Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area

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Cod, haddock, saithe, herring, and capelin are the most important fish species in the Barents Sea and adjacent waters. Ecosystem-based management requires species-specific knowledge of the biological value and vulnerability throughout their life history and distributional range. For each of the five species and four annual quarters, the spawning (egg) areas, nursery areas for larvae and juveniles, and feeding grounds for adults are described and mapped. Areas of eggs (spawning) and larvae were the most important because these are the life stages when fish are most vulnerable to anthropogenic impact. The greatest overlap of spawning areas was from Røstbanken in the south to the Varanger Peninsula in the northeast, and overlap of larval distribution was more extensive.

Keywords: Barents Sea, capelin, cod, haddock, herring, saithe, valuable areas.

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Introduction

The Barents Sea and adjacent waters encompassing the Lofoten–Vesterålen area (Figure 1) play a vital role in the life history of the major fish stocks in the Northeast Atlantic: Northeast Arctic cod (*Gadus morhua*), Northeast Arctic haddock (*Melanogrammus aeglefinus*), Northeast Arctic saithe (*Pollachius virens*), Norwegian spring-spawning herring (*Clupea harengus*), and capelin (*Mallotus villosus*). These fish stocks form the basis for large fisheries in the region as well as being vitally important as prey and predators in the ecosystems of the Norwegian and Barents Seas (Runnstrøm, 1936; Bergstad *et al*., 1987, and references therein). All of them use the oceanic regions of the Barents Sea as feeding grounds for juveniles and/or adults and migrate closer to the coast to spawn between January and May. During these spawning migrations, large numbers of adult fish congregate and produce vast numbers of spawning products within limited time and space. Therefore, the spawning areas and times are crucial to the reproductive success of these stocks. From the perspective of the fish, these areas and periods are the most vital in their life history and also the most vulnerable to negative external impacts.

The Barents Sea faces increasing anthropogenic impact from shipping (Anon., 2004a), oil extraction (Anon., 2003; Hjermann *et al*., 2007), and fisheries (Anon., 2004b). Given the increasing pressure on the Barents Sea ecosystem and the 2002 World Summit on Sustainable Development agreement on implementing an ecosystem-based approach to fisheries management (Anon., 2002), the Norwegian government developed an ecosystem-based management plan for the portion of the Barents Sea under Norwegian jurisdiction (Anon., 2006; Olsen *et al*., 2007). An important tool in this plan is to assess the relative importance of different subareas within the ecosystem, to maintain biodiversity and the biological production of the system as a whole. Such areas of importance for both biodiversity and production are classified as crucial to maintaining the ecosystem in a sustainable state (Olsen and Quillfeldt, 2003; Anon., 2006). Therefore, biological value in the present study is defined as meaning great importance to both biodiversity and biological production. The most important of these areas is the Lofoten–Vesterålen area, the Tromsøflaket Bank, and the 50-km zone along the Norwegian coast to the Norwegian–Russian border. One of the main reasons for focus on these areas is their importance as spawning grounds and as drift and retention areas for eggs and larvae of the major fish stocks. The assessment was made through an expert-based process (Olsen and Quillfeldt, 2003), relying on spatial descriptions of valuable areas for a variety of species. Descriptions and data on valuable areas are also needed to underpin management advice on issues as diverse as marine protected areas, closure of trawling grounds, physical installations on the seabed (e.g. wellheads and pipelines), offshore wind farms, and seismic exploration. Specific spatial data are available in a fragmented manner because studies and articles generally have focused on single species. Moreover, many of the data have not been published through peer review and are only available in the grey literature as survey reports and ICES Working Group documents. This is especially the case for haddock and saithe, where much important information is only available in the grey literature, although for cod, herring, and capelin, more information is published in the primary literature, along with some in the grey literature. A holistic description of valuable areas for major ecological components is, therefore, in demand, and the main goal of this review is to present an integrated analysis of the areas of greatest biological value for the listed commercially important fish stocks in the Barents Sea and adjacent waters in relation to

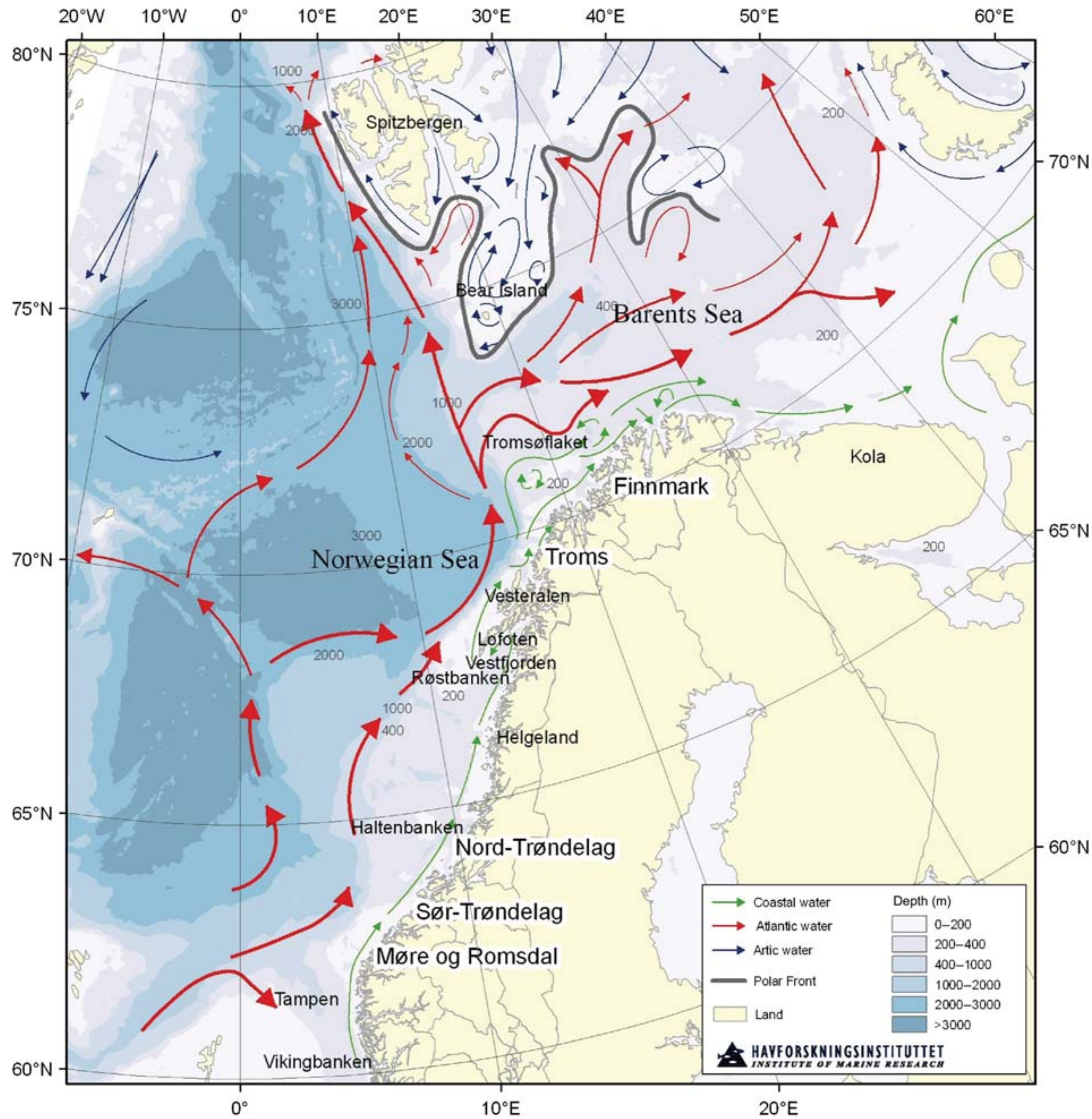

Figure 1. Map of the Barents Sea and adjacent areas, showing the major current systems and geographic features.

their life-history stage and season. Our review is based on knowledge collected from all Norwegian (Institute of Marine Research) and joint Norwegian/Russian surveys in the area, supplemented with information from the fisheries.

Capelin (*Mallotus villosus*)

General description

Capelin are small, pelagic, schooling, planktivorous forage fish that attain a maximum length of ~20 cm at a maximum age of 6 years (Gjøsæter, 1998). The species is semelparous. Capelin has a circumpolar distribution, with major stocks located on both sides of the Bering Sea, in the Newfoundland–Labrador area, on both sides of Greenland, at Iceland, and in the Barents Sea (Carscadden and Vilhjálmsson, 2002). There is one large oceanic stock of capelin in the Barents Sea and additional local stocks in at least one fjord in northern Norway (Gjøsæter, 1998). Barents Sea capelin serve as food for several predators, including other fish, sea mammals, and seabirds. The main predators include cod, harp seals (*Phoca groenlandica*), and various cetaceans.

