



PANEL-BASED ASSESSMENT OF ECOSYSTEM CONDITION OF THE NORTH SEA SHELF ECOSYSTEM

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Panel-based Assessment of Ecosystem Condition of the North Sea Shelf Ecosystem

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Preface:

Mandated by the Ministry of Climate and Environment, the Norwegian Environment Agency is responsible for the development of the "System for assessment of ecological condition" of terrestrial and marine ecosystems in Norway. This report is the second of three from a project funded by the Norwegian Environment Agency on assessing the condition of marine ecosystems. It includes the first assessment of the ecological condition of the shelf ecosystem in the Norwegian sector of the North Sea. The first report focused on the Arctic and sub-Arctic parts of the Barents Sea (Siwertsson et al., 2023) and the third will focus on the assessment of the ecological condition in the pelagic ecosystem in the Norwegian Sea.

For marine ecosystems in Norway, the Panel-based Assessment of Ecosystem Condition (PAEC) has been developed, in cooperation with ecologists working with similar assessments for terrestrial ecosystems, as a methodological framework to assess ecological condition. PAEC forms the basis for a structured, consolidated, evidence-based assessment of the ecological condition of an ecosystem (Jepsen et al., 2019; Jepsen et al., 2020; Jepsen et al., submitted). In 2019, a pilot version of the PAEC protocol was tested for Arctic tundra and the Arctic part of the Barents Sea (Jepsen et al., 2019). Based on lessons learned from these two ecosystems, the PAEC protocol has been improved and translated into English (Jepsen et al., 2020), now providing an easily accessible description of the method.

PAEC for the North Sea has been led by the Institute of Marine Research (IMR) and been conducted by a panel consisting of 24 scientists from IMR and 3 other institutions: Norwegian Institute for Nature Research (NINA), the University of Bergen (UiB) and the University of Oslo (UiO). The work has been led by Per Arneberg in close cooperation with Bérengère Husson and Anna Siwertsson (all IMR). The work has been conducted in the period from 1 June 2021 to 15 January 2023.

The PAEC framework consists of four phases: 1) A scoping phase where new and existing indicators are evaluated for inclusion; 2) the analysis phase; 3) the assessment phase where the scientific panel meets and discusses the significance and validity of indicator analyses, and 4) the report phase where the scientific background material and conclusions from the scientific panel are written up according to the PAEC protocol.

Covid-19 restrictions influenced the project for parts of its duration, and due to these restrictions, there were no physical meetings in the initial phase of the work. Therefore, a digital meeting was held during the scoping phase. A hybrid meeting with the entire scientific panel for the formal assessment phase was held in Bergen on 5 October 2022.

We thank the Marine Biological Association for providing access to data from the Continuous Plankton Recorder Survey, which has greatly improved the assessment by giving information on the long-term changes in the plankton community that are vital for understanding the ecological transformation occurring in the North Sea. We also thank the Norwegian Environment Agency for valuable contributions to the process, in particular Øystein Leiknes and Hanne-Grete Nilsen, who were contacts for the project.

Tromsø 15 January 2023

Per Arneberg

Project leader

Summary (English):

The System for Assessment of Ecological Condition, coordinated by the Norwegian Environment Agency, is intended to form the foundation for evidence-based assessments of the ecological condition of Norwegian terrestrial and marine ecosystems not covered by the EU Water Framework Directive. The reference condition is defined as “intact ecosystems”, i.e., a condition that is largely unimpacted by modern industrial anthropogenic activities. An ecosystem in good ecological condition does not deviate substantially from this reference condition in structure, functions or productivity. This report describes the first operational assessment of the ecological condition of the marine shelf ecosystem in the Norwegian sector of the North Sea and Skagerrak. The assessment method employed is the Panel-based Assessment of Ecosystem Condition (PAEC¹) and the current assessment has considered to what extent the North Sea and Skagerrak shelf ecosystem deviates from the reference condition² by evaluating change trajectories.

Key conclusions from the assessment of the North Sea ecosystem

The scientific panel concludes that the ecosystem in the Norwegian sector of the North Sea and Skagerrak is substantially impacted by human pressures. There is little uncertainty about this conclusion. Climate change is strongly affecting abiotic conditions, mainly through increasing temperatures. This is substantially impacting the rest of the ecosystem, along with other drivers, in particular fisheries. Consequences are largest for functionally important species and seafloor habitats. There are also signs of human-driven changes in diversity of species and ecological functions, as well as in the trophic pyramid of the ecosystem. With further climate change and development of industrial activities in the North Sea, human pressures will remain intensive in the future.

Assessment method

The assessment was done by a scientific panel of 24 experts of the North Sea. In a first phase of scoping, the experts selected sets of indicators relevant to describe temporal changes in seven ecosystem characteristics: *Primary productivity*, *Biomass distribution among trophic levels*, *Functional groups within trophic levels*, *Functionally important species and biophysical structures*, *Landscape-ecological patterns*, *Biological diversity*, and *Abiotic factors*. The method for the assessment is based on developing time series of the indicators and assessing whether there is a trend that indicates a deviation away from the reference condition. First, the experts assigned a phenomenon which contains a description of the indicator under the reference condition (i.e., when largely unimpacted by human activities) and of how the indicator is expected to change with increasing human pressure. Different time periods were considered descriptive for the reference condition for different parts of the ecosystem, and as data for these periods are unavailable for most indicators (except for e.g., 1961-1990 for climate³), the reference condition is generally described qualitatively. The phenomena are assessed as having a high, intermediate or low validity depending on the scientific basis supporting: i) the link between changes in the indicator and the drivers, and ii) consequences of the changes in the indicator's value for the ecosystem. In the second phase of analysis, the data collected allow to build time series of the indicators in predefined geographical regions, and based on those, the evidence for the phenomena (i.e., whether the expected development away from the reference condition caused by increasing human pressure has occurred) are assessed. Finally, the overall condition of each ecosystem characteristic is assessed as belonging to one of three categories with increasing deviation from the reference condition — from no to substantial deviation. Building on this, an assessment is made for the ecosystem as a whole. This report will be peer-reviewed to ensure the validity and robustness of its conclusions.

Datasets and indicators

The assessment of the condition of the North Sea ecosystem is based on 20 datasets (ch.3) supporting 45 indicators. Data to produce the ecosystem time series were collected from stock assessments and population models, satellites, and survey data, e.g., from the International Bottom Trawl Survey (IBTS) operated during the first and third quarter of each year since 2000 and the Continuous Plankton Recorder (CPR) Survey since 1958.

Data coverage for each indicator is evaluated based on spatial and temporal coverage of used datasets relative to reference conditions and relevant dynamics of the biological compartments and was assessed as very good for all but three indicators. Stratification and indicators of ocean acidification were assessed as having only “good” data coverage because of missing information on seasonality and short time series, respectively.

The indicator coverage was assessed as partially adequate for most ecosystem characteristics, as some important information is lacking, except for Abiotic factors which are adequately represented by the selected indicators.

The condition of ecosystem characteristics

Most ecosystem characteristics show signs of human impact and deviate from the reference condition (Table S.1). For ecosystem characteristics *Functionally important species and biophysical structures*, *Landscape ecological patterns* and *Abiotic factors*, there is evidence for substantial deviation from the reference condition due to strong changes in temperature in the water column, widespread impacts of bottom trawling on seafloor and large declines in zooplankton, herring and cod stocks. There are low uncertainties about those assessments, but it can be noted that longer time series on other abiotic factors and more information on the other types of human pressure (noise, pollution) could complete the assessment. For the ecosystem characteristics *Biomass distribution among trophic levels*, *Functional groups within trophic levels* and *Biological diversity* there is evidence for limited deviation from the reference condition due to changes in herbivorous zooplankton, seabirds, copepod body size, biomass of holoplankton relative to that of meroplankton, and zooplankton community composition. There are larger uncertainties for these assessments, mainly due to short time series for several indicators. The same issue is also causing large uncertainty in the assessment of the characteristic *Primary productivity*, for which there is no evidence for deviation from the reference condition.

Table S.1 Summary of assessment of the seven ecosystem characteristics for the North Sea and Skagerrak

Ecosystem characteristic	Assessment of the North Sea ecosystem
Primary productivity	The ecosystem characteristic was assessed as showing no evidence of deviation from the reference conditions. It is based on 2 indicators, with reasonably well-known link to the drivers and well understood consequences on the ecosystem. There are no signs of change in annual primary production or date of start of spring bloom. The main driver of these indicators is climate change. The main uncertainty reside in the length of the time series for both indicators, which do not cover a period of change in the main driver, climate change.
Biomass distribution among trophic levels	The ecosystem characteristic was assessed as showing evidence of limited deviation from the reference conditions. It is based on 6 indicators, with reasonably well-known link to the drivers and well understood consequences on the ecosystem. There is no sign of change in annual primary productivity and biomass of high and low trophic level fish species, but high evidence of decline in herbivorous zooplankton and seabird species. The main driver of these indicators are fisheries and climate change. The main uncertainty resides in the short length of the time series for fish trophic level indicators, which constitutes a major part of the biomass of the ecosystem.
Functional groups within trophic levels	The ecosystem characteristic was assessed as showing evidence of limited deviation from the reference conditions. It is based on 5 indicators, of which one had insufficient data and was not used in the assessment. From the 4 remaining indicators, there were some signs of decline in copepod body size and relative importance of meroplankton to holoplankton. These indicators had relatively good links to the drivers and the consequences for the ecosystem. The main drivers are climate and fisheries. The main uncertainty resides in the short length of the time series for the other indicators.
Functionally important species and biophysical structures	The ecosystem characteristic is assessed as showing evidence of substantial deviation from the reference conditions. It is based on 20 indicators. Several important stocks displayed important declines that are well understood and linked to human pressure. The main drivers are climate change and fisheries. There is little uncertainty in this assessment category.
Landscape-ecological patterns	The ecosystem characteristic is assessed as showing evidence of substantial deviation from the reference conditions. It is based on only one indicator for which link to the driver (fisheries) and consequences for the ecosystem are well understood. There is high evidence of a substantial area being impacted by bottom trawl. There is little uncertainty in this assessment category.
Biological diversity	The ecosystem characteristic was assessed as showing evidence of limited deviation from the reference conditions. It is based on 5 indicators, for which most of the links to the drivers or the impact on the ecosystem are well understood. There are signs of changes in zooplankton community composition. The main driver is climate change. These impacts might be underestimated as other indicators have much shorter time series and are difficult to link to the driver.
Abiotic factors	The ecosystem characteristic is assessed as showing evidence of substantial deviation from the reference conditions. It is based on 7 indicators for which we have moderate to good understanding of the links to the drivers and to the ecosystem. There is strong evidence of increasing temperature and light attenuation linked to climate change. Longer time series for the other indicators could help reduce the uncertainties around this assessment.

Future trajectories for ecosystem condition

Climate change is expected to further impact the North Sea ecosystem unless greenhouse gas emissions are not cut immediately and severely. Already observed changes in the zooplankton community should continue, and many commercial stocks are expected to decline in the region by 2041. It is expected that a northward shift of mobile species would also lead to an increase of other stocks. With climate change, the frequency, duration and severity of extreme climatic events such as storms and heatwaves are expected to increase. This is likely to increase the uncertainties around the future conditions of the ecosystem. As an intensely fished and industrialised region, the future of the Norwegian sector of the North Sea and Skagerrak also strongly depends on development of management of human activities.

Research and monitoring recommendations

This assessment was possible thanks to the long time series available that cover period of change in climate and fisheries. Future changes in these drivers, as well as in other pressures, can only be understood, and their consequences assessed, with continued monitoring of the ecosystem. The Continuous Plankton Recorder (CPR) survey, assessments for a large number of fish stocks, monitoring of key climate parameters and seabirds have all delivered long and important time series. Monitoring needs to be developed further, and in particular for primary producers, jellyfish, benthos and less known fish stocks.

¹ Jepsen, J. U., Arneberg, P., Ims, R. A., Siwertsson, A., and Yoccoz, N. G. 2020. Panel-based Assessment of Ecosystem Condition (PAEC). Technical protocol version 2. NINA Report 1890.

² For consistency with the PAEC protocol, it is generally referred to "deviation from the reference condition" rather than "deviation from good ecological condition" in this report.

³ In the first phase of the work with establishing a framework for assessing condition of Norwegian ecosystems, a joint decision was made for assessments that the climatic normal period 1961-1990 should be considered descriptive for climate under the reference condition (Nybo and Evju 2017, Fagsystem for fastsetting av god økologisk tilstand. Forslag fra et ekspertråd (in Norwegian)). Thus, this was done before the establishment of the North Sea and Skagerrak scientific panel, which noted during the current assessment that climate in the 1961-1990 period cannot be considered unimpacted by anthropogenic emissions of greenhouse gases.

Summary (Norwegian):

System for vurdering av økologisk tilstand, koordinert av Miljødirektoratet, skal utgjøre fundamentet for en kunnskapsbasert vurdering av økologisk tilstand for norske terrestre og marine økosystemer som ikke er omfattet av vanddirektivet. Referansetilstanden er definert som «intakt natur», dvs en tilstand som i stor grad er upåvirket av moderne industrielle aktiviteter. Et økosystem som er i god økologisk tilstand avviker ikke betydelig fra denne referansetilstanden i struktur, funksjon eller produktivitet. Denne rapporten beskriver den første operasjonelle vurderingen av økologisk tilstand i den norske delen av Nordsjøen og Skagerrak. Tilstandsvurderingen følger metoden Panelbasert vurdering av økosystemtilstand (Panel-based Assessment of Ecosystem Condition [PAEC]⁴) og avvik fra referansetilstanden⁵ er vurdert ved å evaluere endringsrater.

Hovedkonklusjon fra vurderingen av økosystemet i Nordsjøen

Fagpanelet konkluderer med at økosystemet i den norske sektoren av Nordsjøen og Skagerrak er vesentlig påvirket av menneskelig aktivitet. Det er liten usikkerhet rundt denne konklusjonen. Klimaendringer har en tydelig påvirkning på de abiotiske forholdene, primært ved å føre til økte temperaturer i havet. Dette, sammen med andre drivere som blant annet fiskeri, påvirker resten av økosystemet i betydelig grad. Konsekvensene er størst for funksjonelt viktige arter og bunnhabitater. Det er også tegn til at menneskelig aktivitet har ført til endringer i artsdiversitet, økologiske funksjoner, og i de trofiske nivåene i økosystemet. På grunn av klimaendringer og industriell utvikling i Nordsjøen, vil menneskelig påvirkning forbli på et høyt nivå i dette havområdet, også i fremtiden.

Vurderingsmetode

Vurderingen ble gjort av et fagpanel på 24 eksperter på Nordsjøen. I en første fase valgte ekspertene ut et sett av indikatorer som er relevant for å beskrive endringer i tid for syv økosystemegenskaper: Primærproduksjon, Fordeling av biomasse mellom trofiske nivåer, Funksjonelle grupper innen trofiske nivåer, Funksjonelt viktige arter og biofysiske strukturer, Landskapsøkologiske mønstre, Biologisk mangfold og Abiotiske forhold. Metoden er basert på å utvikle tidsserier for indikatorene og vurdere om det er en trend i dataene som indikerer en utvikling bort fra referansetilstanden. Først utarbeider ekspertene et fenomen for hver indikator. Det inneholder en beskrivelse av indikatoren under referansetilstanden (dvs når den i stor grad er upåvirket av menneskeskapte aktiviteter) og av hvordan indikatoren er forventet å endres under økende menneskeskapt påvirkning. Ulike tidsperioder ble ansett som beskrivende for referansetilstanden for ulike deler av økosystemet, og fordi det ikke finnes data for disse periodene for de fleste indikatorene (untatt for eksempel 1961-1990 for klima⁶) er referanseperioden i stor grad beskrevet kvalitativt. Fenomenene er vurdert til å ha høy, middels eller lav gyldighet avhengig av i hvilken grad det vitenskapelige grunnlaget gir kunnskap om i) forbindelsen mellom endringer i indikatoren og påvirkningsfaktorene, og ii) konsekvenser av endringer i indikatorverdiene for økosystemet. I den neste fasen, som dreier seg om analyser, blir data samlet inn fra det relevante området slik at tidsserier kan bygges. Basert på disse, blir evidensen for fenomenene vurdert (dvs om det har vært en utvikling bort fra referansetilstanden som kan tilskrives menneskeskapt påvirkning). Til slutt blir tilstanden for hver økosystemegenskap vurdert til en av tre kategorier, fra ingen til betydelig avvik fra referansetilstanden. Basert

på dette blir det gjort en vurdering for økosystemet som helhet. Rapporten vil bli underlagt fagfelleevaluering for å sikre at konklusjonene er gyldige og robuste.

Datasett og indikatorer

Vurderingen av økosystemet i Nordsjøen er basert på 20 datasett (kap. 3) som støtter 45 indikatorer. Dataene som er brukt til å opparbeide tidsseriene ble samlet inn fra bestandsvurderinger og populasjonsmodeller, satellitter og toktdata, for eksempel Det internasjonale bunntålingstoktet (International Bottom Trawl Survey, IBTS), hvor data er brukt fra første og tredje kvartal siden 2000 og planktonundersøkelsen Continuous Plankton Recorder (CPR) Survey, hvor data er brukt fra 1958.

Datadekning for hver indikator er vurdert basert på dekningsgrad i rom og tid til hvert datasett der det tas i betraktning sammenfall med periode som kan anses som beskrivende for referansetilstanden samt relevant dynamikk i tid. Datadekning ble vurdert som «svært god» for alle unntatt tre indikatorer. For indikatorer for stratifisering og havforsuring ble datadekning vurdert som kun «god» på grunn av henholdsvis manglende informasjon sesongvariasjon og korte tidsserier.

Indikatordekning ble vurdert som delvis adekvat for de fleste økosystemegenskapene, fordi noe viktig informasjon gjennomgående mangler. Unntaket er Abiotiske forhold, hvor datadekning er vurdert som adekvat.

Tilstanden til økosystemegenskapene

De fleste økosystemegenskapene viser tegn på menneskeskapt påvirkning og avviker fra referansetilstanden (Tabell S.1). For økosystemegenskapen Funksjonelt viktige arter og biofysiske strukturer, Landskapsøkologiske mønstre og Abiotiske forhold, er det belegg for å si at det er betydelige avvik fra referansetilstanden. Dette er på grunn av betydelige endringer i vanntemperatur, utbredt påvirkning fra bunntåling på sjøbunnen og betydelige nedganger i bestander av dyreplankton, sild og torsk. Det er lite usikkerhet knyttet til disse vurderingene, men det kan bemerkes at lengre tidsserier for andre abiotiske forhold og mer informasjon om andre typer menneskeskapt påvirkning (støy, forurensning) kunne ha utfyllt vurderingen. For økosystemegenskapene Fordeling av biomasse mellom trofiske nivå, Funksjonelle grupper innen trofiske nivå og Biologisk mangfold er det belegg for å si at det er begrenset avvik fra referansetilstanden. Dette er på grunn av endringer for herbivore dyreplankton, sjøfugl, kroppsstørrelse av hoppekreps (en viktig gruppe dyreplankton), biomasse av holoplankton i forhold til meroplankton og sammensetning av dyreplanktonsamfunn. Det er større usikkerhet knyttet til disse vurderingene, hovedsakelig på grunn av korte tidsserier for mange indikatorer. Det samme forholdet forårsaker også stor usikkerhet i vurderingen av egenskapen Primærproduksjon, hvor det ikke er påvist belegg for å si at det er avvik fra referansetilstanden.

Økosystemegenskapen ble vurdert til å vise **evidens for betydelig avvik** fra referansetilstanden. Vurderingen er basert på 7 indikatorer og kunnskapen om forbindelse til påvirkningsfaktorer og konsekvenser for økosystemet er vurdert fra moderat til god for disse indikatorene. Det er betydelig evidens for økning i temperatur og nedgang i lysgjennomtrengning i vannsøylen forbundet til klimaendringer. Lengre tidsserier for de andre indikatorene kunne hjulpet til å redusere usikkerheten knyttet til denne vurderingen.

Tabell S.1.2 Sammendrag av vurderingen for de syv økosystemegenskapene for Nordsjøen og Skagerrak.

Økosystemegenskap	Vurdering av økosystemet i Nordsjøen
Primærproduksjon	Økosystemegenskapen ble vurdert til å vise ingen evidens for avvik fra referansetilstanden. Dette er basert på 2 indikatorer, med rimelig god kunnskap om forbindelse til påvirkningsfaktorene og god kunnskap om konsekvenser for økosystemet. Det er ingen tegn på endringer verken i årlig primærproduksjon eller tidspunkt for start av våroppblomstringen. Den viktigste påvirkningsfaktoren er klimaendringer. Den viktigste årsaken til usikkerhet i vurderingen er knyttet til lengden på tidsserien for begge indikatorene, som ikke sammenfaller med periode for endring i den viktigste påvirkningsfaktoren, klimaendringer.
Fordeling av biomasse mellom trofiske nivå	Økosystemegenskapen ble vurdert til å vise evidens for begrenset avvik fra referansetilstanden. Vurderingen er basert på 6 indikatorer, med rimelig godt forståtte forbindelser til påvirkningsfaktorene og godt forståtte konsekvenser for økosystemet. Det er ikke tegn på endringer for årlig primærproduksjon og biomasse til fisk fra høyt eller lavt trofisk nivå, men evidens for nedgang i mengde herbivort dyreplankton og for sjøfuglarter. De viktigste påvirkningsfaktorene for disse indikatorene er fiskerier og klimaendringer. Den viktigste kilden til usikkerhet er de korte tidsseriene for fisk fra ulike trofiske nivå, som utgjør en betydelig del av biomassen i økosystemet.
Funksjonelle grupper innen trofiske nivå	Økosystemegenskapen ble vurdert til å vise evidens for begrenset avvik fra referansetilstanden. Vurderingen er basert på 5 indikatorer, hvorav en var vurdert til ikke å ha tilstrekkelig data og ikke ble brukt i vurderingen. For de gjenværende 4 var det noe tegn til nedgang i kroppsstørrelse for hoppekreps og den relative viktigheten til meroplankton sammenlignet med holoplankton. For disse indikatorene er kunnskapen om forbindelse til påvirkningsfaktorene og konsekvenser for økosystemet vurdert som relativt god. De viktigste påvirkningsfaktorene er klimaendringer og fiskeri. Den viktigste kilden til usikkerhet er de korte tidsseriene for de andre indikatorene.
Funksjonelt viktige arter og biofysiske strukturer	Økosystemegenskapen ble vurdert til å vise evidens for betydelig avvik fra referansetilstanden. Vurderingen er basert på 20 indikatorer. For flere viktige fiskebestander er det påvist viktige nedganger som er godt forstått og knyttet til menneskeskapte påvirkningsfaktorer. De viktigste påvirkningsfaktorene er klimaendringer og fiskerier. Det er lite usikkerhet knyttet til valg av vurderingskategori.
Landskapsøkologiske mønstre	Økosystemegenskapen ble vurdert til å vise evidens for betydelig avvik fra referansetilstanden. Vurderingen er basert på kun en indikator hvor forbindelsen til påvirkningsfaktoren (fiskeri) og konsekvenser for økosystemet er godt forstått. Det er høy grad av evidens for at et betydelig område er påvirket av bunntåling. Det er lite usikkerhet knyttet til valg av vurderingskategori.
Biologisk mangfold	Økosystemegenskapen ble vurdert til å vise evidens for begrenset avvik fra referansetilstanden. Vurderingen er basert på 5 indikatorer, og for de fleste av dem er kunnskapen om forbindelse til påvirkningsfaktorene og konsekvenser for økosystemet vurdert til å være godt forstått. Det er tegn på endringer for sammensetning av dyreplanktonsamfunn. Den viktigste påvirkningsfaktoren er klimaendringer. Endringene kan være underestimert fordi andre indikatorer har betydelig kortere tidsserier og er vanskeligere å knytte til påvirkningsfaktorer.
Abiotiske forhold	Økosystemegenskapen ble vurdert til å vise evidens for betydelig avvik fra referansetilstanden. Vurderingen er basert på 7 indikatorer og kunnskapen om forbindelse til påvirkningsfaktorer og konsekvenser for økosystemet er vurdert fra moderat til god for disse indikatorene. Det er betydelig evidens for økning i temperatur og nedgang i lysgjennomtrengning i vannsøylen forbundet til klimaendringer. Lengre tidsserier for de andre indikatorene kunne hjulpet til å redusere usikkerheten knyttet til denne vurderingen.

Endringer i fremtiden for økosystemet

Klimaendringer er forventet å påvirke økosystemet i Nordsjøen ytterligere med mindre det gjøres omfattende og umiddelbare kutt i utslipp av drivhusgasser. Endringene som allerede er observert for dyreplankton vil fortsette, og flere kommersielt utnyttede bestander er forventet å minke i området frem mot 2041. Det er forventet at en forflytning nordover av mobile arter vil føre til en økning i andre bestander. På grunn av klimaendringer forventes frekvens og varighet av ekstreme hendelser som stormer og varmebølger å øke. Dette vil sannsynligvis føre til økt usikkerhet om hva forholdene i økosystemet vil være i fremtiden. Som et intenst fisket og betydelig industrialisert område, vil den utviklingen av den norske sektoren av Nordsjøen og Skagerrak i stor grad avhenge av utviklingen av menneskeskapte aktiviteter.

Anbefalinger for forskning og overvåking

Denne vurderingen var mulig å gjøre takket være de lange tidsseriene som dekker perioder med endring i klima og fiskeri. Konsekvenser fra fremtidige endringer i disse og andre påvirkningsfaktorer kan bare forstås med fortsatt overvåking av økosystemet. Undersøkelsen Continuous Plankton Recorder (CPR), bestandsvurderinger for et stort antall fiskebestander, overvåking av sentrale klimaparametere og sjøfugl har alle gitt lange og viktige tidsserier. Overvåkingen må utvikles videre, og i særlig grad for primærprodusenter, maneter, bunndyr og mindre overvåkede fiskebestander.

5 For å være konsistent med PAEC-protokollen er det i stor grad referert til «avvik fra referansetilstanden» heller enn «avvik fra god økologisk tilstand» i denne rapporten.

6 I den første fasen av arbeidet med å etablere Fagsystemet for vurdering av økologisk tilstand ble det tatt en felles avgjørelse for alle økosystemer om at klimanormalperioden 1961-1990 skal anses som beskrivende for klima i referanseperioden (Nybø and Evju 2017, Fagsystem for fastsetting av god økologisk tilstand. Forslag fra et ekspertråd). Dette ble altså gjort før etableringen av fagpanelet for Nordsjøen og Skagerrak. Fagpanelet noterte seg klimaet i perioden 1961-1990 ikke kan anses som upåvirket av menneskeskapte utslipp av drivhusgasser.

Content

Introduction	12
Definition of terms	15
1. Composition of the scientific panel	16
2. Definition of the reference condition	18
3. Ecosystem delineation, data sources, and choice and utility of indicators	21
3.1 Delineation of the ecosystem	21
3.2 General considerations regarding data source	22
3.3 Choice and utility of indicators	24
4. Estimation of indicators and rates of change	27
4.1 General considerations	27
4.2 Framework for trend estimation	29
5. Methods used to assess deviation from the reference condition	33
5.1 Scientific evidence base for the phenomena in the North Sea	35
<i>Annual primary productivity [NI01]</i>	35
<i>Timing of the spring bloom [NI02]</i>	36
<i>Herbivorous copepods [NI03]</i>	36
<i>Carnivorous zooplankton [NI04]</i>	38
<i>Low trophic level fish [NI05]</i>	39
<i>High trophic level fish [NI06]</i>	40
<i>High trophic level seabirds [NI07]</i>	41
<i>Holoplankton vs meroplankton [NI08]</i>	42
<i>Copepod body size [NI09]</i>	43
<i>Gelatinous zooplankton [NI10]</i>	44
<i>Fish body size [NI11]</i>	46
<i>Fish life history [NI12]</i>	47
<i>Calanus species [NI13]</i>	48
<i>Pseudocalanus / Paracalanus species [NI14]</i>	50
<i>Cod stock size [NI15]</i>	51
<i>Cod recruitment [NI16]</i>	52
<i>Haddock stock size [NI17]</i>	54
<i>Haddock recruitment [NI18]</i>	55
<i>Saithe stock size [NI19]</i>	56
<i>Saithe recruitment [NI20]</i>	57
<i>Lesser sandeel stock size [NI21]</i>	59
<i>Lesser sandeel recruitment [NI22]</i>	61
<i>Norway pout stock size [NI23]</i>	62
<i>Norway pout recruitment [NI24]</i>	63
<i>Whiting stock size [NI25]</i>	64
<i>Whiting recruitment [NI26]</i>	65
<i>Herring stock size [NI27]</i>	66
<i>Herring recruitment [NI28]</i>	67
<i>Mackerel stock size [NI29]</i>	68
<i>Mackerel recruitment [NI30]</i>	70
<i>Northern shrimp stock size [NI31]</i>	70
<i>Northern shrimp recruitment [NI32]</i>	72
<i>Area unimpacted by bottom trawling [NI33]</i>	73
<i>Fish species vulnerable to higher temperature [NI34]</i>	74
<i>Fish species benefitting from higher temperature [NI35]</i>	74

<i>Copepod species vulnerable to higher temperature [NI36]</i>	75
<i>Copepod species benefitting from higher temperature [NI37]</i>	78
<i>Fish species vulnerable to fisheries [NI38]</i>	81
<i>Temperature [NI39]</i>	81
<i>Stratification [NI40]</i>	82
<i>Flow conditions [NI41]</i>	83
<i>Nutrients [NI42]</i>	85
<i>Light attenuation [NI43]</i>	88
<i>pH [NI44]</i>	90
<i>Aragonite saturation [NI45]</i>	90
6. Ecosystem characteristics	92
7. Assessments	96
7.1 Assessment of the knowledge base	96
7.2 Assessment of the phenomena	100
7.3 Assessment of ecosystem condition	106
7.3.1 Assessment of the condition of individual ecosystem characteristics	106
7.3.2 Assessment of the condition of the ecosystem as a whole	118
7.3.3 Future trajectories for ecosystem condition	123
7.3.4 Recommendations for monitoring and research	124
8. Appendices	128
9. References	129

Introduction

Based on a mandate from the Norwegian Ministry of Climate and Environment, the *System for Assessment of Ecological condition*¹ was developed with the aim — for each of the major terrestrial and marine ecosystems not covered by the EU Water Framework Directive in Norway — to 1) define criteria for what could be considered good ecological condition and 2) develop methods for assessing the degree of deviation from “good condition” (Nybø and Evju, 2017). The results will be used to follow up the national action plan for biodiversity (Ministry of Climate and Environment, 2015) and holistic ecosystem-based ocean management plans (Ministry of Climate and Environment, 2020). For the latter, results from the assessments will have a central role in the description and evaluation of status of the marine environment, a key part of the scientific advisory work established for the management plans.

Two alternative assessment methods have been developed under the *System for Assessment of Ecological Condition* (Jepsen et al., 2020; Jakobsson et al., 2021). For all assessments of marine ecosystems, the method *Panel-based Ecosystem Assessment of Ecosystem Condition* (PAEC) is used.

The background for developing PAEC is an increasing demand for integrated assessments of the condition of entire ecosystem units under intensified anthropogenic pressures. PAEC is inspired by approaches used in several national and international bodies, including the *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (IPBES, 2020), *Intergovernmental Panel on Climate Change* (IPCC, 2020) and the *French national ecosystem assessment* (EFESE, 2020). These bodies share the common belief that the condition or state of complex systems (e.g., climate systems, ecosystems), and the level of evidence for change in the condition of such systems as a result of anthropogenic and natural drivers, is best assessed by broad scientific panels following stringent and structured protocols. PAEC is a structured protocol for a panel-based assessment of the condition of an ecosystem relative to a specific reference condition (Jepsen et al., 2020; Jepsen et al., submitted). A principal goal of PAEC is that it should provide a framework for making reproducible qualitative assessments based on quantitative analyses of the underlying data.

The overall question the current assessment aimed to answer was whether there has been a change away from the defined *reference condition* (“intact nature”, see Ch. 2), which can be attributed to anthropogenic impacts. Anthropogenic impact on climate is commonly measured relative to the 1850-1900 period (IPCC, 2021), while over-harvesting of fish stocks has been going on for much the 20th century and possibly even longer. Observational time series covering these time periods do not exist in the marine realm and, as a consequence, the current assessment did not include quantitative estimates of indicators for when the ecosystem was not significantly impacted by humans (reference values). In other assessment frameworks, lack of data for the reference condition has been dealt with by assigning values for the reference condition using expert judgement, observations from least impacted sites or modelling (e.g. Pedersen et al. (2016); Direktoratgruppen vanndirektivet (2018); Pedersen et al. (2018)). Values for the current state have then been compared with these estimates, setting a threshold value for substantial deviation from the reference condition as for example 60% of the reference values (Nybø and Evju, 2017; Nybø et al., 2019; Jakobsson et al., 2021). There are several major shortcomings with this approach, including high uncertainty in expert-based reference values (Morgan, 2014; Pedersen et al., 2018) and low robustness of the threshold values set for deviation from the reference condition (Mupepele et al., 2016; Jepsen et al., 2019). PAEC has therefore been developed as an alternative to the requirement of reference and threshold values, instead focusing on the direction and rate of change (trajectories). The use of expert-based reference and threshold values is replaced by first describing how we expect an indicator to change as a result of anthropogenic drivers acting on the ecosystem and then use time series data to assess whether this development has indeed taken place. This involves qualitatively describing each indicator under the reference condition (to help describing how we expect indicators to change from anthropogenic impact) but only to the extent that information from published literature allows.

Structurally, PAEC is conducted in a hierarchical manner and consists of four phases: 1) *Scoping*, 2) *Analysis*, 3)

Assessment, and 4) *Reporting and peer review* (Fig. 1). Key to the *Scoping Phase*, is the selection of relevant indicators within a set of *ecosystem characteristics* covering structural and functional components (biotic and abiotic) of the ecosystem as well as the formulation of specific formalised expectations (termed *Phenomena*) describing expected directional changes in a given indicator or state variable as a result of relevant drivers acting on the system (when there are large uncertainties about the effects from drivers, the phenomena are sometimes formulated as simply change in any direction). Phenomena are thus the equivalent of a scientific hypothesis formulated prior to a scientific study. The *Analysis Phase* consists of a statistical analysis of the underlying data to permit an assessment of the level of evidence for each phenomenon. This is based on evaluating whether rates of change seen in indicator time series can, as described above, be attributed to anthropogenic impact as described in the phenomena. The *Assessment Phase* consists of a plenary session where the assessment panel scrutinises and assesses the knowledge base underlying the assessment, assesses the condition of each ecosystem characteristic, and finally assesses the condition of the entire ecosystem. An independent *Peer review* of the final assessment report will be undertaken, with the aim of continuous improvements, and is seen to be a fundamental step in PAEC. An assessment according to PAEC is primarily a scientific exercise, and the scientific assessment panel should consist of a group of scientists with in-depth knowledge of the focal ecosystem characteristics, as well as relevant quantitative methodologies (study design and statistical modelling). However, PAEC is also envisioned to be a tool for adaptive management of ecosystems, or specific ecosystem components. Thus, the protocol allows for the integration of a stakeholder group (consisting for instance of representatives from management agencies responsible for the specific ecosystem) into the assessment process (Fig. 1). This is not mandatory but may serve to broaden PAEC, from a purely scientific assessment to an operational and policy-relevant tool for developing management goals and adaptive management strategies for the implementation and assessments of specific management actions. Depending on the type of process in which the protocol is used, the level of stakeholder involvement in the assessment phase may vary across the different phases. For the assessments of marine ecosystems, the Advisory Group on Monitoring (“Overvåkingsgruppen” in Norwegian), which is established to support the ocean management plans, has been informed about the work regularly (4 times yearly), throughout all phases of the work, with possibilities to provide feedbacks.

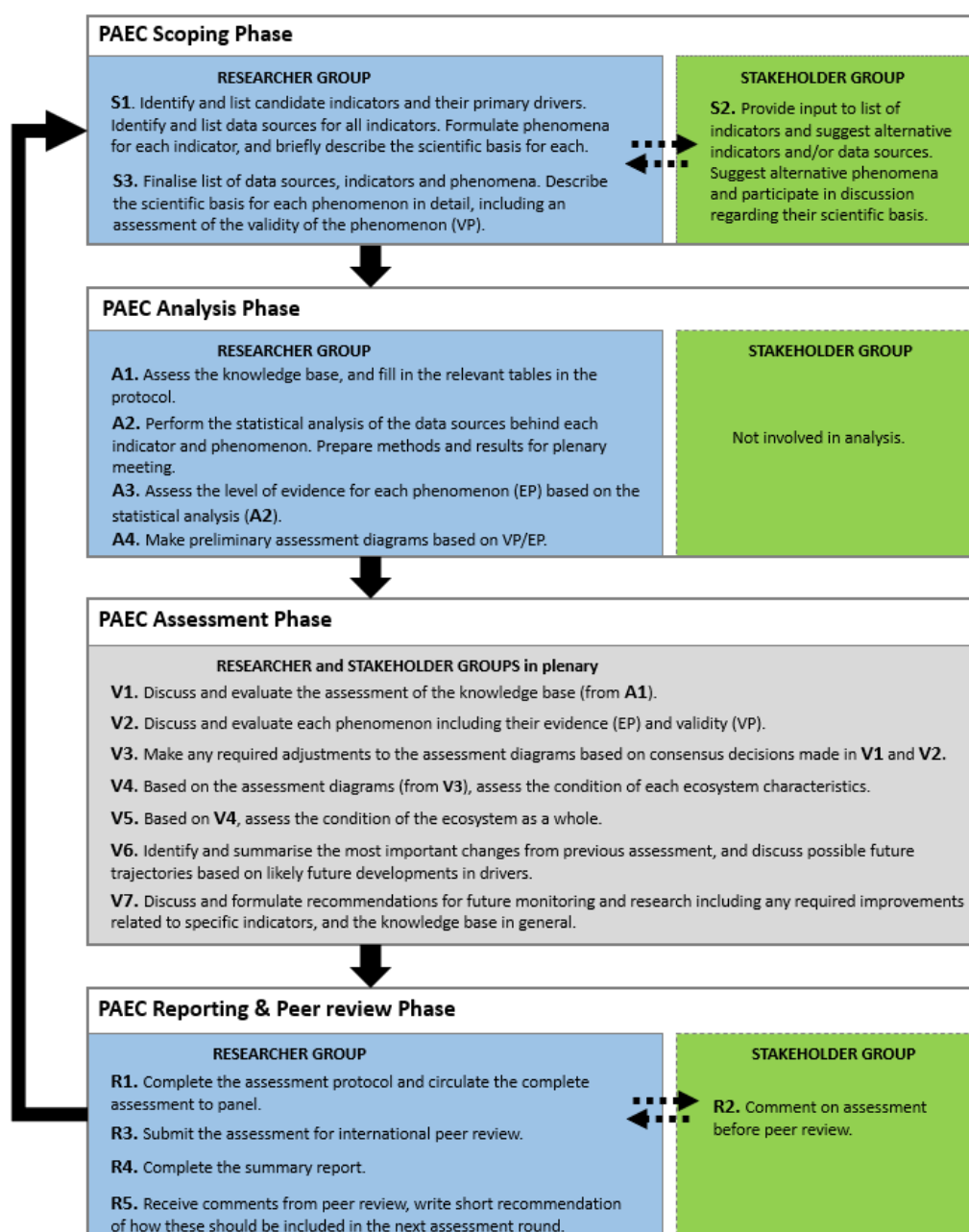


Figure 1: Summary of the four phases of ecosystem condition assessment according to PAEC, and the main tasks involved in each phase. PAEC allows non-mandatory involvement of a stakeholder group in the assessment panel in addition to the scientific panel. In such cases, the stakeholder group would provide input during the Scoping Phase (Task S2), participate in all or parts of the plenary assessment meeting (Tasks V1-V7) and provide comments on the assessment report prior to peer review (Task R2). Stakeholders were not involved in the North Sea assessment, and tasks S2 and R2 hence not included. From (Jepsen et al., 2020).

⁴ In Nybø and Evju (2017) termed "Technical system for determining good ecological condition".

Definition of terms

Table 1. Definition of key terms used in PAEC (Jepsen et al., 2020).

Term	Definition
Ecosystem characteristics	Characteristics of an ecosystem underlying how abiotic factors, ecosystem structure and functions interact. In the current assessment framework, seven characteristics are considered: primary productivity, biomass distribution among trophic levels, diversity of functional groups, functionally important species and biophysical structures, landscape ecological patterns, biological diversity, and abiotic factors.
State variable	Ecosystem feature describing an ecosystem characteristic. A state variable measures directly the functions and processes of its corresponding ecosystem characteristic(s). State variables can be used to build models for estimating causal relations between ecosystem characteristics and external drivers and to make quantitative predictions across space and time. One state variable can be associated with several ecosystem characteristics.
Ecosystem condition	The current state of the ecosystem across all ecosystem characteristics, summarizing the state variables, often in terms of their dynamical regime. We consider here the term ecosystem condition synonymous with 'ecosystem state'. State is often used in the context of alternative states, when the ecosystem can shift between regimes that persist at a particular spatial extent and temporal scale, but state changes may also be gradual.
Reference condition	A reference condition describes the state of the ecosystem at a pre-defined time period (e.g., "a climatic reference period"), or according to specific criteria such as in the absence of local and global human influences ("a pristine state"), or the maintenance of important functional or structural components (e.g., population cycles, "a functional ecosystem"). The reference condition is characterized by the range of variation and covariation among state variables, due to ecosystem dynamics over a period that is long enough to obtain statistically reliable estimates, but with persistent (stable) environmental conditions.
Indicator	A preferably simple and easily interpreted surrogate for a state variable or a driver/pressure (the "canary in the mine"). Because indicators are required to have many properties (e.g., sensitive to changes, applicable over a large area, valid over a wide range of stress, cost-effective), a set of complementary indicators is often required. In this document, the term <i>indicator</i> denotes all metrics that are used to describe the focal ecosystem characteristics. Accordingly, it is important to note that indicators may range from <i>state variables</i> that directly denote ecological functions and structures, to <i>surrogate indices</i> that have more or less validated indirect relations to such functions and structures.
Ecosystem significance	A change in an indicator is of ecosystem significance if it implies ecologically large changes, either in the ecosystem characteristic the indicator is associated with, in other ecosystem characteristics, or generally in ecosystem condition. This is not related to statistical significance.
Phenomenon	An expected directional change in an indicator which is of ecosystem significance, and which can be attributed to one or more relevant drivers. Phenomena are thus the equivalent of scientific hypotheses formulated prior to a scientific study.
Quantitative phenomenon	A phenomenon is quantitative if one can identify and estimate a threshold value for the change in the indicator which, if exceeded, results in a change away from the reference condition which is of ecosystem significance.
Qualitative phenomenon	A phenomenon is qualitative if one cannot identify and estimate such a threshold value, but rather focuses on the type and direction of changes away from the reference condition linked to drivers that can lead to changes of ecosystem significance.
Validity of Phenomenon (VP)	Addresses the links between drivers and ecosystem significance by assessing 1) how well we understand the mechanisms by which drivers affect an indicator, and 2) how well we understand how the change in an indicator leads to changes that are of ecosystem significance.
Evidence for Phenomenon (EP)	Assessment of the quality of empirical evidence that 1) the expected change in an indicator has occurred (incl. statistical significance) and 2) the change is of ecosystem significance. The assessment hence considers both the relationship between state variables and indicators, and between indicators and ecosystem condition. The assessment relies upon the consistency in observed changes (over space and time), and the uncertainty of the estimated changes. In particular, a distinction is made between the absence of evidence for a phenomenon due to large uncertainties, and evidence that no change of ecosystem significance has occurred.
Design-based sampling and estimation	Given that one can define a target population with a list of units, design based sampling uses either probability sampling where the probability that each unit is sampled is known <i>a priori</i> (e.g., stratified sampling with more variable strata being sampled more intensively) or some form of systematic sampling (e.g., grid). In the former case, one can use the design to estimate parameters of interest (e.g., averages) with known uncertainty without relying on statistical models.
Model-based sampling and estimation	Aims at maximizing the accuracy of estimates of relationships between predictors (e.g., drivers) and responses (e.g., ecosystem state variables). Designs combine two things: 1) precision of estimates by having large contrasts in predictor values, and 2) accuracy of the functional response by allowing for non-linear responses and by sampling intermediate values of predictors. Model-based estimation uses the model to extrapolate to non-sampled units and is sensitive to the model used, and therefore robustness needs to be evaluated.

1. Composition of the scientific panel

Below we list participants in the scientific panel assessment, as well as their respective roles and expertise (Table 1.1).

Table 1.1. The composition of the scientific panel with definitions of roles and expertise. The list is sorted alphabetically on last name, except for panel leader listed first.

Name, institution, email	Role	Expertise	Expert on single indicators
Per Arneberg, IMR ¹ , per.arneberg@hi.no	Project manager, leader of the scientific panel, expert	Ecosystem overview/ understanding	
Jon Albretsen, IMR ¹ , jon.albretsen@hi.no	Expert, participant in scientific panel	Oceanography	Temperature, Stratification, Flow conditions, Nutrients
Knut Yngve Børsheim, IMR ¹ , yngve.borsheim@hi.no	Expert, participant in scientific panel	Primary production	Annual primary production, Timing of spring bloom
Côme Denechaud, IMR ¹ , come.denechaud@hi.no	Expert, participant in scientific panel	Cod	Cod stock size and cod recruitment
Joël Durant, UiO ² , joel.durant@ibv.uio.no	Expert, participant in scientific panel	Ecosystem overview/ understanding	
Tone Falkenhaus, IMR ¹ , tone.falkenhaus@hi.no	Expert, participant in scientific panel	Zooplankton	Herbivorous copepods, Carnivorous zooplankton, Holoplankton vs meroplankton, Copepod body size, Gelatinous zooplankton, Calanus species, Pseudocalanus/ Paracalanus species, Copepod species vulnerable to higher temperature, Copepod species benefiting from higher temperature
Per Fauchald, NINA ³ , per.fauchald@nina.no	Expert, participant in scientific panel	Seabirds, Ecosystem overview/understanding	High trophic level seabirds
Anders Martin Frugård Opdal, UiB ⁴ , Anders.Opdal@uib.no	Expert, participant in scientific panel	Ecosystem overview/ understanding	Light attenuation
Bérendère Husson, IMR ¹ , Berengere.Husson@hi.no	Expert, participant in scientific panel, data management	Ecosystem data and models	
Sissel Jentoft, UiO ² , sissel.jentoft@ibv.uio.no	Expert, participant in scientific panel	Fish, genetics	
Tore Johannessen, IMR ¹ , tore.johannessen@hi.no	Expert, participant in scientific panel	Fish	Cod stock size, Cod recruitment, Haddock stock size, Haddock recruitment, Saithe stock size, Saithe recruitment, Lesser sandeel stock size, lesser sandeel recruitment, Norway pout stock size, Norway pout recruitment, Mackerel stock size, mackerel recruitment, Herring stock size, herring recruitment
Espen Johnsen, IMR ¹ , espen.johnsen@hi.no	Expert, participant in scientific panel	Lesser sandeel and Norway pout	Lesser sandeel stock size, lesser sandeel recruitment, Norway pout stock size, Norway pout recruitment
Elizabeth Jones, IMR ¹ , elizabeth.jones@hi.no	Expert, participant in scientific panel	Ocean acidification	pH, Aragonite saturation
Cecilie Kvamme, IMR ¹ , cecilie.kvamme@hi.no	Expert, participant in scientific panel	Herring	Herring stock size, herring recruitment
Gabriella Ljungström, UiB ⁴ , Gabriella.Ljungstrom@uib.no	Expert, participant in scientific panel	Ecosystem models, climate change impacts	
Pål Mortensen, IMR ¹ , paal.mortensen@hi.no	Expert, participant in scientific panel	Benthos, trawling impact	Area unimpacted by bottom trawling
Yves Reecht, IMR ¹ , yves.reecht@hi.no	Expert, participant in scientific panel	Haddock, saithe and whiting	Haddock stock size, Haddock recruitment, Saithe stock size, Saithe recruitment, Whiting stock size, Whiting recruitment
Anna Siwertsson, IMR ¹ , anna.siwertsson@hi.no	Expert, participant in scientific panel	Ecosystem overview/ understanding	
Hiroko Solvang, IMR ¹ , hiroko.solvang@hi.no	Statistical analyses	Statistical analyses	
Morten D. Skogen, IMR ¹ , morten.skogen@hi.no	Expert, participant in scientific panel	Ecosystem models/ understanding, zooplankton	
Aril Slotte, IMR ¹ , aril.slotte@hi.no	Expert, participant in scientific panel	Mackerel	Mackerel stock size, mackerel recruitment
Espen Strand, IMR ¹ , espen.strand@hi.no	Expert, participant in scientific panel	Zooplankton	Herbivorous copepods, Carnivorous zooplankton, Holoplankton vs meroplankton, Copepod body size, Gelatinous zooplankton, Calanus species, Pseudocalanus/ Paracalanus species, Copepod species vulnerable to higher temperature, Copepod species benefiting from higher temperature
Guldborg Søvik, IMR ¹ , guldborg.soevik@hi.no	Expert, participant in scientific panel	Shrimp	Shrimp stock size, shrimp recruitment

Gro I. van der Meeren, IMR ¹ , groM@hi.no	Expert, participant in scientific panel	Ecosystem overview/ understanding	
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1 IMR - Institute for Marine Research, 2 UiO - University of Oslo, 3 NINA - Norwegian Institute of Nature Research, 4 UiB -University of Bergen

2. Definition of the reference condition

All assessments of ecological condition done to follow up Norway's national biodiversity action plan (Ministry of Climate and Environment, 2015) apply the methodological framework described in the *System for Assessment of Ecological Condition* (Nybø and Evju, 2017). Note that this includes both marine and terrestrial ecosystems. The reference condition in this framework is defined as “intact ecosystems” and the assessment should consider the extent to which the current condition of the ecosystem deviates from this reference condition. The term “good ecological condition” is used herein to characterise a condition in which the structure, functions and productivity of an ecosystem do not deviate substantially from the reference condition.

Below, the complete definitions from Nybø and Evju (2017) of what constitutes “intact ecosystems” are given first. This includes the climatic reference on which the assessment should be based (Box 1). We further reiterate their normative description of the condition of each ecosystem characteristic under the reference condition (Box 2) before going on to describe how these definitions have been incorporated into the current assessment.

Box 1. Definitions from (Nybø and Evju, 2017). Translation from Norwegian from (Pedersen et al., 2021). Note that the choice of time period as descriptive for the reference period for climate is discussed in the main text below

Intact ecosystems

Intact, natural and semi-natural, ecosystems are characterised by the maintenance of fundamental structures, functions and productivity. Intact ecosystems are further characterised by having complete food webs, and element cycles. The majority of the food web consists of native species which dominate at all trophic levels and in all functional groups. The species composition, population structure and genetic diversity of native species is a result of natural processes occurring through the ecological and evolutionary history of the ecosystem. Intact ecosystems possess characteristics which are not changing systematically over time but vary within the boundaries of the natural dynamics of the system. Human influences can be present, but should not be pervasive or dominating, or be a factor which changes the structure, function or productivity of the ecosystem. This means that human influences should not be at a scale which exceeds the impacts of natural pressures (e.g., disturbance) or dominating species (e.g., top predators) in the ecosystem. Further, human influences should not lead to changes which are more rapid or more pervasive than natural pressures in the ecosystem. In semi-natural ecosystems, the human activities which define the system (e.g., grazing, hay cutting) are considered an integral part of the ecosystem.

Reference climate

The climate used as a basis for the assessment of intact ecosystems is a climate as described for the climatic normal period 1961–1990.

Box 2. *The normative description from Nybø and Evju (2017) of “good ecological condition” for each of the seven ecosystem characteristics, i.e., when there are no substantial deviations from the reference condition (Translation from Norwegian from Pedersen et al. (2021)).*

Primary productivity:

The primary productivity does not deviate substantially from the productivity in an intact ecosystem. Reason: Elevated or decreased primary productivity indicates a system impacted for instance by eutrophication, overgrazing or drought.

Biomass distribution among trophic levels:

The distribution of biomass among trophic levels does not deviate substantially from the distribution in an intact ecosystem. Reason: Substantial shifts in biomass distribution between trophic levels indicate a system impacted for instance by removal of top predators.

Functional groups within trophic levels:

The functional composition within trophic levels does not deviate substantially from the composition in an intact ecosystem. Reason: Substantial changes in the functional composition within trophic levels indicate a system impacted for instance by loss of functional groups (e.g., pollinators), loss of open habitat species due to encroachment, or super-dominance of certain functional groups or species (e.g., jellyfish in marine habitats).

Functionally important species and biophysical structures:

The functions of functionally important species, habitat building species and biophysical structures do not deviate substantially from the functions in an intact ecosystem. Reason: Functionally important species (e.g., small rodents), habitat building species (e.g., coral reefs, kelp forest), and biophysical structures (e.g., dead wood) have vital importance for the population size of a number of species, and changes in their occurrence will hence have functional implications for the ecosystem.

Landscape-ecological patterns:

Landscape-ecological patterns are compatible with the persistence of species over time, and do not deviate substantially from an intact ecosystem. Reason: Human influences can lead to changes in landscape-ecological patterns which have implications for the population size and population structure of native species, for instance through habitat fragmentation. Fragmented habitats may not be sufficiently large or connected to permit long-term survival of native species. Climate change, altered area use, pollution and invasive or introduced species may also influence landscape-ecological patterns with implications for population size and composition of native species.

Biological diversity:

The genetic diversity, species composition and species turnover do not deviate substantially from an intact ecosystem. Reason: Loss of biological diversity can cause the ecosystem to be less resilient towards pressures and disturbances, and influence the structure, functions and productivity of the ecosystem. Changes in rates of species turnover, due to extinction or colonisation can indicate a modified system.

Abiotic factors:

Abiotic condition (physical and chemical) does not deviate substantially from an intact ecosystem. Reason: Human influences (e.g., environmental toxins, fertilization, changed hydrology or acidification) can lead to substantial changes in the physical/chemical structure and function of the ecosystem, which in turn will impact the species composition, function and dynamics of the ecosystem.

The main implications of the definitions provided above (Box 1 and 2) for the assessment of the North Sea shelf ecosystem are as follows:

- Human influence, under the definition of the reference condition, can be present but not pervasive or dominating. The current assessment focuses on the extent to which an ecosystem deviates from a condition that is under little or no influence from anthropogenic pressures. When operationalising this, an obvious question is how human pressures have historically changed the North Sea shelf ecosystem, and related to this, how the recent time periods for which we have data from systematic monitoring can be considered descriptive for the reference condition.
- Industrial fisheries have a long history, dating back to at least the 19th century, when large scale trawling was developed (Kerby et al., 2012). The entire North Sea was fished by 1900 (Cushing, 1988) and fishing effort increased throughout the 20th century (Holden, 1978; Rijnsdorp et al., 1996; Greenstreet et al., 1999; Jennings et al., 1999a), possibly except during years in the First and second World Wars (Beverton and Holt, 1957). This caused large changes in fish stocks, including substantial declines in abundance of several target species (e.g., cod, Rijnsdorp et al. (1996)) but also increases in abundance of some smaller target species (Greenstreet et al., 1999). Although data on individual body size lack for the early part of the 20th century, models based on macroecological theory suggest that the abundance of large individuals within the stocks was reduced dramatically through the 20th century, with an estimated decline of more than 98 % for the largest fishes (16-66 kg, Jennings and Blanchard (2004)). Reconstructions of past population abundance trajectories for cod based on genetic data suggest that declines in the stock caused by fisheries may have started a millennium ago (Sodeland et al., 2022). Analyses of landings from UK demersal fisheries from 1889 and onwards indicate that landings per unit fishing effort was reduced by 94% over the following 118 years, suggesting a huge decline in demersal fish abundance from the end of the 19th to the beginning of the 21st century (Thurstan et al., 2010). Thus, the conditions during most of the 20th century may not be considered descriptive for the reference condition for fish.
- Whaling has a long history in the North Sea and in historical times the large whale populations were depleted or extirpated with unknown consequences for the ecosystem (ICES, 2021b). Thus, any recent period may not be considered descriptive for the reference condition for the marine mammal community. It should be noted that data on marine mammals were not used in the current assessment for capacity reasons.
- Input of nutrients, largely from rivers, and to a smaller extent from the atmosphere, has led to eutrophication in the

North Sea. The main increase in nutrient load to the coastal areas probably took place from the late 1940s to the late 1970s (Ærtebjerg et al., 2001) and has later declined (see phenomenon for the indicator on nutrients (NI42) in Ch. 5.1).

- **P**ollution of other substances than nutrients have a long history in the North Sea. Offshore exploration and production of oil and gas started in 1959 and was developed through the next decades, leading to pollution of hydrocarbons and other substances. Mass production of persistent organic pollutants such as PCB started in the 1930s (Markowitz, 2018) and pollution through local and long range transport of these substances became widespread in the subsequent decades.
- For climate, the period that should be considered descriptive for the reference condition has been pre-set to 1961-1990 for all assessments of ecological condition in Norway (Nybø and Evju (2017), Box 1). It should be noted that this period is already part of the strong increase in global temperatures after 1950 (IPCC, 2021) and therefore is not pre-industrial, i.e., it is already and increasingly impacted anthropogenically. IPCC AR6 (IPCC, 2021) uses 1850-1900 as their reference period as a compromise between a climate state that can still be considered pre-industrial, but that has a reasonable coverage of reliable climate records.
- Systematic monitoring of the North Sea shelf ecosystem used for this assessment generally started after the periods that can be considered descriptive for the reference condition, with monitoring of temperature (start in 1950), plankton (1958) and cod, haddock and saithe stocks (1963-1972) representing the longest time series, with Secchi depth registrations (1903-) as an exception (Table 3.1). This has two important implications for how the assessment is done (Jepsen et al., submitted). First, it is not possible to describe the reference condition quantitatively, and this has therefore been done qualitatively to the extent possible from literature sources. Second, the assessment is based on *phenomena*. In short, and as described in the introduction, this is done by describing the direction we expect an indicator to change away from the (qualitatively described) reference condition with increasing pressure from the most important anthropogenic drivers (i.e. describe a phenomenon), and then assessing whether this development has indeed occurred using analyses of time series data (i.e. assess the evidence that a phenomenon has occurred, see the protocol (Jepsen et al., 2020) for details). Descriptions of the reference condition for each indicator are found in the phenomena descriptions (Ch. 5, note that when there are large uncertainties about the link between drivers and the indicator, the phenomena are sometimes simply formulated as change in any direction).
- Evidence for deviation from the reference condition is classified into one of four categories: (1) no evidence for deviation, (2) evidence for limited deviation, (3) evidence for substantial deviation, or (4) insufficient data to assess deviation from the reference condition.

PAEC requires that the assessment of temporal representativity (Fig. 7.1, Tab 7.1) includes an evaluation of the extent to which data underlying the indicators are overlapping with any "temporally defined reference period" used. Following the arguments above about different time periods being representative for the reference condition for different components of the ecosystem, this period has been set differently across indicators.

3. Ecosystem delineation, data sources, and choice and utility of indicators

3.1 Delineation of the ecosystem

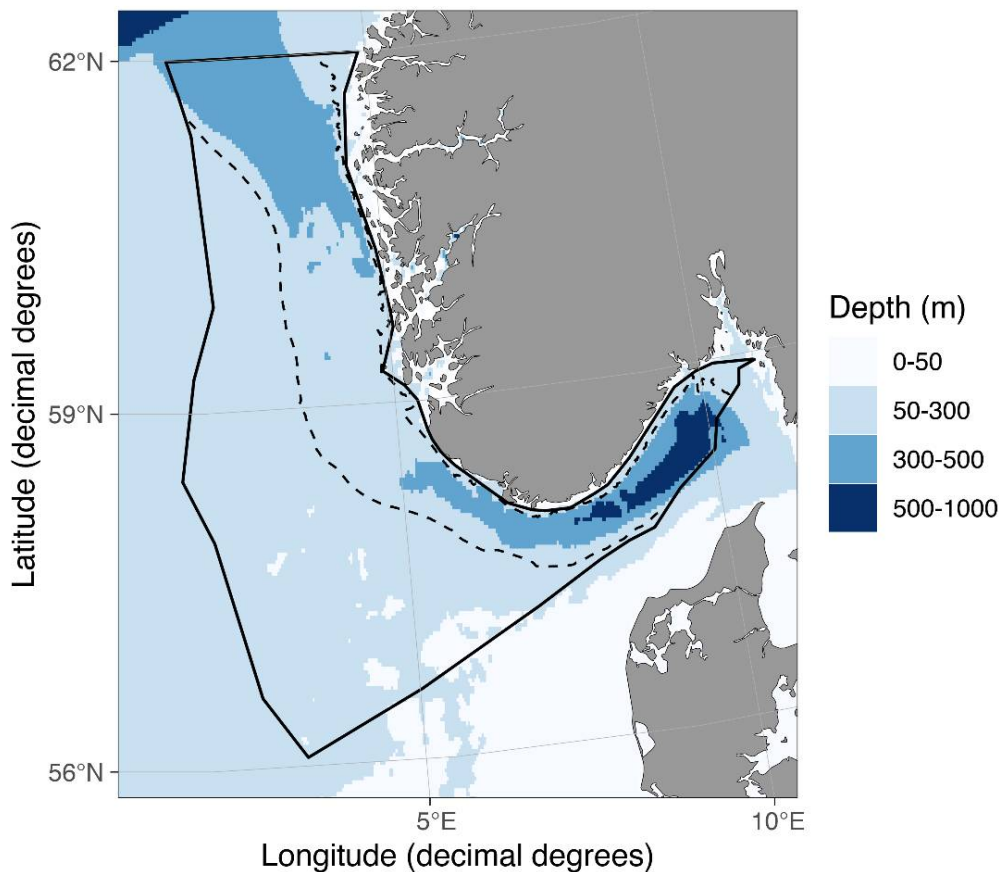


Figure 3.1. Map of the spatial extent of the panel-based assessment of ecosystem condition of the North Sea shelf ecosystem. Note that the water column and sea floor deeper than 200 meters in the Norwegian Trench (indicated by the dotted line) are defined as a separate ecosystem (Nybø and Evju, 2017) and not included in the current assessment. Note that the water column above 200 meters in these areas is included.

The assessment is limited to the Norwegian Management Plan area for the North Sea (Norwegian Ministry of the Environment, 2013) and to areas shallower than 200 meters, thus excluding the deeper parts of the Norwegian Trench, which is characterised by different species and ecological processes than the shallower shelf and therefore considered a different ecosystem type in this work (Nybø and Evju, 2017). The horizontal delineation is shown in Fig. 3.1.

3.2 General considerations regarding data source

The North Sea is a data rich system but with varying coverage of data between different groups of organisms. In this assessment, most datasets are sourced from extensive monitoring programs. In particular, the continuous plankton recorder survey (Richardson et al. (2006) and references therein, hereafter termed CPR), and the international bottom trawl survey (ICES (2020c), hereafter termed IBTS) provided abundance indices for plankton and fish, respectively, covering a large number of the indicators in the current assessment. The CPR was initiated in 1931 (Hardy, 1939) and is the largest multi-decadal plankton monitoring programme in the world (Richardson et al., 2006). The CPR is based on samplers towed at a standard depth (7 meters) after commercial vessels on specific ship routes and provides semi-quantitative (phytoplankton) and quantitative (zooplankton) estimates of relative abundance of large numbers of plankton taxa. Each sampling unit covers 15 miles of towing, and there is a 5 mile overlap between the preceding and following unit (Richardson et al., 2006). The current assessment is based on sampling units from the Norwegian sector (Fig 3.1), and data from 1958 and onwards are used, as this marks the year when *Calanus helgolandicus* was started to be identified as a separate taxon (Richardson et al., 2006).

The IBTS has been conducted in the North Sea since the beginning of the 1960s. It is run yearly in the 1st (target month February) and 3rd (target month August) quarter with participation from Denmark, France (only 1st quarter), Germany, Netherlands, Norway, UK Scotland, UK England (only 3rd quarter) and Sweden. Sampling is done using the GOV trawl (chalut à Grande Ouverture Verticale) with a semi-random or fixed station design (ICES, 2020c). All fish (or a subsample from large catches) are determined to the lowest taxonomic level possible. Due to biases and inconsistencies in multispecies data from the earlier part of the time series from the survey (Daan, 2001) only data from after 2000 were used in the current assessment for multispecies fish indicators. As for CPR, only data from the Norwegian sector (Fig. 3.1) have been used for these indicators.

ICES stock assessments of the main commercial species, which are based on IBTS and other cruises and data sources, were used to evaluate the status of functionally important species, providing data for another large section of the indicators. These assessments cover the entire North Sea and sometimes additional areas, such as the assessment for mackerel, which covers large parts of the northeast Atlantic Ocean (ICES, 2021m). The sandeel assessment as an exception, covering only the Norwegian sector and small additional areas outside this (see Appendix 8.2).

Temperature is measured in two oceanographic sections, the Torungen-Hirtshals section and the Utsira-Orkney Islands section. Together, these are placed to give a good representation of temperature in the entire assessment area. In the current assessment, only data from the Norwegian side and for the 100-200 depth interval are used. Data used to estimate stratification of the upper water column come from the North Sea ecosystem cruise carried out during spring (April and May). Inflow of Atlantic water is estimated using the ocean circulation model NORWECOM (Hjøllo et al., 2009).

Other data sources come from long term monitoring of seabird colonies in the SEAPOP programme (SEAPOP, 2022), satellite monitoring of chlorophyll a concentration for estimation of net primary production (Behrenfeld and Falkowski, 1997), monitoring of nutrients in Skagerrak (Miljøstatus, 2022b), Secchi disk depth measurements for estimation of light attenuation (Opdal et al., 2019) and monitoring of pH and aragonite saturation (Omar et al., 2019).

While monitoring of benthic invertebrates has been carried out by the oil and gas industry and the data made publicly available, the quality of data has been assessed as inadequate for estimation of temporal change on community scale (Ellingsen et al., 2017). There are also data on invertebrates from IBTS, where data are collected on a predetermined set of shellfish, bivalve and squid species and, varying among nations, a general registration of benthic invertebrates caught in the trawl is done. These data were not used in the current assessment due to capacity constraints, except for data on gelatinous plankton (see section 3.3).

Different lengths of time series may introduce uncertainty to PAEC assessments (Siwertsson et al., 2023). The data used from the IBTS survey are used only from 2000 on. This makes the indicator time series below 30 years long, which

might be too short to capture relevant trends. On the contrary, some stocks or CPR data are available since the 50s or 60s. Varying lengths of time series for indicators for the same ecosystem characteristic might induce a bias in its assessment. This is addressed by using information on data coverage (Table 7.1) and also by considering how different lengths of time series introduces uncertainty in the assessment.

Data sources are described in more detail in Table. 3.1.

3.3 Choice and utility of indicators

To assess the status of the ecosystem through its seven ecosystem characteristics, we have grounded our choice of indicators in the panel's knowledge on each ecosystem's key components and functions. Researchers, grouped by area of expertise, have based their selection of indicators on a compromise between parsimony in the number of indicators and their relevance and importance, supported by the scientific literature. Also, some organism groups could not be included because of capacity constraints. This includes marine mammals and benthic invertebrates.

