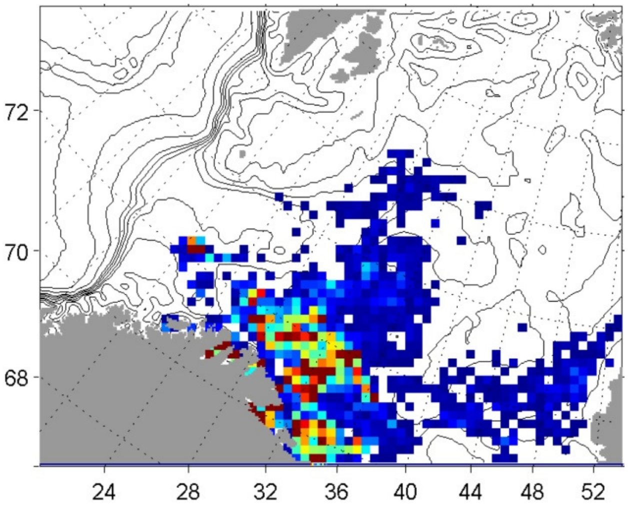
Does juvenile herring (*Clupea harengus*) affect the capelin (*Mallotus villosus*) recruitment in the Barents Sea?

- *A model study for the years 2001 - 2003 focusing on capelin larvae mortality, spawning sites and drift patterns*



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“*Herring is known to reduce the survival of capelin larvae…*” (Gjøsæter 1998)

“…being killed greatly decreases future fitness” (Lima and Dill 1990)

“*…the biomass production of capelin is the driving force behind the obtainable yield of cod, the former being governed by the recruitment and life pattern of the herring*” (Hamre 2003)

‘‘*All models are wrong, but some are useful*’’ (Chatfield 1995)

Abstract

Barents Sea capelin (*Mallotus villosus*) year class strength is thought to be determined during the first months after egg hatching. The now widely accepted Hamre's hypothesis states that young herring (*Clupea harengus*) present in the southern Barents Sea potentially may cause poor capelin recruitment. This hypothesis was presently tested through model scenarios, by simulating a realistic spatio-temporal overlap between young herring and capelin larvae in the Barents Sea during the 2001 - 2003 summer seasons.

Herring totally consumed 10.6 % (2001), 0.06 % (2002) and 25.2 % (2003) of the capelin larvae populations, and up to 2.36 % of the capelin larvae populations were consumed day^{-1}. Hamre's hypothesis is therefore supported. Considering the high capelin larvae abundance in June 2002 and the low herring abundance in the Barents Sea that summer, the capelin 2002 year class became unexpectedly weak. Capelin recruitment is thus probably threatened by other factors than predatory herring as well. Nevertheless, it is presently suggested that predation from herring on capelin larvae strongly contributed to the poor capelin recruitment and abundances in the years 2003 – 2006.

The choice of capelin spawning ground location is highly variable and is presently suggested to be important regarding the capelin recruitment successfulness. Western spawning grounds may lead to prolonged capelin larvae drift periods along the northern coasts of Norway and Russia, where the predatory herring often are abundant. Yet the capelin larvae originating from western spawning areas often become widely dispersed, while the capelin larvae spawned at eastern spawning grounds experience a rapid drift into the eastern Barents Sea. The present study shows that capelin larvae spawned at western locations might be advected northwards, ultimately ending up in the central or north-western Barents Sea.

Survey programs and model studies are characterized by uncertainties and weaknesses. The present study will shed light on such problems and suggest possible enhancements.

Keywords: Capelin larvae, herring, Barents Sea, predation, spawning grounds, drift patterns.

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1 Introduction

The Norwegian spring-spawning herring (*Clupea harengus* Linné) and the Barents Sea capelin (*Mallotus villosus* Müller) are two very important species, both commercially and in relation to the ecosystems where they live (Holst and Slotte 1998; Nakken 1998; Ushakov and Prozorkevich 2002). While the Barents Sea capelin lives in the Barents Sea throughout the lifetime, the herring only uses the Barents Sea as nursing area (Gjøsæter 1995). Both species are plankton feeders, converting energy from low trophic levels into food directly available for larger organisms, including humans (Dragesund *et al.* 1997; Gjøsæter 1998). They are also considered to be key species in the Norwegian Sea - Barents Sea ecosystem (Hamre 2003), and have therefore been studied extensively (Olsen *et al.* 2010, and citations therein). General distribution patterns of the two species are shown in Fig. 1.

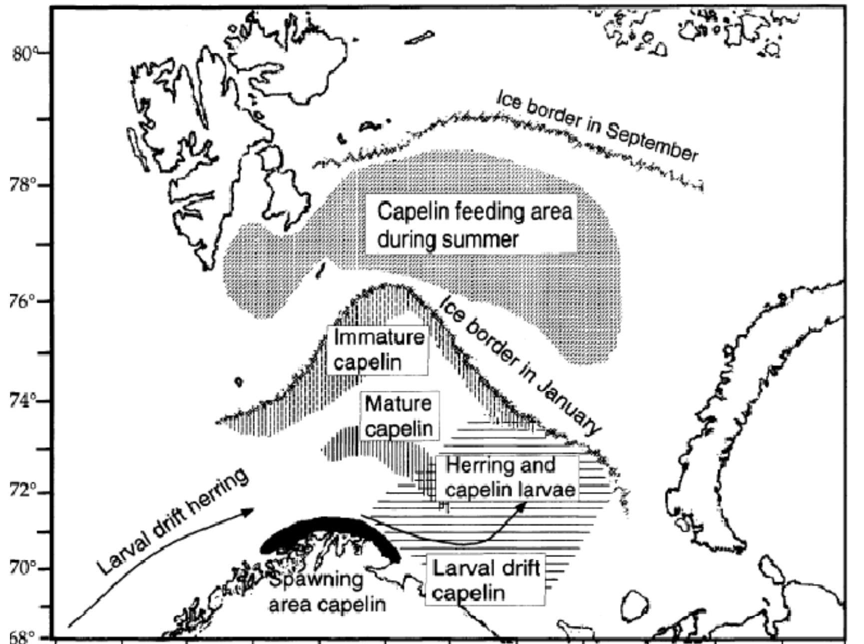

Figure 1: Overview of general capelin and herring distribution patterns in the Barents Sea. The figure was taken from Gjøsæter (1995); the figure is a redrawn version of Fig. 4 in Hamre (1991).

Polar pelagic ecosystems, such as that in the Barents Sea, are consequently unstable; these instabilities are initiated by a highly variable physical environment and continued by large fluctuations in productivity and fish stock sizes (Sakshaug 1997). Thus both the herring and capelin stocks constantly experience very large abundance fluctuations. Yet the Barents Sea has traditionally been important for the fisheries (Sakshaug *et al.* 1992). Harvest due to commercial fisheries may, in addition to natural fluctuations, also have a significant impact on the recruitment of fish stocks (Toresen and Østvedt 2000). Therefore, it seems to be important to develop reliable methods to predict stock recruitment, abundance and possible long-term yields.

The commercially very important Northeast Arctic Cod (*Gadus morhua* Linné) is the most important predator on non-larvae Barents Sea capelin, and the capelin is also the most important prey item for the cod stock in the Barents Sea (Bogstad and Gjøsæter 2001). By feeding on capelin the cod stores energy enabling its long spawning migrations (Marshall *et al.* 1999; Hjermann *et al.* 2004). Capelin larvae are on the other hand preyed upon by young herring (Huse and Toresen 2000). In one of his later papers on this topic, Hamre (2003) stated that the recruitment and life pattern of herring determines the capelin biomass production, which in turn is crucial for the cod yields. Therefore, the knowledge of the survival of the Barents Sea capelin larvae and its link to the herring abundance and distribution in the area should be of the greatest ecological and economical interest.

The Barents Sea capelin, one of several capelin stocks in the northern hemisphere and potentially one of the largest capelin stocks in the world (Gjøsæter 1995), is possibly the most important plankton feeder in the Barents Sea (Hamre 1994). The stock has a total biomass of up to 8 million tons, and up to 3 million tons have been caught by the fisheries annually (Gjøsæter 1995). Although some capelin stocks might spawn several times during a lifetime (i.e. iteroparity), the Barents Sea capelin is commonly considered to be semelparous, where both male and female specimens die subsequently to the first spawning (Christiansen *et al.* 2008). Thus, even though the capelin continues to grow throughout its lifetime, it seldom exceeds a length of 20 cm or a weight of 50 g (Prokhorov 1968). Capelin growth is assumed to be positively correlated to the sea water temperature (Gjøsæter and Loeng 1987), and the growth rate is often faster in the warmer southern and western areas of the Barents Sea compared to the colder areas further north and east (Gjøsæter 1985). Capelin normally undergoes metamorphosis at an age of approximately 12 months (Gjøsæter 1998). Maturation is rather dependent upon length than age (Tjelmeland 1985), and the capelin matures usually by a length of 15 - 19 cm (Gjøsæter and Loeng 1987) or even shorter (Forberg and Tjelmeland 1985).

The Barents Sea capelin stock annually undergoes large feeding and spawning migrations. Generally, the migration patterns of Barents Sea capelin seem to be dependent on the sea water temperature; the distribution areas during the seasons are usually moved further north-easterly in warm years compared to cold ones (Ozhigin and Luka 1985). Capelin eggs are mostly spawned in shallow water (25 - 75 m; Sætre and Gjøsæter 1975) on the northern coasts of Norway and Russia, commonly in March (Gjøsæter 2009). Spawning may fundamentally occur at either eastern or western locations (Ozhigin and Luka 1985), but several common spawning between these two extremes are known (Gjøsæter 1998). The spawners prefer sandy bottom, in which the adhesive eggs are being buried. Depending on temperature, the eggs hatch within 1 - 2 months after spawning, and the larvae (6 - 8 mm length) ascend immediately to the upper water layers (Gjøsæter and Gjøsæter 1986). These newly hatched larvae are probably weakly capable of self-induced movement (Eriksrød and Ådlandsvik 1997), and it is uncertain if they may perform directional movement (Pedersen *et al.* 2009b). They are therefore often considered to be advected passively north- and eastwards along with the ocean currents, which may be quite strong along the North Norwegian coast (Loeng *et al.* 1997).

By late summer, the larvae population (0-group) is usually scattered throughout the central and southern Barents Sea (Anon 2001b, 2002b, 2003). Newly hatched capelin larvae are assumed to prey on small zooplankton organisms commonly found where the larvae are being hatched (Moksness 1982; Fossheim *et al.* 2006). Immature and mature capelin prey on copepods, euphausiids and amphipods, depending on the season and on the length of the specimen (Panasenko 1984). By late autumn (October/November) most capelin aggregate on the southern side of the polar front, where they overwinter near the bottom until February. In February, the maturing component of the capelin stock differentiates from the immature component and initiates the spawning migration southwards towards coastal areas. At the same time as the maturing component of the stock spawns, the immature individuals initiate their spawning migration towards the coast, since the elevated biological spring production is initiated in near-coastal areas (Gjøsæter 1998). As the summer season advances the sea ice melts and retracts north-eastwards towards the North Pole. Now also the capelin migrate north-eastwards, since the zone near the ice edge is characterized by a high biological productivity and thus availability of capelin food (Sakshaug and Skjoldal 1989). By October, before migrating towards the overwintering area south of the polar front, the capelin is distributed throughout the whole northern Barents Sea.

Johannes Hamre pointed out that juvenile herring through predation on capelin larvae possibly may determine the success of the capelin recruitment, presupposed that there is a sufficient spatio-temporal overlap between the two populations (i.e. Hamre's hypothesis; Hamre 1985, 1988, 1991, 1994, 2003; Hamre and Moen 2008). It has been shown that capelin larvae may serve as food for juvenile herring (Huse and Toresen 1995, 2000; Hallfredsson 2006; Hallfredsson and Pedersen 2009), and the Hamre's hypothesis has also been recognized by other authors (e.g. Fossum 1992; Gjøsæter and Bogstad 1998; Hjermann *et al.* 2004; Pedersen *et al.* 2009a). Hamre had several reasons for his hypothesis. First, declines in the capelin recruitment have appeared to occur in years with strong herring year classes, meaning that the larvae possibly were heavily predated upon by herring. Second, the capelin stock had good recruitment in years when the herring abundances were weaker, possibly due to a lower predation pressure.

The Norwegian spring-spawning herring is a small pelagic fish species living in Norwegian waters and spawning during springtime (Holst *et al.* 2004). This stock is potentially the largest herring stock in the world, with a stock size of up to 20 million tons and an annual catch of up to 2 million tons during its most successful periods (Olsen *et al.* 2010). The stock, which is schooling, undergoes large and variable migrations (Dragesund *et al.* 1997). Adult Norwegian spring-spawning herring typically spawn during a period of 50 days along the west coast of Norway in February and March (Sætre *et al.* 2002a; Sætre *et al.* 2002b). Hatching usually occurs during the last half of March (Sætre *et al.* 2002b). The herring eggs and larvae are subsequently carried northwards along the Norwegian coast by the Norwegian Coastal Current (NWCC) (Bjørke and Sætre 1994). A large part of the juvenile herring will ultimately end up in the Barents Sea (Dragesund 1970; Holst and Slotte 1998), where they reside during the first 2 - 4 years of their life cycle (Huse and Toresen 2000).

Several conditions seem to positively correlate with herring year class strength. Sætre *et al.* (2002b) found a coherence between recruitment and the rate of larval retention in spawning areas. They also found that the strength of the wind-induced turbulence during the hatching period strengthened the larvae's capability to survive. The latter observation is supported by the idea that turbulence in the water column increases the encounter rate between the larvae and its food, thereby reducing the larvae's requirement for food density in its vicinity (Rothschild and Osborn 1988; MacKenzie and Kiørboe 1995). Successful herring recruitment also seems to be dependent upon low predation rates from fish and seabirds (Sætre *et al.* 2002a) and a warm climate (Toresen and Østvedt 2000; Hamre 2003). However, good herring recruitment depends primarily upon a large spawning stock; herring year class strength is thought to be proportional to the size of the spawning stock (Hamre 1994). Large numbers of herring appear in the Barents Sea in years with strong inflow of Atlantic Water (Gjøsæter 1995), which in turn depends on a low atmospheric pressure in the Barents Sea region (Ådlandsvik and Loeng 1991).

In the following, the present study has five main objectives:

- First, I attempt to describe the abundances and the spatio-temporal distributions of young herring and larval capelin in the Barents Sea during the summer seasons of 2001 – 2003.
- Second, I will test Hamre's hypothesis through model scenarios, and thus try to determine if the herring could be linked to the 2003 - 2006 collapse in the capelin stock. This will be done by simulating a realistic spatio-temporal overlap between young herring and capelin larvae in the Barents Sea during the three above-mentioned periods. The hypothesis has recently been tested by Pedersen *et al.* (2009a) for the year 2001, but in that study the capelin larvae were exposed to predation from a stationary herring field. In order to increase the realism of the model, I presently exposed the capelin larvae to predation from dynamic herring fields.
- Third, I aim to provide information on recruitment success in relation to the locations of the capelin spawning sites.
- Fourth, I will focus on the capability of the model to transport larvae of coastal origin into the central Barents Sea, and on the general ability of the model to execute such studies.
- Fifth, I will validate the model results with field data, and examine possible ways to enhance future related studies.

2 Material and methods

2.1 General description

The spatio-temporal distributions of the predatory Norwegian spring-spawning herring (*Clupea harengus*) and its prey, the Barents Sea capelin larvae (*Mallotus villosus*) has been simulated for the summer seasons of the years 2001, 2002 and 2003, from the first half of June (when the first mapping of capelin larvae distribution and abundance occur) until the end of September. The simulation end dates were chosen of two main reasons. Firstly, the young herring distribution fields were mapped during surveys in May/June and in September/October. Prolonged simulating times would thus lead to uncertainties considering the herring distributions. Secondly, the distributions fields of the two stocks commonly seem to be very limitedly overlapping by late autumn.

The capelin larvae were assumed to drift passively with the ocean currents. This problem was studied by the use of an Individual Based Model (IBM; Letcher *et al.* 1996), using a high-resolution hydrodynamic model (Fig. 2). Capelin larvae were released in the southern Barents Sea in accordance with the surveyed capelin larvae June distributions in the three years. All the larvae specimens caught during the annual larvae June surveys were simulated independently as super-individuals (Scheffer *et al.* 1995), and they were assumed to represent (i.e. contain) the total estimated number of capelin larvae in the Barents Sea for the three years. The number of the particles contained by each super-particle depended on the capelin larvae density on the survey stations on which the larvae were caught. A constant capelin larvae mortality rate of 1.3 % day^{-1} (Ivarjord *et al.* 2008) was applied, but the effect of other mortality rates has also been considered.

All herring migrations were attempted to be realistically modelled according to information provided in various survey reports and International Council for the Exploration of the Sea (ICES) documents. Surveyed spring and autumn herring distributions were digitized, and the migrations between these surveyed herring fields were assumed to follow a linear spatio-temporal pattern. Any intersection between the distribution fields of young herring and capelin larvae led to a reduction of the capelin larvae abundance by a certain rate depending on the number of herring in the actual area.

The results of the simulations were mainly validated against surveyed capelin 0-group data, both with respect to distribution and abundance. By using catch data and capelin larvae spring distributions as indicators of capelin spawning location, capelin recruitment success has been related to the origin of the larvae. Sensitivity analyses regarding the natural mortality rates of capelin larvae were carried out.

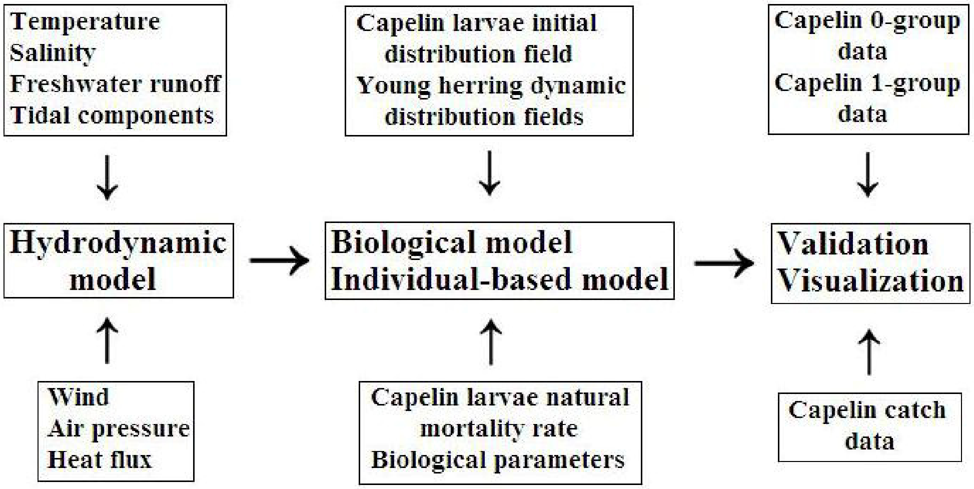

Figure 2: Schematic overview of the main model processes and its input data.

2.2 Study area

The Barents Sea (Fig. 3) is the shallow (average depth 230 meters) shelf sea area that is delimited by Novaya Zemlya as the eastern border and the shelf-break north of Norway as the western border. The northern coasts of Norway and Russia form the southern border of the Barents Sea, while the northern border is defined as the shelf edge of the Arctic Ocean (Sakshaug and Kovacs 2009).

Two main current systems flow northwards along the Norwegian coast and further into the Barents Sea (Furevik 2001): the Norwegian Coastal Current (NWCC) and the Norwegian Atlantic Current (NWAC). The former is found near the coast flowing both northwards along the Norwegian coast and eastwards along the Russian coast; it is renamed to the Murman Coastal

Current (MCC) as it flows into Russian territory. More distant from the coast, the NWAC splits into two branches near 70.5° N latitude. One branch, the West Spitsbergen Current (WSC) continues northwards towards Spitsbergen. The other branch, the North Cape Current (NCC) penetrates the central parts of the Barents Sea (Sætre and Aure 2007). The amount and properties of the inflowing Atlantic Water masses determines the climate in the Barents Sea (Loeng 1991; Loeng *et al.* 1997).

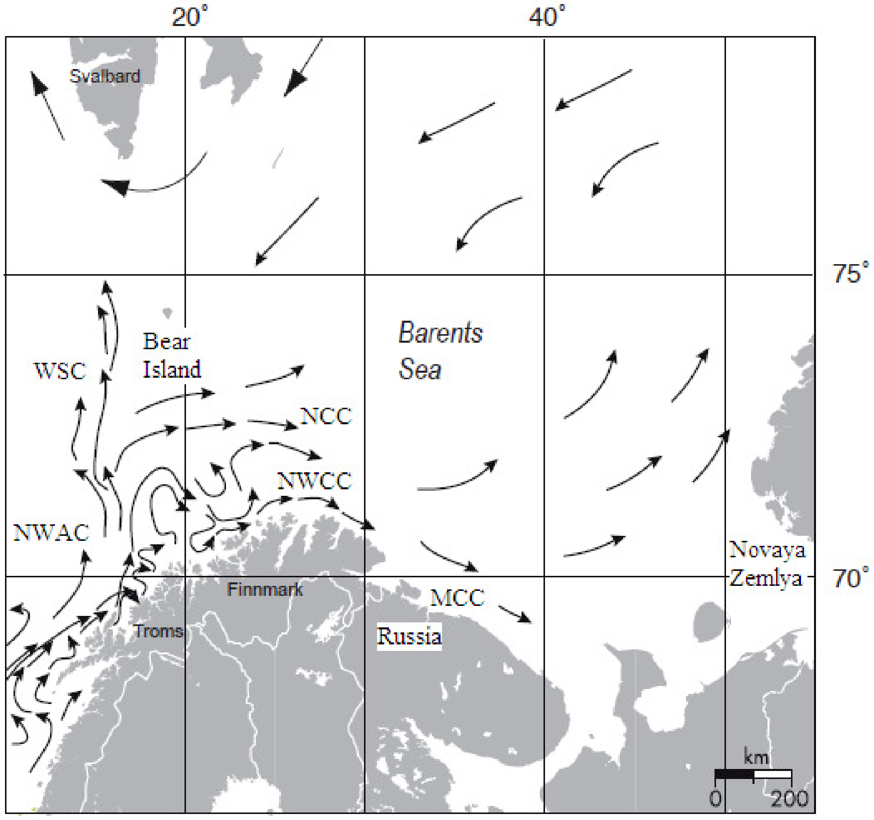

Figure 3: Overview of the Barents Sea with idealized current patterns. All nomenclatures are defined in the text.

