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# Overwintering distribution, inflow patterns and sustainability of *Calanus finmarchicus* in the North Sea

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## ABSTRACT

Calanoid copepods are key taxa in the North Sea as they are the main food source for many fish stocks, such as herring, mackerel and cod. In this study we use an individual-based model for *Calanus finmarchicus* embedded in the NORWegian ECOlogical Model system (NORWECOM) to investigate important population parameters such as biomass and abundance, distribution and interannual variability of the overwintering population, as well as the inflow of *C. finmarchicus* into the North Sea from adjacent areas for the 2000–2016 period. The modelled spatial–temporal patterns of *C. finmarchicus* abundance is comparable with the Continuous Plankton Recorder (CPR) Survey data in the northern North Sea. The simulated annual mean biomass of *C. finmarchicus* amounts to 0.94 million-tonnes of carbon. High overwintering biomass appears in the Norwegian Trench as well as in the north-west shelf region of the North Sea. A decreasing trend in the overwintering biomass has been detected on the path of the East Shetland Atlantic Inflow (ESAI) over the simulated period. The inflow of *C. finmarchicus* biomass into the North Sea from the north constitutes on average 41% of the annual mean biomass in the North Sea during the simulated 17 years, and thus determines the interannual variability of the biomass. We conclude that the *C. finmarchicus* population in the North Sea is not self-sustained and is highly dependent on the inflow of *C. finmarchicus* from the Faroe-Shetland Channel and south of the Norwegian Sea. *C. finmarchicus* enter the North Sea via three branches of the North Atlantic current with variable depths depending on seasons and topography. Beside the western flank of the Norwegian Trench (carrying 57% of the inflow biomass), we suggest that the ESAI is also an important agent carrying 37% of the total *C. finmarchicus* inflow biomass through the shelf area into the north-west of the North Sea. The annual mean outflow biomass is larger than the inflow biomass (0.52 versus 0.39 million-tonnes carbon per year), which indicates that the North Sea serves as a feeding ground and growth region for *C. finmarchicus*. This study is a first step towards a better understanding and quantification of the exchange of *C. finmarchicus* between the open seas, coastal waters and the fjords.

## 1. Introduction

Copepods are dominant taxa in all world oceans and serve as a key link between primary production and upper trophic levels (Mauchline, 1998). In particular, the large and lipid-rich calanoid copepod, *Calanus finmarchicus*, plays a major role in the North Atlantic ecosystems from the Gulf of St. Lawrence and coast of Newfoundland in the west (Dalpadado and Mowbray, 2013) to the Norwegian coast and fjords in the east (Bagøien et al., 2001; Broms et al., 2009). The Norwegian Sea, in the Northeast Atlantic Ocean, represents one of the centers of *C. finmarchicus* production and overwintering. It serves as a source of *C. finmarchicus* dispersal to the surrounding waters, including the North Sea (Heath et al., 1999; Melle et al., 2014).

The North Sea is a continental shelf sea, with an average water depth of 90 m, connecting to oceans through the Norwegian Sea in the north and the English Channel in the south (Fig. 1). It is an area of high human impact and socio-economic importance with some of the most productive fisheries in the world. Several studies have shown that the recruitment of sandeel, cod and herring were positively associated with *Calanus* abundance (Arnott and Ruxton, 2002; Beaugrand and Reid, 2003; van

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Deurs et al., 2009). Therefore, a sustained *Calanus* stock is essential both ecologically and economically for the North Sea.

The *C. finmarchicus* stock in the North Sea is either reproduced locally from the overwintering stock or advected from the southern Norwegian Sea. It is generally believed that the abundance of *C. finmarchicus* is extremely low during winter in the North Sea due to the shallow water depths (Beare et al., 2002; Fransz et al., 1991; Heath et al., 1999) except in some deep Norwegian fjords (Bagøien et al., 2001) and in the Norwegian Trench (Heath et al., 2004). Nevertheless, Maar et al. (2013) have reported a concentration of 1–3 *C. finmarchicus* individuals per $m^3$ in surface waters in January at the northern boundary of the North Sea from Continuous Plankton Recorder (CPR) data. They have also suggested that the abundance of *Calanus* species is very sensitive to the degree of overwintering within the North Sea, because it allows them to utilize the spring bloom more efficiently and independently of the timing and amount of oceanic inflow.

Heath et al. (1999), conversely, have demonstrated that the North Sea *C. finmarchicus* is mainly replenished each spring by an overwintering stock located in the Faroe Shetland Channel in association with the overflow of Norwegian Sea Deep Water (NSDW). They have further elaborated that neither the Fair Isle Current, nor the East Shetland Atlantic Inflow have been important routes for the inflow of *C. finmarchicus* into the North Sea, but rather the Norwegian Trench, according to their statistical analysis of CPR data.

This study aims to 1) investigate the spatial distribution of overwintering *C. finmarchicus* in the North Sea and the variability of this distribution over time; 2) evaluate the importance of *C. finmarchicus* inflow to the local population in the North Sea; 3) elaborate the possible horizontal and vertical position as well as the seasonality of the inflow. We use a three-dimensional coupled ocean physical-biogeochemical model, the NORWegian ECOlogical Model system (NORWECOM.E2E), which includes an individual-based model (IBM) for *C. finmarchicus,* applying to a model area that covers both the North Sea and the Norwegian Sea.

## 2. Material and methods

### 2.1. The North Sea circulation

The North Sea circulation is predominantly anti-clockwise and restricted by the topography with shallower water depth (<50 m) in the south, ~200 m in the north, and the Norwegian Trench (>200 m) in the

