Stock name: Barents Sea capelin **Latin name**: *Mallotus villosus*

Geographical area: Barents Sea (juvenile and adult feeding grounds) and coast of Northern Norway

and Kola Peninsula (spawning grounds) (ICES subarea 1)

Expert: Georg Skaret, Maria Fossheim, Geir Huse

Date: 28 January 2020

Stock Sensitivity Attributes

HABITAT SPECIFICITY: Barents Sea capelin (*Mallotus villosus*, Osmeridae) mainly inhabits the boreal parts of the Barents Sea at the margins of cold Arctic waters. It is a small (maximum length 20 cm) and short-lived (maximum age 5-6 years) osmerid. It is a pelagic species with a wide distribution area. It undertakes pronounced seasonal migrations following the withdrawing ice edge northwards for feeding during summer and migrations towards the coast of North Norway for spawning (Gjøsæter, 1998). A range of spawning localities have been documented along the coast of North Norway and the north-eastern parts of Russia. In other stocks of capelin, spawning has been reported over a wide salinity range from 3 to 35 psu reflecting the differences between beach spawners in fresher water (Newfoundland) and deep-water spawners in more saline environments. Over their distribution area in the North Pacific and Atlantic oceans, capelin is found in temperatures that range from -1.5 to 14 °C (Rose, 2005). However, they are most often found in waters ranging from -1 to 6 °C. As adults, capelin tend to occupy a relatively narrow range of salinities, from 33 to 35 psu.

PREY SPECIFICITY: Adult Barents Sea capelin feeds on plankton, while copepods dominate the diet of small (<12 cm) capelin. Calanus finmarchicus, Pseudocalanus elongatus (Clausocalanidae), Paraeuchaeta norvegica (Euchaetidae) and Metridia longa (Metridinidae) contribute to the diet of small capelin throughout the year (Hassel et al., 1991), while Calanus hyperboreus (Calanidae), Microcalanus pusillus (Clausocalanidae), Oithona similis (Oithonidae) and Oncaea borealis (Oncaeidae) may play an important role during one or more quarters of the year (Gjøsæter, 1998). Of the above-mentioned copepods, C. finmarchicus dominate the diet of small capelin; C. finmarchicus made up more than half of the stomach content over a 4-year study period from 2005-2008 (Dalpadado & Mowbray, 2013). At about 12 cm total length, there is a shift in capelin diet towards larger macroplankton; in particular the euphausiids Thysanoessa inermis (Euphausiidae) and T. raschii and the two amphipods, Themisto libellula (Hyperiidae) and T. abyssorum (Gjøsæter, 1998). Of these, T. inermis dominates in the diets (Dalpadado & Mowbray, 2013; Panasenko, 1984). Both C. finmarchicus and T. inermis are abundant in the Barents Sea and their dominance in capelin diets likely reflect high availability.

SPECIES INTERACTION: As a pelagic species, capelin can take most advantage of the zooplankton production in the central Barents Sea (Gjøsæter, 1998). It has a diet overlap with polar cod (Boreogadus saida, Gadidae) in the northern areas, but polar cod tends to prefer pure Arctic water masses for feeding. In the southern Barents Sea young capelin have overlapping diets with young herring (Huse & Toresen, 1996). Both overlaps may impose competition in some years but likely to a limited extent. The larval stages of capelin in the south spatially overlap with other fish larvae such as those of herring and cod, but capelin larvae hatch later and are typically smaller than herring and cod larvae and diet overlap is hence low (Fossheim et al., 2006; Pedersen & Fossheim, 2008). Herring is well known to prey on larval capelin (Godiksen et al., 2006; Huse & Toresen, 2000) and this is likely the primary cause for the collapse reported for the capelin stock in recent decades (Gjøsæter et al., 2009; Gjøsæter & Bogstad, 1998). Capelin is a major forage fish in the Barents Sea and subject to substantial predation throughout the year in particular by cod, sea mammals and seabirds (Bogstad et al., 2000).