The Barents Sea capelin stock is characterized by large fluctuations in stock size. From more than 7 million tonnes before 1985, the stock collapsed to a few hundred thousand tonnes in 1987. Four years later, the stock had rebuilt to pre-collapse levels. This pattern was repeated in the mid-1990s (Gjøsæter, 1998) and again from 2003 to 2008 (Gjøsæter *et al.*, 2009). During the periods of collapse, the fishery for capelin was halted. Annual landings of capelin have otherwise varied between 100 000 and 3 million tonnes.

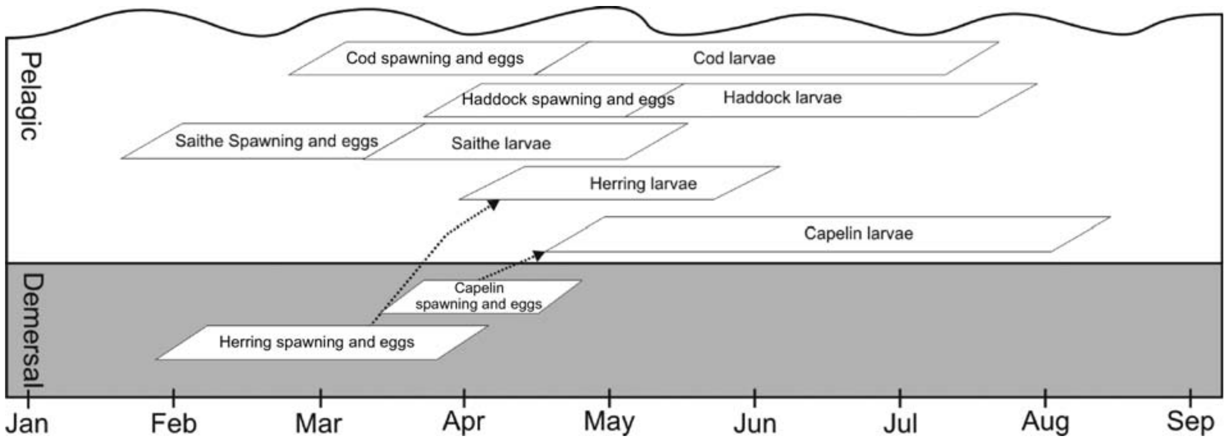

Figure 2. Schematic representation of the temporal and vertical distribution of spawning (eggs) and larvae for cod, haddock, saithe, herring, and capelin in the Barents Sea. The order of species within the pelagic and demersal groups is random.

Spawning

The main spawning season is late March to early April (Figure 2), but some spawning may take place earlier in March and during summer. Capelin spawn in spring (Figure 2) along the Norwegian coast from Vesterålen to the entrance to the White Sea (Gjøsæter, 1998; Figure 3). However, they seldom spawn in all these areas in a single year. Spawning is normally only west of 25°E (western), between 20 and 30°E (central), or east of 25°E (eastern). It has been difficult to predict where capelin will spawn, e.g. based on hydrographical conditions. Luka and Ponomarenko (1983) described a correlation between high sea temperature and eastern spawning, and between low sea temperature and western spawning. In recent years, however, this pattern has been broken, e.g. when far-western spawning was associated with the highest sea temperatures on record, in 2006.

Capelin normally approach spawning areas in large schools (Luka and Ponomarenko, 1983). The main migration routes towards the coast are termed western, central, or eastern according to their direction, but the migration varies unpredictably from year to year. In most years, there are several approaches; capelin following western routes arrive somewhat earlier than those following more eastern routes. Capelin may not necessarily spawn where they reach the coast; quite often, they continue west before settling to the bottom and starting to spawn.

Egg stage

Capelin deposit demersal eggs at depths of 20–100 m along the coast in areas with strong currents (Sætre and Gjøsæter, 1975), although there are indications that Barents Sea capelin can spawn at depths down to 250 m. Capelin prefer sand and gravel substrata for spawning. The eggs adhere to the substratum, but not to each other, may be partially buried by strong currents or wave action, and may sometimes form layers up to 15 cm thick, though 5–7 cm is more common.

On the bottom, the eggs are preyed upon by predators such as fish (mainly haddock), diving birds (mainly eiders, *Somateria* spp.), and benthic organisms (Sætre and Gjøsæter, 1975), and also by capelin (Slotte *et al.*, 2006). Egg mortality was reported to be quite low by Sætre and Gjøsæter (1975); <20% in 75% of the samples, and in just 13% of the samples was mortality as high as 50%. According to those authors, capelin eggs can endure fairly strong mechanical stress, but viability varies with age. At an ambient temperature of 4°C, hatching peaks after ~40 d, and all eggs hatch within 2 months (Gjøsæter and Gjøsæter, 1986; Figure 2).

Larval and 0-group stages

The larvae hatch at a length of 7.6 mm (Gjøsæter and Gjøsæter, 1986), then ascend towards the surface where they are transported by prevailing currents towards nursery areas (Figure 3). The dispersion or retention of larvae is partly governed by eddies along the shelf edge (Fossheim, 2006). Post-yolk-sac larvae feed on coastal zooplankton such as invertebrate eggs, bivalves, and small copepod eggs, nauplii, and copepodites (Fossheim, 2006). As they grow, they also feed on early stages of larger zooplankton, such as *Calanus finmarchicus* (Karamushko and Reshetnikov, 1994). Larvae reach lengths of 5–7 cm during their first feeding season, and metamorphose at lengths of ~8–10 cm during their second year of life. The nursery grounds are in the central or southeastern Barents Sea, but with large year-to-year variations (Figure 3). For western spawning, portions of the larva population may be trapped by the western branches of the current systems in the area and transported towards areas west of Svalbard. With eastern spawning, most larvae end up in the southeastern Barents Sea. The vertical distribution of the various larval and post-larval stages is not well known. During early stages, larvae have been observed concentrating in the upper 40 m. As they grow, they probably do carry out some vertical migration, but even during the 0-group investigations of August, post-larvae 4–7 cm long are mainly in the upper 75 m (Beltestad *et al.*, 1975).

Juvenile stage

Immature capelin feed on copepods, and from a length of ~10–12 cm, larger zooplankton such as krill (Euphausiacea) become more and more dominant in the diet (Gjøsæter, 1998). They start to mature at ~13 cm long, and 50% maturity is attained at ~14 cm. This length is achieved during their third or fourth year of life, depending on growth rate. They spread out horizontally as the capelin grow, and during the feeding season, juveniles are found over nearly the whole Barents Sea, apart from the southwest (Figure 3). During winter, they probably retreat from north of the Polar Front, which is covered by ice. Some immature capelin migrate south during spring to coastal areas, then migrate north

