

Infaunal and epifaunal secondary production in the Barents Sea, with focus on snow crab (*Chionoecetes opilio*) prey resources and consumption

Børge Holte ^{1,*}, Mona M. Fuhrmann ¹, Anne Helene S. Tandberg ², Carsten Hvingel ¹
and Ann Merete Hjelset ¹

¹Institute of Marine Research, Fram Centre, Hjalmar Johansensgt. 14, 9007 Tromsø, Norway

²University Museum of Bergen, Allégaten 14, 4007 Bergen, Norway

*Corresponding author: tel: +47 91630856; e-mail: boerge.holte@hi.no.

Since the first observation of snow crab (*Chionoecetes opilio*) in the Barents Sea in 1996, the population has increased significantly, supporting a commercial fishery on the Norwegian shelf since 2012. To investigate whether the availability of benthic prey organisms may support a continued geographical snow crab expansion, benthic invertebrate production was studied across the central parts of the Barents Sea and around Svalbard, where snow crabs are currently absent or at low densities. Annual productivity (*P/B* ratio) from 66 stations collected by grab and beam trawl was estimated using a multiparameter artificial neural network model. Mean infaunal productivity and production were 0.43 yr⁻¹ and 38.4 g ww m⁻² yr⁻¹, respectively, while the epifaunal production was considerably lower with 2.5 g ww m⁻² yr⁻¹. The proportions of epi- and infaunal production suitable as prey for snow crab were 98 and 96%, respectively. Areas close to the Polar Front represent the most attractive snow crab foraging region, having the highest benthic secondary production, high estimated primary production, and bottom water temperatures within the snow crab's preferences. At snow crab densities of 12800 ind. km⁻², high enough to support commercial fishing, their mean consumption rate was estimated to be around 1.5 g ww m⁻² yr⁻¹, which amounts to 4% of mean infaunal prey production. Food availability is, therefore, not expected to be a hindrance to further population expansion of the snow crab in the Barents Sea.

Keywords: beam trawl, benthic productivity, biomass, grab, high latitude systems, newly established species, *P/B*-ratio, polar front.

Introduction

The snow crab *Chionoecetes opilio* (Fabricius, 1788) population is widely distributed on high-latitude continental shelves, and several valuable fisheries are established in the USA, Japan, and Canada. In 1996, the snow crab was observed for the first time in the south-eastern Barents Sea (Kuzmin *et al.*, 1999) and has later increased its geographical range and established a self-reproducing population in large parts of the Barents Sea (Alvsvåg *et al.*, 2009; Agnalt *et al.*, 2010; Danielsen *et al.*, 2019) and Kara Sea (Zimina, 2014). A new study based on genetic analysis shows that the snow crab presence in the Barents Sea is a result of a recent natural expansion from waters around Alaska (Dahle *et al.*, 2022). The snow crab's native habitat includes the northern Pacific and the cold waters of the Sea of Japan east of the Korean Peninsula, the Sea of Okhotsk, the Chukchi Sea, and adjacent waters, eastern Siberian waters, the Laptev and Beaufort seas as well as the north-western Atlantic Ocean, including waters off western Greenland (Slizkin, 1982; Williams, 1984). In the Barents Sea, a small snow crab fishery started in 2012 and it has since increased in economic importance concurrent to the crabs' expanding geographical distribution (Hvingel *et al.*, 2021).