2.3 Hydrodynamic and particle-tracking model

The hydrodynamic model (SINMOD) used in the present study was mainly the same as developed and described by Støle-Hansen and Slagstad (1991), Slagstad and Wassmann (1996) and Slagstad and McClimans (2005). Shelf sea dynamics reproduced by SINMOD have previously been validated against field data and proven to be realistic (Skarðhamar and Svendsen

2005). The model is based on the primitive Navier-Stokes equations and solved by a finite difference scheme, thus delivering the Barents Sea current fields which were the driving forces in the present model studies. Temperature and salinity data, which were used as initial values, were taken from NODC World Ocean Atlas 1998 data (Levitus database), provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA (http:/www.cdc.noaa.gov/). Data on wind, air pressure and heat flux were taken from met.no's hindcast database (Reistad and Iden 1998). Forcing from freshwater runoff and four tidal components (M2, S2, K1 and N2) were implemented. In order to save computational cost, the model was nested; it consisted of one large-scale and one small-scale component. The large-scale component had a horizontal grid point distance of 20 km and produced boundary conditions for the small-scale model, which had a horizontal resolution of 4 km. The highest resolution was assigned only to the area of interest, i.e. the Barents Sea areas where the larvae could be distributed. The coupling between the model components was executed by a flow relaxation scheme as described by Martinsen and Engedahl (1987). Vertically, a fixed z-level system was applied, with 25 vertical levels. These vertical levels were in the intervals 0 - 10, 10 - 15, 15 - 20, 20 - 25, 25 - 30, 30 - 35, 35 - 40, 40 - 50, 50 - 75, 75 - 100, 100 - 150, 150 - 200, 200 - 250, 250 - 300, 300 - 400, 400 - 500, 500 - 700, 700 - 1000, 1000 - 1500, 1500 - 2000, 2000 - 2500, 2500 - 3000, 3000 - 3500, 3500 - 4000 and 4000 - 4500 meters of depth.

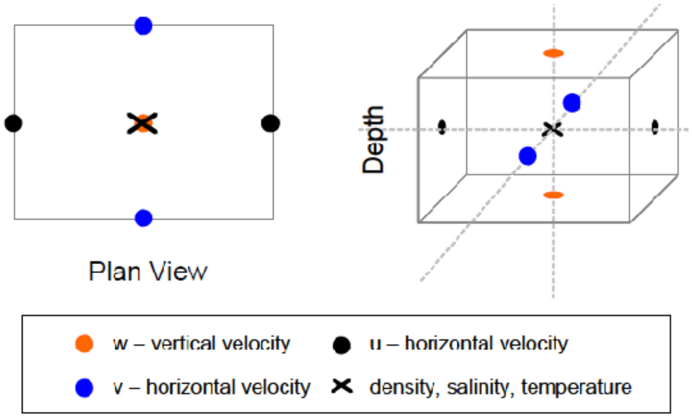

Figure 4: Schematic description of the Arakawa-C grid system. Left: plan view; right: depth view. Water properties are estimated at the locations indicated by the colored symbols, whereas the dashed lines indicate the perspectives. The figure is taken from Lacroix *et al.* (2009).

A structured Arakawa-C grid system was applied (Fig. 4). The surface elevation was thus evaluated between the points where the horizontal u and v current components were calculated; u and v were also calculated in different points. The hydrodynamic model was only run one time, and the resulting physical fields were saved. The current files were further run offline by the particle-tracking model (IBM), and they could thus be used in multiple simulations.

In the particle-tracking model, the super-particles were initially distributed at given positions in the southern Barents Sea determined from the capelin larvae June distributions (Fig. 5). Velocities delivered by the current files were interpolated to the position of the particles, such that the particles were transported to new positions; this was solved using a fourth-order Runge-Kutta routine. The positions, growth and preyed fractions of the larvae were calculated every 20 minutes. The states of the model runs were saved every 24 hours. This particle tracking model tracked all super-particles from the date of release (i.e. the date of cruise sampling) until the end of September. All model runs were carried out in FORTRAN 90. An overview of the 12 simulations presently carried out is shown in Table 1, while all data sources used in the simulations and for validation of the model results are listed in Table 2. All analyses and visualizations were carried out in MATLAB R2007b.

Table 1: Overview of the simulation setups. Main simulations are shown in bold; simulations used in the model sensitivity analysis are written with regular type.

Simulation	Year	Start date	End date	Predation type	Predation start date	Capelin larvae natural mortality rate	Number of simulated super-particles
1	**2001**	**06.06**	**30.09**	**Off**	**-**	**0.013**	**17786**
2	**2001**	**06.06**	**30.09**	**On, dynamic**	**06.06**	**0.013**	**17786**
3	**2002**	**08.06**	**30.09**	**Off**	**-**	**0.013**	**31553**
4	**2002**	**08.06**	**30.09**	**On, dynamic**	**08.06**	**0.013**	**31553**
5	**2003**	**13.06**	**30.09**	**Off**	**-**	**0.013**	**14455**
6	**2003**	**13.06**	**30.09**	**On, dynamic**	**13.06**	**0.013**	**14455**
7	2001	06.06	30.09	On, static	06.06	0.013	17786
8	2001	06.06	30.09	On, dynamic	24.06	0.013	17786
9	2001	06.06	30.09	Off	-	0.005	17786
10	2001	06.06	30.09	Off	-	0.035	17786
11	2001	06.06	30.09	On, dynamic	06.06	0.005	17786
12	2001	06.06	30.09	On, dynamic	06.06	0.035	17786

2.4 Biological model

2.4.1 Capelin larvae: model setups and input data

Only capelin mortality by means of natural mortality and predation from young herring is presently modelled. The 0-group herring was assumed not to consume significant amounts of capelin larvae, as stated by Pedersen and Fossheim (2008). The natural mortality rate of young herring was not taken into account. The rate of predation as a function of the prey density, i.e. the functional response (Solomon 1949; Murdoch 1969) was presently assumed to follow a linear relationship according to Eq.1

$$N_e = 0.256817 \times N_c \qquad \text{(Eq. 1)}$$

where Ne refers the number of capelin larvae eaten by one young herring d^{-1}, and Nc is the number of capelin larvae m^{-2}. Eq. 1 was derived from the formula Ne = Ns x D x 24h (Bajkov 1935; Munk 2002) where Ns (i.e. the number of larvae per herring stomach) was assumed to be 0.0351 Nc (Elvar Hallfredsson pers. comm.) and D is the digestion rate of capelin larvae in herring stomach, estimated to be 0.30 h^{-1} by Hallfredsson *et al.* (2007). This gave the formula (Eq. 2) describing the predation of herring on capelin larvae;

$$N_{pr} = N_h \times N_e \qquad \text{(Eq. 2)}$$

where N_{pr} is the number of capelin larvae preyed upon m^{-2}, and N_h is the average number of herring m^{-2}. The latter parameter varied between the years and during each season according to Table 3. See Section 2.4.2 for explanations on the herring fields.

Capelin larvae growth rate was also implemented in the biological model, and assumed to be 0.25 mm d^{-1}. This rate was estimated by Ivarjord *et al.* (2008) by otolith microstructure analyses, where capelin larvae of known age first had been kept in black, predator-free PVC bags for 35 - 79 days. Due to the absence of comparable autumn field data of cohort length distributions, modelled length compositions were presently not further explored. The hereby general natural mortality rate of 1.3 % day^{-1} was also calculated based on results from the bag studies of Ivarjord *et al.* (2008).

Total capelin larvae abundances and distribution are annually estimated in June by the Institute of Marine Research (Fig. 5). In order to give a visual impression of the capelin larvae distributions the fields (Fig. 5) were interpolated from the discrete field locations using the built-in MATLAB function “griddata”. I had access to the survey data for 2001, 2002 and 2003. All sampling of capelin larvae was carried out with a Gulf III plankton sampler as described by Alvheim (1985), and the abundances were estimated according to the standard method described by Eriksen *et al.* (2006). Each year the estimated capelin larvae abundance is divided by 10^{12} and renamed to the “capelin larvae index”. This index is calculated in the GIS (Geographic Information System) program ArcMap, with a spatial resolution of 1.0 nm^2. The GIS method has lately been introduced, and commonly gives a good correlation (0.991) with the previous method (that was computed in FORTRAN), though the GIS method often results in slightly higher values than the old one. Capelin larvae indices for the years 1981 – 2005 are shown in Appendix E.

The capelin larvae indices used in this study were 12.4 (2001), 24.2 (2002) and 12.1 (2003). Since I have chosen to use GIS-calculated indices throughout my study, the index for 2001 deviates from that used by Pedersen *et al.* (2009a). In general, the larval indices for 2001 and 2002 are probably under-estimates, since research activities were not allowed inside the Russian Exclusive Economic Zone (EEZ) those years (ICES 2004). Thus only capelin larvae in the Norwegian areas are included those years.

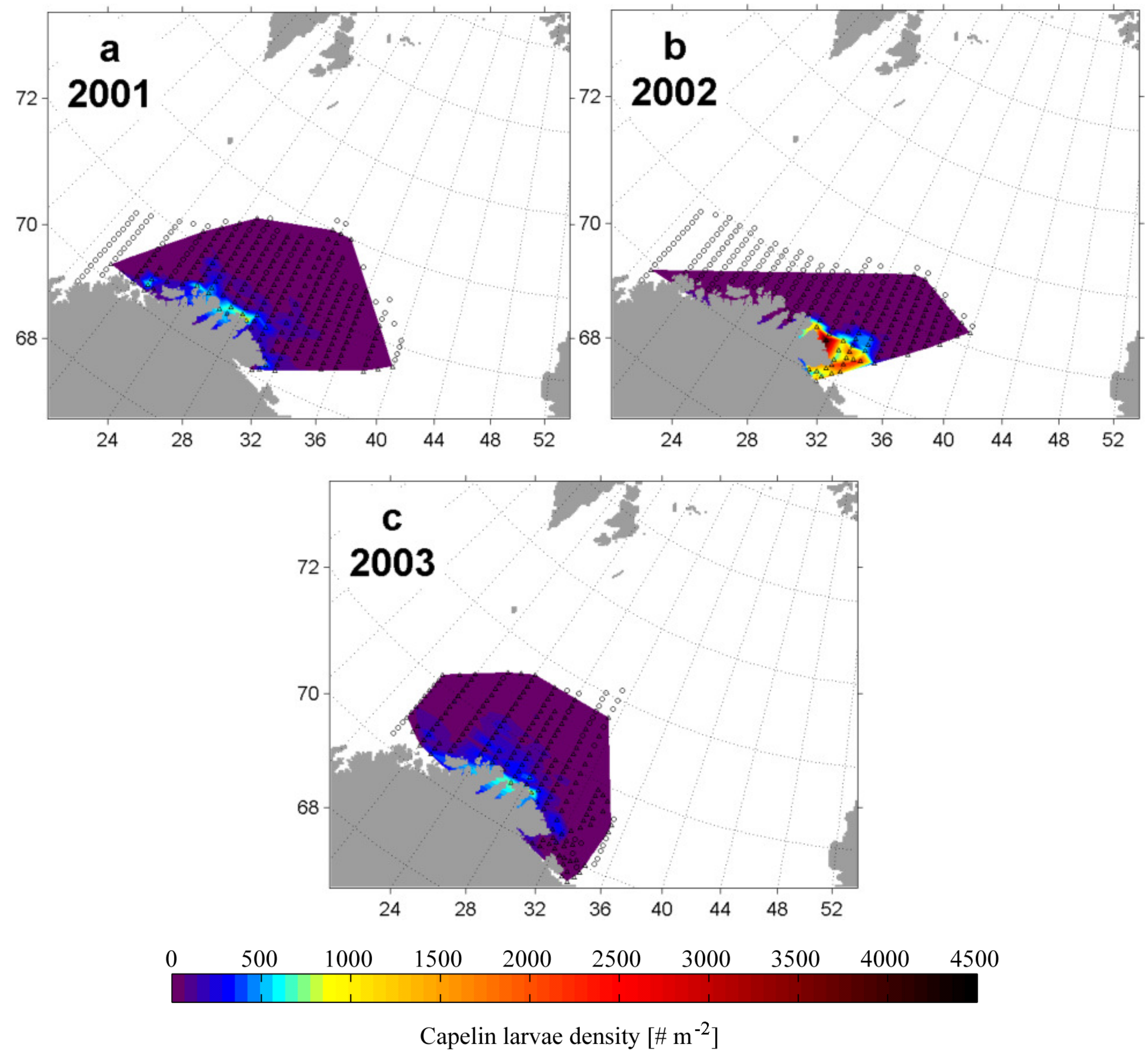

Figure 5: Capelin larvae survey stations and field data in June a) 2001, b) 2002 and c) 2003. The numbers refer to the number of capelin larvae m^{-2}. The figures are based on data sampled by the Institute of Marine Research (2001, 2002, 2003). Black triangles indicate survey stations where capelin larvae were found; black open circles indicate stations were capelin larvae not were found. The density contours illustrate the estimated number of capelin larvae m^{-2}.

Table 2: Overview of the data sources used in the model and in the validation of the modelled results. Immature herring data and capelin larvae data were used as input in the simulations; capelin 0-group and 1-group data were used in the validation of the model. The names mentioned in "Additional notes" refer to the research vessels used. Abbreviations: ICES = International Council for the Exploration of the Sea; IMR = Institute of Marine Research; PINRO = The Polar Research Institute of Marine Fisheries and Oceanography; UiT = University of Tromsø.

Number	Data type	Year	Season	Origin	Additional notes	Source
1	Immature herring	2001	Spring	ICES	Survey with F. Nansen carried out in the Barents Sea 17/5 - 5/6 2001.	ICES (2001)
2	Immature herring	2001	Autumn	IMR/PINRO	Survey with Johan Hjort, G. O. Sars, AtlantNIRO and F. Nansen carried out in the Barents Sea 3/9 - 4/10 2001	Anon (2001a)
3	Immature herring	2002	Spring	ICES	Survey with F. Nansen carried out in the Barents Sea 28/5 - 7/6 2002.	ICES (2002)
4	Immature herring. Capelin 0-group. Capelin 1-group	2002	Autumn	IMR/PINRO	Survey with Johan Hjort, G. O. Sars, M. Sars, AtlantNIRO and F. Nansen carried out 6/9 - 6/10 2002.	Anon (2002a)
5	Immature herring*	2003	Spring	ICES	Survey with G. O. Sars carried out in the Norwegian Sea north of 70 °N from the Norwegian coast to the Spitsbergen area, between 4-20°E.	ICES (2003)
6	Immature herring	2003	Spring	UiT	Survey with Jan Mayen carried out in the Barents Sea from 23/6 - 7/7 2003.	Hallfredsson and Pedersen (2009); Torstein Pedersen pers. comm.
7	Immature herring. Capelin 0-group. Capelin 1-group	2003	Autumn	IMR/PINRO	Survey with Johan Hjort, G. O. Sars, Jan Mayen, Tsivilsk and Smolensk carried out in the Barents Sea and in the western part of the Norwegian Sea 27/7 - 2/10 2003.	Anon (2003)
8	Capelin larvae	2001	Spring	IMR	Survey with Michael Sars carried out in the Barents Sea 4/6 - 25/6 2001.	IMR (2001)
9	Capelin 0-group	2001	Autumn	IMR/PINRO	Survey with G. O. Sars, Johan Hjort, AtlantNIRO and Fridjof Nansen carried out in the Barents Sea and adjacent waters 10/8 - 8/9 2001.	Anon (2001b)
10	Capelin larvae	2002	Spring	IMR	Survey with Michael Sars carried out in the Barents Sea 7/6 - 6/7 2002.	IMR (2002)
11	Capelin 0-group	2002	Autumn	IMR/PINRO	Survey with G. O. Sars, Johan Hjort, AtlantNIRO and Fridjof Nansen carried out in the Barents Sea and adjacent waters 10/8 - 8/9 2002.	Anon (2002b)
12	Capelin larvae	2003	Spring	IMR	Survey with G. O. Sars carried out in the Barents Sea 10/6 - 27/7 2003.	IMR (2003)
13	Capelin 1-group	2004	Autumn	IMR/PINRO	Survey with Johan Hjort, Jan Mayen, Smolensk and F. Nansen carried out in the Barents Sea 1/8 - 4/10 2004.	Anon (2004)

*) No spring survey conducted in Russian Exclusive Economic Zone in 2003. The report yet documents a component of 1-group (2002 year class) Norwegian spring-spawning herring overwintering in the Norwegian Sea.

2.4.2 Young herring input data and migrations

Young herring concentrations as well as horizontal and vertical distributions were mapped by the Institute of Marine Research during spring cruises (2001 - 2002) and autumn cruises (2001 - 2003). The immature herring spring 2003 distribution was mapped by the University of Tromsø (Hallfredsson and Pedersen 2009; Torstein Pedersen pers. comm.), but the total herring spring 2003 abundance was not determined (ICES 2003). Therefore the herring abundance was assumed to equal the herring autumn 2003 abundance throughout the 2003 summer season. The mapping was carried out acoustically with echo sounders, and the back-scattering strengths (S_A values) of the herring were recorded. Anon (2001a, b, 2002a, b, 2003) and Hallfredsson and Pedersen (2009) give detailed equipment descriptions. Target strength (TS; Foote 1987) was used in order to convert the echo intensities into a certain number of fish. The herring TS relationship (Eq. 3) is expressed in decibel (dB) as

$$TS = 10 \times \log \left(\frac{\sigma}{4\pi}\right) = 20.0 \times \log L - 71.9 \tag{Eq.3}$$

where L is the length of the fish (in centimeters); σ is the backscattering cross section, corresponding to $8.1 \times 10^{-7} \times L^{2.00}$.

Table 3: Herring 0-group indices (2000 – 2003) and immature herring age compositions for the years 2001-2003. The numbers (age 1-3) refer to billion individuals; herring 0-group indices are non-denominated. The data were obtained from Anon (2001b, 2002b, 2003).

Year	**2000**	**2001**		**2002**		**2003**	
Season	**Autumn**	**Spring**	**Autumn**	**Spring**	**Autumn**	**Spring**	**Autumn**
Age 0 (indices)	0.30		0.13		0.53		0.51
Age 1		0.302	0.5	0.538	0		99.8
Age 2		7.643	10.5	3.935	0		4.3
Age 3		8.767	1.7	0	0		2.5
Sum (age 1-3)		16.7	12.7	4.473	0	106.6*	106.6

*) Assumed that the young herring abundance was similar in spring as in autumn 2003.

Only herring of age 1 - 3 years (2001 - 2003) were assumed to prey on capelin larvae. Age 0 herring (0-group, 2000 - 2003), which are estimated by trawl hauls, were included in order to validate the strength of immature herring abundance in the subsequent years (Table 3). The data were obtained from Anon (2001b, 2002b, 2003).

Table 4: Young herring input data. Interpolated herring fields are shown in italics.

Year	Parameter	Period 1	Period 2	Period 3	Period 4
2001	Dates	06.06-30.06	*01.07-31.07*	*01.08-30-08*	01.09-30.09
	Size of distribution area [10^9 m^2]	50.8	*131.2*	*211.6*	292
	Number of young herring [10^9]	16.700	*15.4*	*14.1*	12.8
	Number of young herring m^{-2}	0.3287	*0.1174*	*0.0666*	0.0438
	Figure number	**3a**	***3b***	***3c***	**3d**
2002	Dates	08.06-20.06	*20.06-30.06*	*01.07-31.07*	01.08-30.09
	Size of distribution area [10^9 m^2]	196.0	*115.3**	*22.1**	0
	Number of young herring [10^9]	4.473	*6.087*	*7.700*	0
	Number of young herring m^{-2}	0.023	*0.053*	*0.349*	0
	Figure number	**4a**	***4b***	***4c***	**4d**
2003	Dates	13.06-14.07	*15.07-01.08*	01.08-30.09	
	Size of distribution area [10^9 m^2]	56.6	*152.4*	249.2	
	Number of young herring [10^9]	106.700	*106.700*	106.700	
	Number of young herring m^{-2}	1.887	*0.700*	0.428	
	Figure number	**5a**	***5b***	**5c**	

*) A certain proportion of the herring field was extended into the Norwegian Sea (ICES 2002), but it is hereby assumed that all the herring were within the defined area used in the model.

The fields (areas) in which the herring predation were modelled (Figs. 6 - 8) were based on survey-estimated abundances and distribution fields (Table 2). For a given period, the number of herring in the Barents Sea was divided by the size of the distribution area, giving a certain number of herring m^{-2}. The herring were moreover assumed to be evenly distributed within each defined herring field throughout each period, i.e. the number of herring m^{-2} was similar for the whole area until there was a shift in the predation pattern according to Table 4. Start and final herring distribution fields (Figures 6a, 6d, 7a, 7c, 7d, 8a and 8c) are digitized fields based on the estimated density distribution maps of young herring (S_A values). The other fields (Figures 6b, 6c, 7b and 8b) were linearly interpolated between the known fields, both in x and y direction and with respect to abundance. The spring 2003 herring distribution (Fig. 8a) was not mapped further east than 33° E (Hallfredsson and Pedersen 2009). As indicated by their data, the herring distribution had probably an even more easterly extension, introducing a potentially large uncertainty in the input data used in the present study.

