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Assessing the importance of zooplankton sampling patterns with an ecosystem model

Solfrid Sætre Hjøllo^{1*}, Cecilie Hansen¹, Morten D. Skogen¹

1) Institute of Marine Research, 5817 Bergen, Norway
*) Corresponding author: Solfrid Sætre Hjøllo, Solfrid.hjollo@hi.no

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. To estimate the total stock size, observations of zooplankton biomass are collected at a relatively low number of stations, where the number of observations as well as the sampling pattern varies in time and space between the years. However, the sampling patterns applied in the zooplankton monitoring for the period 1995-2004 revealed a lack of robustness over time. Here, the importance of varying the spatiotemporal sampling pattern for estimating the biomass was explored by virtual sampling in *C. finmarchicus* spatial fields from the end-to-end ecosystem model NORWECOM.E2E. Non-consistent sampling patterns during the month of May cause the biomass estimate to be highly dependent on the chosen sampling strategy. Sampling patterns from the first part of the period generally produce the highest biomass estimates. Lastly, we applied the 1995-

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1 2004 sampling patterns as well as the recent (2020) sampling pattern with regular and more
2 numerous sampling stations to a gridded zooplankton observational dataset and found systematic
3 differences. We conclude that the present May sampling regime is much more robust and thereby
4 also more likely to be a good estimate of the interannual variability of the total biomass in the area.
5 This study is an example of how models can be used to mechanistically interpret experimental
6 datasets, and more specifically how models can be used to assess sampling patterns and reveal
7 their limitations.

8

9 **Keywords:**

10 *Calanus finmarchicus* biomass, Norwegian Sea, representation error, virtual sampling,
11 NORWECOM.E2E

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16 **1. Introduction**

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18 The Norwegian Sea, situated north of 60°N, is a section of the Northeast Atlantic Ocean
19 and adjacent to the Arctic Seas. With an area of ~1mill km², it is home for several large pelagic
20 fish stocks which feed intensively on the abundant zooplankton, particularly the copepod *Calanus*
21 *finmarchicus* (Gunnerus 1765,Dalpadado et al. 2000, Broms & Melle 2007, Langøy et al. 2012,
22 Bachiller et al. 2016). *C. finmarchicus* is the dominant species of mesozooplankton in the
23 Norwegian Sea (Melle et al. 2004). A variety of organisms feed on the different stages of *C.*

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1 *finmarchicus*, including large standing stocks of invertebrates and mesopelagic fish and migrating
2 predators (Dalpadado et al. 1998, Skjoldal et al. 2004). *C. finmarchicus* overwinters at depth
3 mainly as copepodite stages 4 (CIV) and 5 (CV). During early spring, they ascend towards the
4 surface where they mature and produce eggs prior to and during the spring phytoplankton bloom
5 (Marshall & Orr 1972, Niehoff et al. 1999, Broms & Melle 2007, Broms et al. 2009). The new
6 generation stays in the upper waters while individuals continue to mature, potentially producing
7 another new generation, and build up fat reserves before descending to overwinter (Hirche 1996,
8 Broms & Melle 2007, Broms et al. 2009). Since 1993, zooplankton have been routinely monitored
9 in the southern Norwegian Sea by the Institute of Marine Research (IMR, Norway) via plankton
10 nets used at stations along standardized sections as well as at stations irregularly distributed both
11 spatially and temporally . Huse et al. (2012) reported a decline in zooplankton biomass since the
12 late 1990s, and ICES (2016) reported a peak in zooplankton biomass around 2000 followed by a
13 decline until a minimum in 2009.. Declining zooplankton biomass causes concerns regarding the
14 consequences it may have on the large stocks of commercial fish in the Norwegian Sea that feed
15 primarily on the copepods (Langøy et al. 2012).

16 The vast size of the Norwegian Sea makes synoptic sampling almost impossible.
17 Traditionally, zooplankton biomass in the Norwegian Sea has been estimated from a temporally
18 and spatially varying number of observations, forming indexes like the arithmetic mean (Mueter
19 et al. 2009, Huse et al. 2012, Toresen et al. 2019). However, zooplankton species like *C.*
20 *finmarchicus* have patchy distributions in the Norwegian Sea (Basedow et al. 2006, Toresen et al.
21 2019), and the temporal and spatial irregularity of the sampling pattern (SP) may also influence
22 biomass estimates and, thus, represent a challenge. Temporal irregularity in sampling was
23 addressed by Dupont et al. (2017) using generalized additive models accounting for adult stage

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1 representation in the dataset, confirming the increase in *C. finmarchicus* spring abundance prior to
2 the year 2000, and a decrease between the years 2000 and 2011. The decrease in abundance was
3 greater for stations closer to the coast, in accordance with the findings of Toresen et al. (2019).
4 Spatial irregularity can be incorporated by the use of aggregated data (in space, time or by e.g
5 water masses) or objective mapping methods. Relating distribution to water masses, Broms et al.
6 (2009) applied principal component analysis to examine the geographical distribution of *C.*
7 *finmarchicus* stages CIV–CVI for the year 1995 and found the highest average abundance in
8 Atlantic- and Arctic water masses. Bagøien et al. (2012) used spatiotemporally aggregated basin-
9 scale data to study the seasonal development of *C. finmarchicus* abundance in different water
10 masses for the period 1993-2008. They found a total delay of about 6 weeks from coastal to Arctic
11 water masses for the first generation of *Calanus* copepods (CI–CIII), and two generations
12 produced in the Atlantic waters. Recently, Kristiansen et al. (2019) used objective mapping of
13 biomass data from the International Ecosystem Survey to identify a post-2003 reduction in the
14 abundance of large *C. finmarchicus* (stage CIV-CVI) north of the Faroe Islands during May. Using
15 objective mapping procedures and data from the continuous plankton recorder (CPR) survey along
16 the Svalbard and other transects, Strand et al. (2020) also found high *C. finmarchicus* abundance
17 west of Svalbard and in the Barents Sea entrance for the period 2008-2014/15.

18 To address temporal and spatial variability in the zooplankton field, a possible approach is
19 to apply an ecosystem model and produce a virtual representation of the dynamic zooplankton
20 distribution, i.e., apply a digital twin. Herein, a full life-cycle model for *C. finmarchicus* embedded
21 in the physical-biological model system NORWECOM.E2E was applied to perform a simulation
22 of *C. finmarchicus* biomass for the period 1995-2004. Motivated by the reported zooplankton
23 variability in time and space, and realizing the temporal and spatial irregularity within the available

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1 data sets for *C. finmarchicus*, we explore different SPs by virtual sampling in the model field. In
2 addition, we applied several SPs to a gridded zooplankton observational dataset for the period
3 1995-2017. The main aim of the study is to utilize the full 3D spatial dimension of a stage-resolving
4 biological model to estimate and compare the biomass from several observational based SPs for
5 the month of May, thus showing how ecosystem models can be used to mechanistically interpret
6 observational datasets, exemplified by assessing zooplankton sampling in the Norwegian Sea.

