

Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change

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Rose, G. A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change. — ICES Journal of Marine Science, 62: 1524–1530.

Capelin (*Mallotus villosus*) is a classic “r” adapted pelagic species that inhabits the northern boreal oceans at the margins of cold Arctic waters. The species originated in the North Pacific and colonized the North Atlantic at least once during interglacial periods of the past few million years. Capelin became the main forage species for many larger predatory fish, and also for seabirds and marine mammals. The colonizing abilities of capelin have been noted in historical anecdotes, typically in concert with climate variations. In this paper, all known shifts in distribution are catalogued. Shifts have taken place at the larval and adult stages, and some result in new spawning locations, others do not. Displacement distance relates to temperature change: $\log_{10}(\text{distance}_{\text{km}}) = 0.28 \times \text{temperature change} + 2.16$ ($p < 0.05$, $r^2 = 0.91$). The persistence of the shifts relates to the displacement distance: $\log_{10}(\text{persistence}_y) = 2.62 \times \log_{10}(\text{distance}_{\text{km}}) - 6.56$ ($p < 0.05$, $r^2 = 0.83$). The quick and consistent response of capelin to temperature change, its importance to the North Atlantic foodweb, and established monitoring methods suggest this species as a sea “canary” for northern boreal marine ecosystem responses to climate variability and change.

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Keywords: capelin, climate change, northern boreal ecosystems, temperature.

Received 14 June 2004; accepted 15 May 2005.

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Introduction

The capelin (*Mallotus villosus*) is a small and short-lived osmerid, a pelagic species with high reproductive potential and intrinsic rate of population growth “r” (Vilhjálmsson, 1994). Its distribution is circumpolar in boreal waters of the North Pacific and North Atlantic oceans (Figure 1). Feeding occurs in the margins of very cold Arctic waters. Capelin originated in the North Pacific, where osmerids are endemic (Ekman, 1953). The species migrated to the North Atlantic during interglacial periods within the past few million years, although the exact timing is difficult to specify (Ekman, 1953; Stergiou, 1989). Capelin then migrated eastwards across the Greenland–Iceland–Jan Mayen region and into the Barents Sea. This range expansion in response to climate change led to genetic separation and the development of somewhat different regional life history strategies, in particular related to reproduction (e.g. Vilhjálmsson, 1994; Carscadden and Vilhjálmsson, 2002).

Capelin have two modes of reproductive behaviour, beach and deeper water spawning, which have a curious geographic distribution. Beach spawning dominates in much of the Pacific and Newfoundland regions, but deeper water spawning dominates in Icelandic and Norwegian waters. This distribution led Stergiou (1989) to speculate that a very recent re-incursion of beach-spawning capelin to the Northwest Atlantic from the North Pacific occurred during the melting of late Wisconsin ice between 6000 and 12 000 years ago. However, there is evidence against this notion. During the last glacial maximum (LGM) about 12 000 years ago, the North Atlantic was much colder than it is today, and land masses and adjacent seas were covered in the massive Scandinavian, Greenland, and Laurentide ice sheets. Models of sea surface temperature (SST) during the LGM show declines of up to 5–6°C in open water, and most current spawning areas would have been ice bound (Sarnthein *et al.*, 2003). The sole contemporary Atlantic spawning ground that was ice-free during the LGM is the southeast shoal of the Grand Bank, which was then above sea level