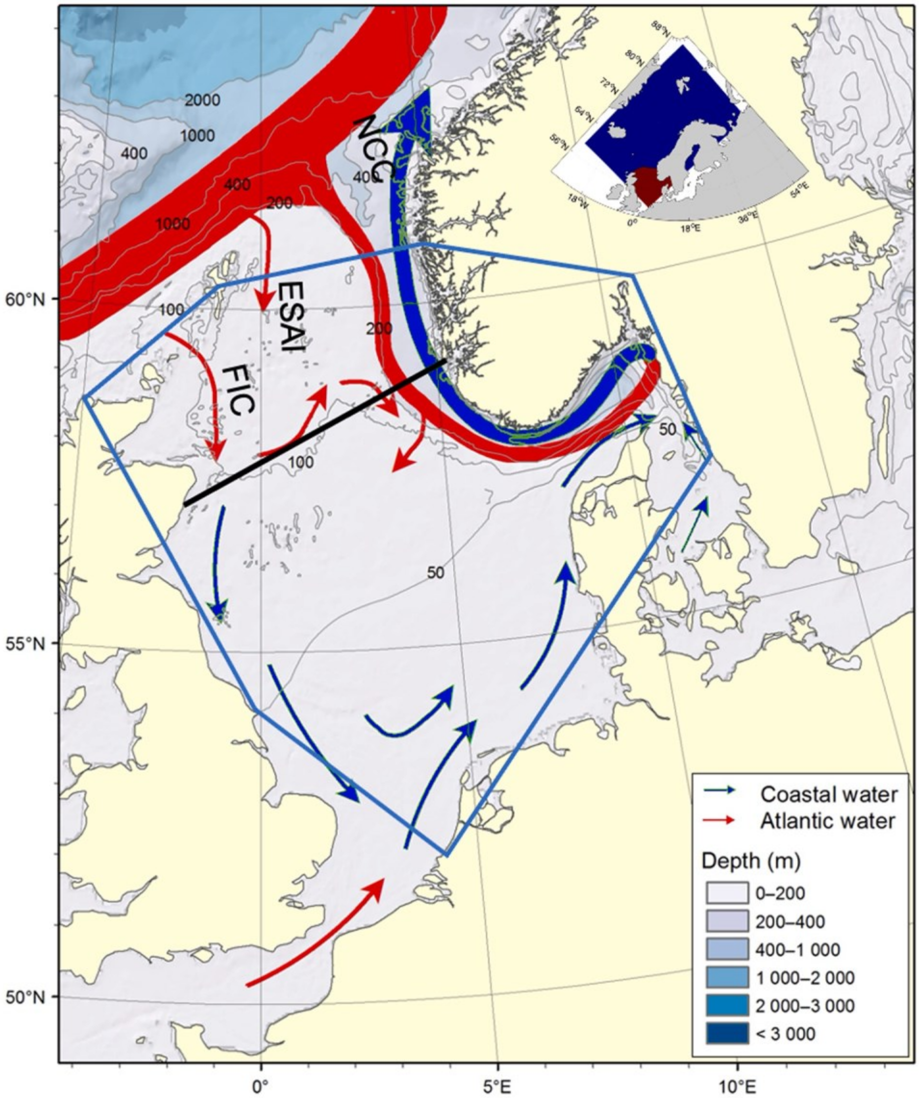

**Fig. 1.** A map of the North Sea showing the main currents and topography. The ocean area covered by the polygon in blue lines is the modelled North Sea area used in the analyses. The entire model domain covers the Norwegian Sea and Barents Sea in addition, shown on the map at the upper right corner. The black line indicates the M transect where the CPR data were collected. FIC: Fair Isle Current; ESAI: East Shetland Atlantic Inflow; NCC: Norwegian Coastal Current.

east. In the northern part it is strongly affected by the large-scale atmospheric forcing (Hjøllo et al., 2009). Warm, saline Atlantic water mainly enters the North Sea from the north, in three branches across the Scotland-Faroe-Norwegian coast section (Fig. 1, red arrows in the upper part). Within the North Sea it mixes with freshwater runoff, and leaves the North Sea as part of the Norwegian Coastal Current. A small amount of Atlantic water also enters through the English Channel, but the inflow of *C. finmarchicus* is negligible there due to its minor importance south of the UK (Helaouët and Beaugrand, 2007).

### 2.2. The physical ocean model

The ocean model used is the three-dimensional baroclinic Regional Ocean Modelling System (ROMS) version 2.1, described in the work by Shchepetkin and McWilliams (2005), and references therein. The model domain covers the Barents Sea, the Norwegian sea and the North Sea. ROMS uses a topography-following coordinate system with 32 sigma-layers in the vertical that permits enhanced resolution near the surface and bottom. The Norwegian reanalysis 10 km high resolution atmospheric reanalysis archive (Reistad et al., 2011) has been applied as atmospheric forcing, while the Simple Ocean Data Assimilation (SODA) dataset version 2.1.6 (Carton et al., 2000; Carton and Giese, 2008) was used both for initial and boundary values. Monthly mean climatological values of river runoff, scaled with the climatological values based on interannual variability in precipitation, have been used. The output of the ROMS model has been used to produce the Nordic Seas 4 km numerical ocean model hindcast archive (SVIM) (Lien et al., 2013) for the period 1960–2019 (available at https://archive.norstore.no/pages/public/datasetDetail.jsf?id=https://doi.org//10.11582/2015.00014). The water masses which are directly influenced by Atlantic Water are realistically represented in the archive, in terms of both advection/transport and hydrographic and dynamic variability, which also applies to the adjacent shallow North Sea. The physical forcing derived from the SVIM archive has been used to run the NORWECOM End-To-End (E2E) model system in offline mode with the same horizontal resolution of 4 km for the period 2000–2016, with a spin up period of seven years.

### 2.3. The biogeochemical model

The nutrients-phytoplankton-zooplankton-detritus (NPZD) part of the NORWECOM.E2E was primarily developed to study primary production, nutrient budgets and dispersion of particles such as fish larvae and pollution (Skogen et al., 1995; Skogen and Søiland, 1998). It has been validated by comparison with field data in the North Sea/Skagerrak (e.g. Skogen et al., 1997, 2004; Søiland and Skogen, 2000; Hjøllo et al., 2009), as well as in the Nordic Seas and Barents Sea (Skogen et al., 2007; Hjøllo et al., 2012; Skaret et al., 2014). The model is forced by physical ocean fields (velocities, salinity, temperature, water level and sea ice) and atmospheric fields (wind and short-wave radiation) in offline mode. It is coupled to the physical model through the light, the hydrography and the horizontal and vertical movements of the water masses. The prognostic variables include dissolved inorganic nitrogen (DIN), phosphorous (PHO), and silicate, two functional types of phytoplankton (diatoms and flagellates), two classes of zooplankton (meso and micro), two detritus pools (dead organic nitrogen and phosphorous), diatom skeleton (biogenic silica) and oxygen. The zooplankton modules are partly based on the ECOHAM4 model (Moll and Stegert, 2007; Stegert et al., 2009; Pätsch and Kühn, 2008). The simulated processes involve primary and secondary production, grazing by zooplankton on phytoplankton and detritus, respiration, mortality, remineralization of dead organic matter, self-shading, turbidity, sedimentation, resuspension, sedimental burial, and denitrification. A fraction of 10% of the dead organic material is instantly regenerated as DIN (in nature as ammonia) and 25% as PHO available for uptake by phytoplankton, while the rest is partly regenerated through the detritus pool (Garber, 1984; Bode et al., 2004). Remineralization takes place both in the water column and in the sediments. Particulate matter has a constant sinking speed and may accumulate on the bottom, when the bottom stress is below a certain threshold. Likewise, resuspension takes place, when the bottom stress is above a limit. Parameters of the biogeochemical processes are taken from literature based on experiments in laboratories and mesocosms, or deduced from field measurements (Pohlmann and Puls, 1994; Aksnes et al., 1995; Mayer et al., 1995; Gehlen et al., 1995; Lohse et al., 1995, 1996).

The incident irradiation used in the biogeochemical model is calculated with a formulation based on the work by Skartveit and Olseth (1986, 1987), using short wave radiation as input. Nutrient initial fields are typical winter values of Atlantic water in the Norwegian Sea (F. Rey, pers. comm.). Both diatoms and flagellates are initialized with a low concentration of 0.10 mg $N/m^3$. These values are also used at the open boundaries. Inorganic nitrogen is added to the system from the atmosphere at each time step, since there is no river input of nutrients. To absorb inconsistencies between the forced boundary conditions and the modelled values, a 7-gridcell “Flow Relaxation Scheme” zone is used around open boundaries (Martinsen and Engedahl, 1987).

