Capelin *Mallotus villosus* (Pisces: Osmeridae), glaciations, and speciation: a nomothetic approach to fisheries ecology and reproductive biology

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ABSTRACT: Capelin *Mallotus villosus* in the North Pacific and Northwest Atlantic are characterized by a wider latitudinal distribution (cool temperate to subarctic), lower number of vertebrae (64.45 to 68.50), lower biomass, lower fecundity and larger eggs than are capelin in the Central-Northeast Atlantic (exclusively subarctic, 69.16 to 71.54 vertebrae). Capelin in the North Pacific and Northwest Atlantic spawn intertidally over a wider range of latitudes (42 to 72° N), temperatures (1 to 14 °C), salinities (from brackish to oceanic water), and at a higher mean temperature (7.5 °C), than do populations in the Central and Northeast Atlantic (offshore spawning, 63 to 76° N, 0.94 to 7 °C, 32.0 ‰ to 34.6 ‰, 4 °C respectively). These differences indicate that capelin are towards the r-endpoint of the r–k continuum of life history strategies in the North Pacific-Northwest Atlantic and towards the k-endpoint in the Northeast Atlantic. A nomothetic explanation is proposed. During the peak of the last glaciation, the major present-day spawning grounds on the Pacific rim were ice-free. Capelin experienced little change in their accustomed environmental conditions and spawned intertidally over a wide geographic range. In contrast, North Atlantic spawning grounds were ice-covered. Accordingly, offshore spawning habits evolved. Intertidal spawning in the North Atlantic probably did occur between 40 to 55° N along the European coast and in the Mediterranean Sea where ice did not reach the sea. Capelin populations underwent k-selection, and stenothermy, stenohalinity, low fecundity, large egg size and high biomass evolved in populations of deep-spawning capelin of the North Atlantic in response to the greater environmental predictability in these offshore habitats. During the Holocene hypsithermal, capelin from the Pacific Ocean (intertidal spawning) repopulated Canadian Arctic waters and Northwest Atlantic. Deep-spawning capelin continued to reproduce in the North Atlantic where bathymetry, spawning temperatures and salinities were optimum (Grand Banks, Iceland, Barents Sea). Minor stocks of beach-spawning capelin which now inhabit some Norwegian fjords may have been derived from the Northwest Atlantic, via the North Atlantic Drift, and/or from relict populations which spawned intertidally along the ice-free Western European/Mediterranean coast. The implications of this hypothesis for the taxonomic status of capelin are discussed.

INTRODUCTION

Capelin *Mallotus villosus* inhabit arctic, subarctic and cool-temperate seas (Walters 1955, McAllister 1963, 1984, Winters 1969, Jangaard 1974, Stergiou 1984) and play a key role in the North Atlantic ecosystem (Zenkevitch 1963, Bailey et al. 1977). They have been fished by many generations of Canadian, Greenlandic, Icelandic, Norwegian and Murman fishermen, and continue to play a major role in the North Atlantic fishery (Perley 1859, Hardy 1867, Sars 1879, Fries et al.

1895, Hjort 1914, Jensen 1925, Prokhorov 1965, Vibe 1967, Corlett 1968, Vilhjálmsen 1968, 1983, Mattox 1973, Cumming 1975, Winters 1975, Stergiou 1984). The capelin fishery presently ranks fourth in world fishery production, with a catch of 2 265 039 t in 1985 (FAO 1987).

There are signs of genetic differentiation of capelin throughout its geographic range. The differences observed in some morphometric and meristic characters between the populations of capelin in the North Pacific and Atlantic Oceans have been used to argue for the recognition of 2 subspecies, one in each ocean (Vladykov 1933, Schultz 1937, Rumyantsev 1946, Schmidt 1965, Kljukanov 1972, Kljukanov & McAllister

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1979). In addition, the spawning mode of capelin in the Barents Sea differs from that in the Northwest Atlantic (Prokhorov 1965, Templeman 1968, Stergiou 1984).

Glacial-interglacial cycles have been widely considered as factors affecting the distribution, abundance and speciation of both marine (e.g. Slobodkin & Rapport 1974, Grant & Utter 1984, Nesis 1984, Scott et al. 1986) and land biota (Gould 1969, Budyko 1974, 1977). Here, the distribution, meristic characters, abundance, spawning conditions, fecundity and egg size of capelin are reviewed and differences between the populations of capelin in the North Pacific-Northwest Atlantic and Central-Northeast Atlantic are established. These differences are heuristically correlated with the changes in oceanographic conditions of the Northern Hemisphere which occurred during the last glacial-interglacial cycle. These patterns are then used to develop a nomothetic (*sensu* Raup & Gould 1974) approach to fisheries ecology and reproductive biology. The implications of this hypothesis for the taxonomic status of capelin are also discussed.