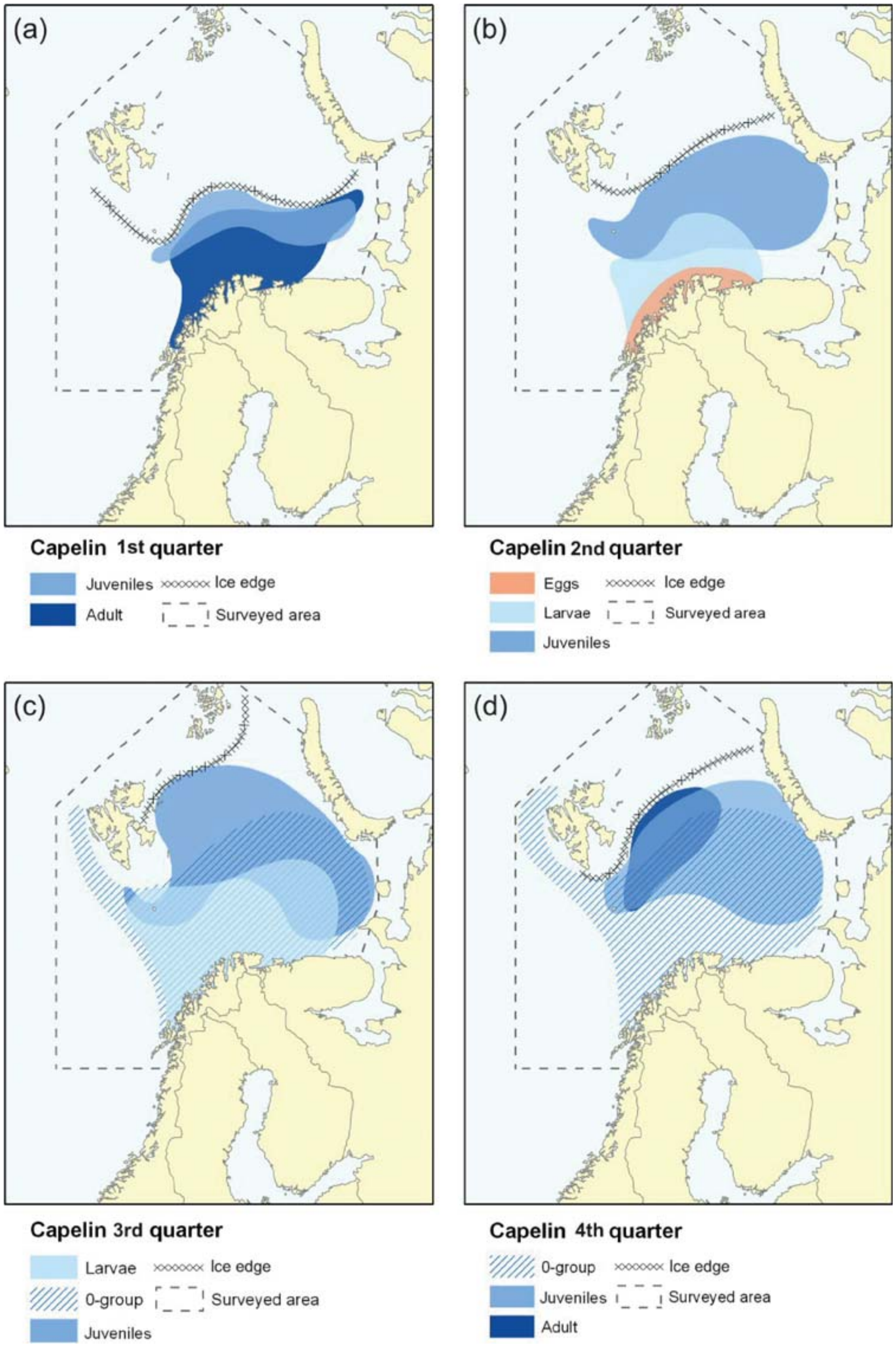

Figure 3. The distribution of capelin eggs, larvae, juveniles, and adult spawning areas, and the main migration patterns by (a) first quarter, (b) second quarter, (c) third quarter, and (d) fourth quarter.

during summer to feed in the plankton-rich areas formed when the ice retracts.

The vertical distribution of capelin was studied by Luka and Ponomarenko (1983), but not the vertical distribution of juveniles compared with that of mature fish. They concluded that the interchange of daylight and darkness triggered vertical migration. By night, capelin disperse and form loose schools or scattering layers in the upper part of the water column, whereas during daylight, they often congregate into more densely packed layers and schools at intermediate depth and may descend towards the seabed. This pattern is not well defined during the polar night. During spring and the onset of daylight, the difference between light conditions by day and night increases, and the amplitude of vertical migrations intensifies. Normally, mature capelin

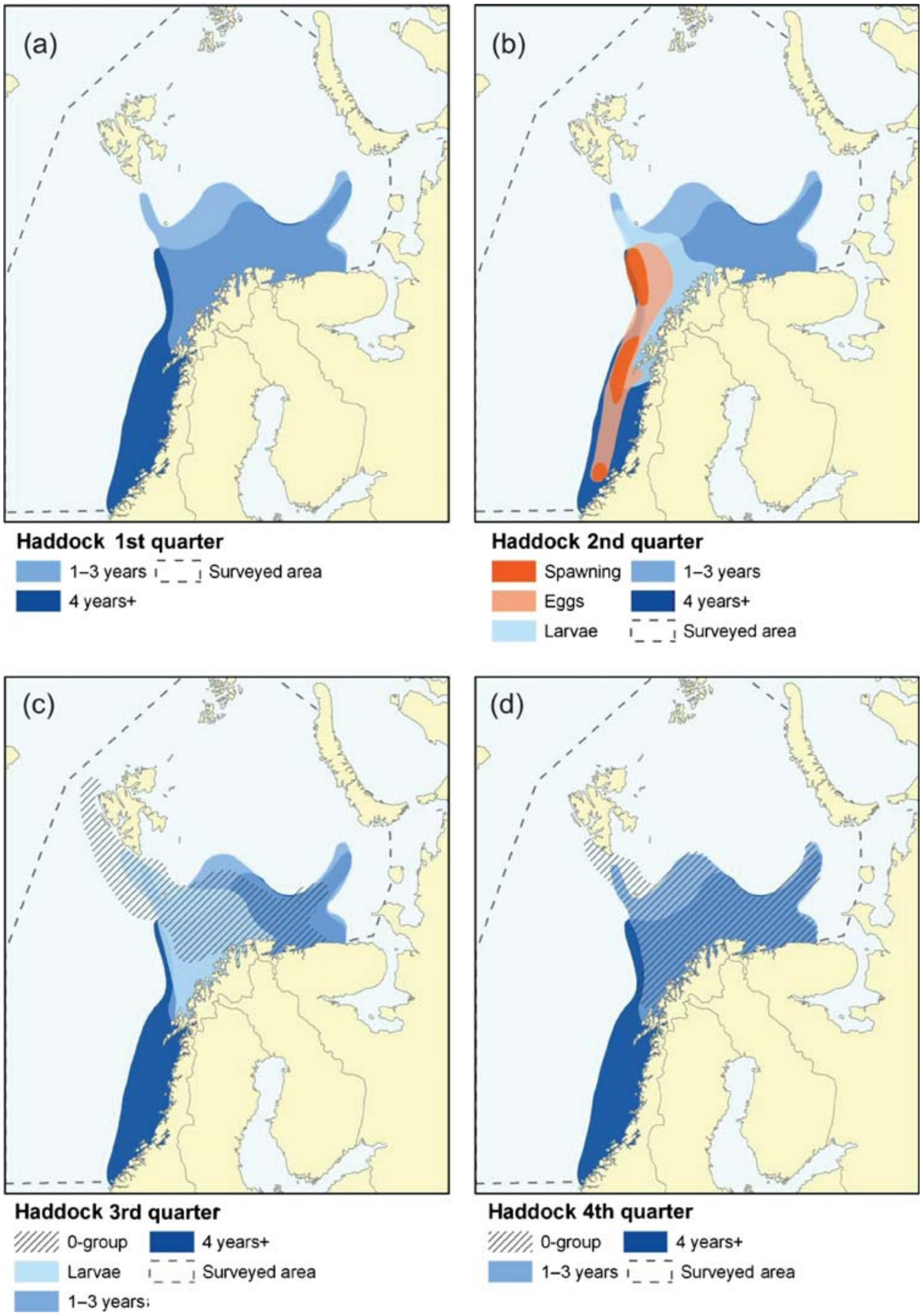

Figure 4. The distribution of haddock eggs, larvae, juveniles, and adult spawning areas, and the main migration patterns by (a) first quarter, (b) second quarter, (c) third quarter, and (d) fourth quarter.

descend to greater depths than immature fish, and capelin caught at or near bottom are normally larger and older than capelin caught at shallow and intermediate depth. Immature fish are preyed upon by a variety of predators (fish, seals, whales, and birds), but their main predator is cod.

Adult and mature stages

Maturation starts in late summer, and during the annual capelin investigations in September, it is possible to identify, by maturity stage, those fish that will spawn the following year. Maturation rate depends on length, and the length at 50% maturity is ~14 cm (Gjøsæter, 1998). Other factors such as seasonal growth patterns, age, and sex also influence maturation. Males mature at somewhat larger size than females (Gjøsæter, 1998). Mature capelin normally migrate farther north during the feeding season than immature capelin (Gjøsæter, 1999). During winter, immature and maturing fish may be found in the same areas, but maturing fish descend to near the seabed (Luka and Ponomarenko, 1983). In February, mature fish gradually segregate from immature fish and start migrating towards the coastal spawning grounds (Figure 3).

They generally form large schools and stay in pelagic layers; in the final phase of the spawning migration, schools may descend and eventually form dense layers at the seabed. During this migration, mature capelin are preyed upon heavily by young cod that gather in these areas and follow the capelin towards the coast (Bogstad and Gjøsæter, 1994). After spawning, dead and dying capelin are found near the spawning grounds, and spent capelin are most likely eaten by predators and scavengers at the surface, in the water column, and at the seabed (Bogetveit *et al.*, 2008).