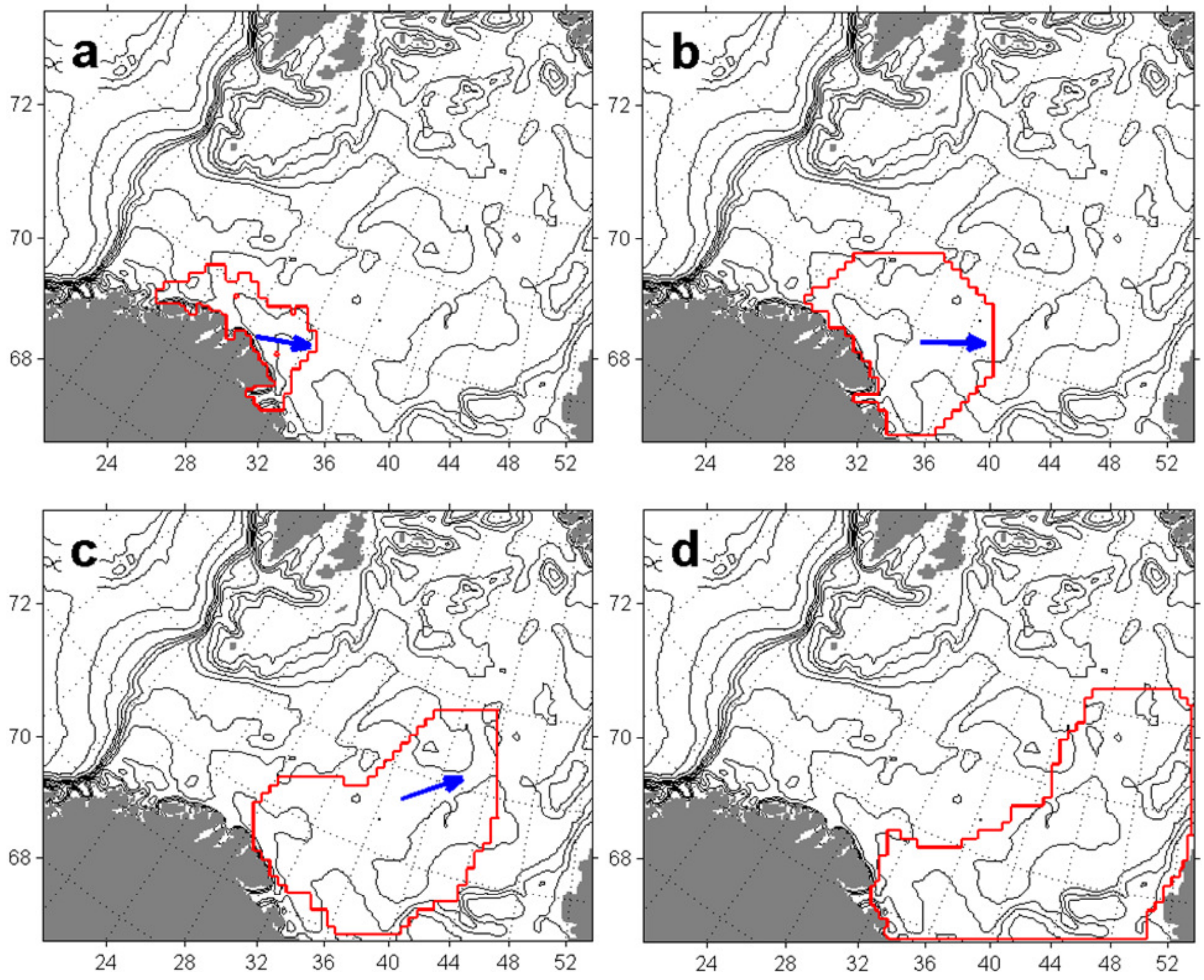

Figure 6: Assumed herring migrations during summer and autumn 2001 according to Table 4. Blue arrows indicate the assumed direction of herring field movement. a) Period 1. Immature herring field in the Barents Sea in June, based on ICES (2001). b) Period 2. Assumed immature herring field in the Barents Sea in July. The field is interpolated between the June field (ICES 2001) and September field (Anon 2001a). c) Period 3. Assumed immature herring field in the Barents Sea in August. The field is interpolated between the June field (ICES 2001) and September field (Anon 2001a). d) Period 4. Immature herring field in the Barents Sea in September, based on Anon (2001a).

Since herring are good swimmers (Huse and Ona 1996), ocean currents were not taken into account in the interpolation of the assumed herring fields. Immature herring natural mortality was not especially taken into account in the model, but eventual shifts in herring abundances during the seasons were reflected by the autumn survey acoustic estimates.

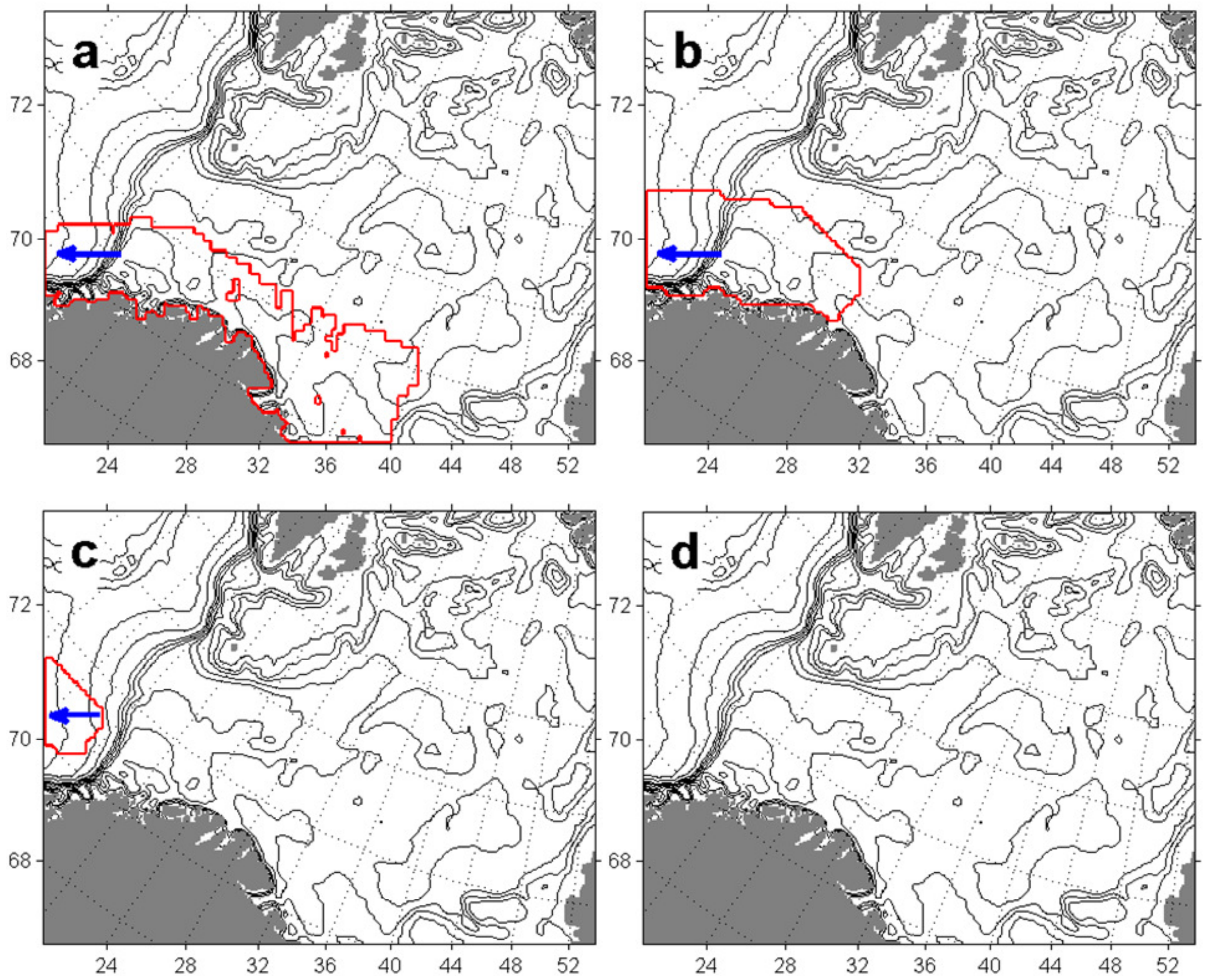

Figure 7: Assumed herring migrations during summer and autumn 2002 according to Table 4. Blue arrows indicate the assumed direction of herring field movement. a**)** Period 1. Immature herring field in the Barents Sea in early June, based on ICES (2002). b**)** Period 2. Assumed immature herring field in the Barents Sea in late June. The field is interpolated between the early June field (ICES 2002) and the September field (Anon 2002a). c**)** Period 3. Assumed immature herring field in the Barents Sea in July. The field is interpolated between the early June field (ICES 2002) and the September field (Anon 2002a). d**)** Period 4. Immature herring field in the Barents Sea in September, based on Anon (2002a); there were apparently no herring in the Barents Sea in the latter period.

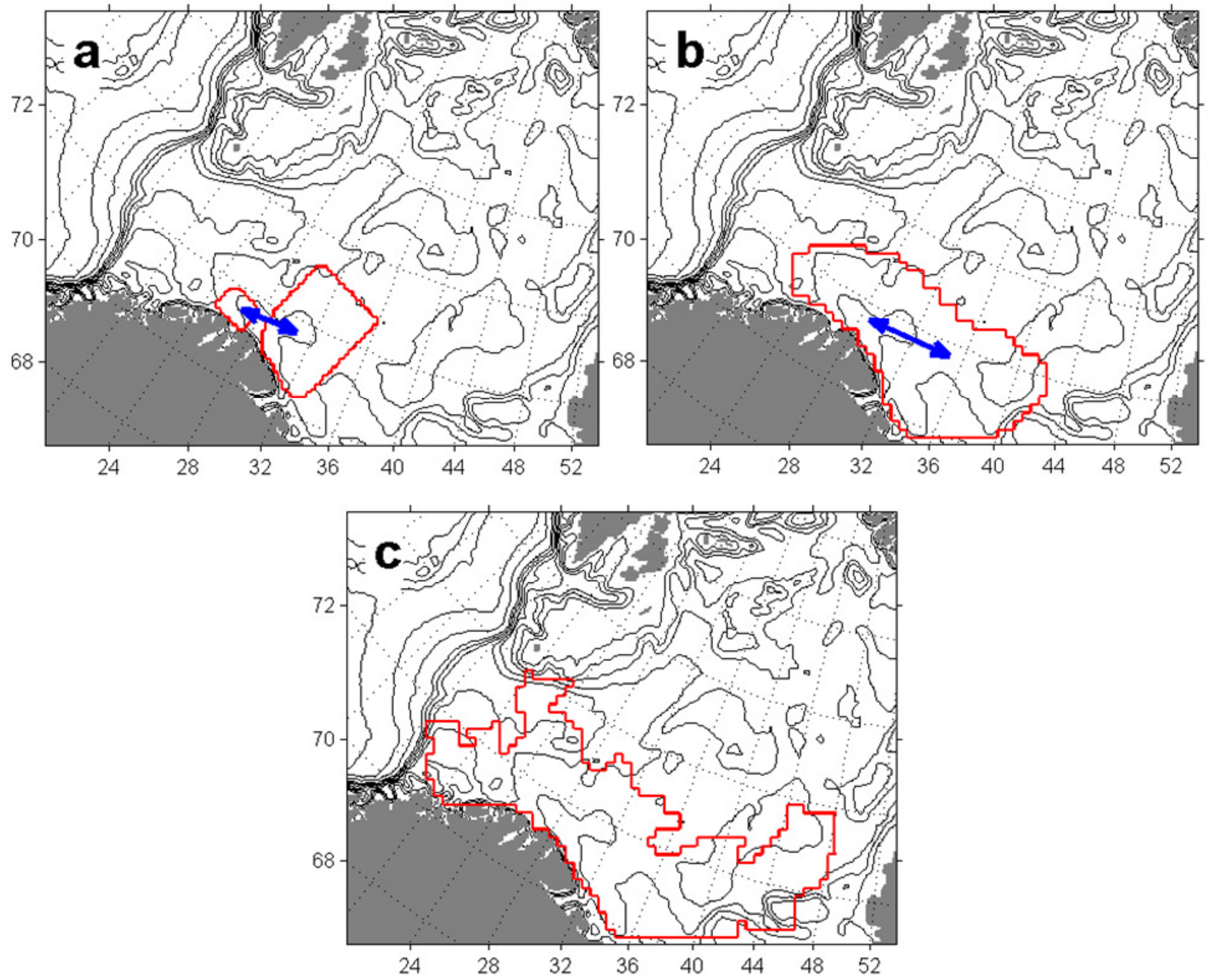

Figure 8: Assumed herring migrations during summer and autumn 2003 according to Table 4. Blue arrows indicate the assumed direction of herring field movement. a**)** Period 1. Immature herring field in the Barents Sea in late June/early July, based on Hallfredsson and Pedersen (2009). b**)** Period 2. Assumed immature herring field in the Barents Sea in late July. The field is interpolated between the late June/early July field (Hallfredsson and Pedersen 2009) and the August/September field (Anon 2003). c**)** Period 3. Immature herring field in the Barents Sea in August and September, based on Anon (2003).

2.5 Sensitivity analysis

The year 2001 was used as a case in the sensitivity analysis. Model runs were carried out with different combinations of predation and natural mortality in order to test the strength of these parameters (Table 1). A capelin larvae natural mortality rate of 1.3 % day^{-1} was used in the main simulations (Table 1; simulations 1 - 6). In the simulations 2, 4 and 6, the capelins were also exposed to herring predation (according to Figs. 6 – 8 and Table 4) throughout the simulation period. In the simulations 1, 3 and 5, the capelins were not exposed to any predation; all mortality was thus natural. Simulation 7 was based on a scenario very similar to that carried out by Pedersen *et al.* (2009a) in their "Scenario 1", where the herring were assumed to follow a static pattern regarding both abundance and size and position of the distribution area. The June herring field was thus applied throughout simulation 7. Simulation 8 was equal to simulation 2, only the herring predation was initiated after the June survey was completed, i.e. June 24 (predation was going on during the survey periods in simulation 2, 4 and 6). Simulations 9 and 11 were carried out with a lowered natural mortality rate (0.5 % day^{-1}), and with predation from herring switched off and on, respectively. This pattern was repeated in simulation 10 and 12, but here an elevated natural mortality rate of 3.5 % day^{-1} was used.

2.6 Validation

Validation of model results to field data was carried out in order to confirm the reliability of the model. The validation was mainly accomplished between modelled autumn data and autumn-surveyed capelin larvae data (i.e. 0-group capelin data). The capelin 0-group data were obtained from Elena Eriksen at the Institute of Marine Research. The 2001 and 2003 data were normalized with respect to trawling distance and the number of trawling depths according to Anon (2005). This method is newly introduced, and it is supposed to correspond better with actual abundances compared to the "old" method. The trawling distances were recalculated based on data of speed and trawling duration. Since the latter data were sparse for 2002, the "standard trawling distances" were used. The start positions for each trawl haul were used as station positions.

Capelin catch data were used as indications of where the capelin spawning had taken place. Catch data from the winter fishery on the North Norwegian coast in 2002 and 2003 were obtained from Roald Oen at Norges Sildesalgslag. Catch data for 2001 were not available. Only capelin catch data from March (2002 – 2003) were used, since most of the fishery activities were carried out that month. Some capelins were also caught both earlier and later than in March, but these were thus not taken into account. The catch data consisted of total catch weight in standard sections along the coast. The data were plotted approximately in the middle of each section (Fig.

13). I assumed that the capelin spawned nearby the catch areas. Moreover, I assumed the spawning to occur in near-coastal waters. Capelins that were caught far from the coast were thereby supposed either to be immature or to be on their way to the spawning site near the coast. In order to relate capelin spawning locations to the sea water temperature, temperature data from the Russian Kola section (70.5 – 72.5° N; 33.5° E) were obtained from the Polar Research Institute of Marine Fisheries and Oceanography (PINRO). Temperature average values and anomalies were freely available at the PINRO webpage (http://www.pinro.ru/labs/indexhid_e.htm?top=hid/kolsec1_e.htm); temperature anomalies (0 - 200 m) for the stations 3 – 7 were used.

In order to compare the modelled number of capelin larvae in the end of September (2001 - 2003) with field data, they were plotted against capelin larvae indices (spring; Institute of Marine Research 2001, 2002, 2003), 0-group indices (autumn; Anon 2001b, 2002b, 2003) and 1-group abundances (the subsequent autumn; Anon 2002a, 2003, 2004).

2.7 Statistical methods

Linear regressions between simulated capelin larvae abundances and 0-group data (see section 2.6) were carried out by the method used by Pedersen *et al.* (2009a). The model domain was divided into square bins of 100 x 100 km, constituting totally 154 bins. Modelled and surveyed data were assigned to bins in accordance to the spatial positions of the organisms. Each bin thereby contained one data pair reflecting simulated and observed abundances. The linear regressions between the data pairs revealed the ability of the model to reproduce documented field distributions through different scenarios.

The modelled and surveyed 0-group capelin distributions were also compared isolated (not including abundance data) by two measures: Jaccard's coefficient (Jaccard 1901; cited in Jackson *et al.* 1989) and Russell/Rao Index (Rao 1948). Both these measures were easily explained by Finch (2005) and Jackson *et al.* (1989), though with some expression differences; I have chosen to use the expressions described by Jackson *et al.* (1989). In both methods, the distribution data were considered as being dichotomous, i.e. the data in each of the 154 bins were assigned the value of either 1 (presence of capelin larvae) or 0 (absence of larvae). For two data rows (modelled and surveyed data), this gives four possible value combinations (Table 5). The variable referred to as a is the number of bins where co-occurrence was evident (i.e. an area in which capelin larvae were found both in modelled and surveyed data), while the d variable refers to bins where co-absence occurred. Variable b refers to the number of bins where larvae where found in the surveyed data but not in the modelled data, and variable c refers to the situation opposite to b. Since these two measures only take distributions into account, the resulting estimates will be constant for all simulations within each year. A perfect fit between modelled and survey data would, for both calculation methods, give a value of 1. No fit would give a value of 0. Obviously, these methods cannot provide statistical information on the model successfulness, but they may give a reasonably good indication of how the actual distribution of organisms could be reproduced by the model.

Table 5: Possible value combinations for dichotomous distribution data. Bins containing larvae were assigned the value of 1; bins not containing larvae were assigned the value of 0. See text for explanations on the variables *a – d*.

Modelled data	Surveyed data	
	1	0
1	*a*	*b*
0	*c*	*d*

The Russell/Rao Index (Eq. 4) has the advantage that it takes into account bins were co-absence of larvae were evident (*d*). This procedure entails however that the areas covered with land were included in the calculations.

$$\text{Russel/Rao Index} = \frac{a}{a+b+c+d} \qquad \text{Eq. 4}$$

To remove possible problems introduced when including bins of co-absence, the Jaccard's coefficient was computed due to Eq. 5. This coefficient excludes all cases where neither of the bins contained larvae, such as the bins which are partly or fully covered by land.

$$\text{Jaccard's coefficient} = \frac{a}{a+b+c} \qquad \text{Eq. 5}$$

3 Results

3.1 Capelin larvae abundance and mortality

Comparison between simulated preyed and non-preyed capelin larvae are shown in Figs. 9 - 11. To make the figures easier to interpret, the capelin larvae were nested into 20 x 20 km squares. Similar color scale for all figures (9 – 11) makes comparison of abundance possible, but an obvious disadvantage is that the actual values of the squares exceed the color scale values. One of the most extreme examples of high abundances compared to the color scale was found in Fig. 10 (July 2002), where some red colored squares were estimated to contain more than 1000 billion individuals (maximum 1.4×10^{12} individuals). On the other hand, some blue colored areas in Fig. 11d (September 2003) only contained considerably less than 100.000 individuals per nested square (minimum 10600 individuals).

Among the three years studied, the 2001 simulations resulted in the most dispersed capelin September distributions. At September 25 2001, the northernmost capelin larvae were found at 76.4° N/36.5° E, while the easternmost larvae were found at 74.2° N/52.9° E. By the same date in 2002, the northernmost and easternmost capelin larvae were found at 74.3° N/44.7° E and 71.7° N/49.4° E, respectively. Finally, by September 25 2003 the northernmost larvae were found at 76.3° N/30.1° E, while the easternmost larvae were found at 71.1° N/43.8° E.

Some particles were about to be advected outside the model domain. Since they could not cross the model domain boundaries, these particles ultimately ended up within 5 gridpoints from one of the boundaries (usually the southern boundary). This was not a big problem in 2001 (only 3 % of the super-particles where within the 5-gridpoint area), but it was more serious in 2002 (45 %) and 2003 (16 %).