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10 **2. Material and Methods**

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12 2.1 *Calanus finmarchicus* dataset 1995-2004

13 In-situ data on size-fractionated zooplankton biomass collected by the IMR were extracted from
14 IMR databases. The dataset was restricted to only cover the Norwegian Sea (west of 18°E and for
15 60-72°N) for the period 1995 to 2004. The basic processing and compilation of this dataset was
16 performed using the free statistical software R (R Core Team 2014). The number of observations
17 as well as the timing and SP varied between the years as the sampling locations were not dedicated
18 to zooplankton monitoring, but rather in connection with other activities at the IMR. Data were
19 sampled throughout the whole year, but the highest sampling frequencies were found during
20 summer, particularly May. The zooplankton biomass analyzed in this paper were collected by WP2
21 nets (Fraser 1966), which have an opening area of 0.25m² and a mesh size of 180 µm (modified
22 from originally 200 µm). The WP2 nets were hauled vertically from 200m (or from near the bottom
23 in shallow areas) to the surface. The unit for biomass in the dataset is dry weight per unit surface

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1 area. If more than one trawl haul were available at a station, only one biomass sample in the dataset
2 was included (the one closest to 200m depth or bottom if in shallow areas). The IMR routine is to
3 split each zooplankton sample in two equally sized parts via a Motoda splitter (Motoda 1959). One
4 part is preserved in formalin for subsequent taxonomic identification and enumeration of
5 individuals, while the other part is used for estimation of size-fractionated biomass, see Melle et
6 al. (2004) for details. Due to the amount of work involved, only selected samples are processed
7 taxonomically in the laboratory, while size-fractionated biomass is estimated for all samples. The
8 size-fractions for zooplankton are 0.18-1mm, 1-2 mm, and > 2 mm, while shrimps, krill and fish
9 are in the > 2 mm fraction and weighed separately. Estimates of observed *C. finmarchicus* biomass
10 for each month were calculated as the arithmetic mean over all relevant stations, using *C.*
11 *finmarchicus* content of 50%, 70% and 0% of the size fractions 0.18-1mm, 1-2 mm, and > 2 mm,
12 respectively (Gjørseter et al. 2000, Skjoldal et al. 2004, W. Melle (IMR), pers. comm.). Dry weight
13 biomass was converted to carbon using C/DW-ratio = 0.45 (Brey et al. 2010). Selecting May
14 produced a time series labelled herein as “Obs-*insitu*”. Figure 1 shows the sampling positions in
15 May of each year, as well as the number of observations in the same month. For model validation
16 purposes, we also combined all observations into a composite annual cycle by averaging all
17 observations from all years in each month. The sum of observations over the period 1995-2004
18 varied from 35 (December) to 559 (May). This dataset is a subset of the Zooplankton dataset
19 (described below).

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21 2.2 Zooplankton dataset 1995-2017

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1 Zooplankton biomass data for the period 1995-2017 are a product of an International Ecosystem
2 Survey in the Nordic Seas (IESNS) and stored in the Planning Group on Northeast
3 Atlantic Pelagic Ecosystem Surveys (PGNAPES) database at Faroe Marine Research Institute.
4 The dataset includes numerous and widely distributed zooplankton observations over the
5 Norwegian Sea, covering Atlantic water, Arctic water, and the Arctic frontal zone. Herein, we use
6 data from the uppermost 200 m sampled by WP2 nets and collected by the DTU Aqua/Technical
7 University of Denmark, Faroe Marine Research Institute, Institute of Marine Research in Norway
8 and Marine and Freshwater Research Institute at Iceland. Spatial fields of Norwegian Sea
9 zooplankton biomass during May throughout 1995-2020 were derived from interpolated
10 zooplankton observations using objective analysis utilizing a Gaussian correlation function (ICES,
11 2016; Figure 2.4, ICES 2020a, ICES 2020b). The routines for the objective analysis were made
12 available through cooperation with the Working Group on Integrated Ecosystem Assessments for
13 the Norwegian Sea (WGINOR)/Dr. Øystein Skagseth, IMR. The biomass distributed in size
14 classes were not available. We used the dataset to compute biomass estimates with the SP for May
15 2020 (with 142 observations) (SP2020) as well as with the SP1995-SP2004 with the aim to explore
16 both the influence of applying different SPs on a dataset with improved quality (longer time span,
17 more numerous and wider & regular spatial distributed observations, gridded by statistical
18 methods), and to investigate to what extent the present sampling pattern (SP2020) gives a more
19 robust estimate of the total biomass.

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22 2.3 Zooplankton model and simulation

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1 The NORWECOM.E2E model system consists of a physical ocean model providing offline
2 forcing fields of hydrography, currents, turbulence and light, a biogeochemical nutrients-
3 phytoplankton-zooplankton-detritus (NPZD) model two-way coupled to a suite of individual based
4 models (IMBs) for zooplankton and fish species, among them one model for *C. finmarchicus*
5 (Hjøllo et al. 2012, Huse et al. 2018). The most important processes of the *C. finmarchicus* model,
6 which are repeated daily, are movement, growth, mortality including predation, and reproduction.
7 The copepod goes through 13 different stages including an egg stage, six nauplii stages N1-N6,
8 five copepodite stages CI-CV, and an adult stage CVI. Here, the NORWECOM.E2E model was
9 run with the *C. finmarchicus* module but without the fish IBMs, thus predation from pelagic fish
10 was parameterized through visibility as a function of *C. finmarchicus* size, depth and light. This
11 mortality was based on the visual feeding model by Aksnes & Giske (1993) for individual species,
12 customized for use at population level. The annual predation from pelagic fish in the model (around
13 82 mill tons averaged over 1995-2004) is comparable to other estimates, e.g., Bachiller et al. (2018)
14 estimated around 84 mill tons of copepods were consumed by mackerel, blue whiting and herring
15 in 2005. There is no information on the size of the pelagic fish stocks, or equivalently, no
16 variability in the top-down control, so the variation in the modeled *C. finmarchicus* biomass herein
17 is due to bottom-up processes. For a full model description, we refer to Supplementary Material
18 S1. The model system has been validated by comparison with field data in the North Sea/Skagerrak
19 (Skogen et al. 1997, 2004, 2007, Søliland & Skogen 2000, Hjøllo et al. 2009, Gao et al. 2021), as
20 well as in the Nordic Seas and Barents Sea (Hjøllo et al. 2012, Skaret et al. 2014, Dalpadado et al.
21 2014). For the purpose of this paper, an extended validation focused on abundance is shown in
22 Supplementary Material S2.