ADULT MOBILITY: Rapid changes in capelin distribution have been reported several times at both the larval stage, as a consequence of drift, and as active feeding or spawning migrations of juveniles and adults (Rose, 2005). The distribution changes have often been associated with climate, and the species has been suggested to be a 'canary' of climate changes in boreal marine ecosystems (Rose, 2005). Changes can be described as: (i) shifts involving distribution changes within the typical stock range (e.g. Barents Sea shifts), or (ii) excursions, which take fish outside their normal range (e.g. Newfoundland Banks–Scotian Shelf excursions of 1990s). New spawning areas have resulted from excursions (North Pacific to North Atlantic excursions), but at other times they have not (Faroe Islands excursion). All stocks exhibit spawning and feeding range displacements associated with climate variations.

DISPERSAL OF EARLY LIFE STAGES: Capelin originated from Pacific waters and then colonized the North Atlantic at some time during inter-glacial periods over the past million years (Ekman, 1953). The adaptation to new habitats has resulted in two different spawning modes, beach spawning and deepwater spawning (Rose, 2005). In the Newfoundland waters the two modes occur in the same stock. The Barents Sea capelin is a deep-water spawner whereas fjordic capelin in Balsfjord, North Norway is a beach spawner (Nyholmen & Hopkins, 1988). Capelin larvae hatch in coastal waters and stay on shallow depths, increasing their likelihood for transport offshelf, where they can take advantage of a greater supply of prey organisms when they have increased in size and grown out of the most critical mortality phases. Further to this, capelin larvae might be associated with a different food chain than other larvae from e.g. herring or cod in the coastal areas. More specifically, capelin larvae prey only sparsely upon copepod nauplii advected onto the shelf from the Norwegian Sea, but rather prey on smaller organisms such as Bivalvia and other small invertebrates occurring in coastal waters (Fossheim et al., 2006). Capelin larvae might be adapted to tolerate low prey abundance in an early phase, contrary to most fish larvae that have relatively low starvation tolerance in this stage. In addition, by omitting C. finmarchicus peaks, capelin larvae may avoid competition on the same prey. Thereby, capelin larvae may avoid substantial top-down control by predators that are attracted by C. finmarchicus flourishing in this area in late spring.

EARLY LIFE HISTORY SURVIVAL AND SETTLEMENT REQUIREMENTS: In general, capelin has high reproductive potential and constitute an intrinsic rate of population growth "r" (Gjøsæter, 1998; Rose, 2005; Vilhjálmsson, 1994). The peak spawning of capelin is in late winter/early spring, as larvae take advantage of a wide variety of coastal prey (Fossheim et al., 2006). However, there is a variable larval survival resulting in different numbers of recruits in Barents Sea capelin (Gjøsæter, 1998). The main top-down control of larval capelin is suggested by young herring the Barents Sea (Gjøsæter & Bogstad, 1998; Hallfredsson, 2006; Huse & Toresen, 2000).

COMPLEXITY IN REPRODUCTIVE STRATEGY: It has been experimentally demonstrated that capelin has two reproductive strategies: semelparous (death for both sexes after one single spawning event) for offshore spawners like the Barents Sea capelin, and iteroparous for beach spawners (Christiansen et al., 2008). It was suggested by these authors that capelin can change between these strategies following changes in habitat, physical forcing and varying predation pressure. Furthermore, they suggested that oceanic capelin like Barents Sea capelin originated from former beach spawners since their eggs are very robust towards changes in temperature and salinity which beach spawned eggs are exposed to.

SPAWNING CYCLE: The main spawning of Barents Sea capelin happens in late winter/early spring over the course of a couple of months, with some spawning extending into the summer (Gjøsæter, 1998). Mature capelin is assumed at age 3-4. Spawning typically occurs over sand or gravel at depths of 25 to 75 m in the North European Atlantic. In the North Pacific and waters off Newfoundland most spawning is on beaches. The eggs adhere to the substrate and *in situ* investigations through diving

have indicated that the preferred habitat for spawning is in current-rich locations in the depth range of 25-75 m at incubation temperatures between 1.5 and 6.5 °C (Bakke & Bjørke, 1971; Sætre & Gjøsæter, 1975).