Three of the seven ecosystem characteristics – “Biomass distribution among trophic levels”, “Functional groups within trophic levels” and “Biological diversity”- are more complex than the other characteristics and require integrating data over ecosystem compartments. This is challenging in the marine environment as the different components of the ecosystem are observed and sampled following different strategies and methods. Therefore, resulting biomass estimates are not directly comparable across indicators. For “Biomass distribution among trophic levels”, we thus decided to select indicators to describe biomass distribution of different trophic level *within* each ecosystem component (phytoplankton, zooplankton and fish). The assessment of if and how the biomass distribution has changed among trophic levels was done by integrating all this information when doing the ecosystem characteristic assessment. Future reiterations of the assessment, however, should try to find a way to combine different indicators to describe the overall variation in biomass across trophic levels. For “Functional groups within trophic levels”, groups of experts have prioritised important functions that were performed by each ecosystem component. Finally, for “Biological diversity”, classical biodiversity indices were difficult to link to anthropogenic drivers. Instead, the selected indicators represented species or groups of species that are known to be sensitive to, or to benefit from, certain anthropogenic pressures and can thus act as “indicator” species. It should be noted that the literature reports increasing species richness in the North Sea associated with poleward shifts of many southern species of calanoid copepods (zooplankton, Beaugrand and Ibañez (2002); Beaugrand et al. (2010)), dinoflagellates (Beaugrand et al., 2010) and fish (Hiddink and ter Hofstede, 2008).

We also attempted to identify important parameters of the ecosystem that are currently missing from the monitoring programs. Thus, issues of data availability or responsiveness to anthropogenic pressure were not considered in the first part of the scoping exercise. A list of additional indicators to consider are presented in Table 7.3.2. This also includes indicators that were attempted to include in the assessment, but where it was realized that the quality was not sufficient. The indicators that were finally used were those for which direct measurements or proxies with sufficient quality were available.

Table 3.1 Description of data sources for assessment of ecological condition in the North Sea

Table 3.1 D escription of data sources for assessment of ecological condition in the Norwegian sector of the North Sea shallower than 200 meters. 1 IMR – Institute for Marine Research, NINA 2 Norwegian institute for nature research, UiB 3 University of Bergen, SAHFOS 4 Sir Alister Hardy Foundation for Ocean Science

Dataset name	ID	Dataset DOI/URL/storage	Owner institution	Contact person for data	Content and methods	Temporal coverage
Chlorophyll, MODIS	D01	Moderate-resolution Imaging Spectroradiometer data (MODIS) Aqua 10.5067/AQUA/MODIS/L3M/CHL/2018 NASA https://lpdaac.usgs.gov/	NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group.	Knut Yngve Børsheim, IMR ¹	Chlorophyll per m ² from satellite. Eight days average with 4x4 km resolution. Primary production is estimated as described in Behrenfeld and Falkowski (1997).	2003–2020
Continuous plankton recorder (CPR)	D02	https://www.cprsurvey.org/services/the-continuous-plankton-recorder/	SAHFOS ⁴	Espen Strand, IMR ¹	The CPR survey gives data on relative abundance of plankton species collected on ship routes covering a large part of the North Sea. The method is described in Richardson et al. (2006)	1958–2016
International bottom trawl survey (IBTS)	D03		ICES	Yves Reeceht, IMR ¹	The survey is described by ICES (2020c). The cruise was run before 2000, but the quality of the data from that period is too low for robust assessment of indicator values (Daan, 2001)	2000–2022
Cod	D04	https://doi.org/10.17895/ices.pub.8211	ICES	Côme Denechaud, IMR ¹	Assessment of spawning stock biomass and recruitment (age 1) of <i>Gadus morhua</i> in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak) (ICES, 2021l)	1963–2022
Haddock	D05	https://doi.org/10.17895/ices.pub.8211	ICES	Yves Reeceht, IMR ¹	Assessment of spawning stock biomass and recruitment (age 0) of Haddock (<i>Melanogrammus aeglefinus</i>) in Subarea 4, Division 6.a, and Subdivision 20 (North Sea, West of Scotland, Skagerrak) (ICES, 2021l)	1972–2022
Saithe	D06	https://doi.org/10.17895/ices.pub.8211	ICES	Yves Reeceht, IMR ¹	Assessment of spawning stock biomass and recruitment (age 3) of Saithe (<i>Pollachius virens</i>) in subareas 4, 6 and Division 3.a (North Sea, Rockall and West of Scotland, Skagerrak and Kattegat) (ICES, 2021l)	1967–2022
Sandeel	D07			Espen Johnsen, IMR ¹	Assessment of total stock biomass and recruitment (age 1) of Sandeel (<i>Ammodytes</i> spp.) in the Norwegian sector of the North Sea (Johnsen, 2021)	1986–2022
Norway pout	D08	https://doi.org/10.17895/ices.pub.8211	ICES	Espen Johnsen, IMR ¹	Assessment of spawning stock biomass and recruitment (age 1) of Norway pout (<i>Trisopterus esmarkii</i>) in the North Sea (ICES, 2021l)	1983–2021
Whiting	D09	https://doi.org/10.17895/ices.pub.8211	ICES	Yves Reeceht, IMR ¹	Assessment of spawning stock biomass and recruitment (age 0) of Whiting (<i>Merlangius merlangus</i>) in Subarea 4 and Division 7.d (North Sea and eastern English Channel) (ICES, 2021l)	1978–2022
Herring	D10		ICES	Cecilie Kvamme, IMR ¹	Assessment of spawning stock biomass and recruitment (age 0) of Herring (<i>Clupea harengus</i>) in Subarea 4 and divisions 3.a and 7.d, autumn spawners (North Sea, Skagerrak and Kattegat, eastern English Channel) (ICES, 2021e)	1947–2022
Mackerel	D11	http://doi.org/10.17895/ices.pub.8298	ICES	Leif Nøttestad, IMR ¹	Assessment of spawning stock biomass and recruitment of mackerel (<i>Scomber scombrus</i>) in the North-east Atlantic (ICES, 2021m)	1980–2021
Seabirds	D12	https://seapop.no/en/	NINA	Per Fauchald, NINA ²	Estimates of breeding colony sizes from the Skagerrak and North Sea coast of Norway, mainly performed by county management authorities and assembled for the first time for this assessment	1970/1980–2020
Temperature	D13	Norsk Marint Datasenter (NMD)	IMR	Jon Albretsen, IMR ¹	Measurements of temperature from the Torungen-Hirtshals and Utsira-Orkney Island oceanographic sections (Institute of Marine Research, 2021)	1950–2021

Mixed layer depth	D14	Norsk Marint Datasenter (NMD)	IMR	Jon Albretsen, IMR ¹	CTD data from the Norwegian ecosystem cruise in the North Sea (Franzè et al., 2021)	2005-2021
Flow conditions	D15	Norsk Marint Datasenter (NMD)	IMR	Jon Albretsen, IMR ¹	Estimates from the NORWECOM model (Hjello et al., 2009)	1980-2021
Nutrients	D16	Norsk Marint Datasenter (NMD)	IMR	Kjell Gundersen, IMR ¹	Data from the Torungen-Hirtshals oceanographic sections (Institute of Marine Research, 2021)	1980-2021
Secchi disk depth measurements	D17	https://doi.org/10.1111/gcb.14810	UiB	Anders Martin Frugård Opdal, UiB ³	Data from locations throughout the northern part of the North Sea.	1903-1998
pH and aragonite saturation	D18	https://doi.org/10.21335/NMDC-1939716216	Norwegian Environmental Agency	Elizabeth Jones, IMR ¹	Mean values from Atlantic Water core present at 3-4 stations along the Torungen-Hirtshals oceanographic section (Skagerrak) each year, regional box 58.00-58.40 N, 8.77-9.37 E	2012-2020
Shrimp	D19	https://doi.org/10.17895/ices.advice.19453658	IMR	Guldborg Søvik, IMR ¹	Assessment of the ratio of spawning stock biomass to $MSYB_{trigger}$ and of recruitment in divisions 3.a and 4.a East (Skagerrak and Kattegat and northern North Sea in the Norwegian Deep) (ICES, 2022d)	1971-2022 (SSB) 1971-2021 (recruitment)
Area unimpacted by bottom trawling	D20	https://www.pnas.org/doi/10.1073/pnas.2109449119 and https://doi.org/10.17895/ices.advice.8188	Proceedings of the National Academy of Sciences and ICES	Pål Mortensen, IMR ¹	Assessment of relative benthic status for the whole North Sea (Pitcher et al., 2022) and distribution of trawling activities in the whole North Sea (ICES, 2021b)	2008-2010 for relative benthic status and 2017-2020 for distribution of trawling activities

4. Estimation of indicators and rates of change

This chapter describes the methods for calculation of indicator values based on the datasets described in Ch. 3 and the analytical framework for estimating rates of change in the resulting time series. First, we give a general description on how the datasets from the Continuous Plankton Recorder Survey (CPR) (Continuous Plankton Recorder Survey, 2022) and the International Bottom Trawl Survey (IBTS) (ICES, 2020c), the main data sources for the assessment, have been treated (Ch. 4.1). This is followed by a description of the framework for estimating rates of change (Ch. 4.2). Brief description of the specific methods for each indicator is given in Table 4.1. Additional descriptions of the methods are given in appendix 8.1, which also includes graphical representation of all indicator values and results from statistical analyses. Statistical analyses were conducted in R (R Core Team, 2019).

4.1 General considerations

The CPR is operated using ships of opportunity and data coverage varies across the North Sea. For this assessment, the North Sea was first divided into grid cells covering 0.5 degree latitude and 1 degree longitude and data density calculated for cells within and in the vicinity of the PAEC area. The locations of the cells are shown in Fig. 4.1.

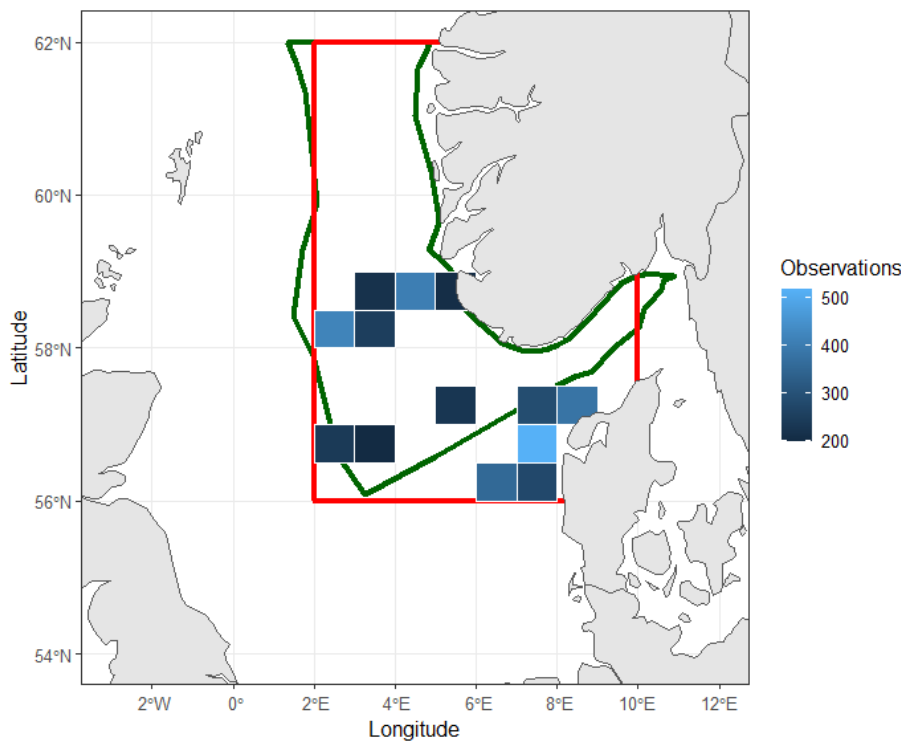


Figure 4.1. Locations of grid cells from which CPR data have been used for the assessment and number of data points for each cell. The PAEC area is indicated by the black line and the area from which data density was evaluated indicated by the red line.

The IBTS catch data were transformed to catch per unit effort (CPUE, per nautical mile). Values were summed per the desired taxonomic or functional groups and averaged over the area. Average number of stations per year is 50 (min:17, max: 122).

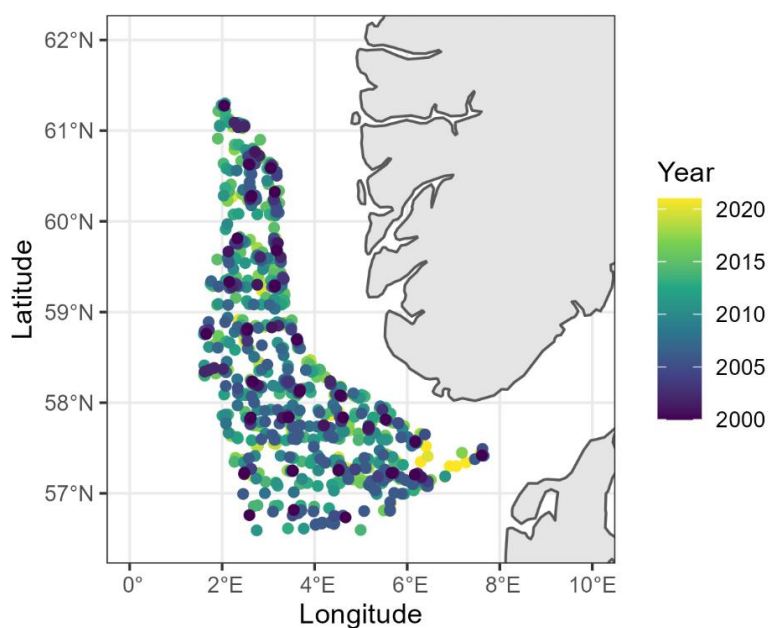


Figure 4.2: Location of IBTS stations within the PAEC area from 2000 to 2020

4.2 Framework for trend estimation

The objective of the method used to assess deviation from the reference conditions is to fit a trend to each indicator's data and to compare it to the phenomena stated by the experts (see Ch. 5.1). Depending on the length of the indicator's time series, two types of trend analyses were done.

- For time series with at least 50 data points, four autoregressive linear models taking into account effects of autocorrelation in time series data were fitted (without autocorrelation or with autocorrelation from first to third order, see Pedersen et al. (2021) for an example of application of such models in PAEC), and the best fitting model was selected based on the AIC criteria. Then, to highlight potential nonlinear trends, the first step of a TREC analysis (Solvang and Planque, 2020; Solvang and Ohishi, 2022) was applied to the standardized time series to compare the fit of polynomial models (from degree 1 to 3). The best fitting model was also selected based on AIC criteria.
- For time series with less than 50 data points, autoregressive models are not robust (Hardison et al., 2019). Only the TREC analysis was applied then. As support information, a linear trend without autocorrelation in the error was applied to give an idea of the direction of the trend, but the interpretation should be done carefully as the trend coefficients and confidence interval may be erroneous (Hardison et al., 2019). For supplementary information, we also applied a moving average smoother. All plots are available in Appendix 8.1.

Table 4.1. Methods for estimating indicator values from datasets for the North Sea

Ecosystem characteristic	Indicator [ID]	Dataset ID	Methods
Primary productivity	Annual primary productivity [NI01]	D01	The indicator is represented by a time series on annual net primary production (gram carbon per m ² per year) based on satellite data on chlorophyll concentration and estimated from a vertically generalized production model (Behrenfeld and Falkowski, 1997).
Primary productivity	Timing of the spring bloom [NI02]	D01	The bloom start days were calculated using the threshold method (Brody et al., 2013), with start day at 0.68 mg chlorophyll m ⁻³ calculated as suggested by Siegel et al. (2002).
Biomass distribution among trophic levels	Annual primary productivity [NI01]	D01	See above
Biomass distribution among trophic levels	Herbivorous copepods [NI03]	D02	The indicator is represented by a time series based on CPR abundance values (annual means in March-September from selected grids with high sampling effort within or in the vicinity of the Norwegian sector) of copepods assigned as omnivore (UK Pelagic Habitats Expert Group, 2021).
Biomass distribution among trophic levels	Carnivorous zooplankton [NI04]	D02	The indicator is represented by a time series based on CPR abundance values (annual means in March-September from selected grids with high sampling effort within the Norwegian sector) of copepods assigned as carnivore (UK Pelagic Habitats Expert Group, 2021).
Biomass distribution among trophic levels	Low trophic level fish [NI05]	D03	The indicator is represented by a time series of planktivorous or herbivorous fish average CPUE (kg/nm) across the PAEC polygon. Feeding mode data were extracted from Beukhof et al. (2019) for the North Sea.
Biomass distribution among trophic levels	High trophic level fish [NI06]	D03	The indicator is represented by a time series of piscivorous fish average CPUE (kg/nm) across the PAEC polygon. Feeding mode data were extracted from Beukhof et al. (2019) for the North Sea.
Biomass distribution among trophic levels	High trophic level seabirds [NI07]	D12	The indicator is represented by time series of total breeding colony sizes for common gull (<i>Larus canus</i>), lesser black-backed gull (<i>Larus fuscus</i>), herring gull (<i>Larus argentatus</i>), great black-backed gull (<i>Larus marinus</i>), common tern (<i>Sterna hirundo</i>), Arctic tern (<i>Sterna paradisaea</i>) and tern (<i>Sterna</i> spp.) on the Norwegian Skagerrak and North Sea coast.
Functional groups within trophic levels	Holoplankton vs meroplankton [NI08]	D02	The indicator is represented by a time series based on CPR abundance values (annual means in March-September from selected grids with high sampling effort within or in the vicinity of the Norwegian sector) of plankton assigned as holoplankton and meroplankton (UK Pelagic Habitats Expert Group, 2021). The time series itself is then calculated as the ratio of holoplankton to meroplankton abundance.
Functional groups within trophic levels	Copepod body size [NI09]	D02	The indicator is represented by a time series based on CPR abundance values (annual means in March-September from selected grids with high sampling effort within or in the vicinity of the Norwegian sector) of copepods assigned as small or large (UK Pelagic Habitats Expert Group, 2021). The time series itself is then calculated as the proportion of large copepods.
Functional groups within trophic levels	Gelatinous zooplankton [NI10]	D03	The indicator is represented by a time series of jellyfish species average CPUE (kg/nm) across the PAEC polygon
Functional groups within trophic levels	Fish body size [NI11]	D03	The indicator is represented by a time series community weighed average size among all stations inside the PAEC polygon. Size data were extracted from length infinity parameter of Von Bertalanffy growth curves described in Beukhof et al. (2019) for the North Sea.
Functional groups within trophic levels	Fish life history [NI12]	D03	The indicator is represented by three time series of the average CPUE (kg/nm) of equilibrium, periodic and opportunistic species among all stations inside the PAEC polygon. Fuzzy clustering of each species to one of the three strategies was based on data from Pecuchet et al. (2017).
Functionally important species and biophysical structures	<i>Calanus</i> species [NI13]	D02	The indicator is represented by a time series based on CPR abundance values (annual means in March-September from selected grids with high sampling effort within or in the vicinity of the Norwegian sector) of stage CV-CIV <i>C. finmarchicus</i> and <i>C. helgolandicus</i> . The time series is then calculated as the proportion of <i>C. finmarchicus</i> .
Functionally important species and biophysical structures	<i>Pseudocalanus/Paracalanus</i> species [NI14]	D02	The indicator is represented by a time series based on CPR abundance values (annual means in March-September from selected grids with high sampling effort within or in the vicinity of the Norwegian sector) of the <i>Para-Pseudocalanus</i> species complex.
Functionally important species and biophysical structures	Cod stock size [NI15]	D04	The indicator is represented by the estimated spawning stock biomass of cod in the entire North Sea, Skagerrak, and the eastern English Channel.
Functionally important species and biophysical structures	Cod recruitment [NI16]	D04	The indicator is represented by the estimated recruitment from cod in the entire North Sea, Skagerrak, and the eastern English Channel.

Ecosystem characteristic	Indicator [ID]	Dataset ID	Methods
Functionally important species and biophysical structures	Haddock stock size [NI17]	D05	The indicator is represented by the estimated spawning stock biomass of haddock in the entire North Sea, West of Scotland, Skagerrak.
Functionally important species and biophysical structures	Haddock recruitment [NI18]	D05	The indicator is represented by the estimated recruitment from haddock in the entire North Sea, West of Scotland, Skagerrak.
Functionally important species and biophysical structures	Saithe stock size [NI19]	D06	The indicator is represented by the estimated spawning stock biomass of saithe in the entire North Sea, Rockall and West of Scotland, Skagerrak, and Kattegat.
Functionally important species and biophysical structures	Saithe recruitment [NI20]	D06	The indicator is represented by the estimated recruitment from saithe in the entire North Sea, Rockall and West of Scotland, Skagerrak, and Kattegat.
Functionally important species and biophysical structures	Lesser sandeel stock size [NI21]	D07	The indicator is represented by the estimated spawning stock biomass of sandeel (<i>Ammodytes</i> spp.) in central (sector 3r) and northern (sector 5r) North Sea.
Functionally important species and biophysical structures	Lesser sandeel recruitment [NI22]	D07	The indicator is represented by the estimated recruitment of sandeel (<i>Ammodytes</i> spp.) in central (sector 3r) and northern (sector 5r) North Sea.
Functionally important species and biophysical structures	Norway pout stock size [NI23]	D08	The indicator is represented by the estimated spawning stock biomass of Norway pout in the entire North Sea, Skagerrak, and Kattegat.
Functionally important species and biophysical structures	Norway pout recruitment [NI24]	D08	The indicator is represented by the estimated recruitment from Norway pout in the entire North Sea, Skagerrak, and Kattegat.
Functionally important species and biophysical structures	Whiting stock size [NI25]	D09	The indicator is represented by the estimated spawning stock biomass of Whiting in the entire North Sea and eastern English Channel.
Functionally important species and biophysical structures	Whiting recruitment [NI26]	D09	The indicator is represented by the estimated recruitment from Whiting in the entire North Sea and eastern English Channel.
Functionally important species and biophysical structures	Herring stock size [NI27]	D10	The indicator is represented by the estimated spawning stock biomass of Herring in the North Sea, Skagerrak and Kattegat, eastern English Channel
Functionally important species and biophysical structures	Herring recruitment [NI28]	D10	The indicator is represented by the estimated recruitment from herring in the North Sea, Skagerrak and Kattegat, eastern English Channel
Functionally important species and biophysical structures	Mackerel stock size [NI29]	D11	The indicator is represented by the estimated spawning stock biomass of mackerel in the northeast Atlantic.
Functionally important species and biophysical structures	Mackerel recruitment [NI30]	D11	The indicator is represented by the estimated recruitment of mackerel in the northeast Atlantic.
Functionally important species and biophysical structures	Northern shrimp stock size [NI31]	D19	The indicator is represented by the ratio of spawning stock biomass to $MSY B_{trigger}$.

Ecosystem characteristic	Indicator [ID]	Dataset ID	Methods
Functionally important species and biophysical structures	Northern shrimp recruitment [NI32]	D19	The indicator is represented by the estimated recruitment (age 0).
Landscape-ecological patterns	Area unimpacted by bottom trawling [NI33]		An indicator for relative benthic status (RBS) is used (Pitcher et al., 2022), which has been recommended as the best performing of three quantitative indicators for bottom trawling impact (Rijnsdorp et al., 2020).
Biological diversity	Fish species vulnerable to higher temperature [NI34]	D03	The indicator is represented by the average CPUE (kg/nm) of species with an affinity for colder temperatures and a limited range of tolerance according to (Dulvy et al., 2008).
Biological diversity	Fish species benefiting from higher temperature [NI35]	D03	The indicator is represented by the average CPUE (kg/nm) of species with an affinity for warmer temperatures and a limited range of tolerance according to (Dulvy et al., 2008).
Biological diversity	Copepod species vulnerable to higher temperature [NI36]	D02	The indicator is represented by a time series on the average number per CPR-sample of copepod species that are assumed to be vulnerable to higher temperatures.
Biological diversity	Copepod species benefiting from higher temperature [NI37]	D02	The indicator is represented by a time series on the average number per CPR-sample of copepod species assumed to benefit from higher temperatures.
Biological diversity	Fish species vulnerable to fisheries [NI38]	D03	The indicator is represented by the time series of species sensitive to bottom trawling according to (Rindorf et al., 2020) that were found regularly in the North Sea.
Abiotic factors	Temperature [NI39]	D13	The indicator is represented by time series based on temperature observations from the Skagerrak (Torungen-Hirtshals transect, once per month) and the Norwegian economic zone in the northern North Sea (Utsira-Orkney transect, four times per year) taken between 100 and 200m depth.
Abiotic factors	Stratification [NI40]	D14	The indicator is represented by estimates based on the maximum of the Brunt–Väisälä frequency, or buoyancy frequency, in the top 100 m of the water column calculated from stations CTD data to preserve the vertical density structure. Indicator values are mean ($\pm$ sd) of station values for the for all North Sea ecosystem cruise CTD-profiles, which are conducted once per year, in April/May.
Abiotic factors	Flow conditions [NI41]	D15	The ocean circulation model NORWECOM (Hjøllo et al., 2009) is conducted to calculate transports of inflowing Atlantic Water through a transect between Utsira, Norway, and the Orkneys as the main inflow pathway into the North Sea is from the north following the western slope of the Norwegian Trench. Indicator values are summarized along the entire transect in all depths using daily estimates from the model.
Abiotic factors	Nutrients [NI42]	D16	The indicator is represented by time series on winter concentrations of phosphorus (PO_4) and nitrogen ($\text{NO}_2 + \text{NO}_3$) from the Torungen-Hirtshals transect.
Abiotic factors	Light attenuation [NI43]	D17	The indicator is represented by a time series based on secchi depth measurements and a statistical model where the effects of season and location of sampling are controlled for to assess the long-term trend (Opdal et al., 2019).
Abiotic factors	pH [NI44]	D18	The indicator is represented by estimates from the core of Atlantic Water at the Torungen-Hirtshals transect. Indicator values are mean of observation ($\pm$ sd).
Abiotic factors	Aragonite saturation [NI45]	D18	The indicator is represented by estimates from the core of Atlantic Water at the Torungen-Hirtshals transect. Indicator values are mean of observation ($\pm$ sd).

5. Methods used to assess deviation from the reference condition

Deviation from the reference condition was assessed by comparing the *expected* variation in an indicators' value with increasing human pressure (phenomenon, see short titles in Table 5.1 and full descriptions in section 5.1) to *observed* trend in the indicators' data (see 4.2). If the fitted trend on the observed data was similar to what is expected given the observed variation in the relevant anthropogenic drivers (see Appendix 8.2), then there is evidence for deviation from the reference condition.

Table 5.1 List of phenomena including overall approach used to determine the extent to which each phenomenon has occurred in the North Sea and Skagerrak. Approach refers to methods used to determine the extent to which the phenomenon has occurred. (1) For quantitative phenomena: The values of the indicator relative to an estimated quantitative threshold value (2) For qualitative phenomena: The value of the indicator relative to variation estimated from the indicator time series or other qualitative or quantitative information about a reference state (3) For all phenomena: Observed and expected effects of changes in the indicator on other components of the ecosystem (i.e., ecosystem significance)

Indicator [ID]	Phenomenon [ID]	Anthropogenic drivers	Approach
Annual primary productivity [NI01]	Increasing annual primary productivity [NP01]	Climate change	2) and 3)
Timing of the spring bloom [NI02]	Change in the spring bloom timing [NP02]	Climate change	2) and 3)
Annual primary productivity [NI01]	Increasing annual primary productivity [NP01]	Climate change	2) and 3)
Herbivorous copepods [NI03]	Decreasing abundance of herbivorous copepods [NP03]	Climate change and eutrophication	2) and 3)
Carnivorous zooplankton [NI04]	Increasing abundance of carnivorous zooplankton [NP04]	Climate change and eutrophication	2) and 3)
Low trophic level fish [NI05]	Change biomass of LTL fish [NP05]	Fisheries and climate change	2) and 3)
High trophic level fish [NI06]	Decreasing biomass of HTL fish [NP06]	Fisheries and climate change	2) and 3)
High trophic level seabirds [NI07]	Decline in abundance of high TL seabirds [NP07]	Fisheries, climate change and eutrophication	2) and 3)
Holoplankton vs meroplankton [NI08]	Changes in Holoplankton vs. Meroplankton composition [NP08]	Climate change	2) and 3)
Copepod body size [NI09]	Reduced average copepod community body size [NP09]	Climate warming	2) and 3)
Gelatinous zooplankton [NI10]	Increasing abundances of gelatinous zooplankton [NP10]	Climate change	2) and 3)
Fish body size [NI11]	Decreasing fish community mean body size [NP11]	Fisheries and climate change	2) and 3)
Fish life history [NI12]	Decreasing proportion of slow-life species and increasing proportion of fast-life species [NP12]	Fisheries and climate change	2) and 3)
<i>Calanus</i> species [NI13]	Decrease in abundance of <i>C. finmarchicus</i> relative to abundance of <i>C. helgolandicus</i> [NP13]	Climate change	2) and 3)
<i>Pseudocalanus</i> / <i>Paracalanus</i> species [NI14]	Declining abundance of <i>Pseudocalanus</i> spp. and <i>Paracalanus</i> spp. [NP14]	Climate change and eutrophication	2) and 3)
Cod stock size [NI15]	Decreasing cod stock size [NP15]	Fisheries and climate change	2) and 3)
Cod recruitment [NI16]	Decreasing cod recruitment [NP16]	Fisheries and climate change	2) and 3)
Haddock stock size [NI17]	Decreasing haddock stock size [NP17]	Fisheries and climate change	2) and 3)
Haddock recruitment [NI18]	Decreasing haddock recruitment [NP18]	Fisheries and climate change and accidental oil blowouts	2) and 3)
Saithe stock size [NI19]	Decreasing saithe stock size [NP19]	Fisheries, climate change and eutrophication	2) and 3)
Saithe recruitment [NI20]	Decreasing saithe recruitment [NP20]	Fisheries, climate change and eutrophication	2) and 3)
Lesser sandeel stock size [NI21]	Decreasing lesser sandeel stock size [NP21]	Fishery, climate change and habitat degradation	2) and 3)
Lesser sandeel recruitment [NI22]	Decreasing lesser sandeel recruitment [NP22]	Fishery, climate change and pollution from petroleum industry	2) and 3)
Norway pout stock size [NI23]	Stable Norway pout stock size [NP23]	Fisheries and climate change	2) and 3)
Norway pout recruitment [NI24]	Stable Norway pout recruitment [NP24]	Fisheries and climate change	2) and 3)
Whiting stock size [NI25]	Decreasing whiting stock size [NP25]	Fisheries and climate change	2) and 3)
Whiting recruitment [NI26]	Decreasing whiting recruitment [NP26]	Fisheries and climate change	2) and 3)
Herring stock size [NI27]	Decreasing herring stock size [NP27]	Fisheries and climate change	2) and 3)
Herring recruitment [NI28]	Decreasing herring recruitment [NP28]	Fisheries and climate change	2) and 3)
Mackerel stock size [NI29]	Decreasing mackerel stock size [NP29]	Fisheries and climate change	2) and 3)
Mackerel recruitment [NI30]	Change in mackerel recruitment [NP30]	Fisheries and climate change	2) and 3)

Indicator [ID]	Phenomenon [ID]	Anthropogenic drivers	Approach
Northern shrimp stock size [NI31]	Decreasing shrimp stock size [NP31]	Fisheries, climate change and pollution	2) and 3)
Northern shrimp recruitment [NI32]	Decreasing shrimp recruitment [NP32]	Fisheries, climate change and pollution	2) and 3)
Area unimpacted by bottom trawling [NI33]	Decreasing area unimpacted by bottom trawling [NP33]	Fisheries	2) and 3)
Fish species vulnerable to higher temperature [NI34]	Decreasing biomass of fish vulnerable to higher temperatures [NP34]	Climate change	2) and 3)
Fish species benefiting from higher temperature [NI35]	Increasing biomass of fish benefitting from higher temperatures [NP35]	Climate change	2) and 3)
Copepod species vulnerable to higher temperature [NI36]	Decrease in number of species sensitive to higher temperatures [NP36]	Climate change	2) and 3)
Copepod species benefiting from higher temperature [NI37]	Increase in number of "Warm-water species" [NP37]	Climate change	2) and 3)
Fish species vulnerable to fisheries [NI38]	Decreasing biomass of fish species vulnerable to fisheries [NP38]	Fisheries	2) and 3)
Temperature [NI39]	Warming of the water column [NP39]	Climate change	2) and 3)
Stratification [NI40]	Increasing stratification of the upper water column [NP40]	Climate change	2) and 3)
Flow conditions [NI41]	Increasing inflow of Atlantic water to the North Sea [NP41]	Climate change	2) and 3)
Nutrients [NI42]	Increasing concentration of nutrients [NP42]	Runoff from land and atmospheric depositions	2) and 3)
Light attenuation [NI43]	Increase in light attenuation [NP43]	Climate change	2) and 3)
pH [NI44]	Decreasing pH [NP44]	Global increase in CO ₂	2) and 3)
Aragonite saturation [NI45]	Decreasing aragonite saturation [NP45]	Global increase in CO ₂	2) and 3)

5.1 Scientific evidence base for the phenomena in the North Sea

Annual primary productivity [NI01]

Phenomenon: Increasing annual primary productivity

Ecosystem characteristic: Primary productivity

Under the reference condition annual primary production is contributed by phytoplankton and is high enough to sustain a food web of naturally occurring species and is not elevated from anthropogenic input of nutrients. During high latitude winters, incoming light intensity is low and vertical mixing is deep, causing phytoplankton cells to be mixed well below the photic zone, making them light limited rather than nutrient limited (Doney, 2006), although other limitations such as grazing are also involved (Behrenfeld, 2010; Behrenfeld and Boss, 2014). In spring, increasing surface light penetrates deeper in the water column, while at the same time, increasing temperatures and reduced winds stabilize the water column, driving the shoaling of the mixed layer. This eventually leads to an exponential increase in phytoplankton concentration, traditionally referred to as the spring bloom, where the vertically integrated gross primary production exceeds phytoplankton losses due to respiration, grazing, and sinking (Sverdrup, 1953). Primary production is highest in the coastal regions due to nutrient inputs from the rivers and mixed water columns (ICES, 2021b). The North Sea receives runoff from vast areas in Central Europe and UK, and management of nutrient runoff in the last century reversed the earlier trend of increasing eutrophication, followed by a gradual decrease in primary production (Capuzzo et al., 2018). The Norwegian administrative area comprises the northern Skagerrak and the north-western North Sea. In the Skagerrak, the outflow from the Baltic Sea mixes with water from the Jutland current forming the Norwegian Coastal Current (Gammelsrød and Hackett, 1981). West of the coastal current Atlantic water dominates, with seasonal temperature driven stratification (van Leeuwen et al., 2015).

The most important anthropogenic drivers of change in the indicator are anthropogenic nutrient input and climate change. Historically, the North Sea underwent strong anthropogenic eutrophication during the middle of the last century, with increasing nutrient input from land use in Europe (Radach and Pätsch, 2007). The trend in nutrient input was reversed in the middle of the 1980s by effects of management decisions (Burson et al., 2016). Following the reversal was a phase of de-eutrophication, with highest effects in the areas impacted by discharges from the large rivers, specifically the southern part of the North Sea (Xu et al., 2020). Building on the experience from the last century, increased input of nutrients is expected to increase the primary production relative to the reference condition (Pätsch and Radach, 1997). Global warming has local consequences for stratification of the surface waters and is predicted to reduce future horizontal larger scale circulation of the North Sea (Holt et al., 2018). A shallower stratification in summer may reduce vertical transport of nutrients for new production and phytoplankton production will be increasingly based on nutrients recycled by grazing (Lindemann and St. John, 2014), causing a possible decline in primary production. It should be noted that there is large natural variation in primary production in the Norwegian part of the North Sea because the area contains different hydrographic regimes with different levels of primary production and that the geographic distribution and size of these may vary from year to year (van Leeuwen et al., 2015; Frelat et al., 2022). This infers a variability to the indicator that leads reduced accuracy of the estimation of the impact of the driver. However, the understanding of the link between the drivers and changes in the indicator is still rated as certain.

Generally, decreasing or increasing annual primary production can lead to corresponding change in total ecosystem production (Chassot et al., 2010). In the North Sea, changes in the net primary production are expected to impact transfer of energy in the food web, with consistent responses over a large range of habitats (Steger et al., 2019; Frelat et al., 2022). Excessive increase in primary production and subsequent degradation of organic material at depth can lead to oxygen deficiency at vulnerable locations (Ciavatta et al., 2016; Breitburg et al., 2018). Increase in water temperature may induce an additional risk of hypoxia. However, such locations exist primarily south of the Norwegian Administrative area. The knowledge about the consequences for change in primary productivity for the rest of the ecosystem is rated as good.

Timing of the spring bloom [NI02]

Phenomenon: Change in the spring bloom timing

Ecosystem characteristic: Primary productivity

Under the reference condition (ca 1900), the timing of the spring bloom in the North Sea is primarily governed by the insolation (Opdal et al., 2019). In winter, phytoplankton growth is at a low level because the mixed layer is deep and insolation low. With the development of thermal stratification and thus shallower mixed layer and increased insolation in spring, the spring bloom is initiated (Opdal et al., 2019).

In temperate regions of the ocean, global warming has been shown to have influenced the onset of the bloom to earlier dates (Racault et al., 2012), and this prolongs the growing season. At higher latitudes, where light is limiting, warmer waters is hypothesized to reduce vertical mixing, also leading to an earlier spring bloom (Doney, 2006). However, coastal ecosystems are often influenced by multiple natural and anthropogenic modifiers, and temperature is only one of these drivers. Water transparency also modifies the light regime for the primary producers, and in the North Sea water clarity has decreased during the last century (Dupont and Aksnes, 2013; Opdal et al., 2019), a phenomenon known as coastal water darkening (Aksnes et al., 2009). Such a reduction in water transparency will on its own, in theory, cause a delayed spring bloom (Opdal et al., 2019). Thus, coastal water darkening may have counteracted an advancement of the spring bloom, as expected from the pronounced warming since 1980 in the North Sea. The substances causing the darkening are likely of terrestrial origin and are known to be increasing in freshwater runoff because of increasing terrestrial vegetation coverage (Larsen et al., 2011; Opdal et al., 2019), as well as more recent (1982-) reduction in sulfur emissions (Monteith et al., 2007).

Seemingly, in the region of interest, global warming produces at least two effects with opposite influence on the timing of the spring bloom. The understanding of the link between drivers and the indicator is therefore rated as less certain.

The spring bloom is a major event in temperate marine ecosystems, and the success of many grazers depends on the high food availability at the height of the bloom. Many species have synchronized their spawning with the expected bloom for optimized food conditions. Changes in the timing of spring bloom may have negative consequences for these grazers (Edwards and Richardson, 2004; Durant et al., 2019). The knowledge about the consequences of changes in timing of the spring bloom for the rest of the ecosystem is rated as good.

Knowledge gaps. Ecological communities are constantly changing due to environmental and anthropogenic pressures, and within the North Sea there are large variation in both ecosystem community structure, and ecosystem responses (Frelat et al., 2022). Research is needed to understand and quantify such changes and variability, as well as studies on the impact of climate change on the multiple controls at work (Lindemann and St. John, 2014).

Herbivorous copepods [NI03]

Phenomenon: Decreasing abundance of herbivorous copepods

Ecosystem characteristic: Biomass distribution among trophic levels

Under the reference condition, the herbivorous zooplankton are a key component for regulating the trophic flow from primary producers to higher consumers. The herbivorous food web, which is dominated by copepods, typically dominates in high nutrient (but not eutrophicated), high turbulent environments. This favors the growth of large phytoplankton ($>5\mu\text{m}$), which are in turn consumed by large grazers (Benedetti et al., 2018). Herbivore-dominated copepod communities are characterized by short food chains and efficient energy transfer towards higher trophic levels (Landry, 1977). Herbivorous grazing by large copepods will also enhance the vertical flux of carbon to deeper layers. The large, filter feeding copepods (e.g., *Calanus* and other large Calanoida) that are dominating the herbivorous zooplankton biomass are able to adapt to extreme seasonal variation in food availability through lipid storing and by employing diapausing strategies. The most important herbivorous species in the North Sea is the copepod *Calanus finmarchicus*, which makes up 70-90% of the zooplankton biomass during spring (Krause and Martens, 1990).

The most important anthropogenic driver of change in the herbivorous copepod community is climate change. Higher temperatures and stronger stratification due to climate change will cause depletion of nutrients in the surface waters, and the primary producers are expected to be dominated by pico- and nano-sized algae and bacteria. This production is consumed by heterotrophic nanoflagellates and microzooplankton and transferred to higher consumers through the microbial food web (Calbet and Landry, 2004). In this state, the food-web is dominated by small omnivores and carnivores, resulting in a longer and less efficient food chain. This is consistent with observations that the relative importance of herbivorous zooplankton decreases in areas with higher temperatures and lower Chl.-a biomass. As a result of climate-induced changes, the North Atlantic ecosystem is expected become less favorable to herbivorous copepods in the next century (McGinty et al., 2021).

In coastal regions the indicator may also be affected by *eutrophication*, which will have a negative effect on the herbivorous food web. Increasing primary production may initially be beneficial for herbivores as it provides more food for grazing copepods. If on the other hand, zooplankton grazing cannot keep pace with increased phytoplankton growth, the result is excessive buildup of organic matter followed by increased bacterial activity and hypoxia. Imbalanced nutrient enrichment will typically modify the plankton community structure towards small-sized phytoplankton, toxic species, bacterioplankton, and detritus production, thus promoting microbially-driven energy pathways (Ndah et al., 2022). This system is less favorable for herbivorous zooplankton, and will be dominated by omnivores and small carnivores, with longer and less efficient trophic pathways. However, the responses by the zooplankton community to increasing nutrient concentrations is unpredictable due to the complex planktonic food webs, and linking zooplankton metrics to eutrophication has been found to be challenging (Ndah et al., 2022).

Given the complex interaction between environmental conditions and the trophic structure of the planktonic community, the links between the drivers (climate and eutrophication) and herbivorous copepods is rated as less certain.

Marine biological productivity depends on the magnitude of phytoplankton production and its trophic transfer through food webs. Numerous studies have demonstrated that changes in the abundance of herbivorous zooplankton will influence the ecosystem productivity, nutrient recycling and carbon transfer (Landry, 1977; Sommer et al., 2002; Castellani et al., 2008; Armengol et al., 2019). A decline in the abundance of herbivorous zooplankton will result in longer trophic pathways, less efficient energy transfer and reduced production on higher trophic levels. A reduction in the large lipid-rich herbivorous species will cause a loss in accessible energy for planktivores. For example, successful cod recruitment in the North Sea is linked to years with high abundance of *C. finmarchicus* (Beaugrand et al., 2003). Furthermore, a change towards less herbivorous grazing is projected to reduce the oceanic uptake of CO₂ by lowering the efficiency of the biological pump to deeper layers (Richardson, 2008). This could contribute to a positive feedback between climate change and the ocean carbon cycle, leading to rapid and potentially unstable climate shifts (Denman and Peña, 2002).

Given the evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Decreasing abundances of herbivorous copepod zooplankton can be considered of ecosystem significance if: i) it causes a decline in the productivity at higher trophic levels (e.g., fish) and ii) it causes significant reduction in the vertical transport of carbon (carbon-pump).

Knowledge gaps: The phenomenon can be monitored by using the CPR time series which provides long term abundance data on large filter feeding copepod species and other herbivores in the North Sea. Indeed, studies based on CPR data have documented that total *Calanus* biomass has declined by 70% since the 1960s, which is in line with the phenomenon described above. However, all copepods (including *C. finmarchicus*) are classified as obligate omnivores in the CPR dataset and most species are known to alter their dietary strategy under changing local conditions (Kleppel, 1993). Dietary preferences of zooplankton species have been compiled in trait databases, (e.g., Benedetti et al. (2015); Brun et al. (2017)) but feeding traits cannot always be considered as species specific. The monitoring of this phenomenon requires improved knowledge on zooplankton feeding traits. Furthermore,

microzooplankton (<200 µm grazers) have been reported as important consumers of the primary production (Calbet, 2008) but data on both abundances and feeding rates of microzooplankton taxa is lacking. Finally, it should be noted that the CPR survey only samples the surface waters. As a result, the CPR data may be affected by potential changes in the vertical distribution of each species in response to changing climate (Pinsky et al., 2013).

Carnivorous zooplankton [NI04]

Phenomenon: Increasing abundance of carnivorous zooplankton

Ecosystem characteristic: Biomass distribution among trophic levels

Under the reference condition, carnivorous zooplankton are secondary consumers constituting an intermediate link between herbivorous zooplankton and higher trophic levels. Common and important carnivorous taxa include carnivorous copepods, amphipods, euphausiids, chaetognaths, ctenophores and cnidarians (jellyfish). These predators are known to feed on smaller copepods and are in turn prey for higher trophic levels. Carnivorous zooplankton can occupy several trophic levels, from secondary consumers to the top predators in the pelagic ecosystem.

The most important anthropogenic driver of change in the carnivorous zooplankton is climate change. Higher temperatures and stronger stratification due to climate change will cause depletion of nutrients in the surface waters. The primary producers are expected to be dominated by pico- and nano-sized algae and bacteria which are consumed by small invertebrate omnivores or carnivores, and transferred to higher consumers through the microbial food web (Calbet and Landry, 2004). In this state, the food-web will be dominated by carnivores, with several intermediate levels, resulting in a longer and less efficient food chain. Carnivore dominated systems often occur in tropical and oligotrophic regions where trophic interactions are more complex and tend to be dominated by top-down as opposed to bottom-up processes (Hébert et al., 2016). As a result of climate-induced changes, the North Atlantic ecosystem is predicted to become more favorable to carnivorous copepods in the next century and the overall habitat area for carnivores will increase (McGinty et al., 2021). This is consistent with Schmidt et al. (2020) who reported that several carnivorous copepods have been increasing in UK shelf waters, despite a decline in overall copepod abundance.

An additional important driver of change in the indicator is *eutrophication*, which will enhance the carnivorous food web. Nutrient enrichment will typically modify the plankton community structure towards small-sized phytoplankton, bacterioplankton, and detritus production, thus promoting microbially-driven energy pathways (Ndah et al., 2022). This system will be dominated by omnivores and small carnivores, with longer and less efficient trophic pathways. However, the responses by the zooplankton community to increasing nutrient concentrations is unpredictable due to the complex planktonic food webs and linking zooplankton metrics to eutrophication has been found to be challenging (Ndah et al., 2022).

Given the complex interaction between environmental conditions and the trophic structure of the planktonic community, the links between the drivers (climate and eutrophication) and carnivorous zooplankton is rated as less certain.

Marine biological productivity depends on the magnitude of phytoplankton production and its trophic transfer through food webs. Numerous studies have demonstrated that increasing dominance of carnivorous zooplankton will decrease the ecosystem productivity and the vertical carbon transfer (Landry, 1977; Sommer et al., 2002; Castellani et al., 2008; Armengol et al., 2019). An increase in the abundance of carnivorous zooplankton will result in longer trophic pathways, less efficient energy transfer and reduced production on higher trophic levels.

Carnivorous zooplankton have been found to have a substantial impact on prey communities and selective predation by zooplankton may influence the trophic structure of the zooplankton community. Carnivorous zooplankton may negatively affect fish populations through direct predation on early life stages or via competition with juveniles and adults (Yen, 1987; Falkenhaus, 1991; Purcell and Arai, 2001).

Given the evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Increasing abundance of carnivorous zooplankton can be considered of ecosystem significance if i) it causes a decline in the productivity at higher trophic levels (e.g., fish) and ii) it causes reduced recruitment of fish populations

Knowledge gaps in monitoring and research: The phenomenon can be monitored through the CPR time series which provides long term abundance data on 27 different zooplankton taxa classified as carnivorous zooplankton. However, improved knowledge on zooplankton feeding traits is required which are not always taxon-specific but vary with season and life stages. Furthermore, monitoring data on important carnivorous components, such as carnivorous microzooplankton and gelatinous plankton are lacking. Future studies should attempt to disentangle the interaction between bottom-up and top-down control in the planktonic food web. Finally, it should be noted that the CPR survey only samples the surface waters. As a result, the CPR data may be affected by potential changes in the vertical distribution of each species in response to changing climate (Pinsky et al., 2013).

Low trophic level fish [NI05]

Phenomenon: Change biomass of LTL fish

Ecosystem characteristic: Biomass distribution among trophic levels

Low trophic level pelagic and demersal fish are key species of the ecosystem functioning in the North Sea that ensure the link from the planktonic production to the upper trophic level both in the upper and lower water column. Under the reference conditions, the biomass of this group is sufficient to fulfil this link in the food web. Examples of low trophic level species include herring (*Clupea harengus*), sprat (*Sprattus sprattus*), Norway pout (*Trisopterus esmarkii*), mackerel (*Scomber scombrus* and *S. japonicus*), sand lances (*Ammodytes* spp.), pipefish (*Syngnathus* spp.) and gobies (Gobiidae).

The main drivers of the biomass of low trophic level species in the North Sea are climate change and fisheries. Engelhard et al. (2010) have observed long term increase of low/mid trophic level demersal species in the North Sea and a general decline of high trophic level species. This community pattern confirms previous size-spectrum analysis suggesting a slow decline in the trophic level of demersal communities (Jennings et al., 2002). Both climate change and fisheries could have led to these observations. First, the northward shift of large Boreal predators decreased their abundance in the North Sea, while small bodied low trophic level Lusitanian species progressed inside the region during the post-1989s warmer regime. Second, fisheries are typically targeting larger, higher trophic level species, thus reducing their abundance in the region and increasing the *relative* abundance of lower trophic level species (Jennings et al., 2002; Engelhard et al., 2010). However, in the North Sea, many of the forage fish species, such as herring, sandeels, sprat and Norway pout, are targeted by commercial fisheries, and fisheries thus have a direct negative effect on the biomass of low trophic level fish. Finally, their productivity (growth, recruitment) is thought to be declining as a consequence of the over-harvesting in the late 1990s and the loss of productivity of the first secondary consumers such as zooplankton (Clausen et al., 2018; Lindegren et al., 2018). Considering the multidirectional direct and indirect effects of climate and fisheries and the uncertainties around the links between biomass and productivity, the understanding of the link between the drivers and change in the indicator is assessed as less certain.

Variation in fisheries and climate change pressures have been shown to have cascading impacts mediated by these key low trophic level species. Multiple studies have shown the dependence of the ecosystem top predators on forage fish stocks, in particular herring, sprat and sandeels, with abundance of forage fish e.g. positively affecting the breeding success of seabirds, the condition of whiting (*Merlangius merlangus*), or negatively impacting zooplankton (Frederiksen et al., 2006; Wanless et al., 2007; Fauchald et al., 2011b; Lauerburg et al., 2018). A modelling study using Ecopath with Ecosim (Smith et al., 2011) suggested that fishing low trophic level species (sandeels, sprat, sardine, krill and mackerel) leads to changes in biomass of more than 40% in other parts of the ecosystem compared to scenarios without fishing. Negatively impacted species included mostly the top predators of the system such as halibut, large demersal fish, rays, seabirds, seals, or whales. Conversely, large abundances of forage fish can also impact larger predators by leading to predator-prey role inversions. This could occur if overfishing of large predators releases predation pressure on forage fish that feed on and compete with early life stages of large predators (Fauchald, 2010). The understanding of the importance of changes in the indicator for the rest of the ecosystem is thus assessed as good.

Changes in the biomass of low trophic level fish species can thus be considered of high ecological significance if predator populations are negatively impacted.

Important knowledge gaps on low trophic level species include the benthic-pelagic coupling and how it is affected by the combined impacts of climate and fisheries. Indeed, changes in trophic level and size structure in the North Sea seem to differ between the pelagic and the demersal compartment (Jennings et al., 2002). Understanding the coupling of flows from the upper to the lower water column and monitoring its changes could inform on how the drivers might affect the ecosystem as a whole.

High trophic level fish [NI06]

Phenomenon: Decreasing biomass of HTL fish

Ecosystem characteristic: Biomass distribution among trophic levels

Under reference conditions, predatory fish biomass is mainly linked to the abundance of their prey, on which they may maintain a top-down control. The smaller demersal or bathypelagic piscivorous species include the whiting (*Merlangius merlangus*), adult haddock (*Melanogrammus aeglefinus*) and grey gurnard (*Eutrigla gurnadus*), feeding on forage fish and juvenile gadoids. Larger high trophic level species are adult individuals of generalist species such as cod (*Gadus morhua*), saithe (*Pollachius virens*), and benthivorous/piscivorous fish such as anglerfish species (*Lophius piscatorius* and *L. budegassa*), and northern lampreys (*Lampetra fuvialitis* and *Petromyzon marinus*). Pelagic species include greater sandeel (*Hyperoplus immaculatus*), the Atlantic bonito (*Sarda sarda*) and porbeagle (*Lamna nasus*, IUCN vulnerable).

The main driver of changes in biomass of high trophic level fish are fisheries. By removing the largest individuals, fisheries have several impacts that drive a decline in the biomass of the population. First, by directly removing individuals and then by depleting the pool of large fecund females that are thought to produce better eggs than the younger spawners (e.g. Hixon et al. (2013)). Second, fisheries can also target the predators prey. The Norwegian fleet in the North Sea is composed mainly of small vessels (<11m) that target mostly demersal species, including potential prey of high trophic levels species (ICES, 2021c). Lastly, fishing affects biological interactions. For example, fishing on cod is suggested to have released the competition pressure on grey gurnard (not fished) which have replaced fished (predator) species in their ecological niche and feeding partially on their early life stages (Floeter et al., 2005; ICES, 2021c). Previous size-spectrum analyses suggest a slow decline in the trophic level of demersal communities (i.e. decreasing biomass of high trophic level fish) since the 1980s supposedly linked to fisheries (Jennings et al., 2002). Climate change also has a negative impact on high trophic level fish as the decreasing abundance of large, lipid rich copepods could impact the condition and survival of their early life stages (Capuzzo et al., 2018). Engelhard et al. (2010) have observed long term generally decreasing or marginally increasing high trophic level demersal species in the North Sea in link with the water column warming and the concomitant northward shift of fish species, driving larger species out of the North Sea. The understanding of the links between fisheries in the indicator is assessed as certain, but the impacts of climate change are rated as less certain.

Impacts of a decreasing biomass of high trophic level species include a change in the trophic structure of the ecosystem, by releasing predation pressure on lower trophic levels. The specific consequences on the North Sea lower trophic levels are however not well understood. The understanding of the importance of changes in the indicator for the rest of the ecosystem is assessed as less good.

Important knowledge gaps for low trophic level species include the benthic-pelagic coupling and how it is affected by the combined impacts of climate and fisheries. Indeed, changes in trophic level and size structure in the North Sea seem to differ between the pelagic and the demersal compartment (Jennings et al., 2002). Understanding the coupling of flows from the upper to the lower water column and monitoring its changes could inform on how the drivers might affect the ecosystem as a whole.

High trophic level seabirds [NI07]

Phenomenon: Decline in populations of piscivorous surface feeding seabirds

Ecosystem characteristic: Biomass distribution among trophic levels

Under the reference condition, the numerous islets and skerries in the archipelago along the coast of the North Sea and Skagerrak host large breeding populations of mainly fish-eating gulls and terns. The gulls include herring gull (*Larus argentatus*), common gull (*Larus canus*), lesser black-backed gull (*Larus fuscus*) and great black-backed gull (*Larus marinus*). Terns include common tern (*Sterna hirundo*) in all areas, and Arctic tern (*Sterna paradisaea*) in the western and northern part of the North Sea. The main food source is small pelagic schooling fish, such as sprat (*Sprattus sprattus*), sandeel (*Ammodytes* spp.) and juvenile fish including herring (*Clupea harengus*) and saith (*Pollachius virens*). The gulls are opportunistic, and when small fish are scarce, they might survive on less nutritious marine resources, including crustaceans, bivalves, echinoderms, and polychaetes (see e.g. Kubetzki and Garthe (2003)). In addition, discards from the fishing fleet has been suggested to be an important alternative food source for gulls in the North Sea (Garthe et al., 1996). However, the availability of small pelagic fish seems to be important for successful reproduction (Byrkjeland, 2015). Enabled by omnivorous and opportunistic foraging behavior, some populations of gulls have, possibly partly as a response to declining food resources, moved the breeding and foraging habitats to urban areas. In the marine environment, gulls and terns are limited to feed from the upper meter of the water column and they are consequently dependent on other predators, such as predatory fish, diving seabirds and marine mammals that “herd” small fish to the surface (Veit and Harrison, 2017). The fish-eating populations of gulls and terns along the coast of the North Sea are accordingly dependent on a diverse and rich coastal fish community.

The most important anthropogenic drivers of change in this indicator are fisheries and to some extent eutrophication and climate change. Following increased capacity and efficiency in the fishing fleet, coastal fish stocks were severely depleted by overfishing from the 1950s to the 1980s (Norderhaug et al., 2020). Experimental evidence from no-take zones suggest that commercial and recreational fishing is still a factor that keep coastal fish stocks at low levels (Moland et al., 2013). Monitoring of the numerous seabird reserves along the coast suggests that food scarcity has been the main factor behind decades of breeding failure and population decline in gulls and terns (Finne and Fjellbakk, 2013; Larsen, 2014; Byrkjeland, 2015; Larsen, 2021). In particular, the management reports point to the decline in the availability of sandeel and sprat (ibid.). In the North Sea, these small pelagic fish species have complex population structures with many more or less distinct populations confined to specific areas and fjord systems (Falkenhaug and Dalpadado, 2014; ICES, 2017a; Saltalamacchia et al., 2022). Unregulated industrial fisheries were developed on sprat and sandeel during the 1950s to 70s. Following a period of high catches, several stocks declined and have remained at low and fluctuating levels. For example, the landings on several historically important sandeel fishing grounds in the Norwegian economic zone showed a dramatic decline from the late 1990s, and were commercially depleted for many years (Johannessen and Johnsen, 2015; ICES, 2017a). Although the stocks are still fished in industrial fisheries, the fisheries are today better regulated according to the population structure (Johnsen et al., 2021). The impact of overfishing on seabirds has been documented in numerous studies world-wide (Cury et al., 2011; Grémillet et al., 2018). Although there are several unresolved questions related to the exact relationship between fishing, the dynamics of local stocks of sprat and sandeel and seabirds (Byrkjeland, 2015), the link between overfishing and the indicator is assessed as relevant (Finne and Fjellbakk, 2013; Larsen, 2014; Byrkjeland, 2015; Larsen, 2021), and the understanding of the link between the indicator and fisheries is assessed as certain. In addition to overfishing, climate change, eutrophication and sea water darkening might affect seabirds through indirect impacts on prey availability. Finally, predation from e.g., white tailed eagles (*Haliaeetus albicilla*) and American mink (*Neovison vison*) may also play a role.

Gulls and terns are a significant part of the top predator guild in the Norwegian part of the North Sea and Skagerrak. A large relative drop in the abundance of these species could impact their role as top predators in the ecosystem and would signal negative changes at lower trophic levels. The understanding of the importance of changes in the abundance of piscivorous surface feeding seabirds is assessed as good.

Decreasing abundance of pelagic seabirds can be considered of ecosystem significance if, for example: i) there is a

sudden drop in the populations caused by a mass die-off of birds following a collapse in the availability of prey due to climate extremes or overfishing, and ii) there is a significant gradual long-term (> 10 years) decrease in the populations associated with climate warming and/or decrease in the availability of prey.

Holoplankton vs meroplankton [NI08]

Phenomenon: Changes in Meroplankton vs. Holoplankton abundance

Ecosystem characteristic : Functional groups within trophic levels

Under the reference condition, holoplankton are likely numerically dominating over meroplankton. Holoplankton are organisms that are planktic for their entire life cycle (“true plankton”) and constitute a very diverse group of taxa of which copepods is the numerically dominating one. Meroplankton on the other hand, spend only parts of their life cycle as plankton before entering other life conditions such as the nekton (e.g., fish and cephalopods) or the benthos community (e.g., sea urchins, crabs and mussels). The Continuous Plankton Recorder (CPR) survey has since 1958 routinely surveyed the North Sea plankton community on an approximately monthly basis. From the start of the survey up to around 1990, the holoplankton have comprised around 80% of the total zooplankton abundance in Norwegian waters. Since then, there has been a marked decline and by 2016 the holoplankton constituted only 35% compared to the 65% meroplankton. Studies have shown that this shift is primarily driven by increased numbers of echinoderm larva (Lindley et al., 1995; Lindley and Batten, 2002), and Kirby and Lindley (2005) showed that this increase was primarily driven by larva of the sea urchin *Echinocardium cordatum*. In contrast, the abundance of bivalve mollusk larvae has declined, suggesting that not all taxa respond similarly to climate change (Kirby et al., 2008).

The most important anthropogenic driver of change in the indicator is climate change, and more precisely increased sea temperature. Analysing the whole North Sea, Lindley and Batten (2002) showed that *E. cordatum* have advanced their spawning season by 47 days over a period of 45 years. Spawning in adult *E. cordatum* is initiated when North Sea winter temperature exceeds 6°C (Nunes and Jangoux, 2004), and Kirby et al. (2007) suggest that an increased thermal regime in the North Sea in winter and spring have benefited reproduction and survival in this benthic species. Increased North Sea phytoplankton biomass is also believed to help facilitate larval growth (Kirby et al., 2007) and improve food supply for benthos through increased sedimentation (Kirby et al., 2008). Given the evidence described above the understanding of the link between climate change and the indicator is rated as certain.

It is well known that the North Sea has gone through a regime shift (Beaugrand, 2004b), and the increase in echinoderm larvae could act to reinforce the new ecological regime by competitive exclusion of other holo-zooplanktonic taxa, such as copepods, during spring and summer (Kirby et al., 2007). Increases in meroplankton abundance may also have an effect on the benthic community, and thereby increase the benthic-pelagic coupling (Kirby et al., 2007; Kirby et al., 2008). However, we lack a clear understanding of how increased levels of meroplankton affect holoplankton abundance in general and food competition in particular. Trophic interactions and other processes in the benthic community may also affect the production of meroplankton (Kirby et al., 2008). Thus, our understanding of the importance of change in the indicator for other parts of the ecosystem is less good.

Increasing abundance of meroplankton relative to holoplankton can be considered of ecosystem significance if, for example, it causes large declines in copepod abundance, and with it, a likely decline in fish recruitment success. The relative abundance of holoplankton and meroplankton will also reflect energy partitioning between the pelagic and benthic environments (Bedford et al., 2020).

Monitoring of this phenomenon is adequate due to the CPR time series, while research should be focused on understanding the level and effect of food competition between abundant holoplankton groups and *E. cordata* larva.

Copepod body size [NI09]

Phenomenon: Reduced average copepod body size

Ecosystem characteristic: Functional groups within trophic levels

Under the reference condition, copepod body size is considered as a key trait in zooplankton as it is related to numerous physiological and ecological processes, e.g., individual growth, metabolic rates, feeding behavior and life strategies (Pope et al., 1994; Kiørboe, 2011; McGinty et al., 2021). In planktonic communities, body size is of particular importance, because food webs are comprised of regular and progressively increasing size spectra (Sheldon et al., 1972). Copepod body size is affecting grazing efficiency, predator prey interactions, and trophic energy transfer and thereby determining the trophic structure and dynamics of pelagic communities (Gorokhova et al., 2013). Zooplankton body size varies with latitude and species tend to be larger in colder, higher latitudes compared to its congeners found in warmer regions (Bergmann's temperature-size rule).

The most important anthropogenic driver of change in zooplankton body size is climate change, in terms of increasing temperature. Higher temperatures cause elevated metabolic rates and energy costs, resulting in smaller body sizes both within species (Record et al., 2012) as well as at the community level (Beaugrand et al., 2002b). Ecological theory and observations suggest that climate warming is expected to favor small copepods over large copepods (Daufresne et al., 2009). This suggests that an increase in temperature should result in an increase in the proportion of smaller-sized species in a community.

As ocean temperatures increase over the next century, these changes are likely to shift communities into states where smaller phytoplankton and zooplankton species dominate. Significant shifts in zooplankton community structure and size-spectra towards the dominance of the small-sized copepod *Oithona similis* relative to large-bodied calanoid copepods have already been observed across the global ocean such as in the Arctic (Balazy et al., 2021), the North Sea (Nielsen and Sabatini, 1996; Bedford et al., 2018), the North Atlantic and the Mediterranean Sea (Beaugrand et al., 2003; Castellani et al., 2015).

The replacement of large copepods with small ones has also been suggested as an indicator of eutrophication in the Baltic region (Gorokhova et al., 2013; HELCOM, 2018) but in marine systems the causal link between eutrophication and body size is ambiguous (Ndah et al., 2022).

Given the solid evidence described above the understanding of the link between temperature and zooplankton body size is rated as certain.

Changes in the average copepod body size are expected to alter the food web structure and the carbon transfer between trophic levels. Zooplankton communities composed of large-bodied copepods have a higher capacity for transfer of primary producers (phytoplankton) to fish, i.e., higher energy transfer efficiency. By contrast, a dominance of small-bodied copepods is usually associated with lower energy transfer efficiency, since it results in longer food chains and thereby higher energetic losses (Lewandowska and Sommer, 2010). Thus, a reduction in the mean copepod body size represents unfavorable fish feeding conditions and less efficient utilization of primary production. According to ecological theories, this would represent a less efficient food web (HELCOM, 2018).

As ocean temperatures increase over the next century, these changes are likely to shift communities into states where smaller phytoplankton and zooplankton species dominate. This will result in a less productive system, with decreased trophic efficiency and reduced fecal carbon flux (Hébert et al., 2016).

A reduction in the zooplankton body size will have direct negative impact on fish feeding conditions, fish larval survival and recruitment (Beaugrand, 2005). Pitois et al. (2012) and Pitois et al. (2021) found strong correlations between herring distribution and larger copepod mean sizes rather than high copepod abundances, confirming that copepod mean size has the potential to reflect food web and ecosystem health status as well as highlight climatic impacts on marine ecosystems.

Given the substantial evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Decreasing zooplankton body size can be considered of ecosystem significance if i) it causes massive declines in the production and recruitment of fish stocks, and ii) it causes reduced vertical carbon flux (carbon pump).

Knowledge gaps in monitoring and research: Based on the classification of UK Pelagic Habitats Expert Group (2021), copepods from the CPR data set can be classified into two size groups: as “Small” (< 2 mm) and “Large” (2> mm). However, dataset including species specific copepod sizes are available (Razouls et al., 2005-2022; Brun et al., 2017).

The interpretation of this phenomenon may be demanding due to top-down effects. Size-selective predation on zooplankton by predators (top-down) will affect the size composition of zooplankton and may counteract climate-induced effects (bottom-up). Future studies should try to disentangle the interaction between top-down and bottom-up control.

Alternative metrics related to copepod size should be investigated further, e.g. “Copepod community body size” as the abundance weighted mean prosome length (Evans et al., 2020). Relative metrics, including both size and abundance may be more informative, e.g. Normalized Biomass Size-Spectra (NBSS) and the Abundance-Size Spectrum of zooplankton, referring to the relative abundance or biomass of zooplankton organisms of different size classes (Thompson et al., 2013).

The MSTS (Zooplankton Mean Size and Total Stock) is a core indicator in the Baltic region, where the lengths of individuals are measured for each species (HELCOM, 2018). A similar indicator exists in the OSPAR area (FW6; Ndah et al. (2022)). However, a major limitation is that zooplankton sizes are not regularly measured in marine monitoring and are usually estimated using mean values from the literature. The lack of in-situ size information will mask any potential long-term change in species-specific size structure. Future monitoring should aim at including size measurements of zooplankton, preferably by the use of image analyzing methods (e.g., FlowCam).

Gelatinous zooplankton [NI10]

Phenomenon: Increasing abundances of gelatinous zooplankton

Ecosystem characteristic: Functional groups within trophic levels

Under the reference condition, gelatinous zooplankton are ubiquitous members of zooplankton communities and can make up 30-60 % of the total plankton carbon biomass (Vinogradov and Shushkina, 1994). “Gelatinous plankton” includes members of at least three different phyla: Cnidaria (Hydrozoan and Scyphozoan medusae and siphonophores), Ctenophora (“comb jellies”) and Chordata (appendicularia and salps). “Jellyfish” usually refers to the hydrozoan and scyphozoan medusae. The diverse groups of gelatinous zooplankton differ in both feeding strategies and life cycles. The cnidarians and ctenophores are carnivorous predators on other zooplankton (copepods and even fish). Pelagic tunicates on the other hand, are filter-feeders on phytoplankton and bacteria, and, thus, are primary consumers in the food web. Cnidarians have a complex life cycle, usually involving benthic stages (polyps), while Ctenophores and tunicates do not have a benthic phase (they are holoplankton).

