



Assessing the importance of zooplankton sampling patterns with an ecosystem model

Solfrid Sætre Hjøllo*, Cecilie Hansen, Morten D. Skogen

Institute of Marine Research, 5817 Bergen, Norway

ABSTRACT: The copepod *Calanus finmarchicus* is the dominant species of mesozooplankton in the Norwegian Sea and an important food source for multiple commercially exploited pelagic fish stocks. In addition to the patchy distribution of species, the vast size of the Norwegian Sea makes synoptic zooplankton monitoring challenging. Monitoring includes relatively few sampling stations, and the number as well as the geographical location of these vary in time and space among years. In the present study, we explored the sampling patterns in 2 existing datasets: (1) for the period 1994–2004: size-fractionated zooplankton biomass, which allows for estimation of *C. finmarchicus* fractions, at irregularly spaced locations, and (2) for the period 1995–2017: non-size-fractionated zooplankton biomass data, gridded by objective analysis. We first assessed the *C. finmarchicus* data set by virtual sampling in *C. finmarchicus* spatial fields from the end-to-end ecosystem model NORWECOM.E2E. We found that non-consistent sampling patterns during the month of May caused the biomass estimate to be highly dependent on the chosen sampling strategy: sampling patterns from the first part of the period generally produced the highest biomass estimates. We then assessed the gridded zooplankton dataset by applying the 1995–2004 sampling patterns as well as a recent (2020) sampling pattern, which included regular and more numerous sampling locations, and found systematic differences. We conclude that the present May sampling pattern is much more robust and thereby also more likely to provide a good estimate of the interannual variability of the total biomass in the area. This study is an example of how models can be used to mechanistically interpret experimental datasets, and more specifically, how models can be used to assess sampling patterns and reveal their limitations.

KEY WORDS: *Calanus finmarchicus* biomass · Norwegian Sea · Representation error · Virtual sampling · NORWECOM.E2E

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1. INTRODUCTION

The Norwegian Sea, situated north of 60°N, is a section of the Northeast Atlantic Ocean and adjacent to the Arctic Seas. With an area of ~1 000 000 km², it is home to several large pelagic fish stocks which feed intensively on the abundant zooplankton, particularly the copepod *Calanus finmarchicus* (Dalpadado et al. 2000, Broms & Melle 2007, Langøy et al. 2012, Bachiller et al. 2016). *C. finmarchicus* is the dominant species of mesozooplankton in the Norwegian Sea (Melle et al. 2004). A variety of organisms feed on the different stages of *C. finmarchicus*,

including large standing stocks of invertebrates and mesopelagic fish and migrating predators (Dalpadado et al. 1998, Skjoldal et al. 2004). *C. finmarchicus* overwinter at depth mainly as copepodite stages 4 (CIV) and 5 (CV). During early spring, they ascend towards the surface where they mature and produce eggs prior to and during the spring phytoplankton bloom (Marshall & Orr 1972, Niehoff et al. 1999, Broms & Melle 2007, Broms et al. 2009). The new generation stays in the upper waters, while individuals continue to mature, potentially producing another new generation, and build up fat reserves before descending to overwinter (Hirche 1996, Broms &

*Corresponding author: solfrid.hjollo@hi.no

Melle 2007, Broms et al. 2009). Since 1993, zooplankton have been routinely monitored in the southern Norwegian Sea by the Institute of Marine Research (IMR, Norway) via plankton nets used at stations along standardized sections as well as at stations irregularly distributed both spatially and temporally. Both Huse et al. (2012) and ICES (2016) reported a low level of zooplankton biomass around 2009, after a decline since the mid-1990s. Declining zooplankton biomass causes concerns regarding the consequences it may have on the large stocks of commercial fish in the Norwegian Sea that feed primarily on the copepods (Langøy et al. 2012).

The vast size of the Norwegian Sea makes synoptic sampling almost impossible. Traditionally, zooplankton biomass in the Norwegian Sea has been estimated from a temporally and spatially varying number of observations, forming indexes like the arithmetic mean (Mueter et al. 2009, Huse et al. 2012, Toresen et al. 2019). However, zooplankton species like *C. finmarchicus* have patchy distributions in the Norwegian Sea (Basedow et al. 2006, Toresen et al. 2019), and the temporal and spatial irregularity of the sampling pattern (SP) may also influence biomass estimates and, thus, represent a challenge. Temporal irregularity in sampling was addressed by Dupont et al. (2017) using generalized additive models accounting for adult stage representation in the dataset, confirming the increase in *C. finmarchicus* spring abundance prior to the year 2000 and a decrease between the years 2000 and 2011. The decrease in abundance was greater for stations closer to the coast, in accordance with the findings of Toresen et al. (2019). Spatial irregularity can be incorporated by the use of aggregated data (in space, time or by e.g. water masses) or objective mapping methods. Relating distribution to water masses, Broms et al. (2009) applied principal component analysis to examine the geographical distribution of *C. finmarchicus* stages CIV–CVI for the year 1995 and found the highest average abundance in Atlantic and Arctic water masses. Bagøien et al. (2012) used spatiotemporally aggregated basin-scale data to study the seasonal development of *C. finmarchicus* abundance in different water masses for the period 1993–2008. They found a total delay of about 6 wk from coastal to Arctic water masses for the first generation of *Calanus* copepods (CI–CIII), and 2 generations produced in the Atlantic waters. Recently, Kristiansen et al. (2019) used objective mapping of biomass data from the International Ecosystem Survey to identify a post-2003 reduction in the abundance of large *C. finmarchicus* (stage CIV–CVI)

north of the Faroe Islands during May. Using objective mapping procedures and data from the continuous plankton recorder survey along the Svalbard and other transects, Strand et al. (2020) also found high *C. finmarchicus* abundance west of Svalbard and in the Barents Sea entrance for the period 2008–2014/15.

To address temporal and spatial variability in the zooplankton field, a possible approach is to apply an ecosystem model and produce a virtual representation of the dynamic zooplankton distribution, i.e. apply a digital twin. Herein, a full life-cycle model for *C. finmarchicus* embedded in the physical-biological model system 'Norwegian Ecological Modeling system End-to-End' (NORWECOM.E2E) was applied to perform a simulation of *C. finmarchicus* biomass for the period 1995–2004. Motivated by the reported zooplankton variability in time and space, and realizing the temporal and spatial irregularity within the available data sets for *C. finmarchicus*, we explored different SPs by virtual sampling in the model field. In addition, we applied several SPs to a gridded zooplankton observational dataset for the period 1995–2017. The main aim of the study was to utilize the full 3D spatial dimension of a stage-resolving biological model to estimate and compare the biomass from several observation-based SPs for the month of May, thus showing how ecosystem models can be used to mechanistically interpret observational datasets, exemplified by assessing zooplankton sampling in the Norwegian Sea.

