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Long-term stability in modelled zooplankton influx could uphold major fish spawning grounds on the Norwegian continental shelf¹

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Abstract: Early life stages of fish spawned on the Norwegian continental shelf have long been suggested to depend on eggs and nauplii from the crustacean zooplankton *Calanus finmarchicus* for survival. *Calanus finmarchicus* overwinters in the deep basins of the Norwegian Sea, and gravid females must be advected onto the shelf prior to spawning if eggs and nauplii larvae are to serve as food for fish larvae. In this study, cross-shelf advection of *C. finmarchicus* is simulated over 52 years (1960–2011) using a numerical ocean model coupled with an individual-based model. The results suggest that cross-shelf transport of *C. finmarchicus* is surprisingly stable across years and that transport is particularly concentrated immediately upstream of the two major spawning areas for the Northeast Arctic cod (*Gadus morhua*) and the Norwegian spring-spawning herring (*Clupea harengus*), namely Lofoten and Møre, respectively. Two large topographical features, the Træna Trough and the Norwegian Trench, appear to be funnelling *C. finmarchicus* onto the shelf in these two areas. This could suggest that the fish spawning grounds outside Møre and Lofoten are, in part, maintained owing to stable interannual food supply in spring.

Résumé : Il a longtemps été suggéré que les premiers stades du cycle de vie de poissons nés sur la plateforme continentale norvégienne dépendent des œufs et nauplius du crustacé zooplanctonique *Calanus finmarchicus* pour leur survie. Les *Calanus finmarchicus* passent l'hiver dans les bassins profonds de la mer de Norvège, et les femelles gravides doivent être amenées par advection sur la plateforme avant le frai pour que les œufs et les nauplius puissent servir de nourriture aux larves de poisson. Dans cette étude, nous avons simulé l'advection de *C. finmarchicus* sur la plateforme sur une période de 52 ans (1960–2011), à l'aide d'un modèle océanique numérique jumelé à un modèle basé sur les individus. Les résultats portent à croire que le transport de *C. finmarchicus* sur la plateforme est étonnement stable d'une année à l'autre et qu'il est concentré plus particulièrement juste en amont des deux grandes aires de frai pour la morue (*Gadus morhua*) du nord-est de l'Arctique et le hareng (*Clupea harengus*) norvégien frayant au printemps, soit les régions de Lofoten et Møre, respectivement. Deux grands éléments topographiques, la dépression de Træna et la fosse norvégienne, semblent convoyer préférentiellement les *C. finmarchicus* vers la plateforme dans ces deux régions. Cela pourrait indiquer que les aires de frai des poissons à l'extérieur de Møre et Lofoten sont en partie maintenues grâce à la stabilité interannuelle de l'apport de nourriture au printemps. [Traduit par la Rédaction]

Introduction

The Norwegian and Barents seas are some of the most productive areas of the North Atlantic and home to two of the world's largest fish stocks, the Norwegian spring-spawning herring (*Clupea harengus*) and the Northeast Arctic cod (*Gadus morhua*) (Skjoldal 2004). Despite vast differences in both habitat and behaviour, herring and cod share a crucial resource, namely the calanoid copepod *Calanus finmarchicus*. This crustacean zooplankton appears in large abundances in the Norwegian Sea (Melle et al. 2004, 2014) as well as in the deep Norwegian fjords (Kaartvedt 1996) and is considered an important food source for several adult pelagic fish in the Norwegian Sea, as well as earlier life stages of both pelagic and demersal fish on the Norwegian continental shelf and in the Barents Sea (Ellertsen et al. 1989; Loeng and Drinkwater 2007).