DISTRIBUTION

The distribution of capelin in the North Atlantic ocean (Fig. 1) coincides with that of the marine subarctic zone, *sensu* Dunbar (1951, 1968, 1972), that is, the

Fig. 1. Map showing the Ortmann line (heavy line marked with an arrow) and the marine subarctic zone in the world ocean (hatched area, reproduced from Dunbar 1968) together with the distribution of capelin (from Stergiou 1984, unpubl.): (●) areas visited on a year-to-year basis; (■) areas visited occasionally; (□) areas where it is not known whether capelin is permanent or a periodic visitor

zone in which water from the Arctic Ocean is found mixed, or in close association with, water from the Atlantic Ocean, and extends vertically to 250 or 300 m depth (Stergiou 1984, unpubl.). In the Pacific (Fig. 1), the distribution of capelin is mainly within the cool-temperate zone (McAllister 1963, Stergiou 1984, unpubl.) the southern limit of which is bounded by the 15 °C isotherm (Ortmann line; Ortmann 1896). The distribution of capelin in the Arctic Ocean is discontinuous and Arctic populations are probably relicts from preceding warm periods (Stergiou 1984, unpubl.). Thus, in the North Pacific and Northwest Atlantic capelin occupy a wider area (cool-temperate, subarctic) than they do in the Central and Northeast Atlantic (exclusively subarctic).

SYSTEMATIC POSITION, NUMBER OF VERTEBRAE

Capelin belongs to the Suborder Salmonoidea and together with the smelts comprises the Family Osmeridae (McAllister 1963). Pacific and Atlantic populations are meristically and morphometrically different and may represent either 2 distinct subspecies (Vladykov 1933, Schultz 1937, Rumyantsev 1946, Schmidt 1965, Kljukanov 1972, Kljukanov & McAllister 1979) or one monotypic species with 2 consubspecific forms in each ocean (McAllister 1963, 1984, Kljukanov & McAllister 1979).

There is an increase in the number of vertebrae from south to north (Table 1), which is not well correlated with environmental temperatures (Pitt 1958, Prokhorov 1965, 1968, Templeman 1968, Vilhjálmsson 1968). This is clearly shown by the similarity in the number of vertebrae in populations from the Grand Banks and the Newfoundland/Labrador/Gulf of St. Lawrence, regions with dissimilar ambient temperatures, and by the differences in number of vertebrae between capelin from the Barents Sea and those from the Grand Banks, regions with similar ambient temperatures. Templeman (1968) and Vilhjálmsson (1968) maintained that genetic differences may account for the differences in the vertebral counts.

What is evident (Table 1), however, is that the number of vertebrae of capelin in the North Pacific and Northwest Atlantic ranges between 64.45 and 68.50, as opposed to 69.16 to 71.54 in populations from the Central-Northeast Atlantic (Barents Sea and Iceland). These distributions are non-overlapping.

BIOMASS

Landings

Over the last 15 to 20 yr, capelin have been heavily exploited by Norwegian and Soviet fleets in the

Table 1. *Mallotus villosus*. Number of vertebrae of capelin in different areas

Location	Lat. °N	Vertebrae		Source
		Male	Female	
Bay of Fundy	44–46	66.03	65.86	(1)
Gulf of St. Lawrence				
Coudres Islands	47.2	66.89 ^a	64.45 ^a	(2)
Grande Riviere	48.2	66.16 ^a	68.50 ^a	(2)
Natashquan	50.5	66.87 ^a	66.57 ^a	(2)
Seven Islands	50.5	66.56 ^a	67.07 ^a	(2)
Newfoundland	43–55	65.34–65.70	65.47–65.83	(3)
Grand Banks	43–45	65.45–65.51	65.55–65.65	(4)
South Labrador	54–58	65.49–65.57	65.54–65.62	(3)
Beaufort Sea	69.3	68.17 ^a	–	(2)
British Columbia	48–55	65.32–65.76	65.05–65.24	(5)
Japan Sea	42–44		67.3 ^b	(6)
Greenland	60–70		68.07–68.32 ^a	(7)
Iceland	63.5–66.5	69.42–69.48 ^a		(8)
		69.40–69.48 ^a	69.45–69.53 ^a	(9)
Barents Sea	67–72	68.34–68.60	–	(10)
		68.25–68.41	–	(10)
		68.16–68.30	–	(10)
		70.83–71.54	69.72–71.12 ^a	(11)

^a Counts including the urostyle
^b May or may not include the urostyle
Sources: (1) Tibbo & Humphreys (1966); (2) Arsenault (1979); (3) Templeman (1948); (4) Pitt (1958); (5) Hart & McHugh (1944); (6) Rumyantsev (1946); (7) Hansen (1943); (8) Fridriksson (1943); (9) Vilhjálmsón (1968); (10) Prokhorov (1965); (11) Nikiforovskaya (1933)

Barents Sea (Dragesund et al. 1973, Cumming 1975, Stergiou 1984). Since the early 1970s, in addition, an international capelin fishery has developed in the Northwest Atlantic (Winters 1975). An important fishery exists also in Iceland (Vilhjálmsón 1984, 1985, 1986). Capelin in the North Pacific are exploited mainly by Japanese and Soviet fleets.