### 2.4. The Calanus finmarchicus individual-based model

The model is a three-dimensional individual-based model taking into account life history, behavior, growth, mortality, and reproduction of *C. finmarchicus*. The model addresses the full 13-stages life cycle of *C. finmarchicus*; from eggs to spawning adults (eggs + 6 nauplii stages + 6 copepodite stages). Individuals develop into the next stages, when stage-specific critical weights (constant in time and space) are reached (Carlotti and Wolf, 1998). The super-individual (SI) approach (Scheffer et al., 1995) is applied, where one SI represents many ($\sim 10^{12}$) identical individuals, and the number of such identical siblings is one of the attributes of the SI. Adult individuals can reproduce when their structural weight is above 100 μg. They have attained enough fat reserves to spawn a batch of eggs, and they are positioned within the upper mixed layer (<40 m). An overview of growth, mortality, movement and reproduction processes is given in Table 1. When it comes to seasonal/ontogenic vertical migration in *C. finmarchicus*, the actual mechanism(s) triggering it are far from understood. Life history and behavioral strategies of individuals are therefore modelled through a strategy vector (Huse et al., 1999), consisting of five behavioral and life-history-adaptive traits, and evolved for a *C. finmarchicus* population inhabiting the Norwegian Sea and the northern parts of the North Sea using a genetic algorithm approach (Huse et al., 2018). This concept involves equipping individuals with “genes” and adapting these by simulating evolution by natural selection over many generations (Huse and Giske, 1998; Huse et al., 1999). The genetic algorithmic approach can be considered as the “spinup” of the model, as it simulates natural selection in the study area over time. The values of the adapted “genes” or strategies are listed in Table 1, including the date for ascent (WUD) from overwintering depth (OWD) to surface waters, the start date for copepodites stage CV to allocate fat (AFD) to prepare for overwintering, the relative fat content (FSR) to be obtained before descending to overwintering and two genes ($VM_1$ and $VM_2$) that determine vertical position (DD) through the following relationship: $DD = VM_1 + VM_2 * L$, where L is the length of the individual. At night, individuals are placed at the maximum chlorophyll depth, while during daytime the larger value between the maximum chlorophyll depth and DD is chosen. An offspring inherits the strategy vector from its parents. For further details the readers are referred to the work by Hjøllo et al. (2012) and Huse et al. (2018). Horizontal movement of a SI is due to passive drift driven by the velocity fields from the ROMS and a fourth order Runge–Kutta method. The initial distribution field for *C. finmarchicus* in the model is based on an overwintering population distributed in the deep Norwegian Sea basin as well as in the Greenland- and Barents Sea, evolved through a four-year long adaptation process (Hjøllo et al., 2012). The IBM for *C. finmarchicus* is coupled to the biogeochemical model and enforces grazing on phytoplankton

**Table 1**
Process overview and scheduling for the *C. finmarchicus* IBM setup.

| Process/ parameter | Scheduling | Reference |
|---|---|---|
| Growth | NI and NII; Belehrádek equation (temperature dependent) NIII and above: functional response, type 2 (as a function of phytoplankton density, temperature and size) | Lynch et al. (1998);Carlotti and Wolf (1998);Campbell et al. (2001) |
| Mortality | Eggs-nauplii: unspecified + tactile<br>Copepodite-adults: unspecified (stage-dependent), fish predation (geographically uniform, daylight- and prey size dependent, restricted to upper 600 m), invertebrate predation (geographically uniform, day/night dependent, exponentially decaying in upper 1000 m), starvation (stage-dependent weight limited), reproduction stress (if > 800 eggs produced), export out of model area | Ohman et al. (2004);Fiksen (2000) |
| Movement | Vertical: daily migration between chlorophyll maximum at night and (for copepodite stage CIV-CVI) to size dependent depth of typically 60 m. Ascent and descent velocity to/from overwintering depth of 1 m hour$^{-1}$<br>Horizontal: by ocean currents | Dale and Kaartvedt (2000); Heath (1999);Huse et al. (2018) |
| Reproduction | Spawning when in the upper mixed layer, structural weight > 90 μg and sufficient fat reserve. Strategy vectors inherited from parents. | Carlotti and Wolf (1998) |
| Life strategies | Initial values from literature. For the adapted start population:<br>Wake-Up-Day (WUD): Date for ascent from overwintering state: Feb 10-April 10<br>Allocation-to-Fat-Day (AFD): Date for initiating fat allocation in stage CV: March 20-July 1<br>Fat-Soma-Ratio (FSR): Fat/soma ratio needed before descending to overwintering, 0.4 ± 0.2<br>Over-Wintering-Depth (OWD): 300–1100 m<br>VM$_1$ and VM$_2$: Two genes that determine the vertical position during day through the following relationship: VM$_1$ + VM$_2$*L | Heath (1999);Fiksen (2000); Edvardsen et al. (2006); Hjøllo et al. (2012);Huse et al. (2018) |

and microzooplankton. The model unit for *C. finmarchicus* is carbon, which can be converted to dry weight by using a conversion factor of two (Hirche et al., 2001).

The *C. finmarchicus* IBM has been validated in previous studies by Hjøllo et al. (2012) in the Norwegian Sea, and by Dalpadado et al. (2014) and Skaret et al. (2014) in the Barents Sea for the period 1995–2007.

### 2.5. Continuous plankton recorder data

The Continuous Plankton Recorder Survey is a long-term, sub-surface marine plankton monitoring program consisting of a network of CPR transects towed monthly across the major geographical regions of the North Atlantic ("CPR Survey Data Catalogue". Continuous Plankton Recorder Survey. Marine Biological Association of the UK. https://data.cprsurvey.org/datacatalog/). It has been operating in the North Sea since 1931 with some standard routes existing with a virtually unbroken monthly coverage back to 1946 (Batten et al., 2003; Reid et al., 2003).

The CPR survey is recognized as the longest sustained and geographically most extensive marine biological survey in the world (Edwards et al., 2010). The dataset comprises a uniquely large record of marine biodiversity covering ∼ 1000 taxa over multi-decadal periods. The CPR data used in this study uses the 'M' route that runs from Aberdeen to southern Norway on a monthly basis.

The CPR is a high-speed plankton recorder that is towed behind 'ships of opportunity' through the surface layer of the ocean (~10 m depth) (Warner and Hays, 1994). Water passes through the recorder and plankton are filtered by a slow-moving silk (mesh size 270 μm). A second layer of silk covers the first and both are reeled into a tank containing 4% formaldehyde. Upon returning to the laboratory, the silk is unwound and cut into sections corresponding to 10 nautical miles and approximately 3 m$^3$ of filtered sea water. There are four separate stages of analysis carried out on each CPR sample, with each focusing on a different aspect of the plankton: (1) overall chlorophyll (the phytoplankton colour index; PCI); (2) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton (zooplankton "traverse"); and (4) larger zooplankton (zooplankton "eyecount"). The collection and analysis of CPR samples have been carried out using a consistent methodological approach, coupled with strict protocols and Quality Assurance procedures since 1958, making the CPR survey the longest continuous dataset of its kind in the world (Richardson et al., 2006). Zooplankton analysis of CPR data is carried out in two stages, with small (<2 mm) zooplankton identified and counted on-silk (representing ∼ 1/50 of the filtering silk) which includes the copepodite Calanus stages I-IV and larger (>2 mm) zooplankton enumerated off-silk which includes a count of *C. finmarchicus* (stages V-VI) that is used in the current study.