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1 The spatial and temporal resolution of the 3D environment within NORWECOM.E2E are
2 user-defined. This experiment covered the Barents Sea, the Norwegian Sea and the North Sea
3 (Figure 1), consisting of ~21000 grid cells with length ~20 km and separated into 32 terrain-
4 following vertical layers. The time step was 1 hour, and the simulation length was 10 years (1995-
5 2004). The model was initialized with a distribution field for *C. finmarchicus* based on an
6 overwintering population distributed in the deep Norwegian Sea basin as well as in the Greenland-
7 and Barents Sea, evolved through a 25 years long adaptation process.

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10 2.4 Simulated time series and description of analyses

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12 For the simulation period 1995-2004, the model fields are stored every second day. *C.*
13 *finmarchicus* biomass and abundance are calculated from stage CI-CVI individuals in the upper
14 200 m. In addition, for validation purposes, a selected year (1997), abundance is also calculated
15 for the intervals 200-500 m and from 500 m to bottom.

16 The full 3D spatial and temporal dimension in the model provided an opportunity to
17 estimate the biomass by several sampling methods, i.e., perform *in-silico* sampling. We
18 constructed in total 14 time series from the model results for the month of May. First, to perform
19 a comparison with the “Obs-*insitu*” (the observed May biomass estimates), a time series from the
20 model was produced by averaging the modelled biomass sampled at the same time and location
21 (the closest corresponding point in the model) as used in the corresponding years in the
22 observational data. The resulting time series was labelled “Obs-*insilico*”. We also produced a
23 composite annual cycle from the model results in the same way as for the observations (mean of

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1 modelled biomass in all observational points from all years in a specific month, at the same day as
2 the observations). Next, we calculated the area averaged model mean biomass estimate (time series
3 “Modelled”) in a subdomain representing the gross part of Norwegian Sea where observations are
4 available (area shown as an insert in Figure 1) and the modelled core biomass are found. This time
5 series represents the most correct model estimate of *C. finmarchicus* biomass in the Norwegian
6 Sea (“the truth”), as the biomass in each grid point is weighted by the area of the grid cell before
7 the mean of all grid point estimates in the domain is found. This is in contrast to the “Obs-*insilico*”
8 and “Obs-*insitu*” biomass time series, which consists of arithmetic means of biomass in the
9 (irregularly distributed) observational points.

10 Thereafter, we began our exploration of the effects of spatial and temporal irregular
11 sampling. First, we considered the effect caused by interannual variations in the sampling scheme
12 (shown in Figure 1) by applying the SPs from *all* 10 years on the modelled May biomass field
13 *every year*, i.e. producing 10 new time series named Obs-*insilico*_SP1995, Obs-*insilico*_SP1996
14 and so on. This means that, for example, the time series “Obs-*insilico*_SP1995” applied the SP of
15 1995 to the modelled field annually from 1995 until 2004.

16 Lastly, we explored the effects on biomass estimates of sampling the highly spatial and
17 temporal variable *C. finmarchicus* biomass field. The combined effects of both spatial and
18 temporal variability were explored by choosing the minimum and maximum values in the
19 modelled *C. finmarchicus* biomass field over a space window of ± 2 grid cells (i.e. $\sim 80 \times 80$ km²)
20 and a time window of ± 10 days (i.e. 21 days) around the observational points, and the resulting
21 arithmetic mean time series were termed “Mod_dxdt_min” and “Mod_dxdt_max”. The time
22 window is chosen to represent the interannual variability during the May survey period, and the

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1 space window is chosen to resolve *C. finmarchicus* patchiness of ~17 km as found by Basedow et
2 al (2006).

3 For all time series, we calculated the mean value, standard deviation, and annual trend over
4 the period 1995-2004, and compared the time series by computing the correlation coefficient and
5 root mean square difference (RMSD) between each time series and the “Obs-*insitu*” and “Obs-
6 *insilico*” time series. Units for all time series are gC m⁻². All analyses are performed in matlab.
7 The description of the different time series and the results from the analyses are summarized in
8 Table 1.

9
10 Model results were compared with biomass estimates from observations in the Results section.
11 Readers are directed to Supplementary material S2 for further model validation, as the focus of
12 this study is the application of the model and not model validation *per se*.

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17 **3. Results**

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20 3.1 Horizontal distribution of biomass

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22 Maximum values of >5 gC m⁻² in modelled *Calanus finmarchicus* biomass in May were found in
23 a dipole pattern, with a local southern maximum outside Mid-Norway, and a local northern

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1 maximum in the Barents Sea entrance area for the years 1995-2004 (Figure 1). The southern
2 boundary of the core distribution ($>4 \text{ gC m}^{-2}$) was around 63°N , although years with more southern
3 distribution (1996, 1999) were found. Biomass patches were found up to 77°N , but were restricted
4 to approximately 73.5°N in some years (1996-1998, 2003-2004). The westward boundary of
5 biomass was at $\sim 7^{\circ}\text{W}$ for the whole period, although for the core area, the boundary was more
6 variable, but could be found around 4°E .

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8

9 3.2 Annual cycle of *C. finmarchicus* biomass from observations and model

10

11 The annual cycle in biomass and corresponding standard errors from the observations
12 (Obs-*insitu*) and model (Obs-*insilico*) (Figure 2) showed the spring bloom starting in March and
13 in May the observations and model estimates reached 2.6 gC m^{-2} and 2.3 gC m^{-2} , respectively. In
14 August, a new maximum was seen; weakly for the observations (1.6 gC m^{-2}), clearly (4.5 gC m^{-2})
15 for the model (Obs-*insilico*). The modelled timing of the spring bloom matched the observations,
16 while the modelled biomass was higher than the observed for June-October. These high biomass
17 values are related to lack of knowledge of the controlling mechanisms for starting diapause in the
18 autumn; an issue that will be elaborated in the Discussion section. On the other hand, the number
19 of observational points in the autumn were low (Figure 2, top panel), e.g., the September value
20 was based on only 62 stations, 40% of them in 1997 and thus in a constrained region (see Figure
21 1), which made the estimates uncertain. The area averaged estimate (black line) was considerably
22 lower than the pointwise estimate for August to October, indicating that for these months the
23 pointwise estimate was biased towards high density areas and thus not representative. In contrast,

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1 in spring, where the number of observations were high, the pointwise estimate from the
2 observations were reproduced both by the modelled pointwise and area-averaged estimates.