Calanus finmarchicus exhibits an annual cyclic life history (Hirche 1996). During the summer months they reach maturity and build

up energy reserves before descending to greater depths for overwintering (>400 m; Heath et al. 2000), either in the deep ocean or in fjord basins (Kaartvedt 1996). *Calanus finmarchicus* overwintering over the shallower Barents Sea or the Norwegian continental shelf are thought to experience relatively higher mortality from visual predators (Bagøien et al. 2001), which is suggested to limit *C. finmarchicus* presence in these areas (Halvorsen et al. 2003). In late winter they start their ascent towards the surface layers to reach spawning season at the onset of the spring phytoplankton bloom (Basedow et al. 2006; Broms et al. 2012).

In the Norwegian Sea, the adult stages serve as an important and energy-rich food source for pelagic fish such as herring, mackerel (*Scomber scombrus*), and blue whiting (*Micromesisteus poutassou*) (Prokopchuk and Sentyabov 2006; Varpe and Fiksen 2010). The adults, eggs, and early life stages of *C. finmarchicus* are also subjected to advective physical forces that result in horizontal transport onto the continental shelf and into the Barents Sea, either from the fjord basins (Kaartvedt 1996) or the Norwegian Sea

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Fig. 1. Initial overwintering distribution of ~88 000 simulated particles in the Norwegian Sea (from Hjøllo et al. 2012). Defined borders to the North Sea (southern dashed line), the Norwegian continental shelf break (whole line), and the Barents Sea opening (northern dashed line) are denoted together with major spawning areas for Northeast Arctic cod (Lofoten) and Norwegian spring-spawning herring (Møre). For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0524.



(Heath et al. 2000; Skjoldal et al. 1987; Skjoldal and Rey 1989). The Norwegian spring-spawning (NSS) herring (Slotte and Fiksen 2000) and the Northeast Arctic (NEA) cod (Bergstad et al. 1987) spawn at a range of spawning grounds along the continental shelf in spring, and *C. finmarchicus* eggs and nauplii are thought to be their primary prey (Melle et al. 2004; Sætersdal and Loeng 1987). Thus, food availability for early life stages of fish is suggested to be dependent on physical transport primarily from the Norwegian Sea, and variation in such cross-shelf transport might in turn influence recruitment success (Loeng and Drinkwater 2007; Sundby 2000).

Owing to the near technically impossible task of measuring in situ horizontal advection of zooplankton, various combinations of general ocean models and Lagrangian particle tracking routines have been applied to model cross-shelf transport of C. finmarchicus. Earlier models, based on a single or a few years of climatic forcing, have suggested that cross-shelf transport varies along the shelf break (e.g., Slagstad and Tande 1996), but were also thought to greatly underestimate cross-shelf transport because of their coarse (~20 km) grid resolution (Torgersen and Huse 2005). Samuelsen et al. (2009) solved this using a nested approach allowing for a finer (~4.5 km) grid resolution in nearshore areas and found seasonal as well as geographical differences in cross-shelf transport of C. finmarchicus in a single-year simulation. Similarly, Slagstad and Tande (2007), using a Eulerian modelling approach, found that particular overwintering areas along the shelf break in the Norwegian Sea were more susceptible to transport into the Barents Sea. However, owing to the lack of long-term climatic forcing archives for high-resolution regional ocean models, these models have been unable to resolve interannual variation.

Here, a newly established 52-year (1960–2011) numerical ocean model hindcast archive (Lien et al. 2013, 2014), coupled to a regional ocean model system (ROMS), a Lagrangian particle tracking model (LADIM), and an individual-based model (IBM) for *C. finmarchicus*, is applied to resolve interannual variation in physical forcing. The

following research questions, focusing solely on *C. finmarchicus* overwintering in the Norwegian Sea, are asked: (*i*) Where are the main cross-shelf transport routes onto the Norwegian continental shelf and into the Barents Sea? (*ii*) How does cross-shelf transport vary between years? (*iii*) Are certain overwintering areas more important for cross-shelf transport?