### 2.6. Empirical orthogonal function (EOF) analysis

EOF analysis can be used to investigate possible spatial patterns of variability of a given variable and how they change with time. Given any space–time field, EOF analysis finds a set of orthogonal spatial patterns along with a set of associated uncorrelated time series or principal components (PCs) (Hannachi et al., 2007). Therefore, EOFs of a space–time process can represent mutually orthogonal space patterns where the data variance is concentrated, with the first pattern being responsible for the largest part of the variance, the second for the largest part of the remaining variance, and so on (Zhang and Moore, 2015).

## 3. Results

### 3.1. Model validation

We have compared our model results with horizontal survey data in the east as well as CPR data from a transect across the northern part of the North Sea. The modelled mean abundance of *C. finmarchicus* (copepodite stages CI-CVI) over upper 100 m water depth in the eastern part of the North Sea at the end of March (Fig. 2d) compares very well with the survey data published by Krause et al. (2003). Both model and data show higher abundance (700–800 individuals/m$^3$) close to the Norwegian coast and the abundance decreases gradually towards offshore to <50–100 individuals/m$^3$.

On a finer scale, we compared the modelled *C. finmarchicus* abundance with the CPR data along a section across the inflow area in the northern North Sea (Fig. 1, black line). Both modelled and CPR data were standardized separately using the standard-score method, where comparable values were calculated by subtracting the mean value of the individual dataset from each data point and then dividing the difference by the standard deviation of the dataset. As the absolute values from the model and the CPR are not directly comparable, the comparison is focused on the temporal and spatial patterns. As shown in Fig. 2a, the CPR data show a clear seasonal pattern with three peaks of copepodite stages CV-CVI in February (generation 0, overwintering ones from previous year), May and August in the eastern part of the transect. It

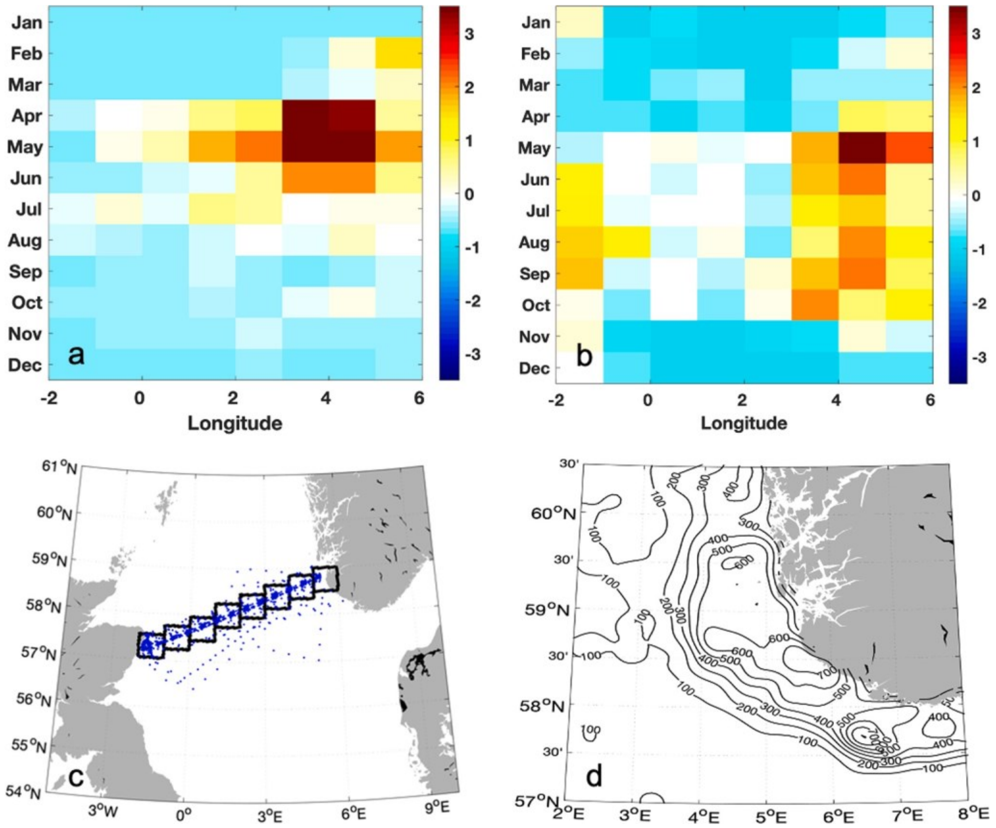

**Fig. 2.** (a) Standardized continuous plankton recorder (CPR) data of *C. finmarchicus* (copepodite stages CV-CVI) on positions shown as blue dots in (c), averaged monthly over 2000–2016; (b) Standardized modelled *C. finmarchicus* (CV-CVI) abundance in areas shown as the black boxes in (c), averaged monthly over 2000–2016. Standard-score method is used for standardization. (d) Modelled abundance (ind./m$^3$) of *C. finmarchicus* (CI-CVI) averaged over upper 100 m water depth on 31st March over 2000–2016.

indicates that there are at least two new generations of *C. finmarchicus* in this area, with the highest abundance during the second peak. Spatially, the first peak occurs close to the Norwegian coast, while the major peak is found approximately on the western shelf break of the Norwegian trench. The pattern looks rather different over the North Sea shelf areas. When moving westwards the signal becomes gradually lower with one peak in April/May and another in July. The model result confirms the main patterns shown from the CPR data (Fig. 2b). There is a weak winter peak of CV-CVI stages in February close to the Norwegian coast, followed by a stronger peak in May with the highest value in the trench and along the western shelf break, and in addition a weaker peak in August/September. Different from the CPR data, when moving westwards along the transect the signal first becomes lower over the shelf area, but then it becomes higher again at the Scottish coast.

### 3.2. Overwintering *C. finmarchicus* in the North Sea

The modelled average abundance of overwintering *C. finmarchicus* in mid-December for the period 2000–2016 is shown in Fig. 3, with the highest value appearing in Skagerrak area of the Norwegian Trench. Interestingly, there is a substantial amount of overwintering *C. finmarchicus* (~600 individuals/m$^3$) in the north-west of the North Sea close to the northern boundary, where the water depths are ~100–150 m. Even in the central North Sea, where the water depths are shallower than 100 m, the average overwintering abundance still amounts to ~360 individuals/m$^3$ in mid-December. By the end of January, shortly before the ascent of *C. finmarchicus*, the modelled abundance of the overwintering population is reduced on average by 22% over the North Sea compared to the values in mid-December, but the general distribution pattern remains the same.

We have analyzed the variability in spatial pattern of *C. finmarchicus* overwintering biomass using the empirical orthogonal function (EOF) analysis (Fig. 4). The first two modes of variability describe a similar fraction of the total variability and shows an east–west (first mode) and north–south (second mode) dipole. The time series of the second mode of variability shows a decreasing trend over time. Based on the spatial pattern of the second mode, which shows high values in the *C. finmarchicus* inflow area close to the east coast of Scotland, we have calculated the overwintering biomass in the marked area as shown in Fig. 4b. A decreasing trend in the overwintering biomass is found over the simulation period (Fig. 4d). In 2005 and 2011, high overwintering biomass were seen, corresponding in time with the high inflow of biomass from the north (Fig. 5a).