2. MATERIALS AND METHODS

2.1. *Calanus finmarchicus* dataset 1995–2004

In situ data on size-fractionated zooplankton biomass collected by the IMR were extracted from IMR databases. The dataset was restricted to only cover the Norwegian Sea (west of 18° E, and 60–72° N) for the period 1995–2004. The basic processing and compilation of this dataset was performed using the free statistical software R (R Core Team 2014). The number of observations as well as the timing and SP varied between years, as the sampling locations were not dedicated to zooplankton monitoring but instead connected to other activities at the IMR. Data were sampled throughout the whole year, but the highest sampling frequencies were found during spring, particularly May. The zooplankton biomass analysed in this paper was based on collections with WP2 nets (Fraser 1966), which have an opening area of 0.25 m² and a mesh size of 180 µm (modified from originally

200 µm). The WP2 nets were hauled vertically from 200 m (or from near the bottom in shallow areas) to the surface. The unit for biomass in the dataset is dry weight per unit surface area. If more than 1 trawl haul was available at a station, only 1 biomass sample in the dataset was included (the one closest to 200 m depth or bottom if in shallow areas). The IMR routine is to split each zooplankton sample in 2 equally sized parts via a Motoda splitter (Motoda 1959). One part is preserved in formalin for subsequent taxonomic identification and enumeration of individuals, while the other part is used for estimation of size-fractionated biomass (see Melle et al. 2004 for details). Due to the amount of work involved, only selected samples are processed taxonomically in the laboratory, while size-fractionated biomass is estimated for all samples. The size-fractions for zooplankton are 0.18–1, 1–2, and >2 mm, while shrimps, krill, and fish are in the >2 mm fraction and are weighed separately. Estimates of observed *C. finmarchicus* biomass for each month were calculated as the arithmetic mean over all relevant stations, using *C. finmarchicus* content of 50, 70, and 0% of the size fractions 0.18–1, 1–2, and >2 mm, respectively (Gjøsæter et al. 2000, Skjoldal et al. 2004, W. Melle pers. comm.). Dry weight biomass was converted to carbon using a carbon:dry weight ratio of 0.45 (Brey et al. 2010). Selecting May observations produced a time series labelled herein as ‘Obs-*insitu*’. Fig. 1 shows the sampling stations in May of each year, as well as the number of observations in the same month. For model validation purposes, we also combined all observations into a composite annual cycle by averaging all observations from all years in each month. The sum of observations over the period 1995–2004 varied from 35 (December) to 559 (May). This dataset is a subset of the zooplankton dataset (described in Section 2.2).

2.2. Zooplankton dataset 1995–2017

Zooplankton biomass data for the period 1995–2017 are a product of an International Ecosystem Survey in the Nordic Seas and stored in the Planning Group on Northeast Atlantic Pelagic Ecosystem Surveys (PGNAPES) database at the Faroe Marine Research Institute. The dataset includes numerous and widely distributed zooplankton observations across the Norwegian Sea, covering Atlantic water, Arctic water, and the Arctic Frontal Zone. Herein, we used data from the uppermost 200 m sampled by WP2 nets and collected by the DTU Aqua/Technical University

of Denmark, Faroe Marine Research Institute, IMR (Norway), and the Marine and Freshwater Research Institute (Iceland). Spatial fields of Norwegian Sea zooplankton biomass during May throughout 1995–2020 were derived from interpolated zooplankton observations using objective analysis utilizing a Gaussian correlation function (ICES 2016, 2020a,b [see Fig. 2.4 in ICES 2020a]). The routines for the objective analysis were made available through co-operation with the Working Group on Integrated Ecosystem Assessments for the Norwegian Sea/Dr. Øystein Skagseth, IMR. The biomass distributed in size classes was not available. We used the dataset to compute biomass estimates with the SP for May 2020 (with 142 observations) (SP2020) as well as with the SP1995–SP2004 with the aim to explore both the influence of applying different SPs to a dataset with improved quality (longer time span, more numerous, and more widely and regularly spatially distributed observations, gridded by statistical methods) and to investigate to what extent the present SP (SP2020) gives a more robust estimate of the total biomass.

2.3. Zooplankton model and simulation

The NORWECOM.E2E model system consists of a physical ocean model that provides offline forcing fields of hydrography, currents, turbulence, and light, and a biogeochemical nutrients–phytoplankton–zooplankton–detritus model 2-way coupled to a suite of individual based models (IBMs) for zooplankton and fish species, among them 1 model for *C. finmarchicus* (Hjøllo et al. 2012, Huse et al. 2018). *C. finmarchicus* is simulated using the superindividual approach (Scheffer et al. 1995), in which a superindividual represents many ($\sim 10^{12}$) identical individuals. The most important processes of the *C. finmarchicus* model, which are repeated daily, are movement, growth, mortality including predation, and reproduction. The copepod goes through 13 different stages, including an egg stage, 6 nauplii stages (N1–N6), 5 copepodite stages (CI–CV), and an adult stage (CVI). Here, the NORWECOM.E2E model was run with the *C. finmarchicus* module but without the fish IBMs; thus, predation from pelagic fish was parameterized through visibility as a function of *C. finmarchicus* size, depth, and light. This mortality was based on the visual feeding model by Aksnes & Giske (1993) for individual species, customized for use at the population level. The annual predation from pelagic fish in the model (around 82 Mt averaged over 1995–2004) is comparable to other estimates; for example,

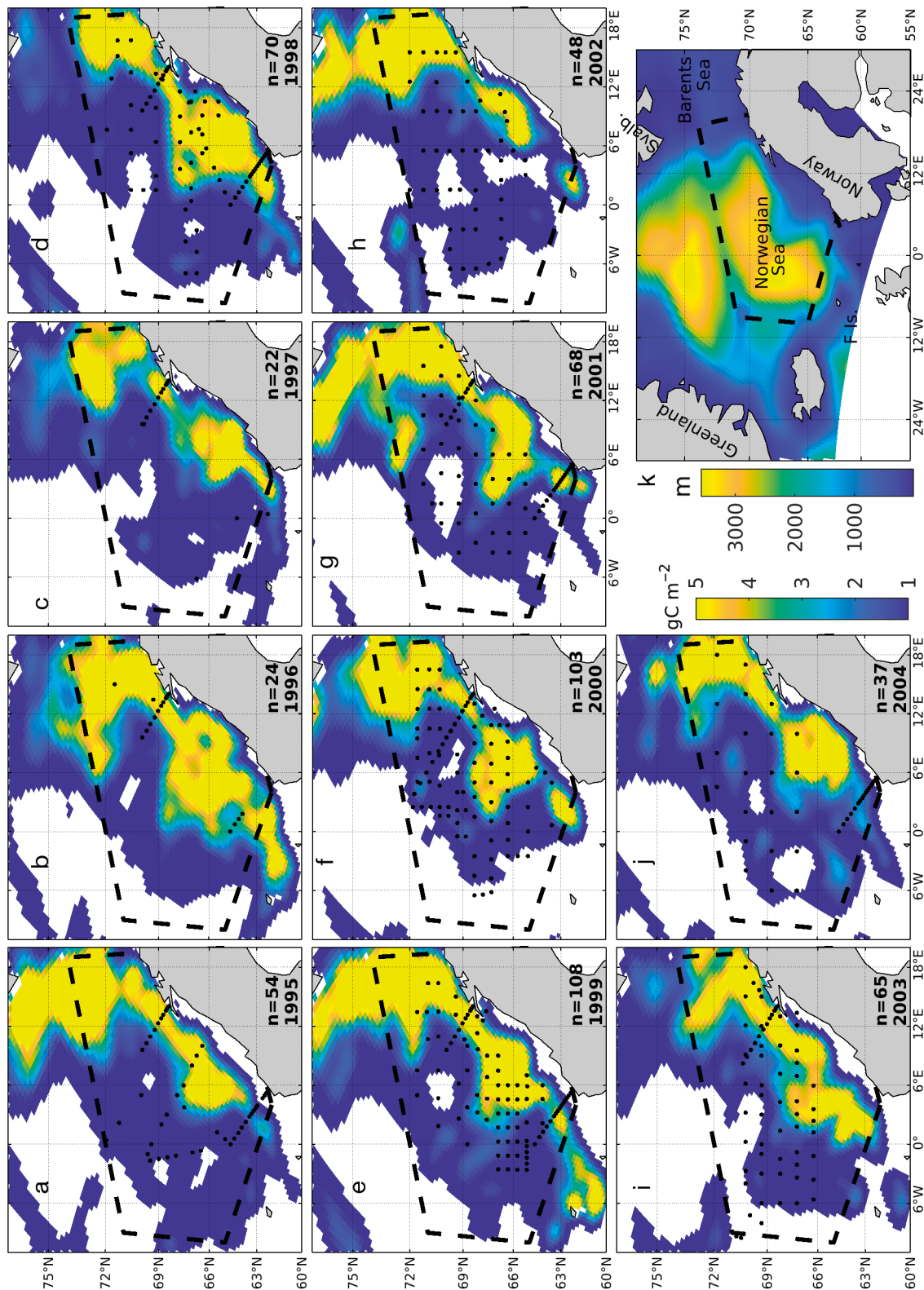


Fig. 1. Stations (dots) for observed May zooplankton biomass superimposed on the modelled mean May *Calanus finmarchicus* biomass (CI-CVI, upper 200 m) from the NORWECOM.E2E model for the period 1995–2004. Only areas with biomass values $>0.3 \text{ gC m}^{-2}$ are plotted. The number of observations for each year (n) is presented. The area enclosed by the dashed line indicates the domain on which Norwegian Sea estimates are based. (k) Model bathymetry. F Is: Faroe Islands