Haddock (*Melanogrammus aeglefinus*)

General description

The haddock is a gadoid found on both sides of the North Atlantic, from North Carolina to Newfoundland in the west and from Portugal to Iceland, Spitsbergen, and Novaja Zemlija in the east (Pethon, 2005). They are most abundant along the coast over the continental shelf, and abundant along the entire Norwegian coast as well as in the Barents Sea. In the Northeast Atlantic, haddock are subdivided into eight stocks: Faroe Islands, Iceland, West of Scotland, Rockall, Irish Sea, English Channel through west of Scotland, North Sea and Skagerrak and Kattegat, and Northeast Arctic along the Norwegian coast from 62°N to Spitsbergen and Novaja Zemlija in the northeast (http://www.ices.dk). Large temporal fluctuations in stock size driven by large cohorts that appear in a cyclic fashion have characterized the dynamics of this stock historically. From 1950 to 2008, stock size varied between an estimated 66 000 and >600 000 t, with an average of ~350 000 t; reported catches have varied between 21 000 and >320 000 t, with an average annual catch of 125 000 t. During recent years, the stock has increased to record high levels mainly because of the input of three consecutive exceptionally large year classes (2004–2006), in contrast to historical observations of cyclic strong year classes (ICES, 2009). Northeast Arctic haddock may grow to 19 kg and 110 cm, and live for up to 20 years (Pethon, 2005).

Spawning

Like cod, Northeast Arctic haddock are batch-spawners with high fecundity, spawning pelagic eggs from March to June, with a peak in late April and early May (Bergstad *et al.*, 1987; Solemdal *et al.*, 1997). Spawning has been reported over a wide range of depths (Bergstad *et al.*, 1987), usually at depths of 300–600 m in temperatures between 4 and 6°C, although spawning in depths ranging from <100 m (Solemdal *et al.*, 1989) to >1000 m (Solemdal *et al.*, 1997) has been reported. Spawning areas have not been properly investigated, and their exact location is diffuse, based on scant data (e.g. Bergstad *et al.*, 1987; Solemdal *et al.*, 1989, and references therein). However, they do spawn along the slope between the continental shelf and the Norwegian Sea. The most important spawning grounds seem to be on the western side of Tromsøflaket and on the banks outside Røstbanken, Vesterålen, the outer part of the Vestfjord, and Møre–Romsdal (see Figure 4b), but spawning along the outer continental shelf from ~62 to ~70°N has been suggested (Sætersdal, 1952; Wiborg, 1957, and references therein; Bjørke, 1984; Bergstad *et al.*, 1987).

Egg stage

The vertical distribution of eggs has not been well investigated, but one study reports large variations in the buoyancy of haddock eggs (Solemdal *et al.*, 1997). The ascending velocity apparently varies between 40 and 170 m per 24 h, with a mean similar to that of cod, and developing eggs seem to concentrate at a depth of 50 m. Newly spawned eggs from the most northern spawning area (Tromsøflaket) have been observed in dense aggregations along the 500-m depth contour, probably drifting north (Figure 4b). Some eggs and larvae, however, drifted east. These observations agree with time-series of density estimates derived from Russian surveys from 1959 to 1993 showing that the highest concentrations of eggs and larvae in April/May were north and west of Røstbanken and at Tromsøflaket (Mukhina, 2005).

Larval and 0-group stages

The larvae continue drifting and dispersing with the currents in a northerly or northeasterly direction and show large spatio-temporal variation in abundance and distribution (Mukhina, 2005). By August and September, they have grown to 30–140 mm, and their distribution as 0-group extends over most of the Barents Sea south of the Polar Front, but also along the west coast of Norway off Spitsbergen (Anon., 2007; Figure 4b). The distribution of 0-group haddock is similar to that of cod, but is generally more to the west and south.

Juvenile stage

Haddock settle to the seabed during the months August–October and prefer temperatures warmer than 1°C. One-year-old haddock have a similar but slightly more southerly distribution than cod (Figure 4b). In some years, large numbers of 1- and 2-year-old haddock are found close to the coast of northern Norway (Troms and Finnmark). Important areas for juvenile haddock (2–4 years) extend from along the northeast Norwegian coast (Finnmark) to the Russian coast off Kola. In recent years, the distribution of juvenile haddock has also extended farther north than previously observed. Juvenile haddock can occupy the entire water column, although they are usually associated with the seabed. They migrate vertically depending on the light, staying closer to the seabed by day, and higher in the water column at night and in winter (Bergstad *et al.*, 1987).

Although juvenile haddock in the pelagic stage feed on planktonic crustaceans, settled juvenile haddock feed mostly on benthic organisms (Burgos and Mehl, 1987). Growth is variable and seems to be cohort-specific (ICES, 2006); on average, haddock grow 7–9 cm each year before maturing, when the growth rate decreases. In some years, cod eat large numbers of juvenile haddock and are likely to significantly impact the survival of young haddock, although the absolute effect has not been quantified (ICES, 2008).

Adult and mature stages

The maturation rate of haddock is variable and depends on age and length as well as other factors such as cohort and sex (Korsbrekke, 1999), but most haddock mature at ages 4–7 and 40–60 cm long. Mature haddock perform more extensive vertical migration than juveniles and are generally found higher in the water column at night. In late summer, large haddock are found high in the water column all day along the coast off eastern Finnmark (Figure 4c).

After age 3, haddock perform seasonal migrations between the eastern and coastal feeding grounds in summer and between western and southerly wintering areas in deeper water (Figure 4c and d). The spawning migration of haddock follows the same pattern, but is poorly understood, especially the distance of the southern migration and the timing and the path of the return.

Adult haddock are rarely preyed on by other Barents Sea fish, although marine mammals such as harp seals, minke whales (*Balaenoptera acutorostrata*) and killer whales (*Orcinus orca*) do take gadids as part of their diet (Bergstad *et al*., 1987). As haddock grow, fish (particularly capelin) become part of the diet. The diet of haddock differs from cod by consisting more of benthic organisms and crustaceans than fish (see Burgos and Mehl, 1987, for further detail).

Saithe (*Pollachius virens*)

General description

Saithe are found only in the North Atlantic. In the western North Atlantic, there is a small stock at the border between the United States and Canada, whereas in the eastern Atlantic, saithe have generally been separated into six stocks, but with poorly defined boundaries. The main eastern Atlantic areas where they are found are west of Ireland and Scotland, Iceland and the Faroe Islands, North Sea, and along the coast of Norway north of 62°N to the Kola Peninsula.

Both total-stock biomass and spawning-stock biomass (SSB) of Northeast Arctic saithe peaked in 1970 and 1971, with an SSB of ~650 000 t in 1970 (ICES, 2009), after which the stock declined steeply, with SSB dropping to 94 000 t in 1987. This was caused partly by record landings (265 000 t in 1970) and rates of fishing mortality that increased to unsustainably high levels (above F_{lim}, the level of fishing mortality at which there is an unacceptably high risk that stocks will collapse), and partly by reduced recruitment caused by unfavourable environmental conditions (Toresen and Østvedt, 2000), probably driven by the declining SSB (ICES, 2009). From 1985 to 1992, the SSB was below B_{lim} (the minimum spawning biomass of a stock below which there is a high risk of a serious decline in the stock and from where recovery would be slow), and landings were low. After a long period of low stock size, the stock recovered during the 1990s, supported by the recruitment of several above-average year classes. From 2000 to 2007, the stock was at a stable, high level, with SSB at ~800 000–1 000 000 t (ICES, 2009), and a low rate of exploitation. Since 2007, the stock size has been decreasing again (ICES, 2009).

Spawning

Northeast Arctic saithe spawn in winter, with a peak in February, at a depth of 150–200 m and at 6–10°C (Pethon, 2005). Spawning takes place over a wider area than for Northeast Arctic cod, and the best known spawning areas are outside Lofoten, on the banks off Helgeland, the banks off Møre and Romsdal, and the banks in the northern North Sea (Figure 5a).

Egg stage

Spawning is pelagic, and the fertilized eggs, lacking an oil globule, ascend to the surface. Each female produces 0.2–8 million eggs. The eggs are 1.0–1.2 mm in diameter and hatch after 6–15 d, depending on temperature. Eggs and larvae drift north with the currents.

Larval and 0-group stages

During the years 1985–1993, an annual 0-group saithe survey was performed in April/May in the northern part of the North Sea, the eastern part of the Norwegian Sea, and along the Norwegian coast north to Troms to obtain an index of year-class strength (Mehl *et al*., 1988). Since 1996, the distribution of larvae and 0-group saithe has been partly covered by the Norwegian spring-spawning herring larva survey in April. The surveys show the densest concentrations of saithe larvae from Møre to north of Haltenbanken. 0-group saithe are also found during the 0-group investigations in the Barents Sea in August, but that survey covers just a fraction of the total distribution of the stock (Stensholt and Nakken, 2001). 0-group fish settle in the littoral zone of the coast from western Norway to the Kola coast in the southeastern part of the Barents Sea in April–June. An observer programme for 0-group saithe started in summer 2000 with 25 observers distributed along the Norwegian coast from 62°N to the Varanger Fjord (Borge and Mehl, 2002; Mehl, 2007). During that programme, the abundance of 0-group saithe is classified visually on a scale from 0 to 10.

