



Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean

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ABSTRACT

An assessment of the potential for 17 fish or shellfish stocks or stock groups to move from the sub-Arctic areas into the Arctic Ocean was conducted. A panel of 34 experts was convened to assess the impact of climate change on the potential movement of the 17 stocks or stock groups. The panel considered the exposure of species to climate change, the sensitivity of species to these changes and the adaptive capacity of each stock or stock group. Based on expert opinions, the potential for expansion or movement into the Arctic was qualitatively ranked (low potential, potential, high potential). It is projected that the Arctic Ocean will become ice-free during the summer season, and when this happens new areas will open up for plankton production, which may lead to new feeding areas for fish stocks. Five stocks had a low potential to move to, or expand in, the high Arctic. Six species are considered as potential candidate species to move to, or expand in, the high Arctic. Six stocks had a high potential of establishing viable resident populations in the region. These six stocks exhibit life history characteristics that allow them to survive challenging environmental conditions that will continue to prevail in the north. This study suggests that several life history factors should be considered when assessing the potentiality of a species moving in response to changing climate conditions.

Key words: Arctic Ocean, Barents Sea, Bering Sea, biogeography, climate change, fish, fisheries, migration

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INTRODUCTION

Global projections of the implications of climate change indicate that the relative magnitude and rate of environmental change will be greatest at the Poles (IPCC, 2007). Previous studies projected shifts in bioclimatic habitats of marine species and concluded that new species will colonize Polar ecosystems at an accelerated rate relative to other regions of the globe (Cheung *et al.*, 2009). However, closer examination of the processes governing fish distributions revealed that range expansions and successful colonization of new regions will depend on a complex suite of factors (Walther, 2010) including habitat suitability, habitat quality and population size (MacCall, 1990; Auster and Link, 2009).

Predicting the responses of commercial species to future climate change in the Arctic is of great interest to scientists, governments and fishing communities. The Arctic marine ecosystem exhibits several unique habitat features including a high proportion of shallow continental shelves, extreme seasonal weather variations, low temperature, extensive permanent and seasonal ice cover, and a large supply of freshwater from rivers and melting ice. These conditions create a challenging environment for marine biota. Arctic marine ecosystems have a large number of specialist species that have, over time, been able to adapt to the environment, but are still challenged by extreme inter-annual variations and the rapid pace of change in the Arctic (ACIA, 2005; Burrows *et al.*, 2011; Duarte *et al.*, 2012).

The possible pathways by which climate variability and change may affect ecological processes are many and can vary across a broad range of temporal and spatial scales (Ottersen *et al.*, 2010). There is ample empirical evidence of the effects of climate variability on the dynamics of marine ecosystems (Bakun, 2010; Overland *et al.*, 2010). Ecological responses to climatic variation can be immediate or time-lagged, linear or nonlinear, and may result from the amplification of climate effects due to fishing (Bakun, 2010; Planque *et al.*, 2010; Simpson *et al.*, 2011).

Climate variability and change affects marine life at all levels of biological organization, from genetics to

ecosystems, with potentially important implications for commercial fisheries (Brierly and Kingsford, 2009; Brander, 2010; Doney *et al.*, 2012). Impacts on the distribution and abundance of fish and shellfish stocks in marine ecosystems can occur through direct and indirect pathways. Direct effects include physiological changes (metabolic and reproductive processes), and indirect effects include changes to the biotic (predators, prey, species interactions) and the abiotic (habitat type and structure) environment (Ottersen *et al.*, 2010; Overland *et al.*, 2010). Significant progress has been made in: (i) identifying mechanisms by which climate change can affect fish population dynamics (O'Brien *et al.*, 2000; Barange and Perry, 2009; Payne *et al.*, 2012), (ii) improving understanding of how climate change will impact shifts in the distributions of fish species (Perry *et al.*, 2005; Dulvy *et al.*, 2008; Mueter and Litzow, 2008; Nye *et al.*, 2009; Last *et al.*, 2011), and (iii) developing models to predict the effects of climate change on future distributions of fish and fisheries (Cheung *et al.*, 2010).

Brown *et al.* (2011a) found that recent attempts to estimate the impact of climate change on fish distribution suffered from methodological shortcomings, and uncertainties remain generally underestimated (Planque *et al.*, 2011). Macroecological analyses of the effects of climate change on the distribution of marine fish assemblages have not accounted for constraints on distributional shifts due to population dependence on essential habitat features (e.g., favored substrates, presence of predators, suitability of prey fields, and proximity to nursery grounds), which are often unknown and difficult to quantify. While fully coupled bio-physical models that could account for these complex processes are under development (Huse and Ellingsen, 2008; Stock *et al.*, 2011), these models require a comprehensive understanding of the relationships governing ecosystem function. A comprehensive understanding of the interactions between atmosphere and ocean, and between climate and marine ecosystems is also needed before the high levels of uncertainty associated with present projections of fish responses to climate change can be significantly reduced.

Acknowledging the present limitations in understanding and projecting commercial fish and shellfish responses to climate change, some authors have synthesized existing information to develop conceptual models of how climate change will impact marine ecosystems (Poloczanska *et al.*, 2007; King *et al.*, 2011; Wassman, 2011). Expert judgement has been synthesized to assess the vulnerability of marine fish and shellfish stocks to fishing (Patrick *et al.*, 2009). This approach was adapted to evaluate the potential for

commercially important fish stocks to migrate from the sub-Arctic areas into the Arctic Ocean or other Arctic continental shelf seas (Fig. 1). Our analysis focuses on potential movements of commercial fish stocks in the Bering Sea and the Norwegian/Barents Sea areas, and does not include an analysis of stocks off the coasts of Newfoundland and Labrador.

ANALYTICAL APPROACH

Daw *et al.* (2009) introduced a conceptual framework for assessing the vulnerability of marine fish and fisheries to climate change. This framework was used to assess vulnerability of fisheries to climate change in several regions of the globe (Johnson and Welch, 2010). It contains four key elements: exposure, sensitivity, potential for impact, and adaptive capacity, which coalesce to define vulnerability. We revised this framework to enable an evaluation of the potential for commercially exploited species in the Bering, Barents and Norwegian Seas to move farther into the Arctic region. In this revised framework we adopted the following definitions:

E: Exposure is the nature and degree to which a species is exposed to variations in the environment that result from climate change.