Bachiller et al. (2018) estimated that around 84 Mt of copepods were consumed by mackerel, blue whiting, and herring in 2005. There is no information on the

size of the pelagic fish stocks, or equivalently, no variability in the top-down control, so the variation in the modelled *C. finmarchicus* biomass herein is due

to bottom-up processes. For a full model description, refer to Supplement 1 at www.int-res.com/articles/suppl/m680p163_supp.pdf. The model system has been validated by comparison with field data in the North Sea/Skagerrak (Skogen et al. 1997, 2004, 2007, Søiland & Skogen 2000, Hjøllo et al. 2009, Gao et al. 2021), as well as in the Nordic Seas and Barents Sea (Hjøllo et al. 2012, Skaret et al. 2014, Dalpadado et al. 2014). For the purpose of this paper, an extended validation focused on abundance is shown in Supplement 2.

The spatial and temporal resolution of the 3D environment within NORWECOM.E2E is user-defined. In this version, our model covered the Barents Sea, the Norwegian Sea, and the North Sea (Fig. 1), consisting of ~21 000 grid cells with length ~20 km and separated into 32 terrain-following vertical layers. The time step was 1 h, and the simulation length was 10 yr (1995–2004). The model was initialized with a distribution field for *C. finmarchicus* based on an overwintering population distributed in the deep Norwegian Sea basin as well as in the Greenland and Barents Seas, evolved through a 25 yr long adaptation process.

2.4. Simulated time series and description of analyses

For the simulation period 1995–2004, the model fields were stored every second day. *C. finmarchicus* biomass and abundance were calculated from stage CI–CVI individuals in the upper 200 m. In addition, for validation purposes, for a selected year (1997), abundance was also calculated for the intervals 200–500 m and from 500 m to the bottom.

The full 3D spatial and temporal dimension in the model provided an opportunity to estimate the biomass by several sampling methods, i.e. perform *in silico* sampling. We constructed a total of 14 time series from the model results for the month of May. First, to perform a comparison with the 'Obs-*insitu*' (the estimated May biomass based on observations), a time series from the model was produced by averaging the modelled biomass sampled at the same time and location (the closest corresponding point in the model) as used in the corresponding years for the observational data. The resulting time series was labelled 'Obs-*insilico*'. We also produced a composite annual cycle from the model results in the same way as for the observations (mean of modelled biomass in all observational points from all years in a specific month, on the same day as the observations). Next,

we calculated the area-averaged model mean biomass estimate (time series 'Modelled') in a subdomain representing the gross part of the Norwegian Sea where observations are available (Fig. 1k) and the modelled core biomass is found. This time series represents the most correct model estimate of *C. finmarchicus* biomass in the Norwegian Sea ('the truth'), as the biomass in each grid point is weighted by the area of the grid cell, before the mean of all grid point estimates in the domain is found. This is in contrast to the 'Obs-*insilico*' and 'Obs-*insitu*' biomass time series, which consist of arithmetic means of biomass in the (irregularly distributed) observational points.

Thereafter, we began our exploration of the effects of spatial and temporal irregular sampling. First, we considered the effect caused by interannual variations in the sampling scheme (shown in Fig. 1) by applying the SPs from all 10 years to the modelled May biomass field every year, i.e. producing 10 new time series named Obs-*insilico*_SP1995, Obs-*insilico*_SP1996, and so on. This means that, for example, the time series 'Obs-*insilico*_SP1995' applied the SP of 1995 to the modelled field annually from 1995 until 2004.

Lastly, we explored the effects on biomass estimates of sampling the highly spatially and temporally variable *C. finmarchicus* biomass field. The combined effects of both spatial and temporal variability were explored by choosing the minimum and maximum values in the modelled *C. finmarchicus* biomass field over a space window of ± 2 grid cells (i.e. $\sim 80 \times 80$ km) and a time window of ± 10 d (i.e. 21 d) around the observational points, and the resulting arithmetic mean time series were termed 'Mod_dxdt_min' and 'Mod_dxdt_max'. The time window was chosen to represent the interannual variability during the May survey period, and the space window was chosen to resolve *C. finmarchicus* patchiness of ~ 17 km as found by Basedow et al. (2006).

For all time series, we calculated the mean, SD, and annual trend over the period 1995–2004 and compared the time series by computing the correlation coefficient and root mean square difference (RMSD) between each time series and the 'Obs-*insitu*' and 'Obs-*insilico*' time series. Units for all time series are gC m^{-2} . All analyses were performed in Matlab R2020b. The description of the different time series and the results from the analyses are summarized in Table 1. See Supplement 2 for further model validation, as the focus of this study is the application of the model and not model validation per se.

Table 1. *Calanus finmarchicus* biomass time series overview and statistical parameters, showing mean (gC m^{-2}), standard deviation, linear trend for each time series ($\text{gC m}^{-2} \text{ year}^{-1}$), correlation coefficient between each time series and the 'Obs-*insitu*' time series, root mean square difference (RMSD) between each time series and the 'Obs-*insitu*' time series. None of the correlation coefficients is significant at $p < 0.05$

Name of time series	Description	Mean	SD	Linear trend	Corr coeff	RMSD
Obs- <i>insitu</i>	Arithmetic mean of observed biomass at all observational locations	2.56	0.79	0.01	1.00	0.00
Obs- <i>insilico</i>	Arithmetic mean of modelled biomass at nearest corresponding location and time to observational locations	2.25	0.46	-0.05	0.34	0.79
Modelled	Area-averaged model mean biomass, all grid cells	1.92	0.28	-0.02	0.24	0.98
Obs- <i>insilico</i> _SP1995	As for Obs- <i>insilico</i> , but for all years using spatial and geographical locations for the year 1995	1.97	0.31	0.02	0.04	0.99
Obs- <i>insilico</i> _SP1996	As above, but for 1996	3.01	0.94	-0.01	-0.27	1.39
Obs- <i>insilico</i> _SP1997	As above, but for 1997	2.52	0.33	-0.03	-0.15	0.85
Obs- <i>insilico</i> _SP1998	As above, but for 1998	2.43	0.46	0.04	0.20	0.80
Obs- <i>insilico</i> _SP1999	As above, but for 1999	2.38	0.59	-0.01	0.16	0.88
Obs- <i>insilico</i> _SP2000	As above, but for 2000	2.35	0.39	-0.01	0.25	0.78
Obs- <i>insilico</i> _SP2001	As above, but for 2001	2.17	0.36	0.00	-0.10	0.94
Obs- <i>insilico</i> _SP2002	As above, but for 2002	2.15	0.45	-0.04	0.14	0.91
Obs- <i>insilico</i> _SP2003	As above, but for 2003	1.90	0.27	0.01	0.25	0.98
Obs- <i>insilico</i> _SP2004	As above, but for 2004	1.92	0.39	0.02	-0.20	1.10
Mod_dxd_t_max	Area-averaged model mean biomass, using maximum values within a time/space window	5.52	1.04	-0.15	0.21	3.16
Mod_dxd_t_min	Area-averaged model mean biomass, using minimum values within a time/space window	0.53	0.21	-0.01	0.54	2.14

3. RESULTS

3.1. Horizontal distribution of biomass

Maximum values of $>5 \text{ gC m}^{-2}$ in modelled *Calanus finmarchicus* biomass in May were found in a dipole pattern, with a local southern maximum off central Norway and a local northern maximum in the Barents Sea entrance area for the years 1995–2004 (Fig. 1). The southern boundary of the core distribution ($>4 \text{ gC m}^{-2}$) was around 63°N , although years with more southern distributions (1996, 1999) were found. Biomass patches were found up to 77°N , but were restricted to approximately 73.5°N in some years (1996–1998, 2003–2004). The westward boundary of biomass was at $\sim 7^\circ \text{W}$ for the whole period, although for the core area, the boundary was more variable, but could be found around 4°E .