Methods

ROMS model and LADIM tracking

For the ocean circulation model, a model archive of daily averaged currents and hydrography covering the period 1960-2011 was utilized. The archive was established with ROMS on a 4 km × 4 km resolution grid covering the Nordic Seas with 32 sigma layers. Modelled and observed temperatures and salinities repeatedly measured at sections along the Norwegian coast from Møre to the Barents Sea intercepting the Norwegian Atlantic Slope Current significantly correlate with an increasing level northwards. Also, modelled and observed variability and net volume flux of Atlantic water at Møre and at the entrance to the Barents Sea significantly correlate (see Lien et al. 2013 and Lien et al. 2014 for more details). Atmospheric boundary conditions, including 6-hourly winds, temperature, sea level pressure, humidity, cloud cover, and precipitation, were collected from the NORA10 archive (Reistad et al. 2011), while short- and net long-wave radiation were calculated internally. Lateral boundary conditions were taken from the daily mean Simple Ocean Data Assimilation (SODA) data (Carton and Giese 2008), except ice that came from an Atlantic-Arctic Micom simulation (Sandø et al. 2012). In addition, the ROMS model included tides (TPX04) and monthly climatological freshwater runoff from land.

Dispersal of particles representing *C. finmarchicus* was carried out with LADIM (Ådlandsvik and Sundby 1994). Individual particles are advected horizontally with a Runge Kutta fourth-order scheme according to the velocities at their spatiotemporal coordinates. It has a built-in behavioural module that handles vertical migration from the overwintering depths at the end of diapauses and developmental rates. The horizontal distribution, depth (300–1100 m), and individual masses (40–60 μ g carbon (C)) of overwintering *C. finmarchicus* in the Norwegian Sea (Fig. 1) were identical for all simulation years and were drawn directly from evolved overwintering fields presented in Hjøllo et al (2012), but scaled to a total of ~88 000 particles released each year.

Overwintering distribution and individual behaviour

Individual behaviour was largely based on the setup from Samuelsen et al. (2009). Simulation onset was set to 4 February for all years and was defined as the end of diapause (hereinafter referred to as wake-up day, WUD = 35) for the overwintering population. This is in accordance with both Heath (1999) and Melle et al. (2014), who reported arrival at surface waters between late winter and early spring. From this point, individuals ascend towards the surface at a speed of 20 m·day⁻¹ (Heath 1999). When approaching the surface layer (<60 m), individuals start to feed and grow, as well as performing length-dependent diel vertical migration. Length was here a function of mass.

Daily growth rate (G, day⁻¹) was set to 0.13 day⁻¹ (Campbell et al. 2001), and individual mass (M, μ g C) follows a modified Chapman–Richards growth equation derived for adult C. finmarchicus:

$$M_t = 2M_0 - M_{\text{max}} + \frac{-2M_0 + M_{\text{max}}}{1 + e^{-G \cdot t}}$$

where M_0 is initial mass at WUD (t = 0), and M_{max} is maximum obtainable mass set to 300 μ g C (Campbell et al. 2001).

Mass (M, μ g C) was converted to length (L, mm) using the following empirical relationship found by Carlotti and Wolf (1998):

$$L = k_1 \cdot M^{k_2}$$

where k_1 is 0.70 mm·µg C⁻¹, and k_2 is a dimensionless constant of 0.278.

At night, defined by surface light < 8 μ E·m⁻²·s⁻¹ (1 microEinstein = 54 lux) (Samuelsen et al. 2009), *C. finmarchicus* ascend towards a minimum depth of 30 m (Dale and Kaartvedt 2000), while during daytime (surface light > 8 μ E·m⁻²·s⁻¹), depth (Z_{day} , m) is selected as a function of body length (L, mm) (Dale and Kaartvedt 2000).

$$Z_{\rm dav} = Z_{\rm min} + k \cdot I$$

where Z_{\min} is minimum daytime depth (30 m), and k is a constant (-20.5). Vertical swimming speed was set to 1 body length·s⁻¹. This would allow a 2–4 mm *C. finmarchicus* copepodite stage CV to migrate ~7–14 m·h⁻¹.