S: Sensitivity is the degree to which a species responds to variations in an aspect of the marine environment that will be affected by climate change.

PI: Potential for impact is the outcome of the combination of E and S on the species.

AC: Adaptive capacity is the ability or capacity of the species to mitigate the projected impact.

The potential of a species for moving into the Arctic is the result of the potential impact mitigated by the adaptive capacity.

Exposure

Projected changes in physical oceanographic conditions. The latest Intergovernmental Panel on Climate Change report (IPCC, 2007) and other Arctic assessments (e.g., ACIA, 2005; SWIPA, 2012) concluded that warming in the Arctic was well underway and that global temperatures were projected to continue to rise. Global models project that annual air temperatures will rise by 4–6°C in the northernmost regions such as the northern Nordic Seas and the Barents Sea, and the highest (up to 7°C) in the Arctic by the end of this century (ACIA, 2005). Due to its high capacity to store heat, the ocean is not expected to warm as much as the land; however, the impact on seasonal timing of

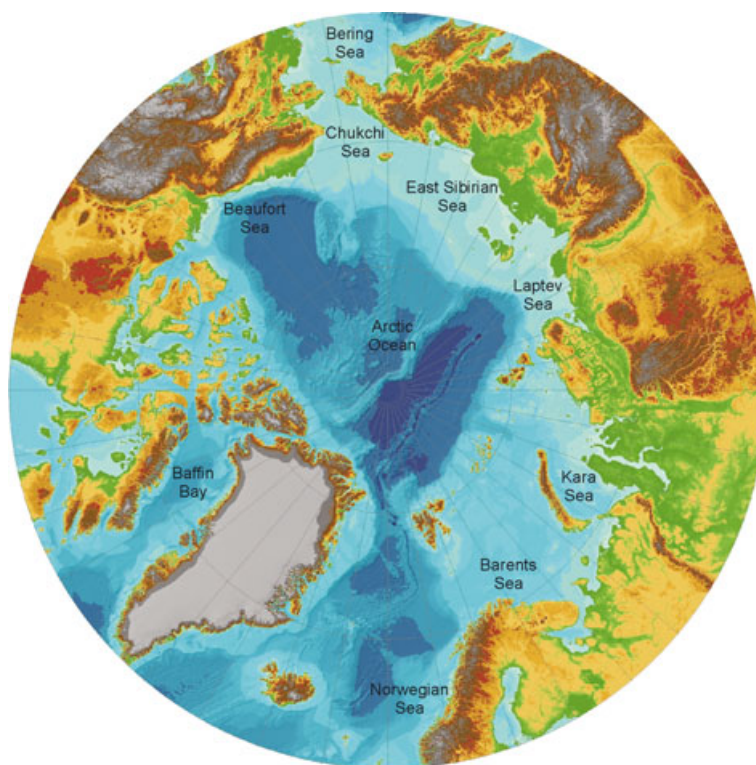


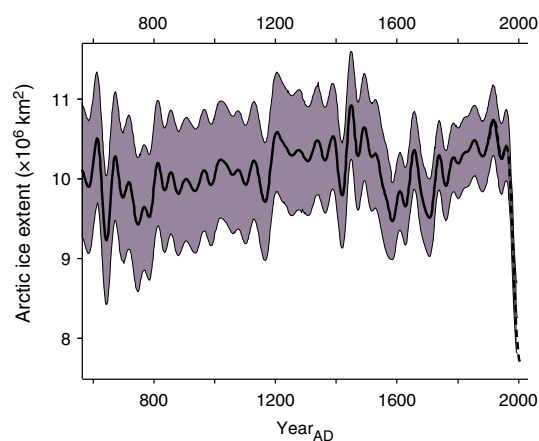
Figure 1. Map of the Arctic Ocean and surrounding seas. Used with permission from ICES Insight (Loeng, 2012).

oceanographic events and its impact on phenology of marine life is expected to be greater in the ocean (Burrows *et al.*, 2011).

As temperatures rise, sea-ice coverage will decrease. Loss of sea ice has been rapid and pervasive in the Arctic during the last decades (Fig. 2; Kinnard *et al.*, 2011; SWIPA, 2012) and several climate models project an ice-free summer in the Arctic by 2100 (Teng *et al.*, 2006; Wang and Overland, 2009). Winter sea ice is expected to continue to form in the Northern Bering and Chukchi Seas, which features a shallow shelf system. This ice formation will continue to form a summer cold pool at depth in these regions during summer (Sigler *et al.*, 2011; Stabeno *et al.*, 2012).

Climate models are often criticized for producing a more or less monotonic-type response to anthropogenic forcing in the 21st century simulations (Easterling and Wehner, 2009) and it is argued that large-scale multi-decadal oscillatory climate features are often not well simulated. Such oscillations can result in periods of a decade or two when the global average surface air temperature shows no trend or even slight cooling despite the presence of longer-term warming (Easterling and Wehner, 2009). The North Atlantic and North Pacific are known as regions of decadal or multi-decadal climate variations (Kushnir, 1994; Mantua *et al.*, 1997; Thompson and Wallace,

Figure 2. Forty-year smoothed reconstructed late-summer Arctic sea ice extent for the last 1450 yr, with 95% confidence interval. The dashed line is from modern observations. Redrawn with authorization from Kinnard *et al.* (2011).



1998; Knight *et al.*, 2005; Di Lorenzo *et al.*, 2008; Kenlyside *et al.*, 2008). Such variability has been observed in the Barents and Bering Seas and it is expected that it will continue to operate in the future. Thus, over time as greenhouse gases accumulate, significant temperature increase is expected to take place in the Arctic Ocean; however, there may be no increase or even a decrease in the average temperature

of the Bering and Barents Seas over the next 10 yr (Drinkwater *et al.*, 2011; Stabeno *et al.*, 2012).