As a newly established large benthic decapod in the Barents Sea, snow crab predation pressure may impact existing ecological interactions through changes in the composition of benthic invertebrate communities (Quijón and Snelgrove, 2005; Lutz-Collins *et al.*, 2016; Oug *et al.*, 2018), potentially affect-

ing trophic interactions (Gebruk *et al.*, 2020), food web structure, and energy flow (Pedersen *et al.*, 2018). The snow crab is known to have a broad dietary range, feeding on both in- and epifaunal species including, among others, amphipods, ophiuroids, polychaetes, shrimp, small bivalves, and gastropods (see e.g. Pavlov, 2007; Chuchukalo *et al.*, 2011; Divine *et al.*, 2017; Zakharov *et al.*, 2020). The snow crab usually feeds on the most abundant prey species, although selective feeding on less abundant prey species has been reported (Wieczorek and Hooper, 1995; Lovrich and Sainte-Marie, 1997). There is, for example, evidence that larger prey items, such as hard-shelled molluscs, are available to large males due to their relatively large chela size (Kolts *et al.*, 2013). However, a study from the Pacific Arctic revealed no major size-dependent diet segregation (Divine *et al.*, 2017). The snow crab thrives in various benthic habitats that may vary with sex and life stage. In Newfoundland waters, immature snow crabs have been found to reside in relatively shallow rocky areas, and when growing, they tend to move to deeper muddy habitats (Comeau *et al.*, 1998). Studies from the eastern part of the Barents Sea indicate that this movement to deeper areas is dominated by males, while females and juveniles typically occupy shallow areas (Zakharov *et al.*, 2020).

The future geographical expansion of the snow crab population in the Barents Sea will largely depend on, among other factors, temperature and prey availability (Kolts *et al.*, 2013; Divine *et al.*, 2017). To date, only two published studies have

Received: March 27, 2022. Revised: September 27, 2022. Accepted: September 28, 2022

© The Author(s) 2022. Published by Oxford University Press on behalf of International Council for the Exploration of the Sea. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

attempted to quantify food resources and estimate consumption by this new predator in the Barents Sea (see Jørgensen *et al.*, 2019; Zakharov *et al.*, 2020). Both studies were based on benthic abundance and biomass estimation solely, which are static measurements providing little information about community response over time. Secondary production of a population integrates density, biomass, and dynamic population measures such as growth, recruitment, and mortality (e.g. Dolbeth *et al.*, 2012) into an overall functional measure of energy flow through the system. Studies on benthic secondary production from the Barents Sea are scarce (see Kedra *et al.*, 2013) but are needed to obtain reliable estimates of energy flow that may elucidate any snow crab prey limitations, provide valuable input to food web models addressing trophic interactions, and contribute to an increased knowledge base for future snow crab management.

Using grab- and beam trawl collected fauna from central and western parts of the Barents Sea, the present study attempts to (1) increase the current knowledge of benthic invertebrate production and its drivers in the Barents Sea; (2) estimate the annual secondary production of prey available for snow crab; (3) estimate snow crab consumption; and (4) identify areas that may be suitable for further snow crab range expansion in the Barents Sea.

Material and methods

Study area

The up to 500 m deep Barents Sea has an average depth of 230 m (Loeng, 1991) and is bounded by Norway and Russia to the south, Novaya Zemlya to the east, and by continental slopes to the west and north. The southern water masses are influenced by Atlantic water, with temperatures typically $>3^{\circ}\text{C}$ and salinities >35 , while subzero temperatures occur in the areas north of 76°N . West of the Central Bank, Atlantic, and Arctic water masses meet and form the relatively stable and strongly topographically controlled Polar Front (Fer and Drinkwater, 2014; Oziel *et al.*, 2016) (Figure 1). In general, the seafloor substrate in the Barents Sea consists of mud and sandy mud with admixed gravel in the relatively shallow bank areas, while sand and gravel dominate in the shallowest parts of the Spitsbergen Bank (Lepland *et al.*, 2014).

The Barents Sea is highly productive, with a modelled annual primary production of $106\text{--}134\text{ g C m}^{-2}\text{ yr}^{-1}$ in the Atlantic-influenced areas and $54\text{--}67\text{ g C m}^{-2}\text{ yr}^{-1}$ in the seasonally ice-covered regions (Reigstad *et al.*, 2011). The mid and northern parts of the Barents Sea are largely ice-covered during the Arctic winter (Loeng and Drinkwater, 2007).