SENSITIVITY TO TEMPERATURE: Adult capelin distribution and migration has been reported to be limited by temperature or temperature-induced changes in plankton distribution. The specific temperature tolerance of capelin has not been investigated, but observations from Newfoundland, Icelandic, and Norwegian waters suggest that 2-years old capelin and older are seldomly found in waters with temperatures of <-1 °C (Gjøsæter & Loeng, 1987; Rose, 2005; Vilhjálmsson, 1994). Nevertheless, capelin occupies the cold waters and may feed and migrate along fronts between cold Arctic and warmer Atlantic waters (Vilhjálmsson, 2002). Although this Arctic-boreal species has evolved to live at the edge of Arctic waters, and to exploit present feeding opportunities, capelin requires higher temperatures for successful reproduction. Maturation has been reported to require temperatures of 2-4 °C (Carscadden et al., 1985). The main part of deep-water spawning occurs at temperatures from 2 to 7 °C (it most likely occurs from 2 to 5 °C), but beach spawning has been reported at temperatures up to or even above 10 °C. The success of such warm-water spawning has been questioned (Vilhjálmsson, 1994), and both the timing and site suitability of the spawning may be regulated by temperature. Among stocks, the temperatures and salinities associated with most spawning appear to vary. Beach spawning occurs in much fresher and warmer waters than would be encountered by deep-water spawners. Their thermal range typically shifts upwards and may contract during spawning. Overall, capelin distribution may be limited by temperature at several stages in the life history. Thermal tolerances of 2-years old capelin and older is relatively wide during feeding with a typical lower limit of -1 °C. Spawning success requires a narrower range of temperatures. Distributions in cold water are risky. Off Labrador, capelin have been observed to freeze to death (Templeman, 1948). Similar observations from Iceland (Vilhjálmsson, 1994) could indicate lethal effects from ice crystal contact in "super-cooled" water. In general, it is almost certain that climateinduced changes affect capelin in the seasonal temperatures of the North Atlantic. Capelin appears to react quickly to environmental changes, and hence act as an early warning sea "canary" for changes that may also affect other species and the ecosystem.

SENSITIVITY TO OCEAN ACIDIFICATION: Capelin are dependent on zooplanktonic crustaceans for food during all life stages; copepod nauplii as larvae, calanoid copepods as juveniles and macrozooplankton, in particular krill, as adults (Dalpadado & Mowbray, 2013; Gjøsæter, 1998). Some crustaceans are sensitive to ocean acidification, and even though the damaging mechanisms are not completely known, low pH water may impact both exoskeleton calcification and intracellular acid-based regulations (Kawaguchi et al., 2013). Adult calanoid copepods have shown robustness towards acidification, but nauplii mortality rates increase threefold when pCO $_2$ concentrations reached 1,000 μ atm (year 2100 scenario) with LC $_{50}$ at 1,084 μ atm pCO $_2$ (Cripps et al., 2014).

POPULATION GROWTH RATE: Capelin normally matures at age 2 to 3 years. Maximum age is 5-6 years. Capelin is a bust-and-boom species meaning it has high reproductive potential and intrinsic rate of population growth (Gjøsæter, 1998).

STOCK SIZE/STATUS: The capelin stock has fluctuated greatly since the stock monitoring started in 1972, also in periods with low fishing pressure. Anecdotal information from times prior to 1972 suggests that the stock size fluctuated greatly also before (Gjøsæter, 1998). There have been four periods after monitoring started with stock biomasses measuring less than 1 million tonnes. On each occasion the stock size has recovered within 5 years. The stock estimate from 2019 was 411,000 tonnes. Due to the fluctuating nature of this stock, an evaluation of resilience based on Stock Size/Status is misleading for Barents Sea capelin.

OTHER STRESSORS: Capelin is experiencing direct stress from fisheries, but the fishing pressure is low due to a conservative management strategy (Gjøsæter et al., 2015). There is also a substantial predation pressure on capelin from for instance cod and harp seals which is indirectly influenced by the harvesting strategies for these predators.