The Arctic Ocean is composed of a three-layer system with cool low salinity water near the sea floor overlaid by warm saline Atlantic waters to approximately 200 m and topped by a lower salinity layer of Pacific origin waters (Carmack and Wassman, 2006). With the exception of the Barents Sea and parts of the Bering and Kara Seas (Fig. 1), the shelf seas are shallow (<100 m). Average inflow of Atlantic water into the Arctic through the Fram Strait and the Barents Sea is more than five times greater than inflow from the Pacific side into the Arctic through the shallow Bering Strait (Carmack and Wassman, 2006; Schauer *et al.*, 2010). The origin of flow through Fram Strait stems from the western branch of the Polar front and the Norwegian Atlantic Slope Current. These currents merge to form the West Spitzbergen Current (WSC). The highest velocities occur on the upper slope of the WSC with average flow of 20 cm s^{-1} (Skagseth *et al.*, 2010). The flow through Bering Strait stems from the northern extension of the Aleutian North Slope Current as it flows out of the Gulf of Anadyr (the Anadyr Current), and the northern extension of the Alaska Coastal Current as it flows along the boundary of the inner domain in the Bering Sea (Danielson *et al.*, 2011).

Nutrient exchange occurs between the shelf and slope through upwelling as a function of river discharge, brine drainage and wind forcing (Carmack and Chapman, 2003). It is uncertain whether intrusions of Atlantic water will intensify under climate change and whether Atlantic water will extend onto Arctic shelves beyond the Barents Sea in the future (Skagseth *et al.*, 2010).

Impacts on fish and shellfish prey - primary and secondary productivity. Winter conditions in the Arctic will remain dark and cold for several months of the year and these conditions will continue to limit the total annual production and deter the invasion of new species into the Arctic region.

Seasonal differences in production have been observed and are expected in the future. Reductions in the spatial extent of sea ice in summer will likely alter the seasonal growing period for plankton production due to the combination of changes in mixing, stratification, deeper light penetration and increased solar heating (Wassman, 2011). Mixing and stratification have long been known to influence primary production (Sverdrup, 1953). In the high Arctic, stratification is formed when ice melts and sea ice also can influence year-to-year variability in phytoplankton

production (Rey and Loeng, 1985). Li *et al.* (2009) hypothesized that increased stratification and extended ice-free periods in summer could cause nitrogen limitation in the upper ocean in the Canadian Basin which could favor of smaller cells and reduced productivity. Timing of production can also be affected by shifts in seasonal sea ice retreat (Skjoldal and Rey, 1989; Nesvetova, 2002; Hunt *et al.*, 2011; Kahru *et al.*, 2011; Leu *et al.*, 2011). Ice algae will continue to be important in selected regions but this contribution may represent a smaller fraction of the total annual open ocean production in the future (Wassman, 2011).

Projected impacts of climate change on primary production differ by region. The region north of St. Lawrence Island in the Bering Sea and the Chukchi Sea is notable for supporting high rates of carbon uptake during ice-free periods (Lee *et al.*, 2011). Grebmeier *et al.* (2006) observed that measurements of benthic standing stock southwest of St. Lawrence Island were decreasing. It is unclear whether this was due to increased foraging pressure or ecosystem change. Relative to the entire Barents Sea region, satellite images in years of reduced seasonal ice cover showed an approximately 30% increase in primary production (Arrigo *et al.*, 2008). This is explained by a combination of increased light levels in areas of decreased ice extent, increased nutrient levels as the Atlantic waters extend farther northward and eastward, and increased turn-over rates of the phytoplankton as a result of warmer temperatures. This observation differs from annual production estimates that do not indicate any trend but rather an annual production varying between 80 and 120 g C m^{-2} in the Barents Sea (Ellingsen *et al.*, 2008). In the Bering Sea, anticipated reduction in sea ice coverage combined with warming is expected to lead to increased primary production (Brown *et al.*, 2011b). Similar productivity increases are expected at a pan-Arctic scale, in response to reduced ice coverage and thickness (Zhang *et al.*, 2010; Slagstad *et al.*, 2011) although such projections for the Arctic region remain uncertain (Grebmeier *et al.*, 2010).

The pace and magnitude of changes in ocean conditions, shifts in the timing of sea-ice retreat, and resulting impacts on the distribution, abundance and species composition of primary production are expected to impact secondary productivity in the Arctic (Leu *et al.*, 2011; Wassman, 2011). Atlantic inflow is expected to advect *Calanus finmarchicus* into the Barents Sea in the spring and summer (Skjoldal and Rey, 1989; Sundby, 2000; Boitsov and Orlova, 2004), a result confirmed by direct measurements

(Edvardsen *et al.*, 2003). It has also been suggested that greater amounts of warm water from the increased Atlantic water inflow would lead to elevated zooplankton productivity because of faster growth and hence lower mortality (Orlova *et al.*, 2004). Model results from Slagstad *et al.* (2011) indicated that increased temperatures in the Barents Sea will increase the production of the copepod *C. finmarchicus* and decrease the production of *Calanus glacialis*. In contrast, on the Eurasian shelf and in the Arctic Ocean, the production of *C. glacialis* is projected to increase with temperature (Slagstad *et al.*, 2011). In the southeastern Bering Sea, observations show that *Calanus marshallae* populations declined in warm temperatures and small less lipid-rich species of copepods increased (Coyle *et al.*, 2011). *Calanus hyperboreus*, a common mesozooplankton in the Greenland Sea (Hirche and Niehoff, 1996) that is also found in the Arctic Basin (Kosobokova and Hirche, 2009), may also be able to exploit the extended growing season in the Arctic (Slagstad *et al.*, 2011).

Fluctuations in abundance of young Euphausiacea, *Thysanoessa inermis* and *Thysanoessa raschii*, in the Barents Sea are determined to a large extent by temperature variability. During warm periods, the abundance of the former species increases along with its expanding distribution area, whereas the abundance of the latter species decreases and its area of distribution contracts. During cold periods, the situation is reversed. The shifts in distribution and abundance are a direct response to thermal habitat preferences with *T. inermis* being a warm-water species and *T. raschii* a cold-water species that is mainly distributed in the eastern part of the Barents Sea (Drobysheva, 1994). In the Chukchi and Beaufort Seas, euphausiids (*T. inermis* and *T. raschii*) have been observed in the Arctic but are thought to be advected into the region from the south (Berline *et al.*, 2008).

In summary, the production of oceanic phytoplankton in the Arctic is expected to increase in response to declines in summer sea ice but this increase in production may be offset by declines in the spatial extent of ice algal blooms, and changes in oceanic species composition to a smaller size. Secondary production is likely to increase with a greater fraction of the annual production being grazed by zooplankton. Warmer ocean conditions and shifts in advection may change the species composition of zooplankton in the Arctic. The size and lipid content of dominant copepods may also change and may increase the production of smaller zooplankton. Temporal mismatches between the onset of spring blooms and peak hatch dates may occur.