3
4 Observed biomass estimates for the period 1995-2004 (Figure 3a, thick blue line) varied
5 between 1.4 and 3.8 gC m⁻², reaching a maximum value in 2002 and thereafter declining. The
6 mean value for the whole period was 2.56 gC m⁻², with a negligible trend (0.01 gC m⁻² year⁻¹;
7 Table 1). The time series for two model estimates, i.e., the corresponding modelled pointwise
8 estimate (Figure 3a, red line), as well as area-averaged estimate for the subdomain (black line),
9 were generally in good agreement over the period (correlation coefficient 0.85, p < 0.05), but with
10 the area-averaged estimate being lower for all years except the last. Both time series showed a
11 weak decreasing trend of -0.05 and -0.02 gC m⁻² year⁻¹, respectively (Table 1), and mean values
12 of 2.25 and 1.92 gC m⁻². The mean values of the modelled time series were within 1 standard
13 deviation of the “Obs-*insitu*” mean value of 2.56 gC m⁻² (Table 1), but for individual years the
14 deviations were large; 2002 being an extreme example. There were no significant correlations
15 between “Obs-*insitu*” and “Obs-*insilico*” or “Modelled” time series.

16

17 3.3 Effect of changing the sampling pattern

18

19 The biomass estimates when sampling the model field for a given year with 10 different SPs are
20 widespread (Figure 3b) . Ideally, the biomass estimates should be independent of the SP applied,
21 so that they all give the same estimate and thus would be placed on top of each other. To be a
22 representative Norwegian Sea biomass value, they should also be close to the area-averaged
23 Norwegian Sea model mean (Figure 3b; black line). This was not the case. Figure 3b can be read

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1 in two directions. Exploring the figure vertically for each of the years 1995-2004, it was evident
2 that several SPs produced biomass estimates that were not representative for the “Modelled” value
3 for that year at all. For instance, in 1995, the estimates varied by a factor of 3.3; between 1.3 and
4 3.98 gC m⁻², the extremes represented by SP2004 and SP1996, respectively. However, the SP1995
5 estimate was very close to the “Modelled” estimate of 1.66 gC m⁻², indicating that SP1995 was
6 actually representing 1995-conditions quite well. This representativeness of the SP was also the
7 case for the years 2002-2004. On the other hand, the spread of the estimates was relatively low in
8 1999, but the deviation between SP1999 value (pink square; 2.83 gC m⁻²) and “Modelled” value
9 (2.14 gC m⁻²) was relatively high. The same can be seen for 1998 and 2000. Overall, SP1996
10 produced high estimates (highest or second highest), and SP2003 low estimates (lowest or second
11 lowest) in 8 of the 10 years (Figure 3b, Table 1). Generally, the SPs from the last part of the
12 simulated period produced lower values compared to the SPs from the first part of the period.

13 By applying all the year-specific SPs on the biomass field for all the years, we created 10
14 time series that ideally should all be similar. Exploring Figure 3b horizontally along the time axis,
15 the mean values of the “Obs-*insilico*_SP” time series range from 1.90-3.01 gC m⁻² (Table 1), with
16 the mean of “Obs-*insilico*_SP2004” corresponding to the area-averaged model mean (“Modelled”
17 time series). The trends of the time series were weak and both positive and negative, and none of
18 the time series were correlated to the “Obs-*insitu*” (Table 1). SP1996 had the highest Root Mean
19 Square Difference (RMSD) and mean value above all other time series.

20

21 3.4 Sensitivity to timing and patchiness

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

12

13 3.5 Sampling interpolated zooplankton fields

14

15 Comparing the estimates from resampling the interpolated fields from the objective analysis with
16 the SP of 2020 (SP2020) (Figure 5, stars) and with SP1995-SP2004 (Figure 5, shaded area), the
17 SP2020 estimates were, except for a few years, in the lower end of the biomass estimate range.
18 The mean SP2020 biomass value for the first period (until 2006) was higher than for the last period
19 (11.0 vs 6.8 g m^{-2}), and the interannual variability was also larger for the first period (up to 100%).
20 The width of the shaded area demonstrated that biomass estimates from the different SPs can vary
21 by up to 100% for each year, and the spread of the dots over the shaded area showed that it is no
22 single SPs that caused the width. For SP1995 to SP2004, the interannual variabilities in biomass

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1 were generally larger than those for SP2020, and were as large as 400% (for SP1996 or SP1997
2 for the 2001- 2002 biomass difference, Figure 5, encircled dots).

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6 **4. Discussion**

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8 Zooplankton, the intermediate trophic link between phytoplankton and fish, is notoriously
9 difficult to sample due to patch variability, and basin-scale monitoring remains challenging.
10 Consequently, the observables suffer from representativeness issues, due to the natural variability
11 of the system but also the large variety in sampling strategies for observing the system. The lack
12 of control of the representation error (the ability of observations to represent a larger area over
13 time) limits their use as reliable indicators of changes, or in constructing model validation fields,
14 as was the starting point for this study. The absence of an objective truth has been discussed by
15 several authors (Lynch et al. 2009, Schutgens et al. 2017, Skogen et al. 2021), and Skogen et al.
16 (2021) advocates that models and observations should be joined to strengthen both in the process
17 of disclosing the truth. Not only should observations be used to validate the models, but also the
18 other way around: how can models validate the observations? In the current paper, we put this idea
19 into practice for a system well modelled and sampled (at least for part of the period studied), to
20 serve as an inspiration for studies on less sampled systems.

21

22 **Model validation**

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1 We have studied the combined impact of spatiotemporal sampling on representation errors
2 for a zooplankton observing system by applying an existing ecosystem model to generate biomass
3 distributions of the *Calanus finmarchicus* population within the Norwegian Sea. The model
4 compared adequately with biomass and abundance reported in the literature (Figure 2 and
5 Supplementary material S2), although with elevated values in the autumn not seen in the utilized
6 observational dataset. Part of the autumn maximum is probably due to the way we have simulated
7 how individuals decide whether to go into diapause or risk staying in the pelagic environment for
8 producing another generation. The controlling mechanisms for these processes are poorly known.
9 In the model, two adapted «genes» or strategies (Allocation-to-Fat-Day AFD and Fat-to-Soma-
10 Ratio FSR, Table S1) are used to determine whether an SI should produce a new generation or
11 build enough fat reserves for enabling overwintering. The model tends to overestimate the number
12 of copepods that decide to produce a new generation. The individuals of this generation will, to a
13 large extent, not mature for overwintering during fall but instead appear as a high autumn biomass
14 that will gradually decrease as these individuals starve and die off before the next spring. On the
15 other hand, when we conclude that the modelled biomass in the fall is too high, it is not because
16 we have precise estimates on this biomass to say that the model is wrong, but simply because the
17 observations say that it should be lower at this time of the year compared to, for example, summer.
18 We also note that for the observations in general, there are issues related to, for example, the
19 catchability of *C. finmarchicus* with the WP2 net (Skjoldal et al. 2000), and the method of
20 separating *C. finmarchicus* from other zooplankton species. For the latter we assumed a *C.*
21 *finmarchicus* content of 50%, 70% and 0% in the size fractions 0.18-1mm, 1-2 mm, and > 2 mm,
22 respectively, but there may be temporal and spatial variations in this relationship that are not taken
23 into account, which will influence the “Obs-*insitu*” time series. We note that the *C. finmarchicus*

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1 fraction also may be biased due to *C. glacialis* and *C. finmarchicus* species misidentification and
2 may subsequently require reinvestigation with the systematic use of molecular tools (Choquet et
3 al 2018). The analysis in this paper is focused on May, where the model sufficiently resembles the
4 average annual values (Figure 2), the horizontal and vertical distribution (Figures S1.1-4), but there
5 are also observations available in July/August showing a weak local maximum (Figure 2). It is left
6 to a follow up study to explore the autumn levels of *C. finmarchicus* biomass.