Scoring of the considered sensitivity attributes

Sensitivity attributes, climate exposure based on climate projections allowing the evaluations of impacts of climate change, and accumulated directional effect scoring for capelin (*Mallotus villosus*) stock in ICES subareas 1 and 2. L: low; M: moderate; H: high; VH: very high, Mean_w: weighted mean; N/A: not applicable. Usage: this column was used to make ad hoc notes, including considerations about the amount of relevant data available: 1 = low, 2 = moderate; 3 = high. N/A = not applicable.

Capelin (Mallotus villosus) in ICES subareas 1 and 2

SENSITIVITY ATTRIBUTES	L	М	Н	VH	$Mean_w$	Usage	Remark
Habitat Specificity	1	3	1	0	2.0		
Prey Specificity	0	3	2	0	2.4		
Species Interaction	0	1	3	1	3.0		
Adult Mobility	0	3	2	0	2.4		
Dispersal of Early Life Stages	0	3	2	0	2.4		
ELH Survival and Settlement Requirements	1	3	1	0	2.0		
Complexity in Reproductive Strategy	0	1	3	1	3.0		
Spawning Cycle	0	1	3	1	3.0		
Sensitivity to Temperature	0	5	0	0	2.0		
Sensitivity to Ocean Acidification	4	1	0	0	1.2		
Population Growth Rate	3	2	0	0	1.4		
Stock Size/Status	0	0	3	2	3.4		
Other Stressors	1	3	1	0	2.0		
Grand mean					2.32		
Grand mean SD					0.65		

CLIMATE EXPOSURE	L	М	Н	VH	Meanw	Usage	Directional Effect
Surface Temperature	0	0	0	0		N/A	
Temperature 100 m	0	2	3	0	2.6		-1
Temperature 500 m	0	0	0	0		N/A	
Bottom Temperature	0	0	0	0		N/A	
O ₂ (Surface)	3	2	0	0	1.4		0
pH (Surface)	0	0	0	0		N/A	
Gross Primary Production	0	3	2	0	2.4		1
Gross Secondary Production	0	2	3	0	2.6		1
Sea Ice Abundance	0	2	3	0	2.6		-1
Grand mean					2.32		
Grand mean SD					0.52		
Accumulated Directional Effect					-		-0.2

Accumulated Directional Effect: NEUTRAL	-0.2
1	

References

Bakke, S., & Bjørke, H. (1971). Diving observations on Barents Sea capelin at its spawning grounds off the coast of northern Norway. *ICES Council Meeting Papers*, *H*: 25, 12.