Juvenile stage

Juvenile saithe are found regularly in schools at specific localities where the bottom depth is 60 m or less. The main prey items of young saithe are *C. finmarchicus*, krill, and other crustaceans (Nedreaas, 1985). Aglen (1995) carried out small-scale acoustic surveys at the coast of western Finnmark for younger age groups of saithe, but observed 0-group saithe only in harbour areas, and very few 1-group saithe at all. There appears to be a tendency for 1-group saithe to stay in shallower water than 2-group fish, so making them less vulnerable to survey capture.

Adult and mature stages

Saithe migrate to the coastal banks from Møre to Finnmark as 2–4-year-olds, depending on climate, food availability, and year-class strength. Migration from the coast during spring in some areas may be explained by the distribution of krill and the competition for food (Nedreaas, 1985). Saithe aged 3–6 are relatively well sampled by the annual coastal survey of October/November (Nedreaas, 1997), but older fish are only partly sampled because they migrate at that time of year (Figure 5d). The greatest concentrations are often at the coastal banks from Møre to Finnmark. During the past 10 years, there has been a trend towards fewer saithe north of 69°30′N, an increase between 67°00′ and 69°30′N up to 2000, and a subsequent decrease, and a marked increase in the southern part of the species' range. This southward shift in distribution may be caused by several factors, such as different exploitation patterns and fishing pressure in certain areas, climate effects, and stock interactions, or a combination of these factors.

Saithe exist in both pelagic and demersal habitats, mainly at depths of 0–300 m. At depths <200 m, they normally remain close to the bottom or in the lower half of the water column, but with increasing depth, they are distributed relatively higher in the water column (Stensholt *et al*., 2002). At depths >300 m, a considerable proportion of the stock may be occupying pelagic waters. Adult saithe feed on fish such as herring, sprat (*Sprattus sprattus*), young haddock, Norway pout (*Trisopterus esmarkii*), and blue whiting (*Micromesistius poutassou*; Mehl, 2005). Along the coast of Finnmark, saithe feed intensively on spawning capelin (Bogetveit *et al*., 2008). Saithe make both feeding and spawning migrations, and adult fish follow Norwegian spring-spawning herring far out into the Norwegian Sea (Figure 5c). Saithe also follow herring on their spawning migration (Runde, 2005). The extent of and changes in these migrations are probably

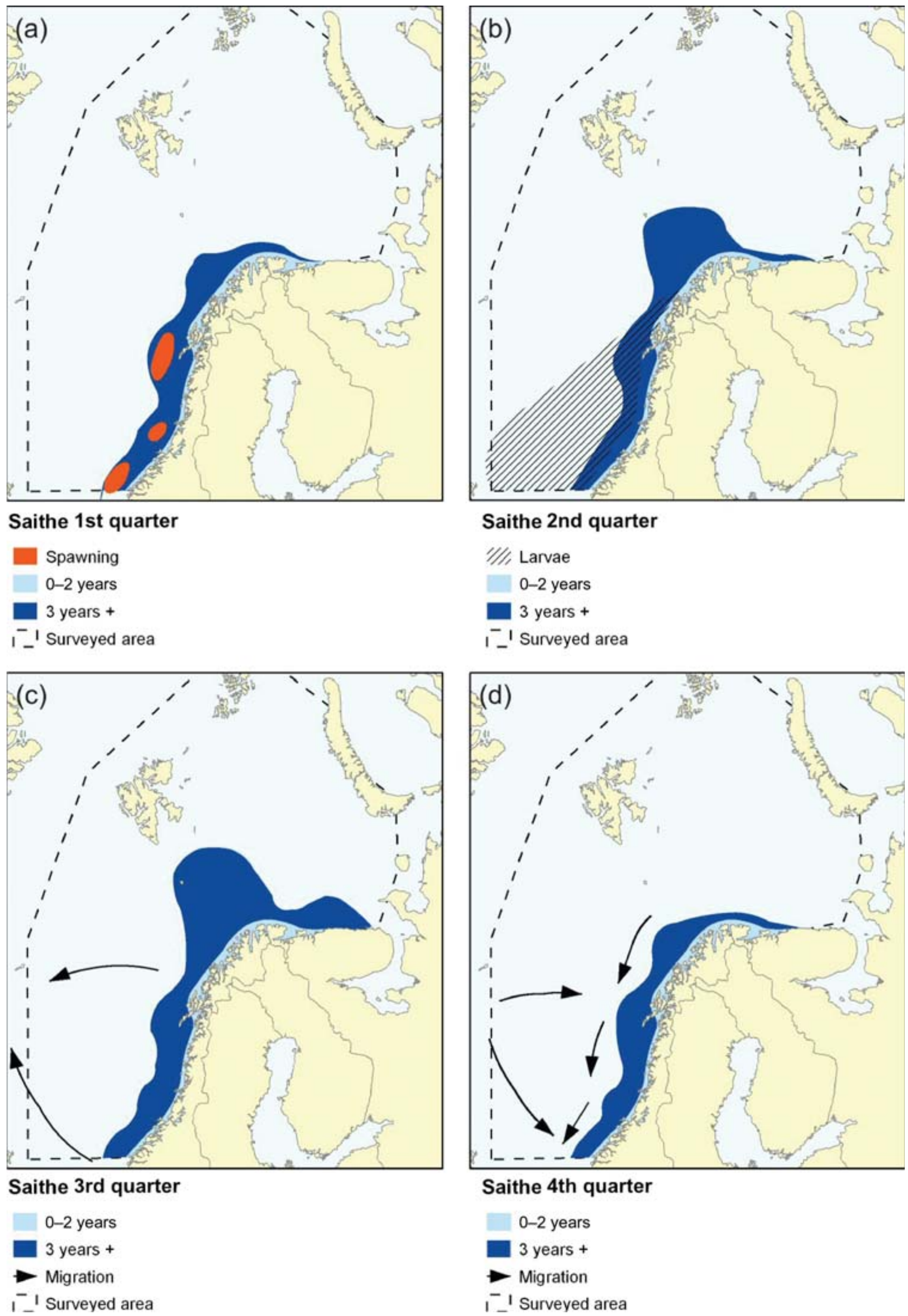

Figure 5. The distribution of saithe eggs, larvae, juveniles, and adult spawning areas, and the main migration patterns by (a) first quarter, (b) second quarter, (c) third quarter, and (d) fourth quarter.

influenced by changes in the migration pattern of the herring, a prey species.

Tagging experiments show regular annual migration of mature saithe from the north coast of Norway to the spawning areas off the Norwegian west coast and also, to a lesser extent, to the northern North Sea. There is also substantial emigration of immature saithe to the North Sea from the Norwegian coast between 62 and 66°N, and this coastal area seems, to a large extent, to serve as a nursery area for the North Sea stock of saithe (Jakobsen, 1981). In some years, there are also examples of mass migration of adult saithe from northern Norway to Iceland and, to a lesser extent, to the Faroe Islands (Jakobsen and Olsen, 1987).

Herring (*Clupea harengus*)

Norwegian spring-spawning herring (NSSH) are found in the Northeast Atlantic, with main areas of distribution along the Norwegian coast (spawning), the Barents Sea (the main area for juveniles), the Norwegian coast and fjords (juvenile area), and the Norwegian Sea bounded by the Norwegian coast, Faroe Islands, the north coast of Iceland, Jan Mayen Island, Spitsbergen, and Bear Island (adult feeding; Figure 6). It is potentially the largest herring stock in the world, with observed stock biomass at nearly 20 million tonnes and annual landings of up to 2 million tonnes. A major characteristic of the NSSH is its plasticity in terms of distribution; spawning, feeding, and wintering areas vary greatly, largely attributable to two factors: changes in stock size and in fish size. The stock collapsed in the late 1960s (Dragesund *et al*., 1980) and went through a long rebuilding period from 1971 to 2000, when it regained the size it had in the early 1950s. Before 1970, the stock occupied a western oceanic wintering area, but during the rebuilding period, it migrated into fjordic wintering areas in northern Norway (Holst *et al*., 2002). From 2002 to 2007, it shifted to eastern oceanic wintering areas.

Spawning

Spawning takes place in February and March on spawning grounds along the Norwegian west coast from ~58 to 70°N, but periodically varying on a north–south scale (Figure 2; Hamre, 1990). The most stable spawning grounds are in the Møre region between 62 and 64°N. In the period with western wintering areas between Iceland and the Faroe Islands, spawning of young herring was also documented east of the Faroe Islands (Figure 6).