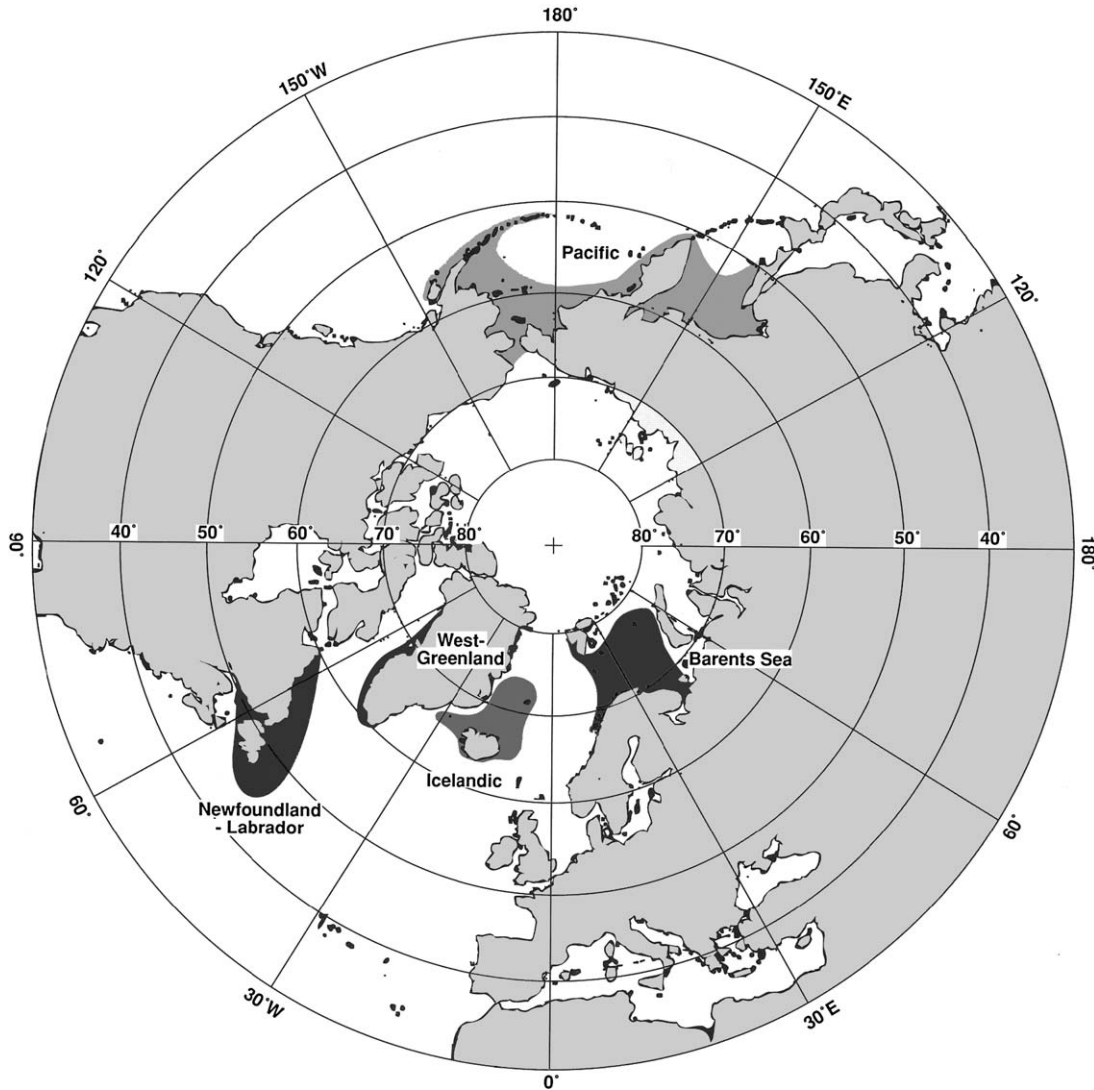


Figure 1. Map of current distribution of capelin (*Mallotus villosus*) and likely migration routes from North Pacific to North Atlantic (redrawn from Vilhjálmsón, 1994).

(Carscadden *et al.*, 1989). During the LGM, capelin distribution in the Northwest Atlantic likely shifted to a southern Grand Bank beach-spawning area (Carscadden *et al.*, 1989). Hence, the original beach-spawning behaviour of capelin in the Atlantic may have survived the ice ages only in Newfoundland waters, and not in the Northeast Atlantic or in Icelandic waters, where contemporary spawning occurs in waters up to 100 m deep (Vilhjálmsón, 1994). Genetic evidence indicates that Pacific and Northwest Atlantic capelin can be distinguished, but beach- and offshore-spawning capelin are indistinguishable in the Newfoundland region, hence adding support for the older migration hypothesis but inconsistent with more recent incursions (Dodson *et al.*, 1991).