3.2. Annual cycle of *C. finmarchicus* biomass from observations and model

The annual cycle in biomass and corresponding standard errors from the observations ('Obs-*insitu*')

and model ('Obs-*insilico*') (Fig. 2) showed the spring bloom starting in March, and in May the observations and model estimates reached 2.6 and 2.3 gC m^{-2} , respectively. In August, a new maximum was seen: weakly for the observations (1.6 gC m^{-2}), clearly (4.5 gC m^{-2}) for the model ('Obs-*insilico*'). The modelled timing of the spring bloom matched the observations, while the modelled biomass was higher than the observed biomass for June–October. These high biomass values are related to a lack of knowledge of the controlling mechanisms for *C. finmarchicus* starting diapause in the autumn (see Section 4.1). The number of observational points in autumn was low (Fig. 2a), e.g. the September value was based on only 62 stations, 40% of them sampled in 1997 and thus in a constrained region (see Fig. 1), which made the estimates uncertain. The area-averaged mean over the area (black line in Fig. 2) was considerably lower than the pointwise estimate for August–October, indicating that for these latter months, the pointwise estimate was biased towards high-density areas and thus is not representative. In contrast, in spring, where the number of observations was high, the pointwise estimate from the observations was reproduced both by the modelled pointwise and area-averaged estimates.

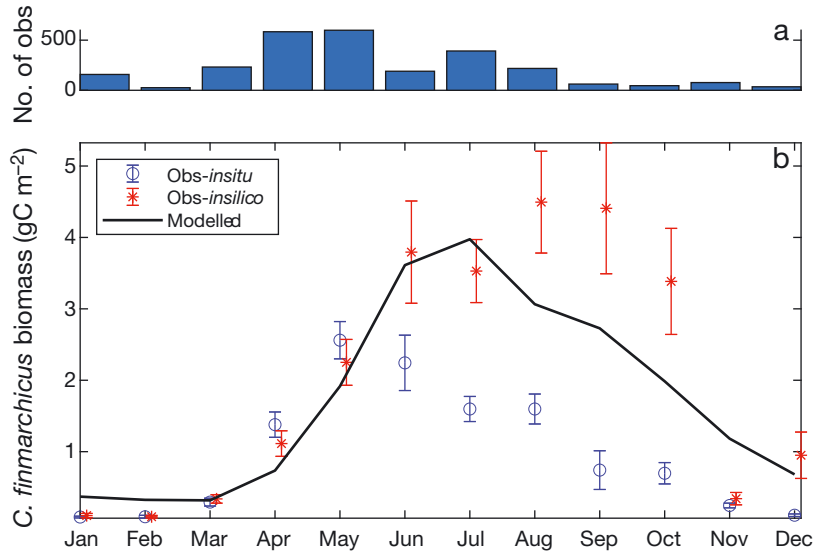


Fig. 2. Monthly (a) number of observations and (b) means (\pm SE) of composite values for *Calanus finmarchicus* biomass in the upper 200 m for the period 1995–2004. Estimates from observations (blue circles), corresponding model estimates (red stars), and area-averaged mean over the area from the model simulation (black line). $SE = \sigma/\sqrt{N}$, where σ is the standard deviation of all observations in each month for all years

Observed biomass estimates for the period 1995–2004 (Fig. 3a) varied between 1.4 and 3.8 gC m⁻², reaching a maximum value in 2002 and declining thereafter. Over the period 1995–2004, there was a negligible trend in biomass (0.01 gC m⁻² yr⁻¹) and a mean value of 2.56 gC m⁻² (Table 1). The time series for 2 model estimates, i.e. the corresponding modelled pointwise estimate (Fig. 3a), as well as area-averaged estimate for the subdomain, were generally in good agreement over the period (correlation coefficient 0.85, $p < 0.05$), but with the area-averaged estimate being lower for all years except the last. Both time series showed a weak decreasing trend of -0.05 and -0.02 gC m⁻² yr⁻¹, respectively (Table 1), and mean values of 2.25 and 1.92 gC m⁻². The mean val-

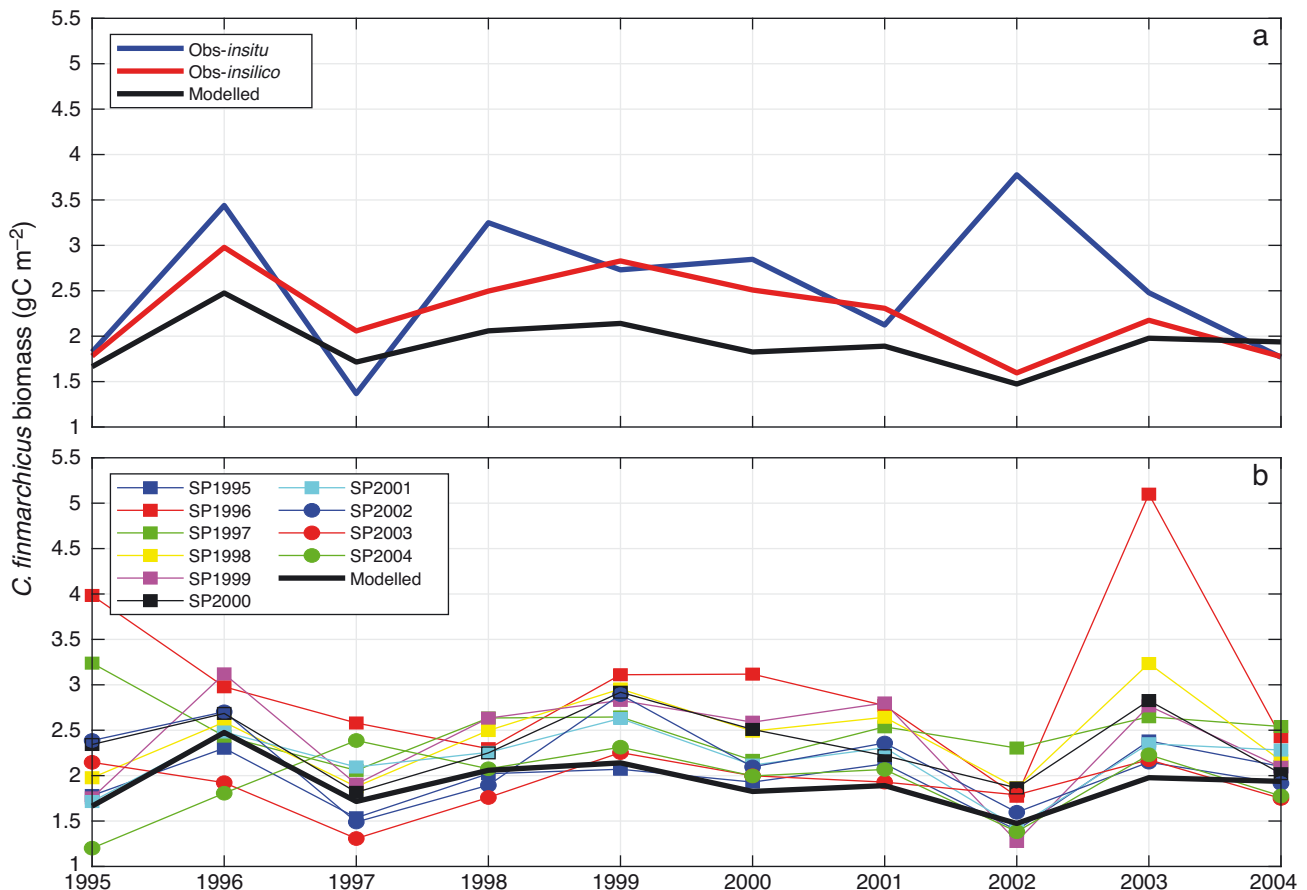


Fig. 3. May *Calanus finmarchicus* biomass in the upper 200 m from observations and the NORWECOM.E2E model for the period 1995–2004. (a) Observed biomass estimate (blue line), the corresponding time series from the model (red line), and area-averaged model estimate (black line). (b) Estimates from different sampling patterns (colored symbols) and the same area-averaged model estimate (thick black line) as in (a)