Larval stage

After hatching, the larvae rise towards the surface and drift with the prevailing northerly and northeasterly currents along the Norwegian coast away from the spawning grounds (Fossum, 1996). Most young NSSH end up in the Barents Sea, where particularly large year classes become significant ecological factors in the ecosystem, as both predator and prey. Smaller numbers of the 0-group end up in fjords along the Norwegian coast and in the northern part of the Norwegian Sea between Jan Mayen and Bear Islands (Figure 6). By late summer, the 0-group has generally settled in the areas where they will live as juveniles for the next 3–4 years (Hamre, 1990).

Juvenile stage

Juvenile herring remain in their juvenile areas until they reach 20–23 cm long at 3–4 years of age. The youngest juveniles in the Barents Sea are generally north of the Kola Peninsula, but they move west as they grow older (Figure 6). The juvenile period in the Barents Sea is also characterized by a northerly dispersal migration in summer, and a southerly concentration migration in winter, which is comparable with the adult feeding migration. In general, herring along the Norwegian coast migrate out of the fjords in summer and return in winter. At ~20–23 cm long, the herring leave the Barents Sea and the fjords for the oceanic area off Troms. During that phase, they are often referred to as "fat herring" because of the large deposition of fat they contain, but still not forming gonads.

Adult stage

First spawning is at lengths of ~28–30 cm, and first-time spawners undertake relatively short southward spawning migrations along the Norwegian coast, which become longer as the fish grow older and larger. During the fjordic wintering period of 1973–2007, the spawning migration began around mid-January. After spawning, the post-spawners quickly move north and northwest into the Norwegian Sea feeding areas (Figure 6). Feeding is a density- and length-dependent process, whereby the largest fish undertake the longest migrations and, depending on individual lengths, the extent of the annual migration is governed by food availability and density-dependent feeding mechanisms. At low stock levels, the feeding areas are along the Norwegian coast, but at higher stock levels, feeding extends into the Polar Front areas between Iceland, Jan Mayen Island, and Bear Island. At the end of the feeding season, the herring move deeper in the water column and retreat towards wintering areas. The wintering areas have varied greatly over the past 50 years, from oceanic waters off eastern Iceland to fjords on the Norwegian coast, and back into the open ocean off northern Norway (Holst *et al*., 2002).

Cod (*Gadus morhua*)

Cod are distributed on both sides of the Atlantic. Its latitudinal distribution is constrained by ~40 and 65°N in the west and by 45 and 80°N in the east (Garrod, 1977). Cod are top predators. In the Barents Sea, adults feed mainly on fish and young cod mainly on planktonic crustaceans. Occasional cod >130 cm and 30 kg (>20 years old) are found, but fish in the weight range of 1–5 kg are the most common in the fisheries. The Northeast Arctic cod stock is distributed mainly in the offshore areas of the Barents Sea. Over the past 60 years, stock size has varied between 0.8 and 4 million tonnes, and over the same period, annual landings have varied between 0.2 and 1.3 million tonnes.

In coastal areas, there are more stationary local cod stocks. During spawning and feeding migrations, parts of the Northeast Arctic stock overlap with the coastal stocks. Figure 7 shows the distribution of Northeast Arctic cod. The stock identity of eggs, larvae, and 0-group cod in fjords and coastal areas has not yet been mapped accurately. North of 67°N, the offshore distributions of all life stages are considered to be totally dominated by Northeast Arctic cod.

Northeast Arctic cod

Spawning areas

The main spawning areas are at Vesterålen, Røstbanken, and outer Vestfjord (coastal areas between 67 and 69°N), but there is also some spawning in coastal areas farther north (in Troms and western Finnmark) and south (Trøndelag and Møre; Figure 7). More scattered spawning may also take place in the Barents Sea. The eggs are spawned pelagically at various depths, mainly deeper than 100 m. Cod are batch-spawners with a high fecundity. For each cod, the total duration from the release of the first to the last batch can be as long as 1 month. A big female may, over this period, spawn several million eggs. Spawning mainly takes place in March and April (Figure 2). The age at sexual maturity is typically 6–7 years for males and 7–8 years for females.

Egg stage

The fertilized eggs are neutrally buoyant near the surface. In calm weather, they tend to be distributed in the upper 20 m of the water column, but strong waves and currents periodically drive them deeper (Vikebø *et al*., 2005). The eggs drift and disperse with the currents in a north–northeasterly direction. In a typical year, eggs are distributed from Røstbanken to Nordkapp and north towards Bear Island, with the greatest concentrations typically at Tromsøflaket (Serebryakov and Aldonov, 1984; Figure 7).

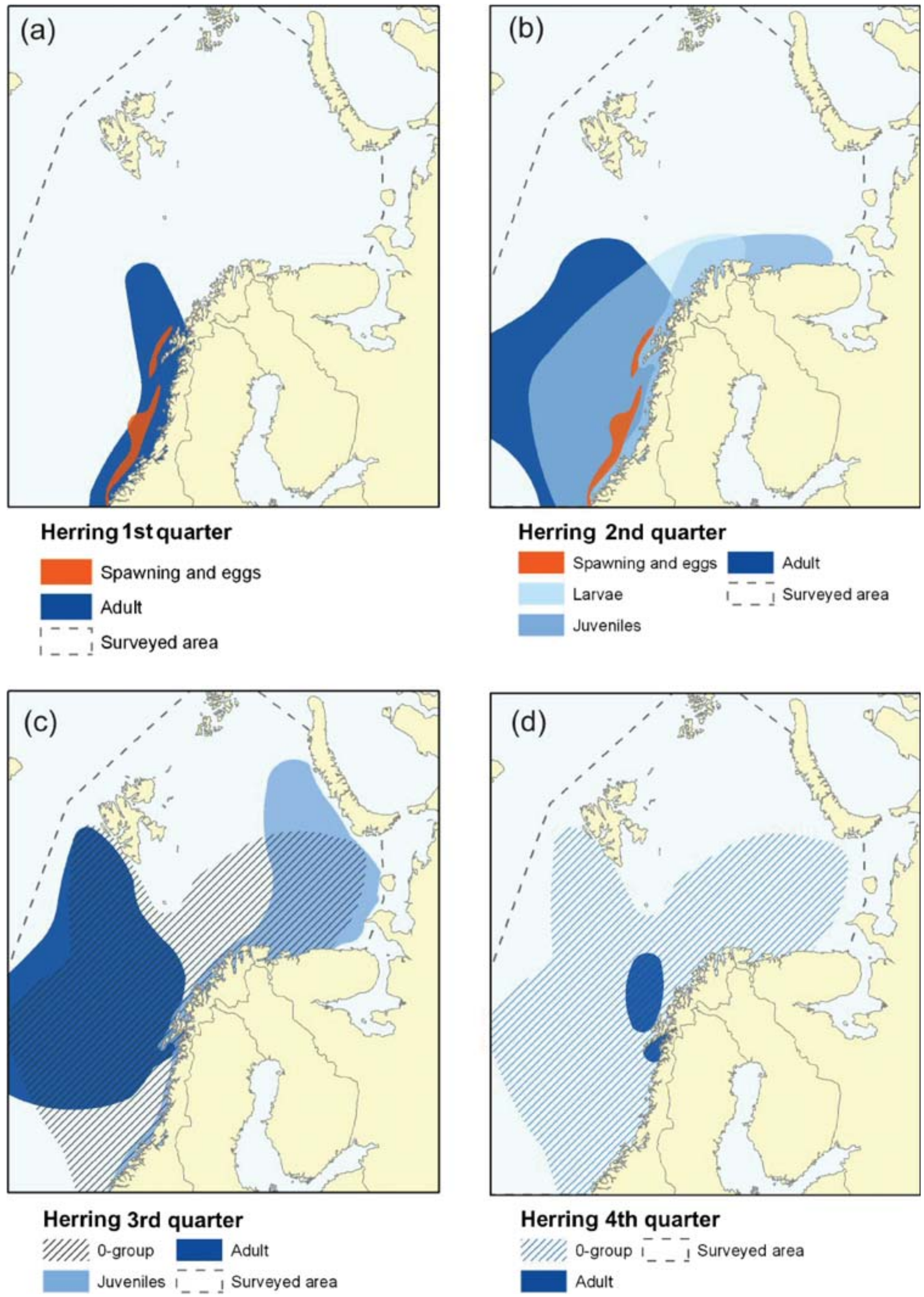

Figure 6. The distribution of herring eggs, larvae, juveniles, and adult spawning areas, and the main migration patterns by (a) first quarter, (b) second quarter, (c) third quarter, and (d) fourth quarter.