Sensitivity of fish and shellfish

Unlike sub-Arctic ecosystems, the Arctic shelf ecosystems are characterized by benthic energy pathways (Grebmeier *et al.*, 2010; Whitehouse, 2011). As the summer growing season is extended by loss of sea ice, pelagic energy pathways may become more important. Whether these changes to trophic energy pathways will be sufficient to support sub-Arctic species is uncertain.

As physical and biological conditions change, new species may be able to colonize the region. Shifts in distributions of fish and shellfish can be a function of changes in the range of suitable habitat and density-dependent expansion of the range. Only a few attempts have been made to quantitatively project climate change effects on sub-Arctic and Arctic fish abundance and these projections are uncertain. Mueter *et al.* (2011) projected that climate change will reduce recruitment of walleye pollock (*Theragra chacogramma*) leading to a decline in stock size. In contrast, Hollowed *et al.* (2009) projected that climate change will have only a modest impact on recruitment of northern rock sole (*Lepidopsetta polyxystra*). Huse and Ellingsen (2008) used an individual-based model to simulate change in the Barents Sea capelin (*Mallotus villosus*) spatial distribution under ocean warming. Their results showed that capelin shifted their feeding areas northwards as the ice edge retreated.

In the absence of models, the future responses of fish and shellfish to changing environmental conditions can be inferred from assessments of observed responses of stocks to climate variability, and knowledge of life history characteristics and physiological attributes. This approach was used in previous assessments of the effect of climate variability on fish stocks (ACIA, 2005; Drinkwater, 2006; Mueter and Litzow, 2008; Simpson *et al.*, 2011). In sub-Arctic seas, shifts in fish distributions in response to changing ocean conditions have been observed in the Barents and Bering Seas (Mueter and Litzow, 2008; Spencer, 2008; Sundby and Nakken, 2008; Heino *et al.*, 2008).

Most fish species are ectotherms (i.e., they do not regulate their body temperature) and their metabolic rates are usually limited by the low temperatures in the Arctic and sub-Arctic regions. An expected increase in temperature has the potential to increase metabolic rates and ultimately growth rates of many fish species and expand the habitat for temperature-limited sub-Arctic species. The geographical expansion of warmer waters, mainly from Atlantic origin, into the Arctic may alter the distribution of suitable habitats for many fish species. Loeng and Drinkwater (2007) projected

that changes in Arctic Ocean conditions would lead to a general increase in fish productivity and a northern shift in geographical distribution of fish. An increase in food and oxygen will be needed to meet the increased metabolic demands of the species (Pörtner, 2010; Coyle *et al.*, 2011). Although oxygen supply may not be a strong limitation in the Arctic, climate impacts on the quality, quantity and timing of the delivery of the food supply remain uncertain. If increased metabolic rates are not matched by a corresponding increase in appropriate food supply this would result in decreased individual growth, higher mortality rates and ultimately a reduction in stock productivity. Climate-induced changes in the geographical distribution of thermal habitats and the associated changes in migration routes may result in shorter (less energy-demanding) or longer (more energy-demanding) movements between spawning, nursery and feeding grounds, directly impacting the metabolic costs associated with ontogenetic migrations (Sundby and Nakken, 2008).

Because of the complex processes and interactions outlined above, there is at present no simple way to predict whether fish productivity will increase or decrease in a warming Arctic and whether new potential habitats will be successfully occupied. Therefore, a qualitative assessment of the sensitivity of the species based on life history characteristics was attempted. The sensitivity of species to changing conditions in the Arctic depends on their ability to respond to the physical and biological conditions of the region. Marine fauna that currently reside in the area are adapted to the challenging conditions of the Arctic. Examples of these adaptations include the following:

- Rapid growth (particularly in the first year) to survive in a short production season.
- Capability to avoid unfavorable conditions. Species that exhibit seasonal movements may be less sensitive to climate change. For example, Greenland halibut (*Reinhardtius hippoglossoides*) may avoid seasonal ice cover and cold temperatures on the Arctic shelf by moving to the deep ocean. Likewise, species that exhibit flexible feeding migrations may be able to adjust to shifts in the distribution and abundance of prey.
- Diversity of diets (e.g., snow crab, *Chionoectes opilio* and some flatfish).
- Broad spawning range with low or moderate site fidelity (e.g., capelin).
- Broad larval or juvenile dispersal to enhance chances for encountering favorable conditions.

Adaptive capacity

- Physiological characteristics of some species make them particularly well suited to Arctic environmental conditions: an example is specific physiological characteristics to survive in cold conditions (e.g., blood antifreeze in polar cod, *Boreogadus saida* and Alaska plaice, *Pleuronectes quadrituberculatus*).
- Phenotypic plasticity.

Several of the species that exhibit the adaptive characteristics listed above, already occupy the Arctic (Table 1).

Potential impact (exposure and sensitivity)

Even if a species exhibits several or all of the attributes listed above that would make them candidates for expansion into the Arctic, the colonization of new regions may not occur unless the thermal windows are suitable for survival at key life stages, sufficient suitable prey are available to meet energetic demands and the advective corridors are available for immigration to the new region. Comparison of the advective corridors for colonization in the Atlantic and Pacific sides of the Arctic indicated that the flows into the Arctic are much stronger on the Atlantic side (Drinkwater, 2011). Ocean currents are more favorable to immigration on eastern boundaries due to the direction and intensity of flow. Distances between similar habitat types are relatively small along the shelf areas of the Bering and Barents seas, but topography may influence the potential for immigration into the Arctic. For example, the shallow shelves of the northern Bering and Chukchi Seas may serve as a barrier to immigration because of either the presence of cold pools (remnant cold water at depth from winter ice cover) or due to depth preferences of fish and shellfish (Sigler *et al.*, 2011).

Although fish that exhibit the appropriate life-history adaptations may be more likely to expand or move into the Arctic, the processes governing survival are spatially and temporally complex. Considerable uncertainty remains as to whether these species will be able to colonize the Arctic successfully. Many species have evolved temporal patterns of feeding and reproductive behavior that maximize survival. If climate change shifts the temporal match with key aspects of the life history, survival may be impacted (Søreide *et al.*, 2010). Several species exhibit seasonal spawning or feeding migrations. If the quality or quantity of habitat is changed, these spawning and feeding migrations may be unsuccessful. Over time, fish often adopt strategies to avoid predation or

Table 1. Evaluation of candidate species for moving to the Arctic Ocean.