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9 **Sampling pattern effects**

10 Modeled data were processed using the same methods as for real surveys, but in addition
11 13 different model generated time series of biomass estimates for *C. finmarchicus* within the
12 Norwegian Sea during the month of May were analyzed (Figure 3 and Table 1). We found the
13 pointwise estimate “Obs-*insilico*” in most years differed from both the corresponding estimate
14 from the observations and the “truth” (in this case the area averaged modelled biomass estimate,
15 i.e., “Modelled”). Reduced biomass estimates in the years 2000-2004 can be related to several
16 causes. The center of gravity for the locations of the observations is found more offshore, where
17 the seasonal cycle of *C. finmarchicus* development differs from the cycle in coastal water masses
18 (Broms and Melle 2007). There is also north/south interannual variability in center of gravity. We
19 did not find any systematic relation between biomass level and mean day of observations (varying
20 from May 8 to 16), or between biomass level and the number of observations, although we do note
21 that the length of the period studied (10 years) is short.

22 The large spread in biomass estimates when applying 14 different SPs to each individual
23 year demonstrates that SPs really matter. The SPs from the last part of the 1995-2004 period

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1 resulted in generally lower mean modelled biomass values than SPs from the first part of the period
2 (Figure 3b; Table 1). The variability in 2004 is lesser than for the previous years, but whether this
3 is due to a more robust sampling scheme achieved, changed *C. finmarchicus* population
4 characteristics such as horizontal extension, patchiness etc, and/or by pure coincidence remains
5 unclear. Generally, the variability in the modelled time series is lower than for the observations
6 (Table 1).

7 Sampling of a spatiotemporal patchy field is challenging, and can only be achieved by
8 high-resolution measurements over space and time. Spatial distributions of *C. finmarchicus* have
9 been found to be highly patchy (Toresen et al. 2019), with a high spatial correspondence between
10 Chl-a and copepods (CV and adult female; Basedow et al. 2006), and with patches from a few
11 kilometers (Trudnowska et al 2016) to several tens of kilometers (Wishner et al. 1988) long
12 horizontally. In contrast, Young et al. (2009) showed that 50% of the spatial variance of copepod
13 nauplii and copepods occurs at the meter scale. In addition, the temporal changes in size and stage
14 of the copepods are rapid, reflecting the intense spring season with the length of different life
15 stages on the order of days, and individuals undergoing their whole life cycle in 22-59 days,
16 depending on temperature and food concentration (Campbell et al. 2001). Sampling along a steep
17 *C. finmarchicus* temporal gradient, such as the one found in the data from May, introduces a large
18 uncertainty, but, as May is the time of the year when research ships are available for either
19 dedicated zooplankton sampling or to combine such sampling with other activities, this is still the
20 main period of zooplankton mapping in the Norwegian Sea. Our results demonstrate that within a
21 zooplankton patch of size 80km, the model biomass estimate can vary by a factor of 10,
22 corresponding to estimates of elevated zooplankton concentration in patches found in the literature

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1 (3-17 times higher biomass than in the surroundings; Trudnowska et al 2016). The sampling
2 patterns applied (Figure 3b) are therefore associated with uncertainty.

3

4 **Recent zooplankton sampling**

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

22 The reasons why the zooplankton time series as sampled by SP2020 (or as presented as the
23 area-averaged mean in ICES (2020a), including all size classes, not directly comparable to the *C.*

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1 *finmarchicus* field modelled) show a decline and thereafter low zooplankton biomass levels after
2 2002 are not well known (ICES 2016), but high predation pressure from pelagic fish has been
3 suggested (Huse et al. 2012). Other explanations involve high predation from carnivorous
4 zooplankton stocks, timing effects (as match/mismatch with the phytoplankton bloom), and lower-
5 than-average heat contents (ICES 2016). Based on the present study, the methodology (sampling
6 design and interpolation) might also be part of the explanation. Dynamical, process-oriented model
7 simulations can be used to explore the reasons for such changes in biomass. For example, in the
8 present model set-up, top-down effects such as predation from pelagic fish and carnivorous
9 zooplankton stocks are not inter-annually varying. If the simulation was extended to cover the
10 period up to present, and assuming that significant correlations between the observed and modeled
11 *C. finmarchicus* biomass were found, top-down forcing should be ruled out as a cause for the
12 decline. Incorporating inter-annual varying top-down effects in the form of full IBMs for the main
13 predators of *C. finmarchicus*, as already introduced into the model (Utne et al. 2012, Holmin et al.
14 2020), the consequences of varying *C. finmarchicus* biomass levels (and other pressures e.g.,
15 climate change) for the food web can be disentangled.

16

17 **Concluding remarks**

18 We have applied results from an ecosystem model to illustrate how spatiotemporal
19 patchiness will impact May biomass estimates through representation errors. When is a model
20 good enough to be used for a certain application? Model validation is meant to answer such claims
21 about the applicability and accuracy of a model regarding the intended purpose as well as to the
22 natural system it represents (Dee, 1995). The model applied in this study has been validated in
23 several articles (e.g., Hjøllo et al., 2012, Skaret et al., 2014, Gao et al., 2021), and we believe that

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1 these works have proven the model's applicability to be used to simulate the life cycle of both *C.*
2 *finmarchicus* individuals and population. In the present work, the question of applicability was
3 redirected to the observations. Zooplankton fields are very patchy, and observations of such
4 quantities will strongly depend on whether a patch is hit or not, thus the representativeness will be
5 a function of the sampling technique and the spatiotemporal resolution (Omori & Hamner 1982).
6 The main objective of the present work was to investigate the latter. Of course, the model is not
7 representing the full truth. It will always be limited to the biological understanding we have; thus,
8 a model is recognized with a basic spatial and temporal resolution, but incomplete representation
9 of processes and components of a natural system, while observations on the other hand give an
10 incomplete access to a natural phenomenon where spatial and temporal resolution is a compromise
11 (Oreskes et al., 1994). Figure 4 in our work clearly demonstrates how this compromise may lead
12 to a large uncertainty based on estimates purely from a small number of observations. One can
13 always argue that with 20km horizontal resolution in the model is not representing the true
14 patchiness, and we agree with this. However, this is not an argument against the present analysis.
15 Using higher-resolution model simulations would change the patchiness of the model, but within
16 the near future the horizontal resolution would be far away from meter-scale, and spatiotemporal
17 patchiness would still be an unresolved process. We think our study illustrates how spatiotemporal
18 patchiness will impact the results, thus hopefully initializing a discussion on what is the best way
19 to measure zooplankton biomass.