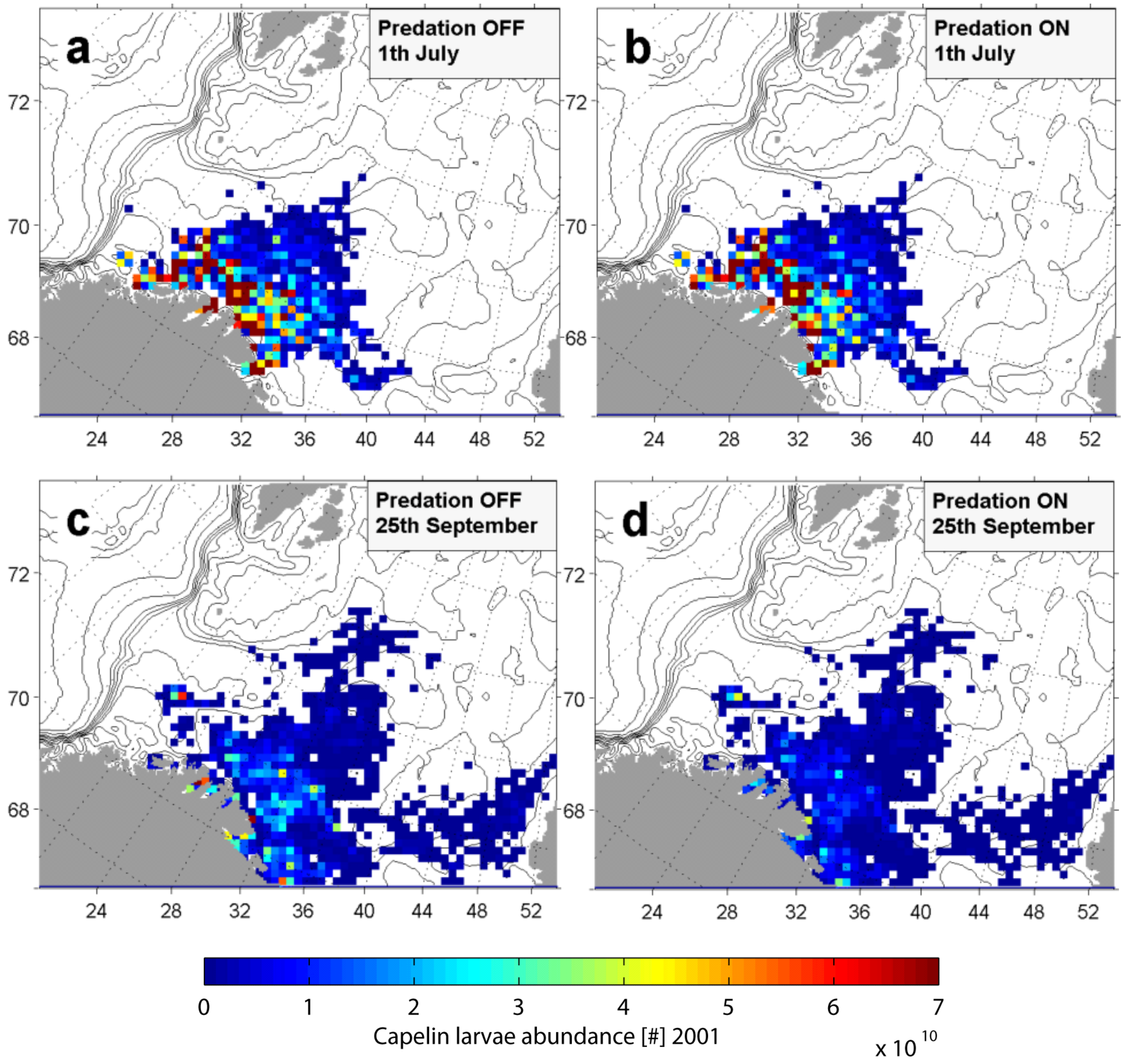

Figure 9: Simulated capelin larvae abundance in the Barents Sea at July 1 (a, b) and September 25 (c, d) 2001. Left figures (a, c) show non-preyed capelin larvae (simulation 1); right figures (b, d) show preyed capelin larvae (simulation 2). The numbers refer to the abundance in each nested grid area.

The 2001 and 2003 distributions showed basically the same pattern, but the 2001 distribution was even more widespread throughout the season. Fjords did to a larger degree contain larvae in September 2001 and 2003 compared to the July situations in the same years. A larger proportion of the larvae seemed to be retained in near-coastal areas in 2001 and 2003 compared to 2002. The only year when any particles were advected north-west of Bear Island during the simulation period was 2003.

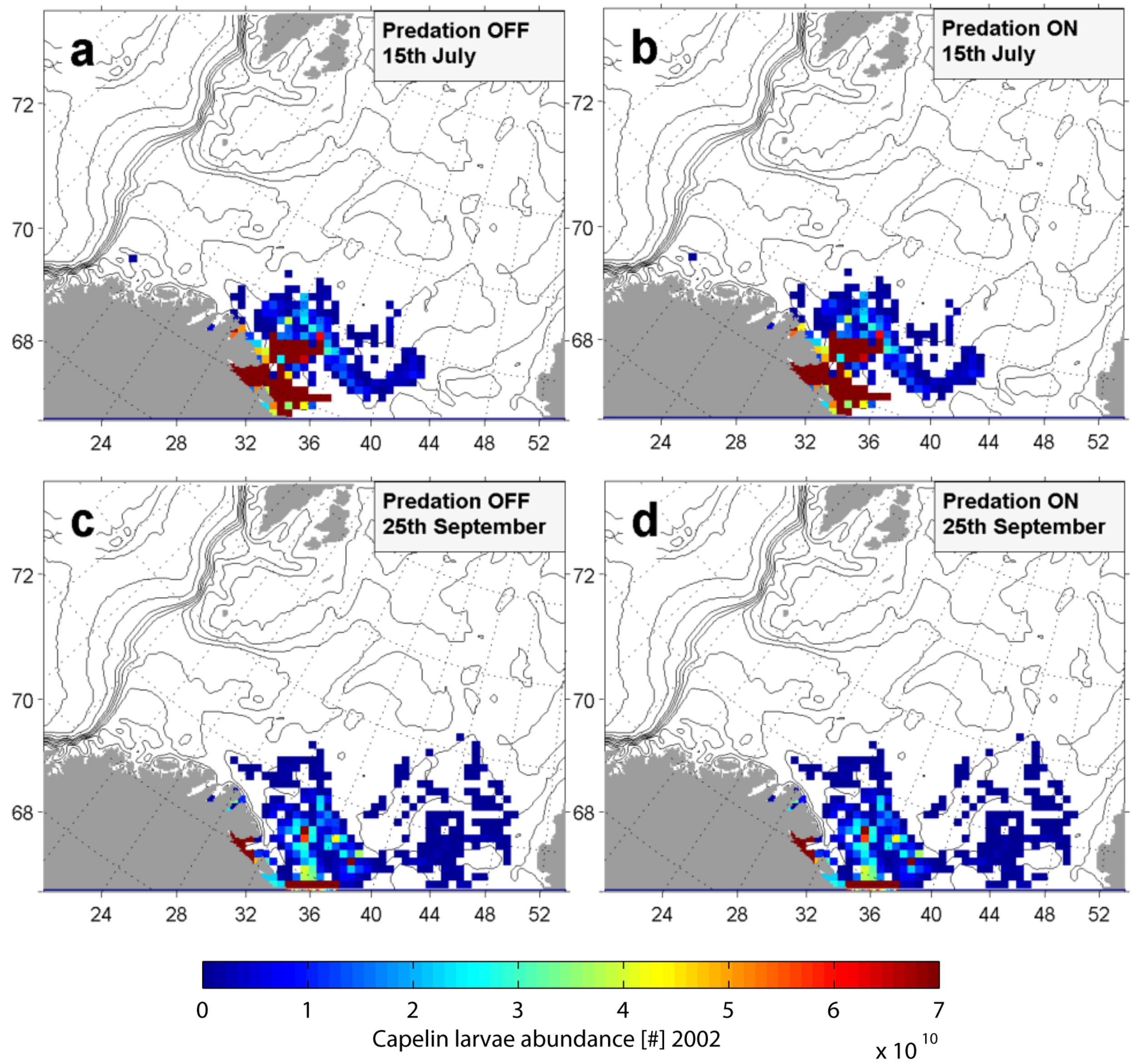

Figure 10: Simulated capelin larvae abundance in the Barents Sea at July 15 (a, b) and September 25 (c, d) 2002. Left figures (a, c) show non-preyed capelin larvae (simulation 3); right figures (b, d) show preyed capelin larvae (simulation 4). The numbers refer to the abundance in each nested grid area.

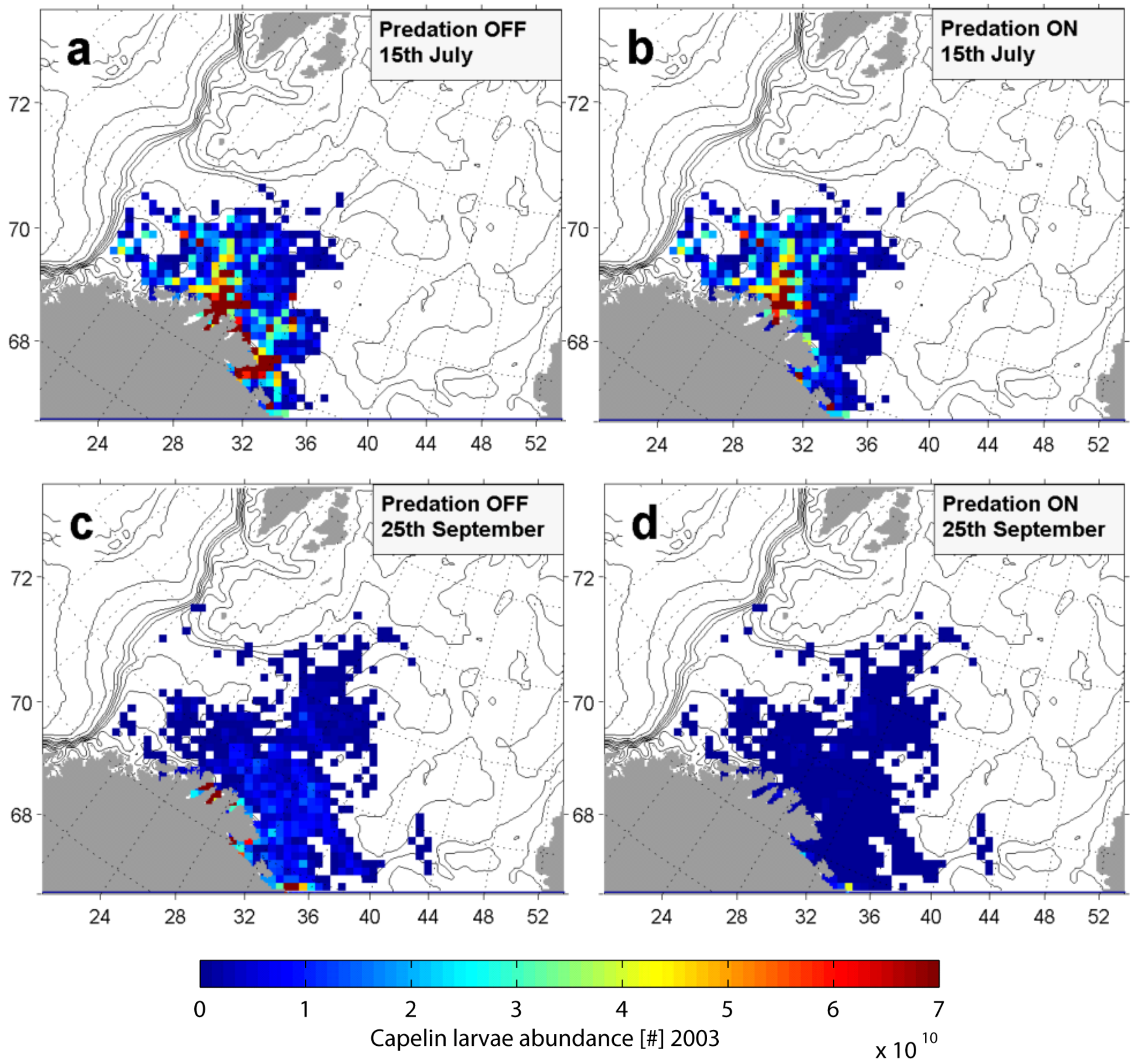

Figure 11: Simulated capelin larvae abundance in the Barents Sea at July 15 (a, b) and September 25 (c, d) 2003. Left figures (a, c) show non-preyed capelin larvae (simulation 5); right figures (b, d) show preyed capelin larvae (simulation 6). The numbers refer to the abundance in each nested grid area.

Simulated capelin survivorships of preyed and non-preyed capelin larvae were compared for the main scenarios (1 - 6), under the assumption of a constant natural mortality rate of 1.3 % day^{-1} (Fig. 12). Capelin larvae mortality was in addition influenced by the spatial and temporal overlap with young herring. Accordingly, the mortality rates of preyed capelin larvae varied considerably between the three years 2001 - 2003. When excluding the effect of natural mortality, the maximum daily mortalities constituted 0.86 % (2001), 0.0064 % (2002) and 2.36 % (2003) of the entire capelin larvae population.

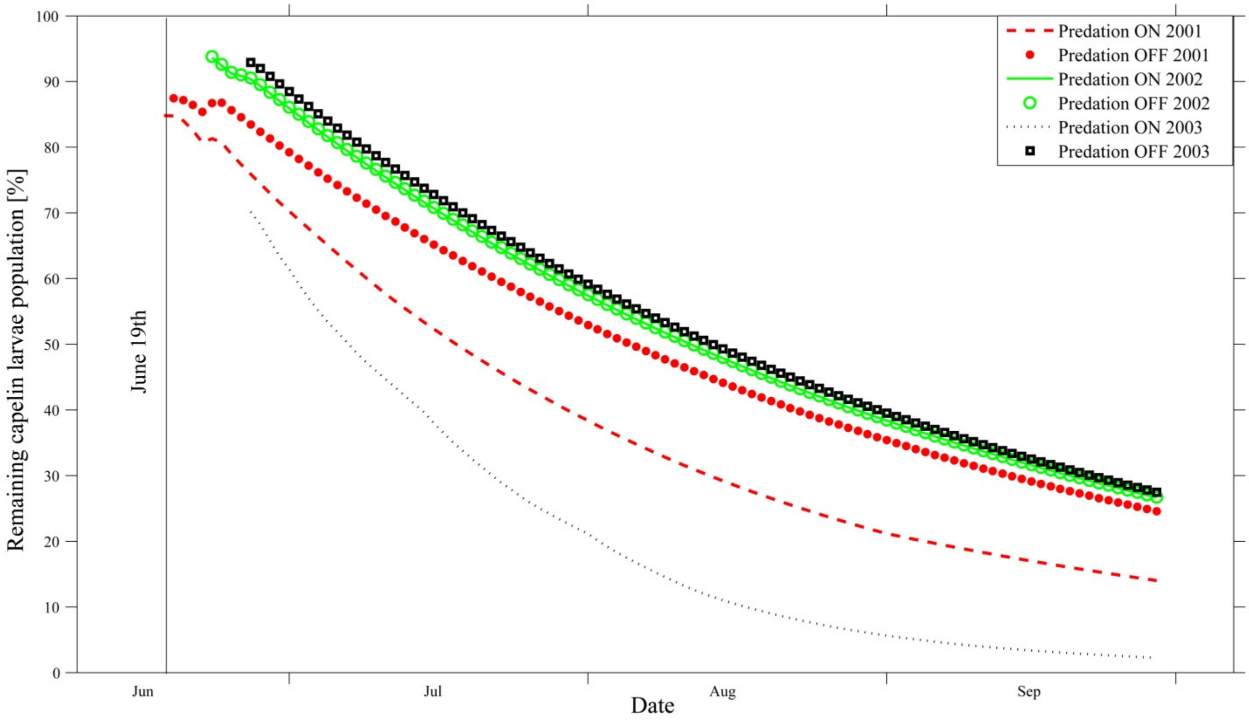

Figure 12: Simulated capelin larvae survivorships in 2001 (red), 2002 (green) and 2003 (black). "Predation ON" curves represent capelin larvae being exposed to predation from a dynamic herring field. "Predation OFF" curves represent capelin larvae not being exposed to any predation, i.e. a capelin larvae natural mortality rate of 1.3% day^{-1}. The curves start by the date of maximum abundance: June 19 (2001), June 23 (2002) and June 27 (2003). Note that the 2002 curves nearly overlap. See legend for symbol explanations.

The initial capelin larvae data were sampled during cruises of 2 - 3 weeks duration. In the subsequent computer simulation, a certain number of capelin larvae would die (either naturally or through herring predation) during the cruise period. The start value (by the date of maximum abundance) of any curve in Fig. 12 could therefore never be as high as 100 % of total larval population size. This aspect is particularly reflected by the "Predation ON 2003" curve, where the larvae suffered a very high mortality during the cruise period; in that scenario. The maximum abundance was never greater than 70 % of the total estimated abundance during the 2003 season. When predation was removed ("Predation OFF 2003"), the maximum abundance increased to more than 90 %. The 2002 curves, on the other hand, where the capelin larvae population was large and the predation pressure was low, showed a maximum abundance of 95 % of the total estimated abundance during that season. Even though the end values of the 2001 curves (Predation ON/OFF 2001) markedly differed, their abundances nearly equaled by June 19 (approximately 12 days after start of the survey). By the end of September, a natural mortality rate of 1.3 % had removed 75.4 % (2001), 73.3 % (2002) and 72.5 % (2003) of the larvae populations. When including predation from herring according to Figs. 6 - 8 and Table 4, 86.0 % (2001), 73.3 % (2002) and 97.8 % (2003) of the capelin larvae were removed. In other words, the herring consumed 10.6 % (2001), 0.06 % (2002) and 25.2 % (2003) of the capelin larvae populations.

3.2 Consequences of capelin larvae origin, in relation to predation

Capelin catch data from March 2002 – 2003 were used as indications of where the spawning took place those years (Fig. 13). Most of the capelin catches in 2002 were carried out in the vicinity of Varanger Peninsula in eastern Finnmark (70 – 71° N; 28 – 31.5° E). Thus the spawning in 2002 probably occurred between 26 – 36° E in the southern Barents Sea. The spawning in 2003 probably occurred mostly between 16 - 22° E along the western North Norwegian coast. A small proportion of the 2003 fisheries were carried out outside the map domain, indicating an even more westerly spawning pattern. Considering the accessible capelin larvae June distribution in 2001 (Fig. 5), one might assume that a widely distributed spawning occurred that year; it was probably carried out along most of the Norwegian coast and possibly also further south-eastwards along the northern coast of Russia.

The locations of the capelin spawning has been related to the mean sea water temperature in the Kola section in the 0 – 200 m depth range (Ozhigin and Luka 1985). Ozhigin and Luka suggested that in years with temperatures of 0.3° C above the long-term average temperature, an easterly spawning pattern was expected. A westerly spawning was expected in years with a mean temperature of 0.3° C below the long-term average. Relative to the long-term mean (3.92° C; 1971 – 2000), the temperature anomalies 2001 – 2003 were 0.56, 0.50 and 0.23, respectively. Spawning-at-location strictly according to this rule of thumb was thus apparently only recognized in 2002, since the spawning seemed to be carried out only at relatively eastern locations that year. Some of the spawning in 2001 also seemed to occur in eastern areas. A very positive temperature anomaly could thus also to some degree explain the spawning pattern that year.

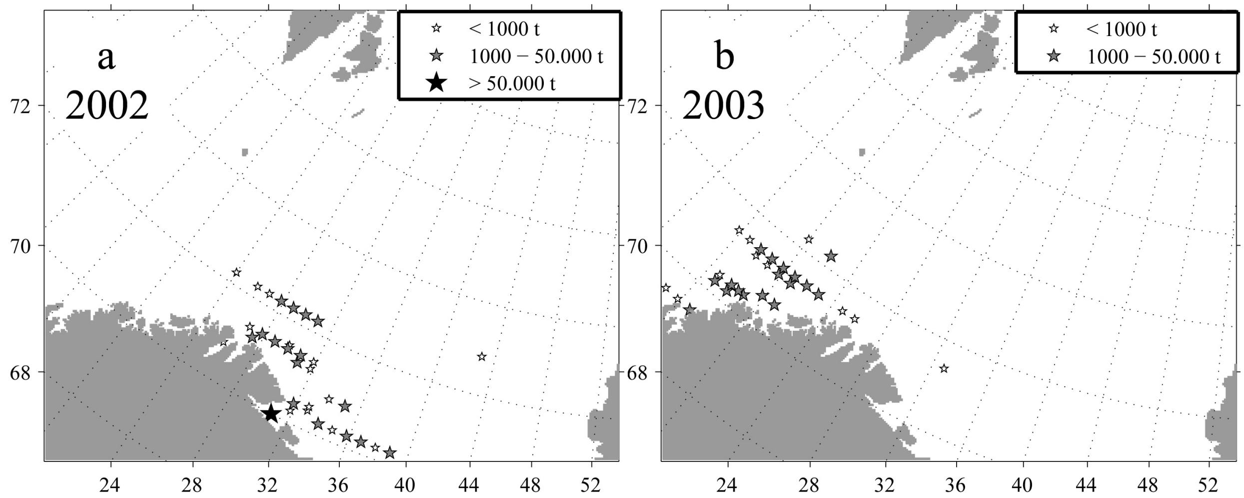

Figure 13: Catch data of maturing capelin in a) March 2002 and b) March 2003. The data were obtained from Norges Sildesalgslag.

The super-particle drift patterns (Fig. 14) had the capelin larvae June distribution fields (Fig. 5) as starting points. Only 200 particles trajectories are shown from each year. Thus, since the capelin larvae abundance was much greater in 2002 compared to the two other years, a smaller proportion of the 2002 paths (Fig. 14b) is displayed relative to in 2001 (Fig. 14a) and 2003 (Fig. 14c). Yet the main Lagrangian paths are assumed to be reflected by these figures. Although some of the same pattern is seen in 2001 and 2003, the 2001 particles were to a much larger degree advected eastwards. All three years, large proportions of the particles seemed to be retained in fjords and near-coastal waters. The small proportion of the capelin larvae that where found at westerly locations in June 2002 were transported eastwards close to the coast (Fig. 14b). One striking property of the modelled advection patterns is the tendency of eddy formations. Retention of particles inside eddies can most easily be observed in areas where a few larvae were spatially isolated from the rest of the population. Such features can be recognized by small circular trajectory paths; the 2001 (Fig. 14a) and 2002 (Fig. 14b) figures hold at least one such example each.