Simulation analysis

To quantify whether individuals in the Norwegian Sea are crossing over the Barents Sea opening, the Norwegian continental shelf break, or into the North Sea, a set of shelf boundary conditions was defined. With respect to depth, both the Barents Sea opening and the continental shelf break were defined as the north-south depth contour of 350 m. The Barents Sea and the Norwegian continental shelf were further separated as north and south of 70°N, respectively. The defined North Sea boundary is not associated with any topographical features and is in fact more of a closure boundary in the southern end of the model domain. Specifically, it was defined as south of 61.2°N following a straight line along 1.9°W, west of Shetland and the Orkney Islands and east of Scotland and England. These boundary conditions resulted in a string of single grid cells stretching from west of Bear Island in the north **Fig. 2.** The NAO winter index (top panel) and the interannual variation in total cross-shelf transport of *C. finmarchicus* quantified by yearly anomaly *z* scores 100 days after wake-up day for the Barents Sea opening, the Norwegian shelf break, and the North Sea cut-off border. Dotted lines denote the 10-year simple moving average (n = 42), and dashed lines are the upper and lower limits of the 80% confidence intervals (CIs). Years with extreme high or low anomalies (outside the 80% CIs) are indicated with dots.



Fig. 3. Regression plots and lines between the 10-year moving average (n = 42) of the NAO winter index and *C. finmarchicus* cross-shelf transport anomaly *z* scores for the Barents Sea opening (circles, R = 0.83, p < 0.001), the Norwegian continental shelf break (triangles, *R* not significant), and the North Sea cut-off border (squares, R = 0.65, p < 0.001).



to northeast England in the south (Fig. 1). Collectively, these are referred to as the eastern shelf boundaries.

For all years, a daily record of each individual particle's horizontal and vertical position, and log time and location for each boundary-cell crossing, is kept. **Fig. 4.** Average number of *C. finmarchicus* transported over time through the Barents Sea opening (top panel), over the Norwegian continental shelf break (center panel), and across the North Sea cutoff border (bottom panel) in years with high (solid lines) and low (dashed lines) cross-shelf transport anomaly *z* scores (see Fig. 2). Shaded areas denote standard deviation.



To check for sensitivity to assumptions of initial overwintering distribution, depth, individual mass, and WUD, the model was also parameterized using uniform overwintering fields (see online supplementary material, Fig. S1²), a fixed overwintering depth (400 m), and fixed initial individual masses (50 μ g C). This setup was then run for all years (1960–2011) for three different WUDs: 20 January (day 20), 4 February (day 35; same as main simulation), and 20 February (day 52).

Results

The interannual variations in yearly averaged transport anomalies across the eastern shelf boundaries by day 100 were moderate (Fig. 2). For cross-shelf transport into the Barents Sea and North Sea, a long-term trend, indicated by the 10-year moving average, suggests a period of negative anomalies before 1980 compared with positive anomalies in the period after 1990. The correlation between the 10-year moving average of the NAO winter index and the cross-shelf transport anomalies are shown in Fig. 3. The NAO winter index explained about 68% (R = 0.83, p < 0.001) of the variability in the cross-shelf transport to the Barents Sea and 42% (R = 0.65, p < 0.001) to the North Sea. In contrast, for cross-shelf transport onto the Norwegian continental shelf, no such pattern in long-term trend was found. These relationships were also found to be robust to change in initial assumptions (Figs. S2 and S3²).