20 Marine monitoring is costly, and if we could efficiently utilize other platforms, we could
21 improve the information underpinning the management decisions. Use of joint model-observations
22 studies have earlier identified preferable sampling frequency for Faroe Island hydrography (Hátún
23 et al. 2005), assessed the representativeness of Barents Sea indicators in management plans

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1 (Hansen et al. 2021) and evaluated the efficacy of both new and existing fishery surveys (Holmin
2 et al. 2020). This study is an example of how dynamical ecosystem models can be used specifically
3 to assess zooplankton SPs in the Norwegian Sea, but also contribute towards the growing
4 recognition of how ecosystem models can contribute to the management of marine ecosystems.

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6

7 **Acknowledgement**

8

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22 Council.

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1 **Figures and tables**

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9 Table 1 Time series overview and statistical parameters. Name of *C. finmarchicus* biomass time
 10 series, short description, and mean (gC m⁻²), standard deviation, linear trend for each time series
 11 (gC m⁻² year⁻¹), correlation coefficient between each time series and the “Obs-*insitu*” time series,
 12 RMSD between each time series and the “Obs-*insitu*” time series, between each time series and
 13 the “Obs-*insilico*” time series. None of the correlation coefficients are significant at a confidence
 14 level of p<0.05.

Name of time series	Description	Mean	Std	Lin trend	Corrcoeff	RMSD
Obs- <i>insitu</i>	Arithmetic mean of observed biomass at all observational locations	2.56	0.79	0.01	1.	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 gridcells	1.92	0.28	-0.02	0.24	0.98
Obs- <i>insilico</i> _SP1995	As above, but for all years using spatial and geographical location 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

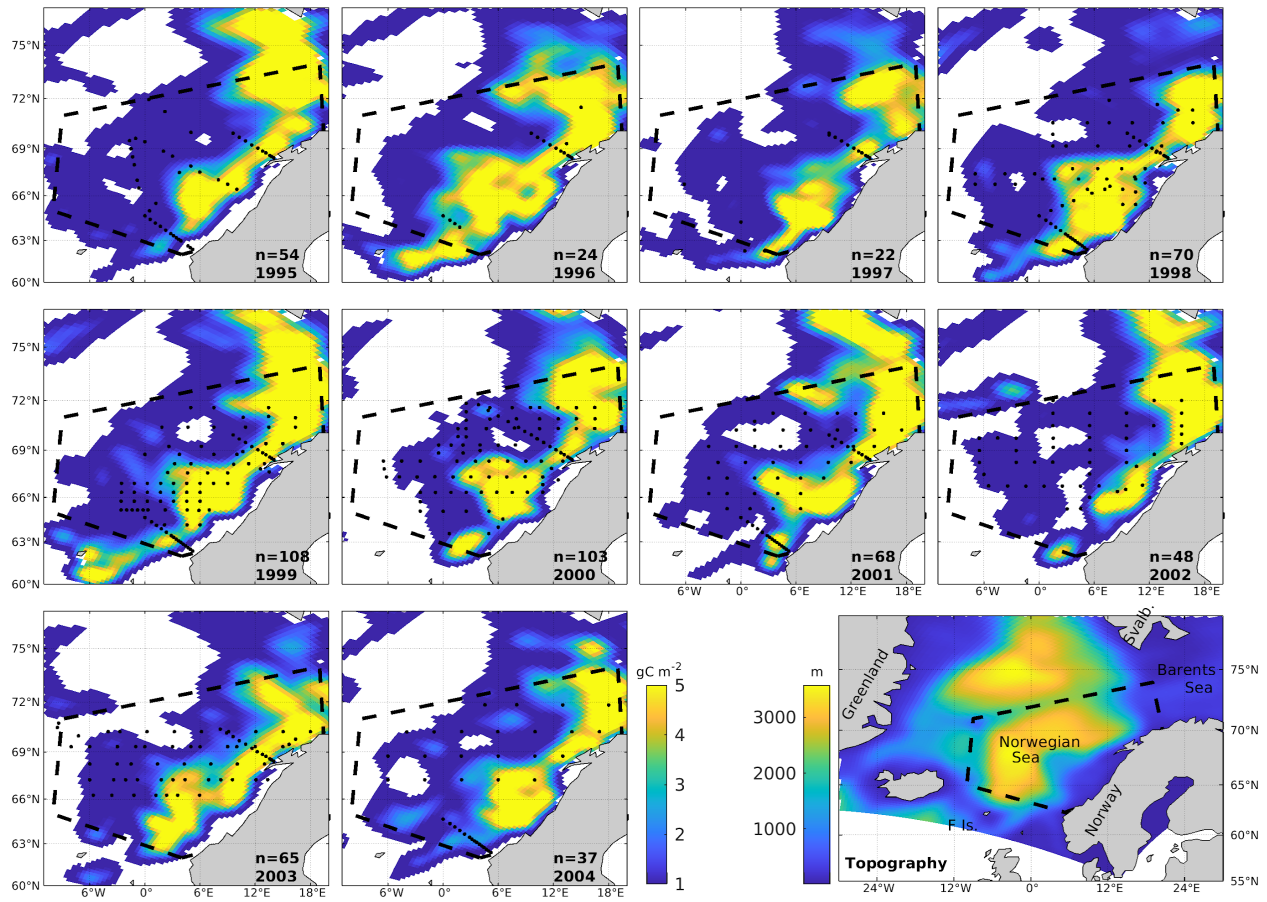
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Obs-insilico_SP1998	As above, but for 1998	2.43	0.46	0.04	0.20	0.80
Obs-insilico_SP1999	As above, but for 1999	2.38	0.59	-0.01	0.16	0.88
Obs-insilico_SP2000	As above, but for 2000	2.35	0.39	-0.01	0.25	0.78
Obs-insilico_SP2001	As above, but for 2001	2.17	0.36	0.00	-0.10	0.94
Obs-insilico_SP2002	As above, but for 2002	2.15	0.45	-0.04	0.14	0.91
Obs-insilico_SP2003	As above, but for 2003	1.90	0.27	0.01	0.25	0.98
Obs-insilico_SP2004	As above, but for 2004	1.92	0.39	0.02	-0.20	1.10
Mod_dxdt_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_dxdt_min	Area averaged model mean biomass, using minimum values within a time/space window	0.53	0.21	-0.01	0.54	2.14