The origin of capelin and its spread from the North Pacific to Northwest Atlantic, then to the Northeast Atlantic, illustrate the influence that large-scale climate change has on marine zoogeography. The North Pacific was not as heavily glaciated as was the North Atlantic, and capelin habitat was likely much closer to contemporary conditions than in the North Atlantic (Stergiou, 1989). Since the big shift from the North Pacific, capelin have been observed to shift their distributions several times.

In this paper, I compile data from reported shifts in capelin distribution. These data are used to quantify the relationship between temperature change and distance displaced for capelin during the feeding and spawning

seasons. The objective of this analysis was to provide a quantitative framework for predicting the likely response of capelin to climate change.

Methods

The literature was searched for descriptions and data on reported capelin locations, environmental data, shifts in distribution, and ancillary information such as temperature changes during the period of the shift and distance moved. In most cases, these data were extracted from tables, maps, or charts documented in the sources cited in Tables 1 and 2. In some cases where there was disagreement among reports, such as occupied temperatures, judgement was used as to what was the more reliable source. In addition, original data from Newfoundland and Labrador were used in the case of temperatures and salinities occupied during the non-spawning period.

Results

Over their range in the North Pacific and Atlantic oceans, capelin are found in temperatures that range from -1.5 to 14°C (Table 1). They are most often found in waters ranging from -1 to 6°C . During spawning, their thermal range typically shifts upwards and may contract. Beach spawning occurs at 2 – 10°C , but deepwater spawning is restricted to about 2 – 7°C (it most likely occurs from 2 to 5°C). As adults, capelin tend to occupy a relatively narrow range of salinities, from 33 to 35 psu. However, spawning has been reported over a wide salinity range from 3 to 35 psu reflecting the differences between beach (fresher) and deepwater (more saline) environments.

Changes in capelin distribution have been reported at both the larval stage, as a consequence of drift, and as

active feeding or spawning range changes of juveniles and adults (Table 2). Changes can be described as shifts, which involve distribution changes within the typical stock range (e.g. Barents Sea shifts), or excursions, which take fish outside their normal range (e.g. Newfoundland Banks–Scotian Shelf excursions of 1990s). Excursions at times have resulted in new spawning areas (North Pacific to North Atlantic excursions), but at times they have not (Faroe Islands excursion). All stocks have exhibited spawning and feeding range displacements associated with climate variations.

The magnitude of capelin distribution changes was associated with sea temperature changes during the same period (Figure 2). The relationship was non-linear and best described by a logarithmic function: $\log_{10}(\text{distance}_{\text{km}}) = 0.28 \times \text{temperature change} + 2.16$ ($p < 0.05$, $r^2 = 0.91$, $n = 12$). This relationship indicates that small changes in temperature (ca. 1°C) are associated with changes in distribution over scales of hundreds of kilometres, but larger changes in temperature (several degrees) may result in much larger displacements. There have been no reported cases of widespread extinction of capelin populations, although vast areas have become relatively vacated as a consequence of distribution shifts.

The persistence of documented changes in distribution correlated with the spatial scale of the change (Figure 3). The best fit model was $\log_{10}(\text{persistence}_y) = 2.62 \times \log_{10}(\text{distance}_{\text{km}}) - 6.56$ ($p < 0.05$, $r^2 = 0.83$, $n = 13$). Changes that persisted for only 1 year (interannual variability) were relatively small, on the order of 100 km, and can be identified as shifts within the normal range. Longer-term changes that result in new spawning locations, such as in the Newfoundland Banks–Flemish Cap–Scotian Shelf–Gulf of St. Lawrence region in the late 1980s and early 1990s, and that result in new