Larval stage

Hatching peaks around mid-April (Figure 2), and thereafter, horizontal dispersion continues. The greatest concentrations of larvae are in June on the banks off northern Troms and at Tromsøflaket (Helle, 1994; Figure 7). During summer, the larvae metamorphose to become 0-group cod, and in August and September, these cod are distributed over most of the Barents Sea south of the Polar Front (Figure 7; Stensholt and Nakken, 2001; Ciannelli *et al.*, 2007). In late autumn, the 0-group cod settle to the seabed and assume a demersal existence (Figure 7).

Nursery grounds

For each cohort, it appears that the horizontal distribution is broadest during the first year after settlement. Then, concentrations tend to be greatest along the Polar Front and occasionally extending into cold water down to -0.5°C (Ciannelli *et al.*, 2007). In general, the centre of the horizontal distribution moves to the southwest as the fish grow older (Ottersen *et al.*, 1998). Cod aged 2 and 3 tend to concentrate in the southeastern Barents Sea, the disputed area (the "grey zone"), and in the Bear Island area. With increasing age, the seasonal migration becomes more

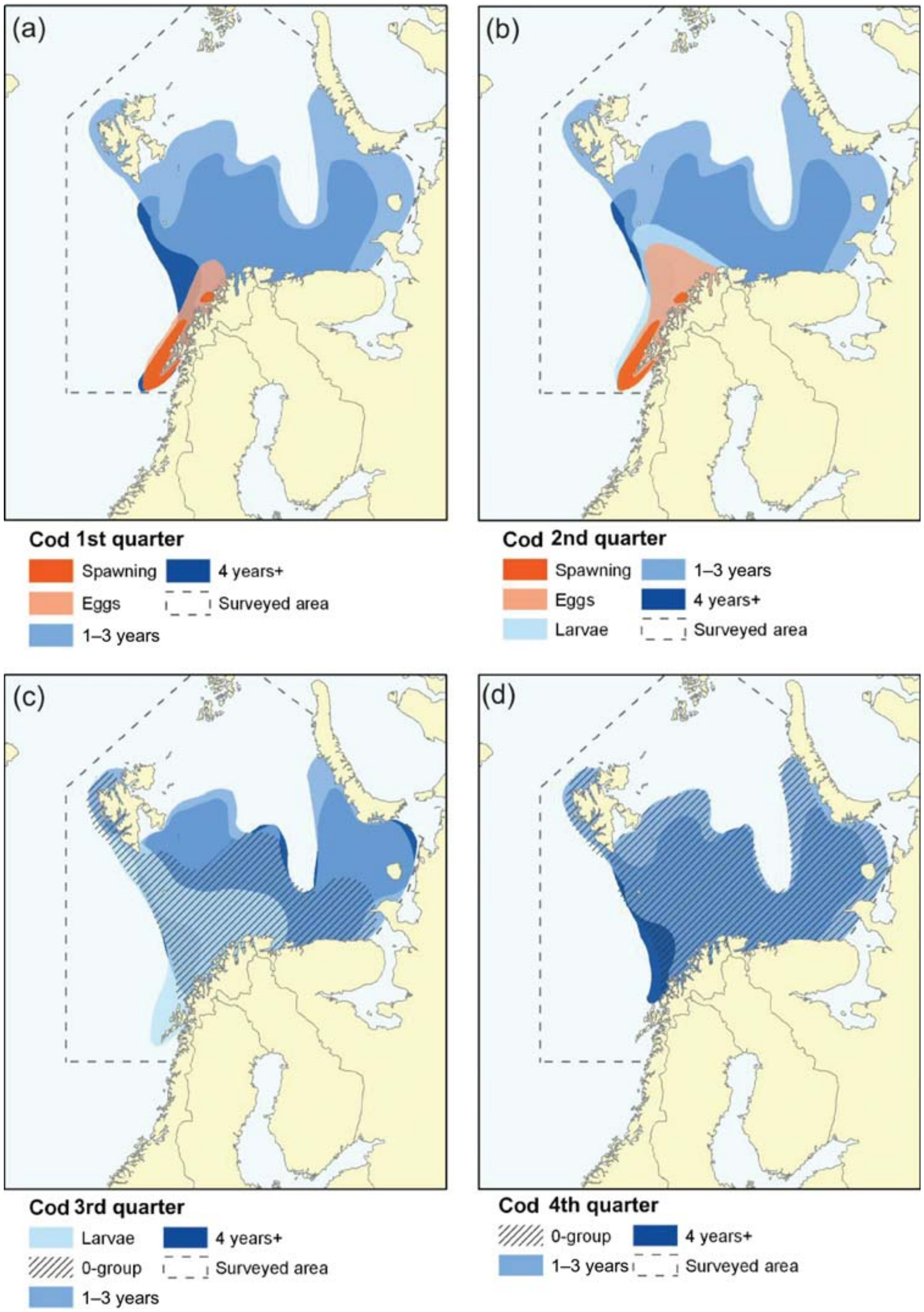

Figure 7. The distribution of cod eggs, larvae, juveniles, and adult spawning areas, and the main migration patterns by (a) first quarter, (b) second quarter, (c) third quarter, and (d) fourth quarter. Coastal cod are not included.

pronounced. At ages 1–3, the seasonal migrations are more limited, and older fish typically feed along the Polar Front during the second half of the year, then migrate south to feed and (as adults) spawn in the first half of the year. Capelin are important food of cod from age 4 (Michalsen *et al*., 1998; Bogstad and Gjøsæter, 2001), and some of the older age groups of cod follow the spawning migration of capelin in spring towards coastal areas between the Kola Peninsula and Troms. Mature cod (age 7 and older) undertake the longest and most pronounced migrations to the spawning areas.

Vertical distribution

Cod are mainly associated with the seabed, but periodically rise higher in the water column (Stensholt *et al*., 2002). Age groups 1 and 2 tend to stay close to the seabed during the increased light of summer, at least at depths <300 m. In the dark winter season, however, these age groups tend to rise above the seabed, especially at night. Older fish exhibit a more variable vertical distribution. During spring and autumn, they tend to be more pelagic by day than by night (Einarsson, 2001).

Coastal cod

Spawning areas

Local spawning of cod has been observed in many fjords along the Norwegian coast. In addition, some coastal cod spawn around some of the islands, e.g. Sørøya, Inner Lofoten, Vikna, and Møre, along the outer coast. There is some evidence that there are several different stocks of coastal cod. Although the stock complex has not been mapped in detail, it is convenient to distinguish between typical fjord stocks and those in the outer coastal areas (so-called "bank cod"). Cod spawning in the fjords seems to be more stationary than the spawning farther out. Some of the outer spawning areas overlap partly with spawning areas of Northeast Arctic cod, but coastal cod typically spawn closer to shore and shallower. Some of the coastal cod also spawn later in the year than Northeast Arctic cod.

Egg and larval stages

The fertilized eggs of coastal cod have a higher specific density than those of Northeast Arctic cod (Kjesbu *et al*., 1992), implying that coastal cod are distributed deeper in the water column. Simulations from current models show that small differences in the vertical distribution of eggs may result in large differences in the drift pattern (Vikebø *et al*., 2005). In a typical fjord, there is an outgoing current in the upper layer and a deeper, inward, compensatory current. In such conditions, eggs distributed deeper would be retained in the fjord, whereas eggs close to the surface would be transported out of the fjord (Myksvoll, 2008).

Nursery grounds

Studies of 0-group cod in some fjords in northern Troms (Berg and Pedersen, 2001) have shown that they settle in shallow areas and even in the littoral zone. Northeast Arctic 0-group cod found in the same fjords as coastal cod settle in the deeper parts of the fjord. There are also indications that, in the outer coastal areas, 0-group coastal cod settle shallower and have shallower nursery areas at ages 1 and 2 than Northeast Arctic cod. Tagging experiments on adult fish show that cod inside fjords are reasonably stationary. The rather wide and open fjords in Finnmark are exceptions. Cod there do migrate to neighbouring coastal areas in autumn and then return in late winter to spawn (Jakobsen, 1987). Tagging of coastal cod in the outer spawning areas of Lofoten and Møre has demonstrated more-extensive migration, both along the coast and into/out of the coastal shelf (Godø, 1984).

Discussion

Our review shows large-scale, area-use patterns at different life stages for five commercially important fish species of the Barents Sea. To present sufficient information for all five species, we have chosen to include data from the grey literature in cases where peer-reviewed publications are lacking. The use of grey literature has been necessary to provide a full description of the life histories. Although these publications have not undergone the strict quality control provided by peer review, the fact that many of them present the same or similar results lends credence to their findings.