Species/stocks	Present distribution	Potential future distribution
Pacific ocean perch (<i>Sebastes alutus</i>)	Pacific ocean perch are a long-lived species (maximum age 90 yr) found along the outer shelf and slope of the Bering Sea (Spencer and Ianelli, 2010). This species is known to occupy rocky untrawlable habitats (Kreiger, 1993). Large commercial removals in the early 1960s led to a population decline. Pacific ocean perch are abundant along the Aleutian Island chain (Spencer and Ianelli, 2010). This indicates that this species may be at the northern end of its range. The diet of Pacific ocean perch consists of calanoid copepods, euphausiids, myctophids, and other miscellaneous prey (Yang, 2003).	There is a <i>low potential</i> for Pacific ocean perch to expand into the Arctic. The shallow shelf area is likely to be a barrier to this species. If larvae were advected into the Arctic, the establishment of resident populations would depend on availability of prey and appropriate thermal conditions.
Beaked Redfish (<i>Sebastes mentella</i>)	Atlantic redfishes are found strictly in Atlantic water masses. Juveniles are largely distributed over the Barents Sea shelf, whereas reproducing adults concentrate over the shelf break when extruding larvae. In the case of <i>S. mentella</i> , adults distribute in open waters during summer feeding migrations.	There is <i>high potential</i> for beaked redfish to expand into the Arctic. Reproducing adults can potentially expand over the northern/eastern side of the shelf break and into the open Arctic ocean during summer months, given appropriate temperature and feeding conditions (Fig. 3).
Greenland halibut (<i>Reinhardtius hippoglossoides</i>)	Greenland halibut is a widely distributed species that is found in northern areas in both the Atlantic and Pacific oceans. In the Atlantic the species is found in Canada, Greenland, Iceland, Faroe Islands and along the continental slope to Svalbard and into the Barents Sea. The stock in the northeast Atlantic has spawning areas along the continental slope of northern Norway and Svalbard where the highest densities are at temperature range approximately from -1 to 4°C . Larvae drift north and east and are found north of Svalbard and eastward to the Kara sea, while immature fish are mostly found in the central areas of the Barents Sea.	There is <i>potential</i> for Greenland halibut adults to expand into the Arctic Ocean shelves and slopes given appropriate temperature and feeding conditions. The potential for northern expansion of spawning sites, and successful reproduction in the Arctic Ocean depends upon suitable topography and transport for larval survival.
Greenland shark (<i>Somniosus microcephalus</i>)	Several elasmobranch species are found in the Barents Sea and in the waters around Spitsbergen. The Greenland shark (<i>Somniosus microcephalus</i>) is particularly adapted to cold and deep waters, and is found in the Arctic Ocean and its adjacent seas.	This species has a <i>high potential</i> to establish viable populations in the Arctic Ocean, or may already be present.
Arctic skate (<i>Amblyraja hyperborea</i>)	Arctic skate (<i>Amblyraja hyperborea</i>) are particularly adapted to cold and deep waters, and are found around in the Arctic Ocean and its adjacent seas.	This species has a <i>high potential</i> to establish viable populations in the Arctic Ocean, or may already be present.
Other elasmobranchs	Other elasmobranch species that currently are widely distributed in the Barents Sea are thorny skate (<i>Amblyraja radiata</i>), round skate (<i>Rajella fyllae</i>), spinytail skate (<i>Bathyraja spinicauda</i>), and common skate (<i>Dipturus batis</i>).	These species <i>potentially</i> may expand their distribution further north and east into the Arctic Ocean.
Atlantic cod (<i>Gadus morhua</i>)	Atlantic cod spawns along the coast of northern Norway (Loefoten) and the larvae drift into the Barents Sea and along the west coast of Spitsbergen. The adults have usually been distributed in the southwestern Barents Sea when it is cold, with a more eastern and northerly distribution in warm years (Drinkwater, 2006). At high latitudes, the light cycle	Atlantic cod have a <i>low potential</i> to establish spawning grounds in the Arctic. Although this species is capable of adjusting its life cycle to latitudinal differences in production cycles, seasonal sea ice will continue to be a barrier to spawning in the Arctic. Atlantic cod is a

Table 1. (Continued)

Species/stocks	Present distribution	Potential future distribution
	controls the timing of seasonal production. Temporal matches between larvae and their prey are more important in regions with short growing seasons with warm years favoring cumulative survival (Kristiansen <i>et al.</i> , 2011). During the last 2 yr, adult cod has been observed in the entire northern Barents Sea during September, almost to the continental slope to the Arctic Ocean. Atlantic cod spawn throughout the North Atlantic having adapted to local differences in timing of spring production in the North Sea, and ocean regions off the coasts of West Greenland, Iceland and Norway.	demersal shelf species, and they are not expected to move into the deep Arctic Ocean to spawn. The bottom topography will deter the northward distribution to the shelf break. Any eastward feeding migration will depend on temperature and food conditions. At northern latitudes, matches between prey quantity and quality are crucial.
Atlanto-scandic herring (<i>Clupea harengus</i>)	Herring is a pelagic species that prefers water masses with temperature higher than 2°C, but might migrate into frontal areas during the feeding season. It spawns along the Norwegian coast, and the stock has its nursery area in the Barents Sea. It migrates to the Norwegian Sea when it is 3–4 yr old to overwinter and feed. Herring is observed as far north, as west of Spitsbergen, but so far there have been no indications of moving even further north.	Potential for expansion; however, colonization will depend on population density and on appropriate temperature increase in the Arctic.
Capelin (<i>Mallotus villosus</i>)	Capelin are a small pelagic species currently found in Bering and Barents Seas and the Arctic. Capelin consume planktonic prey. Capelin spawn in summer in shallow waters. Simulation modeling shows climate change will alter the distribution of capelin spawning and feeding grounds (Huse and Ellingsen, 2008). This stock has exhibited population expansions and collapse in response to shifts in predators and prey. They are capable of rapid growth. Capelin are already observed on the shelf break to the Arctic Ocean. Capelin is also observed in the Kara Sea (Gjørseter <i>et al.</i> , 2011).	Capelin <i>potentially</i> could expand in the Arctic if prey concentrations were sufficient to sustain increased populations.
Northern rock sole (<i>Lepidopsetta polyxystra</i>)	Northern rock sole is a demersal species that is currently found in the Bering Sea. The diet is primarily composed of polychaetes and benthic amphipods and fisheries data suggest that this species exhibits strong fidelity to spawning locations in the outer domain of the southern shelf of the eastern Bering Sea during winter (Wilderbuer and Nichol, 2011).	Northern rock sole have a <i>low potential</i> to move to Arctic because of its life history and fidelity to spawning locations.
Pacific cod (<i>Gadus macrocephalus</i>)	Pacific cod are broadly distributed throughout the eastern Bering Sea shelf. Pacific cod prey on a broad range of species including polychaetes, amphipods, crangonid shrimps, euphausiids, miscellaneous fishes and crustaceans. The species spawns in winter over the outer domain of the southern shelf (Thompson and Lauth, 2011). Pacific cod has been observed in Beaufort Sea (Rand and Logerwell, 2011). Currently tends to avoid ice during spawning and shows fidelity to spawning regions. Pacific cod show fidelity to spawning locations in the Bering Sea (Conners and Munro, 2008).	Pacific cod have a <i>low potential</i> to move to Arctic. Although Pacific cod are capable of large feeding migrations and they exhibit an eclectic prey base. Pacific cod exhibit strong fidelity to spawning locations which would restrict expansion into the Arctic. It is less likely that spawning locations will be established in ice-covered regions of northern Bering Sea and Chukchi Sea.
Polar cod (<i>Boreogadus saida</i>)	Polar cod have a circumpolar distribution and belong to the high-Arctic systems. The species is often associated	There is <i>high potential</i> for polar cod to expand into the Arctic Ocean given