Table 1. Depths, temperatures, and salinities where capelin are found and where they spawn in all stocks. Depth in m, temperature in $^{\circ}\text{C}$, start and end in months, salinity in psu. NL means Newfoundland. Note that feeding temperatures have two interpretations. Unbracketed ranges are where capelin can be located; ranges in parentheses are where most are located or concentrated. It was not always possible from the literature to make this interpretation, and in those cases only one range is reported. As an example, capelin are reported to be concentrated in $<2^{\circ}\text{C}$ Icelandic waters (Vilhjálmsón, 1994), but maps in the same report show capelin extending to 6°C . This is less of a problem with spawning characteristics, which are better specified in the literature.

Stock	Feeding		Spawning			References		
	Depth	Temperature	Start	End	Depth		Temperature	Salinity
NL coastal	1 to 450	-1.5 to 6 (-1 to 2)	6	7	0 to 10	3.5 to 10	14 to 33	Nakashima and Wheeler, 2002; unpubl. data
Grand Bank	1 to 250	-1.5 to 6 (-1 to 2)	6	7	40 to 50	2 to 5	34 to 35	Carscadden <i>et al.</i> , 1989; unpubl. data
Barents Sea	10 to 250	(-1 to 2)	3	4	10 to 100	1.5 to 6.5	32 to 34.6	Loeng <i>et al.</i> , 1983; Gjøsæter and Loeng, 1987
Icelandic	10 to 400	-1.5 to 6 (-1 to 2)	3	4	10 to 150	2 to 7	35+	Vilhjálmsón, 1994
Greenland	1 to 600	(-1 to 2)	4	7	0 to 10	1.9 to 8.5	15 to 33	Hansen, 1943; Friis-Rødel and Kannevorf, 2002
Pacific	1 to 100	(0 to 4)	6	7	0 to 5	2 to 14	3 to 33	Stergiou, 1989; Brown, 2002

Table 2. Documented changes in capelin (*Mallotus villosus*) distribution and spawning sites. GOA is Gulf of Alaska; NE NL is northeast Newfoundland and Labrador; GOSL is Gulf of St. Lawrence; BOF is Bay of Fundy. D is distance moved for feeding (if different, spawning distance are in parentheses); P is persistence (note that the recent shifts in the Northwest Atlantic have not yet reverted, so P is underestimated.); T is temperature change.

Stage	Spawn	Mechanism	Region	Year	D (km)	P (years)	T (°C)	References
Larval	No	Drift	Faroes	1991	780	3		Jákupsstovu and Reinert, 2002
	Yes	Drift	GOA	1978–1979	280			Doyle <i>et al.</i> , 2002
Adult	No	Temperature (currents, food)	Iceland	1960–1980	445	1	3	Vilhjálmsson, 1994
	Yes	Temperature	Trans-Arctic	Pleistocene	12 000	50 000	6	Vilhjálmsson, 1994; Sarnthein <i>et al.</i> , 2003
	Yes	Temperature	Barents	1972–1983	509 (225)	1	2	Ozhigin and Luka, 1984; Gjørseter and Loeng, 1987
	Yes	Temperature	Barents	1987–1988	280 (100)	1	1	Gjørseter, 1998
	Yes	Temperature	Barents	1995–1996	200 (100)	1	0.6	Gjørseter, 1998
	Yes	Temperature (food)	Scotian Shelf	1987–	550	18	2.7	Frank <i>et al.</i> , 1996
	Yes	Temperature (food)	NE NL	1990–	500	15	1.5	Lilly, 1994; Shackell <i>et al.</i> , 1994; O’Driscoll and Rose, 2000
		Temperature	Flemish Cap	1990–	445	15	1.7	Frank <i>et al.</i> , 1996
	Yes	Temperature	GOSL	1990–	890	15	2.7	Frank <i>et al.</i> , 1996
	Yes	Temperature	BOF	1915–1919	1 200	4	2	Bigelow and Schroeder, 1953; Frank <i>et al.</i> , 1996
	Yes	Temperature	BOF	1965–1968	1 200	4	3.2	Tibbo and Humphrey, 1966; Frank <i>et al.</i> , 1996
	Yes	Temperature	Trans-Arctic	4000 BC	6 000	6 000	6	Vilhjálmsson, 1994; Sarnthein <i>et al.</i> , 2003

spawning sites, typically persist longer. The longest-term changes during the Pleistocene that have persisted for tens of thousands of years were large, up to approximately 10 000 km.