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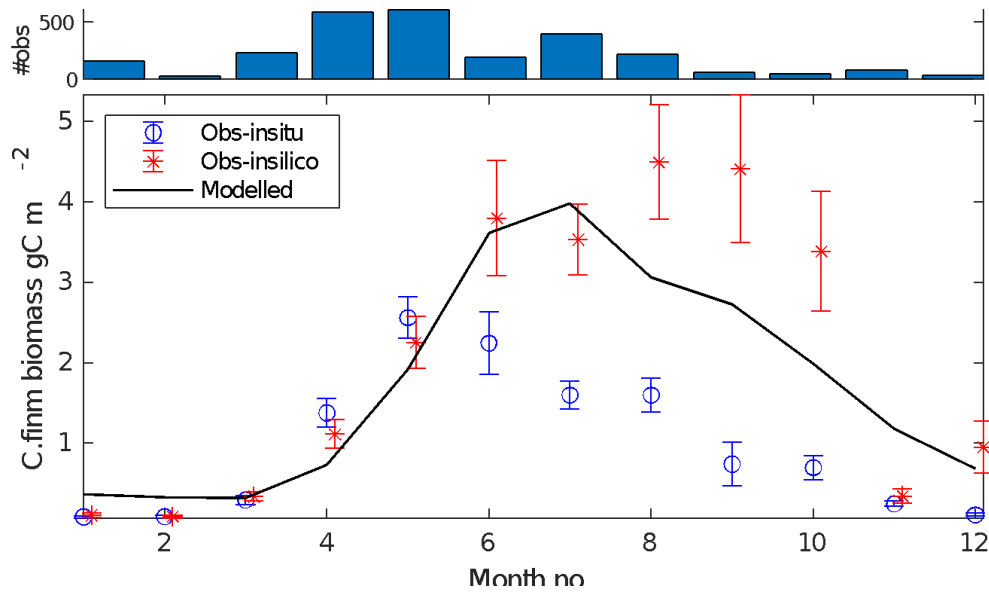
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7 **Figure 1** Stations (dots) for observed May zooplankton biomass locations superimposed on the
 8 modelled mean May *C. finmarchicus* biomass (CI-CVI upper 200m) from the norwecom.e2e
 9 model for the period 1995-2004. Only areas with biomass values $> 0.3 \text{ gC m}^{-2}$ are plotted. The
 10 number of observations for the year (n) is presented. Stippled area indicates the domain of which

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1 Norwegian Sea estimates are based. Lower right panel shows model topography. F Is = the Faroe
2 Islands.

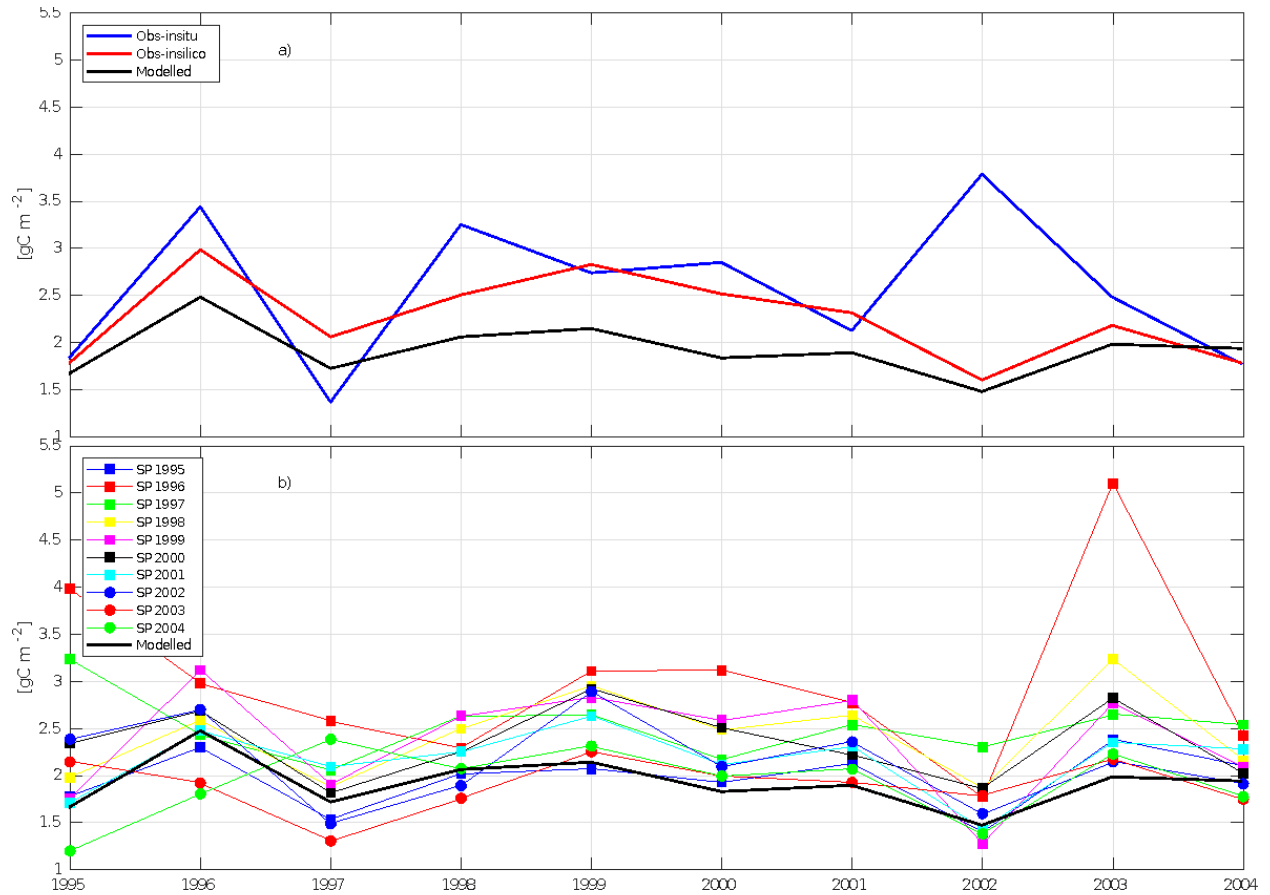
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Figure 2 Monthly means of composite values for *C. finmarchicus* biomass in the upper 200 meters for the period 1995-2004. Estimates from observations (blue circles), corresponding model estimates (red stars), and area-averaged mean over area from model simulation (black line). The error bars are the standard error on the mean (SE), calculated as $SE = \sigma / \sqrt{N}$, where σ is the standard deviation of all observations (N) in each month for all years (x). N is shown above the figure.