Most gelatinous species have evolved a bloom-forming life cycle with rapid growth and high fecundity during suitable conditions. This rapid response to environmental conditions has proven to be a successful strategy in variable and patchy marine environments. Large seasonal blooms of gelatinous zooplankton are thus a natural feature of all marine ecosystems, dating back to the Cambrian Period (Graham et al., 2001).

The most important anthropogenic driver of increasing abundance of gelatinous zooplankton is climate change. Rising temperatures are likely to directly impact gelatinous zooplankton through increasing growth and reproduction rates and through increasing species ranges (Brotz et al., 2012; Condon et al., 2014). Gelatinous zooplankton will be indirectly affected by climate change from increasing stratification, resulting in reduced mixing of nutrients, eutrophication and hypoxia. However, it is currently unclear what impact this will have on gelatinous zooplankton populations (Gibbons and

Richardson, 2013; Lucas and Dawson, 2014).

There is currently no agreement about the underlying drivers of gelatinous blooms. Among the most cited is climatic conditions (Molinero et al., 2005; Lavaniegos and Ohman, 2007; Lynam et al., 2011; Condon et al., 2013) and rising temperatures (Lynam et al., 2004; Lynam et al., 2005; Gibbons and Richardson, 2009; Brodeur et al., 2019). However, a number of additional hypotheses have been suggested, including ocean acidification (Attrill et al., 2007), eutrophication (Arai, 2001), reduced water-clarity (Eiane et al., 1999), an increase in hard substrata for polyp attachment in the case of cnidarians (Parsons and Lalli, 2002), invasion of alien species (Purcell and Arai, 2001; Purcell et al., 2007), and over-fishing (Pauly et al., 2002; Lynam et al., 2011).

Several studies have indicated that blooms of gelatinous plankton are increasing globally, both in frequency and magnitudes (Mills, 2001; Purcell et al., 2007; Richardson et al., 2009). However, opposite declining trends in gelatinous plankton have also been reported (Hosia et al., 2014; Long et al., 2021). There has been a significant debate around the question of whether gelatinous zooplankton has or will increase in the future due to climate change. This *perceived* global increase in gelatinous zooplankton lacks proof from rigorous scientific data and is known as the *jellyfish paradigm* (Brotz et al., 2012; Condon et al., 2013; Gibbons and Richardson, 2013).

Given the limited knowledge on drivers behind gelatinous blooms, the understanding of the link between climate change and gelatinous zooplankton is rated as less certain.

Increasing abundances of gelatinous zooplankton may negatively impact commercially harvested fish stocks (Pauly et al., 2009), limit bioavailable carbon to higher trophic levels and promote microbially mediated food webs (Condon et al., 2014). A change in the relative abundance of crustaceans and gelatinous zooplankton may indicate alternative energy flows through the food web, reducing the production on higher trophic levels, such as fish populations (Purcell and Arai, 2001; Richardson et al., 2009). Predatory jellyfish and ctenophores often feed on the same prey items as planktivorous fish and thus have the potential to adversely impact fish recruitment through both competition and predation. Furthermore, an increase in gelatinous zooplankton also alters the quality of the food available for fish, as gelatinous zooplankton contains 65-95% less carbon than crustacean zooplankton (McConville et al., 2016).

Mass-occurrences of gelatinous zooplankton have also been reported to have negative socio-economic impacts, such as clogging of fishery nets, aquaculture fish mortality, obstruction of cooling systems of power plants, adverse human health, tourism and coastal infrastructure (Purcell et al., 2007; Wright, 2019).

There are also ecological processes and groups that are positively affected by gelatinous zooplankton. An increase in gelatinous filter-feeders (appendicularians and salps) may provide an alternative energetic pathway between primary producers and higher trophic levels, resulting in shorter food chains, and higher trophic efficiency (Heneghan et al., 2021). Additionally, post-bloom jelly-falls may accelerate the biological pump and increase carbon sequestration from the upper ocean to the deep-sea floor (Lebrato et al., 2012). Gelatinous zooplankton have been viewed as trophic dead-ends, but research has shown that they make up some of the diets of 124 fish species and 34 other marine species (Pauly et al., 2009). There has clearly been an underestimation of the importance of gelatinous zooplankton in pelagic food webs as well as in benthic food webs where gelatinous carcasses are rapidly scavenged (Sweetman et al., 2014; Hays et al., 2018; Brodeur et al., 2019).

Given the contradictions and uncertainties described above the understanding of the importance of change in gelatinous zooplankton for other parts of the ecosystem is rated as less good.

Increasing abundance of gelatinous zooplankton can be considered of ecosystem significance if: i) it causes massive declines in fish populations, ii) it causes structural changes in the zooplankton community, or iii) it alters the carbon pump.

Knowledge gaps: One of the main limitations when addressing the phenomenon is the lack of long time-series of the abundance and diversity of gelatinous zooplankton (Brodeur et al., 2016). Available time series are usually found in

coastal areas, where the environmental drivers may differ from the open North Sea. The Continuous Plankton Recorder (CPR) survey does not include gelatinous zooplankton due to the sampling method. However, data on the presence of coelenterate tissue from the CPR survey have been used to examine trends in gelatinous zooplankton (Gibbons and Richardson, 2009). CPR is not an ideal jellyfish sampler, and several limitations must be borne in mind when using jellyfish data from this device. There is a large potential in obtaining monitoring data on gelatinous zooplankton from ongoing monitoring activities and fish surveys (Aubert et al., 2018). Standardized sampling and registration of gelatinous zooplankton should be implemented on e.g., the North Sea IBTS survey and Ecosystem cruises.

As discussed above, to lump hundreds of species from three different phyla into a single category “gelatinous zooplankton” complicates the interpretation of the phenomenon (*comparable to lumping lions and gazelles into a single ecological group called mammals*, c.f. Condon et al. (2012)). Environmental drivers are often species-specific which highlight the need to monitor gelatinous zooplankton with a high taxonomic resolution. E.g., the common Lion mane jellyfish (*Cyanea capillata*) is a boreal, cold-water species and is expected to decrease during climate warming, while *C. lamarckii* thrives in warmer water and is expected to increase. Environmental drivers, such as temperature may also have opposite effects on different phases in the life cycles of Cnidarian species (i.e., benthic polyps vs pelagic medusae).

Alternative indicators should be explored: e.g., species specific indicators, where environmental drivers may be better known. Change in the *frequency* and/or *magnitude of blooms* may be more adequate indicators than the general “abundance of gelatinous zooplankton”.

Fish body size [NI11]

Phenomenon: Decreasing fish community mean body size

Ecosystem characteristic: Functional groups within trophic levels

Reference conditions for a community size structure are difficult to describe. A theoretical unexploited fish community of the North Sea estimated from macroecology theory suggested that the biomass of large fish (4-16 and 16-66kg) was 97-99% lower in the early 2000s than in a situation without fisheries (Jennings and Blanchard, 2004). In this model, the mean turnover time of biomass was twice as slow.

The main driver of change in fish community mean size is fishing. Climate change could also be a driver of change in fish community size, but the links are less well understood. Jennings et al. (2002) suggested that changes in body size was a stronger and more universal indicator of fisheries impact on fish communities than trophic level. By removing the larger individuals, fisheries have reduced the number of large fish species such as cod (*Gadus morhua*), saithe (*Pollachius virens*), ling (*Molva molva*), sturgeon (*Acipenser sturio*) and some elasmobranchs (ICES, 2021b), and would also drive a shift towards smaller size and lower age at maturity (Jørgensen et al., 2007). Abundant literature supports this link. Long term studies of changes in trophic level on size-classed survey data showed a slow decline in abundance of larger fish species as a consequence of intense fishing pressure (Frid et al., 1999; Jennings et al., 1999b; Jennings et al., 2002; Greenstreet and Rogers, 2006). Similarly, a modelling study has shown that an indicator for large fish (Large Fish Index: proportion of fish captured larger than 40cm, ICES (2007)) was mainly driven by cod fishing mortality (Speirs et al., 2016). Furthermore, abundance of small fishes has increased (Daan et al., 2005).

Climate change can have similar effects on fish size. Size-dependent physiological and physical constraints on energy and oxygen uptake might imply that higher temperatures, leading to increased energy and oxygen consumption, can be more easily supported by small-bodied fish, although studies fail to reach a consensus on the underlying mechanisms (Audzijonyte et al., 2019). This is supported by studies in the North Sea that have observed synchronous decreases in body size of commercial fish species of diverse life history traits concomitant with a period of increasing temperature (Baudron et al., 2014; Ikpewe et al., 2020). Engelhard et al. (2010) have observed long term generally decreasing or marginally increasing high trophic level demersal species in the North Sea in link with the water column warming and the northward shift of fish species, driving larger species out of the North Sea. However, the mechanisms linking body size and temperature are less well understood than those linking fisheries and fish body size. The understanding of the

link between change in the indicator and fishing is thus assessed as certain while that between the indicator and climate change is assessed as less certain. As fisheries is the main driver, the overall link to drivers is assessed as certain.

Body size is an important determinant of fish physiology, behaviour, interspecific interactions and might also mediate the relationship between species richness and ecosystem functioning (Brown et al., 2004; Fisher et al., 2010; Andersen et al., 2016). Changes in body size may thus affect ecosystem functioning in multiple ways, including changes in trophic controls (Brose et al., 2012). The understanding of the impacts on the ecosystem of changes in fish size is consequently assessed as good.

The extent to which ecosystem functions, such as carbon fluxes and benthic-pelagic coupling, are affected by changes in body size structure is uncertain. In addition, it is uncertain how other trophic levels might compensate for changes in fish community size structure.

Fish life history [NI12]

Phenomenon: Decreasing proportion of slow-life species and increasing proportion of fast-life species

Ecosystem characteristic: Functional groups within trophic levels

Estimating the relative proportion of life history strategies under reference conditions in the North Sea is not possible without long time series covering periods without human modern activities.

The main drivers of change in fish life history are fisheries and climate change. Climate oscillations are suspected to have triggered a shift in the structure of the North Sea ecosystem, by driving r-selected species (low age and size at maturity, many small offspring with low survival rate and low trophic level) into the North Sea from the Eastern English Channel (McLean et al., 2018). Pecuchet et al. (2017), showed that the proportion of equilibrium species (large body size, few but large offspring with high survival chances), periodic (large body size but small eggs with low survival chances) and opportunistic species (small bodied, short lifespan, high demographic resilience, Winemiller and Rose (1992); Winemiller (2005)) was related in part to sea surface temperatures. Pecuchet et al. (2017) also observed a decline in periodic species but an increase in equilibrium and opportunistic species in the North Sea from 1980 to 2014, probably linked to increased temperatures and decreased fishing effort. By removing the larger individuals, fisheries should decrease the biomass of periodic and equilibrium species (slow-life species, Jennings et al. (1999b)). Although the marginal effect of climate and fisheries are quite certain, their combined effect and mechanisms underlying the response are unclear, and the understanding of the link between the drivers and change in the indicator is assessed as less certain.

The different life history strategies are linked to different degrees of population resilience and to resource and mortality variability and predictability (Winemiller, 2005; Petrik, 2019). Opportunistic species are associated with increasing environmental disturbances and higher unpredictability of resources and mortality, periodic species are associated with large scale, but predictable, spatio-temporal variability, and equilibrium species occur more often in areas of more stable resources. The relative proportion of the three strategies should thus provide insight into the general resilience of the ecosystem. A modelling study also showed that species life history strategy affected the spatio-temporal match-mismatch of first-feeding larvae and their prey (Daewel et al., 2011). The understanding of the specific impacts of a change in the proportion of slow-life versus fast-life strategy is assessed as less good.

There are still knowledge gaps on the response of life-history strategies to climate change, and on the impact of changes in the community life history strategy distribution on the ecosystem functions.

Calanus species [NI13]

Phenomenon: Decrease in abundance of *C. finmarchicus* and increase in abundance of *C. helgolandicus*

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, *Calanus finmarchicus* is the dominating of the two species in the northern North Sea. *C. finmarchicus* is an important grazer on phytoplankton and an important prey for larvae of many fish species and of larger planktivorous fish species. Being a spring spawner, *C. finmarchicus* is a particularly important food source for spring spawning fish species, such as cod, haddock and herring, and high production of the species can be important for recruitment in these species (Beaugrand, 2004b). Through the Continuous Plankton Recorder (CPR) survey, abundance of zooplankton species have been estimated since 1958, before anthropogenic climate change started to affect the zooplankton community in the North Sea (e.g., Beaugrand (2004b)). As climate change is the most important anthropogenic driver of change in this indicator, there is robust evidence from the CPR survey that the abundance of *C. finmarchicus* by far exceeds that of *C. helgolandicus* under the reference condition (Beaugrand, 2004b).

The most important anthropogenic driver of change in the indicator is climate change. Temperature has been found to be the most important factor influencing both spatial distributions and seasonality in the two species (Planque and Fromentin, 1996; Montero et al., 2021). The cold-temperate *C. finmarchicus* has a known temperature range of 0–14°C (Melle et al., 2014; Strand et al., 2020), whereas the warm-temperate copepod *C. helgolandicus* ranges from 9 to 20°C (Bonnet et al., 2005).

When the two species co-occur, they tend to be separated in time: The seasonal peak in abundance of *C. finmarchicus* usually occurs in spring at 0–9°C, while *C. helgolandicus* reaches its seasonal maxima later in the year, at 13–17°C (Bonnet et al., 2005; Falkenhaug et al., 2022). This has been interpreted as thermal niche differentiation between the two species (Helaouët and Beaugrand, 2007). Experimental studies have shown that *C. finmarchicus* develops faster than *C. helgolandicus* at temperatures below 12°C, whereas *C. helgolandicus* develops faster than *C. finmarchicus* at temperatures above 13 °C (Wilson et al. (2015) and references therein). Based on model results, Møller et al. (2012) suggested that a temperature increase to above 11 °C would trigger a shift from a *C. finmarchicus* to a *C. helgolandicus* dominated system.

Abundances of the *Calanus* species may be indirectly affected by climate change through ocean currents. The population of *C. finmarchicus* in the North Sea is not self-sustained and is highly dependent on the inflow from the north (the Faroe-Shetland Channel and the Norwegian Sea; Gao et al. (2021)). Furthermore, the substantial reduction of *C. finmarchicus* in the North Sea has been related to the decrease in Norwegian Sea Deep Water (Heath et al., 1999a). Such climate induced changes in the current system are related to large scale atmospheric processes occurring beyond the North Sea region (North Atlantic Oscillation, North Atlantic Subpolar Gyre; Hátún et al. (2009)).

It has also been suggested that top-down processes acting through grazing from planktivores can have significant effects on the abundance of both *C. finmarchicus* and *C. helgolandicus* (Fauchald et al., 2011a; Johannessen, 2014; Papworth et al., 2016; Lynam et al., 2017). Thus, while this mechanism implies that fisheries may affect zooplankton biomass indirectly through changes in fish stock sizes, climate change is still considered the most important anthropogenic driver for *Calanus* species in the North Sea (Montero et al., 2021). Given the solid evidence described above, the understanding of the link between climate change and the indicator is rated as certain.

C. helgolandicus and *C. finmarchicus* are of major importance as food for higher trophic levels in the North Sea ecosystem. Several studies have shown that the recruitment of cod, herring and lesser sandeel are associated with *Calanus* abundance (Munk and Nielsen, 1994; Arnott and Ruxton, 2002; Heath and Lough, 2007; Heath, 2007; Beaugrand et al., 2009; van Deurs et al., 2009).

Due to species-specific differences in seasonality, life cycle and production, changes in their relative abundances have major ecological impacts on the North Sea ecosystem.

1) *Temporal mismatch with higher trophic levels*: *C. helgolandicus* spawns later in the year compared to *C. finmarchicus*. A replacement of *C. finmarchicus* by *C. helgolandicus* will result in a temporal mismatch between the larvae of spring spawning fish (e.g., cod) and the availability of suitable food (Beaugrand et al., 2003; Durant et al., 2005; van Deurs et al., 2009). *C. helgolandicus* occurs later in the season and is therefore not important for spring spawning fish species but may contribute to success of summer and autumn spawning fish (Beaugrand et al., 2003; Beaugrand and Kirby, 2010).

2) *Reduction in the abundance and quality of food for higher trophic levels*: *C. finmarchicus* contributes to >70 % of the zooplankton biomass in the northern North Sea in spring. In contrast, *C. helgolandicus* never reaches high population densities. A successive replacement of *C. finmarchicus* with *C. helgolandicus* will therefore provide lower total zooplankton biomass available for higher trophic levels. It has also been suggested that *C. helgolandicus* has a lower lipid content and therefore is of lower dietary quality for fish. However, the lipid content of *C. helgolandicus* has been debated, and Wilson et al. (2016) found no significant inter-specific differences in the wax ester levels when comparing specimens of similar size.

3) *Vertical carbon flux*: During autumn, *C. finmarchicus* descend to deeper waters and spend the winter months at 500-1000m depth living on accumulated lipid reserves at low respiration rates (Melle et al., 2014). In contrast, *C. helgolandicus* does not enter diapause but rather is feeding actively through winter (Bonnet et al., 2005). In their seasonal migration, *C. finmarchicus* actively transport a significant amount of carbon (lipids) from the surface to larger depths (Jónasdóttir et al., 2015). A replacement of *C. finmarchicus* with *C. helgolandicus* will thus reduce the vertical carbon flux (the biological carbon pump).

Given the substantial evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Decreasing abundance of *C. finmarchicus* relative to abundance of *C. helgolandicus* can be considered of ecosystem significance if, for example: i) it causes massive declines in recruitment of fish populations, and ii) a reduction in the biological carbon pump

Knowledge gaps:

It must be noted that the CPR species abundance data on *C. finmarchicus* and *C. helgolandicus* only includes stages V and adults. Younger copepodite stages (which usually dominate the populations) cannot be identified to species based on morphology. This may have implications on the value of the ratio *C.finmarchicus*:*C.helgolandicus* (C.f:C.h), depending on the state of the population. The indicator (ratio) will also be highly sensitive to the season. Samples should be available for all seasons (all month) if an annual average is to be calculated. Preferably, separate ratios should be calculated for spring and autumn.

By using a ratio (C.f:C.h), the mechanisms behind observed changes may be challenging to interpret. I.e., a decline in the ratio may indicate a reduction in the abundance of *C. finmarchicus* , or an increase in *C. helgolandicus*.

When co-occurring in time, the two species have been found to be separated in terms of their vertical distributions (Jónasdóttir and Koski, 2010; Lindegren et al., 2020). In cases of increasing temperatures, *C. finmarchicus* is expected to seek refuge in cooler, deeper waters. The CPR survey only samples the surface waters. As a result, the indicator may be affected by potential changes in the vertical distributions in response to temperature changes. However, data on *Calanus* from full ocean depths is available from the IMR North Sea plankton monitoring program.

We have little knowledge on how high temperatures (>12°C) affect development, growth, fecundity and mortality in *C. finmarchicus*, nor how *C. helgolandicus* is affected by low temperatures. Clarifications of the relationship between growth and temperature are therefore a priority of *Calanus* research. An important area for future research is the ability for species to adapt to wider temperature ranges. It has also been speculated that *C. finmarchicus* can hybridize with *C. helgolandicus* in the North Sea which may further increase the species ability to adapt to changing environments

(Wilson et al., 2016).

Food quality may also influence fecundity and development time in both species, but the relationships are not fully understood. The two species do not differ in their food selectivity (Meyer et al., 2002) which indicates that the phytoplankton composition is not an important driver for changes in the indicator.

The importance of advection for *C. finmarchicus* populations in the North Sea has been well documented. However, the role of advection for *C. helgolandicus* abundance has not been studied.

***Pseudocalanus* / *Paracalanus* species [NI14]**

Phenomenon: Declining abundance of *Pseudocalanus* spp. and *Paracalanus* spp.

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, *Pseudocalanus* spp. and *Paracalanus* spp. are small calanoid copepod genera, which tend to dominate the zooplankton community numerically in the North Sea. In particular, *Pseudocalanus* spp. is described to be one of the most important stock-forming copepod taxa and contributes up to 46% of the copepod stock in the southern North Sea (Krause and Martens, 1990; Fransz et al., 1991).

The genus *Pseudocalanus* includes six accepted species, which all have been reported to occur in the North Atlantic Ocean (Corkett and McLaren, 1979; Frost, 1989). *Paracalanus* includes 12 accepted species of which at least 3 occur in the North Sea. However, both genera are considered as pseudo-cryptic species-complex (lack of morphological diagnostic characters) and genetic methods may be necessary for species delimitation (Cornils and Held, 2014; Aarbakke et al., 2014; Bucklin et al., 2015).

Copepods of the genera *Pseudocalanus* and *Paracalanus* are linked to temperate and boreal, neritic shelf-waters and reach peak abundances in summer and autumn (Wiborg, 1954; Beaugrand, 2004a). However, the various species have been found to differ in biogeographical distributions, life history characteristics and have different ecological roles in the pelagic ecosystem (Crouch et al., 2020; Ershova et al., 2021).

The most important anthropogenic drivers of change in the abundance of *Pseudocalanus*/ *Paracalanus* spp. is declining primary production, as a result of climate change. In the past decade, a decrease in the abundance of *Pseudocalanus*/ *Paracalanus* spp. across the North Sea has been documented (Johannessen et al., 2011; Alvarez-Fernandez et al., 2012). Pitois and Fox (2006), and later Capuzzo et al. (2018) found evidence for a link between declining small copepods (including *Pseudocalanus* and *Paracalanus*) and reduced primary productivity, suggesting an overall bottom-up control of the food web structure in the North Sea. Alvarez-Fernandez et al. (2012) hypothesized that the decrease in *Pseudocalanus*/ *Paracalanus* spp. was caused by a decrease in dinoflagellates (Hinder et al., 2012) associated with a third regime change at the end of the 1990s. Dinoflagellates are a major food source for these copepods, and the summer dinoflagellate bloom typically co-occur with the seasonal peak in *Pseudocalanus*/ *Paracalanus* spp. Reduction in the abundance of *Pseudocalanus* spp. and *Paracalanus* spp. has also been linked to ocean warming and acidification (Garzke et al., 2015). This suggests a close link between climate, temperature, primary producers, and the abundance of *Pseudocalanus*/ *Paracalanus* spp.

Given the solid evidence described above the understanding of the link between climate change and declining abundance of *Pseudocalanus*/ *Paracalanus* spp. is rated as certain.

Because of their high abundance and small size, *Pseudocalanus* spp. and *Paracalanus* spp. play important roles in the trophic ecology of marine systems (Corkett and McLaren, 1979), for example, as prey for larval fish (Turner, 2004; Robert et al., 2010). *Pseudocalanus* spp., and *Paracalanus* spp. are the main prey items for larvae of several important fish species in the North Sea, such as herring and sprat (Hardy et al., 1924; Last, 1989; Arrhenius, 1996) and cod and whiting (Shaw et al., 2008), for which year class strength is dependent on either a large year class of *Calanus* or *Pseudocalanus* (Rothschild, 1998; Beaugrand et al., 2003). *Pseudocalanus*/ *Paracalanus* spp. are typically most abundant around July in the northern North Sea. This period has been identified as critical for survival and recruitment

of 0-group cod in Skagerrak (Blaxter, 1965; Johannessen et al., 2011). Blaxter (1965) showed that *Pseudocalanus* spp. were an important prey for herring larvae of smaller sizes (<20 mm), in particular during the winter period when *Calanus* species are absent from the North Sea shelf. As detritivores, *Pseudocalanus* spp. have a high relative dominance in winter (Krause and Martens, 1990). Abundances of *Pseudocalanus*/ *Paracalanus* spp. may thus be of particular importance for the winter survival of autumn spawned herring larvae (Payne et al., 2009; Alvarez-Fernandez et al., 2015).

Given the substantial evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Decreasing abundance of *Pseudocalanus*/ *Paracalanus* spp. can be considered of ecosystem significance if it causes massive declines in recruitment of fish populations.

Knowledge gaps: Long-term time-series on *Pseudocalanus*/*Paracalanus* spp. are available from the CPR survey. According to the plankton counting procedures of the CPR survey, *Pseudocalanus* spp., *Paracalanus* spp. as well as unidentifiable copepods smaller than 2 mm, are all classified as “*Para-Pseudocalanus*”. To combine several taxa into one category may hamper the interpretation of the phenomenon. For example, *Pseudocalanus acuspes* prefers low temperatures and seems to be restricted to the northern North Sea, while *P. elongatus* is distributed in the temperate eastern North Atlantic Ocean and the western Mediterranean (Frost, 1989). Future monitoring should seek to improve the taxonomic resolution (at least to genus) and to reveal species specific trends. Research is needed to improve our knowledge on the interaction between climate induced environmental variations and observed changes at species level.

Cod stock size [NI15]

Phenomenon: Decreasing cod stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, the cod stock is one of the largest demersal fish stocks in the North Sea and an important predator. Cod is distributed throughout the North Sea (Hislop, 2015). The diet of cod in the North Sea was comprehensively studied by The Stomach Sampling Project in 1981 and 1991 under the umbrella of ICES (Daan, 1989; ICES, 1997). Cod feed opportunistically on a wide variety of organisms with Crustaceans and fish as their main prey, but prey varied substantially between years, seasons, and the size of the cod. Cod is an important predator on krill, northern shrimp, Norway lobster, sandeels, Norway pout, whiting, haddock, herring, sprat, and various flat fishes. The proportion of fish in the diet increases with the age of cod. In a recent literature review of potential substocks in the North Sea, ICES (2020d) concluded that there are two genetically distinct components, Viking in the northern and deeper parts (>100 m) of the North Sea, and Dogger in the southern and shallower parts of the North Sea and along the east coast of the UK (~west of 0°). However, ICES (2020d) did not exclude the possibility of a more subtle stock structure. A similar review of West of Scotland cod pointed toward a subtler separation of the Viking population into two, with the north-western component interacting through migration with West of Scotland cod (ICES, 2022h). Viking is dominating in the Norwegian sector with adults centred around Vikingbanken. Viking juveniles are more spread out and Skagerrak serve as a nursery area. Despite acknowledgement of substocks, ICES (2021a) continued to treat cod in the North Sea (including the eastern English Channel and Skagerrak) as a unit stock, mainly due to data shortcomings, but the population is due for a new benchmark in 2023.

The most important anthropogenic drivers of change in the indicator are fisheries and climate change. Landings of cod reached extraordinarily high levels during the so-called gadoid outburst in the 1960s and 1970s (Hislop, 1996). However, by the early 1990s, the spawning stock reached a historically low level, concurrent with fishing mortality increasing to the highest level on records (Hislop, 1996). Since then, the spawning stock has decreased further and has been below B_{pa} since the late 1990s and in many years below B_{lim} (not sustainable; ICES (2021a)). In the last 20 years, fishing mortality has decreased substantially and has been below F_{pa} since around 2010, but still above F_{MSY} (MSY- Maximum Sustainable Yield). The decreasing spawning stock concurred with historically low recruitment after the late 1990s (see recruitment below). In addition, there is evidence of reduced age at maturity in cod, which has been

ascribed to evolutionary impacts of fishing and climate warming (Marty et al., 2014). Our understanding of the impact of fisheries on the cod stock is rated as certain.

Having so-called “supergenes” (Sodeland et al., 2022), cod is robust towards environmental changes, including rising temperatures. In a modelling study based on the worst-case IPCC scenario (RPC8.5), Núñez-Riboni et al. (2019) projected that the southern Skagerrak, the central and northern North Sea, and the edge of the Norwegian trench will remain thermally suitable for North Sea cod throughout the 21st century. Hence, cod is unlikely to become extinct in the North Sea in this century. During the past 100 years, the distribution of the North Sea cod has shifted towards northeast, where the eastern shift is mainly attributed to fishing pressure and the northerly shift to climate change (Engelhard et al., 2014). The impact of climate change is mainly indirect, acting through changes in the plankton community, in particular reduction in the cods preferred prey during early life stages, *Calanus finmarchicus* and *Paracalanus/Pseudocalanus* (Beaugrand et al., 2003; Nicolas et al., 2014), and is projected to exacerbate with increasing temperatures (Frederiksen et al., 2013). Our understanding of the impact of climate change on the cod stock is rated as certain.

As cod is an important predator on a variety of organisms, both drivers, fisheries and climate change, have potentially great implications for the functioning of the North Sea ecosystem. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in the North Sea and the understanding of ecosystem impacts are therefore rated as good.

There are some major knowledge gaps related to the North Sea cod stock that need to be filled. First, comprehensive diet studies of fish in the North Sea were carried out in 1981 and 1991. The two studies showed substantial deviations. During the last three decades there have been major changes in the North Sea ecosystem. Hence, new diet studies are needed to evaluate the ecological impact of the indicator in the ecosystem. Second, it is essential to speed up implementation of separate assessments for the substocks, Viking and Dogger (and possibly an even more detailed substock structure). When a fish stock consists of several substocks, unbalanced fishing effort may result in the collapse of substocks, even under moderate overall fishing mortality (Frank and Brickman, 2001). Violation of the unit stock assumption may thus severely impact both fishing yield and biodiversity (Cowen et al., 2000; Sterner, 2007; Reiss et al., 2009). This concern is particularly relevant for Dogger cod in the warmer and shallower parts of the North Sea as evidence suggests that the Dogger stock has been reduced substantially more than the Viking stock (ICES, 2020d). In addition to the genetically different Viking and Dogger stocks, these stocks might consist of additional substocks. Genetic homogenisation of substocks will take place with a very limited exchange of individuals (Palumbi, 2003), without the two substocks being demographically connected (Lowe and Allendorf, 2010). For example, homing to natal spawning grounds may give rise to substocks with similar genetic traits, e.g., as indicated for sandeel (Johannessen and Johnsen, submitted).

Cod recruitment [NI16]

Phenomenon: Decreasing cod recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, cod recruitment is high and sufficient to sustain a large stock. Although recruitment varies considerably from year to year, it is not characterized by the large fluctuations (poor recruitment most years and very high recruitment in single years at long intervals) seen in haddock (see phenomenon for haddock recruitment (NI18)). After the late 1990s, recruitment of North Sea cod has been historically low, with the last strong year-class in 1999 (ICES, 2021a).

The most important anthropogenic drivers in the indicator are fisheries and climate change. Although there is generally a poor relationship between SSB and recruitment in marine fishes, (e.g., Pierre et al. (2017)), management assumes that there is a lower limit, B_{lim} , where a fish stock has a high likelihood of impaired recruitment (EU, 2015). After the turn of the century the North Sea cod stock has been below B_{lim} around 50% of the time and well below B_{lim} in the last assessment (e.g., ICES (2021a)). This may have contributed to the low recruitment after 2000. Another potential impact

on recruitment is truncation of the age distribution generally observed in fisheries targeting larger fishes (e.g., Bianchi et al. (2000)), as larger females produce large eggs and more viable larvae (e.g., Green (2008)). However, as the recruitment puzzle has not yet been resolved, this remains an untested hypothesis (Johannessen, 2014). An indirect impact of fisheries on cod recruitment is harvesting of predators, in particular gadoids (Daan, 1989; ICES, 1997). As gadoid stocks have generally been decreasing the North Sea due to both fishing and climate change, this may have dampened other negative impacts on cod recruitment such as density-dependent competition and predation (but see below). Due to the general lack of a clear relationship between SSB and recruitment, the impact of the driver (fishing) on recruitment is rated as less certain.

Factors affecting recruitment of cod along the Norwegian Skagerrak coast have been studied in more detail (Johannessen, 2014). The main finding was that year-class strength is mainly determined after settlement, between June and August at the 0-group stage. Good condition and high survival of the 0-group cod was found in relation to a diet of a high proportion of larger, energy rich copepods (e.g., *C. finmarchicus*), whereas a diet of hyperbenthic prey (e.g., fish and mysids) and small, carnivorous copepods was related to poor condition and low survival. Accordingly, a positive relationship has been found between the abundance of copepods, *C. finmarchicus* and *Paracalanus/Pseudocalanus*, and recruitment of North Sea cod (Beaugrand, 2004b; Beaugrand and Ibanez, 2004; Beaugrand et al., 2014). These copepod species/groups have shown substantial reduced abundances concurrent with increasing temperatures (Beaugrand et al., 2003; Nicolas et al., 2014), which affect the survival of larvae and post-larvae cod through food limitation (Beaugrand and Kirby, 2010). The evidence of reduced abundances of these species/groups in warmer climate this is strong, and the current understanding of the link between the driver (climate change) and the indicator is thus rated as certain.

Another factor influencing recruitment in cod is increased predation, probably due to both fisheries and climate change. Grey gurnard is the most important predator on 0-group cod (50-60 %; ICES (2021k), and during the 1990s the stock increased substantially (ICES, 2020a). This concurred with both reduced biomass of demersal gadoids and increasing temperatures, and it has been suggested that grey gurnard may have been able to occupy substantial parts of the ecological niche freed by the diminishing gadoids (Floeter et al., 2005). There is no targeted fishery for grey gurnard and no major predators have been identified (ICES, 1997). A modelling study based on the 1991 stomach sampling project, and the increased biomass of grey gurnard suggested that predation of 0-group cod by grey gurnards may impede recovery of the North Sea cod stock (Floeter et al., 2005). On the other hand, as grey gurnards are important predators of 0-group whiting and older whiting are important predator of 0-group cod, the outcome depends on much whiting is affected by grey gurnard predation relative to predation of 0-group cod. In conclusion, the current understanding of the link between predation (fisheries and climate change) and the indicator is rated as less certain.

The effect of fisheries and climate on recruitment also propagates as an effect on total cod stock biomass (Beaugrand and Kirby, 2010; ICES, 2021a). As cod has been a functionally important species under the reference condition (see references under the cod-section), the observed changes should be considered of ecosystem significance. However, due to lack of updated diet studies of cod, the impact of the indicator is rated as less good.

An important knowledge gap in relation to cod in the North Sea, is the mechanism underlying recruitment variability. For cod along the Norwegian Skagerrak coast, the critical period for formation of the year-class strength was found to be after settlement, between June and August at the 0-group stage (Johannessen, 2014). As described above, high survival during the critical period was observed in relation to a diet of larger, energy rich copepods (e.g., *C. finmarchicus*), whereas diet of hyperbenthic prey (e.g., small fish and shrimps) resulted in poor condition and high mortality. For the North Sea cod, a few diet studies of the diet of pre-settled and settled cod 0-group cod have been carried out (e.g., Bromley et al. (1997); Demain et al. (2011)). However, none of these studies have included condition of the cod. Hence, there is no information to relate diet and condition to recruitment success. Given the close relationship between the North Sea cod and the Skagerrak coastal cod (Sodeland et al., 2022), such studies could be important for predicting climate change impact on future cod recruitment. Another knowledge gap related to the recruitment of cod in the North Sea is how much grey gurnard predation affects 0-group cod relative to 0-group whiting.

Haddock stock size [NI17]

Phenomenon: Decreasing haddock stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, the haddock stock is one of the large demersal fish stocks in the North Sea and an important predator and prey species. It is mainly found in the northern part of the North Sea (north of the diagonal from 55°N on the west side towards 57°N on the east side; Hedger et al. (2004)). Haddock is an opportunistic feeder on benthic invertebrates, fish and zooplankton (Bromley et al., 1997; Greenstreet et al., 1997; Greenstreet et al., 1998; Schuckel et al., 2010; Demain et al., 2011; Engelhard et al., 2013; Tam et al., 2016), and is prey for piscivorous fish, such as cod (Floeter and Temming, 2003; Fujii, 2016), seals and white beaked dolphins (Hammond et al., 1994; Canning et al., 2008). Haddock in the North Sea is managed as one stock (ICES, 2021d). However, a recent study indicated that haddock around Shetland represents a genetically separate stock (also from haddock on the east coast of Scotland (Berg et al., 2020)). In addition, both growth and length of first maturity differ between east and west of the Greenwich meridian (Wright et al., 2011; Wright and Tobin, 2013), and although they are not found to be genetically different (Berg et al., 2020), this may indicate substocks with low demographic connectivity because of different spawning grounds (González-Irusta and Wright, 2016).

The most important anthropogenic drivers of change in the haddock stock size are fisheries and climate change (Linderholm et al., 2014; ICES, 2021d). Landings of haddock decreased from ~400 kt in the 1970s to ~50 kt after 2010 (including discards and industrial bycatch; ICES, 2021 advice). Between 1972 and 2001, SSB was below B_{lim} several years concurrent with a period with high fishing mortality ($F \sim 0.8$). After 2000, recruitment has generally been poor compared to historic year-classes, although the 2019- and 2020-year classes were the highest since 2000. However, SSB has been kept above the precautionary level due to substantially reduced fishing mortality (ICES, 2021d). There is also evidence of reduced age of maturity (from age 3 to age 2) which has been ascribed to evolutionary impact of fishing (Wright et al., 2011; Marty et al., 2014). Given the strong links between fisheries and haddock stock size, the understanding of the link between the driver and changes in the indicator is rated as certain.

In contrast to many other demersal fishes in the North Sea (Perry et al., 2005), no displacement has been observed in haddock in relation to increasing temperatures (Hedger et al., 2004). On the other hand, increasing temperatures have resulted in faster growth of juveniles, but a substantial reduced age at first maturity and reduced maximum size which, in turn, is likely to result in reduced fishery yield (Baudron et al., 2011). Another impact of global warming on the haddock stock is related to potentially reduced recruitment (see below). The understanding between the driver (global warming) and the indicator is rated as less certain.

Given that haddock is an important predator and prey for many species in the North Sea (see references above), large changes in the stock are likely to affect many species. Benthic invertebrates, which are major prey for haddock (Daan, 1989; ICES, 1997), are likely to be more affected than fish. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the knowledge about consequences ecosystem from change in the indicator are therefore rated as good.

There are important knowledge gaps related to the North Sea haddock stock that need to be filled. First, comprehensive diet studies of fish in the North Sea were carried out in 1981 and 1991 (Daan, 1989; ICES, 1997). The two studies showed substantial deviations. During the last 3 decades there have been major changes in the North Sea ecosystem. Hence, new diet studies are needed to evaluate the ecological impact of the indicator in the ecosystem. Second, a potential threat to the North Sea haddock is management based on one unit-stock. There is evidence of genetically different substocks (Berg et al., 2020) as well as indication of substocks with low demographic connectivity east and west of the Greenwich meridian (Wright et al., 2011; Wright and Tobin, 2013). When a fish stock consists of several substocks, unbalanced fishing effort may result in the collapse of substocks, even under moderate overall fishing mortality (Frank and Brickman, 2001). Violation of the unit stock assumption may thus severely impact both fishing yield and biodiversity (Cowen et al., 2000; Sterner, 2007; Reiss et al., 2009). Genetic homogenisation of substocks can take place with a very limited exchange of individuals (Palumbi, 2003), without the two substocks being demographically

connected (Lowe and Allendorf, 2010). For example, homing to natal spawning grounds may give rise to substocks with similar genetic traits, e.g., as indicated for lesser sandeel (Johannessen and Johnsen, submitted).

Haddock recruitment [NI18]

Phenomenon: Decreasing haddock recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, haddock recruitment is high and sufficient to sustain a large stock. Recruitment in haddock is characterised by occasionally very strong year classes and intermittent periods with relatively limited recruitment (ICES, 2021d). It has been suggested that this could be related to a contracted spawning period and relatively low tolerance of haddock larvae to variability in salinity and temperature (Fogarty et al., 2001). However, it could also be related to adaptations in more long-lived species to more rare events that give rise to extraordinary high survival and more offspring during the lifetime of an organism than adaptation to “average conditions” (Johannessen, 2014). In agreement with this, there is a general increase in recruitment variability with longevity (Longhurst, 2002).

The most important anthropogenic drivers in the indicator are fisheries, global warming, and accidental oil blowouts. Although recruitment overfishing is generally difficult to confirm in high fecundity species like haddock (e.g., Pierre et al. (2017)), management assumes that there is a lower limit, B_{lim} , below which a fish stock has a high likelihood of impaired recruitment (EU, 2015). There has been generally poor recruitment after the turn of the century, with the present perception being that SSB of the North Sea haddock stock has been below the precautionary limit (B_{Pa}). This perception lasted until 2021, when recruitment increased rapidly likely due to a combination of the relatively strong year class from 2019-2020 in combination with reduced fishing pressure at this time, probably due to substantially reduced fishing mortality around 2000 (ICES, 2022b). Hence, reduced recruitment appears not to be fully explained by reduced SSB. Another potential impact on recruitment is truncation of the age distribution generally observed in fisheries targeting larger fishes (e.g., Bianchi et al. (2000)), as larger females produce large eggs and more viable larvae (e.g., Green (2008)). However, as the recruitment puzzle has not yet been resolved, this remains an untested hypothesis (Johannessen, 2014). An indirect impact of fisheries on haddock recruitment is harvesting of predators, in particular gadoids (Daan, 1989; ICES, 1997). As gadoid stocks have generally been decreasing in the North Sea due to both fishing and climate change, this may have dampened other negative impacts on haddock recruitment. In conclusion, the impact of the driver (fishing) on the indicator is rated as less certain.

Haddock feeds on copepods during early pelagic stages (Bromley et al., 1997). Several important copepod species/groups have shown substantial reduced abundances in relation to increasing temperatures, including *Calanus finmarchicus* and *Paracalanus/Pseudocalanus* (Beaugrand et al., 2003; Nicolas et al., 2014). Hence, relatively poor recruitment after 2000 might be related to changes in the plankton community. Another potential impact of global warming is related to the preference of age 0 haddock to areas with summer temperatures below 11°C, which is limited to a narrow region of the northern North Sea (Asjes et al., 2016). This habitat is predicted to decrease in the following decades and may thus negatively affect recruitment in haddock. In conclusion, our current understanding of the link between the driver (climate change) and the indicator is rated as less certain.

Laboratory studies have shown that haddock eggs are very sensitive to exposure to both crude oil and dispersed crude oil due to a sticky surface, and oil droplet fouling makes the haddock embryo extremely vulnerable to even short, low concentration oil exposures (Sørhus et al., 2015; Sørhus et al., 2021). Accidental oil blowout during the relatively short spawning period in haddock could therefore negatively impact the year-class strength. If there is low demographic connectivity between the eastern and western side of the North Sea, which some studies have indicated (Wright et al., 2011; Wright and Tobin, 2013), an oil blowout in the Tampen-Vikingbank area might have a particularly negative impact on the year-class strength in the Norwegian sector. In conclusion, our current understanding of the link between oil pollution and the indicator is rated as less certain.

The effect of fisheries, climate and oil blowouts on recruitment also propagate as an effect on total haddock stock biomass. As haddock has been a functionally important species under the reference condition (see references under

the haddock section), the observed changes should be considered of ecosystem significance. However, due to lack of updated diet studies in haddock, the impact of the indicator is rated as less good.

Changes in the indicator could be considered of ecological significance if, for example: i) recruitment was poor several years in a row, ii) adult population decreases as a result of bad recruitment, or iii) important predators switch prey or see their population decline.

There are some important knowledge gaps in relation to recruitment in haddock. First, as for most fishes, factors affecting recruitment remains obscure, except that recruitment is mainly determined during early life stages. On the other hand, after Hjort(1914) suggested the first recruitment hypothesis followed by more than 100 years of research, the recruitment puzzle is obviously very difficult to resolve. Numerous correlations between recruitment and environmental and biological variables have been carried out, of which most “significant” correlations have not stood the test of time (e.g., Myers (1998)). Hence, significant correlations must be confirmed by field studies before being accepted. Second, it remains uncertain whether haddock on the west and east side of the North Sea, which have different spawning grounds (González-Irusta and Wright, 2016; Sundby et al., 2017), are substocks or belong to the same stock. Third, updated stomach studies of predators preying on juvenile haddock are needed to estimate how haddock recruitment has been affected in recent years.

Saithe stock size [NI19]

Phenomenon: Decreasing saith stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, saithe is one of the larger demersal (benthopelagic) fish stocks in the North Sea. Older saithe (~age 3+) are found on the banks in the northern parts of the North Sea (mainly north of 57°N) and along the west side of the Norwegian deep, whereas younger saithe are found in shallower waters along the northern coasts of Scotland and Shetland, in Skagerrak/Kattegat and skerries and fjords along the west coast of Norway (Heino et al., 2012; Hislop, 2015). Older saithe are important predators on a variety of fish species, in particular Norway pout but also herring and sandeel (Daan, 1989; ICES, 1997). Juvenile saithe feed mainly on appendicularians - *Oikopleura dioica*, copepods - *Calanus finmarchicus*) and krill - *Thysanoessa inermis* (Nedreaas, 1987). Coastal juveniles are preyed on by sea birds (Loretsen et al., 2018), seals (Wilson and Hammon, 2016; Sørli et al., 2020) and probably also larger gadoids. Saithe in the North Sea and west of the British Islands is managed as a unit stock (ICES, 2022e). However, genetic analyses suggest that Rockall saithe is separated from the North Sea stock, while there is little support for genetic barriers among North Sea, Icelandic, Faroes and the south of the Northeast arctic stock (Saha et al., 2015).

The most important anthropogenic drivers of change in the saithe stock size are fisheries, climate change and eutrophication. Both landings and SSB reached a maximum in the 1970s during the gadoid outburst (ICES, 2022e). Except for a period around 1990 concurrent with high fishing mortality ($F=0.7$), SSB has been above the precautionary limit. Recruitment (age 3) has shown a slight decreasing trend since the early 2000s, and a more pronounced decline after 2015. This has resulted in SSB below the precautionary limit in 2021. Given the strong relationship between fisheries and the saithe stock size, the understanding of the link between the driver and changes in the indicator is rated as certain.

Mean weight-at-age and growth in saithe have decreased in recent years (Cormon et al., 2016), which, in turn, may cause reduced fishery yield. This has occurred concurrently with a substantial increase in the biomass of European hake (Staby et al., 2018), and Cormon et al. (2014) suggested that competition for food, especially Norway pout, between saithe and hake might have a negative impact on growth and biomass of saithe. No direct relationship was found between saithe and increasing temperatures, but Cormon et al. (2014) suggested that increasing temperatures could indirectly affect saithe through increase in the biomass of hake. As saithe is distributed in the northern and deeper part of the North Sea, available habitat in the North Sea is likely to decrease as temperatures continue rising. The distribution of saithe has so far not shifted northwards as temperatures have risen (Perry et al., 2005), but saithe is now found in deeper waters (Dulvy et al., 2008). Temperatures might also have affected recruitment of saithe (see

recruitment section below), but there is little information about juvenile saithe prior to migration from the coastal nursery grounds into the North Sea. The impact of the driver (climate change) and the indicator is rated as less certain.

As saithe is an important predator on a variety of organisms, both drivers, fisheries and climate change, have potentially great implications for the functioning of the North Sea ecosystem. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the knowledge about ecosystem impacts from change in the indicator is therefore rated as good.

There are some important knowledge gaps related to the North Sea saithe stock that should be filled. First, comprehensive diet studies of fish in the North Sea were carried out in 1981 and 1991 (Daan, 1989; ICES, 1997). The two studies showed substantial deviations. During the last three decades there have been major changes in the North Sea ecosystem. Hence, new diet studies are needed to evaluate the ecological impact of the indicator in the ecosystem. Second, there is very little information about the abundance of saithe during the juvenile stages in coastal waters. Hence, the relative importance of the component growing up along the west coast of Norway versus along the northern coasts of Scotland and Shetland is unknown. Two main spawning concentrations have been identified, one along the continental shelf west of Shetland and one at Tampen and Viking in the Norwegian sector (Sundby et al., 2017). There is no genetic evidence of substocks in the North Sea. On the other hand, as the main current from Tampen is directed southwards into Skagerrak, before leaving Skagerrak as the Norwegian coastal current (Otto et al., 1990), it cannot be excluded that saithe growing up along the west coast of Norway belong to a substock with low demographic connectivity to saithe growing up along the coasts of Scotland and Shetland. Furthermore, advection of saithe larvae following the main current system into Skagerrak and settling on the west coast of Norway is unlikely due to the long distance. Hence, saithe settling on the west coast of Norway probably cross the Norwegian coastal current. This opens for adaptation in saithe larvae to take advantage of current systems that bring the larvae to this area. In support of this, there is increasing evidence of fish larvae being able to cope with moving water masses (see Leis (2006)), either in terms of a return-based or retention strategy, or a strategy in which dispersal or transport to favourable habitats is important (Armsworth et al., 2001; Forward and Tankersley, 2001). In conclusion, the potential existence of subpopulations of saithe with low demographic connectivity in the North Sea and beyond is important to identify for sustainable harvesting.

Saithe recruitment [NI20]

Phenomenon: Decreasing saithe recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, saithe recruitment is high and variable and sufficient to sustain a large stock. There are no estimates of recruitment prior to age 3 due to lack of sampling at coastal nursery grounds. Since 2000, recruitment in the off-shore fishery (age 3) has been decreasing and has been historically low in recent years (ICES, 2022e). Younger saithe (mostly age 2 and 3, occasionally 4) are also targeted by a small-scale purse seine fishery in Norwegian coastal waters when they aggregate over seamounts, before they undertake offshore migrations and start recruiting in the North Sea fishery. In the absence of abundance monitoring, the magnitude of fishing pressure at this stage remains uncertain but is probably low (usually <1000 tonnes per year in the last decade, Yves Reece (IMR), pers. comm.).

The most important anthropogenic drivers for the indicator are fishery, climate change and eutrophication. Although recruitment overfishing is generally difficult to confirm in high fecundity species like saithe (e.g., Pierre et al. (2017)), management assumes that there is a lower limit, B_{lim} , below which a fish stock has a high likelihood of impaired recruitment (EU, 2015). Due to the general lack of a clear relationship between SSB and recruitment, the knowledge about impact of the driver (fishing) on the indicator is rated as less certain.

In a study from 1991 in the north-western North Sea, the diet of 1-3 cm saithe consisted of mainly copepods, e.g., *Calanus finmarchicus*, followed by a shift to the dominance of other crustaceans and fish prey as the saithe grew larger (Bromley et al., 1997). In contrast, in a similar study in 1974 copepods dominated the diet along with fish (Robb, 1981). Bromley et al. (1997) stated that it is uncertain if this reflects normal inter-annual variability or is evidence of long-term

changes in feeding patterns. As substantial changes in the plankton community in the North Sea has been observed in relation to increasing temperatures (e.g., Beaugrand et al. (2003)), the change in the diet of 0-group saithe might reflect environmental changes in relation to global warming. The reduction in saithe recruitment has not been as pronounced as for cod. This might be related to different growth rate in the two species (Johannessen, 2014). Cod and saithe settle at about the same time and size along the Norwegian Skagerrak coast, from late April and onwards. However, by mid-June saithe has reached a mean length of about 7 cm, whereas the mean length of cod is only about 4.5 cm. The critical period for recruitment for cod along the Norwegian Skagerrak coast was found to be between June and August, and survival was positively related to a high proportion of energy-rich, large copepods in the diet. At this time of the year, the substantially larger saithe has probably become more robust towards reduced nutritional value of its prey and experiences a more diverse prey window. In conclusion, as saithe recruitment may be less dependent on climate sensitive zooplankton, our understanding of the impact of the driver (climate change) on the indicator is rated as less certain.

Apart from the obvious relationship between saithe recruitment and size of the saithe stock, little is known about how variation in saithe recruitment affects other parts of the ecosystem. The understanding of this is thus rated as less good.

Along the Norwegian Skagerrak coast, several incidents of abrupt and persistent recruitment collapses have been observed in gadoids locally in relation to gradually increasing eutrophication (Johannessen, 2014). Evidence suggested that the underlying mechanism was abrupt shifts in the plankton community which was propagated to higher trophic levels by causing recruitment failure in the gadoids (Johannessen et al., 2011; Johannessen, 2014). The last event occurred in ~2002 in relation to increasing temperatures. In this case nutrient loads were decreasing, but still above pristine levels (Johannessen et al., 2011; Johannessen, 2014). Hence, it was concluded that the combination of increasing temperatures and elevated nutrients may have induced the abrupt shift in the plankton community. The shift in the plankton community also severely reduced the abundance of goby species that live for only one year (Aanonsen, 2018), particularly the two-spotted goby which is a key prey for 0-group cod during late summer and the first winter (Johannessen, 2014). Following the regime shift in 2002, survival of age-0 cod through this period appears to have been very low. As the saithe habitat along the west coast of Norway is subjected to the same environmental stress as along the Norwegian Skagerrak coast, i.e., increasing temperatures and nutrient loads from various sources including a growing aquaculture industry, potential shifts in the plankton community might already have affected saithe recruitment or could affect recruitment in the future. Our understanding of the impact of the driver (eutrophication in combination with global warming) and the indicator is rated as less certain.

Changes in the indicator could be considered of ecological significance if, for example: i) recruitment was poor several years in a row, ii) adult population decreases as a result of bad recruitment, or iii) important predators switch prey or see their population decline.

There are some knowledge gaps related to saithe recruitment along the west coast of Norway that should be filled. First, how much does recruitment along the west coast of Norway contribute to the total saithe stock in the North Sea, and does this component comprise a substock with low demographic connectivity with a potential western stock? Second, has there been shifts in the plankton community along the west coast of Norway, or is there a potential for such shifts? In relation to the latter, the nutrient loads from various sources should be mapped to evaluate whether they are increasing. Third, except for limited work done on saithe along the Norwegian Skagerrak coast (Johannessen, 2014; Aanonsen, 2018), there are apparently no studies during the first year along the west coast of Norway. As for cod along the Norwegian Skagerrak coast (Johannessen, 2014), the year-class abundance could potentially be determined after settlement. Such monitoring would help evaluating potential consequences of increasing nutrient loads on saithe recruitment. Fourth, identification, mapping and protection of important habitats for settled saithe might contribute to improving or preserving saithe recruitment. For example, eelgrass beds have been identified as important habitats for coastal cod (Johannessen, 2014).

Lesser sandeel stock size [NI21]

Phenomenon: Decreasing lesser sandeel stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, the lesser sandeel stock (hereafter sandeel) is one of the largest fish stocks in the North Sea. Sandeel is a key species in the North Sea ecosystem by forming a mid-trophic link between plankton and higher trophic levels and a very important prey for a variety of predators, including fishes (Daan, 1989), seabirds (Rindorf et al., 2000; Frederiksen et al., 2005), and sea mammals (MacLeod et al., 2007; Anderwald et al., 2012). Due to its burial behaviour in sandy bottom substrate with a limited range in grain sizes (Macer, 1966; Wright et al., 2000), sandeel grounds are spread like a patchwork in the North Sea (Jensen et al., 2010). Most of the sandeel grounds are found south of 58°N (Jensen et al., 2010) at depths between 20 and 70m (Wright et al., 2000), except for at Shetland and Vikingbanken (~60°N) where the latter has a bottom depth of 90-100 m. Sandeels have demersal eggs which are laid on the ground they inhabit (Proctor et al., 1998). Larvae are pelagic and drift away from the natal grounds (Macer, 1965; Proctor et al., 1998; Munk et al., 2002). After settlement, sandeels show high site fidelity and do not migrate over longer distances (Gauld, 1990; Jensen et al., 2010). Since 2011, sandeel has been managed as seven substocks (ICES, 2017a), of which two (SA3r and SA5r) are found in the Norwegian sector (NEEZ). There are an unknown number of small, unexploited sandeel grounds along the west coast of Norway (Bergstad et al., 2002; Jiménez-Mena et al., 2020).

The most important anthropogenic drivers of change in the sandeel stock size are fishery, climate change, and habitat degradation. The impact of overfishing has been particularly severe in NEEZ where the majority of sandeel ground were commercially depleted in the early 2000s (ICES, 2010). This had severe impact on the productivity due to a close relationship between presence of local spawning stock and local recruitment (Johannessen and Johnsen, 2015; Johannessen and Johnsen, submitted). It has been suggested that the underlying mechanism is post-larvae returning and settling in natal habitats, which would imply low demographic connectivity between sandeel grounds in NEEZ (Johannessen and Johnsen, 2015; Johannessen and Johnsen, submitted). This led to the implementation of a unilateral, spatial management system in NEEZ in 2010 to prevent local depletions (see details in Johnsen et al. (2021), App. 2)). Since the implementation of this system, several of the depleted sandeel grounds in SA3r have recovered and the stock has been well above B_{pa} (precautionary limit) since 2015 (ICES, 2021h). Being unexploited, the coastal sandeel grounds along the west coast of Norway are mainly affected by environmental factors. Another fishery impact on sandeels in the North Sea is exploitation of their predators. Bioenergetics modelling indicates that predatory fish take more sandeels than taken by the industrial fishery or marine mammals and seabirds (Furness, 2002). Accordingly, as predator stocks decreased substantially from the 1970s onwards, in particular cod and mackerel, VPA and CPUE data suggest that abundance of sandeels increased in parallel with increased harvesting of sandeels (Furness, 2002). On the other hand, there have been several incidents in NEEZ where sandeel grounds have recovered after having been depleted, and then depleted again by the fishing fleet within just one fishing season (Johannessen and Johnsen, submitted). Depletion of sandeel grounds may cause long-term local recruitment failure, e.g., the highly productive Vikingbanken has remained depleted since 1997 (Johnsen, 2021). Our understanding of the impact of the fishery on the sandeel stock is rated as certain.

Due to high habitat specificity, site fidelity and limited depth range of sandeel habitats, sandeels in the North Sea are particularly vulnerable to climate change. In lack of suitable habitats, sandeels have limited opportunities to migrate to deeper water as temperature increases, nor are there known habitats in more northerly and deeper parts of the North Sea. Evidence suggests that higher temperatures affect sandeels directly through increased metabolic costs resulting in reduced fecundity (Wright et al., 2017). Further, van Deurs et al. (2011) estimated the critical threshold size for sandeel to hibernate through the winter is 9.5 cm at 10°C, and increased to 10.5 cm at 11°C. However, the greatest impact of climate change on sandeels is likely to be indirect through reduction in their main prey, i.e., larger copepods, in particular *Calanus finmarchicus* (van Deurs et al., 2009; van Deurs et al., 2011). The size of calanoid copepods in the North Sea has decreased substantially since the 1980s, and the boreal *C. finmarchicus* has been specially negatively affected by increasing temperatures (Beaugrand et al., 2003). The area suitable for *C. finmarchicus* has declined in southern areas of the North Sea and is predicted to spread northwards during the 21st century (Frederiksen et al., 2013). An increase in

the temperate *Calanus helgolandicus* is not expected to offset this negative trend for sandeel prey as this species has a later spring burst not coinciding with hatching of sandeel larvae (Jónasdóttir et al., 2005; van Deurs et al., 2009). In NEEZ, the negative impact of increasing temperatures on sandeels is likely to be somewhat delayed due to a more northerly position. Another impact of climate change on sandeels acts through the impact on their predators, which to some degree might offset other negative impacts on sandeels. Our understanding of the impact of climate change on the sandeel stock is rated as certain.

The dependency on suitable habitat makes sandeels vulnerable to physical and chemical habitat degradation. Trawling has the potential to affect bottom communities and habitats negatively (Jones, 1992). Sandeel trawls are equipped with relatively light metal chain footrope (Johannessen and Johnsen, submitted), and despite intensive trawling for decades on clearly defined fishing banks, there are no reports of reduced habitat quality due to trawling. The lack of impact of trawling on sandeel habitats is further supported by the fact that after the introduction of the spatial management system in NEEZ, many of the heavily trawled sandeel grounds within SA3r have recovered, and in 2020 the highest landings since 1998 were taken in SA3r (ICES, 2021h). Extraction of sediments is probably not a problem as sandeel grounds are generally found deeper than 20 m. On the other hand, debris from construction work, e.g., deployment of pipelines and drilling for oil, might affect sandeel habitats. During extraction of oil, produced water containing a variety of substances (Meier et al., 2020; Nepstad et al., 2021) might also affect sandeel habitats. Vikingbanken is the most exposed sandeel ground to oil activities in NEEZ. However, there is insufficient knowledge about potential impact on the habitat on the local sandeel stock. Another potential threat from the oil industry is accidental blowouts. Experience from the Deep Water Horizon accident in 2010 showed that “oil snow” was formed and covered large areas of the bottom (Daly et al., 2016). Offshore windfarms are a growing industry in the North Sea and could potentially affect local sandeel stocks. A study before and after the establishment of a windfarm in Danish waters found a short-term increase in abundance of sandeels followed by a slight decrease in the longer term, but the mechanism remained obscure (van Deurs et al., 2012). The impact of habitat degradation has so far not been a significant problem but has the potential to affect sandeels in the future. Our understanding of the impact of habitat degradation is rated as certain.

As sandeels are important prey for a variety of predators, all three drivers have potentially great implications for the functioning of the North Sea ecosystem. Along the east coast of the UK, the breeding success of various seabirds have been related to fluctuations and trends in sandeel abundance (Furness and Tasker, 2000; Rindorf et al., 2000; Furness, 2002). In Scottish waters an increase in harbour porpoises starving to death was observed in relation to a substantial reduction in the proportion of sandeel in their diet (MacLeod et al., 2007), and body condition of various predatory fishes was linked to the availability of sandeels (Engelhard et al., 2013). As the commercial sandeel grounds in NEEZ are situated on west-southwest side of the Norwegian Trench and thus far longer from the coast than breeding seabirds forage (Thaxter et al., 2012), changes in sandeel abundance on the commercial grounds in NEEZ are unlikely to affect the breeding success of seabirds. On the other hand, changes in the non-commercial sandeel grounds along the west coast of Norway may influence breeding in seabirds. Our understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Lesser sandeel has been subjected to substantial research over the years, including impact of fisheries, habitat requirements, identification of sandeel grounds, top-down control by predation, and impact of climate change. Hence, there is generally good knowledge about the anthropogenic drivers affecting the commercial sandeel stocks. However, there is insufficient knowledge about how effluents from the oil industry might affect sandeel habitats. Knowledge about the non-commercial, sandeel populations along the Norwegian coast is also limited.

Lesser sandeel recruitment [NI22]

Phenomenon: Decreasing lesser sandeel recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

The main anthropogenic drivers of sandeel recruitment are fishery, climate change and pollution. Sandeel is a short-lived species in the fishery with a mean age of fish landed in the first half of the year (main fishing season) of 1.4 years (Johannessen and Johnsen, submitted). In contrast, on an unexploited bank, older age groups (up to 8 years) contributed substantially to the local stock (Bergstad and Høines, 2001). Due to the short lifespan on exploited grounds and the dependency on local spawning stocks, sandeels are highly vulnerable to recruitment overfishing (Johannessen and Johnsen, submitted). Implementation of the spatial management system in NEEZ in 2010 aims at protecting local spawning stocks. Our understanding of the impact of fishing on sandeel recruitment is rated as certain.

A dietary study of sandeel larvae revealed high dependency on *C. finmarchicus* (van Deurs et al., 2009). The abundance of the lipid rich *C. finmarchicus* has decreased in parallel with increasing temperatures in the North Sea (Beaugrand et al., 2003) and is projected to decrease further as temperature rises (Frederiksen et al., 2013). Another important, lipid rich group of copepods, *Paracalanus/Pseudocalanus*, has also decreased in the North Sea concurrent with increasing temperatures (Nicolas et al., 2014) and may thus exacerbate the recruitment problems for sandeels. Recruitment is also likely to be affected directly by increasing temperatures causing reduced fecundity (Wright et al., 2017) and reduced survival through the first winter (van Deurs et al., 2011). Our understanding of the impact of climate change on sandeel recruitment is rated as less certain.

Pollution from oil and gas activities (e.g., produced water and acute oil spills) may potentially affect recruitment during the approximately two months sandeel eggs lie glued to the bottom and during the subsequent larval stage (Johnsen, 2021). It is worth noting that the highly productive Vikingbanken, which has remained depleted since 1997 (Johnsen, 2021), is the most exposed sandeel ground to oil and gas production in the Norwegian sector. Our understanding of the impact of pollution on sandeel recruitment is rated as less certain.

Several studies shows that 0-group sandeels are the main prey of many seabirds during the breeding season (MacDonald et al. (2019) and references therein). Hence, any reduction in sandeel recruitment will influence the breeding success in many seabird species in the northern North Sea (Monaghan, 1992). These studies have mainly been conducted in UK waters and around Shetland, but also the breeding success of seabirds along the Norwegian coast is impacted by the availability of sandeel (Hagenlund, 2011). Sandeel is also important prey for several sea mammals (Das et al., 2003), as it is shown that the density distribution of sandeel affect the distribution of minke whales in the North Sea (de Boer, 2010). As many juvenile fishes feed on larval and post-larval sandeels, e.g., cod, whiting, haddock and saithe (Robb and Hislop, 1980; Bromley et al., 1997; Demain et al., 2011), factors affecting recruitment in sandeels might in turn affect recruitment in predators. Our understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Changes in the indicator could be considered of ecological significance if, for example: i) recruitment was poor several years in a row, ii) adult population decreases as a result of bad recruitment, or iii) important predators switch prey or see their population decline.

There are some knowledge gaps in relation to recruitment in sandeels. First, as for most fish species, factors affecting recruitment remains obscure, except that recruitment is mainly determined during early life stages. On the other hand, after Hjort(1914) suggested the first recruitment hypothesis followed by more than 100 years of research, the recruitment puzzle is obviously very difficult to resolve. Numerous correlations between recruitment of various fishes and environmental variable and biological variables have been carried out, of which most "significant" correlations have not stood the test of time (e.g., Myers (1998)). Hence, significant correlations must be confirmed by field studies before being accepted. Second, there is a need for knowledge about how oil and gas activities might affect recruitment in sandeels. Third, updated stomach studies of predators preying on juvenile sandeels is needed to estimate how haddock recruitment has been affected in recent years.

Norway pout stock size [NI23]

Phenomenon: Stable Norway pout stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, Norway pout is one of the largest demersal (benthic-pelagic) fish stocks in the North Sea. It is a small (mainly <20 cm; Hislop (2015)), highly numerous species and important prey for a variety of predators such as cod, whiting, haddock, saithe, and mackerel (Daan, 1989; ICES, 1997). Norway pout is short-lived (rarely reaching 5 years) and mature as I- (~20%) and II-group (~100%) (Lambert et al., 2009). It is mainly distributed in the northern part of the North Sea and along the west and south side of the Norwegian deep, with the highest concentrations found between 100 and 200m (Albert, 1994; Hislop, 2015). Spawning occurs over a wide area in the northern part of the North Sea (Sundby et al., 2017). A proportion of the larvae drift into Skagerrak but return to the northern North Sea when approaching maturity (Lambert et al., 2009). There is no evidence of sub-populations in the North Sea (ICES, 2017b). Being short-lived and recruitment varying substantially interannually, SSB fluctuates accordingly.

The most important anthropogenic drivers of change in the Norway pout stock size are fisheries and climate change. Landings of Norway pout reached a maximum of ~700 kt in 1974 (ICES, 2017b), but has since decreased to a present level varying between 34 and 130 kt (ICES, 2020b). It should be noted that in the mid-1970s, there were substantial bycatches of juvenile haddock, whiting, and other species in the Norway pout fishery (ICES, 2017b). Since then, bycatches have been substantially reduced. In addition, a relatively large area in the UK sector has been closed for Norway pout fishing since 1977 to protect juvenile gadoids, and two areas in the Norwegian sector have been closed since 2002 (Patchbanken) and 2005 (Egersundbanken). Altogether, these closed areas cover a substantial part of the distribution range of Norway pout in the North Sea (ICES, 2017b). SSB has generally been above the precautionary limit the last four decades, and Kempf et al. (2009) found no relationship between SSB and recruitment. The stock appears mostly influenced by natural processes (ICES, 2017b). However, as a close relationship between the Norway pout stock and the abundance of predators have been demonstrated (Kempf et al., 2009), fisheries targeting predators will probably have a positive influence on the stock. Our understanding of the link between the driver (fisheries) and the indicator is rated as certain.