The mean annual total capelin catch from 1965 to 1984 was 1 994 164 t. The total catch of capelin peaked in 1977 (Fig. 2), at 4 000 000 t and ranked second in world catch production. Although overfishing may be implicated in the decline of the capelin biomass in the North Atlantic during the 1970s (Fig. 2), indications are that abiotic factors, independent of parent stock size, are the major contributors to the decrease in catches in both the Northwest Atlantic (Leggett et al. 1984) and the Barents Sea (Stergiou 1984). In general, the distribution and abundance of capelin throughout their range is closely related to large-scale hydrographic processes (air and water temperature, intensity and direction of currents, direction of winds) (see Table 2 for references).

Capelin catches in the Central-Northeast Atlantic (area east of 42° E) have consistently exceeded those in the Northwest Atlantic and North Pacific by 5 to 202 times (mean = 63) (Fig. 2). The mean (1965 to 1984) annual catch in the Northeast Atlantic, 1 890 927 t, was

18 times higher than that of the Northwest Atlantic and North Pacific, 103 237 t.

Stock size

Estimates of capelin biomass by means of acoustical, photogrammetric, mathematical, tagging, and eggs and larval survey techniques have been produced since the early 1970s for stocks in the North Atlantic (Table 3). These estimates indicate, when the size of the areas involved is taken into account, that the biomass of capelin is much higher in the Northeast than in the Northwest Atlantic.

SPAWNING

Spawning modes

Capelin spawn in 2 habitats: on intertidal beaches and on subtidal sediments offshore (Table 4). These habitats differ considerably with respect to their variability and predictability; intertidal regions are more variable and/or unpredictable environments than subtidal regions offshore (Slobodkin & Sanders 1969, Pianka 1970). Beach-spawning occurs on ebb tides at

Fig. 2. *Mallotus villosus*. Catches of capelin in (a) North Pacific and Northwest Atlantic; (b) Northeast Atlantic; (c) proportion of the catches in (NE Atlantic)/(N Pacific + NW Atlantic)

night; eggs adhere to the gravel and are buried in the substrate to depths of 15 to 20 cm by wave and tidal action. In areas where beach-spawning takes place, capelin may also enter rivers as for instance in Northwest River, Labrador (Kendall 1909, Backus 1957), St. Lawrence River, Quebec (Parent & Brunel 1976), Tumen River, Korea (Mori 1930), rivers entering the Gulf of Maine (Huntsman 1922, Bigelow & Welsh 1924), and in some rivers of the Sakhalin island (Vel-

Table 2. *Mallotus villosus*. Areas where the abundance and distribution of capelin have been shown to be greatly affected by hydrometeorological processes

Area	Source
Barents Sea	Konstantinov (1965), Prokhorov (1965, 1968), Corlett (1968), Konstantinov & Svetlov (1974), Loeng et al. (1983), Stergiou (1984), Ozhigin & Luka (1985), Ozhigin & Ushakov (1985), Gjøsæter & Loeng (1987)
Ungava Bay	Dunbar (1976, 1983)
Greenland	Jensen (1939, 1948), Hansen & Hermann (1953), Vibe (1967), Stergiou (1984)
Iceland	Saemundsson (1934), Jensen (1939, 1948), Fridriksson (1948), Tåning (1948), Magnusson (1966, 1968), Malmberg (1983)
Newfoundland	Templeman & Fleming (1953), Frank & Leggett (1981a, b, 1982a, b), Leggett et al. (1984)
Gulf of Maine/ Bay of Fundy	Kendall (1917, 1919), Bigelow & Welsh (1924), Bigelow & Schroeder (1953), Taylor et al. (1957), Bigelow (1963)
Japan Sea	Rumyantsev (1946), Velikanov (1987)
Korea	Stergiou (1984)

ikanov 1984). Offshore, spawning takes place on the bottom in areas with coarse gravel. In the Barents Sea (Sætre & Gjøsæter 1975), White Sea (Altukhov 1977) and around Iceland (Thors 1981) these areas have been shown to have well-developed bottom currents.

It is evident (Table 4) that capelin in the North Pacific, Northwest Atlantic (except the populations on the Grand Banks and, sporadically, on the southwest coast of Newfoundland) and in the waters off West Greenland spawn on intertidal beaches and enter rivers quite frequently. In the Central-Northeast Atlantic (Iceland and Barents Sea, except minor stocks in some Norwegian fjords) spawning takes place in deep waters offshore.

Table 3. *Mallotus villosus*. Biomass estimates of capelin (in millions of tons) in the North Atlantic

Location	Biomass	Method	Period	Source
Barents Sea	0.8–10.1	Acoustic	1973–75	(1)–(3)
Iceland	0.6–1.5	Acoustic	1980–83	(4)–(7)
Labrador/Newfoundland ^a	1.3–4.8	Sequential model	1972–78	(8)
		Photogrammetric	1974	(9)
Grand Banks	1	Photogrammetric	1977	(10)

^a 2J3K NAFO Div.
 Sources: (1) Dragesund et al. (1973); (2) Nakken & Dommasnes (1975); (3) Midttun & Nakken (1977); (4) Vilhjálmsson (1983); (5) Vilhjálmsson (1984); (6) Vilhjálmsson (1985); (7) Vilhjálmsson (1986); (8) Serebrov et al. (1975); (9) Miller & Carscadden (1979); (10) Klovchov & Seliverstov (1978)