Discussion

Capelin range shifts have occurred at both the larval and adult stages. In 1991, the Faroe Islands region experienced an influx of capelin larvae, perhaps from spawning near Iceland. There is no Faroe Islands capelin spawning population, and the 1991 influx did not result in spawning at the Faroes (Jákupsstovu and Reinert, 2002). Distribution change can also occur through changes in feeding areas and migrations. Some of these changes result in changes in spawning locations, and some do not. The largest change in capelin distribution occurred with migrations from the North Pacific to the Northwest Atlantic. This movement resulted in changes in both feeding and spawning areas. At shorter time scales, changes in both feeding and spawning areas have been documented at annual scales in the Barents Sea (Loeng *et al.*, 1983; Ozhigin and Luka, 1984; also see references in Russian cited in Gjørseter, 1998). Even larger-scale changes have occurred in the Grand Bank region,

although the life stage of the migrants (larval or adult) is not entirely clear (Frank *et al.*, 1996). Similar changes in capelin distribution to the Flemish Cap are unlikely to result in spawning there, but shifts to the southern Gulf of

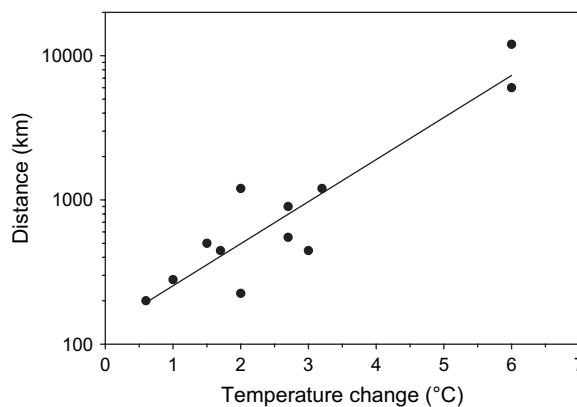


Figure 2. Relationship between displacement of capelin (*Mallotus villosus*) and temperature change. The best fit model was $\log_{10}(\text{distance}_{\text{km}}) = 0.28 \times \text{temperature change} + 2.16$ ($p < 0.05$, $r^2 = 0.91$, $n = 12$). The two longest distance points might be replaced by a single value, depending on whether one or two incursions occurred, but it will influence the model little.

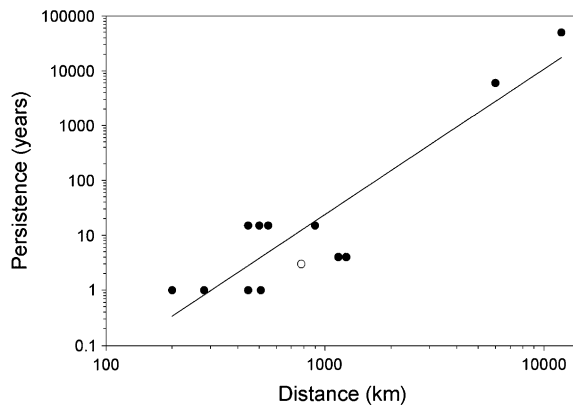


Figure 3. Relationship between persistence of displacement and extent of distribution shift in capelin (*Mallotus villosus*) for adults (closed) and larvae (open). Best fit model was $\log_{10}(\text{persistence}_y) = 2.62 \times \log_{10}(\text{distance}_{\text{km}}) - 6.56$ ($p < 0.05$, $r^2 = 0.83$, $n = 13$). Inclusion of the single larval point (open circle) has little influence on the relationship. The two longest distance points might be replaced by a single value, depending on whether one or two incursions occurred, but it will influence the model little. The model fit is highly dependent on these points.