In contrast to many other demersal fishes in the North Sea that have shown a northerly displacement, displacement of Norway pout has been southwards (Perry et al., 2005). The authors (ibid.) suggested that this could be a result of temperature decreasing with higher latitudes in the southern part of the North Sea but increasing slightly in the northern part due to the current system. On the other hand, as the Norway pout stock is substantially affected by predation, displacement of predators might have shifted the relative predation pressure northwards and belie the response of Norway pout to increasing temperatures. Being dependent on zooplankton during early life stages, climate changes induced changes in zooplankton might potentially affect recruitment in the future (see recruitment section below). In conclusion, our understanding of the link between the driver (climate change) and the indicator is rated as less certain.

Given that Norway pout is an important prey for variety of species (Daan, 1989; ICES, 1997), large changes in the stock might have substantial impact on the functioning of the northern part of the North Sea ecosystem. On the other hand, larger fish rarely experience starvation mortality (Johannessen, 2014). Hence, the most likely effect of reduced food availability is reduced growth, which, for example, has been suggested for saithe in the North Sea due to increased competition for Norway pout related to the rapidly rising stock of European hake in the North Sea (Cormon et al., 2014; Cormon et al., 2016). The impact of a reduced Norway pout stock is uncertain though, as it depends on complex food-web processes (e.g., Valentine et al. (2008)), including the ability of the predators to switch to alternative prey. Norway pout feeds mainly on plankton throughout its life, mostly calanoid copepods and euphausiids (Albert, 1994; Bromley et al., 1997). How Norway pout affects the abundance of their prey is unclear as this depends on complex feedback processes (e.g., Johannessen (2014)). Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the ecosystem impacts are therefore rated as good.

An important knowledge gap for Norway pout in the North Sea is related to how changing abundance will affect

predators. Hence, it is recommended the stomach sampling projects carried out in 1981 and 1991 should be repeated. Another knowledge gap is related to the mechanism underlying the southerly displacement of Norway pout.

Norway pout recruitment [NI24]

Phenomenon: Stable Norway pout recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

In contrast to most of other gadoid species in the North Sea, recruitment in Norway pout has remained quite stable over the past 4 decades (ICES, 2020b).

The most important anthropogenic drivers in the indicator are fisheries and climate change. Although recruitment overfishing is generally difficult to confirm in high fecundity species like Norway pout (e.g., Pierre et al. (2017)), management assumes that there is a lower limit, B_{lim} , where a fish stock has a high likelihood of impaired recruitment (EU, 2015). During the last 4 decades, SSB of Norway pout has generally been above B_{Pa} and recruitment has shown no trend (ICES, 2020b). Hence, with the present low level of fishing mortality and a substantial part of the distribution area being closed for fishing, recruitment will probably not be affected directly by the fishery. On the other hand, fisheries on predators of juvenile Norway pout will probably influence recruitment of Norway pout indirectly. How this will affect recruitment is uncertain though. Reduced abundance of predators will probably benefit recruitment in Norway pout, whereas potential increased abundance in nontarget species, as seen in grey gurnard (Floeter et al., 2005), might have a negative impact on recruitment. In conclusion, the impact of the driver (fishing) on the indicator (recruitment) is rated as less certain.

0-group Norway pout feed mainly on calanoid copepods, in particular *Calanus finmarchicus* (Robb, 1981; Bromley et al., 1997). Although important calanoid copepods like *C. finmarchicus* and *Paracalanus/Pseudocalanus* have decreased concurrent with increasing temperatures (Beaugrand et al., 2003; Nicolas et al., 2014), recruitment in Norway pout has not decrease in parallel (ICES, 2020b). Kempf et al. (2009) reported that the combination of sea surface temperature in spring and geographical overlap with potential predators could explain much of the recruitment variability in Norway pout, and Huse et al. (2008) found a significant, negative correlation between the abundance of Norway pout and that of herring, and suggested that this could be due to herring predation on Norway pout larvae. Unfortunately, most “significant” correlations between fish recruitment and physical and biological variables have not stood the test of time (Myers, 1998), and potential relationships should therefore be confirmed by field studies. On the other hand, predation is obviously a factor that should be considered, but the present level of knowledge does not allow firm conclusions to be drawn. As for most fishes, there is no information about the critical period for recruitment in Norway pout, nor about potential shifts in the diet of larvae and 0-group to compensate for reduced abundances calanoid copepods. Hence, it is not possible to evaluate whether reduced predator stocks have belied potentially reduced recruitment from lower availability of calanoid copepods. In conclusion, our current understanding of the link between the driver (climate change) and the indicator is rated as less certain.

The effect of fisheries and climate on recruitment also propagates as an effect on total Norway pout stock biomass. As Norway pout has been a functionally important species under the reference condition, potential future changes in the recruitment of Norway pout changes should be considered of ecosystem significance. However, due to lack of updated diet studies of predators on juvenile Norway pout and the opportunity for predators to shift to other prey, the impact of the indicator is rated as less good.

Changes in the indicator could be considered of ecological significance if, for example: i) recruitment was poor several years in a row, ii) adult population decreases as a result of bad recruitment, or iii) important predators switch prey or see their population decline.

There are some important knowledge gaps in relation to Norway pout. First, as for most fishes, factors affecting recruitment remains obscure, except that recruitment is mainly determined during early life stages. On the other hand, after Hjort(1914) suggested the first recruitment hypothesis followed by more than 100 years of research, the

recruitment puzzle is obviously very difficult to resolve. Numerous correlations between recruitment and environmental variable and biological variables have been carried out, of which most “significant” correlations have not stood the test of time (e.g., Myers (1998)). Hence, significant correlations must be confirmed by field studies before being accepted. Second, only a few studies of the diet of pre-settled 0-group Norway pout have been carried out and the last one took place in 1991 (Bromley et al., 1997). These studies should be repeated to determine whether Norway pout have shifted to alternative prey to compensate for the decreasing abundance of *C. finmarchicus*. As experience from diet studies in 0-group cod shows that the diet may be highly different between years and that the diet affects the condition of the fish (Johannessen, 2014), such studies should be carried out in more than one year and include the condition of the fish (liver index). Third, knowledge about how changing abundances of predators of juvenile Norway pout are affecting recruitment need to be updated. Hence, the stomach sampling projects carried out in 1981 (Daan, 1989) and 1991 (ICES, 1997) should be repeated.

Whiting stock size [NI25]

Phenomenon: Decreasing whiting stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, the whiting stock is one of the large demersal fish stocks in the North Sea and important prey and predator. Whiting is distributed throughout the North Sea and Skagerrak, with the highest concentrations along the east coast of UK and the southern part of Skagerrak at depths between 30 and 150m (Hislop, 2015). Growth is slow after the first year of living but varies locally so that a fish of 30 cm may vary in age between 2 and 6 years (Daan, 1989). Most whiting mature at the age of 2 (Hislop, 2015). Whiting in the North Sea and Skagerrak is managed two stock units one for Skagerrak and Kattegat and one for the North Sea and The English Channel (ICES, 2022g; ICES, 2022f), but genetic evidence suggests at least 3 distinct population units (Charrier et al., 2007). The diet of whiting in the North Sea was comprehensively studied during The Stomach Sampling Project in 1981 and 1991 under the umbrella of ICES (Daan, 1989; ICES, 1997). Whiting feed opportunistically on a wide variety of organisms but shift gradually with size towards the dominance of fish. Whiting is considered as one of the main predators on commercial fishes in the North Sea (Hislop et al., 1991).

The most important anthropogenic drivers of change in the indicator are fisheries and climate change. Landings of whiting have dropped from around 200 kt in the latter half of the 1970s to the present level of 20-30 kt, of which up to 50% are discards (ICES, 2021i). Fishing mortality dropped substantially around the turn of the century is now estimated to have been below the precautionary level since then. Despite stable recruitment (0-group) over the last 4 decades and reduced fishing mortality, SSB dropped from close to 400 kt in the late 1970s staying at a level below B_{Pa} (180 kt) until 2019. This apparent paradox has been ascribed to increased predation on 0-group whiting (ICES, 2021k) from the substantial increase in the biomass of grey gurnard in the North Sea (ICES (2020a); see section on whiting recruitment), which has been suggested to be an indirect impact of reduced stocks of gadoids from fisheries and climate change (Floeter et al., 2005). In addition, there is evidence of both reduced length and age of maturity in whiting which has been ascribed to evolutionary impact of fishing (Marty et al., 2014). Since 2019 SSB has increased substantially and is now estimated to be close to 300 kt (ICES, 2022g). Our understanding of the impact of fisheries on the whiting stock is rated as certain.

Kerby et al. (2013) found no distinct latitudinal and deepening of whiting in the North Sea over time. However, recruitment might be affected in the future because of changes in the plankton community from climate change (see recruitment section). Our understanding of the impact of the climate change on the indicator is rated as less certain.

As whiting is an important predator and prey of a variety of species, both drivers, fisheries and climate change, have potentially great implications for the functioning of the North Sea ecosystem. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the understanding of ecosystem impacts from changes in the indicator is therefore rated as good.

There are some major knowledge gaps related to the North Sea whiting stocks. First, comprehensive diet studies of fish in the North Sea were carried out in 1981 and 1991 (Daan, 1989; ICES, 1997). The two studies showed substantial deviations. During the last three decades there have been major changes in the North Sea ecosystem. Hence, new diet studies are needed to evaluate the ecological impact of the indicator in the ecosystem. Second, a potential threat to the North Sea whiting stock is lack of implementing separate assessment and management of substocks. When a fish stock consists of several substocks, unbalanced fishing effort may result in the collapse of substocks, even under moderate overall fishing mortality (Frank and Brickman, 2001). Violation of the unit stock assumption may thus severely impact both fishing yield and biodiversity (Cowen et al., 2000; Sterner, 2007; Reiss et al., 2009). Genetic homogenisation of substocks may take place with a very limited exchange of individuals (Palumbi, 2003), without the two substocks being demographically connected (Lowe and Allendorf, 2010). For example, homing to natal spawning grounds may give rise to substocks with similar genetic traits, e.g., as indicated for lesser sandeel (Johannessen and Johnsen, submitted).

Whiting recruitment [NI26]

Phenomenon: Decreasing whiting recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition whiting recruitment is high and sufficient to sustain a large stock. Recruitment varies substantially less from year to year than seen in other gadoids (e.g., haddock), and recruitment has shown no significant trend over the last 4 decades (ICES, 2021i) at the 0-group stage. However, stochastic multispecies modelling (SMS) has suggested that increased predation of 0-group whiting has led to substantially reduced recruitment to the spawning stock (ICES, 2021k).

The most important anthropogenic drivers in the indicator are fisheries and climate change. Although there is generally a poor relationship between SSB and recruitment in marine fishes, (e.g., Pierre et al. (2017)), management assumes that there is a lower limit, B_{lim} , below which a fish stock has a high likelihood of impaired recruitment (EU, 2015). Since the late 1990s, SSB of the North Sea whiting stock has generally been below B_{Pa} (ICES, 2021i), which has been ascribed to substantial increase in the abundance of grey gurnard preying on 0-group whiting (ICES, 2020a; ICES, 2021k). The increase in grey gurnard concurred with both reduced biomass of demersal gadoids and increasing temperatures, and it has been suggested that grey gurnard may have been able to occupy substantial parts of the ecological niche freed by the diminishing gadoids (Floeter et al., 2005). Hence, both fisheries and climate change might have contributed to the increase in grey gurnard. There is no targeted fishery for grey gurnard and no major predators have been identified (ICES, 1997). A modelling study based on the 1991 stomach sampling project (ICES, 1997) and the increased biomass of grey gurnard suggested that predation of 0-group cod by grey gurnards may impede recovery of the North Sea cod stock (Floeter et al., 2005). As grey gurnard is also an important predator on 0-group whiting, this might also be the case for the whiting stock. In conclusion, the understanding of the link between the driver (fishing) and the indicator is rated as less certain.

Whiting larvae feed mainly on juvenile copepods (Last, 1978), and shift to copepods, euphausiids, appendicularians and larval fish during the juvenile, pelagic stage (Robb and Hislop, 1980; Bromley et al., 1997). Despite substantial changes in meso-zooplankton in the North Sea in relation to increasing temperatures (Beaugrand et al., 2003; Nicolas et al., 2014), estimated recruitment of 0-group whiting has shown no trend over last 4 decades (ICES, 2021i). On the other hand, repeated incidences of abrupt and persistent recruitment collapses in 0-group gadoids, including whiting, have been observed in relation to gradually changing environmental conditions along the Norwegian Skagerrak coast (Johannessen et al., 2011; Johannessen, 2014). These collapses were attributed to abrupt shifts in the plankton community depriving juvenile gadoids of adequate planktonic prey. Prior to 2000, these shifts concurred with increasing nutrient loads, whereas the last shift in ~2002 took place during a period of increasing temperatures but decreasing eutrophication. It has been suggested that changing environmental conditions that affect competition in plankton, reduces ecosystem resilience and the system becomes vulnerable to shift to an alternative stable state consisting of plankton better adapted to the altered environment (Johannessen, 2014). With continuing increasing temperature in the

North Sea, this might induce shifts in the plankton community affect recruitment in whiting as seen along the Norwegian Skagerrak coast. In conclusion, our understanding of the link between driver (climate change) and the indicator is rated as less certain.

The effect of fisheries and climate change on recruitment also propagates as an effect on total whiting stock biomass. As whiting has been a functionally important species under the reference condition (see references under the whiting section), the observed changes should be considered of ecosystem significance. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the ecosystem impacts are therefore rated as good.

Changes in the indicator could be considered of ecological significance if, for example: i) recruitment was poor several years in a row, ii) adult population decreases as a result of bad recruitment, or iii) important predators switch prey or see their population decline.

There are some important knowledge gaps in relation to recruitment in whiting. First, as for most fishes, factors affecting recruitment remains obscure, except that recruitment is mainly determined during early life stages. On the other hand, after Hjort(1914) suggested the first recruitment hypothesis followed by more than 100 years of research, the recruitment puzzle is obviously very difficult to resolve. Numerous correlations between recruitment and environmental variable and biological variables have been carried out, of which most “significant” correlations have not stood the test of time (e.g., Myers (1998)). Hence, significant correlations must be confirmed by field studies before being accepted. Second, only a few studies of the diet of pre-settled and settled 0-group whiting have been carried out (e.g., Bromley et al. (1997); Demain et al. (2011)). These studies should also be repeated to determine whether 0-group whiting have shifted to alternative prey in relation to the observed changes in zooplankton in the North Sea (Beaugrand et al., 2003; Nicolas et al., 2014). As experience from diet studies in 0-group cod shows that the diet may be highly different between years and that the diet affects the condition of the fish (Johannessen, 2014), these studies should be carried out in more than one year and include the condition of the fish (liver index). Third, there is a need for knowledge about how changing abundance of predators might affect recruitment in whiting in the North Sea. Hence, the stomach sampling projects carried out in 1981 and 1991 (Daan, 1989; ICES, 1997) should be repeated.

Herring stock size [NI27]

Phenomenon: Decreasing herring stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, the North Sea autumn spawning (NSAS) herring stock is one of the largest pelagic fish stocks in the North Sea and an important predator and prey species. Herring is preyed on by a variety of predators, including several commercial species of fish, sea mammals and seabirds(Daan, 1989; Gannon et al., 1997; ICES, 1997). NSAS herring is distributed throughout the North Sea, Skagerrak, Kattegat and the English Channel (ICES, 2021f) with the highest abundance between 20 and 100m (Dickey-Collas et al., 2015). The NSAS herring spawn in the autumn and winter by disposing their eggs in a thick layer on coarse or solid substrate such as mearl, gravel or boulders. The larval stage lasts for up to 180 days and modelling of larval drift have indicted both retention and long-distance drift (Dickey-Collas et al., 2009). There are 4 main spawning areas along the east coast of the UK, from Shetland to the English Channel (Dickey-Collas et al., 2010; Sundby et al., 2017), and the Downs herring from the most southern spawning area can be separated genetically from other NSAS herring components (Bekkevold et al., In press). After spawning, herring spread out over wide areas of the North Sea to feed during the productive season. Circumstantial evidence suggests the various spawning groups return to their natal spawning grounds (Blaxter and Hunter, 1982). NSAS herring is managed as a unit stock (ICES, 2021f).

The most important anthropogenic drivers for the indicator are fisheries and climate change. The spawning stock biomass (SSB) of the NSAS herring dropped from around 5 million tonnes in the late 1940s to around 3 million in the mid-1960s, followed by a rapid collapse to a minimum of 100-150 kt in the mid-1970s (ICES, 2021f). The stock recovered in the 1980s and has fluctuated around 2 million tonnes after 2000. In recent years SSB has decreased to

around 1.4 million tonnes but is still within safe biological limits. The collapse concurred with increasing landings and substantial increased fishing mortality, and has been attributed to recruitment overfishing (Cushing, 1992; Dickey-Collas et al., 2010). Our understanding of the impact of the driver (fisheries) on the indicator is rated as certain.

NSAS herring are close to the centre of the north-south distribution range of herring in the Northeast Atlantic (Blaxter and Hunter, 1982). It is therefore assumed that the recent increase in temperature would have limited effect on their overall distribution (Röckmann et al., 2010). On the other hand, increasing temperatures are predicted to enhance growth of the youngest age-classes, but reduce the growth of older individuals and shorten the lifespan of herring (Brunel and Dickey-Collas, 2010). A more severe impact of increasing temperatures is on recruitment which has been unprecedentedly low after the turn of the century, despite of a SSB above the precautionary limit (Payne et al., 2013; ICES, 2021f). This has been attributed to a regime shift that occurred in the North Sea around 2000 (Payne et al., 2009) which had substantial impact on the zooplankton community (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014) (see phenomenon for the indicator on herring recruitment (NI28) for more details). Our understanding of the link between the driver (climate change) and changes in the indicator is rated as certain.

Being an important prey for a variety of predators (Daan, 1989; Gannon et al., 1997; ICES, 1997), changes in the herring stock might influence the functioning of the North Sea ecosystem. However, how much this will impact predator stocks is complicated as it depends on opportunities for predators to shift to alternative prey. The impact of herring as predator is also highly uncertain. It is generally assumed that the main drivers of changes in zooplankton are bottom-up processes, e.g., changing temperatures (e.g., Alvarez-Fernandez et al. (2012); Beaugrand et al. (2014)), and top-down processes by large stocks of planktivorous fishes reducing the abundances of their zooplankton prey (e.g., Papworth et al. (2016)). The latter is in accord with the classical perception of an antagonistic predator-prey relationship (e.g., Loreau (1995)). Interestingly though, during the heydays of the two largest planktivorous stocks, herring (SSB of 4-5 million tonnes; ICES (2021f)) and mackerel (SSB ~2.5 million tonnes; Hamre (1990)) in the 1950s and first half of the 1960, one of their key prey species, *Calanus finmarchicus*, had the highest abundance ever observed in the North Sea (Reid et al., 2003). Concurrent with the collapse of these stocks due to overfishing in the latter half of the 1960s (Cushing, 1992; Jansen, 2013), the abundance of *C. finmarchicus* dropped substantially. Although there is evidence to suggest that environmental conditions were unfavourable for *C. finmarchicus* at that time (Fromentin and Planque, 1996), the reduction in *C. finmarchicus* is surprising since the predation pressure must have decreased substantially (the total SSB of herring and mackerel decrease by 6-7 million tonnes). Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the understanding of consequences of change in the indicator for other parts of the ecosystem is therefore rated as good.

An important knowledge gap related to changes in the herring stock in the North Sea is lack of understanding of the importance of bottom-up versus top-down processes, and whether the top-down processes are antagonistic or synergistic.

Herring recruitment [NI28]

Phenomenon: Decreasing herring recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition herring recruitment is sufficiently large to sustain a large stock. As for most marine fishes, recruitment in herring varies considerable interannually (ICES, 2021f).

The most important anthropogenic drivers in the indicator are fisheries and climate change. Concomitant with the collapse of the spawning stock of herring in the 1970s due to overfishing (Cushing, 1992; Dickey-Collas et al., 2010), herring recruitment was historically low (ICES, 2021f). After the recovery the stock in the 1980s, recruitment increased to pre-collapse levels or even slightly higher. The abundance of total *Calanus* (mostly *C. finmarchicus*) followed the same pattern as the SSB and recruitment in herring, with high abundances in the 1950s and -60s followed by a depression in the seventies and recovery in the early 1980 (Reid et al., 2003). One could therefore be tempted to

speculate if the recruitment failure during 1970s was a result of bottom-up processes. However, in the latter half of the 1980s, the abundance of *Calanus* dropped to well below that observed during the 1970s (Reid et al., 2003) without herring recruitment showing a similar drop as during the collapse of SSB (ICES, 2021f). Hence, the main cause of the recruitment failure was most likely a result of recruitment overfishing, as suggested by (Cushing, 1992). In conclusion, our understanding of the link between driver (fisheries) and the indicator is rated as certain.

After 2000 recruitment in herring has been unprecedented low (except for in the 1970s during the collapse of SSB), in spite of SSB being within safe biological limits (Payne et al., 2013; ICES, 2021f). The poor recruitment has been attributed to a regime shift that occurred around 2000 (Payne et al., 2009), as a result of altered physical environment affecting the plankton community, including increasing temperatures (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014). Denis et al. (2016) found that small herring larvae (8–11 mm) are omnivorous and feed on a higher diversity of small prey, mainly small copepods, diatoms and dinoflagellates, whereas bigger larvae (13–15 mm) feed on a lower diversity of larger prey, mainly copepods and dinoflagellates. The authors suggested that this shift in diet might be a critical period for recruitment in herring. Payne et al. (2013) analysed growth in larvae before (1998, 1999) and after (2003, 2004) the onset of the 2000s productivity reduction in the North Sea and found evidence of reduced growth after the regime shift. However, the authors underlined that the results should be interpreted with caution. Although the recruitment puzzle remains unresolved for herring as for most marine fishes, the relationship between climate change, regimes shifts and recruitment failure appears to be robust (Alvarez-Fernandez et al., 2012; Johannessen, 2014). In conclusion, our understanding of the link between the driver (climate change) and the indicator is rated as certain.

The effect of fisheries and climate on recruitment also propagates as an effect on total herring stock biomass. As herring has been a functionally important species under the reference condition, changes in herring recruitment should be considered of ecosystem significance. However, due to lack of updated diet studies of predators on herring (the last took place in 1991; ICES (1997)), the understanding of the consequences of change in the indicator for other parts of the ecosystem is rated as less good.

There are some important knowledge gaps in relation to recruitment in herring. First, as for most fishes, factors affecting recruitment remains obscure, except that recruitment is mainly determined during early life stages. On the other hand, after Hjort (1914) suggested the first recruitment hypothesis followed by more than 100 years of research, the recruitment puzzle is obviously very difficult to resolve. Numerous correlations between recruitment and environmental variable and biological variables have been carried out, of which most “significant” correlations have not stood the test of time (e.g., Myers (1998); Garcia et al. (2020)). Hence, significant correlations must be confirmed by field studies before being accepted. Second, updated stomach studies of predators preying on juvenile herring are needed to estimate how herring recruitment has been affected in recent years.

Mackerel stock size [NI29]

Phenomenon: Decreasing mackerel stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, the mackerel stock is one of the largest pelagic stocks in the North Sea. Mackerel is a highly migratory species, and ICES currently uses the term “Northeast Atlantic (NEA) mackerel” to define the mackerel present in the area extending from the Iberian Peninsula in the south to the northern Norwegian Sea in the north, and Iceland in the west to the western Baltic Sea in east (ICES, 2013). Mackerel in these waters are managed as a unit stock (ICES, 2021g), although historically it has been described to be composed by three main spawning components; the Southern (along the Iberian Island and the Bay of Biscay), the Western (west of the British Isles) and the North Sea component (Iversen, 2002; ICES, 2013). However, no scientific proof for consistent natal homing or repeat spawning can be traced in the year class structures over time to support the idea of these three separate spawning components. Rather the data from for instance the main pelagic survey (PELACUS) in the southern spawning area show that the main bulk of spawners are the oldest and biggest mackerel that to a large degree must have spawned at other sites farther north at younger ages (ICES, 2019). In fact, tagging experiments on mackerel in 1994 at the coast of Spain on large spawners revealed that most recaptures came from the fishery in the wintering area in northern North Sea or early

southward spawning migration west of British Isles and Ireland (Uriarte and Lucio, 2001). In addition, currently there is no genetic structure to support such components being maintained over time (Gíslason et al., 2020). The more updated interpretation is therefore that NEA mackerel is one stock with a dynamic distribution (Jansen and Gislason, 2013), using the North Sea mainly as a wintering ground (Jansen et al., 2012) and nursery area (Jansen et al., 2015). It is further suggested that spawning in the North Sea area may occur more dynamically when the environmental and biological conditions are favourable (Jansen, 2013), and the fraction has been minor (<10%) for the last two decades. New research reveal that the NEA mackerel is highly dependent on its energetic status and feed heavily during the spawning period (Jansen et al., 2021), which ultimately may have significant influence on migration choices for a large population under strict competition for prey. Furthermore, a new large scale tagging program have shown that the mackerel undertake size dependent spawning and feeding migrations with the wintering area in Northern North Sea as basis, and that recruits growing up in the North Sea migrate out of the area to feed far west into Icelandic Waters and spawn west of British Isles and farther south as they grow older and larger (ICES, 2021g; Ono et al., 2022). This suggests that any fidelity for a mackerel growing up in the North Sea to maintain spawning there is low. Furthermore, one should expect that any dynamics in growth and condition (Olafsdottir et al., 2015) may be an important driver for the migration and distribution of the stock.

Hence, when interpreting the phenomenon of decreasing abundance of NEA mackerel in the North Sea region, the above-mentioned updated understanding of the migrations and distribution of the stock is of great importance, as the dynamics in the North Sea are to a large degree driven by the dynamics of the total stock and not the small fraction spawning (ICES, 2021g) choosing to spawn there. First of all, for mackerel North Sea is the main wintering area (Jansen et al., 2012), so any change in abundance in the North Sea is directly linked to the total stock size, i.e. they return to this area every year in September after feeding in the Norwegian Sea and adjacent areas and stay until spawning migration southwards start in January. One thing that is certain is that the stock levels reached historical maximum around 2014 after increasing continuously since bottom levels around 2000, but are now reduced to the same level as in the mid-1980s, and the abundance of mackerel using North Sea as a wintering area is directly linked to these dynamics in total stock.

The most important anthropogenic drivers of change in abundance of mackerel as a whole, and therefore also for the abundance in the North Sea are fisheries and climate change. Under the recent condition with warming of NEA waters from 2000 onwards (Asbjørnsen et al., 2020; ICES, 2021j; Kjesbu et al., 2022), the NEA mackerel as had a series of large year classes leading to high stock levels (ICES, 2021g), but at the same time the fishing pressure has been high with overshooting quotas around 40% since 2010. Under the continuous high fishing pressure with no large recent year classes this has ultimately led to the decreasing stock size after 2014. Our understanding of the link between the driver (fisheries) and changes in the indicator is therefore rated as certain, whereas the link to climate change and actual underlying processes for the recruitment variation is less certain as there is little research describing this. However, Jansen (2014) characterised the collapse in the North Sea spawning as a “pseudocollapse” and proposed that low temperatures between the mid-1970s and mid-1980s resulted in mackerel from the North Sea spawning along the west side of the British Isles and possibly further south, followed by increased temperatures resulting in reduced zooplankton biomass that were unfavourable for recruitment of mackerel in the North Sea. The reduced abundances of zooplankton have been attributed to large-scale hydro-meteorological forcing and increasing temperatures inducing a regime shift in the North Sea in 1980s (Reid and Edwards, 2001; Beaugrand, 2004b).

Mehl and Westgaard.T. (1983) analysed the diet from “year of the stomach” in the North Sea 1981 and estimated that the mackerel at that time may have consumed as much as a million ton, twice its own biomass in the area at the time, in which a large proportion was 0-1 group fish, yet with clear variation spatially and over the year. The last “year of the stomach” in 1991 also revealed that mackerel at all ages had a large proportion of fish (dominated by sandeel) in the stomach, being comparatively just as important prey as zooplankton, yet varying spatially and over the year (ICES, 1997). This are very old data, still they suggest that the presence of mackerel in the North Sea may have significant effect on other fish populations. The year of the stomach data 1991 are used as input to ecosystem models (Mackinson and Daskalov, 2007), still the scenario of ecosystem effects of fluctuating mackerel biomass in the area spatially and

temporally remains undescribed and regarded as less certain. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the ecosystem impacts are therefore rated as good.

Mackerel recruitment [NI30]

Phenomenon: Change in mackerel recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Following the argumentation for decreasing stock size above, decreasing recruitment of mackerel into the North Sea is also directly linked to the changes in the total stock. This is because mackerel recruits in the North Sea most likely is a product of spawning west of the British Isles and further egg/larval drift into the North Sea rather than local recruitment which is assumed to be low due to the low presence of spawners in the area (ICES, 2021g).

The most important anthropogenic drivers in the indicator are fisheries and climate change. The effect of fisheries as a whole is reduced stock, and there is a relation between stock size and recruitment. More spawners produce more eggs, but also an expanding distribution that ultimately may affect survival of progeny (ICES, 2021g), so drivers affecting the stock size also indirectly affect the recruitment. Under the recent condition with warming of NEA waters from 2000 onwards (Asbjørnsen et al., 2020; ICES, 2021j; Kjesbu et al., 2022), the NEA mackerel has had series of large year classes. This has happened simultaneously with a north and westward shift in spawning (Brunel et al., 2017; dos Santos Schmidt et al., In prep.), which ultimately also has led to more progeny ending up in the North Sea area (Nøttestad et al., 2021). It is uncertain whether the shift in spawning areas is related to temperature (Brunel et al., 2017), or more related to migration potential following the size structure and condition of the stock as such and the need for feeding while spawning (Jansen et al., 2021), both factors may play a role. In conclusion, as it is hard to predict whether the overall effect of fisheries and climate change will give an increase or decrease in mackerel recruitment, and the understanding of the link between fisheries and climate change and recruitment of mackerel into the North Sea is regarded as less certain.

In 2018-2021 a swept area survey July covering the North Sea deeper than 50m showed that immature mackerel (1–2-year-old) probably from spawning west of British Isles, dominated in 2021. The biomass was estimated to 560 kt in 2021, which was almost twice as high as in 2019 and 2020 (Nøttestad et al., 2021). This suggests that in addition to the large aggregations of adults wintering in the North Sea from September to January, there may also be a substantial mackerel biomass comprised of young recruits in the area that potentially could impact the ecosystem all year round as revealed by year of the stomach data (ICES, 1997) until they also leave the area for feeding and spawning at older ages, as proved by tagging experiments (Ono et al., 2022). The fact that recruits tagged in the North Sea choose to migrate southwards along the British Isles to spawn, and west to Iceland to feed when growing older, is a proof in itself that they are not belonging to a specific component with high fidelity to the area. As with adult fish there is lack of knowledge of the effects of the spatial and temporal variation in consumption of the mackerel recruits in the North Sea. Hence, knowledge on the impact of variation in mackerel recruitment on the North Sea ecosystem is rated as less good.

Northern shrimp stock size [NI31]

Phenomenon: Decreasing shrimp stock size

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition northern shrimp (*Pandalus borealis*) (hereafter shrimp) is a key component in continental shelf and fjord ecosystems in the northern hemisphere. Shrimp graze on plankton during vertical nocturnal migrations (Barr, 1970; Hudon et al., 1992; Bergström, 2000) and is in turn important food for demersal fish (Parsons, 2005), thereby linking trophic levels, as well as benthic and pelagic components of the ecosystem. Shrimp prefer soft mud or sand/silt substrate (Shumway et al., 1985) which are very common in Skagerrak and the Norwegian Trench (MAREANO, 2022). In this area, the species is found at depths between 100 and 500m (Søvik and Thangstad, 2021). In the North Sea, shrimp obtain their food from the macroplankton at nighttime, while they feed on benthic organisms like crustaceans, polychaetes and molluscs, as well as detritus during the day (Wienberg, 1981). Females in some

areas migrate to shallower areas in late winter to release their larvae, and juveniles are often found in these waters, separate from the adult stock (Shumway et al., 1985). Skagerrak serve as a nursery area as most 1-year old shrimp are found here, and there seems to be a westward migration of juvenile shrimp out of Skagerrak (Søvik and Thangstad, 2021). The shrimp in Skagerrak and the Norwegian Trench, together with coastal shrimp north to Kvænangen in Troms comprise one genetic population (Knutsen et al., 2014; Jorde et al., 2015; Hansen et al., 2021). A modelled time series of shrimp spawning stock biomass (SSB) from Skagerrak and the Norwegian Trench back to 1908 shows high abundance of shrimp in the area at the beginning of the 20th century when the fishery was in its infancy (Hjort and Ruud, 1938; ICES, 2022d; Melaa et al., 2022). The size of shrimp populations depends on the size of predator stocks. Unusually high shrimp densities occur in an arctic fjord environment in the inner part of Porsangerfjorden in Finnmark, where large predator fish are absent (Søvik et al., 2020). The shelf ecosystems in the Northwest-Atlantic were characterized by large demersal fish stocks until they collapsed in the late 1980s (Myers et al., 1996), after which shellfish stocks like northern shrimp increased substantially (Lilly et al., 2000; Pérez-Rodríguez et al., 2017). Worm and Myers (2003), however, found no negative relationship between stocks of shrimp and cod in Skagerrak as opposed to the rest of the North-Atlantic and explained this by shrimp hiding in deep trenches and cod partly being replaced by more southern predator species. Fish stomach analyses in Skagerrak and the Norwegian Trench show that cod, saithe, whiting, velvet belly, roundnose grenadier, blue whiting, angler fish, hake, Norway pout, and poor cod prey on shrimp (Bergstad et al., 2003; Skorda, 2018). Shrimp has furthermore been reported in the diet of marine mammals and sea birds (Bergström, 2000).

The most important anthropogenic drivers of change in this indicator are fisheries (bottom trawling), climate change and pollution. The Norwegian and Swedish trawl fisheries for shrimp commenced in Oslofjorden and the eastern Skagerrak in 1898 (Hjort and Ruud, 1938; Melaa et al., 2022). Norwegian landings peaked in 1963 followed by a sharp decline around 1970. Landings (both Norwegian and total international) then increased and remained at a high level throughout the 1980s, 1990s and 2000s (ICES, 2022d; Melaa et al., 2022). Fishing pressure remained below F_{MSY} (MSY-Maximum Sustainable Yield)

throughout most of this period. Since 2011, landings have decreased, fishing pressure has been above F_{MSY} , and the spawning stock (SSB) has declined and is currently at B_{lim} (not sustainable) (ICES, 2022d) and at 13% of the SSB in 1908 (ICES, 2022c). The decreasing spawning stock concurred with historically low recruitment since 2008 (see recruitment below) (ICES, 2022d). Shrimp have more or less disappeared from the northern part of the Norwegian Trench (Søvik and Thangstad, 2021), and likewise in fjords and coastal areas in western Norway (Zimmermann et al., 2021). Local fisheries in the Oslofjorden region and in fjords in western and mid-Norway have decreased or disappeared (Melaa et al., 2022). Causal relationships may be complex and decreases in stock size not necessarily due to over-fishing (see below). Northern shrimp is a boreal species with its southernmost distribution in the Northeast-Atlantic in Skagerrak and the North Sea. The species has been reported in waters with temperatures ranging from -1.6 °C to 12 °C (Shumway et al., 1985); in Skagerrak and the North Sea it occurs at 4-9 °C (Søvik and Thangstad, 2021). Populations may be adapted to local temperature conditions (Jorde et al., 2015). Rasmussen (1967) explained marked declines in shrimp landings in Skagerrak in 1963-1966 with unusual cold bottom water (4-5 °C), temperatures which are normal in shrimp areas further north (NAFO and ICES, 2021). As shrimp in Skagerrak and the North Sea are found at the species' southernmost distributional limit, the stock is sensitive to rising temperatures (Kjesbu et al., 2022). Furthermore, as a crustacean, shrimp may be affected by ocean acidification, specifically during early life stages and molting (Kjesbu et al., 2022). The disappearing shrimp stocks in the fjords and coastal areas of western Norway (Zimmermann et al., 2021) may be linked to warming through increased stratification causing less frequent renewal of basin water in deep Norwegian fjords (Aksnes et al., 2019), as shrimp metabolism (Dupont-Prinet et al., 2013) and growth (Båtevik, 2020) is negatively affected by hypoxia. Bottom water of poor quality led to the disappearance of shrimp in Bunnfjorden close to Oslo in the late 1940s as the human population, and pollution, increased (Stålesen, 1963). Of recent concern are the demonstrated negative effects on shrimp of delousing chemicals used in salmon aquaculture (Bechmann et al., 2019; Frantzen et al., 2020), relevant in near-coastal areas, while offshore stocks may be vulnerable to oil spills (Bechmann et al., 2010a). The understanding of the links between the drivers (fishing pressure, climate change and pollution) and shrimp stock size is rated as certain.

As shrimp constitute important prey for many species of demersal fish, declining or disappearing shrimp stocks may potentially have considerable consequences for the Skagerrak and North Sea ecosystems. Despite the lack of detailed knowledge of the ecological impacts of changes in stock, the (relatively) high biomass of the stock makes the species an important factor in North Sea and the knowledge of consequences of change in shrimp SSB on other parts of the ecosystem is therefore rated as good.

Decreasing abundance of shrimp can be considered of ecosystem significance if, for example, it causes massive declines in sizes of demersal fish stocks.

Knowledge gaps: The phenomenon can be monitored by using the modelled time series of shrimp spawning stock biomass (SSB) from the ICES stock assessment model (Stock Synthesis) (1908-present) based on fisheries-independent data from the annual Norwegian shrimp bottom trawl survey in the Skagerrak and Norwegian Trench (1984-present) and time series of landings/catch (1908-present). There is insufficient knowledge about stock connectivity, i.e., both larval drift (see recruitment below) and the connection between the nursery grounds in Skagerrak and areas further west and north along the Norwegian coast. With poor recruitment and critically low stock sizes for several years, the population in Skagerrak and the Norwegian Trench has entered a new regime of higher fishing mortality, and there is need for knowledge on how this affects individual growth, mortality, and maturity (timing of transition from males to females), as well as stock composition (number of age groups). Knowledge about the populations in fjords and along the Norwegian coast is also limited.

Northern shrimp recruitment [NI32]

Phenomenon: Decreasing shrimp recruitment

Ecosystem characteristic: Functionally important species and biophysical structures

Under the reference condition, recruitment to the northern shrimp (*Pandalus borealis*) (hereafter shrimp) stock in Skagerrak and the North Sea is high and variable. Recruitment is measured as the abundance of 1-year old shrimp on the annual Norwegian shrimp bottom trawl survey in the Skagerrak and Norwegian Trench (1984-present) (Søvik and Thangstad, 2021), and modelled as the abundance of the 0-group (ICES, 2022c). Since 2008, recruitment has been substantially lower compared with earlier years, except for two good year-classes in 2013 and 2021, and coincides with a historically low stock level which has fluctuated around B_{lim}

since 2011-2012 (ICES, 2022d). Shrimp is a protandric hermaphrodite (Shumway et al., 1985), and sex change from male to female in the Skagerrak and Norwegian Trench stock takes place at an age of 2 years. Females carry the roe under the abdomen from spawning and mating in autumn until hatching in spring the following year (Shumway et al., 1985). The planktonic larval stage lasts for 2-3 months depending on water temperature (Shumway et al., 1985). Currents can cause advection and result in substantial transport distances of the pelagic larvae (Pedersen et al., 2003; Jorde et al., 2015; Le Corre et al., 2020). Constraints on the extent of larval drift in Skagerrak are suggested by the presence of a large-scale surface gyre (Rodhe, 1987; Gustafsson and Stigebrandt, 1996). The 1-year old shrimp are mainly found in Skagerrak (Søvik and Thangstad, 2021), which seems to serve as a nursery area for the whole stock in the area. Under the reference condition (data from unfished fjord populations) the shrimp population will be composed of 7-8 year classes (including the 0-group), with the 1 to 4 year-old age groups dominating the stock biomass (Båtevik, 2020). It is not possible to age crustaceans, but in the fast-growing shrimp stock in Skagerrak and the Norwegian trench, age groups can be discerned as modal peaks in length distributions.

The most important anthropogenic drivers for the indicator are fishery, climate change and pollution. Low recruitment preceded the currently low stock size, suggesting that initially, low recruitment caused the low stock size and not vice versa. Presently, however, a stock size fluctuating around B_{lim} may contribute to continued impaired recruitment, although the relationship between the spawning stock biomass (SSB) and recruitment is not very strong (ICES, 2022a). Shrimp enter the fishable biomass at an age of approximately 1.5 years when they are still male and have not yet reproduced as females (Søvik and Thangstad, 2016). In earlier years, discarding of the smaller and less valuable males were high (ICES, 2022c). Recently, there has been an increased focus on selective fishing gear (e.g. Ingólfsson and

Jørgensen (2020)), but fishing (and discarding) of juveniles still takes place. Another potential impact on recruitment is truncation of the length (and age) distribution, as larger sized females produce more eggs (Parsons and Tucker, 1986). Recently, the mean size of shrimp in the area has decreased (unpublished data), which may result from the presently higher fishing mortality (ICES, 2022d). T

he understanding of the impact of fishing on the indicator is rated as less certain. Interannual variability in shrimp recruitment in the Northwest-Atlantic may be explained by the hypothesis of match/mismatch between hatching and favourable oceanographic conditions in the upper water level (Ouellet et al., 2007; Ouellet et al., 2011). Koeller et al. (2009) showed that across the North-Atlantic, hatching of eggs in shrimp stocks was correlated with the timing of the spring phytoplankton bloom and concluded that populations have adapted to local temperatures and bloom timing, thereby matching egg hatching to food availability under average conditions. Although similar studies from the North Sea and Skagerrak area are lacking, it seems clear that climate changes that shift the spring bloom may increase the risk of mismatch and, thus, recruitment failure. Results from laboratory experiments suggest a slower development of shrimp early life stages under ocean acidification conditions (Bechmann et al., 2010b; Arnberg et al., 2013). The understanding of the impact of climate change on the indicator is rated as certain. Different kinds of pollution have severely negative effects on shrimp larvae as demonstrated by laboratory studies, with both lethal and non-lethal effects (reduced feeding and swimming behaviour). This has been shown for chemical delousing agents used in coastal salmon aquaculture (Bechmann et al., 2018; Bechmann et al., 2020), and oil (Bechmann et al., 2010a). Extrapolating from laboratory studies to natural populations should be done with care, and population-level effects are less certain, but see Moe et al. (2019). The understanding of the impact of pollution on the indicator is rated as less certain. The understanding of the overall impact from fisheries, climate change and pollution on the indicator is rated as less certain.

Sustained low recruitment will likely result in a sustained low stock biomass. In the Skagerrak and Norwegian Trench stock, occasionally good year-classes (after 2008) have only led to transitorily higher stock biomass (ICES, 2022d). As shrimp constitute important prey for many species of demersal fish, declining or disappearing shrimp stocks may potentially have negative consequences for the Skagerrak and North Sea ecosystems. Our understanding of the importance of change in the indicator for other parts of the ecosystem is rated as less good.

Sustained low recruitment leading to sustained low stock biomass of shrimp can be considered of ecosystem significance if, for example, it causes massive declines in sizes of demersal fish stocks.

Knowledge gaps: The phenomenon can be monitored by using the modelled time series of shrimp recruitment (abundance of 0-group) from the ICES stock assessment model (Stock Synthesis) (1984-present) based on fisheries-independent data from the annual Norwegian shrimp bottom trawl survey in the Skagerrak and Norwegian Trench and time series of landings/catch. We have insufficient knowledge on larval drift patterns in Skagerrak and the North Sea, and how these vary with time and space. Preliminary simulations of larval drift in the area suggest that larvae released in Skagerrak mainly will settle there while larvae released further west will drift north along the coast and out of the area (unpublished data). Furthermore, connectivity of the shrimp stocks in Skagerrak and the Norwegian Trench and on the Fladen Ground farther west in UK waters of the North Sea is unknown, although genetic studies indicate separate populations (Knutsen et al., 2014). Connectivity of fjord and offshore stocks is also unknown. The interannual variability of shrimp recruitment, and in particular the reduced recruitment since 2008 is not understood and may be influenced by a range of drivers, including increased predation by pelagic predators.

Area unimpacted by bottom trawling [NI33]

Phenomenon: decreasing area unimpacted by bottom trawling

Ecosystem characteristic: Landscape-ecological patterns

Under the reference condition, the area unimpacted by bottom trawling is large enough to ensure that ecological structure and processes are not significantly impacted by trawling induced area reductions. Industrial scale trawl fisheries in the North Sea date back to the nineteenth century, with the development originating in the UK and later spreading to other countries around the North Sea (Kerby et al., 2012).

The driver of change in the indicator is fisheries performed using bottom trawling. Only a small fraction of the seabed shallower than 200 meters in the North Sea can be classified as untrawled today (Eigaard et al., 2017). As trawling can have significant impacts on bottom communities (see below), reductions in untrawled area in the North Sea clearly has a potential to have affected ecological structure and processes. The link between the driver and change in the indicator is thus rated as certain.

Bottom trawling will reduce the biomass and biodiversity of the benthic ecosystem and may reduce the complexity of seabed habitats (Collie et al., 2000; Kaiser et al., 2006; Buhl-Mortensen et al., 2016) and affect the functioning and productivity of the benthic ecosystem (Jennings et al., 2001; Hiddink et al., 2011; van Denderen et al., 2013) through a progression of state changes (Smith et al., 2016). The ecosystem effects of bottom trawling will be determined by the type of gear deployed, the type of seabed, direct effects of the passage of a trawl, the footprint of the trawl, the trawling frequency, and the sensitivity of the seabed and benthic ecosystem (Jennings et al., 2005; Lucchetti et al., 2012; Rijnsdorp et al., 2015). The understanding of the importance of changes in the indicator for the rest of the ecosystem is rated as good.

Fish species vulnerable to higher temperature [NI34]

Phenomenon: Decreasing biomass or deepening of fish species vulnerable to higher temperature

Ecosystem characteristic: Biological diversity

Under reference conditions, species sensitive to temperature above reference conditions in the North Sea occupy the northernmost areas of the region.

The most important driver of change in this indicator is climate change. Engelhard et al. (2010) showed that Boreal species are slowly being replaced by Lusitanian species (warm temperate marine species, from the Lusitania biogeographic province, from Cape Juby or Blanco in the south to Southern Eastern Channel in the north, Almada et al. (2013)), concomitant with the recent warming. Similarly, Dulvy et al. (2008) revealed a deepening of some North Sea fish species with colder affinities. Atlantic wolffish (*Anarhichas lupus*) is an example of a boreo-Arctic species which was formerly occurring widespread in the central and northern North Sea, has now retracted, as early life stages and more southern part of the stock might have been affected by higher temperatures (Dulvy et al., 2008; Bluemel et al., 2022). Thermal buffering by migration into deeper waters has also been observed for boreal flatfish species (van Hal et al., 2016). The understanding of the link between the driver and change in the indicator is assessed as certain.

Boreal species tend to be bigger and thus to occupy higher trophic levels than Lusitanian species (Engelhard et al., 2010). A decrease in the abundance of the former in the North Sea would thus imply large transformations in the ecosystem functioning, acting via alterations of the food web and the size-structure of communities. The specific impacts on the North Sea population are however still poorly understood. The understanding of the importance of changes in the indicator for the rest of the ecosystem is therefore assessed as less good.

Although there are some examples of cold-affiliated species that were impacted by the recent warming, little is understood about the possible effects of long- and short-term temporal variability on those species and the consequences for the ecosystem functioning.

Fish species benefitting from higher temperature [NI35]

Phenomenon: Increasing biomass of fish benefitting from higher temperatures

Ecosystem characteristic: Biological diversity

Under reference conditions, species sensitive to temperature below reference conditions in the North Sea occupy the southernmost areas of the region.

The most important driver of change in this indicator is climate change. (Engelhard et al., 2010) showed that Boreal species are slowly being replaced by Lusitanian species, concomitant with the recent warming. Previously, Ehrich and Stransky (2001) had also reported on the increasing frequency of southern species in the North Sea, in link with a

series of mild winters. Similarly, van Hal et al. (2010) observed a northward shift of two non-commercial flatfish in link with changes in thermal habitats during mild winters and better recruitment with increasing temperature. The understanding of the link between the driver and change in the indicator is assessed as certain.

Species benefiting from increasing temperature are generally Lusitanian which are characterised by smaller bodies and lower trophic level compared to Boreal species. An increase in their abundance in the North Sea would thus imply large transformations in the ecosystem functioning, via alterations of the food web and the size-structure of communities. van Hal et al. (2010) projected that the northward progression of two small flatfish species would affect the food web and commercial species by predation on juveniles and competition for benthic food resources. ter Hofstede et al. (2010) also highlighted that warming and incoming Lusitanian species most likely have caused an increase in species richness in the North Sea. The specific impacts on the North Sea population are however still poorly understood. The understanding of the importance of changes in the indicator for the rest of the ecosystem is thus assessed as less good.

Little is understood about the possible effects of long- and short-term temporal variability on species movement and physiology, and the consequences for the ecosystem functioning.

Copepod species vulnerable to higher temperature [NI36]

Phenomenon: Decrease in number of species sensitive to higher temperatures

Ecosystem characteristic: Functionally important species and biophysical structures

Zooplankton are poikilothermic, and temperature affects physiological processes, such as ingestion, respiration, mortality, growth and reproduction, which in turn influences survival from the individual to the population level (e.g. Carlotti et al. (1993)). Consequently, zooplankton taxa that are sensitive to changes in temperatures can be used as indicators to monitor changes in biodiversity due to rising temperatures.

The North Sea belongs to the North East Atlantic Shelves Biogeographic Province, as defined by (Longhurst, 1998). The zooplankton communities in the northeastern North Sea (Norwegian sector) are influenced by Atlantic inflow, and characterized by boreal and temperate species (Fransz et al., 1991). However, a mixture of neritic, oceanic, and even subarctic and arctic species (e.g. *Euchaeta norvegica*, *C. hyperboreus* and *Metridia longa*) co-occurs in this region (Beaugrand et al., 2019). In contrast, the southern North Sea is dominated by neritic, warm-temperate species which are dependent on local production in tidally mixed waters.

The most important anthropogenic driver of change in the indicator is climate change. Water temperature is probably the single most important physical variable affecting the abundance, distribution and phenology of plankton populations. Rising temperatures are causing species to expand at the northern edge of their distribution, while they are retreating at the southern edge (Beaugrand et al., 2009). Species tend to be most sensitive to changes in temperature when they occur near their range edges. Accordingly, species occurring near the *southern* boundary of their distributional range in the North Sea are expected to *be vulnerable to* higher temperatures (Poloczanska et al., 2013). One example is *C. finmarchicus*, which in the North Sea, is close to its southernmost range edge, and has shown a strong declining trend during the last decades related to rising temperatures in this area (Beaugrand et al., 2003). In the North Sea *C. finmarchicus* is the dominant *Calanus*- species at temperatures below 11°C (Bonnet et al., 2005). If temperatures increase to above 11°C, *C. helgolandicus* is expected to take over the habitat currently dominated by *C. finmarchicus* (Møller et al 2012). The decrease in *C. finmarchicus* is thus a useful indicator of the warming trend in the North Sea.

Boreal and polar species generally have lower tolerance and less adaptive capacity than temperate and neritic species, making them more vulnerable to increasing temperatures. As a result, boreal species have shown a declining trend in the North Sea due to rising temperatures, e.g. *C. finmarchicus*, *C. hyperboreus*, and *Euchaeta norvegica* (Pitois and Fox, 2006).

Species specific information on additional species that are vulnerable to higher temperatures can be found in Fransz et al. (1991) who listed North Sea zooplankton species in relation to their preferred environment.

Species-specific information is essential in many circumstances for interpreting climate change impacts. However, studies focusing on individual species may have limited potential for inferring changes to the ecosystem level. Beaugrand et al. (2002a) identified nine calanoid copepod species assemblages on the basis of their distribution and variability (Table 5.2). These species assemblages were related to biotopes defined by several environmental variables (bathymetry, salinity, water masses, stratification). Their species assemblage-number 7, 8 and 9 comprises boreal and polar taxa that are vulnerable to increasing temperatures, and that have been found to decrease in the North Sea during the last decades (Beaugrand et al., 2009). However, these species groups, are associated with biogeographic regions, characterized by several environmental factors (Beaugrand et al., 2009). Thus, the species assemblages may not be directly linked to temperature *per se*, but represents an integrated effect from several drivers, and can be considered as indicators of *water-mass dynamics* (Ndah et al., 2022).

Ocean currents modify the coupling between climate change and biogeographical shifts (García Molinos et al., 2017) and advection has been found to introduce species of different origins to the North Sea (Fransz et al., 1991; Reid and Edwards, 2001). The substantial reduction of *C. finmarchicus* in the North Sea has been related to the decrease in Norwegian Sea Deep Water (Heath et al., 1999b). Fransz et al. (1991) concluded that *Paraeuchaeta norvegica*, *Calanus hyperboreus*, and *Metridia longa* can be considered as indicators of arctic-boreal oceanic inflow to the North Sea, while Beaugrand et al. (2002a) classified the same taxa as subarctic to arctic species.

Given the uncertainties described above, the understanding of the link between climate change and the indicator is rated as less certain.

Because higher temperatures are expected to contribute to increased reproduction and survival for species near the poleward edges of their ranges (Poloczanska et al., 2013), species tend to shift their distributions towards higher latitudes during warming conditions. Indeed, strong biogeographical shifts in copepod populations have been documented in the North Atlantic with a northward extension of more than 1100 km of warm-water species during the last 50 years (Beaugrand et al., 2002a). As a result, the diversity of the zooplankton community is expected to increase, while the overall total zooplankton biomass decreases. The change in species composition community will alter the productivity and seasonal phenology of the plankton community. This may produce trophic mismatches, affect predator-prey interactions, alter the carbon transfer and change the ecosystem functioning. The clearest example of this has been the replacement of *C. finmarchicus* by *C. helgolandicus*, as water has warmed in the North Sea. *C. helgolandicus* spawn later in the year compared to *C. finmarchicus*, which has resulted in a reduction in total zooplankton biomass, and a temporal mismatch between the spawning of cod in spring and the availability of suitable food (Beaugrand et al., 2003).

Zooplankton communities characterized by warm-water species tend to be smaller, exhibit less biomass and are less energy-rich than polar and boreal species (Kattner et al., 2007). A reduction in lipid rich species may reduce growth and survival, and in turn affect recruitment in fish or seabirds (Wanless et al., 2005; Beaugrand et al., 2009). Communities dominated by cold-water species are expected to have shorter food chains, high trophic efficiency and represent favorable fish feeding conditions. A reduction in the biomass of cold-water species will result in a less productive system, with decreased trophic efficiency and reduced biological carbon pump (Hébert et al., 2016).

Given the substantial evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Increasing abundance of warm-water species can be considered to be of ecosystem significance if: i) it causes massive declines in the production and recruitment of fish populations, and ii) it causes reduced vertical carbon flux (carbon pump).

Knowledge gaps: To select adequate indicators of the phenomenon is challenging since knowledge on species specific responses to temperature changes is limited. Furthermore, the interpretation of the phenomenon may be hampered by intercorrelations and indirect effects from temperature increases, e.g., changes in stratification, phytoplankton composition and ocean currents. Future research should attempt to disentangle the coupling between

biogeographical shifts, temperature, and advection.

The CPR survey provides abundance data on copepod species that are vulnerable to higher temperatures. However, data on other ecologically important taxonomic groups in the North Sea are lacking, such as euphausiids.

We have limited knowledge on how species are able to adapt to changing temperatures. In order to interpret and predict temperature effects on zooplankton communities, research on temperature tolerance and adaption is needed

In cases of increasing temperatures, species are expected to seek refuge in cooler, deeper waters, The CPR survey only samples the surface waters. As a result, the CPR data may be affected by potential changes in the vertical distribution of each species in response to temperature changes (Pinsky et al., 2013). Zooplankton data from full ocean depths are available from the IMR North Sea plankton monitoring program

Table 5.2 Biological composition of species assemblages and their ecological preferendum. From Beaugrand et al. 2002a. The time period considered in the analyses was 1958–1999. The names of some species assemblages have been slightly modified in comparison to those used in Beaugrand et al. (2002b; their Table 1).

Name of the assemblage	Species or taxa	Ecological preferendum
1. Subtropical and warm-temperate species assemblage	<i>Undeuchaeta major</i> , <i>Acartia danae</i> , <i>Paracandacia bispinosa</i> , <i>Euchaeta media</i> , <i>Temora stylifera</i> , <i>Scolecithrix danae</i> , <i>Euchaeta marina</i> , <i>Candacia ethiopica</i> , <i>Eucalanus attenuatus</i> , <i>Lucicutia</i> spp., <i>Eucalanus elongatus</i> , <i>Candacia pachydactyla</i> , <i>Rhincalanus cornutus</i> , <i>Euchaeta pubera</i> , <i>Centropages violaceus</i>	Oceanic and pseudo-oceanic species generally found near shelf edges and in the northward extension of the Gulf Stream
2. Warm-temperate oceanic species assemblages	<i>Euchaeta acuta</i> , <i>Undeuchaeta plumosa</i> , <i>Euchirella restrata</i> , <i>Neocalanus gracilis</i> , <i>Clausocalanus</i> spp., <i>Nannocalanus minor</i> , <i>Pleuromamma borealis</i> , <i>P. gracilis</i> , <i>P. abdominalis</i> , <i>P. xiphias</i> , <i>P. piseki</i> , <i>Calocalanus</i> spp., <i>Mesocalanus tenuicornis</i> , <i>Heterorhabdus papilliger</i> , <i>Centropages bradyi</i> , <i>Mecynocera clausi</i>	Oceanic warm water species, generally south of 52°N but concentration associated with the path of the North Atlantic Current above 52°N east of the mid-Atlantic ridge
3. Warm-temperate pseudo-oceanic species assemblage	<i>Euchaeta gracilis</i> , <i>Euchaeta hebes</i> , <i>Ctenocalanus vanus</i> , <i>Calonoides carinatus</i>	Warm water shelf-edge species found south of about 50°N along the European shelf edge for years prior to the 1980s
4. Temperate pseudo-oceanic species assemblage	<i>Rhincalanus nasutus</i> , <i>Eucalanus crassus</i> , <i>Centropages typicus</i> , <i>Candacia armata</i> , <i>Calanus helgolandicus</i>	Species can be found in oceanic and neritic water but their abundance is higher along shelf edges until about 55 before the 1980s
5 Shallow-water species assemblage	<i>Isias clavipes</i> , <i>Anomalocera patersoni</i> , <i>Labidocera wollastoni</i>	Species generally found above the continental shelf but mainly abundant in shallow coastal regions
6 Continental shelf species assemblage	<i>Centropages hamatus</i> , <i>Temora longicornis</i> , <i>Pseudocalanus adult</i> , <i>Para-Pseudocalanus</i> spp.	Species generally found above the continental shelf
7. Cold-temperate mixed-water species assemblage	<i>Aetideus armatus</i> , <i>Pleuromamma robusta</i> , <i>Acartia</i> spp., <i>Metridia lucens</i>	Species indicative of mixed water more usually found at the boundary between warm water and subarctic water
8 Subarctic species assemblage	<i>Heterorhabdus norvegicus</i> , <i>Scolecithricella</i> spp., <i>Euchaeta norvegica</i> , <i>Calanus finmarchicus</i>	Species indicative of subarctic water
9. Arctic species assemblage	<i>Calanus hyperboreus</i> , <i>Metridia longa</i> , <i>Calanus glacialis</i>	Species indicative of arctic

Copepod species benefitting from higher temperature [NI37]

Phenomenon: Increase in number of “Warm-water species”

Ecosystem characteristic: Biological diversity

Zooplankton are poikilothermic, and temperature affects physiological processes, such as ingestion, respiration, mortality, growth and reproduction, which in turn influences survival from the individual to the population level (e.g. (Carlotti et al., 1993)). Consequently, zooplankton taxa that are sensitive to changes in temperatures can be used as indicators to monitor changes in biodiversity due to rising temperatures.

The North Sea belongs to the North East Atlantic Shelves Biogeographic Province, as defined by Longhurst (1998). The zooplankton communities in the northeastern North Sea (Norwegian sector) are influenced by Atlantic inflow, and is characterized by boreal and temperate species (Fransz et al., 1991). However, a mixture of neritic, oceanic, and even subarctic and arctic species (e.g. *Euchaeta norvegica*, *C. hyperboreus* and *Metridia longa*) co-occurs in this region (Beaugrand et al., 2019). In contrast, the southern North Sea is dominated by neritic, warm-temperate species which are dependent on local production in tidally mixed waters.

The most important anthropogenic driver of change in the indicator is climate change. At the species level, temperature is the single most important physical variable affecting the abundance, distribution and phenology of plankton populations. Rising temperatures are causing species to expand at the northern edge of their distribution, while they are retreating at the southern edge (Beaugrand et al., 2009). Species tend to be most sensitive to changes in temperature when they occur near their range edges. Accordingly, species occurring near the *northern* boundary of their distributional range in the North Sea are expected to *benefit* from higher temperatures (Poloczanska et al., 2013). One example is *C. helgolandicus*, which in the North Sea, reaches its northernmost distributional range edge, and has shown a strong increasing trend to rising temperatures during the last decades in this area. In the North Sea *C. helgolandicus* is the dominant *Calanus*- species at temperatures above 11°C (Bonnet et al., 2005). If temperatures increase to above 11 C, *C. helgolandicus* is expected to take over the habitat currently dominated by *C. finmarchicus* (Møller et al., 2012). The abundance of *C. helgolandicus* is thus a useful indicator of the warming trend in the North Sea.

Species that have high thermal tolerance and adaptive capacity are also expected to benefit from higher temperatures. Temperate and neritic species generally have a wider thermal tolerance window than boreal and polar species, making them more robust to changes in temperature. One example is the small-sized copepod *Oithona similis* which thrives under conditions that are thermally unfavourable to other species, including a wide range of temperatures from < 0°C (Balazy et al., 2021) up to ~ 17 °C (Castellani et al., 2007). This species has been observed to increase in the North Sea (Bedford et al., 2018). Hence, the ratio of *O. similis* relative to calanoid copepods may be a strong indicator of fundamental biodiversity changes linked to temperature (Ndah et al., 2022).

Some non-indigenous species are also expected to benefit from higher temperatures. For example, the spreading and establishment of the alien ctenophore *Mnemiopsis leidyi* and the cladoceran *Penilia avirostris* are closely linked to increasing temperatures in the North Sea (Johns et al., 2005; Hosia and Falkenhaus, 2015).

Species specific information of additional species that are expected to benefit from higher temperatures can be found in Fransz et al. (1991), who listed North Sea zooplankton species in relation to their preferred environment.

Species-specific information is essential in many circumstances for interpreting climate change impacts. However, studies focusing on individual species may have limited potential for inferring changes to the ecosystem level. Beaugrand et al. (2002a) identified nine calanoid copepod species assemblages on the basis of their distribution and variability (Table 5.2). These species assemblages were related to biotopes defined by a number of environmental variables (bathymetry, salinity, water masses, stratification). For example, the presence of warm-temperate pseudo-oceanic species in the north-western part of the North Sea (assemblage number 2) may be a good indicator of the warm dynamic regime of North Sea marine ecosystems (Beaugrand et al., 2002a). Their species assemblages number 1,2,3,

and 4 comprises taxa that are expected to benefit from increasing temperatures in the North Atlantic and North Sea (Table 5.2). However, these species groups are associated with biogeographic regions characterized by several environmental factors (Beaugrand et al., 2009). Thus, such species assemblages are not directly linked to temperature *per se*, but represents an integrated response to multitude drivers, and should rather be considered as indicators of *water-mass dynamics* (Ndah et al., 2022).

Ocean currents modify the coupling between climate change and biogeographical shifts (García Molinos et al., 2017) since advection may introduce “warm-water species” to the North Sea (Reid et al., 2001). The increased intensity of the European shelf-edge current may have played an important role in advecting more warm-water species northwards (Reid and Edwards, 2001). Furthermore, the substantial reduction of *C. finmarchicus* in the North Sea has been related to the decrease in Norwegian Sea Deep Water (Heath et al., 1999b). Fransz et al. (1991) concluded that *C. typicus*, *Candacia armata* and *Metridia lucens* can be considered as indicators of the inflow of oceanic and coastal waters to the North Sea from the north, while Beaugrand et al. (2002a) classified the same taxa as temperate pseudo-oceanic species. Accordingly, Beaugrand et al. (2019) suggested to use variations in species of the warm-temperate association (association 2) as a proxy to evaluate the strength of the North Atlantic Current and oceanic advection through the Celtic Sea to the English Channel.

Given the uncertainties described above the understanding of the link between increases in temperature and the indicator is rated as less certain.

Because higher temperatures are expected to contribute to increased reproduction and survival for species near the poleward edges of their ranges (Poloczanska et al., 2013), species tend to shift their distributions towards higher latitudes during warming conditions. Indeed, strong biogeographical shifts in copepod populations have been documented in the North Atlantic with a northward extension of more than 1100 km of warm-water species during the last 50 years (Beaugrand et al., 2002a). As a result, the diversity of the zooplankton community is expected to increase, while the overall total zooplankton biomass decreases. The change in species composition community will alter the productivity and seasonal phenology of the plankton community. This may produce trophic mismatches, affect predator-prey interactions, alter the carbon transfer and change the ecosystem functioning. The clearest example of this has been the replacement of *C. finmarchicus* by *C. helgolandicus*, as water has warmed in the North Sea. *C. helgolandicus* spawn later in the year compared to *C. finmarchicus*, which has resulted in a reduction in total zooplankton biomass, and a temporal mismatch between the spawning of cod in spring and the availability of suitable food (Beaugrand et al., 2003).

Zooplankton communities characterized by warm-water species tend to be smaller, exhibit less biomass and are less energy-rich than polar and boreal species (Kattner et al., 2007). A reduction in lipid rich species may reduce growth, survival and in turn affect recruitment in fish or seabirds (Wanless et al., 2005; Beaugrand et al., 2009). Communities dominated by warm-water species are expected to have longer food chains, reduced trophic efficiency and represent unfavorable fish feeding conditions and less efficient utilization of primary production. This will result in a less productive system, with decreased trophic efficiency and reduced biological carbon pump (Hébert et al., 2016).

Given the substantial evidence described above the understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Increasing abundance of warm-water species can be considered to be of ecosystem significance if: i) it causes massive declines in the production and recruitment of fish populations, and ii) it causes reduced vertical carbon flux (carbon pump).

Knowledge gaps: To select adequate indicators of the phenomenon is challenging since knowledge on species specific responses to temperature changes is limited. Furthermore, the interpretation of the phenomenon may be hampered by intercorrelations and indirect effects from temperature increases, e.g., changes in stratification, phytoplankton composition and ocean currents. Future research should attempt to disentangle the coupling between biogeographical shifts, temperature, and advection.

The CPR survey provides abundance data on copepod species that may benefit from higher temperatures. However, data on other ecologically important taxonomic groups in the North Sea are lacking, such as small copepod species (e.g., *Oithona*), appendicularians, chaetognaths, cladocerans, and gelatinous zooplankton. These are all groups that are expected to benefit from higher temperatures.

We have limited knowledge on how species are able to adapt to changing temperatures. In order to interpret and predict temperature effects on zooplankton communities, research on temperature tolerance and adaption is needed

In cases of increasing temperatures, species are expected to seek refuge in cooler, deeper waters. The CPR survey only samples the surface waters. As a result, the CPR data may be affected by potential changes in the vertical distribution of each species in response to temperature changes (Pinsky et al., 2013). Zooplankton data from full ocean depths are available from the IMR North Sea plankton monitoring program.