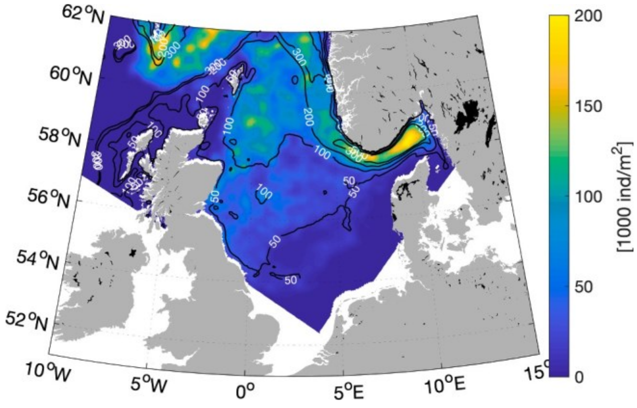

**Fig. 3.** The modelled abundance (1000 individual/m$^2$) of overwintering *C. finmarchicus* copepodite stage CV integrated through the whole water column, on December 16th averaged over 2000–2016. The contour lines and white labels indicate the bathymetry.

### 3.3. Inflow of *C. finmarchicus* into the North Sea

The simulated annual mean biomass of *C. finmarchicus* during

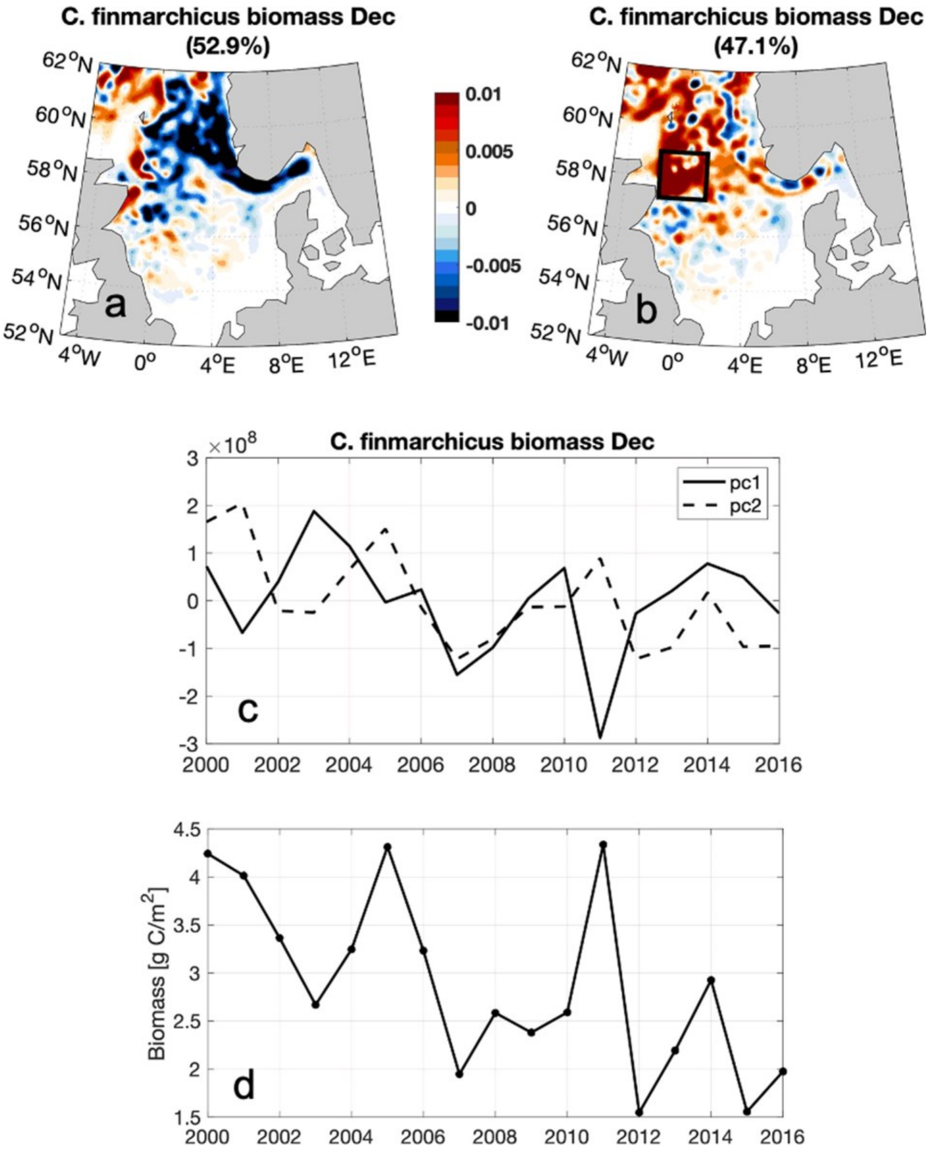

**Fig. 4.** The first two modes of the empirical orthogonal function (EOF) for *C. finmarchicus* overwintering biomass in December during 2000–2016; (a) first mode where 52.9% of the variance is explained, (b) second mode where 47.1% of the variance is explained, (c) the principal component (pc) time series of each mode, (d) overwintering biomass of *C. finmarchicus* in December in the core inflow area marked as a black square in (b).

2000–2016 (Fig. 5a) averages 0.94 (ranging 0.81–1.05) million-tonnes of carbon in the North Sea. It is rather stable over the simulation period. We have also calculated the inflow biomass into the North Sea, by counting the numbers of individuals (multiplied by body weight) that have entered the blue polygon, shown in Fig. 1, across the boundary from the north. The average inflow biomass is 0.4 million-tonnes of carbon per year with the highest value of 0.7 in 2005 and the lowest value of 0.3 in 2010. The values differ with a factor of 2.5 between the years, but there is no trend over the whole period (Fig. 5a). Compared to the mean North Sea *C. finmarchicus* biomass, the inflow biomass contributes on average 41% (27–65%) over the 17 years (Fig. 5b), and therefore, is an important contribution to the interannual variability of the biomass. We have quantified the inflow biomass via three main currents into the North Sea. The Fair Isle Current Inflow, the East Shetland Atlantic Inflow (ESAI) and the inflow along Norwegian Trench contribute to 6%, 37% and 57% to the total inflow biomass, respectively.

The horizontal and vertical positions of the inflow of *C. finmarchicus* super-individuals in 2001 are shown in Fig. 6 as an example. During summer months, *C. finmarchicus* flows into the North Sea mainly in the upper 50 m water depth, spreading over the whole transect. In winter months, the inflow of *C. finmarchicus* into the North Sea occurs deeper, mainly via the ESAI and the western flank of the Norwegian Trench. The *C. finmarchicus* that are transported into the North Sea in winter are likely at their overwintering depth, and their vertical position in the water column during transportation is constrained by topography. Therefore, they enter the North Sea in winter mainly close to the bottom of the sea, which is usually shallower than their natural overwintering depth in the source region. The depth gradient from the west to the east shown in Fig. 6 in winter months reflects the topography gradient of the transect.

Fig. 7 shows the seasonal variation in the inflow of *C. finmarchicus* biomass as well as abundance. The inflow of *C. finmarchicus* biomass drops to the lowest value of a year in late April to May and reaches relatively high values in late August to September. This reflects the seasonal biomass development of *C. finmarchicus* in the source region of the inflow, which is the Faroe-Shetland Channel and the south of the Norwegian Sea. The abundance of the inflowing *C. finmarchicus* peaks around May, co-occurring with the peak in *Calanus* spawning and thus high numbers of eggs and nauplii.