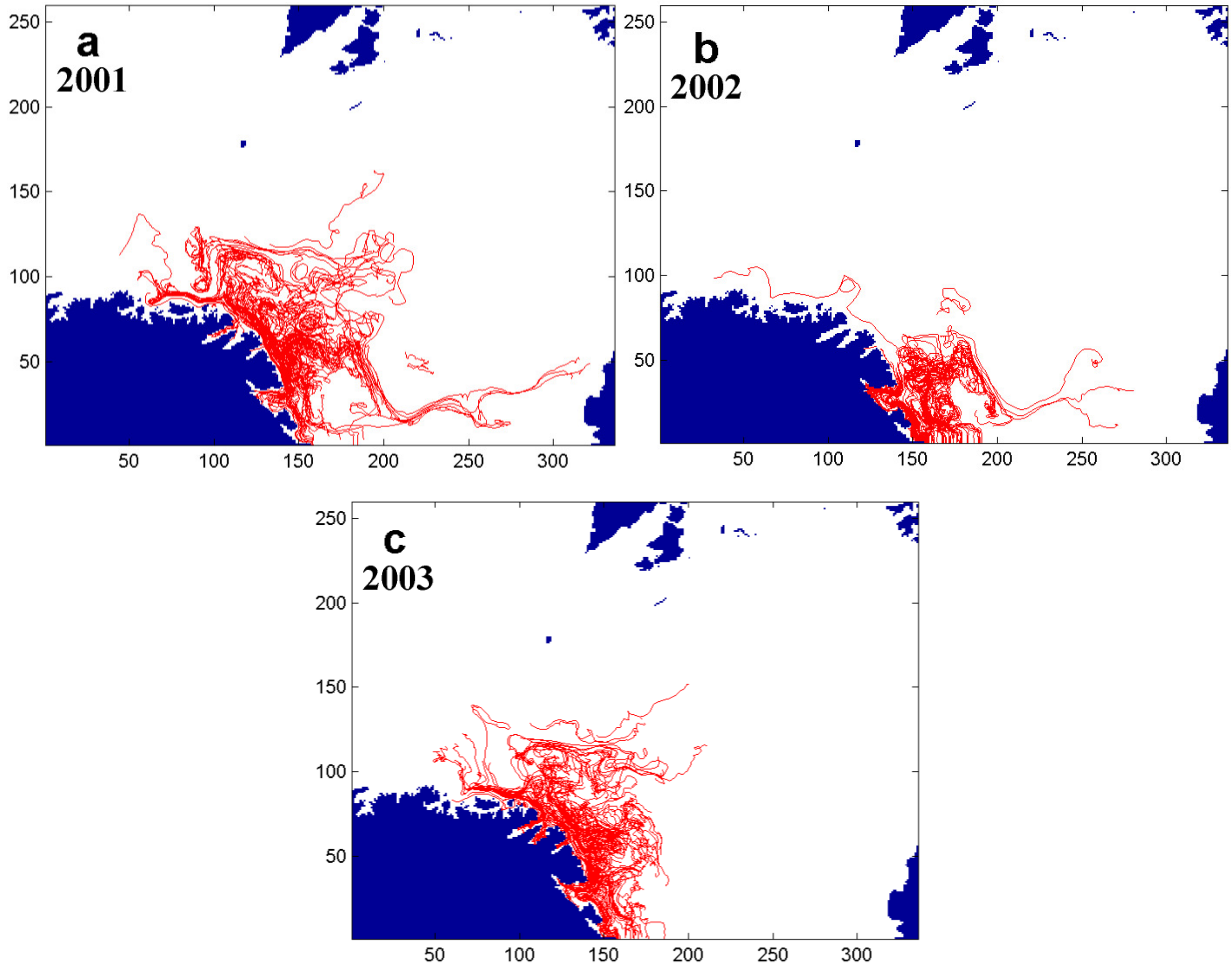

Figure 14: Lagrangian trajectories of 200 random super-particles simulated in June – September in a) 2001, b) 2002 and c) 2003. Axes values are grid points.

Directions and distances of larval movement induced by advection throughout a summer season varied between years and due to the effect of predation (Fig. 15). The super-particle drift trajectories were independent of biological setups; predation from herring did not alter super-particles trajectories. Predation could however modify the relative proportion of particles (i.e. individual capelin larvae) drifting certain directions, since the opportunity of survival would be higher in some areas than in others. Therefore, the average values (μ) as well as the standard deviations (s.d.) of drift distances and directions were calculated. The number of individuals in the end of each simulation (n) is hereby also mentioned. In scenario 2 (2001; predation ON), the drift direction was slightly more northerly (n = 1843813545356; 17786 super-particles; μ = 116.9°, s.d. = 48.2°; Fig. 15a) compared to in scenario 1 where the larvae not were preyed upon by herring (n = 3211062373088; μ = 121.2°, s.d. = 45.6°). The effect of predation also increased the advected distance of the capelin larvae (μ = 185.3 km, s.d. = 138.6 km; Fig. 15b) relative to when the larvae not were exposed to predation (μ = 173.4 km, s.d. = 134.3 km). Least differences in advected directions and distances due to variations in the simulation setups were observed in 2002. The average 2002 drift direction was 100.5° (s.d = 9.6°; Fig. 15c) both for preyed (n = 6796230328224; 31553 super-particles) and non-preyed (n = 6812488071952) larvae. The larvae drifted 333.9 km (s.d. = 82.9 km; Fig. 15d). When predation was included in 2003 the advected direction became more northerly (n = 308011997247; 14455 super-particles; μ = 139.0°, s.d. = 69.9°; Fig. 15e) and the drift distance became shorter (μ = 123.5 km, s.d. = 82.8 km; Fig. 15f) compared to when the predation was removed. Non-preyed 2003 larvae had on average a drift direction of 155.3° (n = 3499558629216; s.d. = 54.8°) and a drift distance of 126.8 km (s.d. = 73.7 km).

To give a visual impression of the importance of capelin larvae spatial origin in relation to the location of the herring field, the mortality as a function of origin was calculated (Fig. 16). The calculations were based on the spring survey capelin larvae data (Fig. 5) and on the capelin larvae end fields resulting from the main scenarios where predation was included according to Table 4 (September 25; simulations 2, 4 and 6). Capelin larvae that were exposed to herring predation during a prolonged period obviously had smaller chances of survival compared to the larvae whose drift pattern bypassed any herring field. For instance, there was a tendency in 2001 that the larvae found at south-eastern locations during spring were more disposed to be eaten compared to those found in more north-western areas (~ 90 % and ~ 75 % mortality, respectively; Fig. 16a).

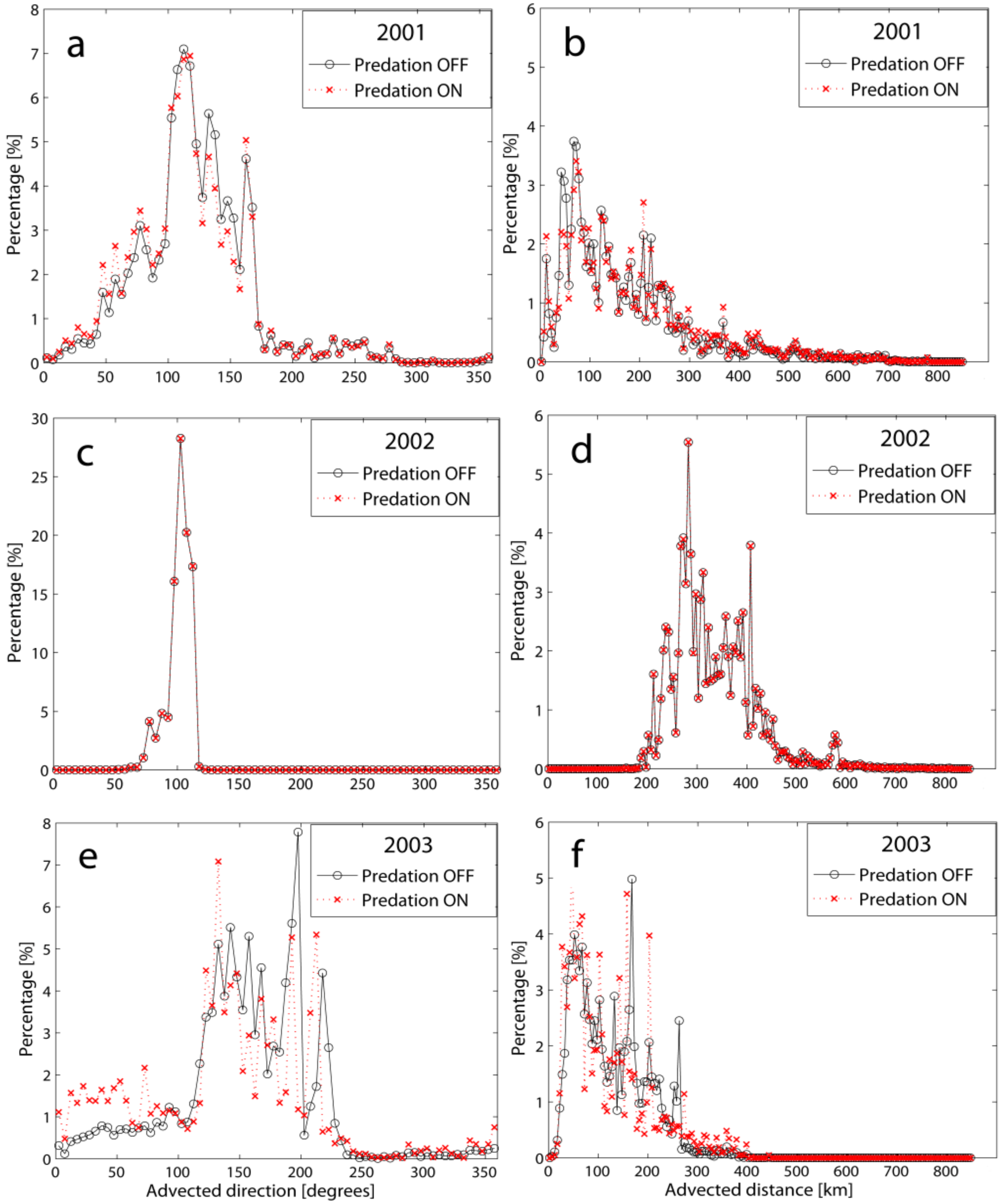

Figure 15: Advected directions (a, c, e) and distances (b, d, f) of the capelin larvae in the end of the simulations compared to the initial positions. The figures represent the years 2001 (a, b), 2002 (c, d) and 2003 (e, f). Note differences in y-axes ranges. Solid, black lines broken by circles represent simulations in which no predation occurred; dotted, red lines broken by crosses represent simulations in which predation occurred. Directions are given in degrees, distances are given in kilometers.

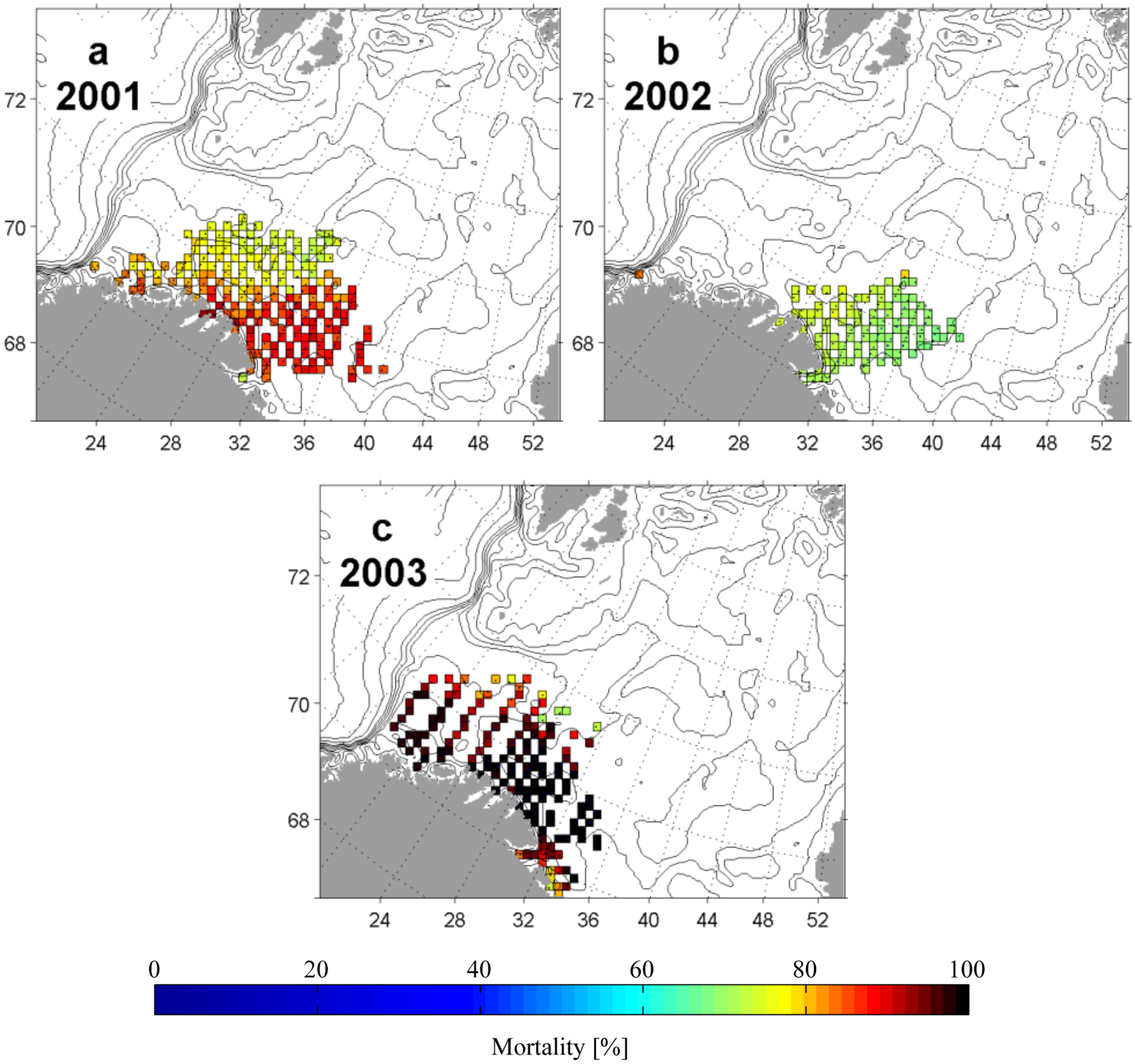

Figure 16: Simulated capelin larvae mortality [%] by the end of September as a function of origin. a) 2001; b) 2002; c) 2003. Based on spring survey data and on the main scenarios which included predation (simulations 2, 4 and 6).

In 2002, the herring initially had a typical, widespread distribution along the North Norwegian coast. However, in early summer the herring population seemed to move westwards out of the Barents Sea. Thus, most of the capelin larvae had obviously only a brief overlap with the herring. The capelin larvae having the westernmost origin therefore seemed to be spatially overlapping with herring for a longer period than those originating from more eastern areas; consequently the former suffered higher mortality rates than the latter (~ 75 % and ~ 65 % mortality, respectively; Fig. 16b). This pattern was emphasized by the small proportion of the

2002 capelin larvae originating from the very western part of the model domain (69.5° N/17.0° E). These larvae drifted eastwards through the westward-migrating herring field, and thereby suffered the highest mortality rates among the whole capelin larvae population that year (~ 90 %). A large proportion of the capelin larvae population spatially overlapped with the strong herring 2002 year class (Table 3) distribution field throughout the 2003 summer season; this led to a nearly total mortality among these larvae (Fig. 16c). Capelin larvae originating from the outermost oceanic areas or from southeasterly coastal locations were subjected to a moderate mortality (~ 70 – 90 %) due to predation from herring. Since most of the ocean currents in the near-coastal part of the study area run eastwards, and since the herring fields presently also were assumed to migrate eastwards into the Barents Sea in 2001 and 2003, large proportions of the capelin larvae were preyed upon by the young herring.

3.3 Validation to field data

The modelled capelin larvae September distributions (Figs. 9 - 11) were in general agreement with those mapped during the 2001 – 2003 capelin 0-group autumn surveys (Anon 2001b, 2002b, 2003; Fig. 17). However, the modelled distributions were generally less widespread than documented by the surveys. Modelled capelin larvae were advected shorter than the real larvae regarding both easterly, westerly and northerly directions, and the model was not able to recreate any capelin patches in near-Svalbard waters. Unlike the actual distributions, large proportions of modelled larvae also seemed to be retained within fjords and in near coastal areas. Nevertheless, the central Barents Sea distributions in 2001 and 2003 are seen both in modelled and field data. The modelled data of 2002 also resulted in a pattern largely consistent with the field data, however the survey participants found that the larvae had a more easterly distribution that year. Considering abundance-at-locations, a reverse pattern is often evident between field and modelled data. The surveys detected dense larvae concentrations in oceanic areas far from the assumed spawning areas, whereas the modelled data showed dense near-coastal concentrations and lower offshore concentrations.

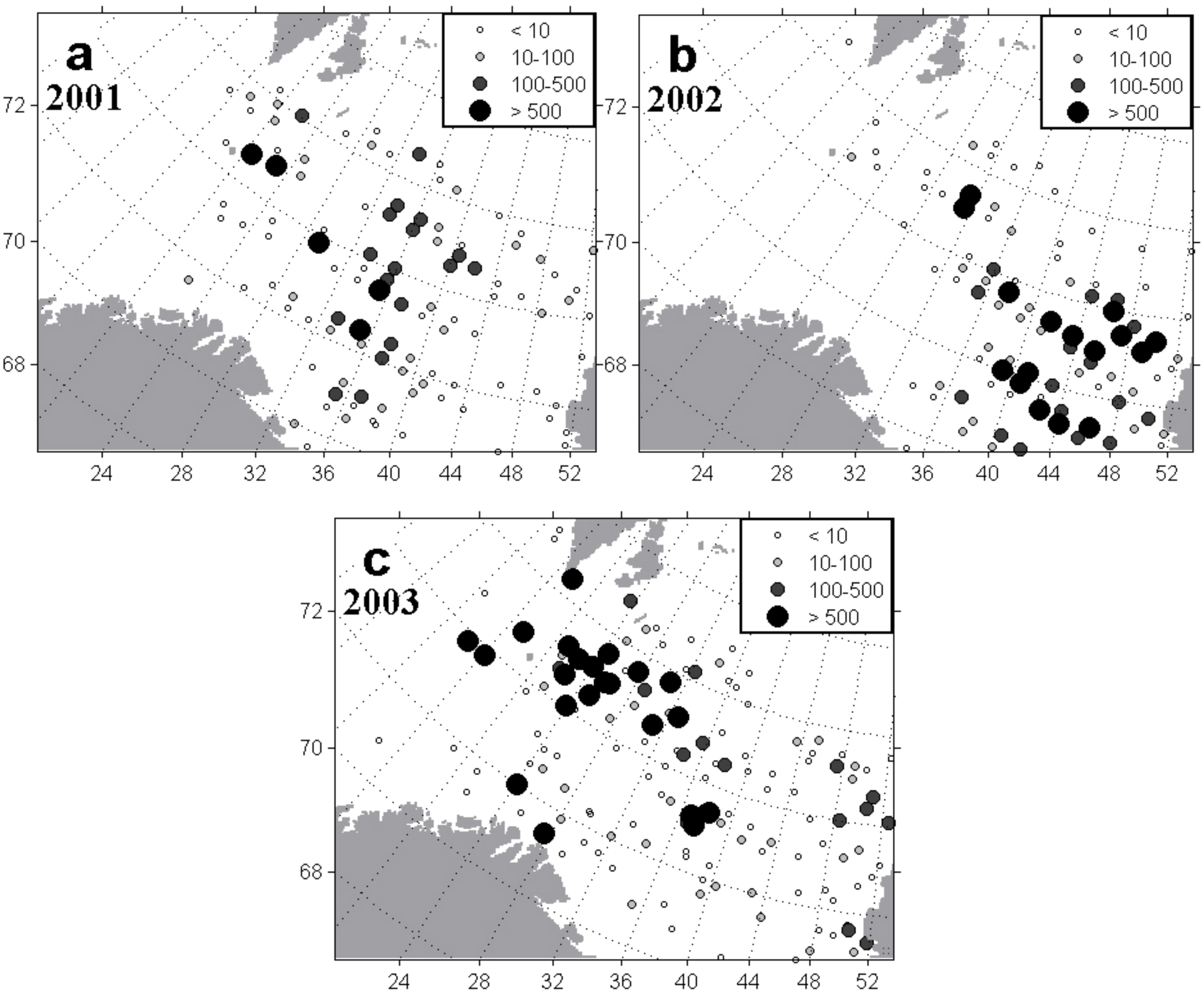

Figure 17: Capelin 0-group survey data in August-September 2001 (a), 2002 (b) and 2003 (c). The data were obtained from the Institute of Marine Research.

The Jaccard's coefficient and the Russell/Rao Index (Table 6) were conducted to test the similarity between model results and survey data. As explained in section 2.7, the total model domain was divided into 154 bins in order to make such calculations more robust. In all three years, the number of bins containing capelin larvae was greater in the survey data than in the model data. The modelled data had nearly equally many bins containing capelin larvae as the survey data in 2001 (58 vs. 60 bins), though the bins containing larvae were not always co-occurring. Co-occurrence of larvae in survey data and model results was nevertheless greatest in 2001 (46 bins), thereby leading to the highest values of the Jaccard's coefficient (0.6389) and Russell/Rao Index (0.2987). The larvae distribution was more restricted in 2002, and the coherence between model and survey data also was lower than in 2001 and 2003. This coherence was especially low (0.1429; Russell/Rao Index) when co-absent bins were included. In 2003, the largest surveyed larvae distribution among the years 2001 – 2003 was given; 65 of the survey bins contained larvae. The number of co-absent bins was smallest in 2003 (77 bins) and largest in 2002 (100 bins). In any case, the model capelin larvae were most widespread in 2001, while the surveyed 0-group capelin population was most widespread in 2003. The least widespread distribution patterns were evident in 2002.

Table 6: Comparisons between modelled and surveyed data, in the end of September 2001 – 2003. "Total survey" denotes the total number of bins containing larve in the survey data. "Total model" refers to the total number of bins containing larvae in the model data. Case a refers to the number of bins where both the model and the survey data contained larvae. Case b refers to the number of bins where only the model data contained larvae. Case c refers to the number of bins where only the survey data contained larvae. Case d refers to the number of bind where neither the model data or the survey data contained larvae. The Jaccard's coefficient and the Russell/Rao Index for the data are given.