Table 4. *Mallotus villosus*. Mode of spawning of capelin in different areas: I, intertidal beach spawning; O, offshore deep spawning

Location	Lat. °N	Mode	Source
Greenland	60–70	I	(1)–(4)
Labrador	52–58	I	(5), (6)
Newfoundland ^a	46–51	I	(5)–(7)
Gulf of St. Lawrence	48–50	I	(7)
Bay of Fundy ^b	44–46	I	(8)
Hudson Bay			
Belcher Island	56–57	I	(9)
Beaufort Sea			
Herschel Island	69.5	I	(10)
British Columbia	48–50	I (3–4 m)	(11)–(13)
Kamchatka	52–60	I	(14)
Okhotsk Sea	55	I (1–7 m)	(15)
Sakhalin Island	46–52	I (1–2 m)	(16)
Sea of Japan			
Peter The Great Bay	42–44	I (3–4 m)	(17)
Newfoundland			
Southwestern coast	46–47	O (35–55 m)	(5), (6)
Grand Banks	43–55	O (30–60 m)	(18), (19)
Iceland ^c	63–66	O (20–90 m)	(20), (21)
Barents Sea ^d	67–72	O (10–280 m)	(22)–(31)
White Sea	64–67	O	(32)

^a Sporadically on the west coast (5–7)

^b Occasionally present (8)

^c Information given by Saemundsson (1934) that capelin spawn in lagoons and estuaries was considered doubtful by Vilhjálmsón (1968)

^d Minor stocks of capelin spawn intertidally in some Norwegian fiords (33–35)

Sources: (1) Jensen (1925); (2) Jensen (1948); (3) Hansen & Hermann (1953); (4) Kanneworff (1968); (5) Templeman (1948); (6) Templeman (1968); (7) Parent & Brunel (1976); (8) Bigelow & Welsh (1924); (9) Dunbar pers. comm.; (10) McAllister (1962); (11) Hart & McHugh (1944); (12) Clemens & Wilby (1961); (13) Hart (1973); (14) Schultz (1937); (15) Savicheva (1982); (16) Velikanov (1984); (17) Rumyantsev (1946); (18) Pitt (1958); (19) Dragesund & Monstad (1973); (20) Vilhjálmsón (1968); (21) Thors (1981); (22) Rass (1933); (23) Prokhorov (1965); (24) Prokhorov (1968); (25) Møller & Olsen (1962); (26) Bjørke et al. (1972); (27) Gjøsæter & Sætre (1973); (28) Gjøsæter et al. (1974); (29) Sætre & Gjøsæter (1975); (30) Gjøsæter & Martinsen (1975); (31) Hamre & Sætre (1976); (32) Altukhov (1977); (33) Davenport et al. (1979); (34) Davenport & Stene (1986); (35) Mork & Friis-Sørensen (1983)

Spawning seasons and conditions

The latitude for spawning extends from 42 to 76° N, and spawning takes place from March to October (Table 5). Capelin spawn later at higher latitudes. This spatial-temporal pattern in spawning implies that capelin are sensitive to thermal conditions or to those biological phenomena such as plankton blooms which occur successively later with an increase in latitude. In the North Atlantic, spawning occurs earlier in areas, such as West Greenland, Southwest Iceland and Barents Sea, influenced by warm Atlantic waters (Irminger current, North Cape current) than in areas influenced by cold Arctic waters (e.g. Labrador, Newfoundland). The timing of spawning, however, changes from year to year depending on the varying oceanographic conditions (Sars 1879, Jensen 1939, 1948, Templeman 1948, Hansen & Hermann 1953, Templeman & Fleming 1953, Prokhorov 1965, 1968,

Galkin & Ushakov 1978, 1979, 1980, 1981, 1983, Stergiou 1984).

Capelin spawn at temperatures ranging from 0.94 °C, in the White Sea, to 14 °C, along the Sakhalin coasts (Table 6). Available information pertinent to spawning salinities is scanty (Table 7). It can be assumed, however, that capelin populations that spawn intertidally (and in estuaries) are subjected to wider fluctuations of salinities than those that spawn offshore in deep waters. The available data confirm this assumption (Table 7).

From Tables 5, 6 and 7 it becomes apparent that the populations inhabiting the North Pacific and Northwest Atlantic spawn over a wider range of latitudes (42 to 72° N), temperatures (1 to 14 °C), salinities (from brackish to oceanic water), and at a higher mean temperature (7.5 °C) than do populations in the Central-Northeast Atlantic (63 to 76° N, 0.94 to 7 °C, 32.0 ‰ to 34.6 ‰, 4 °C respectively).