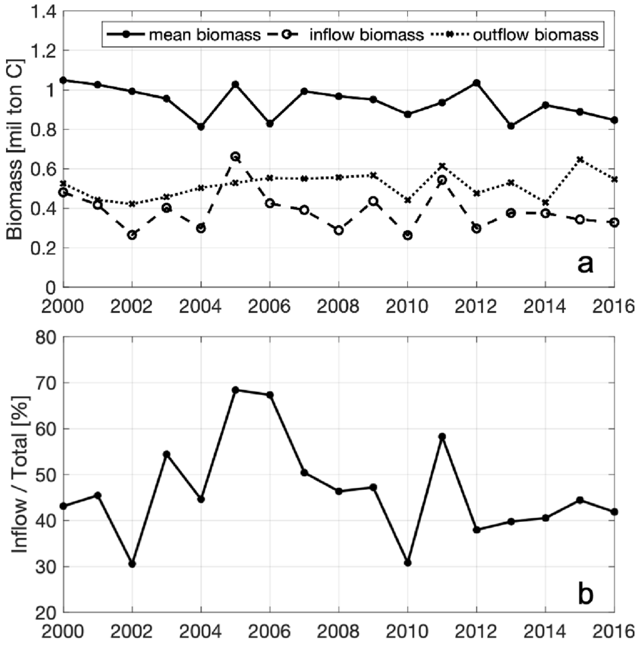

**Fig. 5.** (a) Time series of annual mean daily biomass of *C. finmarchicus* (million tonnes carbon) in the North Sea, and the biomass flow into and out of the North Sea across the northern boundary (blue polygon in Fig. 1). The biomass is vertically integrated over the whole water column with all life-stages included. (b) The inflow biomass relative to the total *C. finmarchicus* biomass in the North Sea.

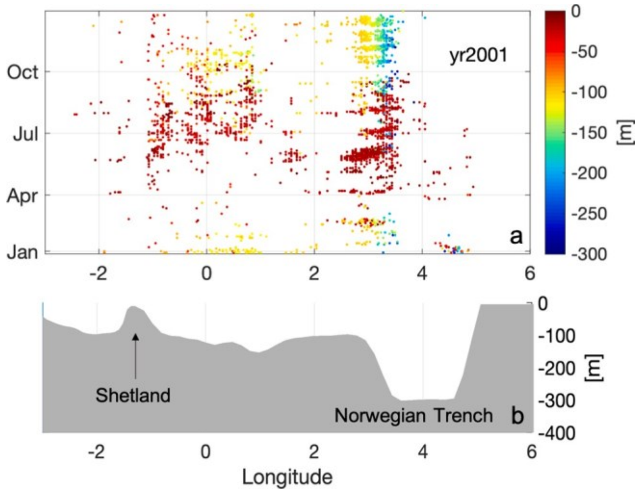

**Fig. 6.** (a) Horizontal and vertical positions of *C. finmarchicus* as they entered the North Sea from the Norwegian Sea in 2001. Every colored dot indicates a super-individual. Eggs are excluded in this figure as there are too many of them. (b) Bathymetry of the northern boundary of the modelled North Sea.

### 3.4. Sustainability of *C. finmarchicus* in the North Sea

We have traced the native North Sea *C. finmarchicus* population through generations to explore its sustainability. The native population is defined as the ones found inside the North Sea on 1st January in 2000 (the starting date of the simulation after spin-up), as well as their offspring through generations. The number of native individuals drops from $1.7\text{x}10^{16}$ to half of the size after one year and decreases to 1% of the initial size after 12 years in our simulation (Fig. 8). Conversely, the total number of individuals in the North Sea varies between $1.0\text{x}10^{16}$ and $1.8\text{x}10^{16}$, with no significant trend over the modelled period (Fig. 8). It indicates that the *C. finmarchicus* population in the North Sea is not self-sustained, but strongly depends on the inflow of *C. finmarchicus* from the north.

## 4. Discussion

Despite the important role of *C. finmarchicus* in the North Sea ecosystem, surprisingly few studies have quantified vital indexes such as biomass, abundance and interannual variability covering full ocean depth. Previous studies have mainly been based on observational data from coastal monitoring stations (Melle et al., 2014; Bresnan et al., 2015) or from near-surface abundance estimates obtained by the CPR (Pitois and Fox, 2006; Strand et al., 2020). In the present work, an IBM for *C. finmarchicus,* coupled to a three-dimensional NPZD ecosystem model, has been used to study *C. finmarchicus* biomass, abundance, interannual variability in the North Sea, as well as the exchange with the Norwegian Sea and self-sustainability.

### 4.1. The biomass estimates: overwintering, inflow and outflow

To our knowledge, quantitative estimate of either total or overwintering biomass of *C. finmarchicus* in the North Sea is scarce. Our study suggests an annual overwintering biomass of 0.44 million-tonnes of carbon within the North Sea, with an interannual variability range of the order of 0.2 million-tonnes. High overwintering biomass appears in the Norwegian Trench and in the north-western North Sea. We have recognized a decreasing trend in overwintering biomass in the north-western North Sea over the simulated 17 years, indicating a decrease in the East Shetland Atlantic Inflow (ESAI). The overwintering biomass in the Norwegian Trench, on the other hand, is relatively stable.

The modelled annual mean biomass of *C. finmarchicus* is 0.94 million-tonnes of carbon within the North Sea. On average, over 40% of the annual mean biomass (0.39 million tonnes carbon) is supplied by the inflow from the Norwegian Sea, which thus contributes to a major part of the interannual variability. The *C. finmarchicus* population in the North Sea is not self-sustained but depends on this inflow, which is in agreement with a previous modelling study by Speirs et al. (2006). Without this annual import the model suggests a decline of >30% per year on average and that means the native population would become extinct (<1%) in ~12 years (Fig. 8).

The annual mean outflow biomass (calculated as the number of individuals that leave the blue polygon shown in Fig. 1, multiplied by body weight) amounts to 0.52 million-tonnes per year, mainly carried by the Norwegian coastal current. It is worth to notice that the annual mean outflow biomass is larger than the mean inflow biomass (0.52 versus 0.39 million-tonnes carbon per year), which indicates that the highly productive North Sea plays an important role as feeding ground and growth region for *C. finmarchicus*. This becomes clearer from comparing Fig. 7a and 7b, which shows a tremendous inflow of eggs and young stages in May/June, and due to their small body mass, they do not contribute to the inflow biomass (minimum in May). Theses eggs and juveniles develop, feed and grow in the North Sea during summer and contribute then to the biomass outflow from the North Sea via the Norwegian Coastal Current later in the year, so that the annual biomass outflow from the North Sea exceeds the biomass inflow.

We note that the biomass estimates are influenced by the predation pressure in the model, which may be underestimated (see below), thus the biomass estimates are likely on the high end.