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2 **Figure 3** May *C. finmarchicus* biomass in upper 200 meters from observations and the
3 norwecom.e2e model for the period 1995-2004. a) Observed biomass estimate (thick blue line),
4 the corresponding time series from the model (red line), area-averaged model estimate (black line),
5 b) estimates from different SPs (colored symbols) and area-averaged model estimate repeated
6 (black line)

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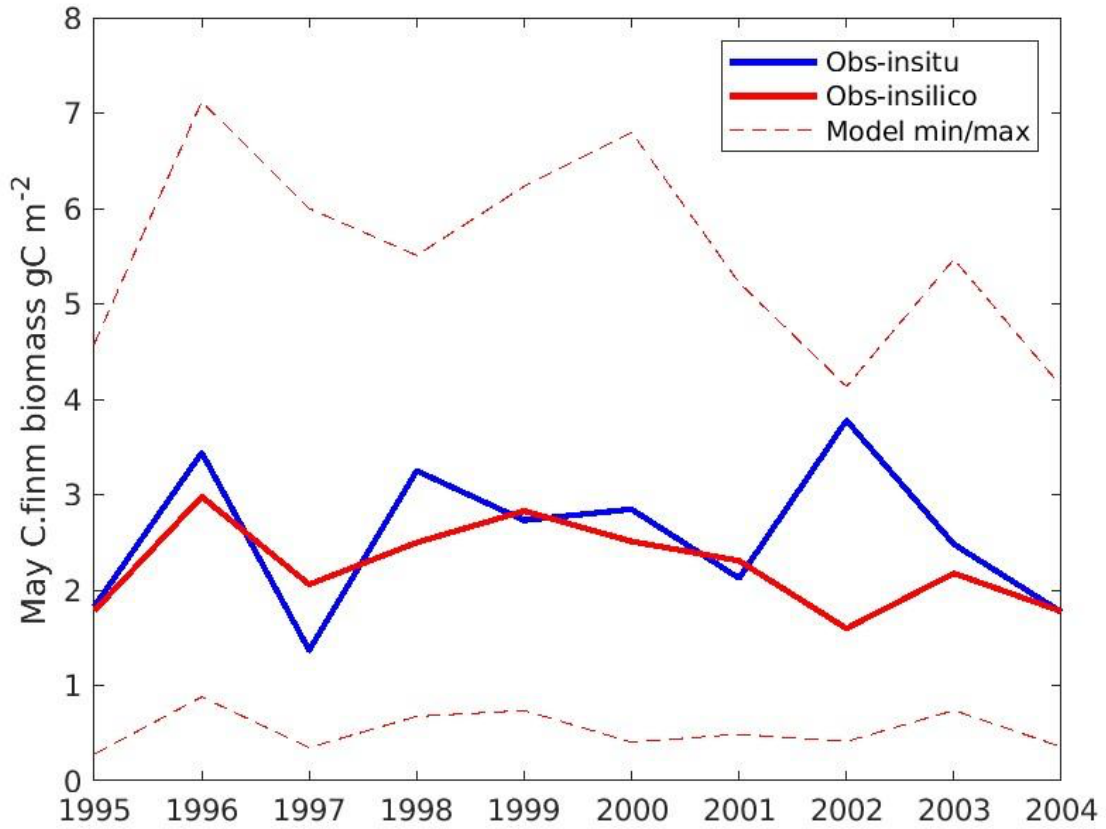
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4 **Figure 4** Observed (blue) and modeled (red) *C. finmarchicus* biomass as in Figure 3, and in
5 addition stippled lines for minimum and maximum values in the modeled *C. finmarchicus* biomass
6 field over a space window of ± 2 grid points and time window of ± 10 days.

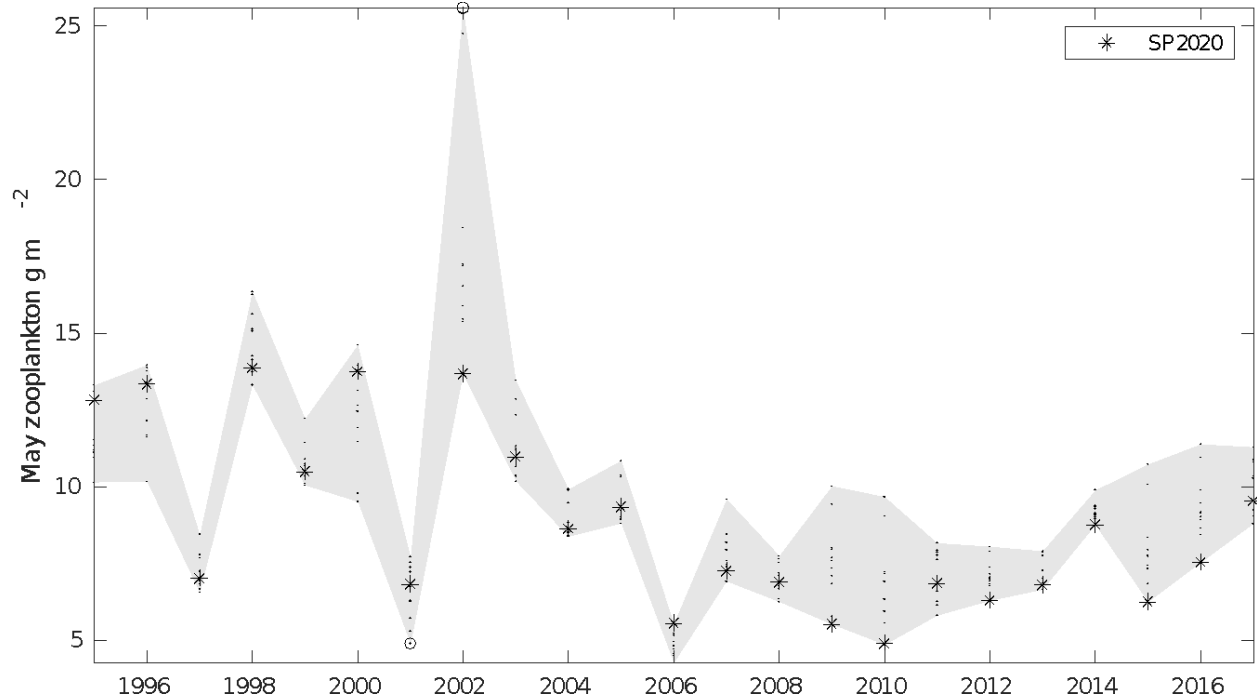
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3 Figure 5 Annual zooplankton biomass indexes (g dry weight m⁻²) from spatially interpolated
4 observations, estimated 1) by SPs from year 2020 (stars), and 2) by SPs from the years 1995-2004

5 (grey shade and dots). The encircled dots are the biomass estimates from SP1997. Biomass is
6 sampled by WP2 in May in the Norwegian Sea and adjacent waters (delimited to east of 14°W and
7 west of 20°E) from 1995-2017, and spatial fields derived from interpolation using objective
8 analysis utilizing a Gaussian correlation function (see details on methods and areas in (ICES 2016).

9 Data from PGNAPES database at Faroe Marine Research Institute and interpolated fields from Dr.
10 Ø. Skagseth, Institute of Marine Research, Norway.

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