St. Lawrence may have resulted in new spawning areas. Changes in feeding areas of Icelandic capelin have, in general, not been accompanied by changes in established spawning grounds (Vilhjálmsón, 1994).

Capelin distribution appears to shift quickly. The larval changes reported from the Faroes occurred within months, and overall historical changes in capelin adult biomass seasonally (Vilhjálmsón, 1994). Large changes such as those in Newfoundland and Labrador waters occurred within a year (Frank *et al.*, 1996).

The limiting factor to adult capelin distribution and migration has been reported to be temperature or temperature-indexed changes in plankton distribution. No studies have been done to determine the specific temperature tolerance of capelin, but observations of location in Newfoundland, Icelandic, and Norwegian waters suggest that capelin 2-years old and older are seldom found for very long in waters with temperatures of $< -1^\circ\text{C}$ (this paper; Gjosæter and Loeng, 1987; Vilhjálmsón, 1994). Nevertheless, capelin make use of the coldest waters and may feed and migrate along fronts between cold Arctic and warmer Atlantic waters (Vilhjálmsón, 2002). Although this Arctic-boreal species has evolved to live at the edge of Arctic waters, and to exploit the feeding opportunities there, capelin require higher temperatures for successful reproduction. Deepwater spawning occurs for the main part at temperatures of $2\text{--}7^\circ\text{C}$, 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 (Vilhjálmsón, 1994), and maturation has been reported to require temperatures of $2\text{--}4^\circ\text{C}$ (Carscadden *et al.*, 1989). Capelin spawning timing may be regulated by temperature, as is the suitability of spawning sites. The temperatures and

salinities associated with most spawning appear to vary among stocks. Beach spawning occurs in much fresher and warmer waters than would be encountered by deepwater spawners.

Capelin distribution may be limited by temperature at several stages in the life history. Thermal tolerances of capelin 2-years old and older when feeding are relatively wide with a typical lower limit of -1°C . Spawning success requires a narrower range of temperatures. Distributions in cold water are not free of risk. Capelin have been observed to freeze to death off Labrador (Templeman, 1948) and Iceland (Vilhjálmsón, 1994), presumably when they contact ice crystals in super-cooled water. In general, it is almost certain that capelin are affected by climate-induced changes in the seasonal temperatures of the North Atlantic. Capelin appear 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. A similar role for capelin has been suggested by Jákupsstovu and Reinert (2002), who thought capelin to be a “messenger of harsh times”.

It is important to point out that the relationship between temperature and capelin distribution may not always be one of cause and effect. Capelin is a cold-water species, and its distributional limits may be more firmly determined by warm than cold waters. It is noteworthy that capelin can be found in very cold waters (ca. -1.5°C) on the Grand Bank of Newfoundland. In the habitat of capelin, cold and warmer waters tend to originate from very different water masses, and the plankton (food) content may differ greatly. Little is known about how capelin select habitat, and there is likely to be a density-dependent component, but it is possible that food (zooplankton) distribution has as much impact as temperature (Mowbray, 2002). Indeed, the shift in the Northwest Atlantic in the 1990s during a very cold period occurred within waters having similar temperatures (O’Driscoll and Rose, 2000), but capelin moved to southern areas adjacent to warmer waters where food may have been more available. Too little is known of capelin feeding, or plankton abundance during this period, to draw specific conclusions. However, as an analogy at higher trophic levels, the distribution of cod shifted to mirror those of capelin during the same period (O’Driscoll and Rose, 2000).