Table 1. (Continued)

Species/stocks	Present distribution	Potential future distribution
	with ice and can tolerate temperatures well below 0°C, but its final temperature preference may actually be in the 3–4°C range (Christiansen <i>et al.</i> , 1996). Its distribution in the Barents Sea is rather static (Hop and Gjørseter, in press). Spawning takes place mainly in the southeastern parts of the Barents Sea but judged from the distribution of larvae in late summer, spawning also occurs east of Svalbard.	appropriate temperature and feeding conditions. Since spawning normally takes place under ice, the spawning areas will likely change if winter ice cover should be lacking in the traditional spawning areas.
Walleye pollock (<i>Theragra chalcogramma</i>)	Walleye pollock are broadly distributed throughout the eastern and western Bering Sea shelves. They are a relatively fast-growing species. Adult and juvenile walleye pollock consume euphausiids and fishes, with adults also exhibiting a more piscivorous diet (cannibalism). Warmer temperatures are expected to reduce recruitment of walleye pollock (Mueter <i>et al.</i> , 2011). Pollock spawn in winter in southern regions of the outer domain of the eastern Bering Sea shelf. They have been observed to avoid the cold pool (Overland and Stabeno, 2004). Therefore, less likely to establish spawning locations in the northern Bering Sea and Chukchi Sea where winter ice will continue to form (Sigler <i>et al.</i> , 2011). Walleye pollock have been observed in low densities in the Beaufort Sea (Rand and Logerwell, 2011).	Walleye pollock have a <i>low potential</i> to move to Arctic because of reliance on euphausiids as prey, apparent avoidance of the cold pool by adult pollock, and possible declines in spawning stock biomass due to lower recruitment.
Yellowfin sole (<i>Limanda aspera</i>)	Yellowfin sole are broadly distributed throughout the southern portions of the eastern Bering Sea. They undergo annual migrations from wintering grounds over the outer domain to spawning grounds in the shallow inner domain. Spawning occurs in late spring–early summer. Yellowfin sole exhibit an eclectic diet of benthic prey. Exploratory surveys of the northern Bering Sea shelf identified high concentrations of yellowfin sole in Togiak Bay, Kuskokwim Bay and Nunivak Island (Wilderbuer <i>et al.</i> , 2011a).	<i>Potential</i> movement to Arctic because of evidence of populations in northern Bering Sea in summer and eclectic diet.
Alaska plaice (<i>Pleuronectes quadrituberculatus</i>)	Alaska plaice are a boreal species found throughout the northern and southern regions of the eastern Bering Sea shelf (Wilderbuer <i>et al.</i> , 2011b). Summer distributions of Alaska plaice tend to be limited to the middle and inner domains. Alaska plaice principally prey on polychaetes and clams.	<i>Potential</i> movement to Arctic because of current occupation of the northern Bering Sea shelf within the cold pool. However, this species exhibits a narrower spectrum of prey items in diet.
Bering flounder (<i>Hippoglossoides classodon</i>)	Bering flounder occupy the northern regions of the eastern Bering Sea shelf. This species occupies the outer domain of the eastern Bering Sea shelf. This species has been observed in the Beaufort Sea (Rand and Logerwell, 2011).	Bering Flounder have a <i>high potential</i> for movement to Arctic because this species already occupies the northern Bering Sea shelf and has been observed in the Beaufort Sea.
Snow crab (<i>Chionoectes opilio</i>)	Snow crab currently occupy the northern regions of the eastern Bering Sea shelf. This species occupies the middle and domain of the eastern Bering Sea shelf. It has been observed in the Beaufort Sea (Rand and Logerwell, 2011). Modeling studies identified corridors for advection of larvae north (Parada <i>et al.</i> , 2010). Previous studies showed the population expanded northward in warm years (Orensanz <i>et al.</i> , 2004).	Snow crab have a <i>high potential</i> for movement to Arctic shelf seas because this species is a demersal shelf forager that already occupies the northern Bering Sea shelf and has been observed in moderate densities in the Beaufort Sea.