### 4.2. Drivers of interannual variability of *C. finmarchicus* biomass

Fromentin and Planque (1996) showed that the abundance of *C. finmarchicus* in the North Sea was inversely correlated to the NAO (the relationship broke down in 1996), which again is correlated to the volume transported into the North Sea (Hjøllo et al., 2009). The possible reasons of the breakdown were suggested by Reid et al. (2003) as a

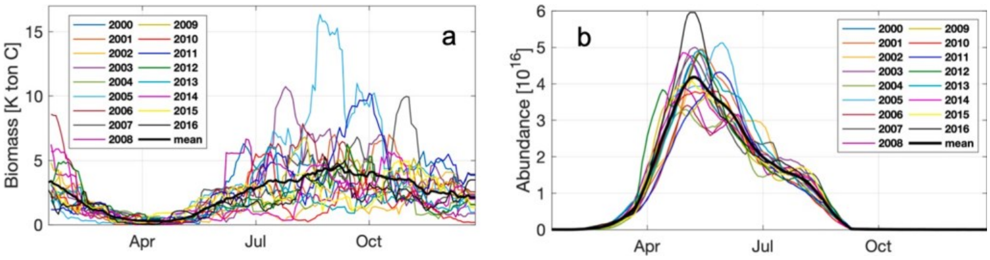

**Fig. 7.** Seasonal variation of the inflow of *C. finmarchicus* (a) biomass ($10^3$ tonnes carbon) and (b) abundance (number of individuals) from the Norwegian Sea across the northern boundary of the modelled North Sea. The values are vertically integrated over the whole water column and all stages are included. The colored lines are 11-day running mean quantities for each year and the thick black lines are the mean values over all years.

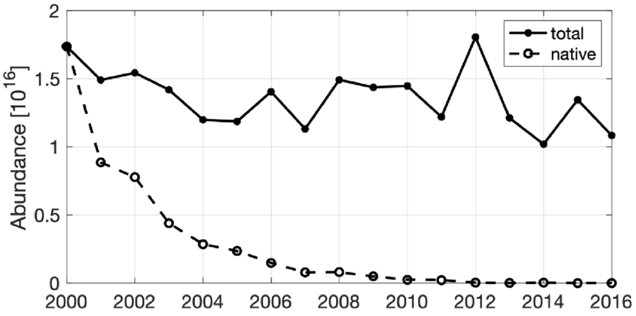

**Fig. 8.** Number of total and native North Sea *C. finmarchicus* individuals on 1. January of the period 2000–2016. Native population is defined as the individuals that are found in the North Sea on 1. January of 2000 and their offsprings.

decline in the overwintering stock in the Norwegian Sea and a general warming resulting in a northward biogeographic shift of boreal species like *C. finmarchicus*. Another hypothesis was raised by Edwards et al. (2013) who have related the relationship breakdown to a shift in the Atlantic Multidecadal Oscillation (AMO) cycle to a positive phase in 1996 that affected the inflow of the North Atlantic Current to the North Sea.

In the present study, the interannual variability of the inflow of *C. finmarchicus* biomass is driven by the inflow water volume ($r = 0.58$, $p < 0.02$) and by the variation of biomass in the Faroe-Shetland Channel as well as in the south of the Norwegian Sea as the source region of the inflow (insignificant) (Fig. A2). In order to identify the drivers of interannual variability of the mean North Sea *C. finmarchicus* biomass, the inflow biomass via the Norwegian Trench (INF) (as the most important inflow), the sea surface temperature (SST) and net primary production (NPP) have been incorporated in a multiple linear regression analysis. The result suggests that the INF has the strongest correlation among the three ($r = 0.52$, $p < 0.05$) with the *C. finmarchicus* biomass in the North Sea, which is in agreement with the findings by Madden et al. (1999). The SST and NPP only explain a very small part of the variation in annual mean *C. finmarchicus* biomass regardless of the productive or unproductive season. This result is unlike what we usually see in an NPZD model, whose phytoplankton and zooplankton dynamics are very tightly coupled in space and time (with lag), and thus also on a multiple-year level (Fennel and Neumann, 2004). However, in our IBM the *C. finmarchicus* biomass is an emergent property resulting from all different individual traits that respond to not only food availability, but also other factors such as temperature, current and predators (Huse et al., 2018). This complicates the picture of the mechanism that controls *C. finmarchicus* biomass. Nevertheless, this might be closer to the reality in nature rather than the almost perfectly correlated phytoplankton and zooplankton dynamics.

### 4.3. Stairway to heaven, swept by currents, where do *C. finmarchicus* enter?

We have found that the exchange of *C. finmarchicus* between the Norwegian Sea and the North Sea plays an essential role in driving the spatial–temporal variation in *C. finmarchicus* stock in the North Sea. Backhaus et al. (1994) have illustrated that the overwintering *C. finmarchicus* associated with the NSDW along the continental slope were transported into the North Sea mainly by wind-driven Ekman transport via the Fair Isle Current and the Norwegian Trench. Heath et al. (1999) have further elaborated on the two different pools of overwintering *C. finmarchicus* along the continental slope and have confirmed that the pool in the Faroe Shetland Channel associated with the NSDW was the most important reservoir for the North Sea. But they stated that neither the Fair Isle Current, nor the East Shetland Atlantic Inflow have been important routes for the *C. finmarchicus* inflow to the North Sea. Sundby (pers. comm., IMR) has found a correlation between the presence of Norwegian Sea Intermediate Water (NSIW) at the bottom of the Norwegian Trench (from observed temperatures in spring and modelled transport in winter) and the abundance of *C. finmarchicus* from CPR data in the following summer. He concluded that overwintering *C. finmarchicus* in the Norwegian Sea might be transported into the North Sea along the bottom of the western flank of the Norwegian Trench with the NSIW. We agree with Backhaus et al. (1994), Heath et al. (1999) and Sundby (pers. comm., IMR) on the Norwegian Sea origin of the inflow and the most important route via the Norwegian Trench. Backtracking the super-individuals shows that they have been caught in the Faroe Shetland Channel, before entering the North Sea, mainly through recirculation of Norwegian Sea water along the Iceland-Faroe ridge (Fig. 9a). This confirms the conclusion by Backhaus et al. (1994) that the *C. finmarchicus* cycle in the northern North Sea should not be considered in isolation, but as a part of an interwoven network of cycles involving the neighboring shelf areas of Faroe Islands and south-east Iceland. The super-individual tracking approach also shows that the main inflow of *C. finmarchicus* to the North Sea is carried by three branches of the North Atlantic current, with the most important inflow going southward along the western flank of the Norwegian Trench (accounts for 57% of the total inflow biomass) and the second important one being the East Shetland Atlantic Inflow (ESAI) (37%) (Fig. 6a and Fig. 9b) in contrast to the conclusion by Heath et al. (1999). The inflow via the Fair Isle Current as suggested by Backhaus et al. (1994) plays only a minor role (accounts for only 6% of the total inflow biomass) in our study. Our results have confirmed the deep inflow of *C. finmarchicus* during winter and early spring (Fig. 6), but there is also inflow into the North Sea over most parts of the shelf throughout the whole year.

### 4.4. Model refinements

There are three issues related to model-observation comparison, mortality by fish predation and ending of diapause in spring that should be taken into account when interpreting the results.