Year	Total survey	Total model	a	b	c	d	Jaccard's coefficient	Russell/Rao Index
2001	60	58	46	14	12	82	0.6389	0.2987
2002	45	31	22	23	9	100	0.4074	0.1429
2003	65	48	36	29	12	77	0.4675	0.2338

The coherences between the modelled abundances and the capelin larvae indices, and between the modelled abundance and 0-group indices, were poor (Fig. 18a, b). Even though dense concentrations of 0-group capelin were found in the areas near Bear Island (74.3° N/ 19.1° E) during the autumn surveys in 2001 and 2003, such patterns were rear in the modelled distributions. There seemed however to be some accordance between the modelled final abundances (September 30, predation ON) and the capelin 1-group autumn estimates (Fig. 18c). Very little connection was seen between the 0-group indices and 1-group abundances, which both are estimated during surveys (Fig. 18d). Due to too few data pairs (three years), no regression analyses were carried out between the abundance data in Fig. 18.

Thus, a reasonably similar spatial pattern was seen between 0-group field data and the modelled larvae distributions by the end of the simulations (Table 6). Considering abundances, there was also some agreement between the modelled abundances in the end of September, and the surveyed 1-group abundance estimates (Fig. 18c).

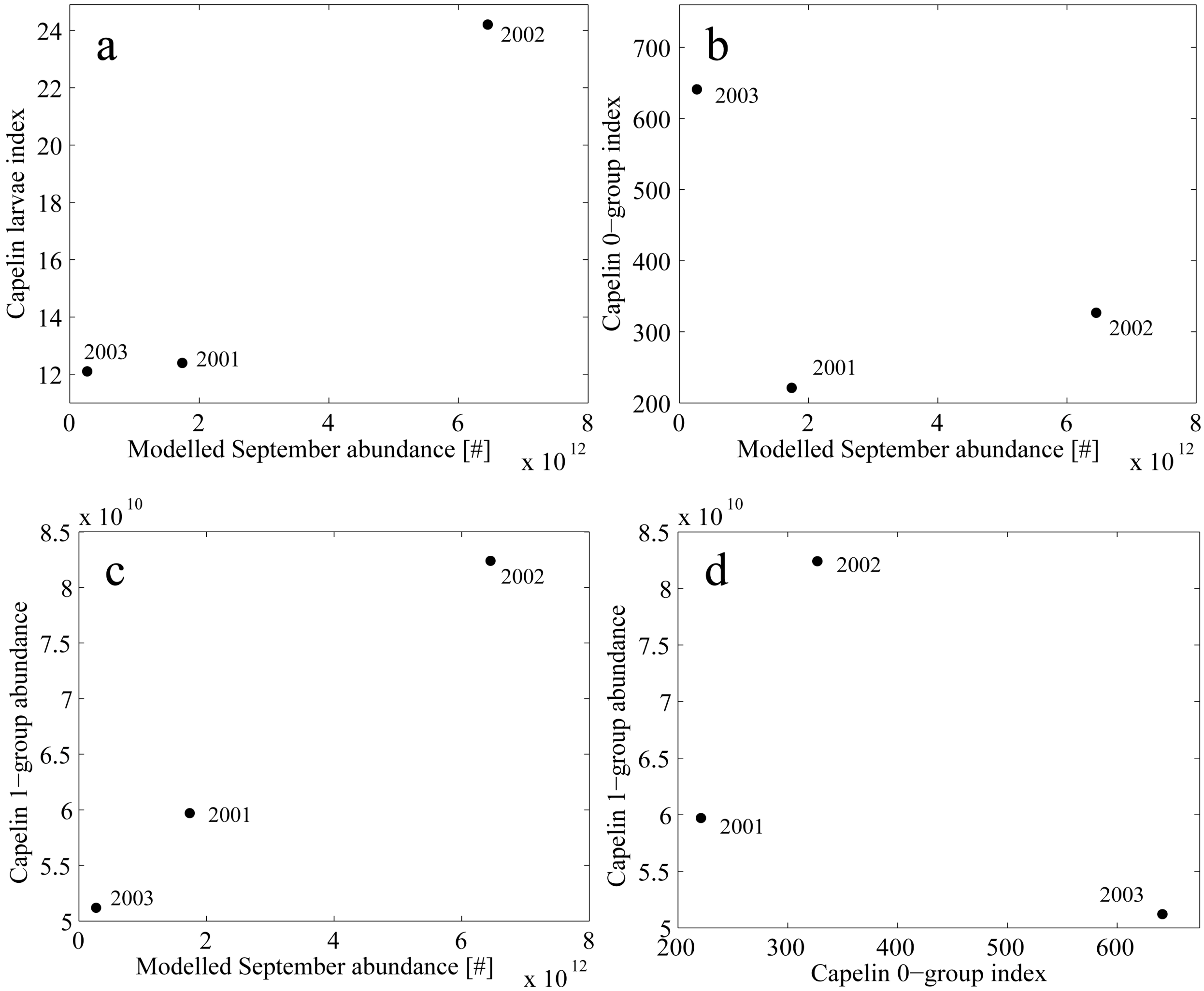

Figure 18: Modelled September abundance plottet against a) capelin larvae index, b) capelin 0-group index and c) capelin 1-group abundance; d) capelin 0-group index against capelin 1-group abundance.

However, when considering both abundances and distributions simultaneously by regression analyses, the correlations between field and modelled data were very poor (Table 7). Among the 6 main simulation setups (simulations 1 - 6), the 2002 scenarios and the 2003 scenario without predation had the best fits with the 0-group data. The 2001 scenarios had poorer fits, whereas the 2003 scenario with predation was worst.

Table 7: Results of regression analyses between field and modelled abundances and distributions. The factor n denotes the number of bins.

Simulation	Year	Predation type	Capelin larvae natural mortality rate day^{-1}	r^2	n
1	2001	Off	0.013	0.00072357	154
2	2001	On, dynamic	0.013	0.00060269	154
3	2002	Off	0.013	0.00159130	154
4	2002	On, dynamic	0.013	0.00158860	154
5	2003	Off	0.013	0.00114700	154
6	2003	On, dynamic	0.013	0.00033362	154
7	2001	On, static	0.013	0.00017974	154
8	2001	On, dynamic from end of survey	0.013	0.00075013	154
9	2001	Off	0.005	0.00067713	154
10	2001	Off	0.035	0.00085963	154
11	2001	On, dynamic	0.005	0.00056566	154
12	2001	On, dynamic	0.035	0.00071308	154

3.4 Model sensitivity

Besides the effect of predation, only natural mortality was investigated by the present model setup. The resulting mortality rates of all the eight 2001 scenarios are shown in Fig. 19. As expected, large variations in mortality rates were observed, depending on the total exposures of predation and natural mortality. The lowest mortality rate (uppermost curve; simulation 9) demonstrates that even at a low natural mortality (0.5 % day^{-1}) and absent herring, only 58.3 % of the population survived from June to September. When the predation was turned on (simulation 11) another 25 % of the larvae suffered mortality. Increasing the natural mortality to 1.3 % day^{-1} and switching off the predation (simulation 1) the surviving proportion was even 9 % smaller than in simulation 11. The September abundance was thereby only 24.6 % compared to the total abundance throughout the simulation period. Maintaining a natural mortality rate of 1.3 % day^{-1} and including predation (simulation 2) led to a predation mortality of 10.6 % and thus a remaining fraction of 14 %. Two simple variations of simulation 2 were also carried out, both with a natural mortality rate of 1.3 % day^{-1}. The first variant (simulation 7) was run with the June herring field being functional throughout the season (static). This scenario caused a predation mortality of 12.2 % of the larvae. A static herring field thus caused 1.6 % higher larval mortality compared to the dynamic approach. The second variant (simulation 8) exposed the capelin larvae to predation from a normal dynamic herring field, but the predation from herring was not activated before from the end of the survey (i.e. June 24).

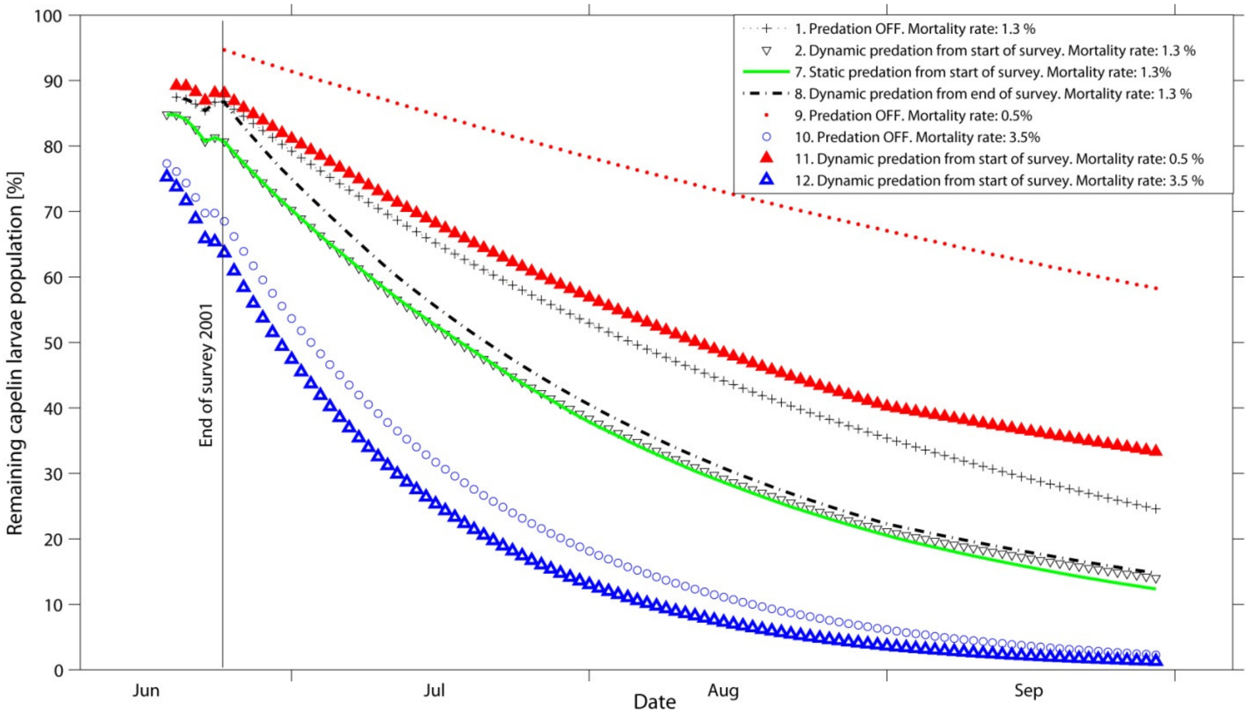

Figure 19: Capelin larvae mortality rates in different 2001 scenarios according to the legend and Table 1. The curves start by the days of maximum abundances. See legend for scenario numbers and symbol explanations.

The remaining larvae proportion due to simulation 8 was 14.8 %. The latter three scenarios gave thus roughly the same result, with a slightly larger proportion eaten by the static herring predation field. In simulation 10, the natural mortality was altered to 3.5 % day^{-1}; without predation 2.3 % of the population survived. When turning on predation (simulation 12), only 1.3 % of the capelin larvae survived. Although only 1 % more of the population survived in simulation 10 compared to simulation 12, this proportion constitutes more than 1.2 x 10^{11} individuals. Simulation 9 (predation OFF; 0.5 % day^{-1} mortality rate) resulted in a nearly linear decrease in abundance, while the simulations 10 and 12 (natural mortality rates of 3.5 % day^{-1}) resulted in decreasing mortality rates during the simulation periods. In simulation 11 (predation ON), when a low natural mortality rate (0.5 % day^{-1}) was applied, a marked decrease in mortality appeared from the start of September.

4 Discussion

This thesis focuses on capelin larvae mortality caused by predation from young herring in the Barents Sea during the summer seasons of 2001 - 2003. The capelin larvae are thereby assumed to behave in a planktonic manner, i.e. they are passively transported around in the Barents Sea by ocean currents. Young herring migrates in schools, thus actively altering their distributions in the Barents Sea during the seasons (Dragesund 1970). An overlap in time and space between the predator (young herring) and its prey (capelin larvae) is necessary for predation to occur (Huse *et al.* 2004).

In the following I will mainly focus on the capelin larvae survivability as a function of the intra- and interannual distributions of both capelin larvae and young herring. Moreover, the observed differences between modelled and surveyed capelin larvae distributions will be discussed as well as improvements for further studies will be pointed out.

4.1 Spatial considerations

4.1.1 Capelin larvae initial distributions

The choice of capelin spawning area and subsequent drift patterns of the capelin larvae can be crucial factors, possibly determining the capelin survival and year class strength. Several authors have defined typical spawning areas (Sætre and Gjøsæter 1975; Ozhigin and Luka 1985; Hamre 1994) and the capelin larvae June distributions (Serebryakov *et al.* 1985). It seems obvious that the location of the capelin larvae distribution field in June is at least partly dependent on the locations where the capelin spawning occurred. Gjøsæter (1998) collected information on known and assumed capelin spawning sites both on the Norwegian and the Russian side of the border for the years 1967 - 1996, and plotted the sites together with the capelin larvae spring distributions. The capelin spawning sites had been determined by egg samples (collected with Petersen grab), sampling of mature capelin, stomach samples of capelin predators, and observations of diving ducks feeding on capelin eggs. Since capelin spawning has been shown to occur in the depth range 12 – 280 meters, eggs in the shallowest of such areas can also be observed by SCUBA divers (Sætre and Gjøsæter 1975). Independent of the easterly or westerly spawning, Gjøsæter found that the western extremities of the capelin spawning sites corresponded well with June larvae distributions. In some years, such as in 1990, 1993 and 1996, the capelin larvae distributions were however far more westerly than any of the observed spawning sites along the coast (Gjøsæter 1998). According to the general Barents Sea current patterns (Fig. 3) a south-westward drift of capelin larvae is probably unlikely, which was also confirmed by the 2001 – 2003 Lagrangian super-particle trajectories (Fig. 14). I thus find it plausible that incomplete information of some parts of the coast give rise to the observed inconsistencies.

Due to the general conformity of capelin spawning areas and June capelin larvae catch areas (Gjøsæter 1998) I assumed that the capelin spawned close to the areas where adult capelins were caught in March (Figs. 5 and 13). However, since catch data for 2001 were not available, the capelin larvae distribution in June was used as information about spawning ground locations that year. Generally, these June distributions substantially varied between the studied years. In the years 2001 and 2003 the capelin larvae seemed to be distributed over large areas between 70 – 74° N/18 - 35° E, whereas the 2003 distribution was slightly more westerly compared to 2001. Hallfredsson and Pedersen (2009) proposed that the spawning was typically western in 2003, while it occurred both at easterly and westerly locations in 2001. The capelin were on the other hand caught at very easterly locations in 2002; some of the most easterly of those (32 - 40° E) may indicate that the spawning during that year possibly also occurred further south and east compared to the model domain (Fig. 13a). The capelin larvae distribution in 2002 could thus likely be defined as “extremely easterly” (Hamre 1994).

Capelin were caught at very westerly locations in 2003, and some were even caught outside (on the southwestern side) of the model domain (Fig. 13b). Capelin are generally assumed not to spawn further south than 69° N (Bjørke and Sætre 1994), which is well reflected by the catch data from 2003. It seems anyway likely that the capelin spawned along most of the northern coast in 2001, while they spawned easterly (east of 24° E) in 2002 and westerly (west of 24° E) in 2003.

4.1.2 Herring migrations and distributions

Young herring functioned as the sole capelin predators in the Barents Sea in the present model study. Herring are highly migrating individuals (Dragesund 1970), and realistic model studies should in my opinion therefore include herring migrations patterns. The present study involves predation on capelin larvae from a dynamically behaving field of young herring, which is an improvement of the earlier version of this biological model (Pedersen *et al.* 2009a). However, since the presently modelled herring migrations were based on few (2 - 3) annual survey estimates, they must be considered as not totally realistic. The present model approach moreover assumed that the herring were evenly distributed within a distribution field. This assumption is probably an over-simplification, particularly in those cases where the herring were very widespread, but in which the major part of the population was accumulated within one or a few small areas (e.g. in September 2001; Fig. 6d; Anon 2001a). Besides, it was assumed that the distributions of young herring were not influenced by ocean currents, due to their strong swimming capacity (Huse and Ona 1996). If currents had been taken more into account, the herring field for July 2001 (Fig. 6b) would probably have assumed a spatial shape more similar to the August 2001 field (Fig. 6c). Nevertheless, I found that migration patterns according to a rather linear approach would be most logical in this study.

The herring populations seemed to migrate in a fairy similar manner in 2001 and 2003, although the herring became more easterly extended in 2001 than in 2003. In the start of the seasons, most or all of the herring were accumulated in dense schools outside the North Norwegian coast. As the summer seasons developed, these fields became eastwardly extended and thereby larger, probably mirroring the herring feeding migration. Both in 2001 and in 2003, the herring were distributed even more north-easterly in August – September compared to most of the simulated capelin larvae (Figs. 17 and 9 - 11). If the model had been totally realistic, the latter would in my opinion mean that the herring migrated by other reasons than just to prey upon capelin larvae. Surveyed 0-group data (Fig. 17) do, however, reveal that the autumn distribution of 0-group capelin was even more northerly, easterly and north-westerly than indicated by the model. Thus, when the 2001 and 2003 survey-mapped distributions of immature herring and 0-group capelin are compared, it appears as if the herring migrated into the central Barents Sea in order to prey on capelin. The herring stock had an entirely different migration pattern in 2002 (Fig. 7). Although the stock resided along the North Norwegian coast in springtime (though in a much more widespread manner than in 2001 and 2003), the stock was apparently absent in the Barents Sea three months later (Anon 2002a). This total herring emigration from the Barents Sea was possibly due to the age composition of the herring stock at that time, which mainly consisted of the 2000 year class (Table 3). Dragesund *et al.* (1980) described the herring life pattern and related herring growth rate to the time (age) of migration to the Norwegian Sea. Some fast-growing individuals were ready for the emigration by an age of two years, while others with a lower growth rate did not join the maturing stock before an age of four years. A collective unification of the younger individuals in the Barents Sea with the maturing stock during the summer of 2002 may thus have happened given that the herring 2000 year class had a reasonably fast growth rate. Linearly interpolating a westward movement of the herring stock over the time period June to September (Fig. 7) involved a serious uncertainty, since the herring just as well could have moved out of the Barents Sea much earlier during that summer. An earlier migration out of the Barents Sea would have decreased the predation pressure upon the capelin larvae. However, since the herring abundance in the spring of 2002 was estimated to be very low (ICES 2002), the potential consequences of other herring migration patterns had probably been relatively unimportant in terms of capelin larvae survival. This impression is also strengthened by the facts that the capelin larvae were very abundant in 2002, and that nearly all the capelin larvae in any case bypassed any herring field most of the time. I therefore assume that the presently implemented herring migrations were fairly realistic.

4.2 Capelin larvae mortality and survival as functions of origin, drift patterns and predation

An overlap in time and space between a predator and its prey is a prerequisite for predation to occur (Huse *et al.* 2004). Capelin larvae drift patterns ensuring limited exposure to predation from young herring could thus be crucial for the survival of the capelin larvae. Integrated over the whole summer seasons (June – September), the herring presently consumed 10.6 % of the capelin larvae in 2001, 0.06 % in 2002 and 25.2 % in 2003 (Fig. 12). Distinction between preyed and non-preyed larvae scenarios was thus mainly observed in 2003 (Fig. 11), where a lot of predation occurred. The corresponding figure for 2002 (Fig. 10) showed no difference between preyed and non-preyed larvae; minor differences could possibly have been observed if the abundances not had been accumulated into 20 km^2 squares. Such nesting makes on the other hand a comparison between figures much easier.

Pedersen *et al.* (2009a) conducted a study very similar to the present one, although they exposed the capelin larvae to predation from a static herring field fairly alike the one shown in Fig. 6a. They found that the capelin larvae population had suffered more than 80 % mortality within the start of September 2001. Even if the assumption that herring behave in a static manner might sound like a rough simplification, the present analyses showed that the implementation of dynamic herring behavior not resulted in any great modification of the capelin larvae mortality rates. A total predation mortality of 12.2 % due to the static herring scenario (simulation 7) is rather close to the 10.6 % predation mortality due to the main 2001 scenario (dynamic herring field; simulation 2). A similar conclusion may not necessarily be drawn for other years, but I find the problem unnecessary to be further explored since the dynamic approach obviously is more realistic.

The presently obtained drift patterns of the surviving capelin larvae population reflected to some degree the ocean areas in which the chances of survival were good. The 2002 scenarios resulted in the longest advections, while the 2003 scenarios resulted in the shortest. During 2003, non-preyed larvae had the southernmost average drift pattern, while the 2002 scenarios resulted in a nearly eastward drift direction for most of the larvae. Peaks in the numbers of larvae drifting in certain directions or distances were not necessarily reflections of the average values. For instance, the average advected direction in a simulation of the situation in 2003 without predation (simulation 5) was approximately 156°, while there was a peak at nearly 200°. There was an especially sound difference in the drift direction between 2003 preyed and non-preyed larvae. While preyed larvae mainly drifted in northern directions (0 - 50°), a smaller proportion drifted in a more southern direction (150 - 175°). Predation from herring in 2003 also resulted in a larger proportion of capelin larvae drifting long distances (300 – 400 km). The standard deviations can be considered as measures of dispersion. The relatively large standard deviations in 2001 and 2003 reflected higher levels of dispersion than in 2002. Thus, those larvae drifting long distances or in directions away from the herring fields often had the greatest chances of survival.