Fish species vulnerable to fisheries [NI38]

Phenomenon: Decreasing biomass fish species vulnerable to fisheries

Ecosystem characteristic: Biological diversity

Under reference condition, species sensitive to fisheries are thriving in the North Sea. Species vulnerable to fisheries are target species and by-catch in the fisheries. Demersal fish sensitive to fisheries are usually considered to be large and to harbour traits linked to slow life history (late age at maturity, demersal egg-layer). An example is the Atlantic wolffish (*Anarhichas lupus*), which is a frequent by-catch of mixed demersal fisheries in the North Sea (Bluemel et al., 2022). However, many small pelagic forage fish are also caught by fisheries in the North Sea (ICES, 2021c). It should be noted that this functional group also includes IUCN vulnerable species such as Atlantic halibut (*Hippoglossus hippoglossus*, IUCN Endangered), small-eyed ray (*Raja microocellata*, IUCN near threatened), and sharks (e.g., tope shark *Galeorhinus galeus*, IUCN Critically endangered, gulper shark *Centrophorus granulosus*, IUCN endangered, and porbeagle *Lamna nasus*, IUCN vulnerable).

The main driver of change in this indicator is fishing. The North Sea was intensely fished in the late 80s (Gislason, 1994; ICES, 2021c). Direct removal of biomass from fisheries has impacted the stocks of fish species such as sandeels (e.g. Lindegren et al. (2018)), cod (*Gadus morhua*), saithe (*Pollachius virens*), the ling (*Molva molva*), the sturgeon (*Acipenser sturio*), and some elasmobranchs (ICES, 2021b). Fisheries also affect target species life history. For example, the North Sea plaice (*Pleuronectes platessa*) has been shown to suffer a decrease in length and age at maturation, partly caused by fisheries-induced adaptation (Grift et al., 2003). In addition, incidental by-catches of marine mammals and IUCN listed species occur in several fisheries (ICES, 2021c). The understanding of the link between the driver and change in the indicator is rated as certain.

The removal of large fish by the fisheries has severe impact on the overall size-structure of the ecosystem. With the size of the fish being generally linked to its trophic level, fishing of large species will affect the top-down controls of the food web. Furthermore, fisheries of low or intermediate trophic level such as forage fish have been shown to have strong impacts on upper trophic level species (Frederiksen et al., 2006; Wanless et al., 2007; Fauchald et al., 2011b; Smith et al., 2011; Lauerburg et al., 2018). As one of the indicators of fishing impact in the region, the abundance of fish sensitive to fisheries can also give an indication on possible other impacts of fisheries such as by-catch of untargeted species, damage to the seafloor, of disruption of the ecosystem food chain and size structure (Gislason, 1994; Bergman and van Santbrink, 2000; Rumohr and Kujawski, 2000; Cook et al., 2014; Church et al., 2019). The understanding of the consequences of a decline in biomass of species sensitive to fisheries for the rest of the ecosystem is assessed as good.

The mechanisms underlying the combined effects of climate and fisheries is an important knowledge gap in the North Sea.

Temperature [NI39]

Phenomenon: Warming of the water column

Ecosystem characteristic: Abiotic factors

Under the reference condition, which for abiotic factors is defined as the climate in the period 1961-1990, the deep-water in the North Sea was characterised by relatively low temperatures with a subsequent warming after the reference period. The most consistent temperature indicator for the North Sea is quantified from the deep-water defined as the depths between 100 and 200m. The surface layer and the entire North Sea shelf area is subject to considerable variation due to the fluctuating atmospheric conditions with short time periods and will appear noisy in long time series. Although the temperature indicator is based on the conditions at depths between 100 and 200m, the temperature variability and trends are also noticeable in the more fluctuating surface layer climate. Data on temperature exists from the 1950s from the Skagerrak (Torungen-Hirtshals) and from the 1980s from the northern North Sea (Utsira-Orkneys),

meaning that the quantitative information for the indicator exists for the entire period that has been defined as descriptive for the reference condition for climate.

The most important anthropogenic driver of change in the indicator is climate change, causing the water column to warm (Pörtner et al., 2019). Anthropogenic global warming leads to increasing ocean temperature in the inflowing Atlantic Water (Schrum et al., 2016) although a minor part of the warming can be attributed to natural variation (Albretsen et al., 2012). Given the massive evidence of anthropogenic influence on the climate in general (Masson-Delmotte et al., 2021), the understanding of the link between drivers and change in the indicator is rated as certain.

Change in temperature can have large implications for the ecosystem in the North Sea and Skagerrak, either directly or through an influence on other aspects of the abiotic environment, such as stratification (see phenomenon for the indicator on stratification (NI40) below). Changes in temperature have been linked to several processes in the plankton community, such as a decrease in the abundance of herbivorous zooplankton (see phenomenon for indicator NI03) and increase in abundance of carnivorous zooplankton (see phenomenon for indicator NI04), changes in meroplankton vs. holoplankton abundance (see phenomenon for indicator NI07), reduction in copepod body size (see phenomenon for indicator NI08), increasing abundance of gelatinous zooplankton (see phenomenon for indicator NI09), changes in the abundance of key zooplankton species (see phenomenon for indicator NI12) and declining abundance of *Pseudocalanus* and *Paracalanus* species (see phenomenon for indicator NI13). These effects can propagate to other parts of the ecosystem and affect key processes such as fish recruitment (Beaugrand et al. (2003), see also phenomena for indicators NI12, NI13, NI16, NI18, NI20, NI22, NI24, NI26, and NI28). Our understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

Examples of consequences of increasing temperatures in other parts of the ecosystem for the zooplankton community are described above. In addition, it includes declining recruitment of cod and herring (see phenomena for NI16 and NI28).

Warming of the water column depends mainly on the southward inflow of Atlantic Water between Norway and the Orkney. Since we excluded the upper 100m in the temperature indicator, the very fluctuating conditions in the surface layer will not disturb the trend analysis. The temperature climate in the deep-water in the North Sea and the Skagerrak follows the same long-term variability as we see in the Norwegian Sea, but improved understanding is needed to address future changes and biological impacts.

Stratification [NI40]

Phenomenon: Increasing stratification of the upper water column

Ecosystem characteristic: Abiotic factors

Under the reference condition, which for abiotic factors is defined as the climate in the period 1961-1990, there are no data coverage of CTD (salinity and temperature) measurements available for deriving stratification. The only time series available are the hydrographic observations within the Norwegian economic zone of the northern and central North Sea and the Skagerrak as a part of the ecosystem cruise conducted in April/May each year. Data are only available from 2005 and onwards, and based on all available data we see a weak, but significant, decrease in stratification during spring in the upper water column of the northern North Sea and the Skagerrak. The surface layer water masses in the northern North Sea are primarily dominated by relative saline Atlantic water, while the Skagerrak contains a mixture of saline water from the North Sea and less saline water associated with the Baltic and local runoff from rivers. There is some uncertainty in deriving stratification from the ecosystem cruise CTS stations since the cover varies between regions dominated by low-saline and Atlantic waters, respectively. Also, the fact that the time series starts as late as 2005 creates a potential uncertainty in the trend of the timeseries since the noticeable temperature increase in the North Sea area was visible from the late 1980s.

The most important anthropogenic driver of change in the indicator is climate change (Pörtner et al., 2019). The upper water column stratification in the northern North Sea during spring (April/May) is relatively weak with well-mixed waters.

In the Skagerrak we normally find a persistent layered system, particularly the Norwegian Coastal Current flowing along the Norwegian coast, and the overall stability is to a large degree dependent on the weather conditions before and during the ecosystem cruise. However, increasing temperatures and decreasing salinity (and thus density) toward the surface will positively affect the stability. Anthropogenic global warming leads to surface warming as well as freshening due to increased precipitation and increased runoff in the adjacent rivers (Sætre, 2007). This will cause a strengthening of the stratification and a shallower mixed layer depth in summer, but since the data used are snapshots of the conditions every spring, the variable weather conditions and thus the variable mixing will influence the overall indicator values. The understanding of the link between driver and change in the indicator is rated as certain.

A shallower stratification in summer reduces vertical transport of nutrients for new production and phytoplankton production will be increasingly based on nutrients recycled by grazing (Lindemann and St. John, 2014), causing a possible decline in primary production. It should be noted that there is large natural variation in primary production in the Norwegian part of the North Sea because the area contains different hydrographic regimes with different levels of primary production and that the geographic distribution and size of these may vary from year to year (van Leeuwen et al., 2015; Frelat et al., 2022). The knowledge of the importance of change in the indicator for the rest of the ecosystem is still rated as good.

The stratification in the open ocean is highly dependent on the weather conditions before and during the measurement period, which in fact is just a snapshot of the hydrographical state of the surface waters. Signals in stratification that would appear from increased surface heating or increased precipitation and runoff from rivers are difficult to disentangle from such an indicator, and conclusions related to the phenomenon must be handled with care.

Flow conditions [NI41]

Phenomenon: Decreasing inflow of Atlantic water to the North Sea

Ecosystem characteristic: Abiotic factors

Under the reference condition, which for abiotic factors is defined as the climate in the period 1961-1990, quantitative information for the indicator exists only for a small part of the reference condition as the modelled inflow of Atlantic Water was estimated from 1985 and onwards, only. The major proportion of water inflow to the North Sea is the southward drift between Scotland and Norway, where the water masses usually can be defined as Atlantic Water. Since no currents measurements are available, we use the numerical ocean model NORWECOM (Hjøllo et al. (2009) and references therein) to quantify the inflow of Atlantic Water. The data series show that the inflow was relatively high in the end of the 1980s and the beginning of the 1990s. In the 1990s and the next decade the inflow decreased while the indicator has been stably low the last 10 years. However, there are considerable fluctuations in the time series, and some quarters/seasons experience very low or high inflows.

The most important anthropogenic driver of change in the indicator is climate change, but there are large uncertainties associated with this link. While the most important driver is the large-scale weather conditions, related to the NAO (Hjøllo et al., 2009), the strength of the North Atlantic Drift may also have an influence. How the latter may be influenced by climate change is associated with large uncertainties (Zickfeld et al., 2007), but may include a change from the current strong state to a substantially weaker state (Boers, 2021). Should this happen, the flow of Atlantic water into the North Sea may be reduced. Given the uncertainties described here, the understanding of the link between the driver and change in the indicator is rated as less certain.

Species resident in the North Atlantic will have a larger potential for drift into the North Sea when this indicator denotes high values (as demonstrated for zooplankton in Gao et al. (2021)). The strength of the flow can also affect temperature and salinity in the North Sea and thus have an influence on other parts of the abiotic environment. The consequences of change in the indicator for other parts of the ecosystem is thus rated as good.

Ocean modelling have considerably improved their abilities to describe the physical climate the last decade, and when applied correctly can serve as a valuable supplement to observational data. Without a substantial monitoring network of

current measurements in the northern North Sea, it would have been impossible to estimate the inflow of Atlantic Water without an ocean model. However, we must be aware that there can be dynamical processes in the model that may affect the indicator and that is not fully included in the model. Future developments will probably reveal potential weaknesses, and new ocean model systems may eventually replace the suggested system.

Nutrients [NI42]

Phenomenon: Increasing concentration of nutrients

Ecosystem characteristic : Abiotic factors

Under the reference condition, the levels of nutrients in the North Sea and Skagerrak are high enough to sustain a food web with naturally occurring species but not elevated by excessive anthropogenic input to levels that may adversely affect naturally occurring species and ecological processes.

The most important anthropogenic driver of change in the indicator is increased runoff from land linked to river discharges from agriculture and other anthropogenic sources via the Baltic, from Central Europe, western part of Sweden and the eastern and southern part of Norway. In addition to the runoff from land, there is also atmospheric deposition in the order of one fifth of the nitrogen generated from land run-off. The total nutrient budgets in the North Sea and the Skagerrak are primarily regulated through water exchange with the open Atlantic that contributes around 90% of the total (Brockmann et al., 1990). However riverine sources of nutrients, mostly associated with inflow from the German Bight and the Baltic Sea through the Kattegat area, are dominant in most of the areas where eutrophication occurs. In 1988, the PARCOM Recommendation on reducing nutrients to the North Sea was signed by the contracting parties. This paper outlined that the inorganic nitrogen and phosphorus inputs to the coastal areas should be reduced by 50% of the 1985 concentrations (OSPAR, 1988) for those areas where nutrients cause, or are likely to cause, pollution. This decision was made because the loads in many European rivers were extremely high. OSPAR developed the Common Procedure (OSPAR CP) for the Identification of the Eutrophication Status of Maritime Areas of the Oslo and Paris Convention (1997) which was updated in 2005 (OSPAR, 2005). It provides the common framework for Contracting Parties to assess and classify the eutrophication status of the waters of the OSPAR maritime area under their jurisdiction. The reporting through OSPAR CP is a national process that also includes the report on source loads and total loads of DIN and DIP in the rivers to the OSPAR Eutrophication Committee (EUC), and OSPAR are publishing reports on nutrients inputs, nutrient concentrations, and eutrophication status in the North Sea and Skagerrak (e.g., OSPAR (2017)). Given the evidence described above the understanding of the link between runoff from land and the indicator is rated as certain.

After PARCOM there has been a significant decline in inputs of nutrients to the area, especially for phosphorous (Fig. NI42.1). A similar decrease has also been seen in atmospheric depositions (OSPAR, 2017). The decrease in nutrient inputs has led to a reduction in eutrophication in the region (Fig. NI42.2). The decrease is expected to continue, with a further decrease in Problem and Potential Problem Areas. Our understanding of the importance of change in the indicator for other parts of the ecosystem is good.

High concentrations and excess nutrients (particularly nitrogen and phosphorous) can lead to eutrophication. While eutrophication in marine systems normally is caused by elevated nutrient concentration or a skewed molar N/P-ratio deviating from 16, the direct effects of nutrient enrichment can often be seen through elevated chlorophyll concentrations, appearance of harmful algal blooms and a shift from long-lived to short-lived nuisance species such as opportunistic cyanobacteria and green macroalgae. Indirect, secondary effects may result in oxygen deficiency (hypoxia or anoxia). Enrichment of organic carbon, particularly in bottom sediments, may change the invertebrate fauna (hypoxia) or kill off sessile organism (anoxia) as larger non-sessile organisms (e.g., fish and larger invertebrates) are vacating the area (Fig. NI42.3, OSPAR (2017)).

Seasonal monitoring of the North Sea and Skagerrak regions is conducted by most countries adjoining these waters. Extensive time-series, e.g., macronutrients (nitrate, nitrite, ammonium, phosphate, silicate), dissolved oxygen and chlorophyll-biomass were started decades ago. In some regions we have equally long time-series of particulates (suspended particles, particulate organic carbon, nitrogen, and phosphorus) and dissolved organic matter (color DOM, dissolved organic nitrogen and phosphorus). Time-series of macronutrients and Chl-a biomass are probably most extensively covered in the North Sea and the Skagerrak, while other parameters are often associated with near shore, coastal monitoring programs and technically, outside the preview of this chapter. In addition, operational models within the Copernicus system are producing daily high-resolution ocean biogeochemistry analysis and forecast for the whole

Northwest shelf area (<https://marine.copernicus.eu/>).

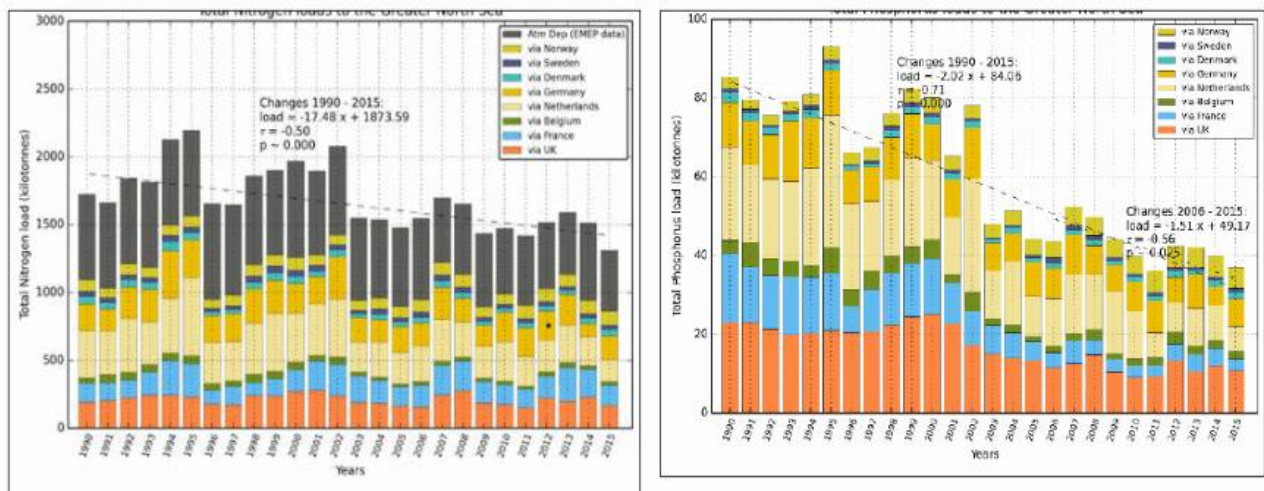


Figure NI42.1: Total nitrogen (left) and total phosphorous (right) inputs to the Greater North Sea in kilotonnes. Dashed line statistically significant ($p < 0.05$) trends. (Fig. 4.6 in OSPAR (2017))

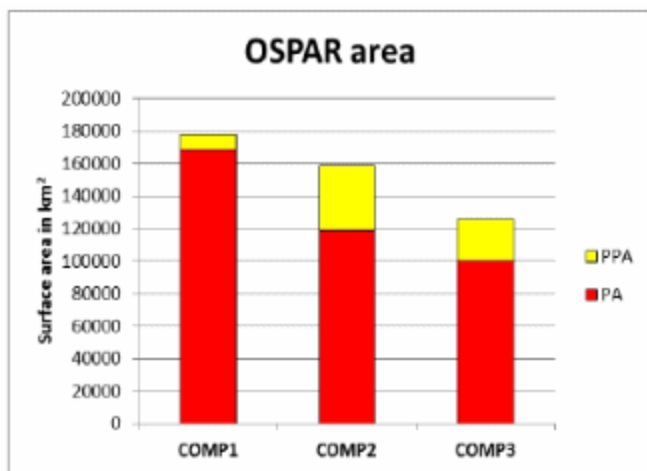


Figure NI42.2: Surface area (km²) of problem areas (PA) and potential problem areas (PPA) in the entire OSPAR area (except for Portugal and Spain) in the three applications of the Comprehensive Procedure (COMP1: 1990-2001; COMP2: 2001-2005; COMP3: 2006-2014). Fig. 4.14 in OSPAR (2017)).

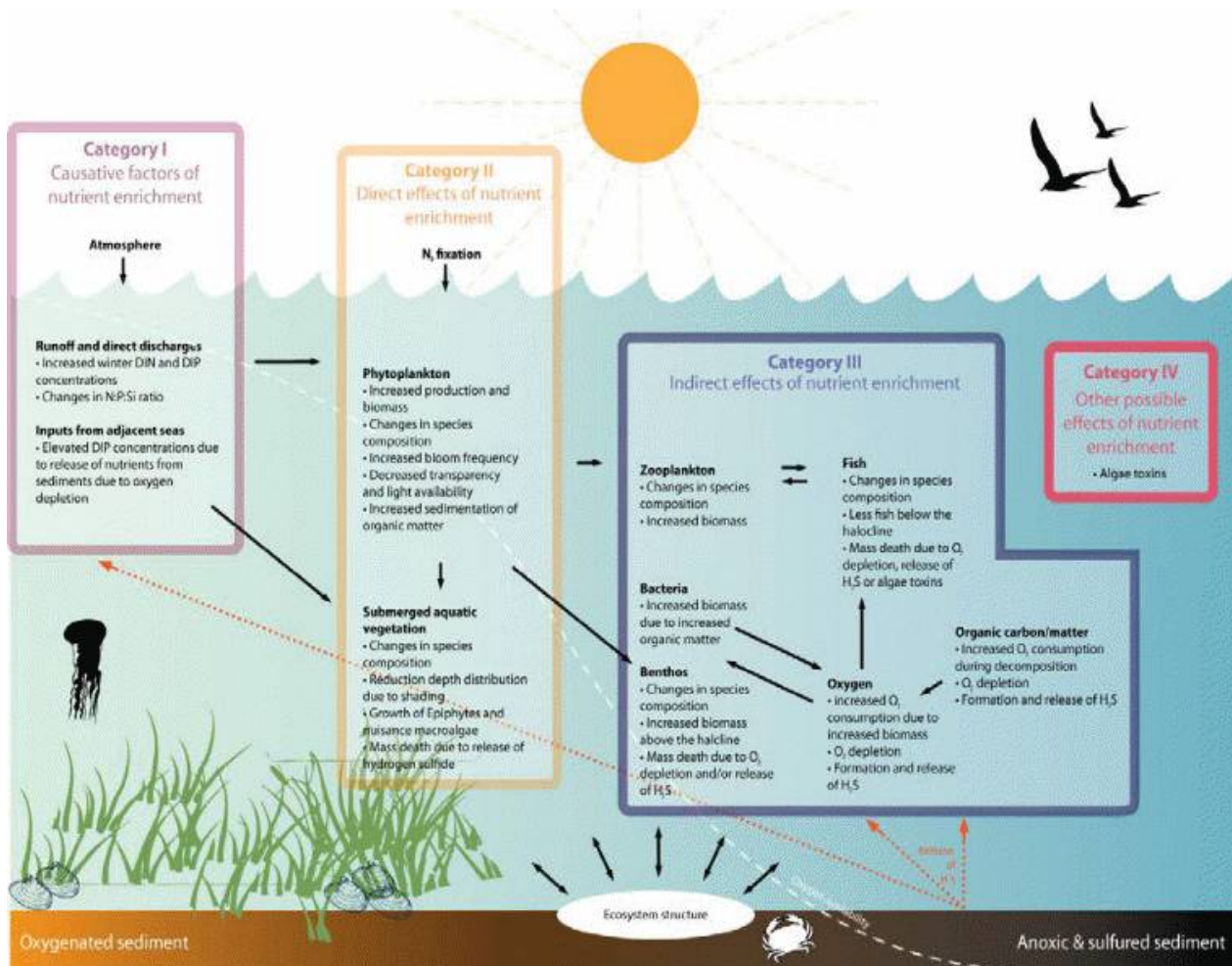


Figure NI42.3: Simplified illustration of many of the issues associated with eutrophication. DIN is dissolved inorganic nitrogen and DIP is dissolved inorganic phosphorus. N:P:Si is the ratio between nitrogen, phosphorus, and silicate (after Ferreira et al. (2011) and Fig. 1.2 in OSPAR (2017).

Light attenuation [NI43]

Phenomenon: Increase in light attenuation

Ecosystem characteristic: Abiotic factors

Under the reference condition (ca 1900) the background light attenuation (K_B) has likely been lower, and euphotic depth deeper, compared to today. The light attenuation coefficient (K , m^{-1}) describes reduction of light with depth. In coastal waters, we find a mix between clear, saline oceanic water ($K_B < 0.05$), and less clear freshwater ($K_B > 1$). Variation in the fraction, and the background light attenuation, of freshwater itself (K_{FW}), is likely the most important driver of K_B in most coastal waters. A spectrophotometer can be used to measure K_B directly, but such measurements are relatively scarce, and only available after around 1950. For longer timeseries, and better coverage, the Secchi disk depth can be used to obtain an approximation (Lee et al., 2015). For the North Sea and Skagerrak, Secchi disk depth measurements are available from 1903 with decent geographical coverage (Aarup (2002), Fig. NI43.1). Conveniently, Secchi disk depth (S , m) scales reciprocally to the total light attenuation, such that $K_S = 1.48/S$ (Lee et al., 2018). In low-phytoplankton conditions (winter), $K_S \sim K_B$. Otherwise, it is possible to correct for phytoplankton shading (K_{PHY}), $K_B = K_S - K_{PHY}$ (e.g. Opdal et al. (2019)). Several studies have suggested that the K_B in the North Sea and Skagerrak have been increasing over the last century (Dupont and Aksnes, 2013; Opdal et al., 2019), a phenomenon referred to as coastal water darkening (Aksnes et al., 2009).

The most important anthropogenic drivers of change in the indicator are likely increased freshwater runoff and increased freshwater light attenuation (K_{FW}) – both associated with climate change. Increased river runoff is caused by increased precipitation which in boreal areas is expected to increase with global warming. When more freshwater enters the coastal water, it becomes fresher and K_B increases (Aksnes et al., 2009). Higher K_{FW} is associated with increased plant growth on land (Kritzberg, 2017; Škerlep et al., 2020), which in turn is caused by improved plant growing conditions (warmer and wetter) and afforestation. More vegetation leads to more degraded plant-litter, higher concentrations of CDOM, and subsequent increase in K_{FW} . In the parts of Northern Europe that drains to the Skagerrak and North Sea, forest cover has increased with 25 %, most of which is driven by the Fennoscandian countries Norway, Sweden and Finland (Fuchs et al., 2015; Tomter, 2019). Also, a reduction in atmospheric sulphur deposition starting in the early 1980s, likely also explain parts of the latest increase in freshwater CDOM concentrations (Evans et al., 2006; Monteith et al., 2007). The understanding of the links between proposed drivers and the indicator is rated as certain.

Increased light attenuation reduces the depth to which surface light penetrates, and the euphotic depth, the depth at which 1% of the surface light is present, becomes shallower. This leads to a reduction of available habitat for organisms dependent on light, such as visual feeding fish (Aksnes, 2007), phytoplankton (Sverdrup, 1953) and macroalgae (Blain et al., 2021). In spring-bloom systems, the phytoplankton spring bloom is expected to be delayed (Opdal et al., 2019), while the maximum growing depth of kelp and seagrasses will likely become shallower (Blain et al., 2021). Secondary effects are poorly understood. To what degree the increase in light attenuation is a new phenomenon (post- 1900) or have been even higher before (pre-1900) is unknown. Both historical and paleo records suggest considerably more forest and higher CDOM concentrations in freshwater lakes before the onset of large-scale logging, livestock grazing and agricultural development in the 15th century (Meyer-Jacob et al., 2015). Our understanding of the importance of change in the indicator for other parts of the ecosystem is rated as good.

A reduction in the kelp and seagrass habitat is suggested to have ramifications for the associated fauna, including nursery habitats for a range of coastal fish species (Christie et al., 2009). It will also reduce the overall production (Blain et al., 2021). A delay in the phytoplankton spring bloom, could influence the match-mismatch dynamics between fish spawning time and the available prey for the first feeding larvae (Cushing, 1990). Increased light attenuation may provide non-visual feeders, such as jellyfish, with a competitive advantage over fish (Aksnes et al., 2009).

Monitoring by Secchi disk measurements has been adequate so far. However, in recent years, Secchi disk measurement appear to disappear from many scientific cruise protocols. These have not been replaced by alternative light- or light attenuation measurements.

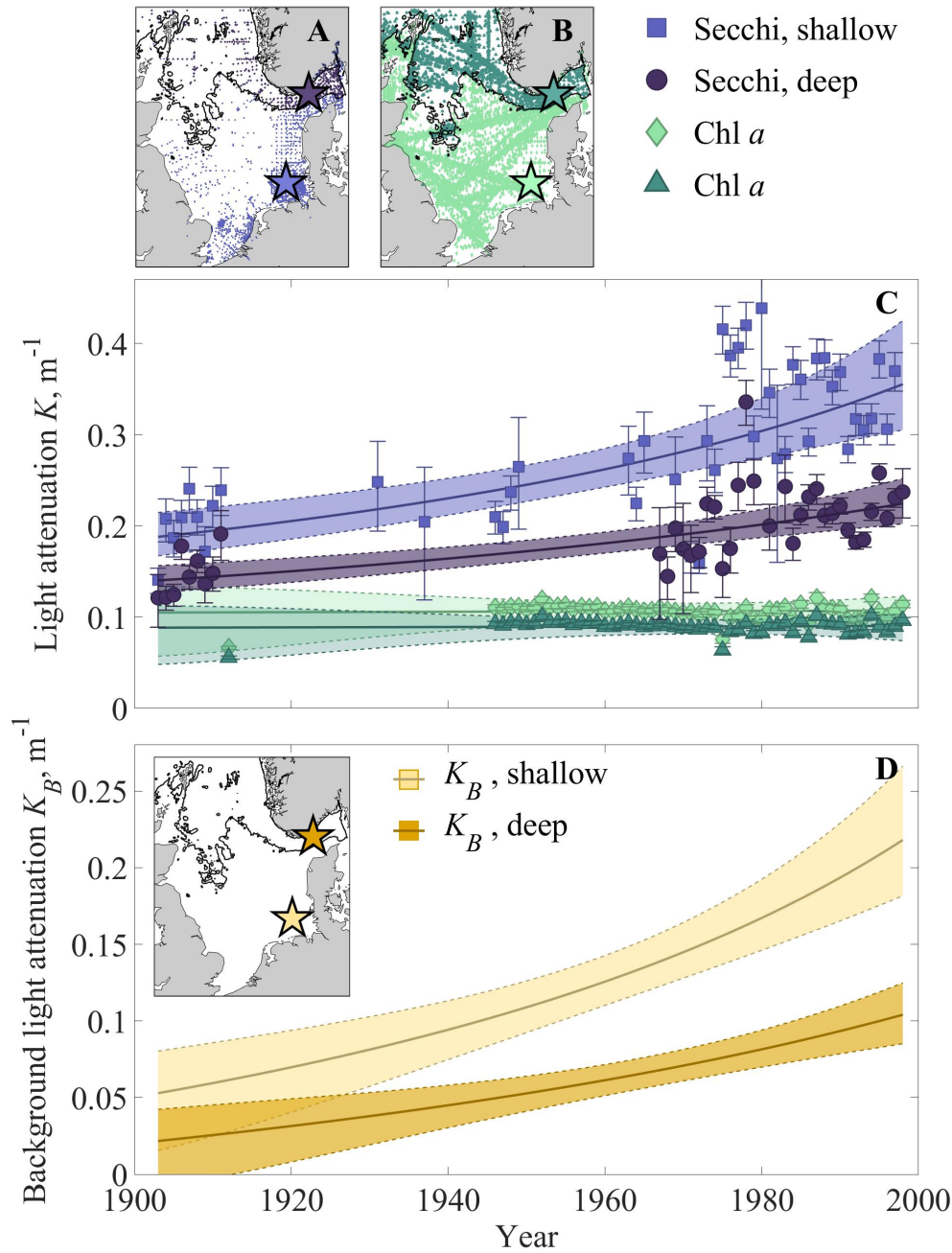


Figure NI43.1. Composite light attenuation in the shallow (<100 m) and deep (>100 m) areas of the North Sea. Panels A and B show the geographical locations of the Secchi disk and chlorophyll *a* sampling stations, respectively. The stars denote the shallow and deep location at which annual mean Secchi disk depth and chlorophyll *a* concentrations have been statistically estimated. Panel C shows light attenuation estimated from Secchi disk depth measurements (K_S) and chlorophyll *a* concentrations (K_{PHY}) at shallow and deep locations (marked with stars in top panels). Error bars denote the standard error of the mean, while blue and green lines and shading indicate mean and confidence intervals of the models. Panel D denotes the corresponding background light attenuation (K_B) for same the deep (dark brown) and shallow (light brown) locations. Modified from Opdal et al. (2019).

pH [NI44]

Phenomenon: Decreasing pH

Ecosystem characteristic: Abiotic factors

Under the reference condition, the water column is basic with a surface pH of about 8. The most important anthropogenic driver of change in the indicator is anthropogenic greenhouse gas emissions. Oceanic uptake of excess atmospheric CO₂ released by human activities, such as burning of fossil fuels and industrialisation, have increased the amount of CO₂ in the oceans over a relatively short time period. Since 1750, the oceanic pH has decreased by about 0.1 units, corresponding to a 30% increase of hydrogen ions (less basic ocean). Currently, observations of the global ocean show that pH has decreased by about 0.02 units per decade (Copernicus Marine Services, 2021). For the Nordic Seas region, pH has decreased at a faster rate relative to the global ocean by 0.002-0.003 per year in the period 1981-2019 (Fransner et al., 2022). Continued pH decrease is rated as highly likely (Pörtner et al., 2019). The understanding of the link between driver and change in the indicator is rated as certain.

Altered pH may directly affect the internal cellular processes in marine organisms, such as the ion pumps and other redox reactions. Changes in pH may also affect the availability and toxicity of vital metals, potentially changing biological production. Also, increased pCO₂ may lead to hypercapnia in fish if exceeding levels 1000 ppm (McNeil and Sasse, 2016). However, the current understanding of the effect of reduced pH on ecosystems is mainly based on acute, short term-experiments and ecosystem modelling (e.g. Browman (2016)). Hence the understanding of the importance of changes in the indicator for the ecosystem is rated as less good.

There are large knowledge gaps of the effect of reduced pH directly on marine organisms and ecosystems. The effects need to be related to studies of adaptive capacity and multi-stressors. This also requires multi-disciplinary observational long-term data sets in relevant areas (Browman, 2016).

Aragonite saturation [NI45]

Phenomenon: Decreasing aragonite saturation

Ecosystem characteristic: Abiotic factors

Under the reference condition, aragonite saturation is high enough for calcifying organisms with aragonitic shells and skeletons to occur with biomasses high enough to sustain North Sea food webs and ecological processes characterising these regional ecosystems.

The most important anthropogenic driver of change in the indicator is anthropogenic greenhouse gas emissions. Oceanic uptake of excess atmospheric CO₂ released by human activities, such as burning of fossil fuels and industrialisation, has increased the amount of CO₂ in the oceans over a relatively short time period. The oceanic carbonate ion concentration (CO₃²⁻) is driving the saturation of calcium carbonate (CaCO₃) biominerals, including aragonite, and the chemical dissolution of the CaCO₃ biominerals. Decreasing pH (from increasing ocean CO₂) has resulted in a decrease in the calcium carbonate saturation state (Ω), with consequences for the dissolution potential and calcification process. Aragonite is the most labile form of CaCO₃ in the ocean and the Nordic Seas region has shown decreased Ω of 0.012 per year in the period 1981-2019 (Fransner et al., 2022). Continued decrease of Ω is rated highly likely (Pörtner et al., 2019). The understanding of the link between driver and change in the indicator is thus rated as certain.

The lowering of CaCO₃ saturation states impacts CaCO₃ shell-forming marine organisms from plankton to benthic molluscs, echinoderms, and corals. Many calcifying species exhibit reduced calcification and growth rates in laboratory experiments under high-CO₂ conditions (e.g., Kroeker et al. (2013); Manno et al. (2017)). Another consequence is also the shoaling of aragonite saturation horizon ($\Omega < 1$) in the ocean, which will continue and has consequences for cold water corals and their ability to withstand erosion and continue to grow (ICES, 2014). At $\Omega < 1$ more energy is required by organisms to produce CaCO₃ (e.g., Comeau et al. (2013)). Climate-driven changes such as ocean warming enhance the effect of low saturation states. However, the current understanding of the effect of Ω in the ecosystem is mainly

based on acute, short term-experiments and ecosystem modelling (Browman, 2016).

Several economically important shellfish species can be weakened by ocean acidification (e.g. Agnalt et al. (2013); Andersen et al. (2013)), and this could also be the case for cold-water coral reefs that are found along the Norwegian coast (Turley et al., 2007). Cold-water corals build their structures out of aragonite and have compensation mechanisms to be able to calcify when $\Omega_{Ar} < 1$. However, the calcification rates and strength of the structures are reduced under low Ω_{Ar} (Hennige et al., 2015). Cold-water coral reefs and their ecosystems are therefore likely to be adversely affected if seawater becomes undersaturated with respect to aragonite. The cold-water coral sites in the Nordic Seas are generally located between 0 and 500m depth and currently the aragonite saturation horizon is located at greater depths, however, model projections show that shoaling of the horizon may expose cold-water reefs to corrosive waters by the end of this century (Fransner et al., 2022). Further, some non-calcareous organisms have shown to be adversely affected by changes in CO_2 or low pH, and other organisms even respond positively to high CO_2 content and low pH (Dupont and Pörtner, 2013).

There are large knowledge gaps about the thresholds and adaptive capacity of organisms to perform calcification at low saturation states in the ocean. The effect on the marine ecosystem is little understood and the effects need to be related to studies of adaptive capacity and influence of several different environmental stressors (Rastrick et al., 2018). This also requires multi-disciplinary, observational long-term data sets in relevant areas. Overall, the understanding of the importance of changes in the indicator for the ecosystem is rated as less good.

6. Ecosystem characteristics

This section describes the role that each indicator and the associated phenomena are perceived to have for the assessment of the ecosystem characteristic they are assigned to. Closely related indicators associated with the same ecosystem characteristic are described together. The description is given in a **Table 6.1**

Table 6.1. Description of the indicators per ecosystem characteristic in the North Sea, indicators gaps and justification of assessment of indicator coverage for ecosystem characteristics

Ecosystem characteristic	Indicator(s)	The role of the indicator(s) in the assessment of the ecosystem characteristic	Indicator gaps and rationale for indicator coverage assessment of the ecosystem characteristic
Primary productivity	Annual primary productivity [NI01] Timing of the spring bloom [NI02]	Annual primary productivity is a key indicator for this ecosystem characteristic, as it seeks to estimate the total input of photosynthetically fixed carbon for the ecosystem. Timing of the spring bloom can influence how the primary production matches or mismatches in time with other important ecological processes, such as reproduction in herbivorous zooplankton.	There is no indicator on species composition of phytoplankton. Variation in species composition can have impacts on other parts of the ecosystem, in particular the type of herbivorous zooplankton that dominates. There is also a lack of direct (in situ) measurements of primary production with the aim of calibrating satellite-based estimates. Given these gaps, the indicator coverage for this ecosystem characteristic is rated as partially adequate .
Biomass distribution among trophic levels	Annual primary productivity [NI01]	This indicator represents the producers (phytoplankton) in the ecosystem, making photosynthetically fixed carbon available for consumers.	Indicators on biomass of benthos and marine mammals are lacking in the assessment. This is an important gap in the indicator coverage, as these groups constitute a considerable part of the biomass at the trophic levels above secondary consumers and also partly at the level of secondary consumers. Generalist and benthivorous species (pelagic, demersal fish, but also benthos) are not included as changes in their biomass does not inform on changes in trophic flows in the system, and changes in their diet cannot be linked to drivers. However, generalist species in the North Sea constitute important biomass stocks (cod, haddock, saithe), and not including them bias our assessment of this ecosystem characteristic. Indicators on microbes are lacking altogether, meaning that there is no information on an important process such as the microbial loop. More generally, the indicators do not give a clear picture of the biomass distribution across the entire ecosystem because the biomass classifications differ too much between groups to allow for robust comparisons of biomass trends. However, the included indicators cover the most important biomass pools of the ecosystems. Given the gaps described here, the indicator coverage for this ecosystem characteristic is rated as partially adequate .
Biomass distribution among trophic levels	Herbivorous copepods [NI03] Carnivorous zooplankton [NI04]	Copepods constitute the trophic link between primary production and major other parts of the ecosystem. Whether this link mainly goes through herbivorous copepods, or whether also carnivorous species are important, can have large implications for overall energy flow in the ecosystem. This gives the background for why the development in these two indicators are important for assessing this ecosystem characteristic. In addition, it is of interest to observe whether the biomass held by zooplankton increases or decreases relative to other groups, such as fish, as such development has been observed due to strong anthropogenic impact in other ecosystems.	
Biomass distribution among trophic levels	Low trophic level fish [NI05] High trophic level fish [NI06]	These two indicators are important to understand the distribution of biomass among trophic levels as fish constitute a large portion of the biomass in the system and of the preys and predators. Understanding how the low versus high trophic level biomass changes among fish species can tell us about changes of controls (top-down, bottom-up) in the food web. It should be related to changes in biomasses of zooplankton and predators such as seabirds.	
Biomass distribution among trophic levels	High trophic level seabirds [NI07]	Fish eating seabirds are a significant part of the top predator guild in the Norwegian part of the North Sea and Skagerrak. A large relative drop in the abundance of these species could impact their role as top predators in the ecosystem and would signal negative changes at lower trophic levels.	
Functional groups within trophic levels	Holoplankton vs meroplankton [NI08]	Change in the relative abundance of holoplankton and meroplankton may affect other parts of the ecosystem. Although the general understanding of this is limited, the indicator can give information about the potential for change in other parts of the ecosystem.	
Functional groups within trophic levels	Copepod body size [NI09]	Changes in the average copepod body size is expected to alter the food web structure and the carbon transfer between trophic levels.	Relevant indicators for functions performed by phytoplankton , microbes and parasites (including virus and parasitic bacteria) are missing, for the latter group due to lack of data. Indicators are also lacking for functions performed by seabirds , marine mammals and benthos not covered by the indicator for meroplankton. Given the gaps described here, the indicator coverage for this ecosystem characteristic is rated as partially adequate .

Ecosystem characteristic	Indicator(s)	The role of the indicator(s) in the assessment of the ecosystem characteristic	Indicator gaps and rationale for indicator coverage assessment of the ecosystem characteristic
Functional groups within trophic levels	Gelatinous zooplankton [NI10]	Increasing abundances of gelatinous zooplankton may negatively affect commercially harvested fish stocks, limit bioavailable carbon to higher trophic levels and promote microbially mediated food webs.	
Functional groups within trophic levels	Fish body size [NI11] Fish life history [NI12]	The role of this set of indicators is to assess changes in size and life history traits, which are important aspects related to the functional characteristics of the demersal fish community. Changes in these indicators have implications for the turnover rates, the cycling rates, the prey-predator interactions, but also the vulnerability of the whole system to perturbations.	
Functionally important species and biophysical structures	Calanus species [NI13]	Due to species-specific differences in seasonality, life cycle and production, changes in the relative abundances of the two major <i>Calanus</i> species have major ecological impacts on the North Sea ecosystem. Because of the observed and expected effects of such changes (see phenomenon for this indicator), the indicator is assigned a higher importance in the assessment.	
Functionally important species and biophysical structures	<i>Pseudocalanus/Paracalanus</i> [NI14]	Because of their high abundance and small size, <i>Pseudocalanus</i> spp. and <i>Paracalanus</i> spp. play important roles in the trophic ecology of marine systems, for example by being prey for larval fish. Because of the observed and expected effects of such changes (see phenomenon for this indicator), the indicator is assigned a higher importance in the assessment.	There are no indicators on microbial species , which could have provided information about the microbial loop. Given the gaps described here, the indicator coverage for this ecosystem characteristic is rated as partially adequate .
Functionally important species and biophysical structures	Cod stock size [NI15] Cod recruitment [NI16]	Cod has been a functionally important species under the reference condition, and changes in the indicator may thus have substantial effects on other parts of the ecosystem. Because of the observed and expected effects of such changes (see phenomenon for these indicators), the indicators are assigned a higher importance in the assessment.	
Functionally important species and biophysical structures	Haddock stock size [NI17] Haddock recruitment [NI18]	Haddock is an important predator and prey for many species in the North Sea and large changes in the stock is likely to affect many species. Benthic invertebrates, which are major prey for haddock are likely to be more affected than fish.	
Functionally important species and biophysical structures	Saithe stock size [NI19] Saithe recruitment [NI20]	Saithe is an important predator on a variety of organisms.	
Functionally important species and biophysical structures	Lesser sandeel stock size [NI21] Lesser sandeel recruitment [NI22]	Sandeels are important prey for a variety of predators, and changes in sandeel abundance may affect several groups, including seabirds, marine mammals, and fish.	
Functionally important species and biophysical structures	Norway pout stock size [NI23] Norway pout recruitment [NI24]	Norway pout is an important prey for a variety of species	
Functionally important species and biophysical structures	Whiting stock size [NI25] Whiting recruitment [NI26]	Whiting is an important predator and prey for many species	

Ecosystem characteristic	Indicator(s)	The role of the indicator(s) in the assessment of the ecosystem characteristic	Indicator gaps and rationale for indicator coverage assessment of the ecosystem characteristic
Functionally important species and biophysical structures	Herring stock size [NI27] Herring recruitment [NI28]	Herring is an important prey for many species and changes in stock size can have considerable consequences for other parts of the ecosystem. Because of the observed and expected effects of such changes (see phenomenon for these indicators), the indicators are assigned higher importance in the assessment.	
Functionally important species and biophysical structures	Mackerel stock size [NI29] Mackerel recruitment [NI30]	Mackerel is an important predator and prey for many species and changes in stock size can have considerable consequences for other parts of the ecosystem.	
Functionally important species and biophysical structures	Northern shrimp stock size [NI31] Northern shrimp recruitment [NI32]	Shrimp is an important prey for many fish species as well as other predators, and changes in shrimp stock size may thus have consequences for other parts of the ecosystem.	
Landscape-ecological patterns	Area unimpacted by bottom trawling [NI33]	Bottom trawling reduces the biomass and biodiversity of the benthic ecosystem, may reduce the complexity of seabed habitats and affect the functioning and productivity of the benthic ecosystem. The role of the indicator is thus to assess the possible extent of these impacts.	This indicator is covering the major landscape-shaping driver in the North Sea. It could be completed by an estimation of area occupied by human infrastructures, noise or light habitats for marine species, or areas invaded by marine species. The indicator coverage for this ecosystem characteristic is therefore rated as partially adequate .
Biological diversity	Fish species vulnerable to higher temperatures [NI34]	The role of the indicator is to assess changes in abundance of fish sensitive to negative impact from climate change	Indicators are lacking for major groups, such microbial species, parasites (including parasitic bacteria and virus), phytoplankton, benthos, seabirds and marine mammals . Given these gaps, the indicator coverage for this ecosystem characteristic is rated as partially adequate .
Biological diversity	Fish species benefitting from higher temperature [NI35]	The role of the indicator is to assess changes in abundance of fish that are expected to benefit from climate change	
Biological diversity	Copepod species vulnerable to higher temperature [NI36]	The role of the indicator is to assess changes in abundance of zooplankton sensitive to negative impact from climate change	
Biological diversity	Copepod species benefitting from higher temperature [NI37]	The role of the indicator is to assess changes in abundance of zooplankton that are expected to benefit from climate change	
Biological diversity	Fish species vulnerable to fisheries [NI38]	The role of the indicator is to assess change in abundance of fish species that due to their life history can be considered vulnerable to negative impact from fisheries. These species typically also have slow recovery after population declines.	The set of indicators are covering the key aspects of the abiotic part of the ecosystem, and the indicator coverage for this ecosystem characteristic is therefore rated as adequate .
Abiotic factors	Temperature [NI39]	The role of the indicator is to assess and quantify changes in temperature over the period with available hydrographic observations 1950-2021. Because this is of high importance to key ecological processes, the indicator is assigned higher importance in the assessment.	
Abiotic factors	Stratification [NI40]	The role of the indicator is to assess changes in stratification, which is of importance for primary production	
Abiotic factors	Flow conditions [NI41]	The rate of inflow of Atlantic water is an important determinant of oceanographic conditions in the North Sea	
Abiotic factors	Nutrients [NI42]	The role of the indicator is to assess the extent of eutrophication in the North Sea	
Abiotic factors	Light attenuation [NI43]	Light attenuation may affect the timing of the spring bloom, particularly in coastal waters. Light attenuation also affects the available habitat for visually feeding predators.	
Abiotic factors	pH [NI44]	The role of the indicator is to assess changes in pH, which is affected by anthropogenic emission of greenhouse gases and can influence ecological processes	

Ecosystem characteristic	Indicator(s)	The role of the indicator(s) in the assessment of the ecosystem characteristic	Indicator gaps and rationale for indicator coverage assessment of the ecosystem characteristic
Abiotic factors	Aragonite saturation [NI45]	The role of the indicator is to assess changes in aragonite saturation, which is affected by anthropogenic emission of greenhouse gases and can influence ecological processes through impact on shell forming organisms.	

7. Assessments

The overall assessment comprises three subsections. Section 7.1 presents the assessment of the overall knowledge base, from the level of individual datasets to the level of ecosystem characteristics. Section 7.2 presents the assessment of the validity of the phenomena used, and the evidence for whether each phenomenon has occurred. Both sections form the basis for the overall assessment (Section 7.3) of the ecological condition of each ecosystem characteristic (based on their indicators and associated phenomena) and of the ecosystem as a whole (based on the condition of their characteristics).

7.1 Assessment of the knowledge base

The overall assessment of the knowledge base is presented in tabular form (Table 7.1). In accordance with PAEC, the knowledge base is assessed at three levels: *Data level*, *indicator level*, and *ecosystem characteristic level*.

1. At a *data level*, we summarise the spatial (SR) and temporal (TR) representativity of the datasets for each individual indicator.
 - a. The spatial representativity (SR) of *each dataset* relative to the target ecosystem (Ch. 3) is determined by the sampling design employed (design-based, model-based, no design). Design-based sampling is evaluated based on three criteria: 1) whether the entire population is included in the sampling (SRd), 2) whether sampling is based on randomisation (SRd2), and 3) whether there is a known probability of including each sampling unit (SRd3). Model-based sampling (SRm) is evaluated based on just one criterium; whether sampling is based on a model (i.e., a sampling design) that is relevant for the indicator or phenomenon in question. It should be noted that randomization is generally not used in the datasets used in this assessment, where the design is to cover everything, e.g., all grid cells in a regular grid, all known seal breeding sites. In these cases, SRd2 (design-based sampling based on randomization) is assessed as fulfilled.
 - b. The temporal representativity (TR) of *each dataset* relative to a relevant temporally defined reference condition. A temporally defined reference condition includes explicit definitions (e.g., the reference condition equals the condition of the ecosystem at a particular point in time), and implicit definitions (e.g., the reference condition equals the condition of the ecosystem in, for instance, a preindustrial climate). It should be noted that the reference condition chosen for this assessment, “intact nature”, is not temporally defined (except for climate), and that different time periods are considered representative for different indicators depending on the history of anthropogenic impact on each indicator (see Ch. 2). Temporal representativity is evaluated with respect to 1) years (TRyr; the length of the time series relative to relevant dynamics and any temporally defined reference conditions), and 2) seasonality (TRse; whether relevant seasonality is taken into account in the sampling). For TRyr we interpret that the time series should cover a time period with reference condition (intact nature) for the indicator to be assessed as adequate.
2. At an *indicator level* we assess the indicator’s total data coverage based on the overall assessment of spatial (SRtotal) and temporal (TRtotal) representativity of each dataset included.
3. At an *ecosystem characteristic level*, we assess indicator coverage for the entire *characteristic*. This reflects the degree to which the set of indicators on which the assessment is based has sufficient coverage and relevance for assessment of the condition of the ecosystem characteristic. Justifications for these assessments are found in Table 6.1.

All assessments are assigned to clearly defined colour-coded categories (Fig. 7.1) as specified in the technical protocol (Jepsen et al. 2020). Each individual assessment is justified in an endnote, which can be found in Appendix 8.3.

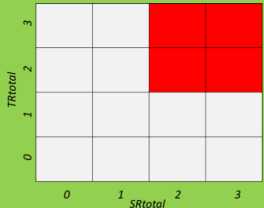
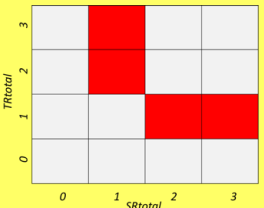
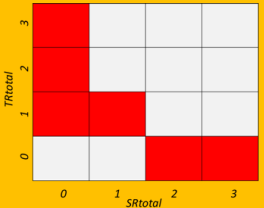
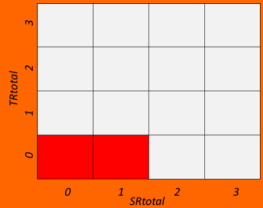
		Categories			
Spatial Representativity (SR)	SRd1	Fulfilled : Design-based sampling where the entire sampling population has a possibility of being included.		Not fulfilled : Design-based sampling where only a SUBSET of the sampling population has a possibility of being included.	
	SRd2	Fulfilled : Design-based sampling based on randomisation.		Not fulfilled : Design-based sampling NOT based on randomisation.	
	SRd3	Fulfilled : Design-based sampling, with known probability of including each sampling unit.		Not fulfilled : Design-based sampling, with UNKNOWN probability of including each sampling unit.	
	SRm	Fulfilled : Model-based sampling based on a model that is relevant for the indicator and the phenomenon in question.		Not fulfilled : Model-based sampling based on a model that is NOT relevant for the indicator and the phenomenon in question.	
	SRtotal	Category 3 : SRm fulfilled with an adequate sample size OR S Rd1 -S Rd3 all fulfilled.	Category 2 : SRm fulfilled with a limited sample size OR two of S Rd1 -S Rd3 fulfilled.	Category 1 : SRm not fulfilled, one of S Rd1 -S Rd3 fulfilled.	Category 0 : SRm not fulfilled, none of S Rd1 -S Rd3 fulfilled.
Temporal Representativity (TR)	TRyr	Adequate : A long time series relative to relevant dynamics. In case of a temporally defined reference condition, time series is partly or fully overlapping with the reference period.		Partially adequate : A long time series relative to relevant dynamics. In case of a temporally defined reference condition, time series are NOT overlapping with the reference period.	
	TRse	Adequate : Seasonal variability is relevant and taken into account in the sampling OR seasonal variability is not relevant.		Inadequate : Seasonal variability is relevant, but not, or to a very limited degree taken into account in the sampling.	
	TRtotal	Category 3 : Both TRyr and TRse are Adequate.	Category 2 : TRyr Adequate and TRse Inadequate OR TRyr Partially adequate and TRse Adequate.	Category 1 : TRyr Inadequate and TRse Adequate OR TRyr Partially adequate and TRse Inadequate.	Category 0 : Both TRyr and TRse Inadequate.
Data coverage	DC	Very good:  Good:  Intermediate:  Poor: 			
Indicator coverage	IC	Adequate : The set of indicators represent the major aspects of the ecosystem characteristic with no obvious shortcomings.		Partially adequate : The set of indicators has certain shortcomings which might limit our ability to assess the condition of the ecosystem characteristic.	
				Inadequate : The set of indicators has severe shortcomings which will definitely limit our ability to assess the condition of the ecosystem characteristic.	

Figure 7.1. Summary of the assessment criteria and colour coding for the knowledge base used in PAEC.

Table 7.1. Assessment of the knowledge base for the datasets, indicators and ecosystem characteristics for the North Sea. See Appendix 8.1 for footnotes. See Table 6.1 for justification of assessment of indicator coverage for ecosystem characteristics.

DATA						INDICATOR			ECOSYSTEM CHARACTERISTIC	
Dataset ID	Spatial representativity (SR)					Temporal representativity (TR)			Data coverage	Indicator coverage
	SRd1	SRd2	SRd3	SRm	SRtotal	TRyr	TRse	TRtotal	DC	IC
D01	1	2	3	4		5	6		Annual primary productivity [NI01]	Primary production (7)
D01	1	2	3	4		5	6		Timing of the spring bloom [NI02]	Primary production (7)
D02	8	9	10	11		12	13		Herbivorous copepods [NI03]	Biomass distribution among trophic levels
D02	8*	9	10	11		12	13		Carnivorous zooplankton [NI04]	Biomass distribution among trophic levels
D03	14	15	16	17		18	19		Low trophic level fish [NI05]	Biomass distribution among trophic levels
D03	14	15	16	17		18	19		High trophic level fish [NI06]	Biomass distribution among trophic levels
D12	20	21	22	23		24	25		High trophic level seabirds [NI07]	Biomass distribution among trophic levels
D02	8	9	10	11		12	13		Holoplankton vs meroplankton [NI08]	Functional groups within trophic levels
D02	8	9	10	11		12	13		Copepod body size [NI09]	Functional groups within trophic levels
D03	14	15	16	17		18	19		Gelatinous zooplankton [NI10]	Functional groups within trophic levels
D03	14	15	16	17		18	19		Fish body size [NI11]	Functional groups within trophic levels
D03	14	15	16	17		18	19		Fish life history [NI12]	Functional groups within trophic levels
D02	8	9	10	11		12	13		<i>Calanus</i> species [NI13]	Functionally important species and biophysical structures
D02	8	9	10	11		12	13		<i>Pseudocalanus</i> / <i>Paracalanus</i> species [NI14]	Functionally important species and biophysical structures
D04	26	27	28	29		30	31		Cod stock size [NI15]	Functionally important species and biophysical structures
D04	32	33	34	35		36	37		Cod recruitment [NI16]	Functionally important species and biophysical structures
D05	38	39	40	41		42	43		Haddock stock size [NI17]	Functionally important species and biophysical structures
D05	44	45	46	47		48	49		Haddock recruitment [NI18]	Functionally important species and biophysical structures
D06				50		51	52		Saithe stock size [NI19]	Functionally important species and biophysical structures
D06	53	54	55	56		57	58		Saithe recruitment [NI20]	Functionally important species and biophysical structures
D07				59		60	61		Lesser sandeel stock size [NI21]	Functionally important species and biophysical structures
D07	62	63	64	65		66	67		Lesser sandeel recruitment [NI22]	Functionally important species and biophysical structures
D08	68	69	70	71		72	73		Norway pout stock size [NI23]	Functionally important species and biophysical structures
D08	74	75	76	77		78	79		Norway pout recruitment [NI24]	Functionally important species and biophysical structures
D09	80	81	82	83		84	85		Whiting stock size [NI25]	Functionally important species and biophysical structures
D09	86	87	88	89		90	91		Whiting recruitment [NI26]	Functionally important species and biophysical structures
D10				92		93	94		Herring stock size [NI27]	Functionally important species and biophysical structures
D10	95	96	97	98		99	100		Herring recruitment [NI28]	Functionally important species and biophysical structures
D10	101	102	103	102		104	105		Mackerel stock size [NI29]	Functionally important species and biophysical structures

DATA									INDICATOR	ECOSYSTEM CHARACTERISTIC
Dataset ID	Spatial representativity (SR)					Temporal representativity (TR)			Data coverage	Indicator coverage
	SRd1	SRd2	SRd3	SRm	SRtotal	TRyr	TRse	TRtotal	DC	IC
D10	106	107	108	107		109	110		Mackerel recruitment [NI30]	Functionally important species and biophysical structures
D19	111	112	113	114		115	116		Northern shrimp stock size [NI31]	Functionally important species and biophysical structures
D19	111	112	113	114		117	116		Northern shrimp recruitment [NI32]	Functionally important species and biophysical structures
D20	118	119	120	121		122	123		Area unimpacted by bottom trawling [NI33]	Landscape-ecological patterns
D03	14	15	16	17		18	19		Fish species vulnerable to higher temperature [NI34]	Biological diversity
D03	14	15	16	17		18	19		Fish species benefiting from higher temperature [NI35]	Biological diversity
D02	8	9	10	11		12	13		Copepod species vulnerable to higher temperature [NI36]	Biological diversity
D02	8	9	10	11		12	13		Copepod species benefiting from higher temperature [NI37]	Biological diversity
D02	14	15	16	17		18	19		Fish species vulnerable to fisheries [NI38]	Biological diversity
D13	124	125	126	127		128	129		Temperature [NI39]	Abiotic factors
D14	130	131	132	133		134	135		Stratification [NI40]	Abiotic factors
D15	136	137	138	139		140	141		Flow conditions [NI41]	Abiotic factors
D16	142	143	144	145		146	147		Nutrients [NI42]	Abiotic factors
D17	148	149	150	151		152	153		Light attenuation [NI43]	Abiotic factors
D18	154	155	156	157		158	159		pH [NI44]	Abiotic factors
D18	160	161	162	163		164	165		Aragonite saturation [NI45]	Abiotic factors

7.2 Assessment of the phenomena

The assessment of the phenomena consists of an assessment of the validity of each phenomenon (VP), and an assessment of the level of evidence that a given phenomenon has occurred (EP). VP and EP are scored according to predefined categories (Fig. 7.2) and presented in Table 7.2. In the table, the columns for VP and EP are colour-coded to present a relatively quick overview of phenomena of higher and lower validity, and the level of evidence for their occurrence.

Validity of Phenomenon (VP)	Evidence for Phenomenon (EP)
High : A CERTAIN link to relevant drivers, and a GOOD understanding of the role of the indicator in the ecosystem.	High : High level of evidence that the expected changes in the indicator have occurred. High (expected or observed) ecosystem significance of observed changes.
Intermediate : A LESS CERTAIN link to relevant drivers, and a GOOD understanding of the role of the indicator in the ecosystem OR A CERTAIN link to relevant drivers, and a LESS GOOD understanding of the role of the indicator in the ecosystem.	Intermediate : High level of evidence that the expected changes in the indicator have occurred. Limited (expected or observed) ecosystem significance of observed changes.
	Low : Low level of evidence that the expected changes in the indicator have occurred. Low or no (expected or observed) ecosystem significance of observed changes.
Low : A LESS CERTAIN link to relevant drivers, and a LESS GOOD understanding of the role of the indicator in the ecosystem.	None : No evidence that the expected changes in the indicator have occurred (sufficient data).
	Insufficient : No evidence that the expected changes in the indicator have occurred (insufficient data).

Figure 7.2. The criteria and color coding used in the assessment of the phenomena (Table 7.2.).

Table 7.2. Assessment of the phenomena in the North Sea. For definitions of categories and criteria see Fig. 7.2. The assessment of the evidence of the phenomenon, EP, can vary in different areas of the ecosystem being assessed and therefore two columns are presented. Details on VP are found under the phenomena description for each indicator in section 5.1.

Ecosystem characteristic	Indicator	Phenomenon [ID]	Validity of Phenomenon (VP)	Evidence for Phenomenon (EP)	Comments EP
Primary productivity	Annual primary productivity [NI01]	Increasing annual primary productivity [NP01]	High	None	There is no evidence of a net change over the entire length of the time series.
Primary productivity	Timing of the spring bloom [NI02]	Change in the spring bloom timing [NP02]	Intermediate	None	There is a tendency towards an earlier start of the spring bloom over the entire length of the time series. However, this trend seems to be driven by the high value in 2006, and the time series is otherwise short and has missing values. It is thus hard to evaluate the interannual variability and whether this value of 2006 is exceptional or not. In addition, the confidence intervals are large independently of the statistical method employed and include the slope 0. There is thus no evidence of a change in the spring bloom timing.
Biomass distribution among trophic levels	Annual primary productivity [NI01]	Increasing annual primary productivity [NP01]	High	None	See above
Biomass distribution among trophic levels	Herbivorous copepods [NI03]	Decreasing abundance of herbivorous copepods [NP03]	Intermediate	High	There is a clear decline in the time series, which is seen also when the data are split into small (which contribute most to the overall pattern) and large species. The pattern for the large group is driven by <i>Calanus</i> I-IV and by <i>Acartia</i> and <i>Para/Pseudocalanus</i> for the small group. For both <i>Calanus</i> and <i>Para/Pseudocalanus</i> , the declines can be linked to climate change, for the former through a direct effect of temperature and possibly advection and for the latter through reduced primary production in the summer and autumn. As the change is also expected to have considerable consequences for other parts of the ecosystem, the evidence for the phenomenon is rated as high.
Biomass distribution among trophic levels	Carnivorous zooplankton [NI04]	Increasing abundance of carnivorous zooplankton [NP04]	Intermediate	Insufficient	CPR is not sampling carnivorous zooplankton well as they may avoid be sampled due to generally larger body size than herbivorous and omnivorous species (the opening of the CPR sampler is fairly small, thus not sampling larger organisms well). They also generally reside deeper in the water column than the CPR sampling depth.
Biomass distribution among trophic levels	Low trophic level fish [NI05]	Change in biomass of LTL fish [NP05]	Intermediate	None	There is a slight increase in biomass of low trophic level species according to the indicator time series, but the slope confidence interval includes 0, so we cannot say that there is a trend over this time period. There is thus no evidence of change in this indicator.
Biomass distribution among trophic levels	High trophic level fish [NI06]	Decreasing biomass of HTL fish [NP06]	Intermediate	None	The linear trend shows a slight decrease, but the slope confidence interval includes 0, so we cannot say that there is a trend over this time period. There is thus no evidence of change in this indicator.
Biomass distribution among trophic levels	High trophic level seabirds [NI07]	Decline in populations of piscivorous surface feeding seabirds [NP07]	High	High	The data show a strong long-term (40 years) decline in all populations of piscivorous surface-feeding seabirds except great black-backed gull. The declines can be attributed to anthropogenic drivers and are assessed to have significant effects on other parts of the ecosystem. The evidence for the phenomenon is thus assessed as high.
Functional groups within trophic levels	Holoplankton vs meroplankton [NI08]	Changes in Meroplankton vs. Holoplankton composition [NP08]	Intermediate	Intermediate	There is a clear decline in the time series that can be attributed to a positive effect of increasing temperature on larval abundance of the echinoderm <i>Echinocardium cordatum</i> . There are considerable uncertainties about consequences of the changes for other parts of the ecosystem, and the evidence for the phenomenon is therefore rated as intermediate.

Ecosystem characteristic	Indicator	Phenomenon [ID]	Validity of Phenomenon (VP)	Evidence for Phenomenon (EP)	Comments EP
Functional groups within trophic levels	Copepod body size [NI09]	Reduced average copepod community body size [NP09]	High	Intermediate	There is a decline in abundance among both small and large copepods, with the large declining more rapidly than the small, resulting in an overall tendency for a decline for the ratio of abundance of large to small species. The decline in the large group is driven by <i>Calanus</i> I-IV and in the small group by <i>Acartia</i> and <i>ParalPseudocalanus</i> . The declines of both of these groups can be linked to climate change (see evaluation of phenomenon for NI03). A development towards smaller copepods is expected to have consequences in the ecosystem, for example for fish larvae. It should be noted that the data only measures change in size as a result of changes in relative species composition and that any changes within species are not measured. Given these points, the evidence for the phenomenon is rated as intermediate
Functional groups within trophic levels	Gelatinous zooplankton [NI10]	Increasing abundances of gelatinous zooplankton [NP10]	Low	Insufficient	As there is no protocol for sampling of gelatinous zooplankton in the parts of the IBTS covering the Norwegian sector of the North Sea and the time series is short, it is considered that the data are insufficient to assess the evidence of this phenomenon
Functional groups within trophic levels	Fish body size [NI11]	Decreasing fish community mean body size [NP11]	High	None	There is large interannual variability in fish community weighed body size. The linear trend is decreasing slowly, and the confidence interval of the slope shows that there might be no trend. There is thus no evidence of change in this indicator.
Functional groups within trophic levels	Fish life history [NI12]	Decreasing proportion of slow-life species and increasing proportion of fast life species [NP12]	Low	None	All three slope confidence intervals include 0 and the obtained trends are very low. There is thus no evidence of change in this indicator.
Functionally important species and biophysical structures	<i>Calanus</i> species [NI13]	Decrease in abundance of <i>C. finmarchicus</i> relative to abundance of <i>C. helgolandicus</i> [NP13]	High	High	There is a clear decline in the abundance of <i>C. finmarchicus</i> relative to that of <i>C. helgolandicus</i> . The time series of <i>C. helgolandicus</i> shows the most pronounced change (a significant increase), while the change in <i>C. finmarchicus</i> abundance is less pronounced (a decline that is not statistically significant). It should be noted that the decline of the latter species is less pronounced in the Norwegian sector of the North Sea than in other parts, probably due to advection from the Norwegian Sea and overwintering part of the population in the Norwegian Trench. The consequences of the changes for the other parts of the ecosystem are well documented and the evidence for the phenomenon this assessed as high.
Functionally important species and biophysical structures	Pseudocalanus/Paracalanus species [NI14]	Declining abundance of Pseudocalanus spp. and Paracalanus spp. [NP14]	High	High	There is clear decline in the time series that can be attributed to effects of climate change. Together, the two taxa constitute the most important group of copepods for higher trophic levels after the <i>Calanus</i> species, and the expected consequences of the changes for other parts of the ecosystem are there considered to be large, and the evidence of the phenomenon assessed as high.
Functionally important species and biophysical structures	Cod stock size [NI15]	Decreasing cod stock size [NP15]	High	High	Strong fisheries pressure brought the stock to low levels until the late 1990s. Climate change might currently limit the recovery of the stock (thermal pressure), also driving northward displacement out of the North Sea. There is thus high evidence of decreasing stock size because of human activities
Functionally important species and biophysical structures	Cod recruitment [NI16]	Decreasing cod recruitment [NP16]	Low	Intermediate	Interannual variability has largely decreased since the late 1990s likely due to climate change (Beaugrand et al., 2003; Beaugrand and Kirby, 2010). There is thus high evidence of decrease of the recruitment away from reference conditions. Although the impact on the ecosystem is potentially high (niche replacement by haddock, importance of juveniles as food items), there are considerable uncertainties about this, and the evidence for the phenomenon is therefore rated as intermediate.
Functionally important species and biophysical structures	Haddock stock size [NI17]	Decreasing haddock stock size [NP17]	Intermediate	Low	SSB was higher and very variable before 2005. It has stabilized at lower levels since then but is now peaking because of good recruitment in 2019-2020. There is thus low evidence of a decline in haddock SSB.