To objectively locate years with relatively low and high crossshelf transport, extreme years (marked with filled circles in Fig. 2) were defined by having anomalies outside the 80% confidence interval (z score = 1.28, dashed line in Fig. 2). Continuous cross**Fig. 5.** Instantaneous distribution of *C. finmarchicus* (abundance) at day 100 after wake-up day for two contrasting years with low (1976) and high (2010) cross-shelf transport. Defined borders to the North Sea (southern dashed line), the Norwegian continental shelf break (solid line), and the Barents Sea opening (northern dashed line) are denoted. For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0524.



shelf transports for all extreme years (Fig. 4) suggest that transport onto the Norwegian continental shelf, for years with both high and low cross-shelf transport (Fig. 4a), was relatively stable over the entire simulation period (linearly increasing and low standard deviation). For the Barents Sea and North Sea (Figs. 4b and 4c), cross-shelf transport in high anomaly years was concentrated between days 20 and 100 (steeper slope), after which it levelled off. For low anomaly years, there was more of a steady moderate flux. In terms of absolute numbers, between 6000 and 12 000 particles was transported across the eastern shelf boundaries during 100 days of simulation. The majority of these (>90%) were transported onto the Norwegian continental shelf. Similar patterns arose when running the model with different initial assumptions (Fig. S4²). For illustrative purposes, cross-shelf transport with high and low cross-shelf transport anomaly is exemplified in Fig. 5 by the years 1976 and 2010, respectively.

By summing up particles transported across the eastern shelf boundaries during the first 100 days for all years and plotting this over geographical location, it is possible to analyse the interannual variation in the locations where cross-shelf transport occurs (Fig. 6). Two areas with consistently high cross-shelf transport stand out. In the north, the Lofoten–Vesterålen area (~68°N) fea-

²Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0524.

Fig. 6. Location and abundance (scale, abundance of individual particles) transported across the eastern shelf boundaries after 100 days, for all years (bottom axis). Superimposed (top axis) is depth contours (grey), coastlines (black), and the assigned border to the North Sea (southern dashed line), the continental shelf (solid line), and Barents Sea (northern dashed line). Areas with contrasting patterns in cross-shelf transport are marked with black and white bars with geographical names (Møre, Helgeland, Lofoten–Vesterålen, and the Barents Sea). For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0524.



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tured two main areas of inflow: the Træna Trough just south of the Lofoten archipelago and the narrow shelf off Vesterålen, north of the archipelago. Further south, in the Møre area (\sim 63°N), inflow appeared to be facilitated through the deep Norwegian Trench. The Lofoten and Møre region made up \sim 30% and 60%, respectively, of all cross-shelf transport along the eastern shelf boundaries. Also, a few minor areas of inflow became evident, such as the Bear Island trough at about 73°N and the narrow shelf off the southern tip of Svalbard at about 74°N. As shown in supplementary Fig. S5², these results did not change significantly when altering initial conditions.

For all years combined, Fig. 7 show the integrated overwintering areas for C. finmarchicus that were advected across the shelf within the first 100 days of the simulation. All latitudinal boundary areas received individuals from overwintering areas in the eastern Norwegian Sea and along the shelf slope from about 62°N to 67°N. In addition, the shelf areas north of 66°N received individuals originating from the rim of the Lofoten Basin, in particular the eastern part. All sections south of the Tromsøflaket, a major bank structure at 70.5°N to 71°N, received individuals that originated from the southern part of the overwintering population between Shetland and Iceland. The southernmost section even encountered individuals coming all the way from Jan Mayen because of the counterclockwise circulation at the rim of the Norwegian Sea. However, in general, most particles that crossed the eastern shelf boundaries originated along the shelf slope. This was true also for different initial conditions (Fig. S6²).

Discussion

By coupling a numerical ocean hindcast archive and an individualbased model for C. finmarchicus with simple rules of behaviour, 52 years of C. finmarchicus transport from the core overwintering areas in the Norwegian Sea and across the eastern shelf boundaries to the Barents Sea, the Norwegian continental shelf, and the North Sea was simulated. The results suggested cross-shelf transport to be stable across years and that more than 90% occurred on the Norwegian continental shelf. Decadal-scale variation in crossshelf transport into the Barents Sea and the North Sea was associated with variation in the NAO winter index, but not so for the Norwegian continental shelf. There, two topographical cross-shelf features, the Træna Trough and the Norwegian Trench, appeared to funnel C. finmarchicus into the major fish-spawning regions of Lofoten and Møre, respectively. Furthermore, the source areas of C. finmarchicus for the various parts of the northeastern Atlantic shelves were limited to the immediate off-shelf areas nearby or upstream, while for decreasing latitudes an increasing but moderate amount of C. finmarchicus were also added from the southern Norwegian Sea and the eastern Icelandic Sea.