Although the present analyses indicate that changes in capelin distribution are certainly associated with climate variations and change, their exact coordinates are uncertain. Coordinates will depend on the spatial dynamics and extent of changes in temperature, salinity, and plankton distribution, and there is considerable uncertainty in the projected patterns of these factors as a consequence of global warming. In general, northward shifts in capelin are to be expected in most areas, with more southerly grounds likely to be abandoned as temperatures rise. If we use the scenario of temperature increases of $2\text{--}4^\circ\text{C}$ in the 21st century, and strictly northerly shifts in capelin (of necessity

oversimplified), the present analyses would suggest maximal shifts of approximately 400–1800 km (4–18° latitude). However, this prediction depends entirely on the coordinates of the shift in the Arctic Polar Fronts, which in general will not move uniformly with respect to latitude, so these estimates describe maximal expected shifts. It is feasible that local cooling of the Northwest Atlantic may accompany overall global warming. Under this scenario, capelin might remain in their present southern distribution with concentrations in the Gulf of St. Lawrence and on the Scotian Shelf. Another global climate scenario predicts more widespread cooling as a result of the weakening of the Gulf Stream and the North Atlantic heat pump (Hansen *et al.*, 2001; Dickson *et al.*, 2002; Hakkinen and Rhines, 2004). Under this scenario, southerly movements of capelin, such as observed in the Northwest Atlantic in the 1990s, might be expected to become more widespread. It is evident that differing climate scenarios have different outcomes for capelin, precisely because it is a quick responder.

Other factors not dealt with directly in this study, but related to capelin distribution and basic biological metrics, are also likely to be influenced quickly by the ocean environment. These include range extensions during the feeding season (Gjøsæter, 1998), changes in vertical distribution (Mowbray, 2002), and spawning timing and somatic growth (Carscadden *et al.*, 2002). Such features enhance the potential of capelin as a sea “canary” to monitor climate change in northern boreal ecosystems. In marine ecosystems that contain more species and are likely more complex, such single-species indicators may not be present, but communities or assemblages of species might be considered necessary to monitor change.

Changes in distribution of an important, perhaps keystone, species such as capelin may be expected to have a direct impact on the many species that feed on them. Nearly 100 years ago, it was reported by Hjort (1914) that fluctuations in capelin in the Barents Sea led to changes in cod distribution and growth. This early recognition has been verified by more complete analyses of nearly a century of data (Gjøsæter, 1998, and references therein). Off Iceland, the mean weight of cod has been shown to be a direct function of capelin biomass (Astthorsson and Vilhjálmsón, 2002; Vilhjálmsón, 2002). In Labrador and Newfoundland waters, the decline and southerly shift of capelin in the 1990s have led to a major dietary change in cod, declines in seasonal condition, and perhaps even mortality (Rose and O’Driscoll, 2002). In addition to influencing cod, changes in capelin are likely to influence other species of predatory fish, such as salmon (Reddin and Friedland, 1993), Arctic char (Dempson *et al.*, 2002), and Greenland halibut, and some seabirds (Carscadden *et al.*, 2002) and marine mammals. These direct effects are likely to cascade through the ecosystem. Although the extent of these changes is beyond our predictive abilities, there is little doubt that they can occur (Dalpadado *et al.*, 2002), and will be impacted by climate change.

As a final comment, because capelin are a “canary” for climate change, a harbinger for changes in boreal-Arctic foodwebs and fisheries of northern oceans, it is suggested that capelin be monitored through concerted international scientific effort by northern hemisphere states. Acoustic monitoring techniques developed over several decades (Vilhjálmsón, 1994; Gjøsæter, 1998) would provide an efficient means of doing this.

Acknowledgements

This work was supported by the NSERC Chair in Fisheries Conservation at Memorial University and NSERC grants held by the author. S. Fudge helped collate the data. I thank Hjalmar Vilhjálmsón for permission to use his figure on capelin distribution, Harald Gjøsæter for pointing to examples of Barents Sea capelin spawning shifts first reported in earlier Russian literature, and Nick Bailey for valuable insights on earlier presentations of the data. Another reviewer suggested that the “canary” analogy was imperfect because the canary had to die to be noticed. The reviewer was correct, but I hope it does not come to this. When the singing changes — a signal has been sent.

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