Firstly, to be assured that our model is competent for the study area

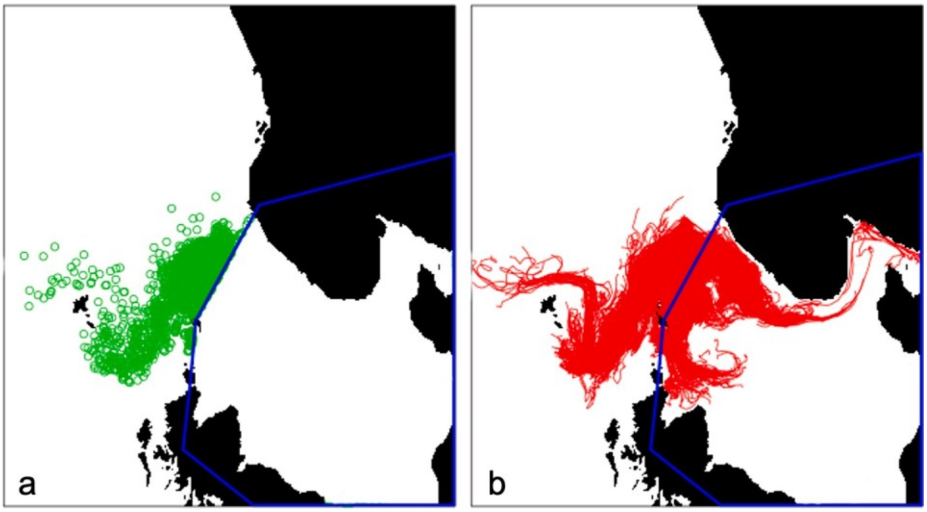

**Fig. 9.** (a) The starting positions of *C. finmarchicus* who have entered the North Sea (marked as the blue polygon) in the course of 2001. (b) The trajectory of those super-individuals in (a) throughout the whole year (2001).

and purpose, we have compared model results with CPR data from a section across the northern end of the area, which is considered as a hot spot of this study. In general, the model and CPR data agree on the timing and location of the maximum abundance of the *C. finmarchicus*. The largest difference between the model and the CPR is the strength of the signal in autumn, as the model shows stronger signal than the CPR data do. The controlling mechanisms for the processes leading copepods either to reproduce and thus producing high autumn abundance, or to go into diapause are unknown. In the model, the AFD (Allocation-to-Fat-Day) "gene" determines whether a SI should produce a new generation or build enough fat reserves for enabling overwintering, and the FSR (Fat-Soma-Ratio) "gene" decides when the fat content is high enough to go into diapause. Compared to the CPR data, the model tends to overestimate the number of SI that decides to produce a new generation. Many individuals of this new generation will not mature for overwintering during autumn but instead appear as a high autumn abundance/biomass that gradually decreases as they starve and die off before the next spring. This is probably partly a model artifact. On the other hand, cautions should be taken when comparing the abundance between the CPR data and the model results, as the way how we process the data and quantification of abundance from CPR (Batten et al., 2003) pose some challenges to the comparison. We use the monthly mean CPR data averaged over one-degree boxes over a 17-year period. The number of CPR data for making such a mean value varies in space and time (Text A1 and Fig. A1). In addition to this irregularity, zooplankton rarely constitute continuous fields in space but rather establish patchy patterns with strong gradients due to the variable and turbulent currents (Mackas et al., 1985; Richardson et al., 2000; Martin, 2003). Observations of such quantities strongly depend on whether a patch is hit or not, and the representativeness is a function of the sampling technique and the spatio-temporal resolution (Omori and Hamner, 1982). For example, in spring when *C. finmarchicus* are positioned mainly at a deep chlorophyll maximum (~20 m), then the abundance would be underestimated by CPR, since the sampling depth is at 7–10 m. Finally, it is well known that zooplankton display diurnal vertical migration (e.g., Forward, 1976), thus the abundance at a fixed depth will depend on the time of the day when the sampling is done. The CPR data are collected at different hours of the day, therefore, they are likely to represent a daily mean, while the model results are always stored at midnight of the model day.

Secondly, in the present model set-up for the North Sea, bottom-up forcing is mechanistically represented while tactile, mesopelagic and pelagic predation are parameterized separately. For an example year (2005), modelled annual zooplankton mortality by predation is on average 2.0 g C/m$^2$ for the whole model domain. Zooplankton consumption by fish in the North Sea has been estimated by Heath (2007) to be 19–25 g C/m$^2$/year. Daewel et al. (2014) found little evidence that predators exerted top-down control on zooplankton in the North Sea, although local top-down control can be expected due to spatial (in front regions between water masses) and temporal (more likely in autumn) variation. In NORWECOM.E2E, during winter copepodite stage IV and later stages are subject to predation by pelagic and mesopelagic predators as a function of light, if *C. finmarchicus* are shallower than 400 m and 600 m, respectively. In the Norwegian Sea, the *C. finmarchicus* overwinter in diapause at depths of 500–1000 m, well below their predators. However, in the North Sea, the overwintering depth is restricted by the water depth, which is on average ~90 m, i.e., much shallower than the Norwegian Sea (~2000 m). This leads to a higher modelled mortality rate in the North Sea compared to the Norwegian Sea during winter, which has been observed by previous studies (Kaartvedt, 2000; Planque and Fromentin, 1996; Heath et al., 1999). Our modelled mortality rate for overwintering *Calanus* is typically 0.6–0.7% per day in the North Sea. This rate is hard to validate, as observations from the deeper areas of the North Sea during winter are scarce. Nevertheless, winter mortality rates of *Calanus* in some of the Norwegian fjords have been reported. Bagøien et al. (2001) have found that the mortality rates of *Calanus* vary within 0.8–2.7% per day and the highest mortality is due to predation from mesopelagic fish. Bagøien et al. (2000) have studied the predation on *Calanus* by krill (*Meganyctiphanes norvegica*) during winter in the Oslofjord (in Skagerrak), where water depths are ~120 m, suggesting a mortality rate of overwintering *Calanus* of 0.1–0.3% per day. However, the authors stated that this low mortality rate might have resulted from a continuous sinking of *Calanus* into the sampling location, thus the rate was considerably lower than the values in other studies, which were generally >0.7% per day (e.g., Bagøien, 1999). A potential model development would be to include more realistic and North Sea adapted fish predation, either directly from fish IBMs or in form of spa- tial–temporal mortality indices created from fish and fish larvae grazing pressure estimates from literature (Maar et al., 2014).

Thirdly, the emergence from diapause is set as an individual trait for each super-individual. The distribution of this trait in the initial population is adapted using a genetic algorithm approach performed for the Norwegian Sea and used a spin-up period of four years (Huse et al., 2018; Hjøllo et al., 2012). The actual mechanism controlling the timing of emergence is unknown, but both surface light and the timing of spring bloom might have an impact. Both factors are different in the North Sea compared to the Norwegian Sea. Thus, the strategies of the initial population are likely to have a bias towards a better fitness for inhabitation in the Norwegian Sea.

The exchange of *C. finmarchicus* between the Norwegian Sea and the North Sea has been demonstrated in this study to play an essential role in driving the spatial–temporal variation in *C. finmarchicus* stock in the North Sea. A further transport of *Calanus* in coastal waters into the fjords is believed to be an important supply to the local *Calanus* population that overwinters well below the sill depths (Lindahl and Hernroth, 1988; Bucklin et al., 2000). Through a two-step exchange, a connection between the large oceanic population of *Calanus* and the local population in the fjords can therefore be established. We have demonstrated the first-step exchange between the Norwegian Sea and the North Sea in the present study. A similar modelling approach with a higher resolution model can be applied to study the second-step exchange between the coastal waters and the fjords with focusing on distinguishing between drifting/exotic and resident/local species in the fjords.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102567.

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