Table 5. *Mallotus villosus*. Spawning periods of capelin in different areas

Location	Lat. °N	Period	Source
British Columbia			
Strait of Georgia	48–50	Sep–Oct	(1), (2)
Eastern Barents Sea			
Cheshkaya-Kolguev-Indiga Bay	67–76	Aug–Sep	(3)–(6)
Beaufort Sea			
Herchel Island	69.5	Jul–Aug	(7)
Alaska			
Point Barrow	72	Jul–Aug	(8)
Iceland			
North, northeast, east coast	63–66	Jul–Aug	(9), (10)
Bering Sea			
Northern part	60–65	End Jul–Aug	(8)
Labrador			
Northern part	57–58	Late Jul–Aug	(11), (12)
Okhotsk Sea			
Shantar Island	55	Late Jul–Aug	(8)
Hudson and James Bays	52–57	Early Jul–Aug	(13)
Newfoundland			
Southwest offshore	46–49	Jul–Aug	(9), (10)
Murman coast			
Mid and eastern part	67–69	Jun–Jul	(3)–(5), (14), (15)
Greenland			
Northwestern coast	65–70	Jun–Jul	(16)
Labrador			
Southern coast	52–57	Late Jun–Jul	(11), (12)
Grand Banks	43–45	Late Jun–Jul	(17), (18)
Newfoundland			
East coast	47–51	Jun–Jul	(11), (12)
West coast	47–51	Early Jun–Jul	(11), (12), (19)
South coast	46–47	Early Jun–Jul	(11), (12)
Kamtchatka			
West and east coast	52–60	June	(8)
Sakhalin			
West, south and east coast	46–52	May–Jul	(20)
Greenland			
Southwestern coast	65–68	May–Jun	(16)
Eastern coast	65.5	May–Jun	(21)
White Sea	64–67	May–Jun	(22)
Bering Sea	55–65	May–Jun	(23)
St. Lawrence Gulf			
North shore	49–51	May–Jun	(19)
Gaspé Peninsula	48–49	May–Jun	(19)
St. Lawrence Estuary	48–49	Apr–Jun	(19)
Southern part ^a	45–47	May–Jun	(24)
Bay of Fundy ^a	44–46	May–Jun	(25), (26)
Iceland			
South and southwest coast	63–64	Mar–Jun	(9), (10)
Finmark coast	67–72	Mar–Apr	(3), (4), (27)–(36)
Murman coast			
West and mid part	68–70	Mar–Apr	(3), (4), (37)–(44)
Sea of Japan			
Peter The Great Bay	42–44	Mar–Apr	(45)

^a Occasionally present

Sources: (1) Hart & McHugh (1944); (2) Hart (1973); (3) Rass (1933); (4) Prokhorov (1965); (5) Prokhorov (1968); (6) Pashkova (1975); (7) McAllister (1962); (8) Andriyashev (1964); (9) Vilhjálmsón (1968); (10) Vilhjálmsón (1979, 1980, 1981, 1983, 1984, 1985, 1986); (11) Templeman (1948); (12) Templeman (1968); (13) Vladykov (1933); (14) Pozdnyakov (1959); (15) Pozdnyakov (1962); (16) Kannevorff (1968); (17) Pitt (1958); (18) Fitzpatrick & Miller (1979); (19) Parent & Brunel (1976); (20) Velikanov (1984); (21) Jensen (1948); (22) Altukhov (1977); (23) Naumenko (1984); (24) Jeffers (1931); (25) Bigelow & Welsh (1924); (26) Tibbo & Messieh (1967); (27) Gjøsaeter & Sætre (1973); (28) Jakobsen & Nakken (1973); (29) Anonymous (1974); (30) Gjøsaeter et al. (1974); (31) Sætre & Gjøsaeter (1975); (32) Anonymous (1975); (33) Gjøsaeter & Martinsen (1975); (34) Hamre & Sætre (1976); (35) Dommasnes & Hamre (1977); (36) Dommasnes et al. (1979); (37) Kovalyov & Benko (1970); (38) Kovalyov (1972); (39) Galkin (1973); (40) Kovalyov & Galkin (1974); (41) Galkin (1975); (42) Galkin & Luka (1976); (43) Galkin & Shulga (1977); (44) Galkin & Ushakov (1978, 1979, 1980, 1981, 1983); (45) Rumyantsev (1946)

Table 6. *Mallotus villosus*. Temperatures of spawning time of capelin in different areas

Location	Lat. °N	T °C	Source
Grand Banks	43–45	1–4.7	(1)–(4), (40)
Gulf of St. Lawrence	48–50	6–9	(5)
Newfoundland			
West coast	48–52	6–9	(5)
East and south coasts	46–51	5.5–10.7	(6)–(9)
Labrador	52–58	5.5–8.5	(6), (7)
Hudson Bay			
Richmond Gulf	52–56	10	(10)
Beaufort Sea			
Herchel Island	69–70	2.3–9.5	(11)
British Columbia			
Georgia Strait	48–55	10–12.5	(12), (13)
Okhotsk Sea			
Shantar Island	55	12.9	(14)
Eastern part	55–60	6–7.8	(15)
Sakhalin			
West, south and east coasts	46–52	2–14	(16)
Japan Sea			
Peter The Great Bay	42–44	2–4	(17)
Barents Sea			
Norwegian coast	67–72	1.5–6.5	(18)–(23), (41)
Western Murman coast	67–72	1.2–3	(24)–(30)
Eastern Murman coast	67–72	2.2–4.9	(24)
White Sea	64–66	> 2	(31)
Estuary of the White Sea	66–68	0.94–0.96	(24)
West Greenland	60–70	1.9–8.5	(32)–(34)
Iceland	63–66	5–7	(35)–(39)