ues of the modelled time series were within 1 SD of the 'Obs-*insitu*' mean value of 2.56 gC m^{-2} (Table 1), but for individual years, the deviations were large, with 2002 being an extreme example. There were no significant correlations between the 'Obs-*insitu*' and 'Obs-*insilico*' or 'Modelled' time series.

3.3. Effect of changing the SP

The biomass estimates when sampling the model field for a given year with 10 different SPs were widespread (Fig. 3b). Ideally, the biomass estimates should be independent of the SP applied, so that they all give the same estimate and the lines in the figure would thus be on top of each other. To be a representative Norwegian Sea biomass value, they should also be close to the area-averaged Norwegian Sea model mean (Fig. 3b). This was not the case. Fig. 3b can be read in 2 directions. Exploring the figure vertically for each of the years 1995–2004, it was evident that several SPs produced biomass estimates that were not representative for the 'Modelled' value for that year at all. For instance, in 1995, the estimates varied by a factor of 3.3, between 1.3 (as estimated by SP2004) and 3.98 gC m^{-2} (as estimated by SP1996). However, the SP1995 estimate was very close to the 'Modelled' estimate of 1.66 gC m^{-2} , indicating that SP1995 actually represented 1995 conditions quite well. This representativeness of the SP was also the case for the years 2002–2004. On the other hand, the spread of the estimates was relatively low in 1999, but the deviation between the SP1999 value (2.83 gC m^{-2}) and the 'Modelled' value (2.14 gC m^{-2}) was relatively high. The same can be seen for 1998 and 2000. Overall, SP1996 produced high estimates (highest or second highest) and SP2003 low estimates (lowest or second lowest) in 8 of the 10 years (Fig. 3b, Table 1). Generally, the SPs from the last part of the simulated period produced lower values compared to the SPs from the first part of the period.

Exploring Fig. 3b horizontally along the time axis, the mean values of the 'Obs-*insilico_SP*' time series range from 1.90 to 3.01 gC m^{-2} (Table 1), with the mean of 'Obs-*insilico_SP2004*' corresponding to the area-averaged

model mean ('Modelled' time series). The trends of the time series were weak and both positive and negative, and none of the time series was correlated to the 'Obs-*insitu*' time series (Table 1). SP1996 had the highest mean value and RMSD of all 10 time series.

3.4. Sensitivity to timing and patchiness

The effect on the biomass time series when introducing a time ($\pm 10 \text{ d}$) and space (± 2 grid cells) window around the observational position was studied by choosing the minimum or maximum values within the window. The maximum value time series Mod_dxd_t_max estimates were much higher than the 'Obs-*insilico*' and 'Obs-*insitu*' values for all years (Fig. 4), and a clear negative trend of $-0.15 \text{ gC m}^{-2} \text{ yr}^{-1}$ was found (Table 1). Similarly, choosing the minimum value led to lower biomass values than the 'Obs-*insilico*' and 'Obs-*insitu*' values, but the deviation was smaller than for the 'Mod_dxd_t_max' values. When separating the temporal and spatial effects, the spatial effect was somewhat larger than the temporal effect (RMSD = 0.21 vs. 0.25, respectively). Choosing the mean value instead of the maximum or minimum value over the window produced an estimate very close to using the pointwise estimate 'Obs-*insilico*' (not shown).

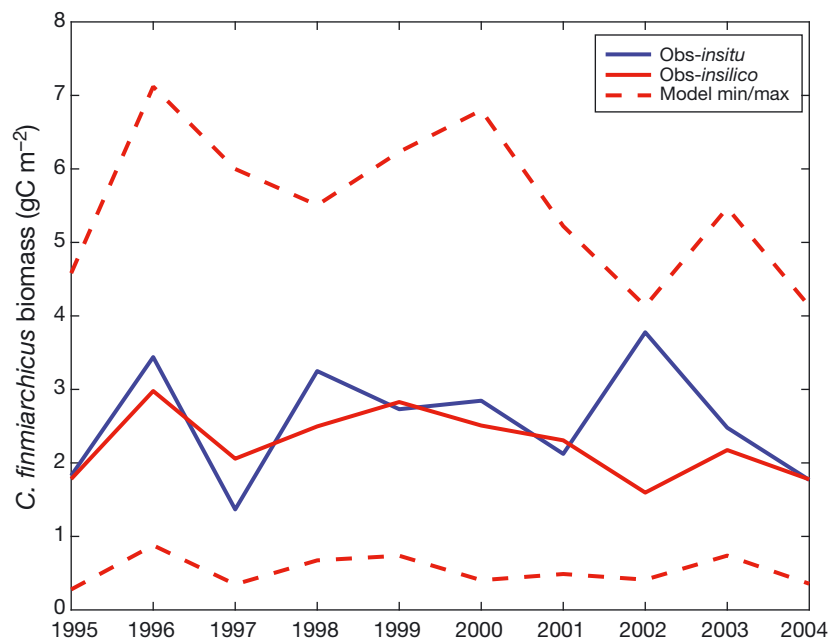


Fig. 4. Observed (blue) and modelled (red) *Calanus finmarchicus* biomass as in Fig. 3; in addition, dashed lines for minimum and maximum values in the modelled *C. finmarchicus* biomass field over a space window of ± 2 grid points and time window of $\pm 10 \text{ d}$ are also shown

3.5. Sampling interpolated zooplankton fields

Comparing the estimates from resampling the interpolated fields from the objective analysis with SP2020 and with SP1995–SP2004, the SP2020 estimates were, except for a few years, in the lower end of the biomass estimate range (Fig. 5). The mean SP2020 biomass value for the first period (until 2006) was higher than for the last period (11.0 vs. 6.8 g m⁻²), and the interannual variability was also larger for the first period (up to 100%). The width of the shaded area demonstrated that biomass estimates from the different SPs can vary by up to 100% for each year, and the spread of the dots over the shaded area showed that it is no single SP that caused the width. For SP1995 to SP2004, the interannual variabilities in biomass were generally larger than those for SP2020 and were as large as 400% (for SP1996 or SP1997 for the 2001–2002 biomass difference, Fig. 5).