Our review has identified the areas of importance to the production of new generations of cod, haddock, saithe, herring, and capelin. Areas related to spawning and survival through the most critical life stages (eggs and larvae) are of the most importance. The two criteria used to define an area as more valuable than another in space and time are its importance to ensure (i) high biodiversity and (ii) production. The five fish species described range from pelagic to demersal, span different temperature regimes, and fill different niches in the ecosystem. Overlaying the spawning, egg, and larval areas for all five species (Figure 8) clearly demonstrates the extensive overlap of the most valuable areas for all five species. However, overlap between many areas cannot be the sole criteria to designate an area as particularly valuable biologically. Areas of great value to one species should also be considered especially valuable in a holistic, ecological context; or one might fail to identify critically important spawning areas for a single species. There is also a spatial factor; fewer smaller areas are more valuable than larger, more numerous ones.

Habitat type is a critical factor for the demersal spawners herring and capelin, which depend on a specific substratum to spawn successfully and to secure egg survival (Sætre and Gjøsæter, 1975). In contrast, the spawning habitat of pelagic spawners is less influenced by external factors and tends to return to "normal" after perturbations, unlike bottom habitats that can be damaged permanently. However, the dynamic hydrographic conditions of the pelagic spawning habitat means that the fish cannot anticipate stable conditions for spawning from year to year (Sundby, 1994). Pelagic and demersal spawning also influences the spatial and temporal extent of spawning areas. Cod, haddock, and saithe spawn over broader areas than the demersal spawners herring and capelin at comparable population size. Spawning season is similar between demersal and pelagic spawners, but the incubation time for eggs is shorter for pelagic than for demersal spawners (Blaxter and Hempel, 1963; Buckley *et al*., 2000). Demersal spawners are, therefore, dependent on smaller areas of specific physical habitat over a longer period than pelagic spawners. Hence, demersal spawning areas are of greater value to spawning fish than pelagic spawning areas, so the spawning and egg areas of herring and capelin have greater biological value than the pelagic spawning areas of cod, haddock, and saithe. Vulnerability, however, will vary according to the type of impact, e.g. seismic activity will affect pelagic and demersal spawning areas differently.

Spawning areas are less extensive than larval areas and tend to be located closer to the coast (Figure 8). The greatest overlap of spawning and larval areas tends to be along the coast from Røstbanken in the south to the Varanger Peninsula in the northeast. Spawning grounds of cod, haddock, saithe, and herring are located at Røstbanken and Lofoten, and farther north along the coast, areas of cod and capelin spawning and eggs overlap. Offshore along the edge of the continental shelf, haddock and cod spawning areas overlap. To the south, there is overlap between herring and saithe spawning areas in the Haltenbanken area. Spawning seasons extend from January to the end of May (Figure 2), with overlap between some species: saithe and herring overlap in February, capelin and cod in March, and haddock overlap with capelin and cod in April.

Species overlap is more extensive for larval areas (Figure 8) because all species have pelagic larvae that are transported by the currents and spread out over extensive areas. Again, the coast from Røstbanken to Varanger Peninsula shows the greatest overlap between larvae of the five species discussed here. Figure 8 also shows a high degree of overlap on the Tromsøflaket bank—an important retention area for fish larvae on their way from spawning areas in Lofoten to the juvenile areas in the Barents Sea (Bergstad *et al*., 1987). Larvae are

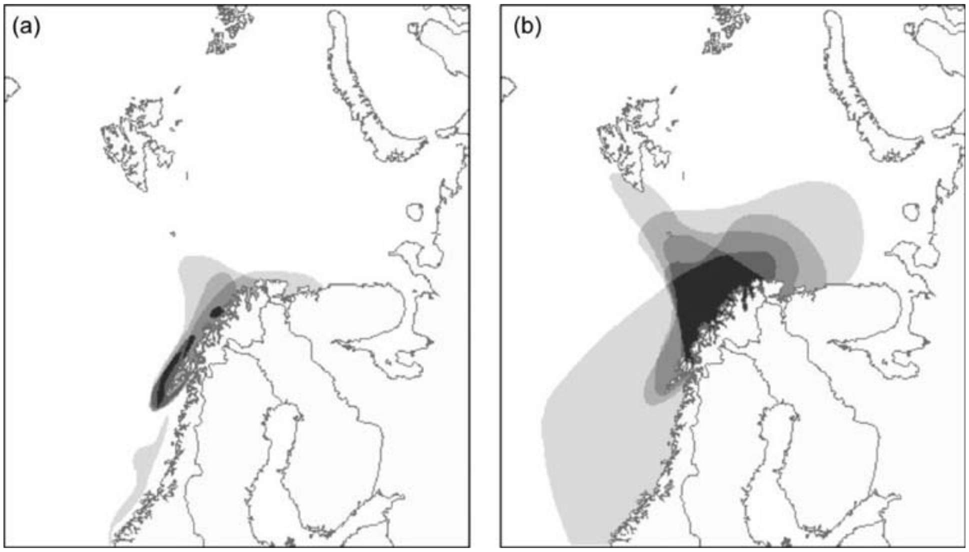

Figure 8. Overlap of biologically valuable areas for cod, herring, haddock, capelin, and saithe (a) spawning areas, and (b) larval areas. The areas for all five species are shown in light grey, and overlap of areas between 2 and 5 species is shown by increasingly darker shades of grey.

carried into the southern Barents Sea and along the continental shelf edge to Svalbard by the North Atlantic Current (Vikebø *et al.*, 2005). The distribution patterns shown in Figure 2 and the species-specific maps (Figures 3–7) are general distribution patterns that will vary from year to year according to both biological and oceanographic factors. This will have a great impact on larval distribution because it depends on the dynamic inflow of Atlantic water (Ingvaldsen *et al.*, 2002), annual surface currents, and larval behaviour (Vikebø *et al.*, 2007). The larval period for all species extends from March to August, but overlaps most at the beginning of May, when saithe, herring, and cod larvae are abundant, and capelin and haddock larvae have just appeared (Figure 2).

Juvenile and adult fish use broader habitats than younger fish because those life stages last longer and allow the fish time to utilize the broader habitats. In addition, older, larger fish have greater potential to move, allowing them to spread out over larger areas. Fish density is less in these areas than in areas used by the younger age classes (Bergstad *et al.*, 1987). Therefore, pollution spills and accidents originating from a point source will only impact a limited part of the distribution of juvenile and adult fish, making them less likely to be impacted. Larger, older fish are also more robust and have less vulnerability to pollution than eggs and larvae (Hjermann *et al.*, 2007). Therefore, the areas occupied by juvenile and adult fish are not as vulnerable to the impacts of pollution as spawning grounds and the areas occupied by eggs and larvae.

The valuable areas described above are associated with the continental shelf or slope (Figure 1). It is in those regions that topography, sediments, and currents have collectively created beneficial habitats for spawning, and gyres over coastal banks create retention areas for the larvae. Such continental shelf areas are also susceptible to impact from other anthropogenic activities, e.g. fishing, subsurface petroleum installations, offshore wind farms, aquaculture, and noise from seismic exploration, and these impacts may cause habitat disruption, especially in the coastal zone where the intensity of aquaculture and offshore wind farms is greatest. Currently, the greatest anthropogenic impact on the stocks and habitats is from fishing (Anon., 2006), but fishing in the area is generally well regulated, with management plans in place for most stocks. Management plans establish rules for exploitation at different stock levels, making management decisions more predictable for managers and fishers alike. Current management plans are not area-based and do not evaluate the effects on valuable habitat from the fishery in question or in relation to other types of human impact. Integrated and sustainable management is the long-term goal of the current management plan for the Barents Sea (Anon., 2006). The challenge for integrated management is to minimize the threat from all human activities that may impact valuable areas. Given the recent concerns about the effects of climate change on Arctic ecosystems, it is important that environmental stress be evaluated in relation to both total human impact and climate effects on habitats and populations.

Fish are most vulnerable to human impact as eggs and larvae. The overlap of nursery grounds (including spawning) for cod, haddock, capelin, saithe, and herring (Figure 8) shows that these grounds are spatially aggregated along areas of frequent human use as fishing grounds, shipping lanes, aquaculture localities, and petroleum fields (Anon., 2006). The most important (hence valuable) of these are the spawning areas, especially for demersal spawners, and the particularly valuable areas are the Møre Banks, the Røstbanken–Lofoten–Vesterålen area, and the coast off Troms and Finnmark. These are also the core spawning areas to where the fish retract at low population density, as was the case for herring during the stock collapse in the 1970s (Dragesund *et al.*, 1997). Areas where eggs and larvae accumulate are also valuable, but are more extensive than spawning habitats. However, because of the extensive overlap of eggs and larvae of most species along the coast and at the Tromsøflaket bank area, it is correct to include these in the list of particularly valuable areas. Therefore, it is imperative to understand the total effects of all human activities in these areas and to employ a precautionary approach when managing existing and new human activities.

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