Detailed studies of ocean current patterns fall outside the scope of this thesis. Yet it seems important to shed light on the role of oceanic features (such as eddies) on the life history of capelin larvae. Some eddies could presently be observed (Fig. 14), and they are known to contribute to spatial structuring of biota (Pedersen *et al.* 2003) since they are often rich in phytoplankton (Falkowski *et al.* 1991) and zooplankton (Mackas *et al.* 2005). Such turbulent waters thus often provide good feeding conditions for larval fish, which leads to higher growth rates and reduced starvation mortalities (Sætre *et al.* 2002b). Several types of organisms also adjust their vertical or horizontal position in order to stay in turbulent waters for prolonged periods; turbulence may increase the encounter rate between a predator and its prey (Rothschild and Osborn 1988). Mesoscale eddies along the North Norwegian coast are fairly well documented. Pedersen *et al.* (2005) recognized several non-linear mesoscale eddies being transported south-eastwards along the North Norwegian shelf by a velocity of about 7 km day^{-1}. Particle-tracking and the SINMOD hydrodynamic model have also been used to observe eddies in roughly the same area (Skarðhamar and Svendsen 2005). The latter study showed that, for particles drifting eastwards along the coast (by the same way as most of the capelin larvae were transported in the present study), winds from the south forced the particles into near-shore areas and increased their velocity. Northern winds led on the other hand to decreased velocities and a more off-shore particle distribution. Finally Pedersen *et al.* (2009b) documented drift and retention of capelin larvae in the waters outside North Norway. They described how most of the capelin larvae hatching along the coast drifted downstream with the Norwegian Coastal Current (NWCC); few larvae were advected offshore. Also mentioned was the presence of small eddies, which were thought to be important both as larvae feeding areas, retention areas and as agents of offshore transport. Regarding the credibility of models, Skarðhamar and Svendsen (2005) did not rule out that a larger number of eddies could be present on the shelf in reality; smaller eddies could also possibly have been observed in a model with higher resolution. Realistic transit times through a given area would thus probably be longer than observed through the present model study. Such argumentation has also previously been addressed by Eriksrød and Ådlandsvik (1997) who simulated drift trajectories of capelin larvae in the Barents Sea. They concluded that a higher horizontal resolution (they used 20 km resolution) probably would have reproduced more widespread and realistic capelin larvae autumn distributions. Moreover, they argued that the same model previously had reproduced current fields in the Barents Sea much more successfully using a horizontal resolution of 4 km (Ådlandsvik and Hansen 1998). Generally, a model needs six to ten grid points across an eddy in order to resolve it, and a model of 4 km resolution can therefore not resolve eddies of smaller diameter than 24 km (Lacroix *et al.* 2009). Several good reasons for enhancing the model resolution are thus evident. The obvious disadvantage is the need of faster computers: a doubling of horizontal resolution entails an eightfold in computational expense (Lacroix *et al.* 2009). The presently applied model used about 45 minutes to simulate one summer season, depending on the duration of the experiment (amount of days) and on the number of simulated super-particles.

General current patterns and the presence of eddies along the North Norwegian coast explain the presently observed drift patterns. Prolonged drift times inside areas where herring resided obviously led to elevated mortality rates. It is hereby demonstrated that the 2002 capelin larvae on average were transported longer distances than observed in 2001 and 2003 (Fig. 15). This pattern was probably a benefit of having the easternmost spawning area and thus the shortest possible distance to offshore waters. There were casually not much herring in the Barents Sea in 2002, but considering common herring distributions, one might expect that the short residence time of capelin larvae in near-coastal waters in most cases would have decreased the larvae's vulnerability to predation. In 2001, when the spawning probably was carried out along most of the North Norwegian coast, the larvae also became widely distributed during the summer season. Larvae having a relatively northerly distribution in June 2001 (Fig. 5a) were apparently least exposed to the more easterly-located herring fields (Fig. 16a). This was probably because their ability to be transported northwards was higher compared to the larvae originating from the south-easternmost areas; the latter suffered higher mortality rates. The same pattern was also seen in 2003: the larvae found far from the coast probably bypassed the herring, and thus experienced the lowest mortalities that year (Fig. 16c). Nevertheless, the capelin larvae must somehow have been transported from the near-coastal spawning sites to the outer locations where they were found in June (Fig. 5). Realistic advection patterns (in contrast to physical fields reproduced by a hydrodynamic model) might be an important factor ensuring such dispersion.

In real situations retention near the shore not only entails disadvantages (increased predation pressure), it may also provide certain benefits. Capelin larvae are thought to prey on small zooplankton found in coastal waters (Fossheim *et al.* 2006), but they are probably too small to feed efficiently on copepod recruits (Pedersen and Fossheim 2008); the latter are most dominant in more offshore (i.e. deeper) waters (Falkenhaug *et al.* 1997). Thus near-coastal waters probably provide the capelin larvae with better growth conditions than more oceanic areas. The risk of being eaten by predators (e.g. young herring) is on the other hand higher near the shore, at least in the three years presently studied (Figs. 6 - 8).

Assuming that the larvae were not spawned at very south-westerly locations (and thus assuming a northward drift) I conclude that western spawning areas generally lead to prolonged drift time for the capelin larvae in near-coastal areas. Larvae residing for long periods in areas where the herring densities often are high might in turn experience a strongly increased risk of predation. Offshore transport of capelin larvae seem to be dependent upon the presence of mesoscale eddies and on events of northerly winds.

4.3 Model sensitivity analysis

Larval-stage fish often suffer high and variable mortality rates (Houde 1997), and small changes in survival rate might severely influence the cohort recruitment success (Houde and Bartsch 2009). Marine fish larvae generally suffer much higher mortality rates than freshwater fish larvae, often experiencing a total loss of 99.98 % before metamorphosis; typically 5.3 % of freshwater larvae survive the equivalent period (Houde 1994). I have hereby focused on two such sources of capelin larvae mortality, namely the natural mortality and the mortality caused by predation from young herring. Considering sensitivity analysis, Pedersen *et al.* (2009a) concluded that the extent of the natural mortality was not important, since scenarios applying other natural mortality rates not affected the correlation with 0-group data significantly. This is in accordance with the analyses in the present study. Yet mortality not caused by predation is obviously important; relatively minor variations in the natural mortality presently led to major variations in the September capelin 0-group abundances (Fig. 19). This relative importance of natural mortality can partly be explained by the fact that this type of mortality presently occurred constantly and thus independently of any drift patterns. Predation, on the other hand, only affected a certain proportion of the capelin stock at a given time. Hallfredsson and Pedersen

(2009), studying predation from young herring on capelin larvae in the Barents Sea in 2001 and 2003, found that herring consumed 7 – 10 % of the capelin population day^{-1} in the area were herring were found, and up to 50 % day^{-1} in areas whose herring densities were highest (2003). When considering all survey stations, Hallfredsson and Pedersen (2009) found that only 0.004 % (2001) and 2.6 % (2003) of the larvae on average were consumed by herring each day. In the present study, the herring consumed a maximum of 0.86 % (2001), 0.0064 % (2002) and 2.36 % (2003) of the capelin larvae population day^{-1}. The latter three mortality rates were evident in early summer (late June/early July), but decreased rapidly with time in 2001 and 2003 as the herring became more widely distributed. Natural mortality in early marine fish life stages generally decrease with increased age and size, and total mortality often decrease from more than 10 % day^{-1} in very early life stages to less than 0.2 % by an age of 1 - 4 years (Houde and Bartsch 2009). A natural mortality rate of 1.3 % day^{-1} is found to be quite low (Hallfredsson and Pedersen 2009), and might in real environments (the rate of 1.3 % day^{-1} was estimated from bag experiments; Ivarjord *et al.* 2008) actually be too low.

These analyses indicate that predation plays a relatively more important role when the natural mortality rate is set to be low. A high natural mortality rate will on the other hand decrease the relative importance of predation. An increased sensitivity to changes in predation pressure when the natural mortality is low may also be evident. It is obviously difficult to distinguish between mortality due to starvation and mortality due to predation, since starvation can increase the susceptibility to be eaten (Bailey 1994). Apart from Ivarjord *et al.* (2008), studies on larval mortality rates in predator-free environments are rarely conducted, and should in my opinion be carried out more extensively in the future in order to provide improved data on mortalities.

4.4 Model validation to field data

As the present study concentrates on three years of seasonal relationship between young herring and capelin larvae, the most natural way to validate the results seems to be a comparison with the annually surveyed 0-group data. These autumn surveys are carried out roughly by the time the model runs are terminated (September/October), and they seek to cover the total capelin larvae distribution area. One, in my opinion large disadvantage, is that these surveys only estimate non-denominated indices. Absolute capelin 0-group abundances are therefore not available, but the estimates can be used as indications of relative interannual capelin 0-group abundance variations.

Possible distribution coherences were explored by calculating the Jaccard's coefficient and the Russel/Rao Index; the former only including areas where larvae were found, the latter also taking co-absence into account. Even though the results of these two methods differed, they pointed in the same direction: the modelled 2001 distribution had the best coherence with survey data, while the coherence in 2003 was somewhat poorer (Table 6). The modelled 2002 distribution had worst fit with the survey data. This information can probably be interpreted in several ways, but it is worth to mention that the same sequence was seen on the degree of modelled capelin larvae distribution (Table 6); the modelled larvae were most widely distributed in 2001 and least widely distributed in 2002. Abundance-at-location regressions were however poor (Table 7). I suggest that any results of such regression analyses in any case must be threaten with great care due to the non-synoptic dimension of the capelin 0-group data; one might expect that the distribution field of the capelin larvae is altered during the survey period. Comparing synoptic (modelled) and non-synoptic (surveyed) data statistically obviously involves uncertainties. Non-synoptic survey distribution data can be transformed into synoptic distributions using forward and backward Lagrangian particle-tracking (Pedersen *et al.* 2000), but some uncertainties could also be reduced by applying a larger number of research vessels and thus reducing the time required for covering the Barents Sea.

Although this study only focuses on the predation from young herring on larval capelin during three seasons, there seems to be some coherence between the simulated capelin larvae abundances in September (by the end of the simulations) and the immature capelin abundances (1-group) by autumn the subsequent years (Fig. 18c and Appendix F). Although capelin 1-group is object of a limited fishery mortality during summer (Gundersen and Gjøsæter 1998), it might potentially constitute a reasonably good indication of the year class strength in the previous year. Capelin recruitment is often measured by means of capelin 1-group abundance in autumn (Tjelmeland 2009). Generally acoustic abundance estimates, such as the capelin 1-group estimate, are thought to be relatively credible (Toresen *et al.* 1998). The model coherence with capelin 0-group indices over the course of the years 2001 - 2003 is much poorer. In the view of a longer time series, the 0-group index is well correlated with the 1-group estimate, while the larvae indices are poorly correlated with both 0-group indices and 1-group estimates (Gundersen and Gjøsæter 1998). For 2001 – 2003, the connection between the 0-group indices and the 1-group estimates was, however, doubtful (Fig. 18d).

4.5 Case study: northern drift of particles

Insufficient model capability to transport particles from the coastal areas and into the central Barents Sea seems to be a well-known problem; the occurrences of larvae in near-Svalbard waters seem to be especially difficult to reproduce, not least in the present study. Intuitively, it seems difficult to explain a northern or north-western drift direction of capelin larvae that originate in areas where the currents above all run eastwards (Eriksrød and Ådlandsvik 1997). This leads to the idea that the larvae found near Svalbard in September *not* originates from the traditional surveyed June distribution field. Bjørke and Sætre (1994) proposed for instance that some of the capelin larvae found in the Barents Sea originate from Iceland, transported to the Barents Sea by the East Icelandic current (EIC).

This problem led me to advocate another hypothesis: the 0-group capelin found far north and east in the Barents Sea originate from typical western north Norwegian spawning grounds, and have been transported northwards by the West Spitsbergen Current (WSC). These capelin larvae are, however, not taken into account during the capelin larvae June survey, simply because they are located far north-east compared to the survey area. In order to explore the possibility that 0-group capelin found near Svalbard in September might originate from the Norwegian coast, I performed a drift simulation where particles where released from known adult capelin catch locations in 2003 (assuming that the capelin were about to spawn in nearby areas). Catch data were obtained from Norges Sildesalgslag and treated as described in section 2.6. All capelin catch locations in 2003 are shown in Fig. 13b. For this simulation, only catch locations of less than 280 water depth (Sætre and Gjøsæter 1975) and with relatively closeness to the shore (Bjørke *et al.* 1972; Sætre and Gjøsæter 1975) were chosen. Thus a total of 30000 particles where released from 16 different locations (1875 particles from each location) at April 7 2003, which is considered to be early in the hatching season (Bjørke *et al.* 1972). The simulation was terminated at September 30. Drift patterns of selected particles are shown in Fig. 20.

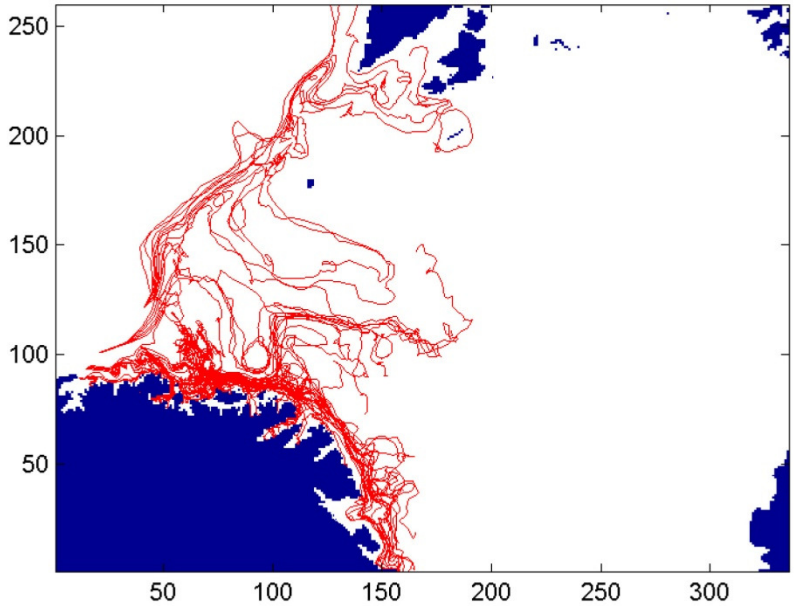

Figure 20: Lagrangian particle trajectories with capelin 2003 catch locations at the as starting points. Axes values are grid points.

A certain amount of the particles were transported northwards by the WSC, while the rest west were carried eastwards by the NWCC and the Murman Coastal Current (MCC) (Fig. 20). None of the northward-drifting particles were advected even futher west compared to the main current direction, but some broke loose from the WSC on their way northwards and continued in a more easterly direction. Skarðhamar and Svendsen (2005) released particles in approximately the same area as done in this case study, and concluded that winds from northerly winds were of crucial importance for a northward particle drift. Northerly winds are dominating in this area during summer (Skarðhamar and Svendsen 2005); a northern transport of capelin larvae is therefor probably common in years when spawning occurs at western localities.

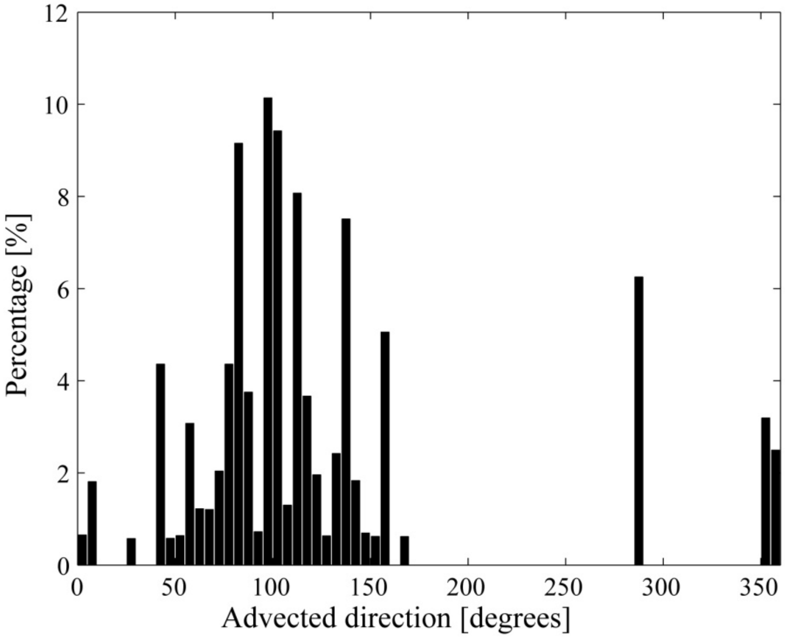

Figure 21: Drift directions of particles with capelin 2003 catch locations as starting points.

Most of the larvae were, as expected, transported in eastern directions (~ 40 - 160°; Fig. 21). These eastern drift patterns may explain why capelin larvae were found along the whole northern coast in June 2003 (even on the Russian side of the border; Fig. 5c) while all the capelin catches were carried out far west along the North Norwegian coast (Fig. 13b). However, more than 20 % of the particles were advected in northern directions (~ 270 - 50°). No particles drifted in directions between ~ 170 – 280° or between ~ 290 – 345°. Approximately 4 % of the particles where within a distance of 5 gridpoints (20 km) to the northern boundary of the model domain, possibly continuing northwards. Whether capelin larvae drifting outside this northern boundary are likely to survive remains unsolved. In any case, this simulation confirms that larvae originating from typical western spawning grounds along the North Norwegian coast might be transported northwards.

A comparance between the capelin 0-group distributions (Fig. 17) for the three years reveal that the concentrations west of 28° E were much denser in 2001 and 2003 than in 2002. In 2003, when the spawning locations were considered to be even more western than in 2001, the north-western autumn 0-group concentrations were by far most dense compared to the two other years. I can not preclude that some of the larvae found near Svalbard originate from Icelandic waters, such as suggested by Bjørke and Sætre (1994). Their suggestion does, however, not explain why large amounts of 0-group capelin could be found near Svalbard in the two years of total or partly western spawning (2001 and 2003), while the larvae were nearly absent in those waters when the spawning was carried out at eastern locations (2002). I thus propose that some of the Barents Sea capelin possibly might originate from Icelandic waters, but the majority are spawned and hatched along the Norwegian-Russian coast.

4.6 Ecological implications and interannual recruitment variability

Relatively large variations in both capelin larvae start populations (i.e. capelin larvae indices) and subsequent model and field abundance estimates are presently documented. Such variations are important to explore with the intention to describe interannual variability in the ecosystem. In this context, the model seems to be able to describe the numerical importance of herring predation on capelin larvae during a given year reasonably well. For instance, the relative autumn amounts of capelin obtained through the present model studies corresponded fairy good with the reported capelin recruitment estimates (1-group; Fig. 18c). However, another aspect seems even more important to pay attention to: despite above-average capelin larvae production (Appendix E), all the three years studied were within a period of decreasing abundance and relatively poor capelin recruitment (Tjelmeland 2009; Appendix A). This recruitment failure possibly led to the stock collapse enduring from 2003 – 2006 (Gjøsæter *et al.* 2009). Two other capelin stock collapses have been observed during the last decades, in the periods 1985 – 1989 and 1993 – 1997. Capelin collapse periods are often associated with large consequences for the several other species in the Barents Sea ecosystem. Knowledge about capelin collapses can naturally be divided into two approaches: what might cause a stock collapse, and what consequences can be expected when a collapse is evident? Hamre (1994) depicted the extraordinary situation in the Barents Sea in 1970's and 1980's. A warm climate in the late 1970's contributed to good growth conditions for herring and cod, but most of the herring were caught by the fisheries. Low densities of herring in the Barents Sea provided favourable recruitment terms for capelin, which in turn was preyed upon by cod. The cod stock rose in abundance during the first half of the 1980's. Although the herring were still heavily exploited, the stock managed to produce a strong year class in 1983 which blocked the capelin recruitment in 1984. By the mid-1980's the large cod stock in the Barents Sea thereby suddenly had insufficient supply of both capelin and herring as food, leading to extended cod cannibalism (Appendix B). The capelin fishery probably also decreased the availability of capelin as cod food (Hopkins and Nilssen 1991). This situation in turn led to starvation among fish and fish predators such as seabirds and sea mammals, and to a collapse in the Barents Sea fisheries. Generally, the zooplankton abundance can be expected to rise if the capelin abundance decreases since capelin feed on zooplankton (Gjøsæter *et al.* 2002; Zhou *et al.* 2009); low capelin abundances can thus be recognized by low zooplankton abundances (Knutsen and Dalpadado 2009; Appendix C). Young herring was also thought to strongly influence the recruitment in the years prior to the two next collapses, in 1993 – 1997 (Gjøsæter and Bogstad 1998) and in 2003 – 2006 (Hallfredsson and Pedersen 2009). The present model experiments suggest that herring to a large degree contributed to the poor survival of the capelin 2001 and 2003 year classes. Yet it is more difficult to explain the relatively poor 2002 year class, since herring was nearly absent in the Barents Sea that year (interannual recruitment is shown in Appendix A). In other years, such as in 1989, the capelin larvae index was below-average (7.2; Appendix E), while the subsequent recruitment in 1990 was exceptionally good. One could therefore expect the capelin 2002 year class to be stronger than it actually became (Appendix A). This indicates that other mechanisms than the predation from herring also can be important regarding capelin year class strength. One such mechanism is suggested to be the lunar cycle. One hypothesis proposed for instance that the fluctuations of all major Barents Sea fish stocks (including both the Barents Sea capelin and the Norwegian spring-spawning herring) are related to the temperature regime in the Kola section (Appendix D) and thus to the lunar cycle (Yndestad and Stene 2002; Yndestad 2004). Predation on young stages of capelin from other species than herring will be discussed in section 4.7.