- Bogstad, B., Haug, T., & Mehl, S. (2000). Who eats whom in the Barents Sea? In G. Vikingsson & F. Kapel (Eds.), *Minke Whales, Harp and Hooded seals: Major Predators in the North Atlantic Ecosystem Book 2* (Vol. 2, pp. 98–119). NAMMCO Scientific Publications.
- Carscadden, J., Winters, G., & Miller, D. (1985). An indirect method of estimating maturation rates of cohorts of capelin (*Mallotus villosus*). *Journal of Northwest Atlantic Fishery Science*, *6*(2), 135–140.
- Christiansen, J. S., Præbel, K., Siikavuopio, S. I., & Carscadden, J. E. (2008). Facultative semelparity in capelin *Mallotus villosus* (Osmeridae)-an experimental test of a life history phenomenon in a sub-arctic fish. *Journal of Experimental Marine Biology and Ecology*, *360*(1), 47–55.
- Cripps, G., Lindeque, P., & Flynn, K. J. (2014). Have we been underestimating the effects of ocean acidification in zooplankton? *Global Change Biology*, *20*(11), 3377–3385.
- Dalpadado, P., & Mowbray, F. (2013). Comparative analysis of feeding ecology of capelin from two shelf ecosystems, off Newfoundland and in the Barents Sea. *Progress in Oceanography*, *114*, 97–105.
- Ekman, S. (1953). The boreal fauna of the North Atlantic. In *Zoogeography of the Sea.* (pp. 100–141). Sidgwick and Jackson.
- Fossheim, M., Tande, K. S., Semenova, T., & Timonin, A. (2006). Capelin larvae (*Mallotus villosus*) and community structure of zooplankton off the coast of northern Norway. *Journal of Plankton Research*, 28(6), 585–595.
- Gjøsæter, H. (1998). The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia*, *83*(6), 453–496.
- Gjøsæter, H., & Bogstad, B. (1998). Effects of the presence of herring (*Clupea harengus*) on the stock-recruitment relationship of Barents Sea capelin (*Mallotus villosus*). *Fisheries Research*, *38*(1), 57–71.
- Gjøsæter, H., Bogstad, B., & Tjelmeland, S. (2009). Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Marine Biology Research*, *5*(1), 40–53.
- Gjøsæter, H., Bogstad, B., Tjelmeland, S., & Subbey, S. (2015). A retrospective evaluation of the Barents Sea capelin management advice. *Marine Biology Research*, 11(2), 135–143.
- Gjøsæter, H., & Loeng, H. (1987). Growth of the Barents Sea capelin, *Mallotus villosus*, in relation to climate. *Environmental Biology of Fishes*, 20(4), 293–300.
- Godiksen, J., Hallfredsson, E., & Pedersen, T. (2006). Effects of alternative prey on predation intensity from herring *Clupea harengus* and sandeel *Ammodytes marinus* on capelin *Mallotus villosus* larvae in the Barents Sea. *Journal of Fish Biology*, 69(6), 1807–1823.
- Hallfredsson, E. (2006). Fish predation on capelin larvae Mallotus villosus in the Barents Sea, in relation to recruitment [Doctor scientiarum thesis]. University of Tromsø.
- Hassel, A., Skjoldal, H. R., Gjøsæter, H., Loeng, H., & Omli, L. (1991). Impact of grazing from capelin (*Mallotus villosus*) on zooplankton: A case study in the northern Barents Sea in August 1985. *Polar Research*, 10(2), 371–388.
- Huse, G., & Toresen, R. (1996). A comparative study of the feeding habits of herring (*Clupea harengus*, Clupeidae, L.) and capelin (*Mallotus villosus*, Osmeridae, Müller) in the Barents Sea. *Sarsia*, *81*(2), 143–153.
- Huse, G., & Toresen, R. (2000). Juvenile herring prey on Barents Sea capelin larvae. Sarsia, 85(5-6), 385-391.
- Kawaguchi, S., Ishida, A., King, R., Raymond, B., Waller, N., Constable, A., Nicol, S., Wakita, M., & Ishimatsu, A. (2013). Risk maps for Antarctic krill under projected Southern Ocean acidification. *Nature Climate Change*, *3*(9), 843–847.
- Nyholmen, O., & Hopkins, C. (1988). Some observations on the population biology of capelin (*Mallotus villosus*) from Balsfjord, northern Norway. *ICES Journal of Marine Science*, 44(3), 264–276.
- Panasenko, L. (1984). Feeding of the Barents Sea capelin. ICES Council Meeting Papers, H: 6, 16.
- Pedersen, T., & Fossheim, M. (2008). Diet of 0-group stages of capelin (*Mallotus villosus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) during spring and summer in the Barents Sea. *Marine Biology*, 153(6), 1037–1046.
- Rose, G. A. (2005). Capelin (*Mallotus villosus*) distribution and climate: A sea "canary" for marine ecosystem change. *ICES Journal of Marine Science*, 62(7), 1524–1530.
- Sætre, R., & Gjøsæter, J. (1975). Ecological investigations on the spawning grounds of the Barents Sea capelin. Fiskeridirektoratets Skrifter Serie Havundersøkelser, 16, 203–227.
- Templeman, W. (1948). The life history of the capelin (*Mallotus villosus* Müller) in Newfoundland waters. *Bulletin of the Newfoundland Government Laboratory*, 17, 1–151.
- Vilhjálmsson, H. (1994). *The Icelandic Capelin Stock: Capelin,* Mallotus villosus *(Müller) in the Iceland-Greenland-Jan Mayen Area*. Hafrannsóknastofnunin.

Vilhjálmsson, H. (2002). Capelin (Mallotus villosus) in the Iceland–East Greenland–Jan Mayen ecosystem. ICES Journal of Marine Science, 59(5), 870–883.