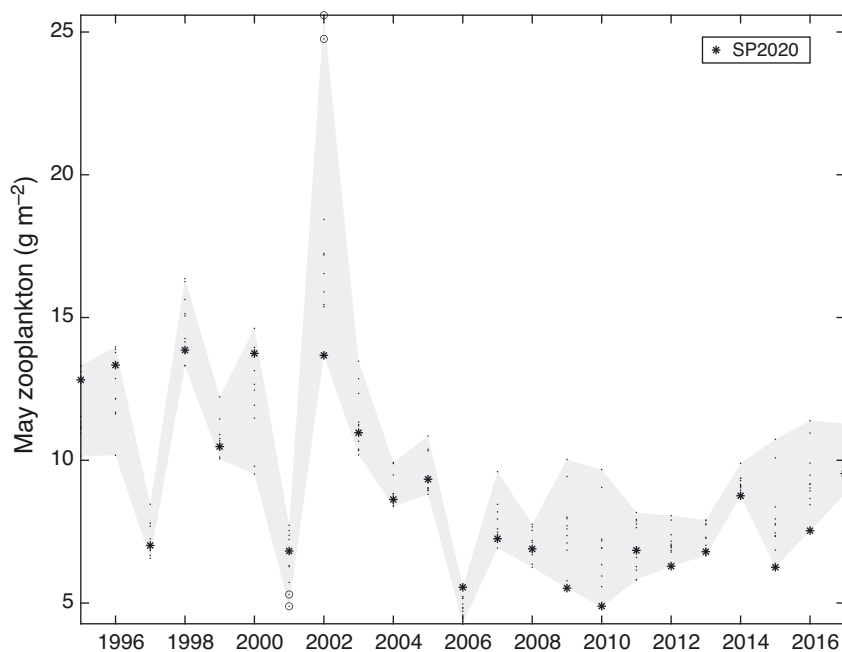


Fig. 5. Annual zooplankton biomass indexes (g dry weight m⁻²) from spatially interpolated observations, estimated (1) by sampling pattern (SP) from the year 2020 (stars), and (2) by SPs from the years 1995–2004 (grey shading and dots). Encircled dots: biomass estimates from SP1996 and SP1997 for 2001 and 2002. Biomass is sampled by WP2 in May in the Norwegian Sea and adjacent waters (delimited to east of 14°W and west of 20°E) from 1995–2017, and spatial fields derived from interpolation using objective analysis utilizing a Gaussian correlation function (see details on methods and areas in ICES 2016). Data from the Planning Group on Northeast Atlantic Pelagic Ecosystem Surveys database at the Faroe Marine Research Institute and interpolated fields from Dr. Ø. Skagseth, Institute of Marine Research, Norway

4. DISCUSSION

Zooplankton, the intermediate trophic link between phytoplankton and fish, is notoriously difficult to sample due to patch variability, and basin-scale monitoring remains challenging. Consequently, the observables suffer from representativeness issues, due to the natural variability of the system but also the large variety in sampling strategies for observing the system. The lack of control of the representation error (the ability of observations to represent a larger area over time) limits the observables' use as reliable indicators of changes, or in constructing model validation fields, as was the starting point for this study. The absence of an objective truth has been discussed by several authors (Lynch et al. 2009, Schutgens et al. 2017, Skogen et al. 2021 in this Theme Section), and Skogen et al. (2021) advocated that models and observations should be joined to strengthen both approaches in the process of disclosing the truth. Not only should observations be used to validate the models, but also the other way around. In the current paper, we show how models can be used to validate *in situ* observation methods, using a system well modelled and sampled (at least for part of the period studied). Our approach will hopefully inspire studies on less well sampled systems.

4.1. Model validation

We have studied the combined impact of spatiotemporal sampling on representation errors for a zooplankton observing system by applying an existing ecosystem model to generate biomass distributions of the *Calanus finmarchicus* population within the Norwegian Sea. The model compared adequately with biomass and abundance reported in the literature (Fig. 2 and Supplement 2), although with elevated values in the autumn not seen in the observational dataset. Part of the autumn maximum is probably due to the way we have simulated how individuals are triggered to go into diapause versus staying in the pelagic environment for producing another generation. The controlling mechanisms for these processes are

poorly known. In the model, 2 adapted 'genes' or strategies ('Allocation-to-Fat-Day' and 'Fat-to-Soma-Ratio', Table S1) are used to determine whether a super-individual should produce a new generation or build enough fat reserves to enable overwintering. The model tends to overestimate the number of copepods that produce a new generation. The individuals of this generation will, to a large extent, not mature for overwintering during autumn but instead appear as a high autumn biomass that will gradually decrease as these individuals starve and die off before the next spring. On the other hand, any conclusion that the modelled biomass in autumn is too high is not based on precise observed estimates of this biomass but simply on the observations showing that biomass should be lower at this time of the year compared to, for example, summer. We also note that for the observations in general, there are issues related to, for example, the catchability of *C. finmarchicus* with the WP2 net (Skjoldal et al. 2000) and the method of separating *C. finmarchicus* from other zooplankton species. For the latter we assumed a *C. finmarchicus* content of 50, 70 and 0% in the size fractions 0.18–1, 1–2 and >2 mm, respectively; however, there may be temporal and spatial variations in this relationship that are not taken into account, which will influence the 'Obs-*insitu*' time series. We note that the *C. finmarchicus* fraction also may be biased due to *C. glacialis* and *C. finmarchicus* species misidentification and may subsequently require reinvestigation with the systematic use of molecular tools (Choquet et al. 2018). The analysis in the present paper is focused on May, when the model sufficiently resembles the average annual values (Fig. 2) and the horizontal and vertical distribution (Figs. S1–S4 in Supplement 2), but there are also observations available in July/August showing a weak local maximum (Fig. 2). Exploring the autumn levels of *C. finmarchicus* biomass is left to a follow-up study.

4.2. SP effects

Modelled data were processed using the same methods as for real surveys, but in addition, 13 different model-generated time series of biomass estimates for *C. finmarchicus* within the Norwegian Sea during the month of May were analysed (Fig. 3, Table 1). We found that the pointwise estimate 'Obs-*insilico*' in most years differed from both the corresponding estimate from the observations and the 'truth' (in this case the area-averaged modelled biomass estimate, i.e. 'Modelled'). Reduced biomass

estimates in the years 2000–2004 can be related to several causes. The centre of gravity for the locations of the observations is found farther offshore, where the seasonal cycle of *C. finmarchicus* development differs from the cycle in coastal water masses (Broms & Melle 2007). There is also north/south interannual variability in the centre of gravity. We did not find any systematic relation between biomass level and mean day of observations (varying from 8 to 16 May), or between biomass level and the number of observations, although we do note that the length of the period studied (10 yr) is short.

The large spread in biomass estimates when applying 14 different SPs to each individual year demonstrates that SPs strongly affect the obtained estimates. The SPs from the last part of the 1995–2004 period resulted in generally lower mean modelled biomass values than SPs from the first part of the period (Fig. 3b, Table 1). The variability in 2004 is less than that for the previous years, but whether this is due to a more robust sampling scheme achieved, changed *C. finmarchicus* population characteristics such as horizontal extension, patchiness, etc., and/or pure coincidence remains unclear. Generally, the variability in the modelled time series is lower than for the observations (Table 1).

Sampling of a spatiotemporally varying and patchy field is challenging, and can only be achieved by high-resolution measurements over space and time. Spatial distributions of *C. finmarchicus* have been found to be highly patchy (Toresen et al. 2019), with a high spatial correspondence between chl *a* and copepods (CV and adult females; Basedow et al. 2006), and with patches from a few kilometres (Trudnowska et al. 2016) to several tens of kilometres in horizontal length (Wishner et al. 1988). In contrast, Young et al. (2009) showed that 50% of the spatial variance of copepod nauplii and copepods occurs at the metre scale. In addition, the temporal changes in size and stage of the copepods are rapid, reflecting the intense spring season with the length of different life stages on the order of days, and individuals undergoing their whole life cycle in 22–59 d, depending on temperature and food concentration (Campbell et al. 2001). Sampling along a steep *C. finmarchicus* temporal gradient, such as the one found in the data from May, introduces a large uncertainty; however, as May is the time of the year when research ships are available for either dedicated zooplankton sampling or to combine such sampling with other activities, this is still the main period of zooplankton mapping in the Norwegian Sea. Our results demonstrate that within a zoo-

plankton patch length scale of 80 km, the model biomass estimate can vary by a factor of 10, corresponding to estimates of elevated zooplankton concentration in patches found in the literature (3–17 times higher biomass than in the surroundings; Trudnowska et al. 2016). The SPs applied (Fig. 3b) are therefore associated with uncertainty.