Ecosystem characteristic	Indicator	Phenomenon [ID]	Validity of Phenomenon (VP)	Evidence for Phenomenon (EP)		Comments EP
Functionally important species and biophysical structures	Haddock recruitment [NI18]	Decreasing haddock recruitment [NP18]	Low	Intermediate		According to the assessment, the recruitment has decreased strongly over the last 50 years. The low level in the 2000s is likely linked to fishing and/or climate change. However, the drivers of the current state of haddock recruitment are hard to identify. The consequences for the ecosystem are not well understood, therefore the evidence for the phenomenon is assessed as intermediate.
Functionally important species and biophysical structures	Saithe stock size [NI19]	Decreasing saithe stock size [NP19]	Intermediate	Low		Although the overall trend is showing a decline when including the gadoid outburst, the recent trend is rather flat and stable. The low biomass of the last 10 years is concomitant with low recruitment. Moreover, due to little evidence of isolation from adjacent stocks, and the high mobility of saithe, it cannot be discounted that this may be linked to changes of the population spatial distribution (changing overlap between the population and the management unit domain). There is thus low evidence for a decline in Saithe SSB caused by anthropogenic activities.
Functionally important species and biophysical structures	Saithe recruitment [NI20]	Decreasing saithe recruitment [NP20]	Low	Intermediate		There is quite high evidence of a decline in saithe recruitment, and a decrease in interannual variability, but the consequences for the ecosystem are not well understood. There is thus intermediate evidence of a decline in saithe recruitment as a consequence of anthropogenic activities.
Functionally important species and biophysical structures	Lesser sandeel stock size [NI21]	Decreasing lesser sandeel stock size [NP21]	High	None	High	Recent management alleviated the fishing pressure and good recruitment has allowed a recovery of the stock. However, in section 5r, fishing on sandeel is prohibited as the stock size is very low and do not seem to recover. There is thus no evidence of recent decline of lesser sandeel stock size due to anthropogenic drivers in the sector 3r, but high evidence in sector 5r.
Functionally important species and biophysical structures	Lesser sandeel recruitment [NI22]	Decreasing lesser sandeel recruitment [NP22]	Intermediate	None	Insufficient	The period of low recruitment between 2000 and 2010 is likely due to overfishing. In the most recent decade, the interannual variability of recruitment is large, and the trend over the time period is not strong. There is thus no evidence of a decrease in lesser sandeel recruitment in sector 3r. Since no data are available for sector 5r, there is insufficient evidence for a decrease in recruitment of lesser sandeel in this sector.
Functionally important species and biophysical structures	Norway pout stock size [NI23]	Stable Norway pout stock size [NP23]	Intermediate	Low		There are no strong signs of increase or decrease in the Norway pout. However, interannual variation cast large uncertainties around that statement, and the stock is currently recovering from high fishing pressure before 2000s. There is low evidence for a stable stock size of Norway pout.
Functionally important species and biophysical structures	Norway pout recruitment [NI24]	Stable Norway pout recruitment [NP24]	Low	Low		There are no strong signs of increase or decrease in the Norway pout recruitment. However, interannual variation cast large uncertainties around that statement, and the stock is currently recovering from high fishing pressure before 2000s. There is low evidence for a stable recruitment of Norway pout.
Functionally important species and biophysical structures	Whiting stock size [NI25]	Decreasing whiting stock size [NP25]	Intermediate	None		The first years of the time series may cover the end of the gadoid outburst, after which the whiting SSB continues a slower decrease until the 2010s, without strong ties to fishing pressure. The current SSB trend is increasing and there is no strong evidence of it being driven by anthropogenic pressure. Whiting remains a low-interest stock with little targeted fishing.
Functionally important species and biophysical structures	Whiting recruitment [NI26]	Decreasing whiting recruitment [NP26]	Low	Low		The earliest years had the highest recruitment estimates, which in turn influenced the slope. While there is high interannual variability in whiting recruitment, no significant downward trend can be seen. There is thus low evidence of a decrease in whiting recruitment resulting from anthropogenic impacts.

Ecosystem characteristic	Indicator	Phenomenon [ID]	Validity of Phenomenon (VP)	Evidence for Phenomenon (EP)	Comments EP
Functionally important species and biophysical structures	Herring stock size [NI27]	Decreasing herring stock size [NP27]	High	Intermediate	The initial decline is likely due to fisheries up to the late 1970s. Species interactions but also climate change (since 2000s: change in zooplankton community, new predators) could be hampering the recovery of the stock despite better management. Impact on the ecosystem might have occurred during the 1980s, but there is high uncertainty about this. There is thus intermediate evidence for the decline of herring SSB.
Functionally important species and biophysical structures	Herring recruitment [NI28]	Decreasing herring recruitment [NP28]	Intermediate	Intermediate	Low levels of SSB are associated with low recruitment in the late 1970s (probably fisheries driven) and since the 2000s the recruitment is at a lower level (likely linked to climate change). This has a known impact on herring SSB. The evidence for decline of herring recruitment is thus intermediate.
Functionally important species and biophysical structures	Mackerel stock size [NI29]	Decreasing mackerel stock size [NP29]	Intermediate	Intermediate	The early decline is likely linked to overfishing. Prolonged overfishing in recent years is hidden by good recruitment and year classes, but the stock size should be higher with less fishing (WGWIDE report). There is thus intermediate evidence for this phenomenon
Functionally important species and biophysical structures	Mackerel recruitment [NI30]	Change in mackerel recruitment [NP30]	Low	Low	After the 2000s, recruitment has improved, maybe because of climate change, but the processes are uncertain. The evidence of the phenomenon is thus assessed as low.
Functionally important species and biophysical structures	Northern shrimp stock size [NI31]	Decreasing shrimp stock size [NP31]	High	Intermediate	The current stock size is very low compared to what is estimated 120 years ago. Predators' stocks are low, and higher shrimp stock levels would be expected under such conditions. Current low recruitment might be driving the low stock size. Fishing pressure is also higher now than in the past. There is high level of evidence that the expected changes have occurred.
Functionally important species and biophysical structures	Northern shrimp recruitment [NI32]	Decreasing shrimp recruitment [NP32]	Low	Intermediate	Productivity level in the stock is now lower than expected under reference conditions. Low recruitment started to occur before the stock size decreased, so the fishing mortality might not be at levels where it becomes problematic for the recruitment. It is uncertain what is driving the current low levels of recruitment. There is thus intermediate evidence for the phenomenon.
Landscape-ecological patterns	Area unimpacted by bottom trawling [NI33]	Decreasing area unimpacted by bottom trawling [NP33]	High	High	There is clear evidence that a significant part of the assessment area is impacted by bottom trawling. This is expected to have major ecosystem consequences. The evidence for the phenomenon is thus rated as high.
Biological diversity	Fish species vulnerable to higher temperature [NI34]	Decreasing biomass of fish vulnerable to higher temperatures [NP34]	Intermediate	None	The biomass of cold-water species has decreased and then increased over the period covered by the time series. The trend is negative, but the confidence interval of the slope includes 0. There is thus no evidence of decrease for this indicator.
Biological diversity	Fish species benefiting from higher temperature [NI35]	Increasing biomass of fish species benefitting from higher temperature [NP35]	Intermediate	None	There is only a slight increase in the biomass of warm-water species. The trend is positive, but the confidence interval of the slope includes 0. There is thus no evidence of increase for this indicator

Ecosystem characteristic	Indicator	Phenomenon [ID]	Validity of Phenomenon (VP)	Evidence for Phenomenon (EP)	Comments EP
Biological diversity	Copepod species vulnerable to higher temperature [NI36]	Decrease in number of species sensitive to higher temperatures [NP36]	Intermediate	Low	There is a tendency for a decline in the time series, but the trend is not significant as the confidence interval for the regression coefficient in the linear model includes 0. There are uncertainties associated with the consequences of the change in the indicator for other parts of the ecosystem. Thus, the evidence for the phenomenon is assessed as low.
Biological diversity	Copepod species benefiting from higher temperature [NI37]	Increase in number of "Warm-water species" [NP37]	Intermediate	Low	There is a tendency for an increase in the time series, but the trend is not significant as the confidence interval for the regression coefficient in the linear model includes 0. There are uncertainties associated with the consequences of the change in the indicator for other parts of the ecosystem. Thus, the evidence for the phenomenon is assessed as low.
Biological diversity	Fish species vulnerable to fisheries [NI38]	Decreasing biomass of fish species vulnerable to fisheries [NP38]	High	None	The biomass of fisheries-sensitive species has decreased and then increased over the period. The trend is negative, but the confidence interval of the slope includes 0. There is thus no evidence of decrease for this indicator
Abiotic factors	Temperature [NI39]	Warming of the water column [NP39]	High	High	High evidence of an increase in temperature that can be linked to anthropogenic impact on the climate and high level of evidence of both observed and expected changes in the ecosystem as a consequence of this.
Abiotic factors	Stratification [NI40]	Increasing stratification of the upper water column [NP40]	High	None	There is no evidence of increased stratification. Rather the evidence points towards a decrease. It should be noted that the data can be strongly influenced by atmospheric conditions (wind) and the coverage of the survey, and thus exhibit large natural year to year variation.
Abiotic factors	Flow conditions [NI41]	Increasing inflow of Atlantic water to the North Sea [NP41]	Intermediate	None	There is no evidence of an overall increase in the indicator when looking at the whole time series.
Abiotic factors	Nutrients [NI42]	Increasing concentration of nutrients [NP42]	High	None	There is a decline in both time series (PO4 and NO2-NO3, respectively), thus indicating a development towards rather than away from the reference condition. This is clearly linked to decreased anthropogenic impact through runoff from land, which has also had impact on other parts of the ecosystem, such as decreased chlorophyll concentrations.
Abiotic factors	Light attenuation [NI43]	Increase in light attenuation [NP43]	High	Intermediate	There is a statistically significant increase in light attenuation through the time series. This is seen in a statistical model where the effects of season and position of sampling is taken into account (Opdal et al., 2019). The time series shown in the appendix do not go beyond year 2000. Unpublished results from an updated time series shows that the increase may have levelled off during the last two decades (Opdal, pers. comm.). As the knowledge of the consequences of change in the indicator for the rest of ecosystem is rated as less good, the overall assessment of EP is set to intermediate.
Abiotic factors	pH [NI44]	Decreasing pH [NP44]	Intermediate	Intermediate	Despite a short time series, there is a clear decreasing trend in pH. As there are considerable uncertainties about the consequences of this for other parts of the ecosystem, the evidence for the phenomenon is rated as intermediate.
Abiotic factors	Aragonite saturation [NI45]	Decreasing aragonite saturation [NP5]	Intermediate	Intermediate	Despite a short time series, there is a clear decreasing trend in aragonite saturation. As there are considerable uncertainties about the consequences of this for other parts of the ecosystem, the evidence for the phenomenon is rated as intermediate.

7.3 Assessment of ecosystem condition

Following the PAEC protocol (Jepsen et al., 2020), the assessment of ecosystem condition consists of the following sections: an assessment of each ecosystem characteristics based on all associated phenomena (Ch. 7.3.1); an assessment of the ecosystem as a whole (Ch. 7.3.2); a discussion of likely future trajectories in the condition of the ecosystem (Ch. 7.3.3); and recommendations for further monitoring and research in order to improve future assessments of the condition of the ecosystem (Ch. 7.3.4).

7.3.1 Assessment of the condition of individual ecosystem characteristics

In this chapter we present the assessment of the condition of each of the seven selected ecosystem characteristics. The assessment is supported by 1) Appendix 8.1, which provide time-series plots and trend analyses for each indicator, and 2) the PAEC assessment diagrams (Fig. 7.3.1). The diagrams summarize information for all phenomena in each characteristic regarding the *validity of the phenomenon* (VP, y-axis) and the *evidence for the phenomenon* (EP, x-axis). In addition, point size is related to *data coverage* (DC) for the indicator, so that phenomena with lower data coverage can be down weighted in the assessment of the characteristic. Note that phenomena which are scored as “insufficient” on the EP-axis are not included in the assessment but are plotted to indicate phenomena which need to be improved for future assessments. Based on the distribution of phenomena in the diagram, the ecosystem characteristic is assessed as being in one of three categories: 1) No change; 2) limited change; or 3) substantial deviation from the reference condition. The criteria for the three categories are described in Box 3. An additional summarising figure is given at the end of this sub-chapter, showing an overview of all indicators discussed in the assessment (i.e., both those included and those not included) with the assessment category for those included, and the assessment category indicator coverage for the ecosystem characteristics (Fig. 7.3.2).

Box 3. Summary of the criteria for the three assessment categories and general considerations for this assessment. Details are described in Jepsen et al. (2020).

No deviation from the reference condition

An ecosystem characteristic assigned to this category shows no or very limited deviations from the reference condition. According to the definition of the reference condition, the ecosystem characteristic can be considered in good ecological condition based on the current set of indicators.

- Most or all of the phenomena should be in the green cells in the PAEC assessment diagram (Fig. 7.3.1).
- Most or all phenomena should have either no evidence (EP=None), or low evidence (EP=Low) in combination with a low validity (VP=Low).
- This category can usually be assigned with high confidence, since there is no evidence that changes of ecosystem significance have occurred. In such cases uncertain links to drivers or a poor understanding of the implications of changes is less of a concern.
- If any phenomena are located in the orange or red cells, the choice of category *No deviations from the reference condition* should be justified in the textual assessment.

Limited deviation from the reference condition

An ecosystem characteristic assigned to this category shows limited deviations from the reference condition. According to the definition of the reference condition, the ecosystem characteristic can still be considered in good ecological condition based on the current set of indicators. However, individual indicators show changes in a direction of a worsened ecological condition, which requires attention.

- Most or all of the phenomena should be in the orange cells in the PAEC assessment diagram (Fig. 7.3.1a, b).
- Most or all phenomena should have either low evidence (EP=Low) or intermediate evidence (EP=Intermediate) in combination with a low-intermediate validity (VP=Low or Intermediate)
- This category is often assigned with lower confidence than the other two categories, since it can include phenomena which both have low-intermediate validity and a high level of evidence for change. These are the most uncertain phenomena to assess.
- If any phenomena are located in the green or red cells, the choice of category *Limited deviation from the reference condition* should be justified in the textual assessment.

Substantial deviation from the reference condition

Ecosystem characteristics assigned to this category show substantial deviations from the reference condition. According to the definition of the reference condition, they can NOT be considered in good ecological condition based on the current set of indicators.

- Most or all of the phenomena should be in the red cells in PAEC assessment diagram (Fig. 7.3.1a, b).
- Most or all phenomena should have intermediate – high evidence (EP=Intermediate or High) in combination with intermediate – high validity (VP=Intermediate or High).
- This category can usually be assigned with high confidence, since most phenomena have high validity, and a high level of evidence.
- If any phenomena are located in the green or orange cells, the choice of category *Substantial deviation from the reference condition* should be justified in the textual assessment.

General considerations for this assessment: The choice of assessment category for an ecosystem characteristic is guided by the “centre of gravity” of the set of phenomena representing the characteristic, as outlined in the definition of the categories above. This can be challenging when the characteristic is represented by a set of indicators that is assessed as “inadequate”, or when phenomena are spread across several or all categories. In such cases, the choice of assessment category is supported by a justification that highlights why more emphasis has been placed on certain phenomena. This can be due to better data coverage, higher validity or an understanding that certain phenomena are of greater relevance (e.g., in terms of ecological significance) than others for the condition of the ecosystem characteristic as a whole. Similarly, the assessment of the ecosystem as a whole has been guided by an understanding of the relative importance of the different characteristics for the condition and/or integrity of the ecosystem as a whole.

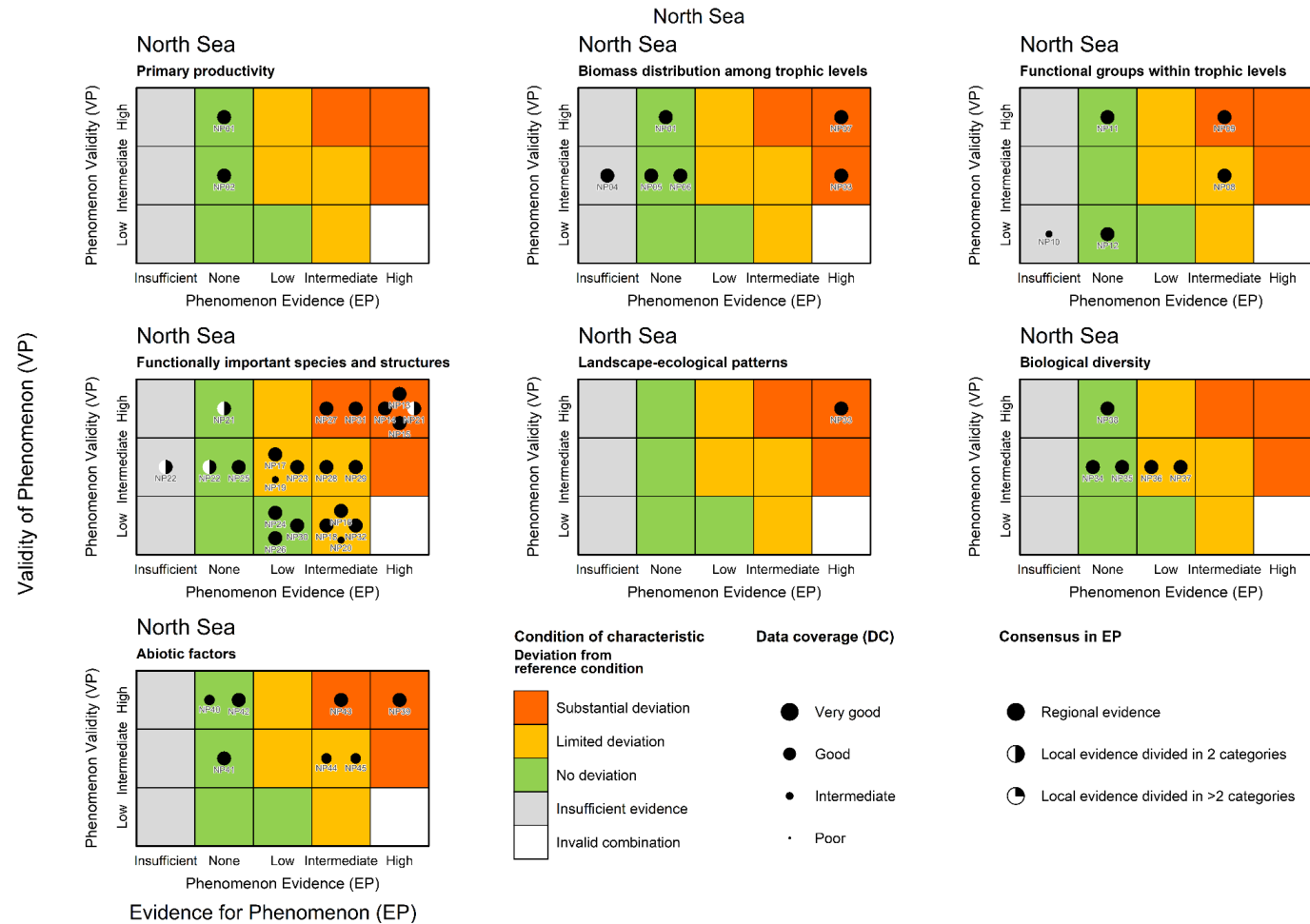


Figure 7.3.1. The PAEC assessment diagram provides an overview of all phenomena for all ecosystem characteristics. Each dot represents the assessment of a phenomenon with ID (from Table 5.1). The size of the dot indicates the data coverage (DC; larger symbols = better coverage, from Table 7.1). The placement of the dot shows the value for the validity (VP) of the phenomenon and the levels of evidence (EP) for the phenomenon (from Table 7.2). Note that phenomena which are scored as EP=Insufficient, should not be accounted for in the assessment, but are plotted to highlight phenomena for which data coverage and/or quality should be improved for future assessments. Bold lines around the coloured boxes, within the diagrams for each of the ecosystem characteristics, indicate the condition of the respective characteristic

North Sea – Primary productivity

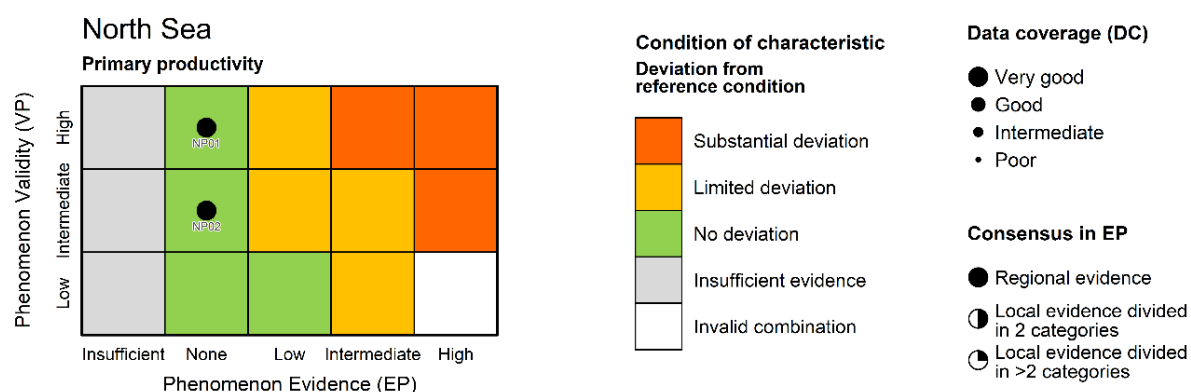


Figure 7.3.1 (i): The PAEC assessment diagram for the Primary productivity ecosystem characteristic of the North Sea. The table below lists the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the set of indicators, this ecosystem characteristic is assessed as showing **no evidence of deviation** from the reference conditions.

Justification for choice of assessment category: This assessment is based on a set of two indicators of intermediate and high validity showing no evidence for increasing primary productivity or change in start date of the spring bloom.

Uncertainties related to the choice of assessment category: High uncertainties surround this assessment, as time series used only go back in time to 2003, when most of the climate warming (the main driver of those phenomena) had already occurred. The time series are thus too short to cover the changes in the main driver.

North Sea – Biomass distribution among trophic levels

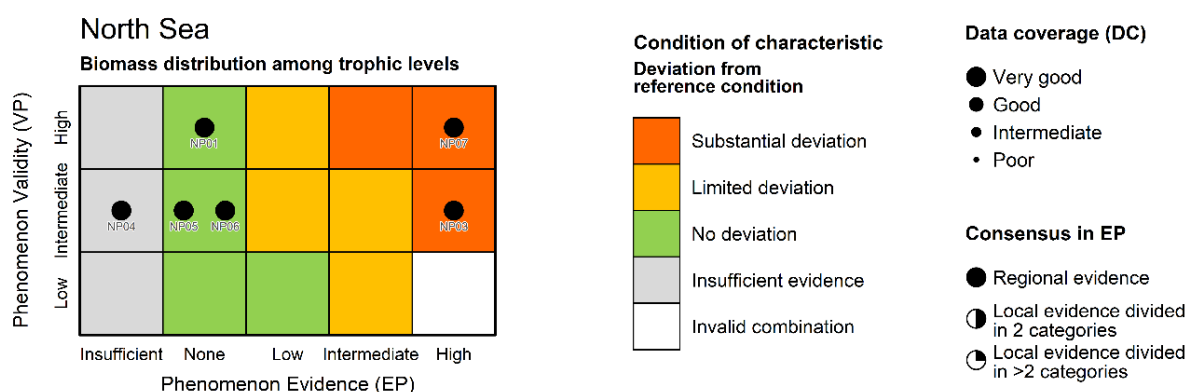


Figure 7.3.1 (ii): The PAEC assessment diagram for the Biomass among trophic levels ecosystem characteristic of the North Sea. The table below lists the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the set of indicators, this ecosystem characteristic is assessed as showing evidence of **limited deviation** from the reference conditions, as some indicators (abundance of high trophic level seabirds and herbivorous copepods) are developing towards impacted conditions and require attention.

Justification for choice of assessment category: This assessment is based on a set of six indicators associated with phenomena of intermediate or high validity. Three of those indicators (NP01 annual primary productivity, NP05 and NP06 biomass of high and low trophic level bottom fish species, respectively) showed no evidence of deviation from the reference conditions but have short time series relative to the period of changes in the main drivers, i.e., climate change and fisheries. One phenomenon (NP04: increasing abundance of carnivorous zooplankton) was not considered in the assessment as it has been categorized as “data insufficient” for the evidence of the phenomenon, which is because the CPR does not sample deep enough to properly catch the carnivorous species. The two last indicators showed high evidence for the phenomena (NP03: decreasing abundance of herbivorous copepods, NP07: decrease in abundance of high trophic level seabirds) and are associated with longer time series and high validity phenomena.

Uncertainties related to the choice of assessment category: The main cause of uncertainty in this assessment is that, because of the short time series available for high and low trophic levels fish species, the choice of assessment category is mainly driven by seabirds and herbivorous copepods. Thus, there is evidence of change in biomass for part of the lower and upper trophic levels, but important information is missing for intermediate trophic levels (fish species, benthos) and other upper trophic levels (high trophic level fish, marine mammals), of which seabirds are only a small portion. Fish species turnover might compensate for the loss or displacement of other stocks, hence the lack of change in the biomass of high and low trophic levels fish species, but longer time series are needed to confirm this and link it to the drivers.

North Sea – Functional groups within trophic levels

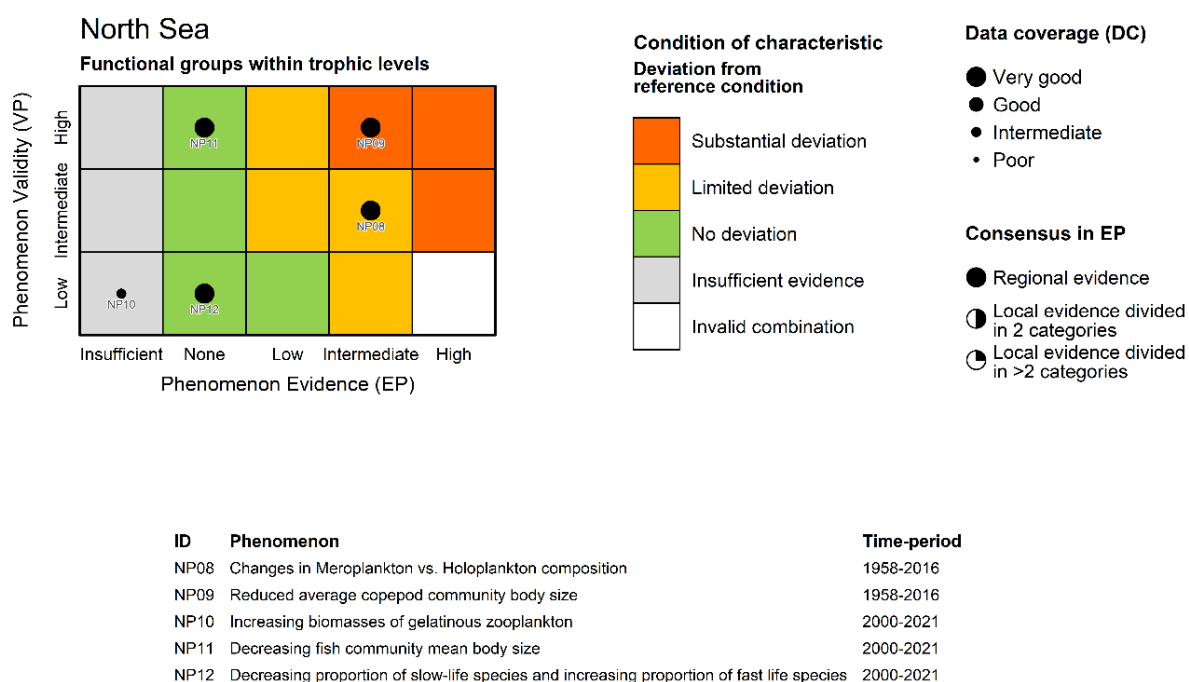


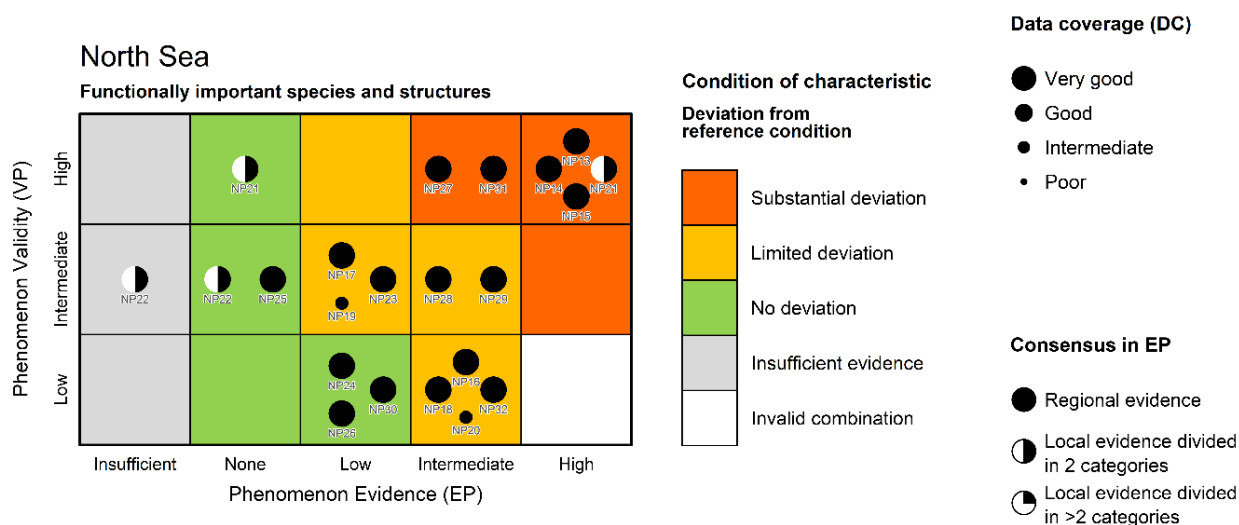
Figure 7.3.1 (iii): The PAEC assessment diagram for the Functional groups within trophic levels ecosystem characteristic of the North Sea. The table below list the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the current set of indicators, this ecosystem characteristic has been assessed as showing evidence for **limited deviation** from the reference conditions. Changes in average copepod body size and the relative abundance of meroplankton versus holoplankton could indicate a more impacted condition, at least in the pelagic system, that require attention.

Justification for choice of assessment category: This assessment is based on five indicators associated with phenomena of low to high validity. One indicator (NI10: biomass of gelatinous zooplankton) has not been considered in this assessment because the time series is too short and because data are not produced using a standardized sampling protocol. Two indicators (NI11 fish community body size and NI12 proportion of slow-life versus fast-life fish species) showed no evidence of decrease, but the time series are short and not overlapping with the period of change in the main drivers. The two other indicators (NI08: the relative abundance of meroplankton versus holoplankton, and NI09: average copepod body size) are associated with intermediate level of evidence for their phenomena and are based on long time series.

Uncertainties related to the choice of assessment category: The main uncertainty around this choice of assessment category is linked to the length of the timeseries among indicators. Because the fish-related indicators are short, this assessment is mainly driven by zooplankton indicators. It should also be noted that CPR data probably give a conservative estimate of change in copepod body size, as it only measures the component due to change in species composition (in the direction of smaller species) and does not cover change in body mass within species (which is expected in the direction of smaller individuals within species). Other uncertainty is associated with missing indicators (e.g., fast/slow growing benthos species, or composition of top predators, Table 6.1)

North Sea – Functionally important species and biophysical structures



ID	Phenomenon	Time-period
NP13	Decrease in abundance of <i>C. finmarchicus</i> relative to abundance of <i>C. helgolandicus</i>	1958-2016
NP14	Declining abundance of <i>Pseudocalanus</i> spp. and <i>Paracalanus</i> spp.	1958-2016
NP15	Decreasing cod stock size	1963-2022
NP16	Decreasing cod recruitment	1963-2022
NP17	Decreasing haddock stock size	1972-2022
NP18	Decreasing haddock recruitment	1972-2022
NP19	Decreasing saithe stock size	1967-2022
NP20	Decreasing saithe recruitment	1967-2022
NP21	Decreasing lesser sandeel stock size	1986-2022
NP22	Decreasing lesser sandeel recruitment	1986-2022
NP23	Stable Norway pout stock size	1983-2022
NP24	Stable Norway pout recruitment	1983-2022
NP25	Decreasing whiting stock size	1978-2022
NP26	Decreasing whiting recruitment	1978-2022
NP27	Decreasing herring stock size	1947-2022
NP28	Decreasing herring recruitment	1947-2022
NP29	Decreasing mackerel stock size	1980-2021
NP30	Change in mackerel recruitment	1980-2021
NP31	Decreasing shrimp stock size	1907-2021
NP32	Decreasing shrimp recruitment	1971-2021

Figure 7.3.1 (iv): The PAEC assessment diagram for the Functionally important species and biophysical structures ecosystem characteristic of the North Sea. The table below list the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the current set of indicators, the panel assessed this ecosystem characteristic as displaying **substantial deviation** from the reference conditions. In particular, zooplankton, herring and cod stocks were given a higher weight prior to the assessment and are showing signs of strong deviation from reference conditions.

Justification for choice of assessment category: This assessment is based on 20 indicators associated with phenomena of low to high validity. Data are lacking on sandeel recruitment in area 5r of the Norwegian sector of the North Sea and this indicator was not considered in the assessment. Fifteen of the other indicators showed low to high evidence of change in the direction expected under increasing human impact. Many of the indicators associated with high

phenomenon evidence also often have higher validity, so the link to the drivers and consequences for the ecosystem are better understood. Zooplankton, herring and cod were prior to the assessment identified as having a higher importance than the other stocks because of their importance in the ecosystem, and those indicators are showing high or intermediate evidence of decrease. There are thus more than warning signals, and this ecosystem characteristic cannot be considered as being close to reference conditions.

Uncertainties related to the choice of assessment category: There is little uncertainty about the category of assessment, considering the number of indicators showing the same signal of impact on the ecosystem characteristic condition. Phenomena with low evidence also have low validity and it is likely that improving their validity through research would further decrease the uncertainty about this assessment. Fourteen indicators are associated with phenomena of low validity. Those are mostly recruitment indicators, and it is often unclear how climate and fisheries jointly impact these indicators, or what consequences they have on the ecosystem. Other species are not included here, such as sharks or whales. These, however, would likely support the current assessment of substantial deviation from the reference conditions (ICES, 2021b). Also, most of the indicators are using ICES stock assessment data for the whole North Sea and are not limited to the Norwegian sector, which is the issue of interest here.

North Sea – Landscape-ecological patterns

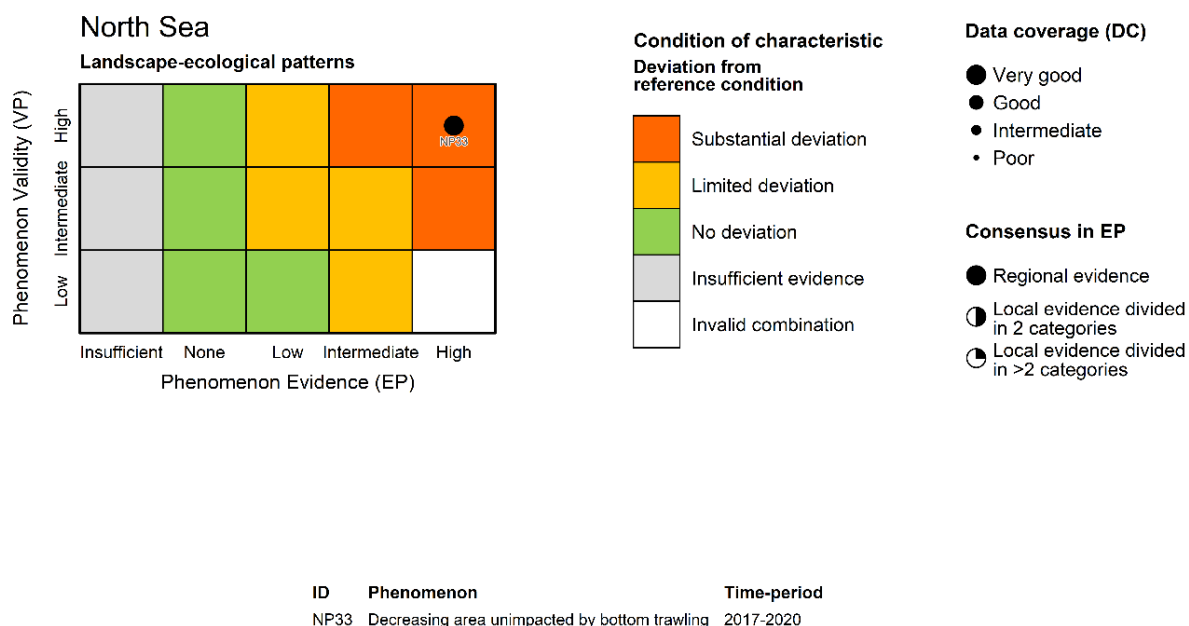


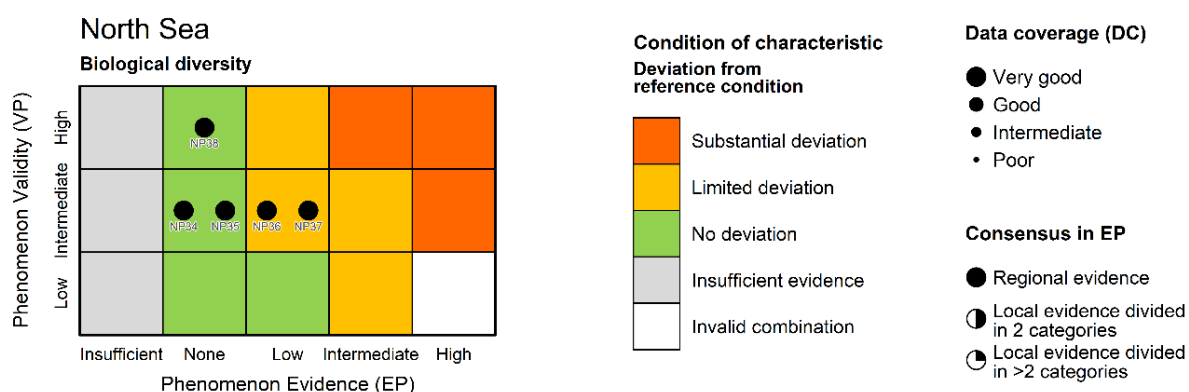
Figure 7.3.1 (v): The PAEC assessment diagram for the Landscape-ecological patterns ecosystem characteristic of the North Sea. The table below lists the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the current set of indicators, this ecosystem characteristic is assessed as showing evidence for **substantial deviation** from the reference conditions.

Justification for choice of assessment category: There is only one indicator in this characteristic, and it has high validity as its link to the driver (fisheries) and its consequences for the ecosystem are well understood. Reference conditions would be that the entire area of interest (Norwegian sector of the North Sea) is unimpacted by bottom trawling. However, this area is clearly reduced.

Uncertainties related to the choice of assessment category: Uncertainties about this assessment category are low. Although there is only one indicator and other habitat and landscape indicators could be added (e.g., area of light or noise habitat that is decreased because of human activities or sizes of other habitat types that are reduced by other sector of activities such as oil and gas, transport, telecommunication etc. see Table 6.1), abounding literature are showing that these new indicators would support the current assessment of substantial deviation from reference conditions.

North Sea – Biological diversity



ID	Phenomenon	Time-period
NP34	Decreasing biomass of fish vulnerable to higher temperatures	2000-2021
NP35	Increasing biomass of fish benefitting from higher temperatures	2000-2021
NP36	Decrease in number of copepod species sensitive to higher temperatures	1958-2016
NP37	Increase in number of "warm-water" copepod species	1958-2016
NP38	Decreasing biomass of fish species vulnerable to fisheries	2000-2021

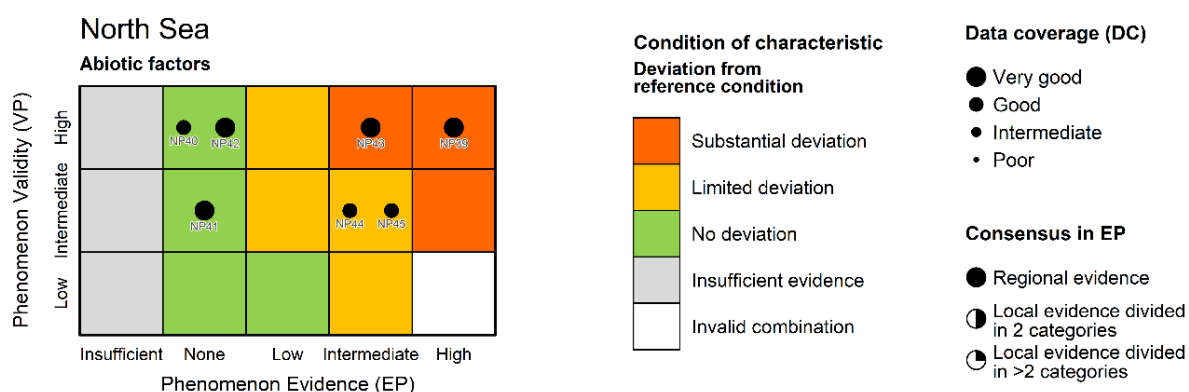
Figure 7.3.1 (vi): The PAEC assessment diagram for the Biological diversity ecosystem characteristic of the North Sea. The table below lists the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the current set of indicators, this ecosystem characteristic is assessed as showing evidence for **limited deviation** from the reference condition. Changes in zooplankton community, with a decline in cold-water and an increase in warm-water copepods, are warning signals that biological diversity in the North Sea require attention.

Justification for choice of assessment category: This assessment is based on five indicators associated with phenomena of intermediate or high validity. Three indicators (NP34, 35 and 38, fish species sensitive to high or low temperatures, or sensitive to fisheries) showed no evidence of change in the direction expected under increasing human impact, but those were based on short time series, not covering the period of change in the drivers (fisheries, climate change). Longer time series available for zooplankton are showing intermediate evidence for a change in zooplankton community composition linked to climate change.

Uncertainties related to the choice of assessment category: The uncertainty linked to this assessment category is that it is currently driven only by the zooplankton indicators, as time series for the other indicators are too short to cover period of change in the drivers. Some important indicators are also missing, such as invasive species or species sensitive to pollution (Table 6.1)

North Sea – Abiotic factors



ID	Phenomenon	Time-period
NP39	Warming of the water column	1952-2021
NP40	Increasing stratification of the upper water column	2005-2021
NP41	Increasing inflow of Atlantic water to the North Sea	1985-2021
NP42	Increasing concentration of nutrients	1980-2021
NP43	Increase in light attenuation	1903-1998
NP44	Decreasing pH	2012-2020
NP45	Decreasing aragonite saturation	2012-2020

Figure 7.3.1 (vii): The PAEC assessment diagram for the Abiotic factors ecosystem characteristic of the North Sea. The table below list the indicators included in this ecosystem characteristic, their associated phenomenon, and the time period covered by the data used to assess the evidence for the phenomenon.

Assessment category: Based on the current set of indicators, this ecosystem characteristic is assessed as showing evidence for **substantial deviation** from the reference condition, mainly driven by increasing temperatures.

Justification for choice of assessment category: This assessment is based on seven indicators associated with phenomena of intermediate or high validity. Temperature was assessed as having a strong weight a priori because of its importance as a proxy of other physical properties and as a driver for the ecosystem structure and functioning. Temperature shows high evidence of deviation from reference condition as a result of climate change. Three indicators are showing no evidence of change away from reference conditions, but their time series are short. There are also signals of increasing light attenuation and acidification.

Uncertainties related to the choice of assessment category : The uncertainty linked to the choice of the assessment category is mainly linked to the short time series of certain indicators. Stratification is only measured for part of the year, hence the poor data coverage score.

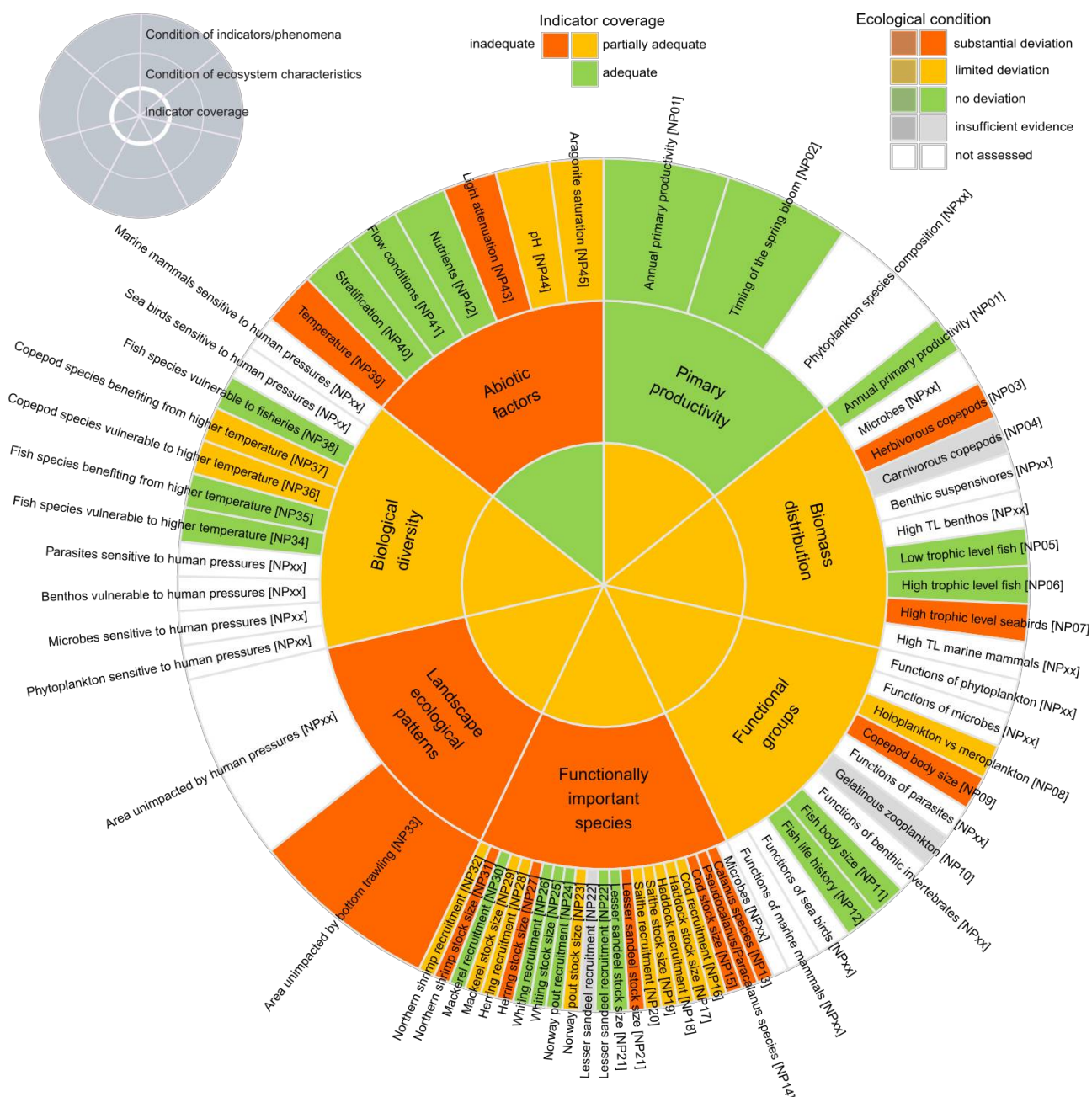


Figure 7.3.2. A graphical summary of the assessment of the Norwegian sector of the North Sea shelf ecosystem. The outer circle shows the assessment of ecological condition at the level of the individual indicators with associated phenomena ID in square brackets. Indicators which have been recommended for inclusion (Table 7.3. 2), but not included in the current assessment are shown in white to illustrate the perceived most important deficiencies in the current indicator set. The two innermost circles show the assessment at the level of ecosystem characteristics, in the form of ecological condition (middle circle) and indicator coverage (innermost circle), based on the set of indicators included in the assessment. TL: trophic level.

7.3.2 Assessment of the condition of the ecosystem as a whole

The scientific panel concludes that the ecosystem in the Norwegian sector of the North Sea and Skagerrak is substantially impacted by human pressures. There is little uncertainty about this conclusion. Climate change is strongly affecting abiotic conditions, mainly through increasing temperatures. This is substantially impacting the rest of the ecosystem, along with other drivers, in particular fisheries. Consequences are largest for functionally important species and seafloor habitats. There are also signs of human-driven changes in diversity of species and ecological functions, as well as in the trophic pyramid of the ecosystem. With further climate change and development of industrial activities in the North Sea, human pressures will remain intensive in the future.

Current state of knowledge of the reference condition

Systematic monitoring rarely stretches back to periods with an unimpacted climate and sustainable fishing and harvesting. Robust quantitative descriptions of the reference condition are therefore beyond reach. The qualitative description that can be made of the reference condition beyond this, is fragmented. While there is good knowledge of the composition of the key species assemblages, i.e., the zooplankton and fish communities, less is known about ecological functions and relationships. Some species groups are also poorly known, such as species involved in the microbial loop and infectious organisms.

Given this and following the description of the phenomena (Ch 5.1), the shelf ecosystem in the Norwegian sector of the North Sea in the reference condition should have had structures and functions which were determined by a temperate climate that was possibly 1°C cooler than the last three decades. Anthropogenic input of nutrients from rivers and the atmosphere did not cause eutrophication and water chemistry was unaffected by anthropogenic greenhouse gas emissions. Other pollutants, such as heavy metals and persistent organic pollutants were absent or found in concentrations that were not significantly elevated above background levels. Water transparency in coastal areas was probably higher due to increased browning in lakes and rivers caused by anthropogenic climate change in the North Sea catchment area during the 20th century (Opdal et al., 2019). As a consequence, the spring bloom may have been earlier during the reference condition (Opdal et al., 2019). The zooplankton community was dominated by cold-water species, in particular *Calanus finmarchicus*, which contributed to favourable conditions for recruitment for many boreal fish stocks, such as cod and herring. Fishing was carried out sustainably, and, based on macroecological models, biomass of the fish community (defined as all fishes with body mass 64 g - 66 kg) appears to have been higher and proportion of large individuals considerably higher than today (Jennings and Blanchard, 2004). That fish biomass was higher under the reference condition is supported by a study of past population abundance trajectories for cod based on genetic data, which suggests that fisheries induced declines in the stock may have started a millennium ago (Sodeland et al., 2022). It is also supported by analyses of landings from UK demersal fisheries from 1889 and onwards, which indicate that landings per unit fishing effort was reduced by 94% over the following 118 years, suggesting a huge decline in demersal fish abundance from the end of the 19th to the beginning of the 21st century (Thurstan et al., 2010). Several marine mammals occurred with substantially larger populations than today because of over-harvesting that took place over several centuries (ICES, 2021b), and benthic habitats and invertebrate populations were not significantly impacted by bottom trawling.

Main drivers of change

As outlined in Ch. 2 (description of reference condition), the main anthropogenic drivers of change in the Norwegian sector of the North Sea above 200 meters depth are climate change and fishing (including disturbance of bottom habitats from trawling). The system may also be affected by pollution, including both long-range transported pollution and local pollution from petroleum extraction activities and underwater noise from seismic activities and ship traffic may also affect the ecosystem.

Following an increase in water temperature relative to the reference period (1961-90) of about 1°C denotable from the end of the 1980s, the North Sea has remained in a warmed state (Fig. 7.3.3).

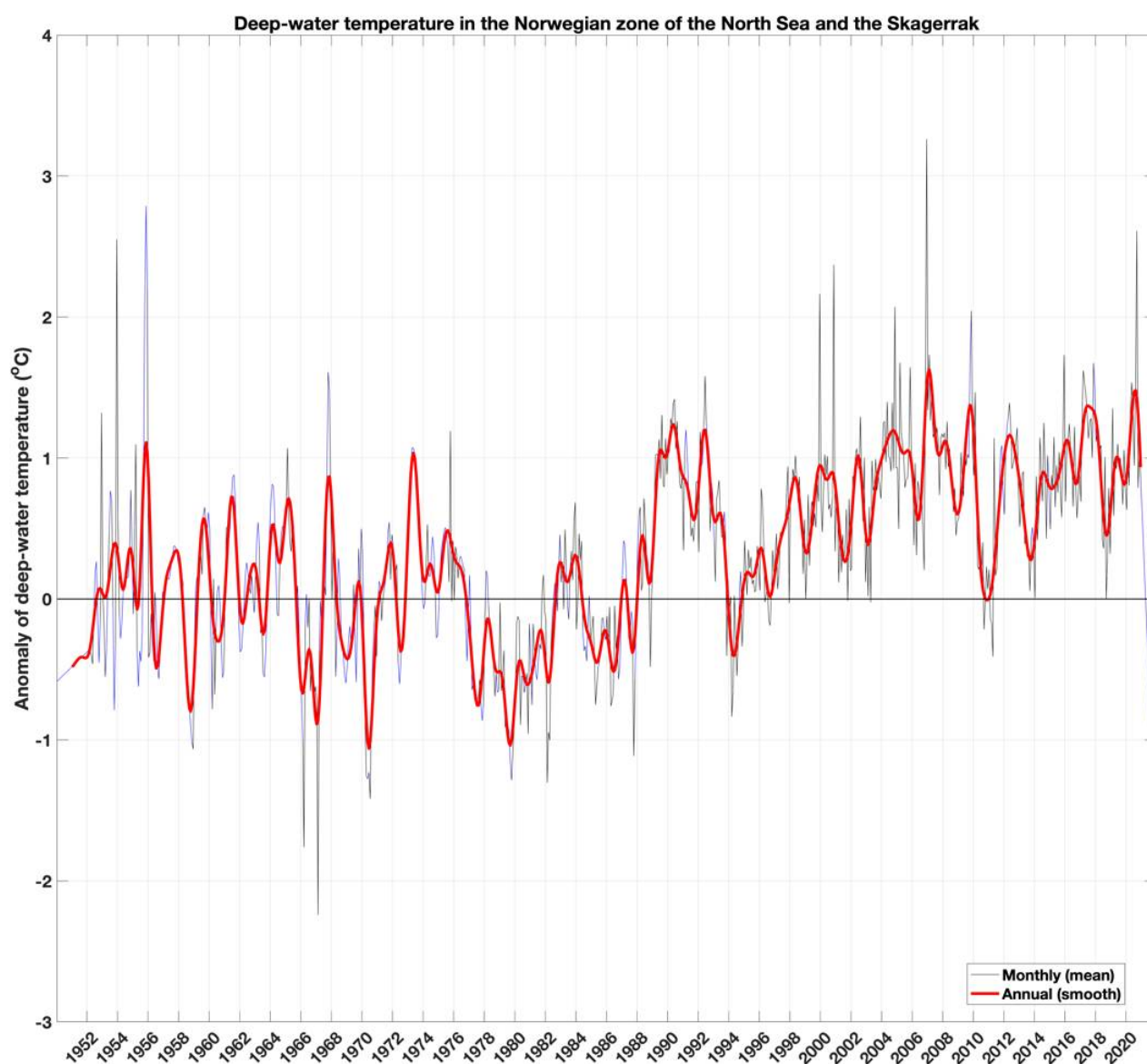


Figure 7.3.3. Time series of deep-water temperature in the Norwegian sector of the North Sea from 1950 to 2021. Temperature observations from the Skagerrak (Torungen-Hirtshals transect) and the northern North Sea (Utsira-Orkney transect) are retrieved from IMR's data base, arranged as monthly values and transferred to anomalies with 1961-90 as the reference period. The black line denotes the monthly data that are available, the blue line is filled in for missing data using an extrapolation method in order to create a lowpass-filtered red line with a one-year long cut-off period.

While fishing pressure increased throughout most of the 20th century, resulting in overfishing of many fish stocks, there was a decline in fishing effort following reforms in the EU Common Fisheries Policy in 2002 (ICES, 2021b). This led to a marked drop in fishing mortality (Fig. 7.3.4). Details in the development of fishing mortality in the fish stocks included as functionally important species in this assessment is given in Appendix 8.2. Some stocks, and in the Norwegian sector most importantly cod, is still fished unsustainably (ICES, 2021a).

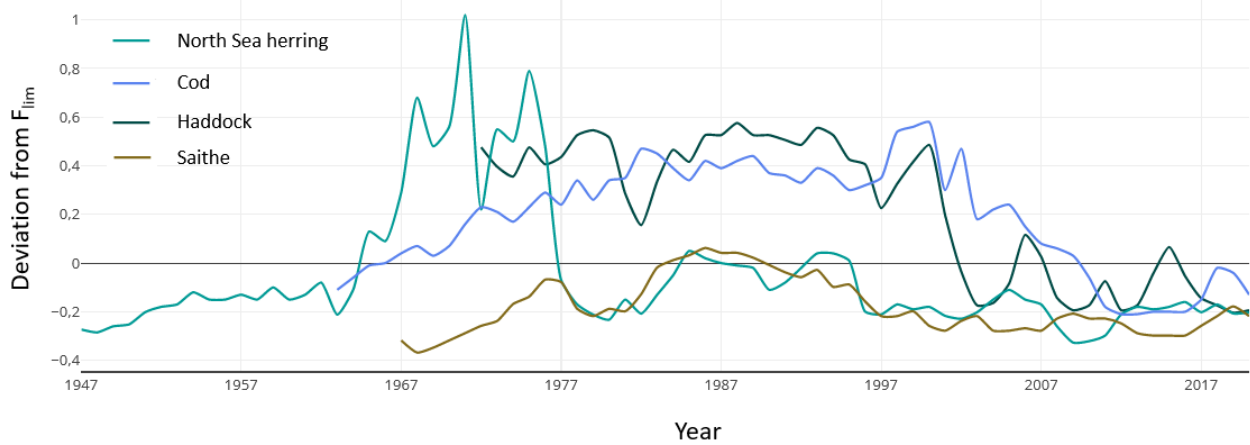


Figure 7.3.4 Fishing mortality of herring, cod, haddock and saithe in the North Sea, expressed as deviation from F_{lim} (F_{lim} represents a critical threshold of fishing mortality, above which recruitment overfishing and stock collapse is possible). This is calculated as F_{lim} subtracted from estimated fishing mortality in the stock, meaning that positive values indicate fishing mortality above F_{lim} . Source (Miljøstatus, 2022a).

Bottom trawling has a long history in the North Sea, and this impact is still pervasive. Using vessel monitoring system (VMS) and logbook data ICES estimates that mobile bottom trawls used by commercial fisheries in the 12 m+ vessel category have been deployed over approximately 490 185 km² of the ecoregion in 2018, corresponding to ca. 73.1 % of the ecoregion's spatial extent (ICES, 2021b). A considerable part of this impact has taken place in the Norwegian sector of the North Sea (Fig. 7.3.5).

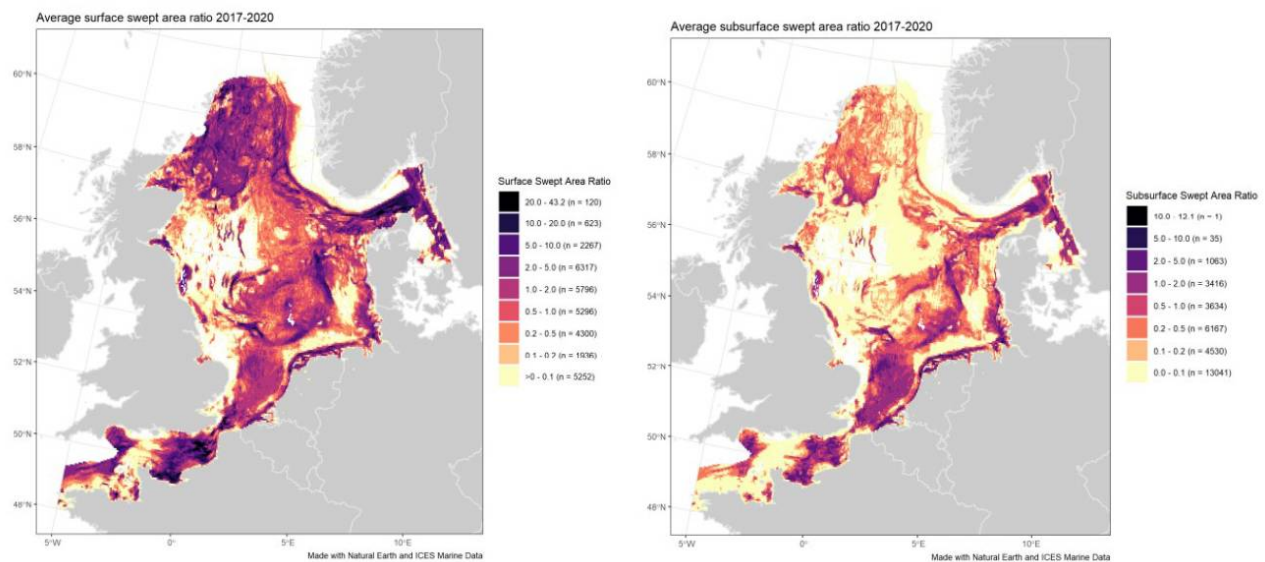


Figure 7.3.5 Average annual subsurface (left) and surface (right) disturbance by mobile bottom contacting fishing gear (Bottom otter trawls, Bottom seines, Dredges, Beam trawls) in the Greater North Sea during 2017-2020 (with available data), expressed as average swept area ratios (SAR). Source ICES (2021b).

The North Sea/Skagerrak is generally more polluted than the other Norwegian waters, yet levels of contaminants in seafood species from the management plan area are below maximum levels for food safety (Frantzen et al., 2022). Concentration of persistent organic pollutants and some other substances, such as mercury, typically increase with

trophic level because of biomagnification (Michelangeli et al., 2022). There is, however, no systematic monitoring and little knowledge about the levels and effects of contaminants in seabirds and sea mammal top predators in the North Sea (Frantzen et al., 2022). The main input of persistent organic pollutants and heavy metals to the North Sea is through atmospheric transport. Levels of these contaminants measured in air on the south-eastern coast of Norway (Birkeland) has declined since around 1990. Some of this decline is reflected in similar declines in biota, but for parts of the biota, no decline is seen (Frantzen et al., 2022).

Routine and legal discharges of oil produced water constitute the largest discharges of oil from oil and gas production in the North Sea. The level of these operational discharges has not changed markedly during the last 20 years. Similarly, there has been no change in the operational discharges of radioactive substances and no indications of an increasing impact from accidental discharges (see Appendix 8.2 for details).

Noise from seismic exploration, ship traffic and other anthropogenic activities can affect behaviour or induce stress in other ways in several groups of species, such marine mammals, fish and several types of invertebrates (Nowacek et al., 2007; Weilgart, 2018; Duarte et al., 2021). There is less information about whether this translates into effects on survival and reproduction in populations, but there is clearly a potential for such effects (Kvadsheim et al., 2017; Kvadsheim et al., 2020; Kvadsheim and Sivle, 2020; Duarte et al., 2021). Anthropogenic sources of noise are widespread in the North Sea and Skagerrak. For example, noise from ship traffic appears to be particularly intense in the Norwegian sector of the North Sea (Farcas et al., 2020). The level of seismic activities is also high in the Norwegian part of the North Sea (Kvadsheim et al., 2020).

Observed deviations from the reference condition

The indicators describing the ecosystem characteristic *Abiotic factors* deviates substantially from the reference condition. This is due to a change in temperature linked to anthropogenic climate change and that have large implications for the rest of the ecosystem. There has also been a significant darkening of the water, which is related to climate change through increased runoff of organic material from land to sea and which may affect several processes in the North Sea and Skagerrak, such as timing of the spring bloom and interactions between predators and prey. Despite short time series (9 years), signs of increased ocean acidification (reduced pH and aragonite saturation) are detected, but there are large uncertainties about the biological consequences of this. Concentrations of nutrients have previously been elevated but have declined during the last decades as a consequence of improved management of runoff from agriculture and other terrestrial sources.

The main rise in temperature occurred at the end of the 1980s as a marked warming of about 1°C above the long term mean over a few years. An important biological response was a change in the zooplankton species that form the main link between the primary producing phytoplankton and higher trophic levels in the ecosystem. During the “cold” state of the ecosystem, the zooplankton species *Calanus finmarchicus* dominated. This species hibernates during winter and generates a large production peak when it spawns in spring. Following the warming, there has been a shift in dominance towards *Calanus helgolandicus*, which feeds throughout the year, spawns in summer and autumn and does not produce marked seasonal peaks in production. The shift in temperature has also caused a general decline in *Paracalanus* and *Pseudocalanus* zooplankton species. Together, these changes in the zooplankton community have had large consequences for the amount and type of food, and the time of the year it is available for higher trophic levels.

The two zooplankton indicators for copepod species described above (*Calanus* species and *Paracalanus/Pseudocalanus* species) are important contributors to the substantial deviation from the reference condition observed for the ecosystem characteristic *Functionally important species and biophysical structures*. The ecosystem characteristic is represented by 20 indicators of which 16 concern fish stocks and 2 the shrimp, covering both biomass and recruitment for each stock. Out of these 20 indicators, 18 show limited to substantial signs of change away from the reference condition. For fish stocks, a contributor to this is overfishing in the 1980s and 1990s that brought several stocks to low levels. After overfishing was reversed following the implementation of the new EU fishery policy from 2003, recovery of several of the stocks has been hampered by low recruitment in the 2000s and 2010s. The

zooplankton groups described above are important food for fish larvae. For cod and herring, which are well studied species, the recruitment failures have been clearly linked to the changes in the zooplankton community driven by the warming. For other fish species, which have been less studied, there are larger uncertainties about the causes of recruitment failures, but given similarities in biology with herring and cod, an influence of the warming-driven changes in the zooplankton community described above is a relevant hypothesis. For shrimp, a recruitment failure which took place in the 2000s caused the stock to collapse under a fishing pressure that was no longer sustainable. Thus, for this species, the recruitment failure preceded the stock decline. Sandeel in the northern part of the North Sea (Vikingbanken) has not recovered from previous overfishing and is at a low level, while sandeel in the southern part of the Norwegian sector of the North Sea has recovered.

Another important aspect of human impact on the ecosystem is the large fraction of the seabed and benthic communities affected by bottom trawling, prompting the ecosystem characteristic *Landscape-ecological patterns* to be assessed as deviating substantially from the reference condition. This may affect complexity of seabed habitats and functioning and productivity of benthic ecosystems, which are aspects of the ecosystem that there are no direct indicators for in the assessment.

For the ecosystem characteristic *Distribution of biomass among trophic levels*, which reflects the overall shape of the trophic pyramid of the ecosystem, it is assessed that there is evidence for limited changes away from the reference condition. This is due to declines in abundance of herbivorous copepods (reflecting to a large extent the same climate-driven changes that are described for *Calanus*, *Paracalanus* and *Pseudocalanus* species above) and fish-eating seabirds likely caused by a combined effect of fisheries and climate change. While the declines in seabird populations are dramatic, seabirds still constitute a small part of the overall biomass in the ecosystem under the reference condition, and the major impact on the shape of the trophic pyramid therefore stems from the changes in herbivorous copepod abundance. There are uncertainties associated with the assessment because time series are short for the lowest (primary production) and intermediate (fish) levels of the trophic pyramid and are lacking for benthos (intermediate trophic level) and marine mammals (top trophic level). It is likely that these two ecosystem compartments were present in higher abundance under the reference conditions. It is however noted that climate driven changes in fish biomass (indicated for many functionally important fish species above), may be compensated by influx of southern species, thus conserving the relative contribution of fish in the trophic pyramid.