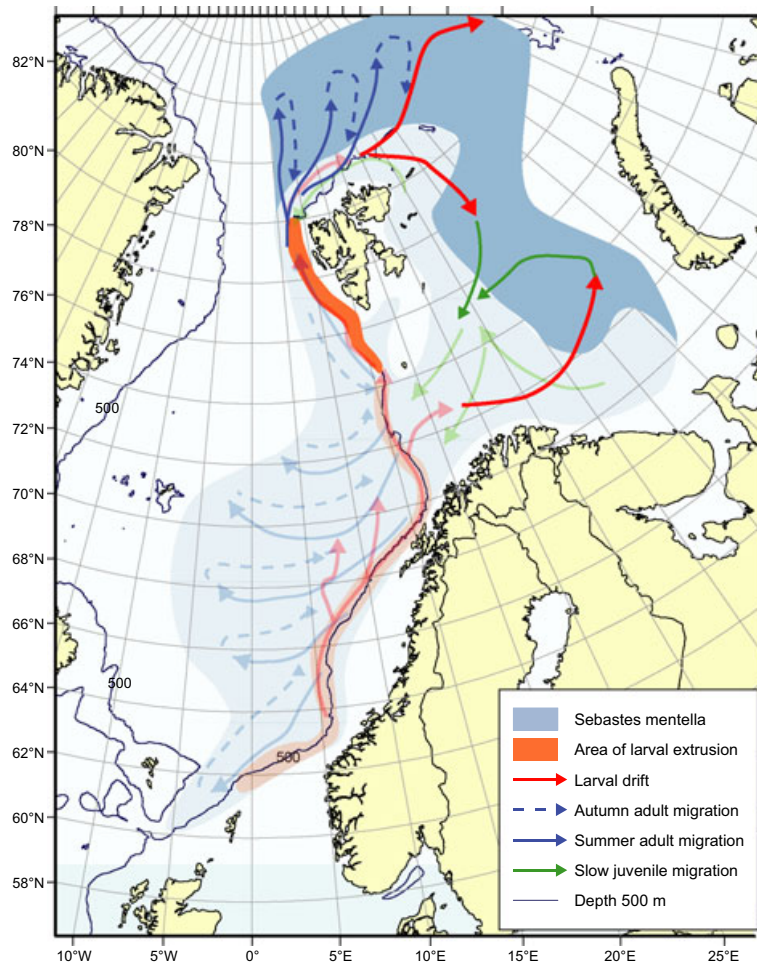


Figure 3. Hypothesized expansion of the distribution area of beaked redfish under future ocean climate in the Barents Sea and surrounding areas. Shaded areas and arrows indicate current distribution areas and migration routes. Plain color areas and arrows indicate the potential expansion of distribution and migration routes. Adapted from Nedreaas *et al.* (2011). Used with permission from ICES Insight.

to partition the limited resources. These strategies result in complex zoogeographic patterns, which allow co-existence (Hollowed *et al.*, 2012). Climate change may influence the effectiveness of these strategies, and new species that colonize the Arctic may disrupt the current dynamics between predator and prey.

POTENTIAL FOR MOVEMENT TO ARCTIC

Assessment of the expected movements of 17 fish and shellfish stocks or stock groups currently found in the Barents, Norwegian and Bering Seas to climate change was qualitatively evaluated by examining the potential impact of climate change as mitigated by the adaptive capacity of each species. Input for this evaluation was provided by 34 stock experts from nine countries during an international workshop held in conjunction with the Ecosystem Studies of sub-Arctic Seas (ESSAS) Open Science meeting sponsored by the International Council for Exploration of the Seas (ICES)

and the North Pacific Marine Science Organization (PICES). Participants provided expert opinions and advice that formed the basis for rankings shown in Table 1. Three ranks were established: low potential, potential or high potential to expand in, or move into, the Arctic. These ranks were based on a review of the life history characteristics identified above, within the context of potential impact and adaptive capacity of the species. Five stocks or stock groups were thought to have a low potential to expand in, or move into, the Arctic: walleye pollock, northern rock sole, Pacific cod (*Gadus macrocephalus*), Atlantic cod (*Gadus morhua*), Pacific ocean perch (*Sebastes alutus*). Six stocks were potentially able to expand or move into the Arctic. Six stocks, polar cod, snow crab, Bering flounder (*Hippoglossoides elassodon*), Greenland shark (*Somniosus microcephalus*), Arctic skate (*Amblyraja hyperborea*), and beaked redfish (*Sebastes mentella*), had a high potential to expand in, or move into, the Arctic. Of these six, several stocks exhibit some of the life history criteria noted above.

Future expansion or movement of sub-Arctic commercial fish stocks from the Norwegian or Barents Seas into the Arctic is more likely because the inflow of warm Atlantic water is stronger and the open water connection with the Arctic Ocean provides greater access to the region. The possible expansion of beaked redfish is illustrated in Figure 3. Pelagic species such as Atlanto-scandic herring (*Clupea harengus*) and capelin potentially could expand and move into Arctic waters if prey resources and temperatures were sufficient to sustain metabolic demands. The persistence of winter sea ice on the shelves is expected to deter the formation of new spawning areas in the Arctic for Atlantic cod. However, Atlantic cod foraging potentially could expand over the Arctic continental shelf areas if appropriate temperature and food conditions were present.

The probability of expansion or movement of commercial fish and shellfish stocks from the Bering Sea to the Chukchi Sea and high Arctic is mixed. The shallow depth of Bering Strait, coupled with the expected persistence of a demersal cold pool in the northern Bering Sea and Chukchi Seas, may deter movement of Pacific Ocean perch (*Sebastes alutus*), Pacific cod (*Gadus macrocephalus*) and walleye pollock into the Arctic. Northern rock sole, was less likely to move or expand into the Arctic because of its restricted diet. Alaska plaice and yellowfin sole (*Limanda aspera*) potentially could expand or move into the Arctic. On the Pacific side, Bering flounder and Greenland halibut, *Reinhardtius hippoglossoides*, exhibited off-shelf spawning movements and were considered potential candidates for expansion if eggs and larvae are advected into the Arctic. Both of these species have been observed in the Arctic in some locations (Rand and Logerwell, 2011).

DISCUSSION

This qualitative assessment identified several factors that will govern the potential expansion and movement of commercial fish and shellfish species into the Arctic. The important environmental factors include: the spatial distribution of suitable thermal conditions, availability of prey, the depth of migration corridors into, or out of, the Arctic Ocean. Key life history and behavioral characteristics included: growth potential, fidelity to spawning sites, foraging plasticity, thermal tolerances, habitat depth and projected spawning stock size.

Ocean conditions in the Arctic are projected to change in response to global warming, ocean acidification and associated changes in the cryosphere (e.g., ACIA, 2005; SWIPA, 2012). Previous studies

concluded that several important commercial stocks would move northwards in response to projected changes in ocean conditions (ACIA, 2005). The vulnerability analysis presented here indicates that different species will react differently to changes in ocean conditions. Only six stocks were highly likely to exhibit expansions sufficient to support commercial fishing in the Arctic Ocean.