Fortunately, the capelin stock usually recover by nearly the same rate as it previously became reduced (Appendix A). Fossum (1992) explained this recover efficiency of capelin stocks by the short generation times and its ability to produce spawning products on the expense of biomass. Another reason for fast capelin recoveries might have been that the herring migrated out of the Barents Sea as maturation was reached, reducing the predation pressure upon the capelin (Tjelmeland and Bogstad 1998). Although each of the three collapse periods lasted for roughly an equally long period, the consequences on the ecosystem were apparently nearly nonexistent in the latter two periods; starving birds or animals were hardly observed. Gjøsæter *et al.* (2009) explained this observation by the hypothesis that the fish predators had better access to other fish preys during the last two collapse periods; this could possibly happen due a warmer climate and thereby better growth conditions for prey species. Such prey switching is common in nature; the mechanism may ensure that the preferred prey species not becomes severely reduced while alternative prey species become too abundant (Murdoch 1969). Isopods are generally regarded as an important food source for seals, sea mammals, polar cod and cod in years when the supply of capelin is insufficient (von Quillfeldt *et al.* 2002). Anyway, predation from herring has above all been given the final responsibility for poor capelin recruitment, while more moderate abundance declines have also been explained by high spawning mortalities (Hamre 1994; Hamre 2003; Hjermann *et al.* 2004).

Although predation from herring on capelin larvae must be considered as a natural event, it does not necessarily lead to healthy conditions in the Barents Sea ecosystem. The capelin stock resides in the Barents Sea throughout the lifetime. Herring use on the other hand the Barents Sea only as a nursery area, and leave to join the maturing stock in the Norwegian Sea by an age of 2 – 4 years (Dragesund 1970). Hjermann *et al* (2004) showed that a warm climate two years prior to a given capelin spawning season often results in a large herring stock preying on the capelin larvae subsequent to the capelin spawning season. Relatively small juvenile herring stocks might block the recruitment of potentially large capelin stocks (Hjermann *et al.* 2004). A large capelin stock is thus replaced by a small herring stock, the latter in any case soon migrating out of the system. As the herring leave the Barents Sea, a large biomass is removed from the region. Strongly reduced amounts of capelin lead to food shortage for cod (Hamre 2000).

As a summary, one might possibly say that the temperature regime at least partly governs the herring recruitment (Hjermann *et al.* 2004), the latter determining the success of the capelin recruitment and thereby the yield of cod (Hamre 2003). The present study confirms that herring had a strong impact on the capelin recruitment both in 2001 and in 2003. Yet, there were apparently no clear reasons for the recruitment fail in 2002, but one might suggest that the capelin larvae were preyed upon by other species than the young herring.

4.7 Model reliability and future directions

4.7.1 Model weaknesses and future enhancement

Modelling the interactions between only two fish species in one entire ecosystem is obviously a serious simplification; herring is not the only species preying on young stages of capelin. According to Bjørke *et al.* (1972) capelin eggs are consumed by haddock (*Melanogrammus aeglefinus* L.), king eiders (*Somateria spectabilis*), common eiders (*Somateria mollissima*) and long-tailed duck (*Clangula hyemalis*). Capelin eggs are even consumed by adult capelin (i.e. cannibalism; Huse and Toresen 1996), but cannibalism is probably not important in a recruitment point of view (Slotte *et al.* 2006). It seems neither not probable that the shape or size of the capelin spawning area is crucial for the rate of cannibalism (Slotte *et al.* 2006). The red king crab (*Paralithodes camchaticus*) is an introduced species whose distribution area partly might overlap with capelin spawning areas. Future studies will show whether also that species will become a threat to the capelin recruitment through predation on capelin eggs. Egg predation is in any case difficult to estimate quantitatively, since the first estimation of cohort strength is carried out after hatching. Regarding predation on capelin larvae, both sandeel (*Ammodytes marinus*; Godiksen *et al.* 2006) and juvenile cod (Hallfredsson and Pedersen 2007) seem to be important. Effects of larvae predation from the latter species can probably be added to the effects of predation from young herring. In some years, such as in 2002, the recruitment failed although the capelin larvae index was high and the herring were scarce. Predation from species other than herring might thus probably contribute to explain unexpectedly poor capelin recruitment in such years. Implementation of predation from the above-mentioned species as well as the availability of zooplankton as food for capelin might contribute to a better performance of the presently used model. Implemented temperature aspects affecting not only the drift patterns but also the species ecology also seem interestingly (Huse and Ellingsen 2008). Finally, Hallfredsson and Pedersen (2009) found the functional response (i.e. the relation between the capelin larvae density and the number of capelin larvae eaten by the herring) to be non-linear; the non-linear approach was particularly superior to the linear one in situation where the capelin densities were high. Due to the lack of time, the linear approach implemented by Pedersen *et al.* (2009a) was continued to be used in the present model runs. However, considering the fact that herring also prey on other species (such as *Calanus finmarchicus*; Dalpadado *et al.* 2000), it is uncertain if the herring regularly become full only preying upon capelin larvae. Nevertheless, future studies should consider the use of the non-linear approach described by Hallfredsson and Pedersen (2009).

One important requirement to realistic particle-tracking models that presently is not fulfilled is the one concerning the size of the model domain. No particles should ever cross any of the model domain boundaries (Brickman *et al.* 2009). Presently, a large proportion of larvae originating at easterly coastal-near locations seemed to be carried southwards by the Murman Coastal Current, thus often ending up at the southern boundary; in reality, these larvae would probably end up somewhere on the southern side of the model domain. Obviously this problem is greatest in years of easterly capelin spawning patterns. As an indication of the proportion of the particles that ultimately would end up outside the model domain in reality, the particles that were within 5 gridpoints (20 km) to the southern boundary by September 25 were registered; most of the particles that approached the southern border would probably be advected further south. While only 3 % of the super-particles where within the 5-gridpoint area in 2001, as much as 45 % and 16 % were within that area in 2002 and 2003, respectively. This suggests that the model domain should be expanded before further studies are conducted, and leads to the important matter-of-fact that the presently obtained capelin distributions and predation estimates must be considered as imprecise or in the worst case wrong. This study thus attempt to shed light on processes such as predation and distribution in detail without regarding the presently used model as an independent management tool. Some of present findings can however possibly be taken into account in more holistic ecosystem models such as the still-active Systmod multispecies model (Hamre 2003; Hamre and Moen 2008).

4.7.2 Recommendations for future survey programs

The present model runs could never be carried out without realistic field data, but the presently used field data were however far from ideal. Some considerations might therefore be done in order to ensure an enhancement of future data sampling.

- The research agreements with Russian authorities considering research activities in the Russian Exclusive Economical Zone should be strengthened; good agreements are still not evident (Institute of Marine Research 2009). Restricted coverage of fish distribution areas may lead to abundance underestimation (Gjøsæter *et al.* 1998). Incomplete or uncertain data time series may also lead to uncertainties in the fisheries management.

- Both herring and capelin abundance surveys should to a larger degree cover near-coastal areas; this should also apply when estimating the abundance of early fish stages (i.e. larval and 0-group capelin). The reasons for this are yet the risks of possible underestimations when only parts of the distribution areas are covered.

- In years when some of the capelin spawning occurs at western locations, it is likely that a certain proportion of the newly hatched larvae assume a northerly drift direction. By the time of the traditional capelin larvae June survey, these larvae will probably be far north of the surveyed area. This might potentially cause an underestimation of the capelin larvae indices, but the problem could theoretically be solved by initiating the survey earlier and at more western locations. Further, increased temperatures due to global warming might also contribute to shifts in the capelin spawning patterns; the areas near Novaya Zemlya are particularly suggested to constitute future spawning grounds (Huse and Ellingsen 2008). I therefore propose that future June capelin larvae surveys should be planned on the basis of catch data.

- If less than two survey stock estimates were made during each season, any approach explaining herring migrations would probably be characterized by uncertainties. More surveys would on the other hand contribute to more certain estimates. Survey programs that attempt to map the spatial distributions of fish stocks such as the Barents Sea capelin and the Norwegian spring spawning herring should strive to counteract data uncertainties due to the fact that the organisms possibly migrate or are being advected long distances during short time intervals. I therefore suggest the use of a larger number of research vessels during each cruise in order to reduce the survey duration without reducing the surveyed area.

Summary and conclusions

Five main questions were initially addressed, and through model and literature studies I suggest the following answers.

How were the abundances and the spatio-temporal distributions of the young herring and the capelin larvae in the Barents Sea during the summer seasons of 2001 – 2003?

The capelin probably spawned along most of the northern coast in 2001, while the spawning was carried out at eastern locations in 2002 and at western locations in 2003. The capelin larvae were initially relatively abundant in 2001 and 2003, while they were very abundant in 2002. During the summer seasons of 2001 and 2003, the simulated capelin became widely distributed within the Barents Sea, while the distribution pattern in 2002 was somewhat more easterly. The herring were fairly abundant in 2001, covering a small area along the coast of North Norway in June and extending north-eastwards during the summer season. In spring 2002 the herring abundance was very low, and most of the herring population migrated out of the Barents Sea and into the Norwegian Sea during the summer. In 2003, the herring were very abundant. They were probably distributed in small areas outside the North Norwegian coast by June, extending their distribution field both eastwards and westwards during the summer.

Is Hamre's hypothesis supported through the present study, and can the herring be linked to the collapse in the capelin recruitment in the years 2003 – 2006?

The modelled capelin larvae population suffered high mortalities due to predation from young herring both in 2001 and in 2003 (10.6 % and 25.2 %, respectively), with maximum daily capelin larvae population mortalities of up to 2.36 % (in 2003). However, the capelin 2002 year class was unexpectedly weak despite a high capelin larvae index and a very limited spatio-temporal overlap with herring; the present model study suggests that herring consumed only 0.06 % of the capelin larvae population in 2002. It is therefore suggested than other recruitment-regulating factors than predation from herring, such as predation from other species, can be important as well. Nevertheless, the present study recognizes the importance of young herring as capelin larvae predators, and suggests that abundant populations of young herring in the Barents Sea may strongly affect capelin year class strengths if the spatio-temporal overlap between the two populations is sufficiently large. Hamre's hypothesis is therefore further supported by the present study.

How can the location of the capelin spawning site be linked to capelin recruitment?

The rate of predation from young herring on capelin larvae is a function of their abundances and the spatio-temporal overlap between the two stocks. The locations of the capelin spawning sites will, together with the prevailing physical environment conditions, determine the drift distances and directions of the capelin larvae. Although the herring population both varies in abundance and perform comprehensive migrations, they seem to be most densely distributed in near-coastal areas early in the summer. Thus capelin spawning areas ensuring a limited capelin larvae residence time in near-coastal waters seem to be important for their survival.

Is the presently used model able to transport capelin larvae realistically into the Barents Sea?

Surveyed capelin larvae June distribution fields are presently used as starting points for the drift simulations of capelin larvae. This method resulted in more realistic offshore drift patterns than have been achieved in previous model studies. The disadvantage of using such larvae fields as initial data is that the June surveys possibly only partly cover the capelin larvae distribution fields. I therefore suggest that a certain proportion of the capelin larvae drift northwards from the most westerly spawning locations in years with a westerly capelin spawning pattern. Northward-drifting capelin larvae can possibly be advected into both central parts of the Barents Sea and to areas near Svalbard, thus explaining such distributions reported from capelin 0-group surveys.

How can future model studies and field surveys be enhanced?

Future model studies must ensure that the model domain is sufficiently large, such that no particles cross the model domain boundaries. Predation from other species, such as cod, should be taken into account. Capelin larvae natural mortality also seems important to study more extensively. A more realistic functional response than the one presently applied is to be considered. I emphasize that more robust agreements should be made between Norwegian and Russian authorities, so that the actual distributions of the organisms in the Barents Sea are covered during surveys. I finally suggest capelin catch locations to be taken more into account when planning the June surveys, and that also near-coastal areas are being surveyed in the future.

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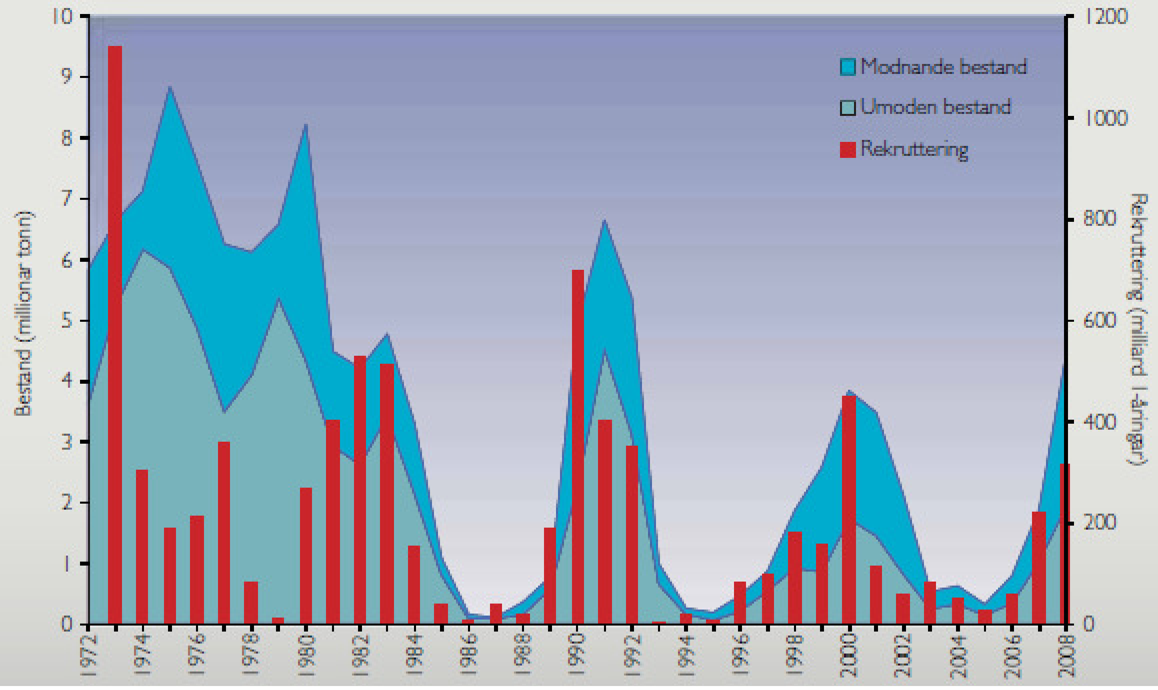
Appendices

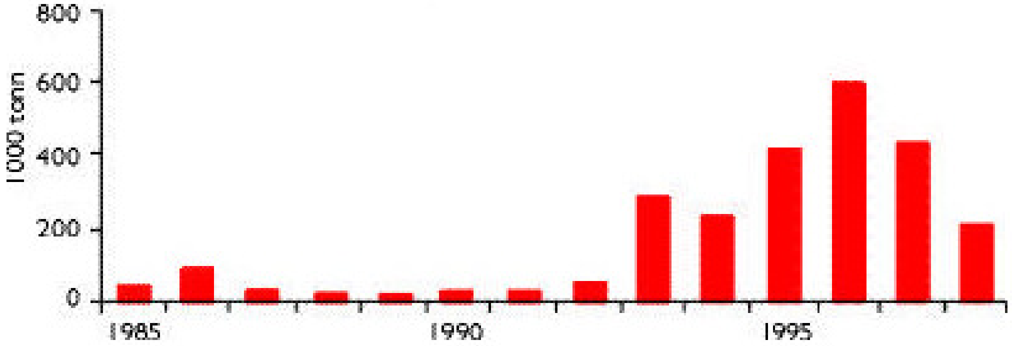
Appendix A: Interannual Barents Sea capelin recruitment and sock size.

Capelin maturing stock size (Modnande bestand), juvenile stock size (Umoden bestand) and recruitment (Rekruttering). Left axis: Stock size in million tons. Right axis: recruitment in billion 1-group individuals. Recruitment was estimeted by autumn. The figure is obtained from Tjelmeland (2009).



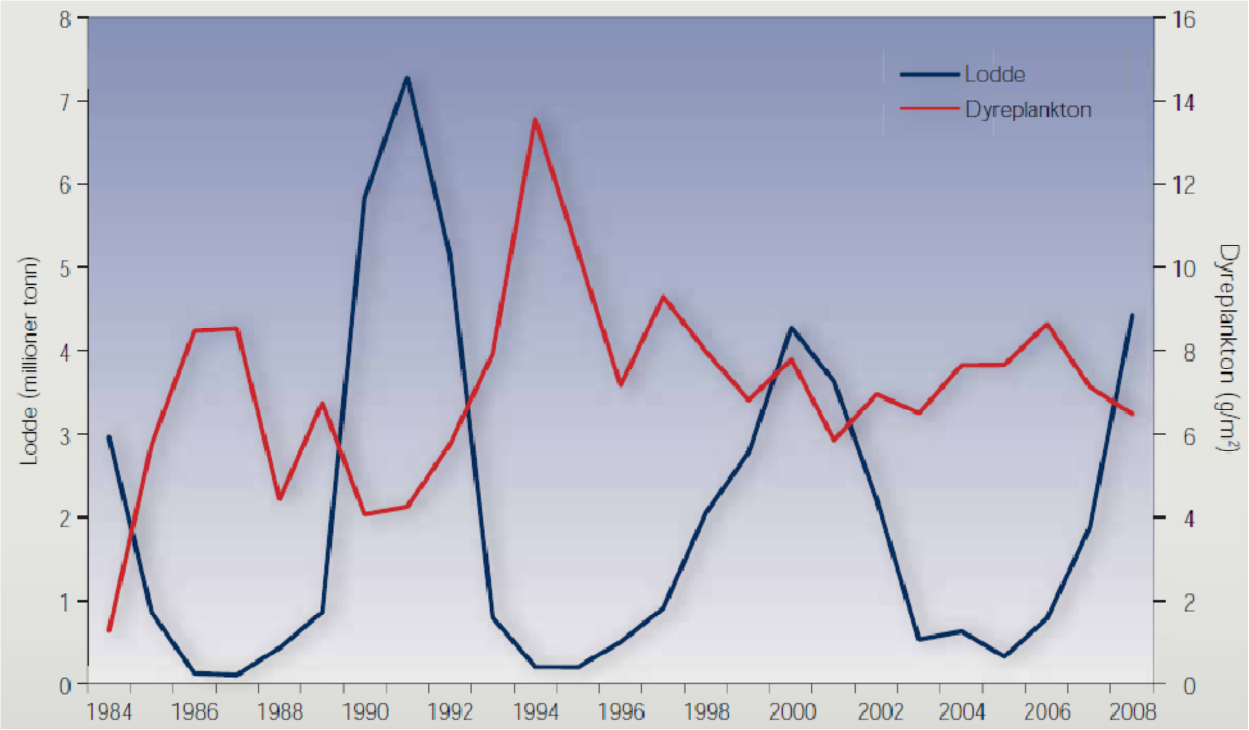
Appendix B: Estimated cod cannibalism in the Barents Sea.

Values are given in 10^3 tonnes (tonn). The figure is obtained from Hamre (2000).



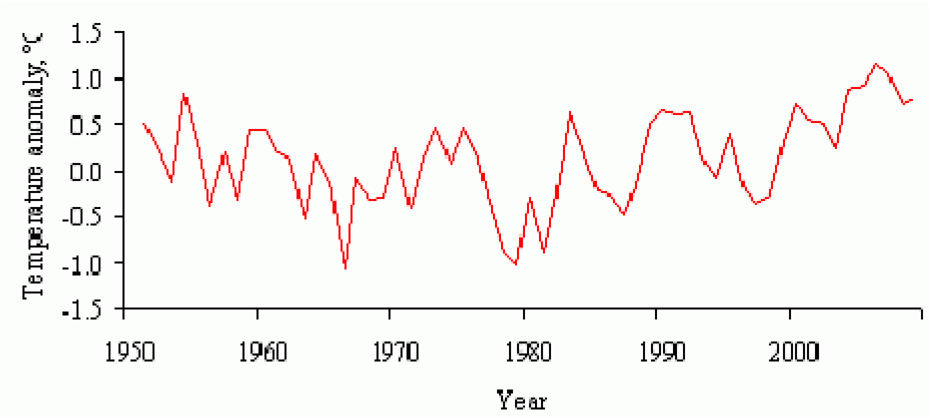
Appendix C: Interannual variations of zooplankton biomass and capelin abundance in the Barents Sea for the years 1984 – 2008.

Capelin (Lodde) abundance is given in 10^6 tons. Zooplankton (Dyreplankton) biomass is given in dry weight (g m^{-2}). The figure is obtained from Knutsen and Dalpadado (2009).



Appendix D: Temperature anomalies in the Kola section 1951 – 2009.

The figure is obtained from the PINRO webpage:
http://www.pinro.ru/labs/indexhid_e.htm?top=hid/kolsec4.php?lang=e.



Appendix E: Capelin larvae indices for the years 1981 - 2003.

The indices used in this study are shown in bold. The numbers refer to the estimated number of capelin larvae (10^{12}) in the Barents Sea in June, and are obtained from Eriksen *et al.* (2006).

Year	New index	Old index
1981*	11	9.9
1982*	10.8	9.9
1983*	6.2	9.7
1984*	8.6	8.2
1985*	11.4	8.6
1987	0.4	0.3
1988	0.2	0.3
1989	7.2	7.3
1990	14.2	13
1991	5.9	3
1992	10.2	7.2
1993	4.7	3.3
1994	0.2	0.1
1995	0	0
1996	2.4	2.4
1997	5.7	6.9
1998	13.7	14.1
1999	41.4	36.5
2000	18.9	19.1
2001	**12.4**	10.7
2002	**24.2**	22.5**
2003	**12.1**	11.9
2004	2.5	2.5
2005	7.9	8.8
Average	9.68	8.42

*) Originally calculated manually according to Alvheim (1985)

**) Reported to be 22.4 by annual cruise reports

Appendix F: Capelin modelled and surveyed abundance estimates.

Capelin larvae indices, model results, 0-group indices and 1-group indices for the years 2001 - 2003.

Year class	Capelin larvae index $[10^9]$	Model result $[10^{12}]$	Capelin 0-group index	Capelin 1-group index $[10^9]$
2001	12.4	1.737	221	59.7
2002	24.2	6.4518	327	82.4
2003	12.1	0.27153	641	51.2