Functional groups within trophic levels is another ecosystem characteristic that is assessed as showing evidence for limited deviation from the reference condition. This is, again, due to changes in the zooplankton community, where long time series show that the important copepod part of this community has changed towards smaller-sized species. This is expected to have significant effects on the predators of the copepods, which includes larva and adults of many fish species, and potentially propagate to other parts of the ecosystem. In addition, there has been a marked increase in the abundance plankton from species that are planktonic only in parts of the life cycle (typically larvae, such as for many benthic species) compared with abundance of species that are planktonic through the whole life cycle (e.g., copepods and other species referred to as zooplankton in this text). Changes are not seen in the biomass of “slow-life” fish species (species growing slowly and maturing) compared with biomass of “fast-life” fish species (growing fast and maturing early), but the time series are short (2000-) and not covering the changes that have been in climate and fishing pressure. Thus, this introduces uncertainty to the assessment.

For the ecosystem characteristic *Biological diversity*, it was assessed that there is evidence for limited anthropogenic impact. Based on long time series, moderate changes linked to climate change are seen for zooplankton species, with a tendency for species sensitive to increases in temperatures to occur less frequently and species expected to benefit from this occurring more frequently. For groups of fish, no changes in species occurrence were seen, but this was assessed with considerably shorter time series not covering changes in climate and fisheries. This introduces uncertainty to the assessment.

Finally, no change was seen for the two indicators contributing to the assessment of the ecosystem characteristic *Primary productivity* (yearly production and timing of the spring bloom). Again, the time series for these indicators are

short and not covering change in the main drivers (temperature, light regime, and nutrients), meaning we do not know whether there has indeed been change due to impact from human activities.

A summary of the assessments of deviation from the reference condition and assessed indicator coverage for the ecosystem characteristics are given in Table 7.3.1.

Table 7.3.1 Graphical summary of the assessment of ecological condition for all ecosystem characteristics in the North Sea

Ecosystem characteristic	Deviation from reference condition			Indicator coverage		
	No	Limited	Substantial	Inadequate	Partially adequate	Adequate
Primary productivity	•				•	
Biomass distribution among trophic levels		•			•	
Functional groups within trophic levels		•			•	
Functionally important species and biophysical structures			•		•	
Landscape-ecological patterns			•		•	
Biological diversity		•			•	
Abiotic factors			•			•

7.3.3 Future trajectories for ecosystem condition

As climate change and fisheries are the two main anthropogenic drivers, scenarios for these are considered here. While quantitative model projections for different emission scenarios (which depend on development of politics and international relations) are available for climate development, fisheries and their management depend on regional politics and international relations in ways that are harder to predict (Planque et al., 2019).

On longer timescales, warming is expected to continue in the North Sea, unless global CO₂ emissions are cut immediately and severely. If emissions remain high, large changes in climate are expected by the end of the century (Fig. 7.3.6). From what we know about climate change as a driver of change in the North Sea (see sections 7.3.2 and 5.1), it is reasonable to expect that substantial future changes in climate will cause large ecological changes. There has already been large climate driven changes in the zooplankton community, such as the increasing dominance of *Calanus helgolandicus* relative to that of *Calanus finmarchicus*, which has set off cascading effects in the ecosystem, including recruitment failure in fish stocks (Beaugrand and Kirby, 2010; Clausen et al., 2018). Many commercial stocks are predicted to suffer from climate change by 2041 (Kjesbu et al., 2022), in particular coastal and North Sea cod, saithe and lesser sandeel. Other species are predicted to benefit from the warming, in particular southern/Lusitanian species (Ehrich and Stransky, 2001), such as Northern hake (*Merluccius merluccius*) and North Sea sprat (*Sprattus sprattus*) (Kjesbu et al., 2022).

With climate change, the frequency, duration and intensity of extreme events (heatwaves or cold spells, storms) will increase (Frölicher et al., 2018; Oliver et al., 2018; Laufkötter et al., 2020; Perkins-Kirkpatrick and Lewis, 2020). There is little information about the impact of extreme climatic events in the North Sea, however, abundant literature reported their impacts across the globe (Smale et al., 2019; Smith et al., 2023). More complex statistical models linking the indicator's dynamic to those different spatial and temporal scales of pressure could help develop these forecasts although knowledge gaps and stochastic events will always be part of the uncertainties and risks.

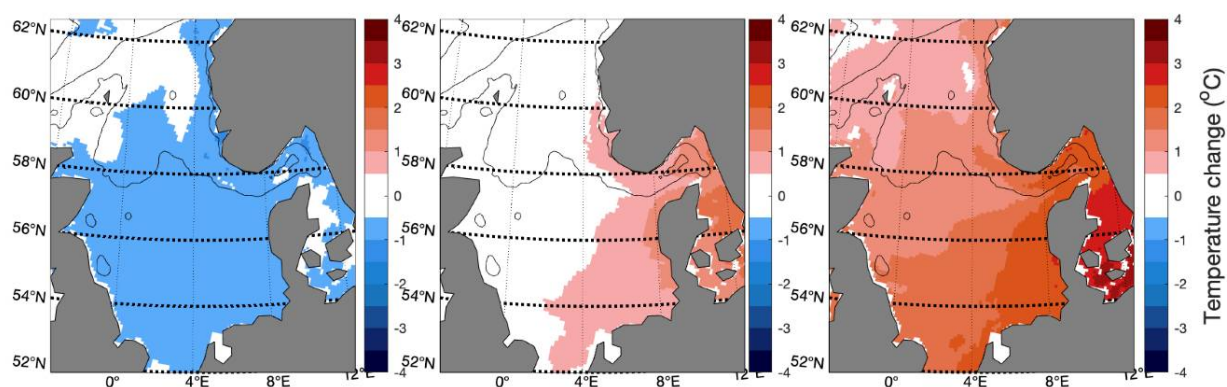


Figure 7.3.6 Projected change in temperature from 2015 to 2100 in the North Sea under three different emission scenarios, SSP1-2.6 (left panel), SSP2-4.5 (middle panel) and SSP5-8.5 (right panel). Projections are downscaled from the model NorESM2 using the regional ocean model NEMO NAA10km. Source: Anne Britt Sandø, Institute of Marine Research, personal communication.

Considering fisheries, one key question is whether the principles of sustainable exploitation of the stocks, laid down in the reforms in the EU Common Fisheries Policy in 2002 (ICES, 2021b) will be continued. As the North Sea is shared by several countries both inside and outside the EU, this will depend not only on the development of EU policies, but also on cooperation with countries outside the union. It is beyond the scope of this assessment to go into this issue, but it seems reasonable to note that considerable uncertainty is associated with the outcome. Another important question related to the impact of fisheries in the future, is whether there will be a change in the impact on benthic communities from bottom trawling. This will depend on many factors, including development of trawling technology. It will also depend on sizes of the fish stocks and the management discussed above, as less trawling time is required when fishing on stocks that are large, which, again, depends on management.

Finally, an important question is how effects of fisheries will interact with other drivers, in particular climate change. For example, with significant declines in the fish species that made up the largest fish stocks under the reference conditions, other fish species, such as the southern species are now increasing in the area. Thus, if the North Sea and Skagerrak are to remain an ecosystem with several large fish stocks, the building of these new stocks will have to be allowed by management, meaning that any fisheries on them will have to be sustainable. However, it should be emphasized that such process would not necessarily lead to a biomass-equivalent replacement and could take longer than the end of the century.

7.3.4 Recommendations for monitoring and research

The present assessment was made possible by the long time series that overlap with periods when the climate was less impacted by greenhouse gases emissions. The data from the Continuous Plankton Recorder Survey (CPR) have been particularly important, as they capture key impacts from climate change on a large number of zooplankton species that affect a range of processes in the ecosystem, including recruitment in large fish stocks. Thus, to assess how climate change will impact the North Sea and Skagerrak shelf ecosystem in the future, it is vital that this survey is continued. It is also important to note that the CPR samples are taken from about 7 meters depth, meaning that additional information from other parts of the water column is needed to validate the CPR data and provide information on important groups we know are not covered well by CPR, such as carnivorous zooplankton. Such data has been collected (with high taxonomic resolution) since 2006 at the North Sea Ecosystem Cruise (Franzè et al., 2021) and at three sections (Torungen - Hirtshals, Utsira - Orkney Islands and Hanstholm - Aberdeen). Thus, continuing this monitoring is crucial for following adequately the ecological status of the North Sea.

In addition, it is necessary to conduct more research to widen the understanding of the (cascading) effects of the changes in the zooplankton communities and on trophic interactions in general. For example, based on dedicated studies on cod and herring, we have a good understanding of how the zooplankton changes have had a negative

impact on recruitment in these species (Beaugrand, 2004b; Beaugrand and Ibanez, 2004; Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014). Similar declines are seen in several other major fish stocks and shrimp but are less well understood due to lack of dedicated studies. Therefore, more studies are needed, combining both *in situ* observations and ecosystem modelling (Skogen et al., 2021), to improve not only our understanding of current patterns of change but also our ability to assess likely future trajectories of change in the ecosystem.

The level of annual primary production is the main determinant of the amount of energy coming into the ecosystem. Estimation of this for large ecosystems is typically done using estimates based on satellite data or ecosystem models, both of which rely on *in situ* measurements of production for calibration. Such estimates are scarce for high latitude ecosystems, and increased effort for primary production *in situ* measurement is therefore needed.

Data on benthic invertebrate species were not included in the assessment largely due to limited access to high quality data. For example, while some data are available from the environmental monitoring of the petroleum industry, they are not of sufficient quality for developing the type of indicators required in this assessment (Ellingsen et al., 2017). Improvements of benthos monitoring are therefore needed, for example by implementing relevant protocols at the International Bottom Trawl Survey (IBTS).

Changes in abundance of gelatinous zooplankton have the potential to set off large ecosystem changes, including significantly reducing the flow of energy to higher trophic levels with negative impacts on key fish stocks as one possible outcome (Purcell and Arai, 2001; Pauly et al., 2009; Richardson et al., 2009; Condon et al., 2014; McConville et al., 2016). Systematic monitoring of the gelatinous zooplankton group is lacking in the North Sea due to lack of standardized protocols and taxonomic knowledge. Thus, developing and implementing a standardized protocol for all monitoring surveys (e.g., the North Sea IBTS survey and Ecosystem cruises) can address this data need (Aubert et al., 2018).

It should also be noted that the IBTS is a source of robust data with good taxonomic resolution for fish (ICES, 2020c). In addition to providing key data for the assessments of fish stocks that have been used in this study, it has also made it possible to develop ecosystem level indicators for fish, which have been important for the assessment of the ecosystem characteristics on functional diversity and biodiversity.

During the assessment, the scientific panel has identified additional indicators which are recommended to be included in the next assessment. An overview of these is given in Table 7.3.2. In this table there are also short evaluations of the possibility for inclusion of each indicator in the next assessment. Future assessments would also benefit from harmonization of indicators used here and in assessments of the Northeast Atlantic done by OSPAR. Indicators used in OSPAR should be considered for the next assessment, however, the relevance of different indicators for the Norwegian Sea pelagic ecosystem needs to be investigated.

*Table 7.3.2. Suggested important missing indicators for the Norwegian Sea. An indication of priority is indicated and represents how easily the indicator can be included in future assessments: 1: data available, can be included in the next assessment; 2: monitoring can be included in current programs or modelling tools are available; 3: monitoring or models must be developed. For recommendations on further development of indicators included in the assessment, see Appendix 8.1. *Indicators that were originally included in the assessment and thus mentioned in Table 4.1, but where data quality was assessed as insufficient during the assessment and development of improved indicators are needed.*

Ecosystem characteristic	Suggested indicator	Relevance to the ecosystem characteristic and obstacles to its inclusion in the current assessment	Possibility of inclusion for the next assessment
Primary productivity	Phytoplankton species composition	Variation in species composition can have impacts on other parts of the ecosystem, in particular the type of herbivorous zooplankton that are successful grazers. In addition, diatoms may have toxic effects and negatively affect growth and development of copepods, and the relationship between diatoms and dinoflagellates may be a relevant indicator. Relevant data exist from CPR (Continuous Plankton Recorder Survey, 2022), but has not been included because of capacity constraints.	1
Biomass distribution among trophic levels	Biomass of benthic suspensivores	The group constitutes a significant part of the biomass in the ecosystem. Data exists from the IBTS (ICES, 2020c) and monitoring of benthos performed by the oil and gas operators (Ellingsen et al., 2017). Not included because of lack of capacity	1
Biomass distribution among trophic levels	Biomass of high trophic level benthos	The group constitutes a significant part of the biomass in the ecosystem. Data exists from the IBTS (ICES, 2020c) and monitoring of benthos performed by the oil and gas operators (Ellingsen et al., 2017). Not included because of lack of capacity	1
Biomass distribution among trophic levels	Biomass of high trophic level marine mammals	The group constitutes a significant part of the biomass in the ecosystem. Data exists from surveys of several whale species (Solvang et al., 2015; Leonard and Øien, 2020b; Leonard and Øien, 2020a). Not included because of lack of capacity	1
Biomass distribution among trophic levels	Carnivorous zooplankton*	The group constitutes a significant part of the biomass in the ecosystem (see phenomenon for NI04). Not included because of lack of data with sufficient quality. Although some carnivorous zooplankton are sampled by CPR, the group typically resides below the depth sampled by CPR (~ 7 m) (John et al., 2001). In addition, important carnivorous groups such as amphipods, euphausiids, amphipods and gelatinous zooplankton are too large to be sampled efficiently by the CPR. Data exist from the IMR North Sea Ecosystem Cruise, and three sections, but with shorter time series (2006 and onwards for the ecosystem cruise, Franzè et al. (2021))	1
Biomass distribution among trophic levels	Microbes	The amount of energy flowing through the microbial loop can significantly affect the overall flow of energy in the ecosystem and thus several important ecological processes. Not included because of lack of data.	3
Functional groups within trophic levels	Gelatinous zooplankton*	Variation in biomass or abundance of the group may have significant effects on energy flow and a substantial number of other species in the ecosystem (see phenomenon for indicator NI10). Data with sufficient quality are lacking because there is no robust protocol for sampling of the group in IBTS and other relevant cruises. If this is developed, data will be available.	2
Functional groups within trophic levels	Indicator(s) for functions performed by phytoplankton	An indicator for the relationship between diatoms and dinoflagellates, discussed for <i>Primary productivity</i> above, may be relevant here. Data are available from CPR but were not included because of capacity constraints.	1
Functional groups within trophic levels	Indicator(s) for functions performed by microbes	It should be evaluated how different types of microbes contribute to different ecosystem functions and indicators should be developed accordingly. Not included because of lack of capacity and data.	3
Functional groups within trophic levels	Indicators for functions performed by parasites	Parasites are here defined to include all types of infectious organisms, i.e., including viruses and bacteria. Parasites constitute a large part of the total biodiversity (suggested as e.g. around 40% by Dobson et al. (2008)) and may significantly affect ecosystem structure and processes (Lafferty, 2008). Work is needed to identify relevant indicators. Not included because of lack of capacity and data.	3
Functional groups within trophic levels	Indicator(s) for functions performed by seabirds	Seabirds are important predators for parts of the ecosystem. Not included because of lack of capacity.	1

Functional groups within trophic levels	Indicator(s) for functions performed by marine mammals	Mammals are important predators in the ecosystem and changes in functional groups may affect several ecological processes. Not included because of lack of capacity.	2
Functional groups within trophic levels	Indicator(s) for functions performed by benthic invertebrates	Benthos is an important component in the ecosystem, and changes in functional groups may have significant impacts on structure and processes in the ecosystem. Data exists from the IBTS (ICES, 2020c). Data from the monitoring of benthos performed by the oil and gas operators, may be of sufficient quality for assessing functional groups (Ellingsen et al., 2017). Not included because lack of capacity.	1
Functionally important species and biophysical structures	Indicator for microbes	Should be included to provide information on the microbial loop. Not included because of lack of capacity and data.	3
Functionally important species and biophysical structures	Area unaffected by human infrastructures and noise	Infrastructures established for oil and gas production (Fujii, 2016) and windmill farms with subsea cables emitting stable magnetic fields have a potential to affect ecological processes (Sivle et al., 2020; Cresci et al., 2022). Noise from seismic activities, ship traffic and other types of anthropogenic activities may affect several groups of organisms (Kvadsheim et al., 2020; Sivle et al., 2020). Thus, indicators for areas unaffected by these factors should be developed. This has not been done due to lack of capacity.	1
Biodiversity	Biomass of tall or slow life benthos species	Tall, long-lived benthic invertebrates are particularly sensitive to trawling. Relevant data may exist from IBTS (ICES, 2020c) and monitoring of benthos performed by the oil and gas operators (Ellingsen et al., 2017). The relevance of the data for a PAEC assessment needs to be evaluated. Not included because lack of capacity.	1
Biodiversity	Number of parasitic species sensitive to impact from climate change, fisheries and other anthropogenic drivers	Parasites (including virus and bacteria) may be more prone to extinctions from anthropogenic drivers than are other types of species (Lafferty and Kuris, 2009). As they constitute a major part of the total biodiversity (Dobson et al., 2008) and may profoundly affect ecosystem structure and processes (Lafferty, 2008), such indicators may have an important role in the assessment. Not included because of lack of capacity and data.	3
Biodiversity	Number/biomass of microbial species/groups sensitive to different anthropogenic drivers	Microbial species may be important for the overall flow of energy in the ecosystem through the microbial loop. Not included because of lack of capacity and data.	3
Biodiversity	Number of phytoplankton sensitive to climate change and nutrient levels	Changes in phytoplankton species composition can be important for processes and structure in the ecosystem (see above). Data exists through the CPR program (see above). Not included because lack of capacity.	
Biodiversity	Numbers/abundance/biomass of species/groups of benthos sensitive to climate change and other human drivers.	Benthos is an important component in the ecosystem, and changes in species composition may have significant impacts on structure and processes in the ecosystem. Data exists from the IBTS (ICES, 2020c). Data from the monitoring of benthos performed by the oil and gas operators, are probably not of sufficient quality for biodiversity assessments (Ellingsen et al., 2017). Not included because lack of capacity.	1
Biodiversity	Abundance of seabird species sensitive to fisheries, climate change and pollution.	Seabirds are important predators for parts of the ecosystem. Not included because of lack of capacity.	1
Biodiversity	Abundance of mammal species sensitive to fisheries (bycatch), climate change and pollution	Mammals are important predators in the ecosystem and change in species composition may affect several ecological processes. Not included because of lack of capacity.	1

8. Appendices

[Appendix 8.1: Indicator times series analyses](#)

[Appendix 8.2: Supplementary information on drivers](#)

[Appendix 8.3: footnotes for data coverage Table 7.1](#)

9. References

- Agnalt, A. L., Grefsrud, E. S., Farestveit, E., Larsen, M., and Keulder, F. 2013. Deformities in larvae and juvenile European lobster (*Homarus gammarus*) exposed to lower pH at two different temperatures. *Biogeosciences*, 10: 7883-7895.
- Aksnes, D. L. 2007. Evidence for visual constraints in large marine fish stocks. *Limnology and Oceanography*, 52: 198-203.
- Aksnes, D. L., Aure, J., Johansen, P.-O., Johnsen, G. H., and Veia Salvanes, A. G. 2019. Multi-decadal warming of Atlantic water and associated decline of dissolved oxygen in a deep fjord. *Estuarine, Coastal and Shelf Science*, 228: 106392.
- Aksnes, D. L., Dupont, N., Staby, A., Fiksen, Ø., Kaartvedt, S., and Aure, J. 2009. Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. *Marine Ecology Progress Series*, 387: 39-49.
- Albert, O. T. 1994. Biology and ecology of Norway pout (*Trisopterus esmarki* Nilsson, 1855) in the Norwegian Deep. *Ices Journal of Marine Science*, 51: 45-61.
- Albretsen, J., Aure, J., Saetre, R., and Danielssen, D. S. 2012. Climatic variability in the Skagerrak and coastal waters of Norway. *Ices Journal of Marine Science*, 69: 758-763.
- Almada, V., Falcón, J., Brito, A., Levy, A., Floeter, S., Robalo, J., Martins, J., et al. 2013. Complex origins of the Lusitania biogeographic province and northeastern Atlantic fishes. *Frontiers of Biogeography*, 5: 20-28.
- Alvarez-Fernandez, S., Licandro, P., van Damme, C. J. G., and Hufnagl, M. 2015. Effect of zooplankton on fish larval abundance and distribution: a long-term study on North Sea herring (*Clupea harengus*). *Ices Journal of Marine Science*, 72: 2569-2577.
- Alvarez-Fernandez, S., Lindeboom, H., and Meesters, E. 2012. Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Marine Ecology Progress Series*, 462: 21-38.
- Andersen, K. H., Berge, T., Gonçalves, R. J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N. S., et al. 2016. Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *Ann Rev Mar Sci*, 8: 217-241.
- Andersen, S., Grefsrud, E. S., and Harboe, T. 2013. Effect of increased $p\text{CO}_2$ level on early shell development in great scallop (*Pecten maximus* Lamarck) larvae. *Biogeosciences*, 10: 6161-6184.
- Anderwald, P., Evans, P. G. H., Dyer, R., Dale, A., Wright, P. J., and Hoelzel, A. R. 2012. Spatial scale and environmental determinants in minke whale habitat use and foraging. *Marine Ecology Progress Series*, 450: 259-274.
- Arai, M. N. 2001. Pelagic coelenterates and eutrophication: a review. *Hydrobiologia*, 451: 69-87.
- Armengol, L., Calbet, A., Franchy, G., Rodríguez-Santos, A., and Hernández-León, S. 2019. Planktonic food web structure and trophic transfer efficiency along a productivity gradient in the tropical and subtropical Atlantic Ocean. *Scientific Reports*, 9: 2044.
- Armstrong, P. R., James, M. K., and Bode, L. 2001. When to Press On or Turn Back: Dispersal Strategies for Reef Fish Larvae. *The American Naturalist*, 157: 434-450.
- Amberg, M., Calosi, P., Spicer, J. I., Tandberg, A. H. S., Nilsen, M., Westerlund, S., and Bechmann, R. K.

2013. Elevated temperature elicits greater effects than decreased pH on the development, feeding and metabolism of northern shrimp (*Pandalus borealis*) larvae. *Marine Biology*, 160: 2037-2048.
- Arnott, S., and Ruxton, G. 2002. Sandeel recruitment in the North Sea: Demographic, climatic and trophic effects. *Marine Ecology Progress Series*, 238.
- Arrhenius, F. 1996. Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* (L.)) in the northern Baltic Sea. *ICES J Mar Sci.*, 53: 701-712.
- Asbjørnsen, H., Årthun, M., Skagseth, Ø., and Eldevik, T. 2020. Mechanisms Underlying Recent Arctic Atlantification. *Geophysical Research Letters*, 47: e2020GL088036.
- Asjes, A., González-Irusta, J. M., and Wright, P. J. 2016. Age-related and seasonal changes in haddock *Melanogrammus aeglefinus* distribution: implications for spatial management. *Marine Ecology Progress Series*, 553: 203-217.
- Attrill, M. J., Wright, J., and Edwards, M. 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, 52: 480-485.
- Aubert, A., Antajan, E., Lynam, C., Pitois, S., Pliru, A., Vaz, S., and Thibault, D. 2018. No more reason for ignoring gelatinous zooplankton in ecosystem assessment and marine management: Concrete cost-effective methodology during routine fishery trawl surveys. *Marine Policy*, 89: 100-108.
- Audzijonyte, A., Barneche, D. R., Baudron, A. R., Belmaker, J., Clark, T. D., Marshall, C. T., Morrongiello, J. R., et al. 2019. Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Global Ecology and Biogeography*, 28: 64-77.
- Balazy, K., Boehnke, R., Trudnowska, E., Søreide, J. E., and Błachowiak-Samołyk, K. 2021. Phenology of *Oithona similis* demonstrates that ecological flexibility may be a winning trait in the warming Arctic. *Scientific Reports*, 11: 18599.
- Barr, L. 1970. Diel vertical migration of *Pandalus borealis* in Kachemak Bay, Alaska. *Journal Fisheries Research Board of Canada* 27: 669-676.
- Baudron, A. R., Needle, C. L., and Marshall, C. T. 2011. Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. *Journal of Fish Biology*, 78: 1874-1889.
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., and Tara Marshall, C. 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20: 1023-1031.
- Beaugrand, G. 2004a. Monitoring marine plankton ecosystems. I: Description of an ecosystem approach based on plankton indicators. *Marine Ecology Progress Series*, 269: 69-81.
- Beaugrand, G. 2004b. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245-262.
- Beaugrand, G. 2005. Monitoring pelagic ecosystems using plankton indicators. *Ices Journal of Marine Science*, 62: 333-338.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature*, 426: 661-664.
- Beaugrand, G., Edwards, M., and H  laou  t, P. 2019. An ecological partition of the Atlantic Ocean and its adjacent seas. *Progress in Oceanography*, 173: 86-102.

- Beaugrand, G., Edwards, M., and Legendre, L. 2010. Marine biodiversity, ecosystem functioning, and carbon cycles. *Proceedings of the National Academy of Sciences*, 107: 10120-10124.
- Beaugrand, G., Harlay, X., and Edwards, M. 2014. Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series*, 502: 85-104.
- Beaugrand, G., and Ibanez, F. 2004. Monitoring marine plankton ecosystems. II: Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Marine Ecology Progress Series*, 284: 35-47.
- Beaugrand, G., and Ibañez, F. 2002. Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. *Marine Ecology Progress Series*, 232: 197-211.
- Beaugrand, G., Ibañez, F., Lindley, J. A., and Reid, P. C. 2002a. Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Mar. Ecol. Prog. Ser.*, 232: 179-195.
- Beaugrand, G., and Kirby, R. R. 2010. Climate, plankton and cod. *Global Change Biology*, 16: 1268-1280.
- Beaugrand, G., Luczak, C., and Edwards, M. 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology*, 15: 1790-1803.
- Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. 2002b. Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science*, 296: 1692-1694.
- Bechmann, R. K., Arnberg, M., Bamber, S., Lyng, E., Westerlund, S., Rundberget, J. T., Kringstad, A., et al. 2020. Effects of exposing shrimp larvae (*Pandalus borealis*) to aquaculture pesticides at field relevant concentrations, with and without food limitation. *Aquatic Toxicology*, 222.
- Bechmann, R. K., Arnberg, M., Gomiero, A., Westerlund, S., Lyng, E., Berry, M., Agustsson, T., et al. 2019. Gill damage and delayed mortality of Northern shrimp (*Pandalus borealis*) after short time exposure to anti-parasitic veterinary medicine containing hydrogen peroxide. *Ecotoxicology and Environmental Safety*, 180: 473-482.
- Bechmann, R. K., Larsen, B. K., Taban, I. C., Hellgren, L. I., Møller, P., and Sanni, S. 2010a. Chronic exposure of adults and embryos of *Pandalus borealis* to oil causes PAH accumulation, initiation of biomarker responses and an increase in larval mortality. *Mar Pollut Bull*, 60: 2087-2098.
- Bechmann, R. K., Lyng, E., Westerlund, S., Bamber, S., Berry, M., Arnberg, M., Kringstad, A., et al. 2018. Early life stages of Northern shrimp (*Pandalus borealis*) are sensitive to fish feed containing the anti-parasitic drug diflubenzuron. *Aquatic Toxicology*, 198: 82-91.
- Bechmann, R. K., Taban, I. C., Westerlund, S., Godal, B. F., Arnberg, M., Vingen, S., Ingvarsdottir, A., et al. 2010b. Effects of ocean acidification on early life stages of shrimp (*Pandalus borealis*) and mussel (*Mytilus edulis*). *Journal of Toxicology and Environmental Health, Part A* 74: 424-438.
- Bedford, J., Johns, D., and McQuatters-Gollop, A. 2018. A century of change in North Sea plankton communities explored through integrating historical datasets. *Ices Journal of Marine Science*, 76: 104-112.
- Bedford, J., Ostle, C., Johns, D. G., Atkinson, A., Best, M., Bresnan, E., Machairopoulou, M., et al. 2020. Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. *Global Change Biology*, 26: 3482-3497.
- Behrenfeld, M. J. 2010. Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms. *Ecology*, 91: 977-989.
- Behrenfeld, M. J., and Boss, E. S. 2014. Resurrecting the ecological underpinnings of ocean plankton blooms.

- In Annual Review of Marine Science*, pp. 167-194. Ed. by C. A. Carlson, and J. Giovannoni. CRC Press, Boca Raton, FL.
- Behrenfeld, M. J., and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, 42: 1-20.
- Bekkevold, D., Berg, F., Polte, P., Bartolino, V., Ojaveer, H., Mosegaard, H., Farrell, E., et al. In press. Genetic stock identification in Atlantic herring (*Clupea harengus*): genome analysis provides new tools for identifying management units and complex migration dynamics. *ICES J Mar Sci*.
- Benedetti, F., Gasparini, S., and Ayata, S.-D. 2015. Identifying copepod functional groups from species functional traits. *Journal of Plankton Research*, 38: 159-166.
- Benedetti, F., Vogt, M., Righetti, D., Guilhaumon, F., and Ayata, S.-D. 2018. Do functional groups of planktonic copepods differ in their ecological niches? *Journal of Biogeography*, 45: 604-616.
- Berg, P. R., Jorde, P. E., Glover, K. A., Dahle, G., Taggart, J. B., Korsbrekke, K., Dingsør, G. E., et al. 2020. Genetic structuring in Atlantic haddock contrasts with current management regimes. *Ices Journal of Marine Science*, 78: 1-13.
- Bergman, M. J. N., and van Santbrink, J. W. 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. *Ices Journal of Marine Science*, 57: 1321-1331.
- Bergstad, O., and Høines, Å. 2001. Effects of exploitation on age and size structure of sandeel, *Ammodytes marinus*, populations in the North Sea. *Archive of Fishery and Marine Research*, 49: 3-18.
- Bergstad, O. A., Høines, Å. S., and Jørgensen, T. 2002. Growth of sandeel, *Ammodytes marinus*, in the northern North Sea and Norwegian coastal waters. *Fisheries Research*, 56: 9-23.
- Bergstad, O. A., Wik, D. A. J., and Hildre, O. 2003. Predator-Prey Relationships and Food Sources of the Skagerrak Deep-water Fish Assemblage. *Journal of Northwest Atlantic Fishery Science*, 31: 165-180.
- Bergström, B. I. 2000. The biology of *Pandalus*. *Advances in Marine Biology*, 38: 57-245.
- Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A., Dencker, T. S., Sólmundsson, J., Punzón, A., et al. 2019. Marine fish traits follow fast-slow continuum across oceans. *Scientific Reports*, 9: 17878.
- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. *Fisheries Investigations Series II*. Ministry of Agriculture, Fisheries and Food, London, UK.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., et al. 2000. Impact of fishing on size composition and diversity of demersal fish communities. *Ices Journal of Marine Science*, 57: 558-571.
- Blain, C. O., Hansen, S. C., and Shears, N. T. 2021. Coastal darkening substantially limits the contribution of kelp to coastal carbon cycles. *Global Change Biology*, 27: 5547-5563.
- Blaxter, J. H. S. 1965. The feeding herring larvae and their ecology in relation to feeding. *CalCOFI Reports*, 10: 79-88.
- Blaxter, J. H. S., and Hunter, J. R. 1982. The Biology of the Clupeoid Fishes. *In Advances in Marine Biology*, pp. 1-223. Ed. by J. H. S. Blaxter, F. S. Russell, and M. Yonge. Academic Press.
- Bluemel, J. K., Fischer, S. H., Kulka, D. W., Lynam, C. P., and Ellis, J. R. 2022. Decline in Atlantic wolffish *Anarhichas lupus* in the North Sea: Impacts of fishing pressure and climate change. *J Fish Biol*, 100: 253-267.

- Boers, N. 2021. Observation-based early-warning signals for a collapse of the Atlantic Meridional Overturning Circulation. *Nature Climate Change*, 11: 680-+.
- Bonnet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., Ceballos, S., et al. 2005. An overview of *Calanus helgolandicus* ecology in European waters. *Progress in Oceanography*, 65: 1-53.
- Breitbart, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., et al. 2018. Declining oxygen in the global ocean and coastal waters. *Science*, 359: eaam7240.
- Brockmann, U. H., Laane, R. W. P. M., and Postma, J. 1990. Cycling of nutrient elements in the North Sea. *Netherlands Journal of Sea Research*, 26: 239-264.
- Brodeur, R. D., Hunsicker, M. E., Hann, A., and Miller, T. W. 2019. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources. *Marine Ecology Progress Series*, 617-618: 149-163.
- Brody, S. R., Lozier, M. S., and Dunne, J. P. 2013. A comparison of methods to determine phytoplankton bloom initiation. *Journal of Geophysical Research: Oceans*, 118: 2345-2357.
- Bromley, P. J., Watson, T., and Hislop, J. R. G. 1997. Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. *Ices Journal of Marine Science*, 54: 846-853.
- Brose, U., Dunne, J. A., Montoya, J. M., Petchey, O. L., Schneider, F. D., and Jacob, U. 2012. Climate change in size-structured ecosystems. *Philos Trans R Soc Lond B Biol Sci*, 367: 2903-2912.
- Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E., and Pauly, D. 2012. Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia*, 690: 3-20.
- Browman, H. I. 2016. Applying organized scepticism to ocean acidification research Introduction. *Ices Journal of Marine Science*, 73: 529-536.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. 2004. Toward a metabolic theory of ecology. *Ecology*, 85: 1771-1789.
- Brun, P., Payne, M. R., and Kiørboe, T. 2017. A trait database for marine copepods. *Earth Syst. Sci. Data*, 9: 99-113.
- Brunel, T., Damme, C., Samson, M., and Dickey-Collas, M. 2017. Quantifying the influence of geography and environment on the northeast Atlantic mackerel spawning distribution. *Fisheries Oceanography*, 27.
- Brunel, T., and Dickey-Collas, M. 2010. Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. *Marine Ecology Progress Series*, 405: 15-28.
- Bucklin, A., McGillicuddy, D. J., Wiebe, P. H., and Davis, C. S. 2015. Habitat usage by the cryptic copepods *Pseudocalanus moultoni* and *P. newmani* on Georges Bank (Northwest Atlantic). *Continental Shelf Research*, 111: 83-94.
- Buhl-Mortensen, L., Ellingsen, K. E., Buhl-Mortensen, P., Skaar, K. L., and Gonzalez-Mirelis, G. 2016. Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition. *Ices Journal of Marine Science*, 73: i98-i114.

- Burson, A., Stomp, M., Akil, L., Brussaard, C. P. D., and Huisman, J. 2016. Unbalanced reduction of nutrient loads has created an offshore gradient from phosphorus to nitrogen limitation in the North Sea. *Limnology and Oceanography*, 61: 869-888.
- Byrkjeland, S. 2015. Hekkande sjøfugl i Hordaland 2014. Forvaltingsplan for 69 sjøfuglreservat, samt oppdatert bestandsoverslag for dei ulike sjøfuglartane i fylket. Fylkesmannen i Hordaland, MVA-rapport x/2015.
- Båtevik, T. 2020. Estimating natural mortality rates for northern shrimp (*Pandalus borealis*) from a wide range of its latitudinal distribution in the Northeast Atlantic. Master Thesis. University of Bergen, Department of Biological Science. 79 pp.
- Calbet, A. 2008. The trophic roles of microzooplankton in marine systems. *Ices Journal of Marine Science*, 65: 325-331.
- Calbet, A., and Landry, M. R. 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography*, 49: 51-57.
- Canning, S. J., Santos, M. B., Reid, R. J., Evans, P. G. H., Sabin, R. C., Bailey, N., and Pierce, G. J. 2008. Seasonal distribution of white-beaked dolphins (*Lagenorhynchus albirostris*) in UK waters with new information on diet and habitat use. *Journal of the Marine Biological Association of the United Kingdom*, 88: 1159-1166.
- Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., McQuatters-Gollop, A., et al. 2018. A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, 24: E352-E364.
- Carlotti, F., Krause, M., and Radach, G. 1993. Growth and development of *Calanus finmarchicus* related to the influence of temperature: Experimental results and conceptual model. *Limnology and Oceanography*, 38: 1125-1134.
- Castellani, C., Irigoien, X., Harris, R. P., and Holliday, N. P. 2007. Regional and temporal variation of *Oithona* spp. biomass, stage structure and productivity in the Irminger Sea, North Atlantic. *Journal of Plankton Research*, 29: 1051-1070.
- Castellani, C., Irigoien, X., Mayor, D. J., Harris, R. P., and Wilson, D. 2008. Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. *Journal of Plankton Research*, 30: 1095-1116.
- Castellani, C., Licandro, P., Fileman, E., di Capua, I., and Mazzocchi, M. G. 2015. *Oithona similis* likes it cool: evidence from two long-term time series. *Journal of Plankton Research*, 38: 703-717.
- Charrier, G., Coombs, S. H., McQuinn, I. H., and Laroche, J. 2007. Genetic structure of whiting *Merlangius merlangus* in the northeast Atlantic and adjacent waters. *Marine Ecology Progress Series*, 330: 201-211.
- Chassot, E., Bonhommeau, S., Dulvy, N. K., Mélin, F., Watson, R., Gascuel, D., and Le Pape, O. 2010. Global marine primary production constrains fisheries catches. *Ecology Letters*, 13: 495-505.
- Christie, H., Norderhaug, K., and Fredriksen, S. 2009. Macrophytes as habitat for fauna. *Marine Ecology-progress Series - MAR ECOL-PROGR SER*, 396: 231-243.
- Church, G., Furness, R., Tyler, G., Gilbert, L., and Votier, S. 2019. Change in the North Sea ecosystem from the 1970s to the 2010s: great skua diets reflect changing forage fish, seabirds, and fisheries. *Ices Journal of Marine Science*, 76.
- Ciavatta, S., Kay, S., Saux-Picart, S., Butenschön, M., and Allen, J. I. 2016. Decadal reanalysis of

- biogeochemical indicators and fluxes in the North West European shelf-sea ecosystem. *Journal of Geophysical Research: Oceans*, 121: 1824-1845.
- Clausen, L., Rindorf, A., Deurs, M., Dickey-Collas, M., Hintzen, N. T., and Arlinghaus, R. 2018. Shifts in North Sea forage fish productivity and potential fisheries yield. *Journal of Applied Ecology*, 55: 1092-1101.
- Collie, J. S., Escanero, G. A., and Valentine, P. C. 2000. Photographic evaluation of the impacts of bottom fishing on benthic epifauna. *Ices Journal of Marine Science*, 57: 987-1001.
- Comeau, S., Carpenter, R. C., and Edmunds, P. J. 2013. Coral reef calcifiers buffer their response to ocean acidification using both bicarbonate and carbonate. *Proceedings of the Royal Society B: Biological Sciences*, 280: 20122374.
- Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., Mianzan, H. W., et al. 2013. Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences*, 110: 1000-1005.
- Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H. D., Sutherland, K. R., et al. 2012. Questioning the Rise of Gelatinous Zooplankton in the World's Oceans. *Bioscience*, 62: 160-169.
- Condon, R. H., Lucas, C. H., Pitt, K. A., and Uye, S. I. 2014. Jellyfish blooms and ecological interactions. *Marine Ecology Progress Series*, 510: 109-110.
- Continuous Plankton Recorder Survey 2022. Continuous Plankton Recorder Survey, <https://www.cprsurvey.org/>.
- Cook, A. S. C. P., Dadam, D., Mitchell, I., Ross-Smith, V. H., and Robinson, R. A. 2014. Indicators of seabird reproductive performance demonstrate the impact of commercial fisheries on seabird populations in the North Sea. *Ecological Indicators*, 38: 1-11.
- Copernicus Marine Services. 2021. Copernicus Marine Services.
- Corkett, C. J., and McLaren, I. A. 1979. The Biology of *Pseudocalanus*. In *Advances in Marine Biology*, pp. 1-231. Ed. by F. S. Russell, and M. Yonge. Academic Press.
- Cormon, X., Ernande, B., Kempf, A., Vermard, Y., and Marchal, P. 2016. North Sea saithe *Pollachius virens* growth in relation to food availability, density dependence and temperature. *Marine Ecology Progress Series*, 542: 141-151.
- Cormon, X., Loots, C., Vaz, S., Vermard, Y., and Marchal, P. 2014. Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. *Ices Journal of Marine Science*, 71: 1342-1355.
- Cornils, A., and Held, C. 2014. Evidence of cryptic and pseudocryptic speciation in the *Paracalanus parvus* species complex (Crustacea, Copepoda, Calanoida). *Frontiers in Zoology*, 11: 19.
- Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B., and Olson, D. B. 2000. Connectivity of Marine Populations: Open or Closed? *Science*, 287: 857-859.
- Cresci, A., Perrichon, P., Durif, C. M. F., Sørhus, E., Johnsen, E., Bjelland, R., Larsen, T., et al. 2022. Magnetic fields generated by the DC cables of offshore wind farms have no effect on spatial distribution or swimming behavior of lesser sandeel larvae (*Ammodytes marinus*). *Marine Environmental Research*, 176: 105609.
- Crouch, K. E., Blanco-Bercial, L., Richardson, D. E., Copley, N. J., Wiebe, P. H., and Bucklin, A. 2020. Species-specific patterns of distribution and abundance of the cryptic copepods *Pseudocalanus moultoni* and

- P. newmani on Georges Bank (NW Atlantic Ocean) during spring 1995–2012. *Continental Shelf Research*, 208: 104242.
- Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A., et al. 2011. Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. *Science*, 334: 1703-1706.
- Cushing, D. H. 1988. *The provident sea*, Cambridge University Press, Cambridge.
- Cushing, D. H. 1990. Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. *In* *Advances in Marine Biology*, pp. 249-293. Ed. by J. H. S. Blaxter, and A. J. Southward. Academic Press.
- Cushing, D. H. 1992. A short history of the Downs stock of herring. *Ices Journal of Marine Science*, 49: 437-443.
- Daewel, U., Peck, M., and Schrum, C. 2011. Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: An individual-based modelling approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 426-443.
- Daly, K. L., Passow, U., Chanton, J., and Hollander, D. 2016. Assessing the impacts of oil-associated marine snow formation and sedimentation during and after the Deepwater Horizon oil spill. *Anthropocene*, 13: 18-33.
- Das, K., Lepoint, G., Leroy, Y., and Bouqueneau, J. M. 2003. Marine mammals from the southern North Sea: feeding ecology data from delta C-13 and delta N-15 measurements. *Marine Ecology Progress Series*, 263: 287-298.
- Daufresne, M., Lengfellner, K., and Sommer, U. 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106: 12788-12793.
- de Boer, M. N. 2010. Spring distribution and density of minke whale *Balaenoptera acutorostrata* along an offshore bank in the central North Sea. *Marine Ecology Progress Series*, 408: 265-274.
- Demain, D. K., Gallego, A., Jaworski, A., Priede, I. G., and Jones, E. G. 2011. Diet and feeding niches of juvenile *Gadus morhua*, *Melanogrammus aeglefinus* and *Merlangius merlangus* during the settlement transition in the northern North Sea. *Journal of Fish Biology*, 79: 89-111.
- Denis, J., Vallet, C., Courcot, L., Lefebvre, V., Caboche, J., Antajan, E., Marchal, P., et al. 2016. Feeding strategy of Downs herring larvae (*Clupea harengus* L.) in the English Channel and North Sea. *Journal of Sea Research*, 115: 33-46.
- Denman, K. L., and Peña, M. A. 2002. The response of two coupled one-dimensional mixed layer/planktonic ecosystem models to climate change in the NE subarctic Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49: 5739-5757.
- Dickey-Collas, M., Bolle, L. J., van Beek, J. K. L., and Erftemeijer, P. L. A. 2009. Variability in transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of Downs herring larvae. *Marine Ecology Progress Series*, 390: 183-194.
- Dickey-Collas, M., Hessen, H., and Ellis, J. 2015. Shads, herring, pilchard, sprat (*Clupeidae*). *In* *Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea*, p. 139 - 151. Ed. by H. Heesen, N. Daan, and J. Ellis. Wageningen Academic Publishers and KNNV Publishing.
- Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., Corten, A., et al. 2010. Lessons learned from stock collapse and recovery of North Sea herring: a review. *Ices Journal of*

Marine Science, 67: 1875-1886.

Direktoratgruppen vanndirektivet 2018. Veileder 02:2018 Klassifisering av miljøtilstand i vann.

<https://www.vannportalen.no/veiledere/klassifiseringsveileder/>.

Dobson, A., Lafferty, K. D., Kuris, A. M., Hechinger, R. F., and Jetz, W. 2008. Homage to Linnaeus: How many parasites? How many hosts? *Proceedings of the National Academy of Sciences*, 105: 11482-11489.

Doney, S. C. 2006. Plankton in a warmer world. *Nature*, 444: 695-696.

dos Santos Schmidt, T. C., Slotte, A., Olafsdottir, A. H., Nøttestad, L., Jansen, T., Jacobsen, J. A., í Homrum, E., et al. In prep. Atlantic mackerel (*Scomber scombrus*) migrates farther north to spawn under the current warm climate scenario.

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., Erbe, C., et al. 2021. The soundscape of the Anthropocene ocean. *Science*, 371: eaba4658.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45: 1029-1039.

Dupont-Prinet, A., Pillet, M., Chabot, D., Hansen, T., Tremblay, R., and Audet, C. 2013. Northern shrimp (*Pandalus borealis*) oxygen consumption and metabolic enzyme activities are severely constrained by hypoxia in the Estuary and Gulf of St. Lawrence. *Journal of Experimental Marine Biology and Ecology*, 448: 298-307.

Dupont, N., and Aksnes, D. L. 2013. Centennial changes in water clarity of the Baltic Sea and the North Sea. *Estuarine, Coastal and Shelf Science*, 131: 282-289.

Dupont, S., and Pörtner, H.-O. 2013. A snapshot of ocean acidification research. *Marine Biology*, 160: 1765-1771.

Durant, J. M., Hjermann, D. Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N., and Stenseth, N. C. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters*, 8: 952-958.

Durant, J. M., Molinero, J.-C., Ottersen, G., Reygondeau, G., Stige, L. C., and Langangen, Ø. 2019. Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. *Scientific Reports*, 9: 15213.

Daan, N. 1989. Data base report of the stomach sampling project 1981. ICES Cooperative Research Report No. 164. pp. 144. <https://doi.org/10.17895/ices.pub.4533> .

Daan, N. 2001. The IBTS database: a plea for quality control. ICES CM 2001/T:03.

Daan, N., Gislason, H., G. Pope, J., and C. Rice, J. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *Ices Journal of Marine Science*, 62: 177-188.

Edwards, M., and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430: 881-884.

EFESE. 2020. l'Évaluation française des écosystèmes et des services écosystémiques [French assessment of ecosystems and ecosystems services]. Accessed on the internet at <https://www.ecologie.gouv.fr/evaluationfrancaise-des-ecosystemes-et-des-services-ecosystemiques> on 29 March 2022.

- Ehrich, S., and Stransky, C. 2001. Spatial and temporal changes in the southern species component of North Sea Bottom fish assemblages. *Senckenbergiana maritima*, 31: 143-150.
- Eiane, K., Aksnes, D. L., BagØien, E., and Kaartvedt, S. 1999. Fish or jellies—a question of visibility? *Limnology and Oceanography*, 44: 1352-1357.
- Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., et al. 2017. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *Ices Journal of Marine Science*, 74: 847-865.
- Ellingsen, K. E., Yoccoz, N. G., Tveraa, T., Hewitt, J. E., and Thrush, S. F. 2017. Long-term environmental monitoring for assessment of change: measurement inconsistencies over time and potential solutions. *Environmental Monitoring and Assessment*, 189: 595.
- Engelhard, G. H., Blanchard, J. L., Pinnegar, J. K., van der Kooij, J., Bell, E. D., Mackinson, S., and Righton, D. A. 2013. Body condition of predatory fishes linked to the availability of sandeels. *Marine Biology*, 160: 299-308.
- Engelhard, G. H., Ellis, J. R., Payne, M. R., ter Hofstede, R., and Pinnegar, J. K. 2010. Ecotypes as a concept for exploring responses to climate change in fish assemblages. *Ices Journal of Marine Science*, 68: 580-591.
- Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. 2014. Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biology*, 20: 2473-2483.
- Ershova, E. A., Nyeggen, M. U., Yurikova, D. A., and Søreide, J. E. 2021. Seasonal dynamics and life histories of three sympatric species of *Pseudocalanus* in two Svalbard fjords. *Journal of Plankton Research*, 43: 209-223.
- EU 2015. Reference points for Europe's Fish Stocks.
- Evans, C. D., Chapman, P. J., Clark, J. M., Monteith, D. T., and Cresser, M. S. 2006. Alternative explanations for rising dissolved organic carbon export from organic soils. *Global Change Biology*, 12: 2044-2053.
- Evans, L. E., Hirst, A. G., Kratina, P., and Beaugrand, G. 2020. Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography*, 43: 581-590.
- Falkenhaug, T. 1991. Prey composition and feeding rate of *Sagitta elegans* var. *arctica* (chaetognatha) in the Barents Sea in early summer. *Polar Research*, 10: 487-506.
- Falkenhaug, T., Broms, C., BagØien, E., and Nikolioudakis, N. 2022. Temporal Variability of Co-occurring *Calanus finmarchicus* and *C. helgolandicus* in Skagerrak. *Frontiers in Marine Science*, 9: 779335.
- Falkenhaug, T., and Dalpadado, P. 2014. Diet composition and food selectivity of sprat (*Sprattus sprattus*) in Hardangerfjord, Norway. *Marine Biology Research*, 10: 203-215.
- Farcas, A., Powell, C. F., Brookes, K. L., and Merchant, N. D. 2020. Validated shipping noise maps of the Northeast Atlantic. *Science of The Total Environment*, 735: 139509.
- Fauchald, P. 2010. Predator-prey reversal: A possible mechanism for ecosystem hysteresis in the North Sea? *Ecology*, 91: 2191-2197.
- Fauchald, P., Skov, H., Skern-Mauritzen, M., Hausner, V. H., Johns, D., and Tveraa, T. 2011a. Scale-dependent response diversity of seabirds to prey in the North Sea. *Ecology*, 92: 228-239.
- Fauchald, P., Skov, H., Skern-Mauritzen, M., Johns, D., and Tveraa, T. 2011b. Wasp-Waist Interactions in the

North Sea Ecosystem. Plos One, 6.

Ferreira, J. G., Andersen, J. H., Borja, A., Bricker, S. B., Camp, J., Cardoso da Silva, M., Garcés, E., et al. 2011. Overview of eutrophication indicators to assess environmental status within the European Marine Strategy Framework Directive. *Estuarine, Coastal and Shelf Science*, 93: 117-131.

Finne, M., and Fjellbakk, Å. 2013. Bestandstrender hos sjøfugl på Østfoldkysten, 1993-2012. Fylkesmannen i Østfold, Miljøvern avdelingen. Rapport 3/13.

Fisher, J. A. D., Frank, K. T., and Leggett, W. C. 2010. Global variation in marine fish body size and its role in biodiversity-ecosystem functioning. *Marine Ecology Progress Series*, 405: 1-13.

Floeter, J., Kempf, A., Vinther, M., Schrum, C., and Temming, A. 2005. Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator? *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 1853-1864.

Floeter, J., and Temming, A. 2003. Explaining diet composition of North Sea cod (*Gadus morhua*): prey size preference vs. prey availability. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 140-150.

Fogarty, M. J., Myers, R. A., and Bowen, K. G. 2001. Recruitment of cod and haddock in the North Atlantic: a comparative analysis. *Ices Journal of Marine Science*, 58: 952-961.

Forward, R. B., and Tankersley, R. A. 2001. Selective tidal-stream transport of marine animals *Oceanography and Marine Biology, an Annual Review*, 39: 305-353.

Frank, K. T., and Brickman, D. 2001. Contemporary management issues confronting fisheries science. *Journal of Sea Research*, 45: 173-187.

Fransner, F., Fröb, F., Tjiputra, J., Goris, N., Lauvset, S. K., Skjelvan, I., Jeansson, E., et al. 2022. Acidification of the Nordic Seas. *Biogeosciences*, 19: 979-1012.

Fransz, H. G., Colebrook, J. M., Gamble, J. C., and Krause, M. 1991. The zooplankton of the north sea. *Netherlands Journal of Sea Research*, 28: 1-52.

Frantzen, M., Bytingsvik, J., Tassara, L., Reinardy, H. C., Refseth, G. H., Watts, E. J., and Evenset, A. 2020. Effects of the sea lice bath treatment pharmaceuticals hydrogen peroxide, azamethiphos and deltamethrin on egg-carrying shrimp (*Pandalus borealis*). *Marine Environmental Research*, 159: 105007.

Frantzen, S., Boitsov, S., Dehnhard, N., Duinker, A., Grøsvik, B. E., Heimstad, E., Hjermann, D., et al. 2022. Forurensning i de norske havområdene - Barentshavet, Norskehavet og Nordsjøen (Pollution in the Norwegian sea areas - Barents Sea, Norwegian Sea and North Sea). Rapport fra havforskningen nr. 2022-3.

Franzè, G., Falkenhaug, T., Nash, R., J., A., Gundersen, K., Heldal, H. E., Meier, S., et al. 2021. North Sea Ecosystem Cruise 2020, Cruise Report. Institute of Marine Research Cruise number JH2020205. Toktrapport/ Havforskningsinstituttet/ ISSN1503 6294/Nr.2–2021.

Frederiksen, M., Anker-Nilssen, T., Beaugrand, G., and Wanless, S. 2013. Climate, copepods and seabirds in the boreal Northeast Atlantic - current state and future outlook. *Global Change Biology*, 19: 364-372.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., and Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, 75: 1259-1268.

Frederiksen, M., Wright, P. J., Harris, M. P., Martin Heubeck, R. A. M., and Wanless, S. 2005. Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Marine Ecology Progress Series*, 300: 201-211.

- Frelat, R., Kortsch, S., Kröncke, I., Neumann, H., Nordström, M. C., Olivier, P. E. N., and Sell, A. F. 2022. Food web structure and community composition: a comparison across space and time in the North Sea. *Ecography*, 2022.
- Frid, C., Clark, R. A., and Hall, J. A. 1999. Long-term changes in the benthos on a heavily fished ground off the NE coast of England. *Marine Ecology-progress Series - MAR ECOL-PROGR SER*, 188: 13-20.
- Fromentin, J.-M., and Planque, B. 1996. Calanus and environment in the eastern North Atlantic. 2. Role of the North Atlantic Oscillation on Calanus finmarchicus and C. helgolandicus. *Marine Ecology Progress Series*, 134: 11-118.
- Frost, B. W. 1989. A taxonomy of the marine calanoid copepod genus Pseudocalanus. *Canadian Journal of Zoology*, 67: 525-551.
- Frölicher, T. L., Fischer, E. M., and Gruber, N. 2018. Marine heatwaves under global warming. *Nature*, 560: 360-364.
- Fuchs, R., Herold, M., Verburg, P. H., Clevers, J. G. P. W., and Eberle, J. 2015. Gross changes in reconstructions of historic land cover/use for Europe between 1900 and 2010. *Global Change Biology*, 21: 299-313.
- Fujii, T. 2016. Potential influence of offshore oil and gas platforms on the feeding ecology of fish assemblages in the North Sea. *Marine Ecology Progress Series*, 542: 167-186.
- Furness, R. W. 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *Ices Journal of Marine Science*, 59: 261-269.
- Furness, R. W., and Tasker, M. L. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, 202: 253-264.
- Gammelsrød, T., and Hacket, B. 1981. The circulation of the Skagerrak determined by inverse methods. *In* The Norwegian Coastal Current, Vol I, pp 311-330. Bergen.
- Gannon, D. P., Read, A., Craddock, J. E., Frstrup, K. M., and Nicolas, J. R. 1997. Feeding ecology of long-finned pilot whales Globicephala melas in the western North Atlantic. *Marine Ecology Progress Series*, 148: 1-10.
- Gao, S., Hjøllø, S. S., Falkenhaug, T., Strand, E., Edwards, M., and Skogen, M. D. 2021. Overwintering distribution, inflow patterns and sustainability of Calanus finmarchicus in the North Sea. *Progress in Oceanography*, 194: 102567.
- García Molinos, J., Burrows, M. T., and Poloczanska, E. S. 2017. Ocean currents modify the coupling between climate change and biogeographical shifts. *Scientific Reports*, 7: 1332.
- Garcia, T., Planque, B., Arneberg, P., Bogstad, B., Skagseth, Ø., and Tiedemann, M. 2020. An appraisal of the drivers of Norwegian spring-spawning herring (Clupea harengus) recruitment. *Fisheries Oceanography*, 30: 159-173.
- Garthe, S., Camphuysen, K., and Furness, R. W. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Marine Ecology Progress Series*, 136: 1-11.
- Garzke, J., Ismar, S. M. H., and Sommer, U. 2015. Climate change affects low trophic level marine consumers: warming decreases copepod size and abundance. *Oecologia*, 177: 849-860.

- Gauld, J. A. 1990. Movements of lesser sandeels (*Ammodytes marinus* Raitt) tagged in the northwestern North Sea. *Ices Journal of Marine Science*, 46: 229-231.
- Gibbons, M. J., and Richardson, A. J. 2009. Patterns of jellyfish abundance in the North Atlantic. *Hydrobiologia*, 616: 51-65.
- Gibbons, M. J., and Richardson, A. J. 2013. Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. *Journal of Plankton Research*, 35: 929-938.
- Gíslason, D., Helyar, S. J., Óskarsson, G. J., Ólafsdóttir, G., Slotte, A., Jansen, T., Jacobsen, J. A., et al. 2020. The genetic composition of feeding aggregations of the Atlantic mackerel (*Scomber scombrus*) in the central north Atlantic: a microsatellite loci approach. *Ices Journal of Marine Science*, 77: 604-612.
- Gislason, H. 1994. Ecosystem effects of fishing activities in the North Sea. *Marine Pollution Bulletin*, 29: 520-527.
- González-Irusta, J. M., and Wright, P. J. 2016. Spawning grounds of haddock (*Melanogrammus aeglefinus*) in the North Sea and West of Scotland. *Fisheries Research*, 183: 180-191.
- Gorokhova, E., Lehtiniemi, M., Lesutiene, J., Strake, S., Uusitalo, L., Demereckiene, N., and Amid, C. 2013. Zooplankton mean size and total abundance. HELCOM Core indicator Report. Retrieved in Dec 2019 from www.helcom.fi. ICES Document December.
- Graham, W. M., Pagès, F., and Hamner, W. M. 2001. A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, 451: 199-212.
- Green, B. S. 2008. Maternal effects in fish populations. *Advances in Marine Biology*, 54: 1-105.
- Greenstreet, S. P. R., Bryant, A. D., Broekhuizen, N., Hall, S. J., and Heath, M. R. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *Ices Journal of Marine Science*, 54: 243-266.
- Greenstreet, S. P. R., McMillan, J. A., and Armstrong, E. 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? *Ices Journal of Marine Science*, 55: 121-133.
- Greenstreet, S. P. R., and Rogers, S. I. 2006. Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. *Ices Journal of Marine Science*, 63: 573-593.
- Greenstreet, S. P. R., Spence, F. E., and McMillan, J. A. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish species assemblage between 1925 and 1996. *Fisheries Research*, 40: 153-183.
- Grémillet, D., Ponchon, A., Paleczny, M., Palomares, M.-L. D., Karpouzi, V., and Pauly, D. 2018. Persisting Worldwide Seabird-Fishery Competition Despite Seabird Community Decline. *Current Biology*, 28: 4009-4013.e4002.
- Grift, R. E., Rijnsdorp, A. D., Barot, S., Heino, M., and Dieckmann, U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology Progress Series*, 257: 247-257.
- Gustafsson, B., and Stigebrandt, A. 1996. Dynamics of the freshwater-influenced surface layers in the Skagerrak. *Journal of Sea Research*, 35: 39-53.
- Hagenlund, M. 2011. Effekten av næringstilgang og havtemperatur på bestandsstørrelsen av krykkje (Rissa

tridactyla), i tre norske kolonier. Bachelor of Science Thesis, Hedemark College, 35pp.

Hammond, P. S., Hall, A. J., and Prime, J. H. 1994. THE DIET OF GRAY SEALS AROUND ORKNEY AND OTHER ISLAND AND MAINLAND SITES IN NORTH-EASTERN SCOTLAND. *Journal of Applied Ecology*, 31: 340-350.

Hamre, J. 1990. Life history and exploitation of the Norwegian spring spawning herring. *In* Biology and Fisheries of the Norwegian Spring Spawning Herring and Blue Whiting in the Northeast Atlantic. Proceedings of the fourth Soviet-Norwegian Symposium – Bergen, 12–16 June 1989., pp. 5-39. Ed. by T. Monstad.

Hansen, A., Westgaard, J.-I., Søvik, G., Hanebrekke, T., Nilssen, E. M., Jorde, P. E., Albretsen, J., et al. 2021. Genetic differentiation between inshore and offshore populations of northern shrimp (*Pandalus borealis*). *Ices Journal of Marine Science*.

Hardison, S., Perretti, C. T., DePiper, G. S., and Beet, A. 2019. A simulation study of trend detection methods for integrated ecosystem assessment. *Ices Journal of Marine Science*.

Hardy, A. C. 1939. Ecological investigations with the continuous plankton recorder: object, plan and methods. *Hull Bulletins of Marine Ecology*, 1: 1-57.

Hardy, A. C., Agriculture, G. B. M. o., and Fisheries 1924. The Herring in Relation to Its Animate Environment: The food and feeding habits of the herring with special reference to the east coast of England, H.M. Stationery Office.

Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., Sandø, A. B., Drange, H., Hansen, B., et al. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography*, 80: 149-162.

Hays, G. C., Doyle, T. K., and Houghton, J. D. R. 2018. A paradigm shift in the trophic Importance of jellyfish? *Trends in Ecology & Evolution*, 33: 874-884.

Heath, M. R., and Lough, R. G. 2007. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fisheries Oceanography*, 16: 169-185.

Heath, M. R. 2007. The consumption of zooplankton by early life stages of fish in the North Sea. *Ices Journal of Marine Science*, 64: 1650-1663.

Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., et al. 1999a. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanography*, 8: 163-176.

Heath, M. R., Beare, D. J., Dunn, J., Fraser, J. G., Hay, S. J., and Turrell, W. R. 1999b. Monitoring the effects of climate change - overwintering abundance of *Calanus finmarchicus* in the Faroe-Shetland Channel. *Fisheries Research Services Report*, 14/99.

Hébert, M.-P., Beisner, B. E., and Maranger, R. 2016. Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. *Journal of Plankton Research*, 39: 3-12.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Andrews, J. 2004. Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using generalised additive models. *Fisheries Research*, 70: 17-25.

Heino, M., Svasand, T., Nordeide, J. T., and Ottera, H. 2012. Seasonal dynamics of growth and mortality

- suggest contrasting population structure and ecology for cod, pollack, and saithe in a Norwegian fjord. *Ices Journal of Marine Science*, 69: 537-546.
- Helaouët, P., and Beaugrand, G. 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*, 345: 147-165.
- HELCOM. 2018. Zooplankton mean size and total stock. HELCOM core indicator report. URL: <https://www.helcom.fi/wp-content/uploads/2019/08/Zooplankton-mean-size-and-total-stock-HELCOM-core-indicator-2018.pdf> ISSN 2343-2543 [Accessed: Dec 2020].
- Heneghan, R., Everett, J., Blanchard, J., Sykes, P., and Richardson, A. 2021. Climate-driven zooplankton shifts could cause global declines in food quality for fish. 10.21203/rs.3.rs-953268/v1. (preprint of submitted manuscript).
- Hennige, S. J., Wicks, L. C., Kamenos, N. A., Perna, G., Findlay, H. S., and Roberts, J. M. 2015. Hidden impacts of ocean acidification to live and dead coral framework. *Proceedings of the Royal Society B: Biological Sciences*, 282: 20150990.
- Hiddink, J. G., Johnson, A. F., Kingham, R., and Hinz, H. 2011. Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. *Journal of Applied Ecology*, 48: 1441-1449.
- Hiddink, J. G., and ter Hofstede, R. 2008. Climate induced increases in species richness of marine fishes. *Global Change Biology*, 14: 453-460.
- Hinder, S. L., Hays, G. C., Edwards, M., Roberts, E. C., Walne, A. W., and Gravenor, M. B. 2012. Changes in marine dinoflagellate and diatom abundance under climate change. *Nature Climate Change*, 2: 271-275.
- Hislop, J. e. a. 2015. Gadoids *In* Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea, p. 189 - 194. Ed. by H. Heesen, N. Daan, and J. Ellis. Wageningen Academic Publishers and KNNV Publishing.
- Hislop, J. R. G. 1996. Changes in North Sea gadoid stocks. *Ices Journal of Marine Science*, 53: 1146-1156.
- Hislop, J. R. G., Robb, A. P., Bell, M. A., and Armstrong, D. W. 1991. The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. *Ices Journal of Marine Science*, 48: 139-156.
- Hixon, M. A., Johnson, D. W., and Sogard, S. M. 2013. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *Ices Journal of Marine Science*, 71: 2171-2185.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. *Rapport Procès-Verbal Reunion Conseil International pour L'Exploration de la Mer* 20: 1-228.
- Hjort, J., and Ruud, J. T. 1938. Rekefisket som naturhistorie og samfundssak. Report on Norwegian Fishery and Marine Investigations Vol. V, No. 4. 158 pp. (In Norwegian).
- Hjøllo, S. S., Skogen, M. D., and Svendsen, E. 2009. Exploring currents and heat within the North Sea using a numerical model. *Journal of Marine Systems*, 78: 180-192.
- Holden, M. J. 1978. Long-term changes in landings of fish from the North Sea. *Rapp P-V Reun Cons Int Explor Mer*, 172: 11-26.
- Holt, J., Polton, J., Huthnance, J., Wakelin, S., O'Dea, E., Harle, J., Yool, A., et al. 2018. Climate-Driven Change in the North Atlantic and Arctic Oceans Can Greatly Reduce the Circulation of the North Sea. *Geophysical Research Letters*, 45: 11,827-811,836.
- Hosia, A., and Falkenhaug, T. 2015. Invasive ctenophore *Mnemiopsis leidyi* in Norway. *Marine Biodiversity Records*, 8: e31.

- Hosia, A., Falkenhaus, T., and Naustvoll, L. J. 2014. Trends in abundance and phenology of *Aurelia aurita* and *Cyanea* spp. at a Skagerrak location, 1992-2011. *Marine Ecology Progress Series*, 498: 103-115.
- Hudon, C., Parsons, D. G., and Crawford, R. 1992. Diel Pelagic Foraging by a Pandalid Shrimp (*Pandalus montagui*) off Resolution Island (Eastern Hudson Strait). *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 565-576.
- Huse, G., Salthaug, A., and Skogen, M. D. 2008. Indications of a negative impact of herring on recruitment of Norway pout. *Ices Journal of Marine Science*, 65: 906-911.
- ICES. 1997. Database report of the Stomach Sampling project 1991. ICES Cooperative Research Report No. 219. pp. 422. <https://doi.org/10.17895/ices.pub.4626>.
- ICES. 2007. Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES Document CM 2007/ACE: 04. 159 pp.
- ICES. 2010. Report of the Benchmark Workshop on Sandeel (WKSAN), 6–10 September 2010, Copenhagen, Denmark. ICES C.M. 2010/ACOM:57. 201 pp.
- ICES. 2013. Report of the Ad hoc Group on the Distribution and Migration of Northeast Atlantic Mackerel (AGDMM) 30–31 August 2011 and 29–31 May 2012 ICES Headquarters, ICES CM 2013/ACOM:58. 215 pp.
- ICES. 2014. Final Report to OSPAR of the Joint OSPAR/ICES Ocean Acidification Study Group (SGOA). ICES CM 2014/ACOM:67. . 141 pp.
- ICES. 2017a. Report of the Benchmark on Sandeel (WKSand 2016), 31 October - 4 November 2016, Bergen, Norway. ICES CM 2016/ACOM:33. 319 pp. <https://doi.org/10.17895/ices.pub.7718>.
- ICES. 2017b. Report of the Benchmark Workshop on Norway Pout (*Trisopterus esmarkii*) in Subarea 4 and Division 3a (North Sea, Skagerrak, and Kattegat), 23–25 August 2016, Copenhagen, Denmark. ICES CM 2016/ACOM:35. 69 pp.
- ICES. 2019. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports. 1:36. . 948 pp.
- ICES. 2020a. ICES Advice on fishing opportunities, catch, and effort. Grey gurnard (*Eutrigla gurnardus*) in Subarea 4 and divisions 7.d and 3.a (North Sea, eastern English Channel, Skagerrak and Kattegat). <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2020/2020/gug.27.3a47d.pdf> .
- ICES. 2020b. ICES Advice on fishing opportunities, catch, and effort. Norway pout (*Trisopterus esmarkii*) in Subarea 4 and Division 3.a (North Sea, Skagerrak, and Kattegat). <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2020/2020/nop.27.3a4.pdf> .
- ICES. 2020c. Manual for the North Sea International Bottom Trawl Surveys. Series of ICES Survey Protocols SISP 10-IBTS 10, Revision 11. 102 pp. <http://doi.org/10.17895/ices.pub.7562> .
- ICES. 2020d. Workshop on Stock Identification of North Sea Cod (WKNSCodID). ICES Scientific Reports. 2:89. 82 pp. <http://doi.org/10.17895/ices.pub.7499> .
- ICES. 2021a. Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). In Report of the ICES Advisory Committee, 2021. ICES Advice 2021, cod.27.47d20. .
- ICES. 2021b. Greater North Sea Ecoregion – Ecosystem overview. ICES Advice: Ecosystem Overviews.