The 'potential for movement' assessment utilized the best available information regarding how different species have responded to environmental conditions in the past and applied these relationships to infer the future distributions and abundance of commercial species. Cheung *et al.* (2009) used this approach to identify how bio-climatic envelopes would shift under climate change, using a narrow suite of factors governing the responses to climate change. Cheung *et al.* (2009) predicted that the Polar Regions would experience a high rate of invasions by new species. However, our approach includes a broader suite of factors governing the potential for movement to the Arctic and concludes that only a few species had a high probability of expanding or moving into the Arctic. This finding suggests that bio-climatic envelope models are insufficient on their own for making projections and that species interactions, life history and behavioral responses must be included.

Pelagic species that exhibit long distance feeding migrations may be capable of utilizing the Arctic Ocean as a summer feeding area if temperature and food conditions are suitable. However, examples of simulation studies suggest that pelagic foragers may predominantly track gradients in prey (Humston *et al.*, 2004). Gradient-tracking foragers are likely to conserve energy and forage on local prey sources. Therefore, the emergence of foraging migrations into the Arctic is likely to evolve over considerable time.

Although the present study identified six fish and shellfish species that are expected to expand or move into the Arctic, additional information would be required to sustainably manage these emerging fisheries through an ecosystem approach to management. Some species, such as sharks and skates, exhibit life history characteristics that make them particularly vulnerable to exploitation and therefore unlikely to become target species (Ormseth and Spencer, 2011). U.S. Fisheries management councils recently closed the Arctic regions within their Exclusive Economic Zone to commercial fishing until sufficient information was available to manage the fisheries sustainably (Wilson and Ormseth, 2009).

There are many unknown factors that might have an impact on the future distribution of fish stocks.

We recognize that complex, non-linear responses are likely to occur. For example, the indirect effect of climate through the food web may be as important as the direct effect of thermal habitat suitability. This assessment provides a first-order projection based on existing knowledge and expert opinion. The framework shows that the potential impact of climate change will likely differ by region and species. This framework can be used to guide future research that will lead to a sufficient understanding of the mechanistic linkages between climate change and fish responses. That understanding would allow the framework to be extended to include numeric weightings to formally quantify the potential movement or expansion of fish and shellfish species into the Arctic. Participants in the ICES/PICES workshop identified the following key items for future research to facilitate quantitative assessments of the potential movement or expansion of fish and shellfish species into the Arctic.

Resolve impacts of Atlantic inflow to Arctic

Platforms to investigate trophic interactions (food web) and species specific migration patterns should be maintained and developed to provide observations and to support modeling. In combination with bioenergetics studies, these will provide the understanding necessary to project trends in biological productivity at various trophic levels and in particular for exploited species.

Conduct periodic fish/plankton surveys to monitor shifts in their distributional and abundance patterns

Studies of fish responses to variability in ocean conditions in the northern/colder limits of contemporary geographical distributions will help to resolve the mechanisms governing how the spatial distribution of fish, shellfish and other species can expand or shift towards the Arctic Ocean. It is therefore essential that biological monitoring surveys extend as far as possible into the Arctic to monitor the edge of Arctic and sub-Arctic species distributions and how these may be affected by fluctuations in the ocean climate.

Promote novel approach to ecosystem modeling

Ecosystems that can be described as 'complex adaptive systems' (CAS; Levin, 1998, 2002) and possess an extremely high degree of complexity, are difficult to observe, display non-linear behavior with abrupt changes (also called regime shifts) and are generally defiant to conventional deterministic predictions. Although not fully predictable, such systems are not totally unpredictable either. To project future possible

states of Arctic Ocean ecosystems, the current challenge is to build simulation models that can combine processes occurring at various scales of organization (from individual to ecosystems), different temporal and spatial scales, and that can explicitly handle the intrinsic complexity, stochasticity and self-organization of marine ecosystems. Progress in this direction is paramount to achieve any degree of reliable projection for the state of Arctic/sub-Arctic marine ecosystems in the future. Future research should therefore promote the development of integrated models that are capable of mimicking multiple trophic levels and processes (taxonomic diversity, population demography, food web structure, trophic fluxes, and spatial structures) and explicitly integrate stochasticity, self-organization and adaptation, while recognizing uncertainties in conceptual representations and numerical model formulations and projections.

Conduct studies of zooplankton community dynamics, with special emphasis on the ratio of boreal/Arctic and large/small species

As noted earlier, increased primary and secondary productivity is expected in an ice-free Arctic (Slagstad *et al.*, 2011; Wassman, 2011), as well as changes in relative species composition (Kosobokova and Hirche, 2009). Model projections portend changes in the distribution of *Calanus* spp. (Slagstad *et al.*, 2011). Edvardsen *et al.* (2003) observed *C. finmarchicus* were advected from the Norwegian Sea to the Barents Sea in the Atlantic Current. This observation suggests that advection of *C. finmarchicus* into the Arctic Ocean could also occur. Careful monitoring of expected changes in the species composition is crucial to quantitatively assess the potential expansion and movement of fish and shellfish into the Arctic.

Conduct studies of fish community dynamics, with special emphasis on the ratio of boreal/Arctic species

Studies of the factors governing fish and shellfish movement are needed to assess the processes underlying spawning or feeding movements. Collections of the diet, size, maturity, fecundity and growth will be needed. Studies of the zoogeography of fish and shellfish are needed to assess how new species will impact the fish and shellfish communities. Fish diets will enable the construction of food webs and will identify differences in prey selection. For example, capelin is a specialized plankton feeder and is the most planktonivorous fish in the Barents Sea. Polar cod primarily utilize larger zooplankton forms (Dolgov *et al.*, 2011; Gjøvsæter *et al.*, 2011).

Conduct studies of benthos community dynamics with special emphasis on fish preys

Benthic species constitute a substantial contribution to the feeding of demersal and bottom fish populations. In the Eastern Bering Sea and Barents Sea, estimates of biomass, consumption and production for macrobenthos are far greater than those of all fish species combined (Gaichas *et al.*, 2009). Although the food web of the Barents Sea is believed to be primarily pelagic, the contribution of the benthic energy pathways is important in the Eastern Bering Sea (Megrey and Aydin, 2009). Dedicated studies are required to determine how benthic communities can respond to novel ocean climate and how this can impact the distribution and abundance of commercial fish stocks in the future.

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