Model setup and parameterization

The setup for the *C. finmarchicus* IBM relied on several simplified assumptions, both in the initial starting distribution and individual behaviour. The model was tested for sensitivity to the most crucial parameters, namely the initial overwintering distribution and the WUD (start of simulation). In comparison with the evolved overwintering distribution, depth, and individual mass

Fig. 7. Integrated overwintering distribution for all years for *C. finmarchicus* that are transported from the Norwegian Sea and across the different shelf boundary areas (denoted with double line). The shelf boundary areas are selected based on the latitudinal variation in modelled cross-shelf transport denoted in Fig. 6 and indicate the Barents Sea (*a*), the Lofoten–Vesterälen area (*b*), the Helgeland area (*c*), and the Møre area (*d*). For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/ 10.1139/cjfas-2014-0524.



(Hjøllo et al. 2012), there was little difference in overall model results when changing initial conditions (Figs. S2–S6²). The main result (Fig. 6), showing that interannual variation in location of cross-shelf transport was consistently high in areas around the deep troughs and trenches, appeared to be robust across different initial assumptions (Fig. S5²). This is also in accordance with Samuelsen et al. (2009), who, using a HYbrid Coordinate Ocean Model (HYCOM; Bleck 2002), observed elevated flux of modelled *C. finmarchicus* through the deep troughs and trenches in the Norwe-

gian continental shelf. Consistency between two different ocean models (ROMS and HYCOM) suggests that location of cross-shelf transport is not a model artefact.

Calanus finmarchicus flux and spawning ground stability

Historically, both the NSS herring and the NEA cod are known to have utilized a range of spawning grounds along the Norwegian west coast (Dragesund et al. 1997; Opdal 2010). The two spawning stocks have their feeding grounds in the Norwegian and Barents seas, respectively, and perform extensive spawning migrations to the coastal areas. Eggs, and later larvae, are subsequently advected northwards by the Norwegian Coastal Current and the North Atlantic Current to their common nursery area in the Barents Sea. Calanus finmarchicus eggs and nauplii spawned on the Norwegian continental shelf are suggested to be the primary food source for herring and cod larvae. Fish spawning ground usage is dynamic and may fluctuate greatly between years (Dragesund et al. 1997; Opdal 2010). It has been suggested that for the NSS herring, both stock size (Dragesund et al. 1997) and individual condition (Slotte and Fiksen 2000) determine how far south the stock will spawn. For the NEA cod, migration distance (Jørgensen et al. 2008) and spawning ground location (Opdal and Jørgensen 2015) are suggested to be influenced by size and age structure of the stock. That is, smaller and younger individuals migrate shorter distances than larger and older individuals, and truncated age and size structure of the stock will lead to a northward shift in spawning grounds. Despite observed interannual fluctuations in spawning ground usage of both NSS herring and NEA cod, it is important to note that their core spawning areas have remained surprisingly stable around the Møre (Dragesund et al. 1997) and Lofoten (Opdal 2010) regions, respectively. It is therefore intriguing to see that these two areas also stood out as the most important locations for interannually consistent cross-shelf transport of C. finmarchicus onto the Norwegian continental shelf (Fig. 6). Surely, in addition to suitable space (Dragesund et al. 1997), substrate (Vikebø et al. 2012), reasonable distance from feeding grounds (Jørgensen et al. 2008; Slotte and Fiksen 2000), and favourable currents (Opdal et al. 2011), stable supply of food could be important for the long-term stability of the cod and herring spawning grounds in these two areas.