Report. <https://doi.org/10.17895/ices.advice.9434>

ICES 2021c. Greater North Sea ecoregion – Fisheries overview In Report of the ICES Advisory Committee, 2021. ICES Advice 2021, section 9.2. <https://doi.org/10.17895/ices.advice.9099> .

ICES. 2021d. Haddock (*Melanogrammus aeglefinus*) in Subarea 4, Division 6.a, and Subdivision 20 (North Sea, West of Scotland, Skagerrak). In Report of the ICES Advisory Committee, 2021. ICES Advice 2021, had.27.46a20.

ICES. 2021e. Herring Assessment Working Group for the Area South of 62° N (HAWG). ICES Scientific Reports. 3:12. 779 pp. <https://doi.org/10.17895/ices.pub.8214> .

ICES. 2021f. ICES Advice on fishing opportunities, catch, and effort. Herring (*Clupea harengus*) in Subarea 4 and divisions 3.a and 7.d, autumn spawners (North Sea, Skagerrak and Kattegat, eastern English Channel).

ICES. 2021g. ICES Advice on fishing opportunities, catch, and effort. Mackerel (*Scomber scombrus*) in subareas 1–8 and 14, and in Division 9.a (Northeast Atlantic and adjacent waters).
<https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2021/2021/mac.27.nea.pdf> .

ICES. 2021h. ICES Advice on fishing opportunities, catch, and effort. Sandeel (*Ammodytes* spp.) in divisions 4.b–c, Sandeel Area 1r (central and southern North Sea, Dogger Bank).
<https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2021/2021/san.sa.1r.pdf> .

ICES 2021i. ICES Advice on fishing opportunities, catch, and effort. Whiting (*Merlangius merlangus*) in Subarea 4 and Division 7.d (North Sea and eastern English Channel).
<https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2021/2021/whg.27.47d.pdf> .

ICES. 2021j. Norwegian Sea Ecoregion - Ecosystem Overview. <https://doi.org/10.17895/ices.advice.8188> .

ICES. 2021k. Working Group on Multispecies Assessment Methods (WGSAM; outputs from 2020 meeting). ICES Scientific Reports. 3:10. 231 pp. <https://doi.org/10.17895/ices.pub.7695> .

ICES. 2021l. Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports. 3:66. 1281 pp. <https://doi.org/10.17895/ices.pub.8211> .

ICES. 2021m. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports. 3:95. 874 pp. <http://doi.org/10.17895/ices.pub.8298> .

ICES. 2022a. Benchmark workshop on Pandalus stocks (WKPRAWN). ICES Scientific Reports. 4:20. 249 pp. <http://doi.org/10.17895/ices.pub.19714204> .

ICES. 2022b. Haddock (*Melanogrammus aeglefinus*) in Subarea 4, Division 6.a, and Subdivision 20 (North Sea, West of Scotland, Skagerrak). In Report of the ICES Advisory Committee, 2022. ICES Advice 2022, had.27.46a20. <https://doi.org/10.17895/ices.advice.19447943> .

ICES. 2022c. Joint NAFO/ICES Pandalus Assessment Working Group (NIPAG). ICES Scientific Reports. 4:38. 25 pp. <http://doi.org/10.17895/ices.pub.19692181> .

ICES. 2022d. Northern shrimp (*Pandalus borealis*) in divisions 3.a and 4.a East (Skagerrak and Kattegat and northern North Sea in the Norwegian Deep). In Report of the ICES Advisory Committee, 2022. ICES Advice, pra.27.3a4a. <https://doi.org/10.17895/ices.advice.19453658> .

ICES. 2022e. Saithe (*Pollachius virens*) in subareas 4 and 6, and in Division 3.a (North Sea, Rockall and West of Scotland, Skagerrak and Kattegat). ICES Advice: Recurrent Advice. Report.
<https://doi.org/10.17895/ices.advice.19453649.v1>

- ICES. 2022f. Whiting (*Merlangius merlangus*) in Division 3.a (Skagerrak and Kattegat). In Report of the ICES Advisory Committee, 2022. ICES Advice 2022, whg.27.3a. <https://doi.org/10.17895/ices.advice.19454252> .
- ICES. 2022g. Whiting (*Merlangius merlangus*) in Subarea 4 and Division 7.d (North Sea and eastern English Channel). In Report of the ICES Advisory Committee, 2022. ICES Advice 2022, whg.27.47d. <https://doi.org/10.17895/ices.advice.19457411> .
- ICES. 2022h. Workshop on Stock Identification of West of Scotland Sea Cod (WK6aCodID; outputs from 2021 meeting). ICES Scientific Reports. 4:5. 24 pp. <http://doi.org/10.17895/ices.pub.10031> .
- Ikpewe, I., Baudron, A., Ponchon, A., and Fernandes, P. 2020. Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. *Journal of Applied Ecology*, 58.
- Ingólfsson, O. A., and Jørgensen, T. 2020. Shorter trawls improve size selection of northern shrimp. *Canadian Journal of Fisheries and Aquatic Sciences*, 77: 202-211.
- Institute of Marine Research. 2021. Report on cruises and data stations 2020 — Oversikt over tokt og stasjoner tatt i 2020. <https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen-en-2021-10> .
- IPBES. 2020. Global Assessment Report on Biodiversity and Ecosystem Services. Accessed on the internet at <https://ipbes.net/global-assessment> on 29.03.2022.
- IPCC. 2020. The Intergovernmental Panel on Climate Change. Accessed on the internet at <https://www.ipcc.ch/> on 29 March 2022.
- IPCC. 2021. Summary for Policymakers. In: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 3–32, doi:10.1017/9781009157896.001.
- Iversen, S. A. 2002. Changes in the perception of the migration pattern of Northeast Atlantic mackerel during the last 100 years. *ICES Marine Science Symposia* 215: 382-390.
- Jakobsson, S., Evju, M., Framstad, E., Imbert, A., Lyngstad, A., Sickel, H., Sverdrup-Thygeson, A., et al. 2021. Introducing the index-based ecological condition assessment framework (IBECA). *Ecological Indicators*, 124: 107252.
- Jansen, T. 2013. Pseudocollapse and rebuilding of North Sea mackerel (*Scomber scombrus*). *Ices Journal of Marine Science*, 71: 299-307.
- Jansen, T., Campbell, A., Kelly, C., Hátún, H., and Payne, M. R. 2012. Migration and Fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter. *Plos One*, 7: e51541.
- Jansen, T., and Gislason, H. 2013. Population Structure of Atlantic Mackerel (*Scomber scombrus*). *Plos One*, 8: e64744.
- Jansen, T., Kristensen, K., van der Kooij, J., Post, S., Campbell, A., Utne, K. R., Carrera, P., et al. 2015. Nursery areas and recruitment variation of Northeast Atlantic mackerel (*Scomber scombrus*). *Ices Journal of Marine Science*, 72: 1779-1789.
- Jansen, T., Slotte, A., Christina dos Santos Schmidt, T., Reedtz Sparrevohn, C., Arge Jacobsen, J., and Sigurd Kjesbu, O. 2021. Bioenergetics of egg production in Northeast Atlantic mackerel changes the perception of fecundity type and annual trends in spawning stock biomass. *Progress in Oceanography*, 198: 102658.

- Jennings, S., Alvsvåg, J., Cotter, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., et al. 1999a. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. *Fisheries Research*, 40: 125-134.
- Jennings, S., and Blanchard, J. L. 2004. Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology*, 73: 632-642.
- Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J., and Lancaster, J. E. 2001. Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology*, 70: 459-475.
- Jennings, S., Freeman, S., Parker, E., Duplisea, D. E., and Dinmore, T. A. 2005. Ecosystem consequences of bottom fishing disturbance. *American Fisheries Society Symposium*, 41: 73-90.
- Jennings, S., Greenstreet, S., Hill, L., Piet, G., Pinnegar, J., and Warr, K. J. 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. *Marine Biology*, 141: 1085-1097.
- Jennings, S., Greenstreet, S. P. R., and Reynolds, J. D. 1999b. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, 68: 617-627.
- Jensen, H., Rindorf, A., Wright, P. J., and Mosegaard, H. 2010. Inferring the location and scale of mixing between habitat areas of lesser sandeel through information from the fishery. *Ices Journal of Marine Science*, 68: 43-51.
- Jepsen, J. U., Arneberg, P., Ims, R. A., Siwertsson, A., and Yoccoz, N. G. 2019. Test av fagsystemet for økologisk tilstand. Erfaringer fra pilotprosjekter for arktisk tundra og arktisk del av Barentshavet. NINA Rapport 1674. Norsk institutt for naturforskning.
- Jepsen, J. U., Arneberg, P., Ims, R. A., Siwertsson, A., and Yoccoz, N. G. 2020. Panel-based Assessment of Ecosystem Condition (PAEC). Technical protocol version 2. NINA Report 1890.
- Jepsen, J. U., Arneberg, P., Ims, R. A., Siwertsson, A., Yoccoz, N. G., Fauchald, P., Pedersen, Å. Ø., et al. submitted. Beyond accounting – panel-based assessment of ecosystem condition as a platform for adaptive and knowledge driven management. *Ecosystems*.
- Jiménez-Mena, B., Le Moan, A., Christensen, A., van Deurs, M., Mosegaard, H., Hemmer-Hansen, J., and Bekkevold, D. 2020. Weak genetic structure despite strong genomic signal in lesser sandeel in the North Sea. *Evolutionary Applications*, 13: 376-387.
- Johannessen, T. 2014. From an antagonistic to a synergistic predator prey perspective. *Bifurcations in marine systems.*, Academic Press, London.
- Johannessen, T., Dahl, E., Falkenhaug, T., and Naustvoll, L. J. 2011. Concurrent recruitment failure in gadoids and changes in the plankton community along the Norwegian Skagerrak coast after 2002. *Ices Journal of Marine Science*, 69: 795-801.
- Johannessen, T., and Johnsen, E. 2015. Demographically disconnected subpopulations in lesser sandeel (*Ammodytes marinus*) as basis of a high resolution spatial management system. *ICES CM*, 2015/E:12. 20 pp.
- Johannessen, T., and Johnsen, E. submitted. Post-larvae returning to natal habitats suggested as a mechanism for low demographic connectivity in lesser sandeel in the north-eastern North Sea. .

- John, E. H., Batten, S. D., Harris, R. P., and Hays, G. C. 2001. Comparison between zooplankton data collected by the Continuous Plankton Recorder survey in the English Channel and by WP-2 nets at station L4, Plymouth (UK). *Journal of Sea Research*, 46: 223-232.
- Johns, D. G., Edwards, M., Greve, W., and Sjohn, A. W. G. 2005. Increasing prevalence of the marine cladoceran *Penilia avirostris* (Dana, 1852) in the North Sea. *Helgoland Marine Research*, 59: 214-218.
- Johnsen, E. 2021. Råd for tobisfiskeriet i norsk sone for 2021. Tobistokt i Nordsjøen 23. april-16. mai 2021. Toktrapport/Havforskningsinstituttet/ISSN 15036294/Nr. 6–2021, <https://www.hi.no/resources/Toktrapport2021-nr-6.pdf> : 35 pp.
- Johnsen, E., Sørhus, E., de Jong, K., Lie, K. K., and Grøsvik, B. E. 2021. Kunnskapsstatus for havsil i norsk sone av Nordsjøen. Rapport fra havforskningen 2021-33 ISSN: 1893-4536.
- Johnsen, E., Sørhus, E., Jong, K., de, L., K. K., and Grøsvik, B. E. 2021. Status of knowledge for lesser sandeel in Norwegian zone of the North Sea. Rapport fra havforskningen. 2021-33: 44 pp. (in Norwegian)
- Jónasdóttir, S. H., and Koski, M. 2010. Biological processes in the North Sea: comparison of *Calanus helgolandicus* and *Calanus finmarchicus* vertical distribution and production. *Journal of Plankton Research*, 33: 85-103.
- Jónasdóttir, S. H., Trung, N. H., Hansen, F., and Gärtner, S. 2005. Egg production and hatching success in the calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* in the North Sea from March to September 2001. *Journal of Plankton Research*, 27: 1239-1259.
- Jónasdóttir, S. H., Visser, A. W., Richardson, K., and Heath, M. R. 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proceedings of the National Academy of Sciences*, 112: 12122-12126.
- Jones, J. B. 1992. ENVIRONMENTAL-IMPACT OF TRAWLING ON THE SEABED - A REVIEW. *New Zealand Journal of Marine and Freshwater Research*, 26: 59-67.
- Jorde, P. E., Søvik, G., Westgaard, J.-I., Albretsen, J., André, C., Hvingel, C., Johansen, T., et al. 2015. Genetically distinct populations of northern shrimp, *Pandalus borealis*, in the North Atlantic: adaptation to different temperatures as an isolation factor. *Molecular Ecology*, 24: 1742-1757.
- Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., et al. 2007. Ecology: Managing Evolving Fish Stocks. *Science*, 318: 1247-1248.
- Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P., and Karakassis, I. 2006. Global analysis and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, 311: 1-14.
- Kattner, G., Hagen, W., Lee, R. F., Campbell, R., Deibel, D., Falk-Petersen, S., Graeve, M., et al. 2007. Perspectives on marine zooplankton lipids. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 1628-1639.
- Kempf, A., Floeter, J., and Temming, A. 2009. Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006: The interplay between climate influence and predation. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 633-648.
- Kerby, T., Cheung, W., Van Oosterhout, C., and Engelhard, G. 2013. Wondering about wandering whiting: Distribution of North Sea whiting between the 1920s and 2000s. *Fisheries Research*, 145: 54–65.
- Kerby, T. K., Cheung, W. W. L., and Engelhard, G. H. 2012. The United Kingdom's role in North Sea demersal fisheries: a hundred year perspective. *Reviews in Fish Biology and Fisheries*, 22: 621-634.

- Kirby, R., Beaugrand, G., and Lindley, J. 2008. Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. *Limnology and Oceanography*, 53.
- Kirby, R., Beaugrand, G., Lindley, J., Richardson, A., Edwards, M., and Reid, P. 2007. Climate effects and benthic-pelagic coupling in the North Sea. *Marine Ecology Progress Series*, 330.
- Kirby, R. R., and Lindley, J. A. 2005. Molecular analysis of Continuous Plankton Recorder samples, an examination of echinoderm larvae in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 85: 451-459.
- Kjørboe, T. 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biological Reviews*, 86: 311-339.
- Kjesbu, O. S., Sundby, S., Sandø, A. B., Alix, M., Hjøllø, Solfrid S., Tiedemann, M., Skern-Mauritzen, M., et al. 2022. Highly mixed impacts of near-future climate change on stock productivity proxies in the North East Atlantic. *Fish and Fisheries*, 23: 601-615.
- Kleppel, G. S. 1993. On the diets of calanoid copepods. *Marine Ecology Progress Series*, 99: 183-195.
- Knutsen, H., Jorde, P. E., Blanco Gonzalez, E., Eigaard, O. R., Pereyra, R. T., Sannæs, H., Dahl, M., et al. 2014. Does population genetic structure support present management regulations of the northern shrimp (*Pandalus borealis*) in Skagerrak and the North Sea? *Ices Journal of Marine Science*, 72: 863-871.
- Koeller, P., Fuentes-Yaco, C., Platt, T., Sathyendranath, S., Richards, A., Ouellet, P., Orr, D., et al. 2009. Basin-Scale Coherence in Phenology of Shrimps and Phytoplankton in the North Atlantic Ocean. *Science* 324.
- Krause, M., and Martens, P. 1990. Distribution patterns of mesozooplankton biomass in the North Sea. *Helgolander Meeresuntersuchungen*, 44: 295-327.
- Kritzborg, E. S. 2017. Centennial-long trends of lake browning show major effect of afforestation. *Limnology and Oceanography Letters*, 2: 105-112.
- Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., et al. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology*, 19: 1884-1896.
- Kubetzki, U., and Garthe, S. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. *Marine Biology*, 143: 199-207.
- Kvadsheim, P. H., Forland, T. N., de Jong, K., Nyqvist, D., Grimsbø, E., and Sivle, L. D. 2020. Effekter av støyforurensning på havmiljø - kunnskapsstatus og forvaltningsrådgiving. FFI-RAPPORT 20/01015.
- Kvadsheim, P. H., and Sivle, L. D. 2020. Effekter av seismikk på sjøpattedyr. Sjøpattedyrutvalget, Tromsø, 22.-23. oktober 2020.
- Kvadsheim, P. H., Sivle, S. D., Hansen, R. R., and Karlsen, H. E. 2017. Effekter av menneskeskapt støy på havmiljø - rapport til Miljødirektoratet om kunnskapsstatus. FFI-RAPPORT 17/00075.
- Lafferty, K. D. 2008. Ecosystem consequences of fish parasites. *Journal of Fish Biology*, 73: 2083-2093.
- Lafferty, K. D., and Kuris, A. M. 2009. Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364: 1659-1663.
- Lambert, G., Nielsen, J. R., Larsen, L. I., and Sparholt, H. 2009. Maturity and growth population dynamics of Norway pout (*Trisopterus esmarkii*) in the North Sea, Skagerrak, and Kattegat. *Ices Journal of Marine Science*,

66: 1899-1914.

Landry, M. R. 1977. A review of important concepts in the trophic organization of pelagic ecosystems. *Helgoländer wissenschaftliche Meeresuntersuchungen*, 30: 8-17.

Larsen, S., Andersen, T., and Hessen, D. O. 2011. Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biology*, 17: 1186-1192.

Larsen, T. 2014. Sjøfuglane i Sogn og Fjordane. Ti års bestandstellingar 2004-2013. Fylkesmannen i Sogn og Fjordane Rapport nr. 6-2013

Larsen, T. 2021. Sjøfuglane i Sogn og Fjordane. Hekkebestandar i sjøfuglreservata 2014-2020. Statsforvaltaren i Vestland, miljøvernavdelinga, rapport 2-2021.

Last, J. M. 1978. The food of three species of gadoid larvae in the Eastern English Channel and Southern North Sea. *Marine Biology*, 48: 377-386.

Last, J. M. 1989. The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. *Journal of Fish Biology*, 34: 489-501.

Lauerburg, R. A. M., Temming, A., Pinnegar, J. K., Kotterba, P., Sell, A. F., Kempf, A., and Floeter, J. 2018. Forage fish control population dynamics of North Sea whiting *Merlangius merlangus*. *Marine Ecology Progress Series*, 594: 213-230.

Laufkötter, C., Zscheischler, J., and Frölicher, T. L. 2020. High-impact marine heatwaves attributable to human-induced global warming. *Science*, 369: 1621-1625.

Lavaniegos, B. E., and Ohman, M. D. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Progress in Oceanography*, 75: 42-69.

Le Corre, N., Pepin, P., Burmeister, A., Walkusz, W., Skanes, K., Wang, Z., Brickman, D., et al. 2020. Larval connectivity of northern shrimp (*Pandalus borealis*) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 77: 1332-1347.

Lebrato, M., Pitt, K. A., Sweetman, A. K., Jones, D. O. B., Cartes, J. E., Oschlies, A., Condon, R. H., et al. 2012. Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia*, 690: 227-245.

Lee, Z., Shang, S., Du, K., and Wei, J. 2018. Resolving the long-standing puzzles about the observed Secchi depth relationships. *Limnology and Oceanography*, 63: 2321-2336.

Lee, Z., Shang, S., Hu, C., Du, K., Weidemann, A., Hou, W., Lin, J., et al. 2015. Secchi disk depth: A new theory and mechanistic model for underwater visibility. *Remote Sensing of Environment*, 169: 139-149.

Leis, J. M. 2006. Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology*, 51: 57-141.

Leonard, D. M., and Øien, N. I. 2020a. Estimated Abundances of Cetacean Species in the Northeast Atlantic from Norwegian Shipboard Surveys Conducted in 2014–2018. NAMMCO Scientific Publications 11. [https://doi.org/ 10.7557/3.4694](https://doi.org/10.7557/3.4694).

Leonard, D. M., and Øien, N. I. 2020b. Estimated Abundances of Cetaceans Species in the Northeast Atlantic from Two Multiyear Surveys Conducted by Norwegian Vessels between 2002–2013. NAMMCO Scientific Publications 11. [https://doi.org/ 10.7557/3.4695](https://doi.org/10.7557/3.4695).

Lewandowska, A., and Sommer, U. 2010. Climate change and the spring bloom: a mesocosm study on the

- influence of light and temperature on phytoplankton and mesozooplankton. *Marine Ecology Progress Series*, 405: 101-111.
- Lilly, G. R., Parsons, D. G., and Kulka, D. W. 2000. Was the Increase in Shrimp Biomass on the Northeast Newfoundland Shelf a Consequence of a Release in Predation Pressure from Cod? *Journal of Northwest Atlantic Fishery Science*, 27: 45-61.
- Lindegren, M., Thomas, M. K., Jónasdóttir, S. H., Nielsen, T. G., and Munk, P. 2020. Environmental niche separation promotes coexistence among ecologically similar zooplankton species—North Sea copepods as a case study. *Limnology and Oceanography*, 65: 545-556.
- Lindegren, M., Van Deurs, M., MacKenzie, B. R., Worsoe Clausen, L., Christensen, A., and Rindorf, A. 2018. Productivity and recovery of forage fish under climate change and fishing: North Sea sandeel as a case study. *Fisheries Oceanography*, 27: 212-221.
- Lindemann, C., and St. John, M. A. 2014. A seasonal diary of phytoplankton in the North Atlantic. *Frontiers in Marine Science*, 1.
- Linderholm, H. W., Cardinale, M., Bartolino, V., Chen, D. L., Ou, T. H., and Svedang, H. 2014. Influences of large- and regional-scale climate on fish recruitment in the Skagerrak-Kattegat over the last century. *Journal of Marine Systems*, 134: 1-11.
- Lindley, J. A., Gamble, J. C., Hunt, and H. G. 1995. A change in the zooplankton of the central North Sea (55° to 58° N): a possible consequence of changes in the benthos. *Marine Ecology Progress Series*, 119: 299-303.
- Lindley, J. A., and Batten, S. 2002. Long-term variability in the diversity of North Sea zooplankton. *Journal of the Marine Biological Association of the UK*, 82: 31-40.
- Long, A. P., Haberlin, D., Lyashevskaya, O., Brophy, D., O'Hea, B., O'Donnell, C., Scarrott, R. G., et al. 2021. Interannual variability of gelatinous mesozooplankton in a temperate shelf sea: greater abundance coincides with cooler sea surface temperatures. *ICES Journal of Marine Science*, 78: 1372-1385.
- Longhurst, A. 1998. *Ecological Geography of the Sea*. Academic Press, London.
- Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fisheries Research*, 56: 125-131.
- Loreau, M. 1995. Consumers as Maximizers of Matter and Energy Flow in Ecosystems. *The American Naturalist*, 145: 22-42.
- Lorentsen, S.-H., Anker-Nilssen, T., and Erikstad, K. E. 2018. Seabirds as guides for fisheries management: European shag *Phalacrocorax aristotelis* diet as indicator of saithe *Pollachius virens* recruitment. *Marine Ecology Progress Series* 586: 193–201.
- Lowe, W. H., and Allendorf, F. W. 2010. What can genetics tell us about population connectivity? *Molecular Ecology*, 19: 3038-3051.
- Lucas, C., and Dawson, M. 2014. What Are Jellyfishes and Thaliaceans and Why Do They Bloom? , pp. 9-44.
- Lucchetti, A., Sala, A., and Jech, J. M. 2012. Impact and performance of Mediterranean fishing gear by side-scan sonar technology. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 1806-1816.
- Lynam, C. P., Hay, S. J., and Brierley, A. S. 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, 49: 637-643.
- Lynam, C. P., Hay, S. J., and Brierley, A. S. 2005. Jellyfish abundance and climatic variation: contrasting

- responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *Journal of the Marine Biological Association of the United Kingdom*, 85: 435-450.
- Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., and Hays, G. C. 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology*, 17: 767-782.
- Lynam, C. P., Llope, M., Mollmann, C., Helaoutet, P., Bayliss-Brown, G. A., and Stenseth, N. C. 2017. Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 114: 1952-1957.
- MacDonald, A., Heath, M. R., Greenstreet, S. P. R., and Speirs, D. C. 2019. Timing of Sandeel Spawning and Hatching Off the East Coast of Scotland. *Frontiers in Marine Science*, 6.
- Macer, C. T. 1965. The distribution of larval sand eels (*Ammodytidae*) in the southern North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 45: 187-207.
- Macer, C. T. 1966. Sand eels (*Ammodytidae*) in the southwestern North Sea; their biology and fishery. *Fishery Investigations. Series 2. Great Britain Ministry of Agriculture, Fisheries and Food*, 24: 1-55.
- Mackinson, S., and Daskalov, G. 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. *Sci. Ser. Tech Rep., Cefas Lowestoft*, 142: 196pp.
- MacLeod, C. D., Santos, M. B., Reid, R. J., Scott, B. E., and Pierce, G. J. 2007. Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? *Biology Letters*, 3: 185-188.
- Manno, C., Bednaršek, N., Tarling, G. A., Peck, V. L., Comeau, S., Adhikari, D., Bakker, D. C. E., et al. 2017. Shelled pteropods in peril: Assessing vulnerability in a high CO₂ ocean. *Earth-Science Reviews*, 169: 132-145.
- MAREANO 2022. The sea in maps and pictures. www.mareno.no.
- Markowitz, G. 2018. From Industrial Toxins to Worldwide Pollutants: A Brief History of Polychlorinated Biphenyls. *Public Health Reports*, 133: 721-725.
- Marty, L., Rochet, M.-J., and Ernande, B. 2014. Temporal trends in age and size at maturation of four North Sea gadid species: Cod, haddock, whiting and Norway pout. *Marine Ecology Progress Series*, 497: 179-197.
- Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., et al. 2021. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. . Cambridge University Press, Cambridge.
- McConville, K., Atkinson, A., Fileman, E. S., Spicer, J. I., and Hirst, A. G. 2016. Disentangling the counteracting effects of water content and carbon mass on zooplankton growth. *Journal of Plankton Research*, 39: 246-256.
- McGinty, N., Barton, A. D., Record, N. R., Finkel, Z. V., Johns, D. G., Stock, C. A., and Irwin, A. J. 2021. Anthropogenic climate change impacts on copepod trait biogeography. *Global Change Biology*, 27: 1431-1442.
- McLean, M., Mouillot, D., and Auber, A. 2018. Ecological and life history traits explain a climate-induced shift in a temperate marine fish community. *Marine Ecology Progress Series*, 606: 175-186.
- McNeil, B. I., and Sasse, T. P. 2016. Future ocean hypercapnia driven by anthropogenic amplification of the natural CO₂ cycle. *Nature*, 529: 383-386.

- Mehl, S., and Westgaard, T. 1983. The diet at consumption of mackerel in the North Sea. ICES C.M. 1983/H4:.
- Meier, S., Karlsen, Ø., Le Goff, J., Sørensen, L., Sørhus, E., Pampanin, D. M., Donald, C. E., et al. 2020. DNA damage and health effects in juvenile haddock (*Melanogrammus aeglefinus*) exposed to PAHs associated with oil-polluted sediment or produced water. Plos One, 15: e0240307.
- Melle, W., Runge, J., Head, E., Plourde, S., Castellani, C., Licandro, P., Pierson, J., et al. 2014. The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits. Progress in Oceanography, 129: 244-284.
- Melaa, K. W., Zimmermann, F., Søvik, G., and Thangstad, T. H. 2022. Historic landings of northern shrimp (*Pandalus borealis*) in Norway. Data per county for 1908-2021. Rapport fra havforskningen nr. 2022-24. 31 s. ISSN:1893-4536. <https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen-en-2022-24> .
- Meyer-Jacob, C., Tolu, J., Bigler, C., Yang, H., and Bindler, R. 2015. Early land use and centennial scale changes in lake-water organic carbon prior to contemporary monitoring. Proceedings of the National Academy of Sciences, 112: 6579-6584.
- Meyer, B., Irigoien, X., Graeve, M., Head, R. N., and Harris, R. 2002. Feeding rates and selectivity among nauplii, copepodites and adult females of *Calanus finmarchicus* and *Calanus helgolandicus*. Helgoland Marine Research, 56: 169-176.
- Michelangeli, M., Martin, J. M., Pinter-Wollman, N., Ioannou, C. C., McCallum, E. S., Bertram, M. G., and Brodin, T. 2022. Predicting the impacts of chemical pollutants on animal groups. Trends in Ecology & Evolution.
- Miljøstatus 2022a. Fiskedødelighet i Nordsjøen (in Norwegian), <https://miljostatus.miljodirektoratet.no/tema/hav-og-kyst/havindikatorer/nordsjoen-skagerrak/menneskelig-aktivitet/fiskedodelighet-i-nordsjoen/> .
- Miljøstatus 2022b. Næringssalter i Skagerrak (in Norwegian). <https://miljostatus.miljodirektoratet.no/tema/hav-og-kyst/havindikatorer/nordsjoen-skagerrak/havklima/naringssalter-i-skagerrak/> .
- Mills, C. E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia, 451: 55-68.
- Ministry of Climate and Environment 2020. Norway's integrated ocean management plans. Barents Sea–Lofoten area; the Norwegian Sea; and the North Sea and Skagerrak. Meld. St. 20 (2019 – 2020) Report to the Storting (white paper). . Ed. by N. M. o. C. a. Environment.
- Ministry of Climate and Environment. 2015. Nature for life. Norway's national biodiversity action plan. Meld. St. 14 (2015–2016) Report to the Storting (white paper). Norwegian Ministry of Climate and Environment.
- Moe, J., Hjermann, D. Ø., Ravagnan, E., and Bechmann, R. K. 2019. Effects of an aquaculture pesticide (diflubenzuron) on non-target shrimp populations: Extrapolations from laboratory experiments to the risk of population decline. Ecological Modelling, 413.
- Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., André, C., et al. 2013. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before-after control-impact study. Proc Biol Sci, 280: 20122679.
- Molinero, J. C., Ibanez, F., Nival, P., Buecher, E., and Souissi, S. 2005. North Atlantic climate and northwestern Mediterranean plankton variability. Limnology and Oceanography, 50: 1213-1220.

- Monaghan, P. 1992. Seabirds and sandeels: the conflict between exploitation and conservation in the northern North Sea. *Biodiversity & Conservation*, 1: 98-111.
- Monteith, D. T., Stoddard, J. L., Evans, C. D., de Wit, H. A., Forsius, M., Høgåsen, T., Wilander, A., et al. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, 450: 537-540.
- Montero, J. T., Lima, M., Estay, S. A., and Rezende, E. L. 2021. Spatial and temporal shift in the factors affecting the population dynamics of *Calanus* copepods in the North Sea. *Global Change Biology*, 27: 576-586.
- Morgan, M. G. 2014. Use (and abuse) of expert elicitation in support of decision making for public policy. *Proceedings of the National Academy of Sciences*, 111: 7176-7184.
- Munk, P., and Nielsen, T. G. 1994. Trophodynamics of the plankton community at Dogger Bank: predatory impact by larval fish. *Journal of Plankton Research*, 16: 1225-1245.
- Munk, P., Wright, P. J., and Pihl, N. J. 2002. Distribution of the Early Larval Stages of Cod, Plaice and Lesser Sandeel across Haline Fronts in the North Sea. *Estuarine, Coastal and Shelf Science*, 55: 139-149.
- Mupepele, A. C., Walsh, J. C., Sutherland, W. J., and Dormann, C. F. 2016. An evidence assessment tool for ecosystem services and conservation studies. *Ecological Applications* 26: 1295-1301.
- Myers, R. A. 1998. When Do Environment–recruitment Correlations Work? *Reviews in Fish Biology and Fisheries*, 8: 285-305.
- Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series*, 138: 293-308.
- Møller, E. F., Maar, M., Jónasdóttir, S. H., Nielsen, T. G., and Tönnesson, K. 2012. The effect of changes in temperature and food on the development of *Calanus finmarchicus* and *Calanus helgolandicus* populations. *Limnology and Oceanography*, 57: 211-220.
- NAFO, and ICES. 2021. NAFO/ICES *Pandalus* Assessment Group Meeting, 01 to 04 November 2021. By WebEx. NAFO SCS Doc. 21/19 Serial No.7250. 68 pp.
- Ndah, A. B., Meunier, C. L., Kirstein, I. V., Göbel, J., Rönn, L., and Boersma, M. 2022. A systematic study of zooplankton-based indices of marine ecological change and water quality: Application to the European marine strategy framework Directive (MSFD). *Ecological Indicators*, 135: 108587.
- Nedreaas, K. 1987. Food and feeding habits of young saithe, *Pollachius virens* (L.), on the coast of western Norway. . *Fiskeridirektoratets Skrifter Serie Hav og undersøkelser* 18: 263-301.
- Nepstad, R., Hansen, B. H., and Skancke, J. 2021. North sea produced water PAH exposure and uptake in early life stages of Atlantic Cod. *Marine Environmental Research*, 163: 105203.
- Nicolas, D., Rochette, S., Llope, M., and Licandro, P. 2014. Spatio-Temporal Variability of the North Sea Cod Recruitment in Relation to Temperature and Zooplankton. *Plos One*, 9: e88447.
- Nielsen, T. G., and Sabatini, M. 1996. Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. *Marine Ecology Progress Series*, 139: 79-93.
- Norderhaug, K. M., Nedreaas, K., Huserbraten, M., and Moland, E. 2020. Depletion of coastal predatory fish sub-stocks coincided with the largest sea urchin grazing event observed in the NE Atlantic. *Ambio*.
- Norwegian Ministry of the Environment. 2013. Integrated Management of the Marine Environment of the North

- Sea and Skagerrak (Management Plan). Meld. St. 37 (2012–2013) Report to the Storting (white paper).
- Nowacek, D. P., Thorne, L. H., Johnston, D. W., and Tyack, P. L. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review*, 37: 81-115.
- Nunes, C., and Jangoux, M. 2004. Reproductive cycle of the spatangoid echinoid *Echinocardium cordatum* (Echinodermata) in the southwestern North Sea. *Invertebrate Reproduction & Development*, 45: 41-57.
- Núñez-Riboni, I., Taylor, M. H., Kempf, A., Püts, M., and Mathis, M. 2019. Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change. *Ices Journal of Marine Science*, 76: 2389-2403.
- Nybø, S., and Evju, M. 2017. Fagsystem for fastsetting av god økologisk tilstand. Forslag fra et ekspertråd., p. 247.
- Nybø, S., Framstad, E., Jakobsson, S., Evju, M., Lyngstad, A., Sickel, H., Sverdrup-Thygesen, A., et al. 2019. Test av fagsystemet for økologisk tilstand for terrestriske økosystemer i Trøndelag. NINA Rapport 1672. Norsk institutt for naturforskning. .
- Nøttestad, L., Anthonypillai, V., dos Santos Schmidt, T. C., Høines, Å., Salthaug, A., Ólafsdóttir, A. H., Kennedy, J., et al. 2021. Cruise report from the International Ecosystem Summer Survey in the Nordic Seas (IESSNS) 30th of June – 3rd of August 2021. Working Document to ICES Working Group on Widely Distributed Stocks (WGWIDE, No. 09), ICES HQ, Copenhagen, Denmark, (digital meeting) 25.-31. August 2021, 60 pp.
- Ólafsdóttir, A. H., Slotte, A., Jacobsen, J. A., Oskarsson, G. J., Utne, K. R., and Nøttestad, L. 2015. Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984 to 2013: effects of mackerel stock size and herring (*Clupea harengus*) stock size. *ICES Journal of Marine Science: Journal du Conseil*.
- Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuyssen, J. A., et al. 2018. Longer and more frequent marine heatwaves over the past century. *Nature Communications*, 9: 1324.
- Omar, A. M., Thomas, H., Olsen, A., Becker, M., Skjelvan, I., and Reverdin, G. 2019. Trends of Ocean Acidification and pCO₂ in the Northern North Sea, 2003–2015. *Journal of Geophysical Research: Biogeosciences*, 124: 3088-3103.
- Ono, K., Slotte, A., Hølleland, S., Mackinson, S., Jónsson, S. Þ., Jacobsen, J. A., and Ólafsdóttir, A. H. 2022. Space-time recapture dynamics of PIT-tagged Northeast Atlantic mackerel (*Scomber Scombrus*) reveal size-dependent migratory behaviour. Provisionally accepted. *Frontiers in Marine Science*.
- Opdal, A. F., Lindemann, C., and Aksnes, D. L. 2019. Centennial decline in North Sea water clarity causes strong delay in phytoplankton bloom timing. *Global Change Biology*, 25: 3946-3953.
- OSPAR. 1988. PARCOM recommendation 88/2: On the reduction in nutrients to the Paris convention area. Publication number 88/2, Paris Commission.
- OSPAR. 2005. Common procedure for the identification of the eutrophication status of the OSPAR maritime area. OSPAR Reference number: 2005-3, 36 pp.
- OSPAR 2017. Third Integrated Report on the Eutrophication Status of the OSPAR Maritime Area. OSPAR report 694/2017, ISBN: 978-1-911458-34-0 . 165pp.
- Otto, L., Zimmerman, J. T. F., Furnes, G. K., Mork, M., Saetre, R., and Becker, G. 1990. Review of the

- physical oceanography of the North Sea. *Netherlands Journal of Sea Research*, 26: 161-238.
- Ouellet, P., Fuentes-Yaco, C., Savard, L., Platt, T., Sathyendranath, S., Koeller, P., Orr, D., et al. 2011. Ocean surface characteristics influence recruitment variability of populations of northern shrimp (*Pandalus borealis*) in the Northwest Atlantic. *Ices Journal of Marine Science*, 68: 747-744.
- Ouellet, P., Savard, L., and Larouche, P. 2007. Spring oceanographic conditions and northern shrimp *Pandalus borealis* recruitment success in the north-western Gulf of St. Lawrence. *Marine Ecology Progress Series*, 339: 229-241.
- Palumbi, S. R. 2003. POPULATION GENETICS, DEMOGRAPHIC CONNECTIVITY, AND THE DESIGN OF MARINE RESERVES. *Ecological Applications*, 13: 146-158.
- Papworth, D., Marini, S., and Conversi, A. 2016. A Novel, Unbiased Analysis Approach for Investigating Population Dynamics: A Case Study on *Calanus finmarchicus* and Its Decline in the North Sea. *Plos One*, 11.
- Parsons, D. G. 2005. Predators of northern shrimp, *Pandalus borealis* (Pandalidae), throughout the North Atlantic. *Marine Biology Research*, 1: 48-58.
- Parsons, D. G., and Tucker, G. E. 1986. Fecundity of northern shrimp, *Pandalus borealis*, (Crustacea, Decapoda) in areas of the Northwest Atlantic. *Fishery Bulletin*, 84: 549-557.
- Parsons, T. R., and Lalli, C. M. 2002. Jellyfish population explosions : Revisiting a hypothesis of possible causes. *Mer*, 40: 111-121.
- Pauly, D., Christensen, V., Gu  nette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., et al. 2002. Towards sustainability in world fisheries. *Nature*, 418: 689-695.
- Pauly, D., Graham, W., Libralato, S., Morissette, L., and Deng Palomares, M. L. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia*, 616: 67-85.
- Payne, M., Ross, S., Wors  e Clausen, L., Munk, P., Mosegaard, H., and Nash, R. D. M. 2013. Recruitment decline in North Sea herring is accompanied by reduced larval growth rates. *Marine Ecology Progress Series*, 489: 197-211.
- Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaus, T., Gallego, A., Gr  ger, J., Licandro, P., et al. 2009. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. *Ices Journal of Marine Science*, 66: 272-277.
- Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., et al. 2017. From traits to life-history strategies: Deconstructing fish community composition across European seas. *Global Ecology and Biogeography*, 26: 812-822.
- Pedersen, A., Alve, E., Alvestad, T., Borgersen, G., Dolven, J. K., Gundersen, H., Hess, S., et al. 2016. Bl  tbunnsfauna som indikator for milj  t  lstand i kystvann. Ekspertvurderinger og forslag til nye klassegrenser og metodikk. M-633, Milj  direktoratet.
- Pedersen, B., Bjerke, J. W., Pedersen, H. C., Brandrud, T. E., Gjershaug, J. O., Hanssen, O., Lyngstad, A., et al. 2018. Naturindeks for Norge – fjell og v  tmark. Evaluering av eksisterende indikatorsett, dets datagrunnlag og behovet for ytterligere tilfang av datakilder. NINA Rapport 1462. Norsk institutt for naturforskning.
- Pedersen, O. P., Aschan, M., Rasmussen, T., Tande, K. S., and Slagstad, D. 2003. Larval dispersal and mother populations of *Pandalus borealis* investigated by a Lagrangian particle-tracking model. *Fisheries Research*, 65: 173-190.

- Pedersen, Å. Ø., Jepsen, J. U., Paulsen, I. M. G., Fuglei, E., Mosbacher, J. B., Ravolainen, V., Yoccoz, N. G., et al. 2021. Norwegian Arctic Tundra: a Panel-based Assessment of Ecosystem Condition. Norwegian Polar Institute Report Series 153. Norwegian Polar Institute, Tromsø.
- Pérez-Rodríguez, A., Howell, D., Casas, M., Saborido-Rey, F., and Ávila-de Melo, A. 2017. Dynamic of the Flemish Cap commercial stocks: use of a Gadget multispecies model to determine the relevance and synergies among predation, recruitment, and fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 582-597.
- Perkins-Kirkpatrick, S. E., and Lewis, S. C. 2020. Increasing trends in regional heatwaves. *Nature Communications*, 11: 3357.
- Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. *Science*, 308: 1912-1915.
- Petrik, C. M. 2019. Chapter 16 - Life history of marine fishes and their implications for the future oceans *In* Predicting Future Oceans, pp. 165–172. Ed. by A. M. Cisneros-Montemayor, W. W. L. Cheung, and Y. Ota. Elsevier.
- Pierre, M., Rouyer, T., Bonhommeau, S., and Fromentin, J. M. 2017. Assessing causal links in fish stock–recruitment relationships. *Ices Journal of Marine Science*, 75: 903-911.
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. 2013. Marine Taxa Track Local Climate Velocities. *Science*, 341: 1239-1242.
- Pitcher, C. R., Hiddink, J. G., Jennings, S., Collie, J., Parma, A. M., Amoroso, R., Mazor, T., et al. 2022. Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, 119.
- Pitois, S. G., and Fox, C. J. 2006. Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. *Ices Journal of Marine Science*, 63: 785-798.
- Pitois, S. G., Graves, C. A., Close, H., Lynam, C., Scott, J., Tilbury, J., van der Kooij, J., et al. 2021. A first approach to build and test the Copepod Mean Size and Total Abundance (CMSTA) ecological indicator using in-situ size measurements from the Plankton Imager (PI). *Ecological Indicators*, 123: 107307.
- Pitois, S. G., Lynam, C. P., Jansen, T., Halliday, N., and Edwards, M. 2012. Bottom-up effects of climate on fish populations: data from the Continuous Plankton Recorder. *Marine Ecology Progress Series*, 456: 169-186.
- Planque, B., and Fromentin, J. M. 1996. *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series*, 134: 101-109.
- Planque, B., Mullan, C., Arneberg, P., Eide, A., Fromentin, J.-M., Heymans, J. J., Hoel, A. H., et al. 2019. A participatory scenario method to explore the future of marine social-ecological systems. *Fish and Fisheries*, 20: 434-451.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change*, 3: 919-925.
- Pope, J. G., Shepherd, J. G., Webb, J., Stebbing, A. R. D., Mangel, M., Beverton, R. J. H., Beddington, J. R., et al. 1994. Successful surf-riding on size spectra: the secret of survival in the sea. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 343: 41-49.
- Proctor, R., Wright, P. J., and Everitt, A. 1998. Modelling the transport of larval sandeels on the north-west

- European shelf. *Fisheries Oceanography*, 7: 347-354.
- Purcell, J. E., and Arai, M. N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia*, 451: 27-44.
- Purcell, J. E., Uye, S., and Lo, W. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, 350: 153-174.
- Pätsch, J., and Radach, G. 1997. Long-term simulation of the eutrophication of the North Sea: temporal development of nutrients, chlorophyll and primary production in comparison to observations. *Journal of Sea Research*, 38: 275-310.
- Pörtner, H.-O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., et al. 2019. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.
- R Core Team 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Racault, M.-F., Le Quéré, C., Buitenhuis, E., Sathyendranath, S., and Platt, T. 2012. Phytoplankton phenology in the global ocean. *Ecological Indicators*, 14: 152-163.
- Radach, G., and Pätsch, J. 2007. Variability of continental riverine freshwater and nutrient inputs into the North Sea for the years 1977–2000 and its consequences for the assessment of eutrophication. *Estuaries and Coasts*, 30: 66-81.
- Rasmussen, B. 1967. Temperaturforhold og rekefiske i Skagerrak 1962-66. *Fiskets Gang* nr. 47. 842-847. (in Norwegian).
- Rastrick, S. S. P., Graham, H., Azetsu-Scott, K., Calosi, P., Chierici, M., Fransson, A., Hop, H., et al. 2018. Using natural analogues to investigate the effects of climate change and ocean acidification on Northern ecosystems. *Ices Journal of Marine Science*, 75: 2299-2311.
- Razouls, C., Desreumaux, N., Kouwenberg, J., and de Bovée, F. 2005-2022. Biodiversity of Marine Planktonic Copepods (morphology, geographical distribution and biological data). Sorbonne University, CNRS. Available at <http://copepodes.obs-banyuls.fr/en> [Accessed February 25, 2022].
- Record, N. R., Pershing, A. J., and Maps, F. 2012. First principles of copepod development help explain global marine diversity patterns. *Oecologia*, 170: 289-295.
- Reid, P., and Edwards, M. 2001. *Plankton And Climate*. pp. 2194-2200.
- Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M., and Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography*, 12: 260-269.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361-395.
- Richardson, A. J. 2008. In hot water: zooplankton and climate change. *Ices Journal of Marine Science*, 65: 279-295.
- Richardson, A. J., Bakun, A., Hays, G. C., and Gibbons, M. J. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, 24: 312-322.

- Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D., et al. 2006. Using continuous plankton recorder data. *Progress in Oceanography*, 68: 27-74.
- Rijnsdorp, A. D., Bastardie, F., Bolam, S. G., Buhl-Mortensen, L., Eigaard, O. R., Hamon, K. G., Hiddink, J. G., et al. 2015. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. *Ices Journal of Marine Science*, 73: i127-i138.
- Rijnsdorp, A. D., Hiddink, J. G., van Denderen, P. D., Hintzen, N. T., Eigaard, O. R., Valanko, S., Bastardie, F., et al. 2020. Different bottom trawl fisheries have a differential impact on the status of the North Sea seafloor habitats. *Ices Journal of Marine Science*, 77: 1772-1786.
- Rijnsdorp, A. D., van Leeuwen, P. I., Daan, N., and Heessen, H. J. L. 1996. Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *Ices Journal of Marine Science*, 53: 1054-1062.
- Rindorf, A., Gislason, H., Burns, F., Ellis, J. R., and Reid, D. 2020. Are fish sensitive to trawling recovering in the Northeast Atlantic? *Journal of Applied Ecology*, 57: 1936-1947.
- Rindorf, A., Wanless, S., and Harris, M. P. 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series*, 202: 241-252.
- Robb, A. P. 1981. Observations on the food and diel feeding behaviour of pelagic O-group gadoids in the northern North Sea. *Journal of Fish Biology*, 18: 183-194.
- Robb, A. P., and Hislop, J. R. G. 1980. The food of five gadoid species during the pelagic O-group phase in the northern North Sea. *Journal of Fish Biology*, 16: 199-217.
- Robert, D., Levesque, K., Gagné, J. A., and Fortier, L. 2010. Change in prey selectivity during the larval life of Atlantic cod in the southern Gulf of St Lawrence. *Journal of Plankton Research*, 33: 195-200.
- Rodhe, J. 1987. The large-scale circulation in the Skagerrak; interpretation of some observations. *Tellus* 39A: 245-253.
- Rothschild, B. J. 1998. Year class strengths of zooplankton in the North Sea and then-relation to cod and herring abundance 12. *Journal of Plankton Research*, 20: 1721-1741.
- Rumohr, H., and Kujawski, T. 2000. The impact of trawl fishery on the epifauna of the southern North Sea. *Ices Journal of Marine Science*, 57: 1389-1394.
- Röckmann, C., Dickey-Collas, M., Payne, M. R., and van Hal, R. 2010. Realized habitats of early-stage North Sea herring: looking for signals of environmental change. *Ices Journal of Marine Science*, 68: 537-546.
- Saha, A., Hauser, L., Kent, M., Planque, B., Neat, F., Kirubakaran, T. G., Huse, I., et al. 2015. Seascape genetics of saithe (*Pollachius virens*) across the North Atlantic using single nucleotide polymorphisms. *Ices Journal of Marine Science*, 72: 2732-2741.
- Saltalamacchia, F., Berg, F., Casini, M., Davies, J. C., and Bartolino, V. 2022. Population structure of European sprat (*Sprattus sprattus*) in the Greater North Sea ecoregion revealed by otolith shape analysis. *Fisheries Research*, 245: 106131.
- Schmidt, K., Birchill, A. J., Atkinson, A., Brewin, R. J. W., Clark, J. R., Hickman, A. E., Johns, D. G., et al. 2020. Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. *Global Change Biology*, 26: 5574-5587.
- Schrum, C., Lowe, C., Meier, M., Grabemann, I., Holt, J., Moritz, M., Pohlmann, T., et al. 2016. Projected

- Change—North Sea. *In* North Sea Region Climate Change Assessment. Regional Climate Studies. Ed. by Q. M., and C. F. Springer, Cham.
- Schuckel, S., Ehrich, S., Kroncke, I., and Reiss, H. 2010. Linking prey composition of haddock *Melanogrammus aeglefinus* to benthic prey availability in three different areas of the northern North Sea. *Journal of Fish Biology*, 77: 98-118.
- SEAPOP 2022. SEAPOP. About seabirds - for a richer ocean. <https://seapop.no/en/> .
- Shaw, M., Diekmann, R., Van DerKooij, J., Milligan, S., Bromley, P., and Righton, D. 2008. Assessment of the diets of cod *Gadus morhua* and whiting *Merlangius merlangus* juveniles in a frontal region close to the Norwegian Trench: co-existence or competition? *Journal of Fish Biology*, 73: 1612-1634.
- Sheldon, R. W., Prakash, A., and Sutcliffe Jr., W. H. 1972. THE SIZE DISTRIBUTION OF PARTICLES IN THE OCEAN1. *Limnology and Oceanography*, 17: 327-340.
- Shumway, S. E., Perkins, H. C., Schick, D. F., and Stickney, A. P. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. NOAA Technical Report NMFS 30. FAO Fisheries Synopsis 144, 59 pp.
- Siegel, D. A., Doney, S. C., and Yoder, J. A. 2002. The North Atlantic Spring Phytoplankton Bloom and Sverdrup's Critical Depth Hypothesis. *Science*, 296: 730-733.
- Sivle, L. D., Forland, T. N., de Jong, K., Nyqvist, D., Grimsbø, E., and Kutti, T. 2020. Havforskningsinstituttets rådgivning for menneskeskapt støy i havet: Sesimikk, elektromagnetiske undersøkelser og undersjøiske spregninger, Rapport fra Havforskningen, 2020-1.
- Siwertsson, A., Husson, B., Arneberg, P., Assmann, K., Assmy, P., Aune, M., Bogstad, B., et al. 2023. Panel-based Assessment of Ecosystem Condition of Norwegian Barents Sea shelf ecosystems. Rapport fra Havforskningen 2022-xx.
- Škerlep, M., Steiner, E., Axelsson, A.-L., and Kritzberg, E. S. 2020. Afforestation driving long-term surface water browning. *Global Change Biology*, 26: 1390-1399.
- Skogen, M. D., Ji, R., Akimova, A., Daewel, U., Hansen, C., Hjøllo, S. S., van Leeuwen, S. M., et al. 2021. Disclosing the truth: Are models better than observations? *Marine Ecology Progress Series*, 680: 7-13.
- Skorda, E. T. 2018. Stomach sampling and analyses of shrimp predators in Skagerrak. Master's Thesis. Aquatic Science and Technology, DTU Aqua.
- Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., et al. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 9: 306-312.
- Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., et al. 2011. Impacts of Fishing Low-Trophic Level Species on Marine Ecosystems. *Science*, 333: 1147-1150.
- Smith, C. J., Papadopoulou, K.-N., Barnard, S., Mazik, K., Elliott, M., Patrício, J., Solaun, O., et al. 2016. Managing the Marine Environment, Conceptual Models and Assessment Considerations for the European Marine Strategy Framework Directive. *Frontiers in Marine Science*, 3.
- Smith, K. E., Burrows, M. T., Hobday, A. J., King, N. G., Moore, P. J., Gupta, A. S., Thomsen, M. S., et al. 2023. Biological Impacts of Marine Heatwaves. *Annual Review of Marine Science*, 15: null.
- Sodeland, M., Jentoft, S., Jorde, P. E., Mattingsdal, M., Albretsen, J., Kleiven, A. R., Synnes, A.-E. W., et al.

2022. Stabilizing selection on Atlantic cod supergenes through a millennium of extensive exploitation. *Proceedings of the National Academy of Sciences*, 119: e2114904119.
- Solvang, H., and Ohishi, M. 2022. trec: An R package for trend estimation and classification to support integrated assessment of the marine ecosystem and environmental factors. *arXiv:2209.06619*. doi:10.48550/arXiv.2209.06619.
- Solvang, H. K., and Planque, B. 2020. Estimation and classification of temporal trends to support integrated ecosystem assessment. *Ices Journal of Marine Science*, 77: 2529-2540.
- Solvang, H. K., Skaug, H. J., and Øien, N. I. 2015. Abundance estimates of common minke whales in the Northeast Atlantic based on survey data collected over the period 2008–2013. Paper SC/66a/RMP8 presented to the Scientific Committee of the International Whaling Commission. Unpublished.
- Sommer, U., Stibor, H., Katechakis, A., Sommer, F., and Hansen, T. 2002. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production:primary production. *Hydrobiologia*, 484: 11-20.
- Speirs, D. C., Greenstreet, S. P. R., and Heath, M. R. 2016. Modelling the effects of fishing on the North Sea fish community size composition. *Ecological Modelling*, 321: 35-45.
- Staby, A., Skjæraasen, J. E., Geffen, A. J., and Howell, D. 2018. Spatial and temporal dynamics of European hake (*Merluccius merluccius*) in the North Sea. *Ices Journal of Marine Science*, 75: 2033-2044.
- Steger, J., Pehlke, H., Lebreton, B., Brey, T., and Dannheim, J. 2019. Benthic trophic networks of the southern North Sea: contrasting soft-sediment communities share high food web similarity. *Marine Ecology Progress Series*, 628: 17-36.
- Sterner, T. 2007. Unobserved diversity, depletion and irreversibility The importance of subpopulations for management of cod stocks. *Ecological Economics*, 61: 566-574.
- Strand, E., Bagøien, E., Edwards, M., Broms, C., and Klevjer, T. 2020. Spatial distributions and seasonality of four *Calanus* species in the Northeast Atlantic. *Progress in Oceanography*, 185: 102344.
- Stålesen, O. 1963. Fisken på rekefeltene i Oslofjorden. Master thesis. University of Oslo. 51 pp. (In Norwegian).
- Sundby, S., Kristiansen, T., Nash, R., and Johannessen, T. 2017. Dynamic Mapping of North Sea Spawning - Report of the KINO Project. 195 pp. .
- Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *J. Conseil perm. int. Explor. Mer.*, 18: 287-295.
- Sweetman, A. K., Smith, C. R., Dale, T., and Jones, D. O. B. 2014. Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. *Proceedings of the Royal Society B: Biological Sciences*, 281: 20142210.
- Sætre, R. 2007. The Norwegian Coastal Current—Oceanography and Climate. p. 159. Tapir Academic Press, Trondheim.
- Sørhus, E., Donald, C. E., da Silva, D., Thorsen, A., Karlsen, Ø., and Meier, S. 2021. Untangling mechanisms of crude oil toxicity: Linking gene expression, morphology and PAHs at two developmental stages in a cold-water fish. *Science of The Total Environment*, 757: 143896.
- Sørhus, E., Edvardsen, R. B., Karlsen, Ø., Nordtug, T., van der Meeren, T., Thorsen, A., Harman, C., et al.

2015. Unexpected Interaction with Dispersed Crude Oil Droplets Drives Severe Toxicity in Atlantic Haddock Embryos. *Plos One*, 10: e0124376.
- Sørli, M., Nilssen, K. T., Bjørge, A., and Freitas, C. 2020. Diet composition and biomass consumption of harbour seals in Telemark and Aust-Agder, Norwegian Skagerrak. *Marine Biology Research*.
- Søvik, G., Nedreaas, K., Zimmermann, F., Husson, B., Strand, H. K., Jørgensen, L. L., Strand, M., et al. 2020. Kartlegging av fjordøkosystemene i Tana- og Porsangerfjorden. Råd og kunnskapsbidrag fra Havforskningsinstituttet i forbindelse med vurdering av en eventuell åpning av direktefiske etter reker med bunntål i Tana- og Porsangerfjorden. Rapport fra Havforskningen 2020-39, ISSN:1893-4536. 140 s. <https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen-2020-39>
- Søvik, G., and Thangstad, T. 2016. The Norwegian Fishery for Northern Shrimp (*Pandalus borealis*) in Skagerrak and the Norwegian Deep (ICES Divisions IIIa and IVa east), 1970-2016. NAFO SCR Doc. 16/057, Serial No. N6608. 28 pp.
- Søvik, G., and Thangstad, T. 2021. Results of the Norwegian Bottom Trawl Survey for Northern Shrimp (*Pandalus borealis*) in Skagerrak and the Norwegian Deep (ICES Divisions 3.a and 4.a east) in 2021. NAFO SCR Doc. 21/001, Serial No. N7157. 38 pp. <https://www.nafo.int/Portals/0/PDFs/sc/2021/scr21-001.pdf>
- Tam, J. C., Link, J. S., Large, S. I., Bogstad, B., Bundy, A., Cook, A. M., Dingsor, G. E., et al. 2016. A trans-Atlantic examination of haddock *Melanogrammus aeglefinus* food habits. *Journal of Fish Biology*, 88: 2203-2218.
- ter Hofstede, R., Hiddink, J. G., and Rijnsdorp, A. D. 2010. Regional warming changes fish species richness in the eastern North Atlantic Ocean. *Marine Ecology Progress Series*, 414: 1-9.
- Thaxter, C. B., Lascelles, B., Sugar, K., Cook, A. S. C. P., Roos, S., Bolton, M., Langston, R. H. W., et al. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*, 156: 53-61.
- Thompson, G. A., Dinofrio, E. O., and Alder, V. A. 2013. Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer. *Journal of Plankton Research*, 35: 610-629.
- Thurstan, R. H., Brockington, S., and Roberts, C. M. 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nature Communications*, 1: 15.
- Tomter, S. M. e. 2019. Landsskogtakseringen (Norway's National Forest Inventory) 1919–2019 [In Norwegian]. - Norsk institutt for bioøkonomi - NIBIO.
- Turley, C. M., Roberts, J. M., and Guinotte, J. M. 2007. Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs*, 26: 445-448.
- Turner, J. 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool Stud. Zoological Studies*, 43: 255-266.
- UK Pelagic Habitats Expert Group 2021. Plankton lifeform traits master list (v4:2021-03-17). The Archive for Marine Species and Habitats Data (DASSH). (Dataset). <https://doi.org/10.17031/1709> .
- Uriarte, A., and Lucio, P. 2001. Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. *Fisheries Research*, 50: 129-139.
- Valentine, J. F., Heck, K. L., Jr., Blackmon, D., Goecker, M. E., Christian, J., Kroutil, R. M., Peterson, B. J., et al. 2008. Exploited species impacts on trophic linkages along reef-seagrass interfaces in the Florida Keys.

Ecol Appl, 18: 1501-1515.

van Denderen, P. D., van Kooten, T., and Rijnsdorp, A. D. 2013. When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. Proceedings of the Royal Society B: Biological Sciences, 280.

van Deurs, M., Grome, T. M., Kaspersen, M., Jensen, H., Stenberg, C., Sørensen, T. K., Støttrup, J., et al. 2012. Short- and long-term effects of an offshore wind farm on three species of sandeel and their sand habitat. Marine Ecology Progress Series, 458: 169-180.

van Deurs, M., Hal, R. v., Tomczak, M. T., Jonasdottir, S. H., and Dolmer, P. 2009. Recruitment of lesser sandeel *Ammodytes marinus* in relation to density dependence and zooplankton composition. Marine Ecology Progress Series, 381: 249-258.

van Deurs, M., Hartvig, M., and Steffensen, J. F. 2011. Critical threshold size for overwintering sandeels (*Ammodytes marinus*). Marine Biology, 158: 2755-2764.

van Hal, R., Smits, K., and Rijnsdorp, A. 2010. How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. Journal of Sea Research, 64: 76-84.

van Hal, R., van Kooten, T., and Rijnsdorp, A. D. 2016. Temperature induced changes in size dependent distributions of two boreal and three Lusitanian flatfish species: A comparative study. Journal of Sea Research, 107: 14-22.

van Leeuwen, S., Tett, P., Mills, D., and van der Molen, J. 2015. Stratified and nonstratified areas in the North Sea: Long-term variability and biological and policy implications. Journal of Geophysical Research: Oceans, 120: 4670-4686.

Veit, R. R., ., and Harrison, N. M. 2017. Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. Frontiers in Ecology and Evolution, 5: 121.

Vinogradov, M. E., and Shushkina, E. A. 1994. Study on vertical distribution of the North Pacific zooplankton based on quantitative estimations from manned submersible. Mir. Trans. P.P. Shirshov Inst. Oceanol, 131: 41-63.

Wanless, S., Frederiksen, M., Daunt, F., Scott, B. E., and Harris, M. P. 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. Progress in Oceanography, 72: 30-38.

Wanless, S., Harris, M. P., Redman, P., and Speakman, J. R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Marine Ecology Progress Series, 294: 1-8.

Weilgart, L. 2018. The Impact of Ocean Noise Pollution on Fish and Invertebrates. Report for OceanCare, Switzerland. https://www.oceancare.org/wp-content/uploads/2017/10/OceanNoise_FishInvertebrates_May2018.pdf .

Wiborg, K. F. 1954. Investigations of Zooplankton in Coastal and Offshore Waters of Western and Northwestern Norway. In Report on Norwegian Fishery and Marine Investigations, Vol. XI. No. 1.

Wienberg, R. 1981. On the food and feeding habits of *Pandalus borealis* Krøyer 1838. Archiv für Fischerei Wissenschaft, 31: 123-137.

Wilson, L. J., and Hammon, P. S. 2016. Harbour Seal Diet Composition and Diversity. Scottish Marine and Freshwater Science Report Vol 7 No 21: 86 pp. .

- Wilson, R. J., Heath, M. R., and Speirs, D. C. 2016. Spatial Modeling of *Calanus finmarchicus* and *Calanus helgolandicus*: Parameter Differences Explain Differences in Biogeography. *Frontiers in Marine Science*, 3.
- Wilson, R. J., Speirs, D. C., and Heath, M. R. 2015. On the surprising lack of differences between two congeneric calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*. *Progress in Oceanography*, 134: 413-431.
- Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 872-885.
- Winemiller, K. O., and Rose, K. A. 1992. Patterns of Life-History Diversification in North American Fishes: implications for Population Regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2196-2218.
- Worm, B., and Myers, R. A. 2003. META-ANALYSIS OF COD–SHRIMP INTERACTIONS REVEALS TOP-DOWN CONTROL IN OCEANIC FOOD WEBS. *Ecology*, 84: 162-173.
- Wright, P. J., Gibb, F. M., Gibb, I. M., and Millar, C. P. 2011. Reproductive investment in the North Sea haddock: temporal and spatial variation. *Marine Ecology Progress Series*, 432: 149-160.
- Wright, P. J., Jensen, H., and Tuck, I. 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research*, 44: 243-256.
- Wright, P. J., Orpwood, J. E., and Scott, B. E. 2017. Impact of rising temperature on reproductive investment in a capital breeder: The lesser sandeel. *Journal of Experimental Marine Biology and Ecology*, 486: 52-58.
- Wright, P. J., and Tobin, D. 2013. Maturation differences between sub-stocks of haddock, *Melanogrammus aeglefinus*. *Marine Biology*, 160: 231-239.
- Wright, R. 2019. The role of gelatinous zooplankton for marine ecosystems and the carbon cycle. Doctoral thesis, University of East Anglia.
- Xu, X., Lemmen, C., and Wirtz, K. W. 2020. Less Nutrients but More Phytoplankton: Long-Term Ecosystem Dynamics of the Southern North Sea. *Frontiers in Marine Science*, 7.
- Yen, J. 1987. Predation by a carnivorous marine copepod, *Euchaeta norvegica* Boeck, on eggs and larvae of the North Atlantic cod *Gadus morhua* L. *Journal of Experimental Marine Biology and Ecology*, 112: 283-296.
- Zickfeld, K., Levermann, A., Morgan, M. G., Kuhlbrodt, T., Rahmstorf, S., and Keith, D. W. 2007. Expert judgements on the response of the Atlantic meridional overturning circulation to climate change. *Climatic Change*, 82: 235-265.
- Zimmermann, F., Nedreaas, K. H., Thangstad, T. H., and Søvik, G. 2021. Kartlegging av bunnfisk og reker på rekefelt i vestlandsfjorder (toktnummer 2021854). Toktrapport/Havforskningsinstituttet/ISSN 15036294/Nr. 16-2021. 41 pp. (in Norwegian).
- Ærtebjerg, G., Carstensen, J., Dahl, K., Hansen, J., Nygaard, K., Rygg, B., Sørensen, K., et al. 2001. Eutrophication in Europe's coastal waters. Topic report 7/2001, European Environment Agency.
- Aanonsen, I. A. N. 2018. Impacts of a regime shift on a shallow water fish community on the Norwegian Skagerrak coast. Master thesis, University of Oslo: 77 pp. .
- Aarbakke, O. N. S., Bucklin, A., Halsband, C., and Norrbin, F. 2014. Comparative phylogeography and demographic history of five sibling species of *Pseudocalanus* (Copepoda: Calanoida) in the North Atlantic Ocean. *Journal of Experimental Marine Biology and Ecology*, 461: 479-488.

Aarup, T. 2002. Transparency of the North Sea and Baltic Sea - A Secchi depth data mining study. *Oceanologia*, 44.



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