4.3. Recent zooplankton sampling

The recent, more spatially regular, sampling design and the use of objective mapping methods resulted in the zooplankton time series for 1995–2017 in Fig. 5. When applying a variety of SPs (SP1995–2004 and SP2020, Fig. 5) to the spatially interpolated observations, it is clear that SP2020, with regular and more numerous sampling stations, is a much better sampling strategy than SP1995–2004 when compared to the area-averaged mean biomass (Fig. 2.4 in ICES 2020a). SP2020 thus represents a large step forward in reducing the representation error. It is also worth noting that, except for a few years early in the period, SP2020 is close to the minimum of the SP1995–2004 interval. This suggests that there may be a bias in the biomass reported from observations in the first decade (Huse et al. 2012), with probably too high values compared to the second half of the period. In addition, the first period is recognized by strong oscillations in the observed biomass using SP2020, with a difference between consecutive years up to 100%. To our knowledge, no signs of such large interannual variations have been reported in other parts of the ecosystem; thus, this finding provides support for the reported mean biomass in this period being strongly influenced by the sampling design. From the consistent SP2020 estimates at the lower end of the interval and the much lower interannual variability after 2006, we conclude that the present sampling regime is much more robust and thereby more likely to provide good estimates of the inter annual variability of the total biomass in the area.

The reasons why the zooplankton time series as sampled by SP2020 (or as presented as the area-averaged mean in ICES (2020a), including all size classes and not directly comparable to the modelled *C. finmarchicus* field) show a decline and low zooplankton biomass levels after 2002 are not well known (ICES 2016). Suggested explanations are high predation pressure from pelagic fish (Huse et al. 2012), high predation from carnivorous zooplankton stocks, timing effects (as match/mismatch

with the phytoplankton bloom), and lower-than-average heat contents (ICES 2016). Based on the present study, the methodology (sampling design and interpolation) might also be part of the explanation. Dynamical, process-oriented model simulations can be used to explore the reasons for such changes in biomass. For example, in the present model set-up, top-down effects such as predation from pelagic fish and carnivorous zooplankton stocks are not interannually varying. If the simulation was extended to cover the period up to the present, and assuming that significant correlations between the observed and modelled *C. finmarchicus* biomass were found, top-down forcing could be ruled out as a cause for the decline. By incorporating interannually varying top-down effects in the form of full IBMs for the main predators of *C. finmarchicus*, as already introduced into the model (Utne et al. 2012, Holmin et al. 2020), the causes and consequences of varying *C. finmarchicus* biomass levels (and other pressures, e.g. climate change) on the food web can be disentangled.

5. CONCLUSIONS

We have applied results from an ecosystem model to illustrate how spatiotemporal patchiness will impact May biomass estimates for *Calanus finmarchicus* through representation errors. When is a model good enough to be used for a certain application? Model validation is meant to answer such claims about the applicability and accuracy of a model regarding the intended purpose as well as to the natural system it represents (Dee 1995). The model applied in this study has been validated in several articles (e.g. Hjøllo et al. 2012, Skaret et al. 2014, Gao et al. 2021), and we believe that these works have proven the model's applicability to be used to simulate the life cycle of both *C. finmarchicus* individuals and populations. In the present work, the question of applicability was redirected to the observations. Zooplankton fields are very patchy, and observations of such quantities will strongly depend on whether a patch happens to occur at a sampling location or not, thus the representativeness will be a function of the sampling technique and the spatiotemporal resolution of sampling locations (Omori & Hamner 1982). The main objective of the present work was to investigate the latter. Of course, the model does not represent the full truth; it will always be limited to the biological understanding we have. A model has a basic spatial and temporal resolution,

but incomplete representation of processes and components of a natural system, while observations give incomplete access to a natural phenomenon as spatial and temporal resolution is a necessary sampling effort compromise (Oreskes et al. 1994). Our Fig. 4 clearly demonstrates how this compromise may lead to a large uncertainty based on estimates from a small number of observations. While 20 km horizontal resolution in the model may not represent the true patchiness, this is not an argument against our present analysis. Using higher-resolution model simulations would change the patchiness of the model, but within the near future, the horizontal resolution would be far from metre-scale, and spatiotemporal patchiness would still be an unresolved process. Our study illustrates how sampling patterns will impact the results, thus hopefully initializing a discussion on what is the best way to measure zooplankton biomass.

Marine monitoring is costly, and if we could efficiently use other methods, we could improve the information underpinning our management decisions. Use of joint model–observations studies has identified preferable sampling frequency for Faroe Island hydrography (Hátún et al. 2005), assessed the representativeness of Barents Sea indicators in management plans (Hansen et al. 2021) and evaluated the efficacy of both new and existing fishery surveys (Holmin et al. 2020). Our study is an example of how dynamical ecosystem models can be used specifically to assess zooplankton SPs in the Norwegian Sea, but also add to the growing recognition of how ecosystem models can contribute to the monitoring of marine ecosystems.

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LITERATURE CITED

- ✦ Aksnes DL, Giske J (1993) A theoretical model of aquatic visual feeding. *Ecol Model* 67:233–250
- ✦ Bachiller E, Skaret G, Nøttestad L, Slotte A (2016) Feeding ecology of Northeast Atlantic mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea. *PLOS ONE* 11:e0149238
- ✦ Bachiller E, Utne KR, Jansen T, Huse G (2018) Bioenergetics modeling of the annual consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. *PLOS ONE* 13:e0190345
- ✦ Bagøien E, Melle W, Kaartvedt S (2012) Seasonal development of mixed layer depths, nutrients, chlorophyll and *Calanus finmarchicus* in the Norwegian Sea—a basin-scale habitat comparison. *Prog Oceanogr* 103:58–79
- ✦ Basedow SL, Edvardsen A, Tande KS (2006) Spatial patterns of surface blooms and recruitment dynamics of *Calanus finmarchicus* in the NE Norwegian Sea. *J Plankton Res* 28:1181–1190
- ✦ Brey T, Müller-Wiegmann C, Zittier ZMC, Hagen W (2010) Body composition in aquatic organisms—a global data bank of relationships between mass, elemental composition and energy content. *J Sea Res* 64:334–340
- ✦ Broms C, Melle W (2007) Seasonal development of *Calanus finmarchicus* in relation to phytoplankton bloom dynamics in the Norwegian Sea. *Deep Sea Res II* 54:2760–2775
- ✦ Broms C, Melle W, Kaartvedt S (2009) Oceanic distribution and life cycle of *Calanus* species in the Norwegian Sea and adjacent waters. *Deep Sea Res II* 56:1910–1921
- ✦ Campbell RG, Wagner MM, Teegarden GJ, Boudreau CA, Durbin EG (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar Ecol Prog Ser* 221:161–183
- ✦ Choquet M, Kosobokova K, Kwaśniewski S, Hatlebakk M and others (2018) Can morphology reliably distinguish between the copepods *Calanus finmarchicus* and *C. glacialis*, or is DNA the only way? *Limnol Oceanogr Methods* 16:237–252
- ✦ Dalpadado P, Ellertsen B, Melle W, Skjoldal HR (1998) Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic seas. *Sarsia* 83:103–116
- ✦ Dalpadado P, Ellertsen B, Melle W, Dommasnes A (2000) Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. *ICES J Mar Sci* 57:843–857
- ✦ Dalpadado P, Arrigo KR, Hjøllø SS, Rey F and others (2014) Productivity in the Barents Sea – response to recent climate variability. *PLOS ONE* 9:e95273
- Dee DP (1995) A pragmatic approach to model validation. In: Lynch DR, Davies AM (eds) Quantitative skill assessment for coastal ocean models. Coastal and estuarine studies, Vol 47. American Geophysical Union, Washington, DC, p 1–13
- ✦ Dupont N, Bagøien E, Melle W (2017) Inter-annual variability in spring abundance of adult *Calanus finmarchicus* from the overwintering population in the southeastern Norwegian Sea. *Prog Oceanogr* 152:75–85
- ✦ Fraser JH (1966) Zooplankton sampling. *Nature* 211: 915–916
- ✦ Gao S, Hjøllø SS, Falkenhaug T, Strand E, Edwards M, Skogen MD (2021) Overwintering distribution, inflow patterns and sustainability of *Calanus finmarchicus* in the North Sea. *Prog Oceanogr* 194:102567