Effect of climate change

The Norwegian continental shelf break accounted for \sim 90% of the total cross-shelf transport, and interannual variation was not explained by the variation in the NAO winter index. However, for the Barents Sea and North Sea, a significant part of the interannual variation in cross-shelf transport could be explained by the NAO. In terms of the Barents Sea, this appears to be in accordance with Skjoldal and Rey (1989), who suggested a link between climate and inflow of Atlantic water, and thereby also *C. finmarchicus*, into the Barents Sea.

The NAO is defined as the first mode of variability in the normalized sea level pressure difference between the Azorean high and the Icelandic low (Hurrell 1995). A strong and positive NAO implies strengthened westerly winds and a strong control of storm tracks across the North Atlantic (Bader et al. 2011). A high positive NAO also implies a relative narrow and deep Norwegian Atlantic Current (Blindheim 2004) and enhanced transport of Atlantic water into the North Sea and the Barents Sea (Ottersen and Stenseth 2001). Thus, this study suggest that cross-shelf transport into the Barents Sea and North Sea is driven by local weather systems, while for the continental shelf, variation in cross-shelf transport might be governed by other, potentially remote drivers of ocean current characteristics. However, the importance of C. finmarchicus flux from the Norwegian Sea to the Barents Sea is debated, with contrasting views on whether they originate from local overwintering areas (Aksnes and Blindheim 1996; Arashkevich et al. 2002; Skaret et al. 2014; Tande 1991) or are advected from overwintering areas in the Norwegian Sea (Edvardsen et al. 2003; Loeng and Drinkwater 2007; Slagstad and Tande 2007).

Because the simulations were run with the same overwintering distribution for all years, potential effects of oceanographic or climatological conditions on initial distribution are unaccounted for. For instance, it is suggested that ocean temperature can explain more than 65% of the variation in both abundance and distribution of zooplankton in general (Beaugrand et al. 2014) and *C. finmarchicus* in particular (Reygondeau and Beaugrand 2011). In turn, this could also have consequences for the *C. finmarchicus* overwintering distribution in the Norwegian Sea and thus influence location of cross-shelf transport.

Implications for future C. finmarchicus harvest

In the 1950s, a small-scale fishery for *C. finmarchicus* started out in the Norwegian fjords (Wiborg and Hansen 1974). By the 1970s, the total annual catches had increased from just a few tonnes to over 50 t (Grimaldo and Gjøsund 2012). The development of the fishery has been slow, and today the annual catches, regulated as a trial fishery, is set to 1000 t.

Considering an estimated total stock size of \sim 50 million tonnes (Hjøllo et al. 2012), the current harvest is negligible. However, there appears to be political will to establish a commercial C. finmarchicus fishery and subsequently an increase of quotas (Anonymous 2012). In this regard, two main counter-arguments arise. With the fishery located along the Norwegian coast, (i) it could cause bycatch of early life stages of commercially important fish species, and (ii) the fishery might harvest adult C. finmarchicus that otherwise should have contributed as food (through potential production of eggs and nauplii) to early life stages of commercially important fish species. However, considerations of spatiotemporal occurrences of early life stages of fish, together with information on which part of the C. finmarchicus that will ensure their food, could alleviate this conflict by determining where and when C. finmarchicus should be harvested. In this regard, results from this study (Fig. 7) suggest that C. finmarchicus overwintering in areas close to the shelf break were most likely to be advected onto the shelf, while C. finmarchicus in areas further east were recycled in the Norwegian Sea basin. Thus, harvest for adult C. finmarchicus in shelf break areas, particularly outside the Lofoten-Vesterålen area and the Møre area, may reduce food resources (in terms of reduction in potential production of C. finmarchicus eggs and nauplii) for early life stages of NEA cod and NSS herring.

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