Sources: (1) Pitt (1958); (2) Fitzpatrick & Miller (1979); (3) Templeman (1965); (4) Klochkov & Seliverstov (1978); (5) Parent & Brunel (1976); (6) Templeman (1948); (7) Templeman (1968); (8) Sleggs (1933); (9) Frank & Leggett (1981a); (10) McAllister (1964); (11) McAllister (1962); (12) Hart & McHugh (1944); (13) Hart (1973); (14) Lindberg & Dulkeit (cited by Prokhorov 1965); (15) Savicheva (1982); (16) Velikanov (1984); (17) Rumyantsev (1946); (18) Olsen (1968); (19) Gjøsæter & Sætre (1973); (20) Gjøsæter et al. (1974); (21) Sætre & Gjøsæter (1975); (22) Gjøsæter & Martinsen (1975); (23) Hamre & Sætre (1976); (24) Pozdnyakov (1959); (25) Prokhorov (1965); (26) Prokhorov (1968); (27) Pozdnyakov (1962); (28) Kovalyov & Galkin (1974); (29) Galkin & Ushakov (1980); (30) Galkin & Ushakov (1983); (31) Altukhov (1977); (32) Jensen (1948); (33) Kanneworff (1968); (34) Bigelow & Schroeder (1953); (35) Saemundsson (1934); (36) Vilhjálmsson (1968); (37) Thors (1981); (38) Jespersen (1920); (39) Magnusson (1966); (40) Carscadden (1978); (41) Corlett (1968)

Table 7. *Mallotus villosus*. Salinities at spawning time of capelin in different areas

Location	Lat. °N	Salinity (‰)	Source
Sakhalin	46–52	3.04–33.00	(1)
Newfoundland	43–55	14.00–33.00	(2)
Barents Sea	67–72	32.00–34.60	(3)–(5)

Sources: (1) Velikanov (1984); (2) Templeman (1948); (3) Rass (1933); (4) Prokhorov (1965); (5) Sætre & Gjøsæter (1975)

FECUNDITY AND EGG SIZE

Although both ovaries of capelin have similar rates of egg development, the left ovary is several times larger than the right one (Winters 1971, Podznyakov 1957).

The available data on the mean (right and left ovary) fecundity and egg diameter of capelin from various areas of their range (Table 8) indicate that the populations of capelin in the Central-Northeast Atlantic (Barents Sea and Iceland) are characterized by lower fecundity and larger eggs than are populations in the Northwest Atlantic and Northeast Pacific. The estimations given by Hart & McHugh (1944) for Northwest Pacific populations were based on specimens shorter than 12.2 mm while the other estimates were based on specimens with lengths between 13 and 20 mm. Hence comparisons cannot be made.

DISCUSSION

To sum up, capelin in the North Pacific and Northwest Atlantic differ from the Central-Northeast Atlantic

Table 8. *Mallotus villosus*. Fecundity and egg diameter (in mm) of capelin in different areas

Location	Fecundity	Egg diameter	Source
British Columbia	3020–6670		(1)
Japan Sea	5400–50700	0.65–0.82	(2)
Okhotsk Sea	6000–53200	0.75–0.86	(2), (3)
Newfoundland	18607–47859	0.97	(4)
Grand Banks	16550–61500		(5)
Iceland		1.12	(6)
Barents Sea	9000–24569	1.17	(7)–(9)

Sources: (1) Hart & McHugh (1944); (2) Velikanov (1987); (3) Savicheva (1975); (4) Templeman (1948); (5) Winters (1971); (6) Fredriksson & Timmerman (cited by Winters 1971); (7) Pozdnyakov (1957); (8) Gjøsæter & Monstad (1973); (9) Galkin & Kovalev (1975)

capelin in: (1) the climatic zones occupied, (2) number of vertebrae, (3) level of biomass, (4) range of latitude for spawning, (5) spawning depth, (6) range of spawning salinities, (7) range of spawning temperatures, (8) mean spawning temperature, (9) fecundity and egg size and (10) predictability of the spawning habitat (Table 9). These differences indicate that the populations of capelin in the North Pacific-Northwest Atlantic are towards the r-endpoint of the r–k continuum of life history strategies, first described by MacArthur & Wilson (1967) and developed further by Pianka (1970). The opposite seems to be true of the populations of capelin in the Central-Northeast Atlantic.

Differential reproduction, in particular, is essential to the r- and k-selection argument (Pianka 1970, Colinveaux 1986). Small-egg strategy is well suited to opportunist, r-selected populations (energy is mainly allotted

to reproduction and less to structures and habits that mediate persistence and competitive abilities). R-strategists inhabit immature, highly variable, unpredictable environments (e.g. upwellings, intertidal and estuarine regions) and their population size is usually below the carrying capacity of the environment. Large-egg strategy, on the other hand, is well suited to k-selected populations (energy is mainly allocated to non-reproductive activities that promote individual survival). K-strategists occupy mature, relatively stable and predictable environments (e.g. coral reefs, deep-sea) and are characterized by population sizes near the carrying capacity of the environment. Although for terrestrial organisms a clear distinction between the 2 strategies can be made in some instances, fish show the full range of the r–k continuum (Pianka 1970).