- ✦ Gjosæter H, Dalpadado P, Hassel A, Skjoldal HR (2000) A comparison of performance of WP2 and MOCNESS. *J Plankton Res* 22:1901–1908
- Hansen C, van der Meeren G, Loeng H, Skogen MD (2021) Assessing the state of the Barents Sea using indicators: how, when and where? *ICES J Mar Sci*, doi:10.1093/icesjms/fsab053
- Hátún H, Sandø AB, Drange H, Bentsen M (2005) Seasonal to decadal temperature variations in the Faroe–Shetland inflow waters. In: Drange H, Dokken T, Furevik T, Gerdes R, Berger W (eds) *The Nordic Seas: an integrated perspective*. Geographical monograph series Vol 158. American Geophysical Union, Washington, DC, p 239–250
- ✦ Hirche HJ (1996) Diapause in the marine copepod, *Calanus finmarchicus*—a review. *Ophelia* 44:129–143
- ✦ Hjøllo SS, Skogen MD, Svendsen E (2009) Exploring currents and heat within the North Sea using a numerical model. *J Mar Syst* 78:180–192
- ✦ Hjøllo SS, Huse G, Skogen MD, Melle W (2012) Modelling secondary production in the Norwegian Sea with a fully coupled physical/primary production/individual-based *Calanus finmarchicus* model system. *Mar Biol Res* 8: 508–526
- Holmin AJ, Mousing EA, Hjøllo SS, Skogen MD, Huse G, Handegard NO (2020) Evaluating acoustic-trawl survey strategies using an end-to-end ecosystem model. *ICES J Mar Sci* 77:2590–2599
- ✦ Huse G, Holst JC, Utne K, Nøttestad L and others (2012) Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea—results of the INFERNO project. *Mar Biol Res* 8:415–419
- Huse G, Melle W, Skogen MD, Hjøllo SS, Svendsen E, Paul Budgell W (2018) Modeling emergent life histories of copepods. *Front Ecol Evol* 6:23
- ICES (International Council for the Exploration of the Sea) (2016) Final report of the Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR). ICES CM 2015/SSGIEA:10. ICES, Copenhagen. www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGIEA/2015/WGINOR%20Final%20report%202015.pdf
- ICES (2020a) Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR; outputs from 2019 meeting). ICES, Copenhagen
- ✦ ICES (2020b) Working Group of International Pelagic Surveys (WGIPS). *ICES Sci Rep* 2:56. <http://doi.org/10.17895/ices.pub.6088>
- ✦ Kristiansen I, Hátún H, Petursdottir H, Gislason A and others (2019) Decreased influx of *Calanus* spp. into the southwestern Norwegian Sea since 2003. *Deep Sea Res I* 149: 103048
- ✦ Langøy H, Nøttestad L, Skaret G, Broms C, Fernø A (2012) Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Mar Biol Res* 8:442–460
- ✦ Lynch DR, McGillicuddy DJ Jr, Werner FE (2009) Skill assessment for coupled biological/physical models of marine systems. *J Mar Syst* 76:1–3
- Marshall SM, Orr AP (1972) *The biology of a marine copepod*. Springer Verlag, Berlin
- Melle W, Ellertsen B, Skjoldal HR (2004) Zooplankton: the link to higher trophic levels. In: Skjoldal HR, Sætre R (eds) *The Norwegian Sea ecosystem*. Tapir Academic Press, Trondheim, p 137–202
- Motoda S (1959) Devices of simple plankton apparatus. *Mem Fac Fish Hokkaido Univ* 7:73–94
- ✦ Mueter FJ, Broms C, Drinkwater KF, Friedland KD and others (2009) Ecosystem responses to recent oceanographic variability in high-latitude Northern Hemisphere ecosystems. *Prog Oceanogr* 81:93–110
- ✦ Niehoff B, Klenke U, Hirche HJ, Irigoien X, Head R, Harris R (1999) A high frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. *Mar Ecol Prog Ser* 176:81–92
- ✦ Omori M, Hamner WM (1982) Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *Mar Biol* 72:193–200
- ✦ Oreskes N, Shrader-Frechette K, Belitz K (1994) Verification, validation, and confirmation of numerical models in the Earth sciences. *Science* 263:641–646
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Scheffer M, Bavaco JM, DeAngelis DL, Rose KA, van Nes EH (1995) Super-individuals a simple solution for modelling large populations on an individual basis. *Ecol Model* 80:161–170
- ✦ Schutgens N, Tsyro S, Gryspeerdt E, Goto D, Weigum N, Schulz M, Stier P (2017) On the spatio-temporal representativeness of observations. *Atmos Chem Phys* 17: 9761–9780
- ✦ Skaret G, Dalpadado P, Hjøllo SS, Skogen MD, Strand E (2014) *Calanus finmarchicus* abundance, production and population dynamics in the Barents Sea in a future climate. *Prog Oceanogr* 125:26–39
- Skjoldal HR, Wiebe PH, Foote KG (2000) Sampling and experimental design. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds) *ICES zooplankton methodology manual*. Academic Press, London, p 33–53
- Skjoldal HR, Dalpadado P, Dommasnes A (2004) Food webs and trophic interactions. In: Skjoldal HR, Sætre R (eds) *The Norwegian Sea ecosystem*. Tapir Academic Press, Trondheim, p 447–506
- ✦ Skogen MD, Svendsen E, Ostrowski M (1997) Quantifying volume transports during SKAGEX with the Norwegian Ecological Model system. *Cont Shelf Res* 17:1817–1837
- ✦ Skogen MD, Søiland H, Svendsen E (2004) Effects of changing nutrient loads to the North Sea. *J Mar Syst* 46:23–38
- ✦ Skogen MD, Budgell WP, Rey F (2007) Interannual variability in Nordic seas primary production. *ICES J Mar Sci* 64: 889–898
- ✦ Skogen MD, Ji R, Akimova A, Daewel U and others (2021) Disclosing the truth: Are models better than observations? *Mar Ecol Prog Ser* 680: 7–13
- ✦ Søiland H, Skogen MD (2000) Validation of a three-dimensional biophysical model using nutrient observations in the North Sea. *ICES J Mar Sci* 57:816–823
- ✦ Strand E, Bagøien E, Edwards M, Broms C, Klevjer T (2020) Spatial distributions and seasonality of four *Calanus* species in the Northeast Atlantic. *Prog Oceanogr* 185: 102344
- Toresen R, Skjoldal HR, Vikebø F, Martinussen MB (2019) Sudden change in long-term ocean climate fluctuations corresponds with ecosystem alterations and reduced recruitment in Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae). *Fish Fish* 20:686–696

- ✦ Trudnowska E, Gluchowska M, Beszczynska-Möller A, Blachowiak-Samolyk K, Kwasniewski S (2016) Plankton patchiness in the Polar Front region of the West Spitsbergen Shelf. *Mar Ecol Prog Ser* 560:1–18
- ✦ Utne KR, Hjøllø SS, Huse G, Skogen M (2012) Estimating the consumption of *Calanus finmarchicus* by planktivorous fish in the Norwegian Sea using a fully coupled 3D model system. *Mar Biol Res* 8:527–547
- ✦ Wishner K, Durbin E, Durbin A, Macaulay M, Winn H, Kenney R (1988) Copepod patches and right whales in the Great South Channel off New England. *Bull Mar Sci* 43:825–844
- ✦ Young KV, Dower JF, Pepin P (2009) A hierarchical analysis of the spatial distribution of larval fish prey. *J Plankton Res* 31:687–700

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