Historical factors may account for these geographic differences in the ecology and reproductive biology of capelin. Climatic changes have occurred in the past in a considerable array of different time scales. Setting aside the periodicity of the major ice ages, a matter of 250 to 300 million yr, the current period of Pleistocene glaciations has existed for at least 2 million yr (Mason 1976, Matthews 1976, Boellstorff 1978) and has been repeatedly interrupted by interglacial warm epochs, each glacial stage lasting about 100 000 yr (Emiliani 1972). Paleoclimatic data suggest that the last glaciation started some 70 000 to 75 000 yr ago (Grootes 1978, Stuiver et al. 1978, Woillard & Mook 1982) and reached a maximum some 18 000 years ago (CLIMAP 1976, Barash & Os'kina 1979, Berger et al. 1985).

During the peak of the last glacial stage, ice sheets in the North Pacific existed only along the northeastern edge of the ocean basin from the Aleutian Islands to Washington and portions of the Kamtchatka Peninsula

Table 9. *Mallotus villosus*. Summary of differences in various aspects of capelin biology and ecology between North Pacific-Northwest Atlantic (NP-NWA) and Central-Northeast Atlantic (C-NEA)

Aspects	NP-NWA	C-NEA
Distribution	Cool-temperate and subarctic	Exclusively subarctic
Number of vertebrae	64.45–68.50	69.16–71.54
Abundance		
Mean 1964–1985 commercial catch	103 237 t	1 890 927 t
Spawning		
Latitude	42–72°N	63–76°N
Depth	Intertidal	Offshore deep water
Predictability of habitat	Low	High
T range	1–14 °C	0.94–7 °C
T mean	7.5 °C	4 °C
Salinity	From brackish to oceanic	32–34.6 ‰
Fecundity	< 65 000 eggs	< 30 000 eggs
Egg size	< 1 mm	> 1 mm

(Fig. 3a; Hopkins 1972, Nesis 1984). Yet, glacial biotic refugia seem to have existed along the eastern Pacific coast (Warner et al. 1982). The major present-day spawning grounds of capelin on the Pacific rim were ice-free. In addition, glacial sea surface temperatures (Fig. 3a) did not differ considerably from present ones (Fig. 3b). Hence during the last glaciation, capelin in these regions experienced little change in the environmental conditions to which they were previously accustomed.

In contrast, the shelf of the North Atlantic was covered by ice (Fig. 3a; Barash & Os'kina 1979, Nesis 1984). Glaciers descended deep into the ocean except in discrete areas between glaciers and along the northern boundary of the boreal region, e.g. along the slope of George Banks, south of the Grand Banks and Iceland, and southwest of the Celtic Sea (Nesis 1984). Hence, during the maximum of the last glaciation (and/or probably during any other Pleistocene glacial stage), present day spawning grounds of capelin were ice-covered. Accordingly, offshore spawning habits evolved. Beach spawning probably did not occur along the western rim of the Atlantic basin. Intertidal spawning in the western Atlantic would have been restricted to areas south of 40°N , which were washed by the ancestral Gulf Stream (Barash & Os'kina 1979), with waters too warm for survival. Intertidal spawning in the Eastern Atlantic probably did occur between 40 and 55°N along the European coast. In addition, intertidal spawning probably occurred in the Northwest and Northern Mediterranean Sea where glacial temperatures were comparable to those in adjacent areas

of the northeastern Atlantic (Thiede 1978), and Pleistocene capelin fossils have been found in Bosnia, Yugoslavia (McAllister 1963). However, the dominant mode of spawning for Atlantic capelin during the last glaciation was probably offshore at depth, across the entire North Atlantic, in a relatively cold zone where the range of temperature and salinity was considerably smaller than in coastal areas. Spawning at depth favored selection toward stenothermy and stenohalinity. Yet, lower fecundity and larger egg size were favored because of the greater environmental predictability of these offshore habitats (Sanders 1968, Slobodkin & Sanders 1969, Grassle & Sanders 1973, Thiery 1982). Increased environmental stability, in addition, has been argued to bring about a decrease in expenditure of energy for regulatory purposes and therefore more energy is available for production and, thus, for biomass (Connell & Orias 1964, Pianka 1970). Hence, spawning at depth favored k-selection.

With the opening of the Bering Strait and the warming up of the Canadian Arctic Archipelagos during the Holocene hypsithermal, capelin from the Pacific Ocean (intertidal spawning) repopulated the Canadian Arctic waters and Northwest Atlantic. However, deep spawning capelin continued to populate areas where bathymetry and spawning temperatures and salinities were optimum (Grand Banks, Iceland, Barents Sea). Minor beach-spawning capelin stocks inhabiting some Norwegian fjords may have been derived from the Northwest Atlantic, via the North Atlantic Drift, and/or from beach spawning populations inhabiting the ice-free Western European/Mediterranean coast. The

Fig. 3. (a) Sea-surface temperature and ice extent for Northern Hemisphere in August 18 000 yr Before Present (reproduced from CLIMAP 1976); (b) present day sea-surface temperature in August (from Harvey 1976)

populations of capelin in the Arctic are most likely of postglacial origin and may represent relict populations of a wider Arctic distribution during the Holocene hypsithermal, the date of which varied with latitude and in the Arctic occurred 4500 to 6000 yr ago (Hattersley-Smith 1972, Hopkins 1972, Alt 1983).

It is worthy of mention that capelin spawning intertidally have the ancestral number of vertebrae as opposed to the deep-spawners that have a more derived number of vertebrae (Table 1). Hence, this scenario would be disproved should a stock of deep-spawning capelin be found in the Pacific ocean.

This evolutionary ecological scenario may also apply to other fisheries. Herring exhibits a differentiation with regard to spawning mode similar to that of capelin. It spawns intertidally in the North Pacific and on sediments offshore in the North Atlantic. This, and other aspects of its reproductive biology, parallel those of capelin (see Blaxter 1985 for a review), may be explained by this scenario. Other investigators have also related glacial-interglacial cycles to speciation of both marine (e.g. Nesis 1984: arctic marine benthos; Grant et al. 1984: Pacific halibut) and land biota (e.g. Gould 1969: land snails; Budyko 1977: man's ancestors).

Important in this scenario is not the tempo (i.e. when this took place) but the mode (i.e. how this was mediated); in other words it is the effect of the glacial-interglacial cycle(s) on the distribution and differentiation of capelin throughout its range that concerns us. Although the scenario proposed here is placed, with respect to time, in the last glacial-interglacial cycle (75 000 to 0 yr Before Present) (because this cycle has been extensively studied and the paleoceanography of the seas has been successfully reconstructed), the same argument may hold for any other Pleistocene glacial-interglacial cycle. In this context, the capelin, which probably evolved in the Pacific (McAllister 1963), equipped with mechanisms of dispersal (pelagic larvae) and with mechanisms favoring rapid population growth (high fecundity) – essential characteristics of an opportunist, r-strategist – penetrated the North Atlantic via the Bering Sea/Arctic Ocean route, when conditions for dispersal were optimum (open strait either due to glacio-eustatic sea level changes or geological reasons). During the following glacial period the r-selected populations of capelin were subjected to k-selection to produce endemic populations of capelin in the North Atlantic that were able to reproduce in the new conditions (spawning at depth).

Undoubtedly, such widely separate populations of capelin are unlikely to be panmictic and genetic differences are expected to be established (distance-dependent gene flow, isolation by distance). Indeed Payne (1975, 1976) found, using electrophoretic analy-

sis of liver and skeletal muscle esterases, that populations of capelin from Northwest Territories, Newfoundland and Greenland are genetically distinct. Isolation by distance has been also found in cod throughout the North Atlantic (Mork et al. 1985), Pacific herring (Grant & Utter 1984) and Pacific halibut (Grant et al. 1984). There remains the question to what degree the populations of capelin of the North Pacific-Northwest Atlantic and Central-Northeast Atlantic represent taxonomically distinct groups (subspecies, incipient species, species). Multivariate discriminant analysis performed on morphometric characters of capelin from the Gulf of St. Lawrence, Newfoundland and Grand Banks (Sharp et al. 1978, Carscadden & Misra 1979), as well as data on the seasonal distribution and possible migration patterns of capelin in the Newfoundland area (Campbell & Winters 1973), indicate that the populations of deep-spawning capelin on the Grand Banks and Newfoundland are distinct. It cannot be stated with certainty, however, that these populations are reproductively isolated. Larvae from these 2 areas intermingle by means of the Labrador current system (Sharp et al. 1978). Nevertheless, the spawning behaviors described above are closely related to stock separation.

In the Barents Sea, 2 stocks can be distinguished. A major oceanic stock, which spawns offshore, thrives in the northern part of the sea during summer and starts its spawning migration to the Norwegian and Soviet coast in autumn (Prokhorov 1965, Loeng et al. 1983, Stergiou 1984). Minor stocks, which spawn intertidally, permanently inhabit various Norwegian fjords (Sars 1879, Davenport et al. 1979, Davenport & Stene 1986). However, analysis of tissue extracts from oceanic and fjord capelin by means of isoelectric focusing and histochemical enzyme detection failed to prove reproductive isolation between the 2 stocks (Mork & Friis-Sørensen 1983).

Thus the confirmation of the existence of 2 distinct taxonomic groups of capelin remains open for further study. Morphometric, meristic, genetic and behavioral characteristics of populations from different localities in the Pacific, Atlantic and Arctic oceans must be systematically compared. Nevertheless, it is now possible to conclude that the contemporary differentiation of capelin into 2 recognizably different groups (subspecies, incipient species or species) is probably the result of geographic isolation for a period of less than 100 000 yr. If this scenario is correct, speciation rates for this genus of fish, at least, should be reckoned in thousands of years, not longer.

Acknowledgments. The author thanks Drs B. M. Marcotte and M. J. Dunbar for their invaluable assistance in reading the manuscript and making many constructive criticisms and suggestions, and is grateful for the great hospitality and the use of the excellent library of McGill University. Many thanks are due to M. Cheilakea for typing the references.

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