Field sampling

A total of 66 stations were sampled in the period 2013–2017, all years between March and November, and at depths between 85 and 458 m during the Norwegian Mareano seafloor mapping programme's field campaigns (Table 1; see www.mareano.no). Each station was visited once. The sampled areas (Figure 1) were preselected by the Norwegian Government to increase seafloor-related ecological and geological knowledge relative to the future management of the Barents Sea (Anon., 2011). Sampling followed a stratified design using unsupervised classification maps (Isocluster) based on multi-beam bathymetry and backscatter data (substrate type, depth, terrain variables), modelled seafloor temperature and veloc-

ity (Buhl-Mortensen *et al.*, 2015; Bøe *et al.*, 2020). The stations were generally located to cover the entire environmental range in the study area without taking distances between adjacent stations into account. Detailed station data is available at the Norwegian Marine Data Center (<https://nmdc.no/>) and through the European Marine Observation and Data Network (<https://emodnet.eu>).

At each grab station, a total bottom area of 0.5 m^2 was sampled using van Veen grabs with a sampling area of 0.1 m^2 (62 stations; five replicate samples) or 0.25 m^2 (four stations; two replicates). The lowering speed was reduced to 0.2 m s^{-1} when approaching the sea floor. Fauna collected using these grab sizes is suggested to be quantitatively comparable (Holte and Buhl-Mortensen, 2020). The samples were sieved using 1 mm mesh sieves. Each replicate was treated separately during fauna identification and quantification, whilst pooled per station in the data analysis and the presentation of results.

Epifauna was sampled using a 2 m wide beam trawl equipped with a bottom chain, a belly net mesh of 20 mm, and a 4 mm mesh size for the cod end (Rees, 2009). The beam trawl hauls were standardized to a 5 min tow time at a speed of 1.5 knots. The sampling area was calculated using the swept area method (distance travelled on the seafloor $\times 2\text{ m}$). The beam trawl samples were sieved through 5 mm mesh sieves. All samples (grab and beam trawl) were fixed in borax-buffered 4–6% formaldehyde solutions. Sampling periods for the three sub-areas studied and their position ranges are shown in Table 1.

After the field surveys, the organisms were sorted and transferred to 70% ethanol and identified to the lowest possible taxon (Supplementary Table S1) by largely the same taxonomic experts throughout the sampling period. All taxa names were standardized according to the World Register of Marine Species (WoRMS; last accessed February 2022). For each taxon identified, wet weight (ww) was measured with an accuracy of 0.0001 g. The Polychaeta tube weight was subtracted from the total weight after estimating the average individual tube weight by temporary species-specific subsampling (undertaken by the taxonomic experts). Unidentified animal fragments, pelagic taxa (e.g. jellyfish and copepods), fish, and meiofauna (e.g. Nematoda) were excluded from the dataset.

The sampled areas are largely within the present distribution area for snow crab in the Barents Sea (Figure 1).

Environmental variables

At each station, one extra grab sample was taken for collecting sediments for analyses of total organic carbon (TOC) and grain size (clay + silt/ $<0.06\text{ mm}$) from the uppermost 5 cm of the sediment column, using two 6 cm diameter corers. TOC content was determined by baking samples in an induction oven at 1300°C (European Standard, 2012). Grain size was measured using mechanical ($>0.06\text{ mm}$) and wet-sieving ($<0.06\text{ mm}$) techniques. The TOC and silt + clay proportion varied between 0.5–3.6% and 37–98% of total sediment weight, respectively (Table 1).

Mean monthly bottom water temperatures, salinities, and velocities for the period 2012–2017 were extracted from the SVIM model on a 4 km grid resolution (Lien *et al.*, 2014), varying from ca. -1.5°C in the north to ca. 2°C in the south at the sampled stations (Table 1). During the field sampling (2013–2017), temperature and salinity were routinely

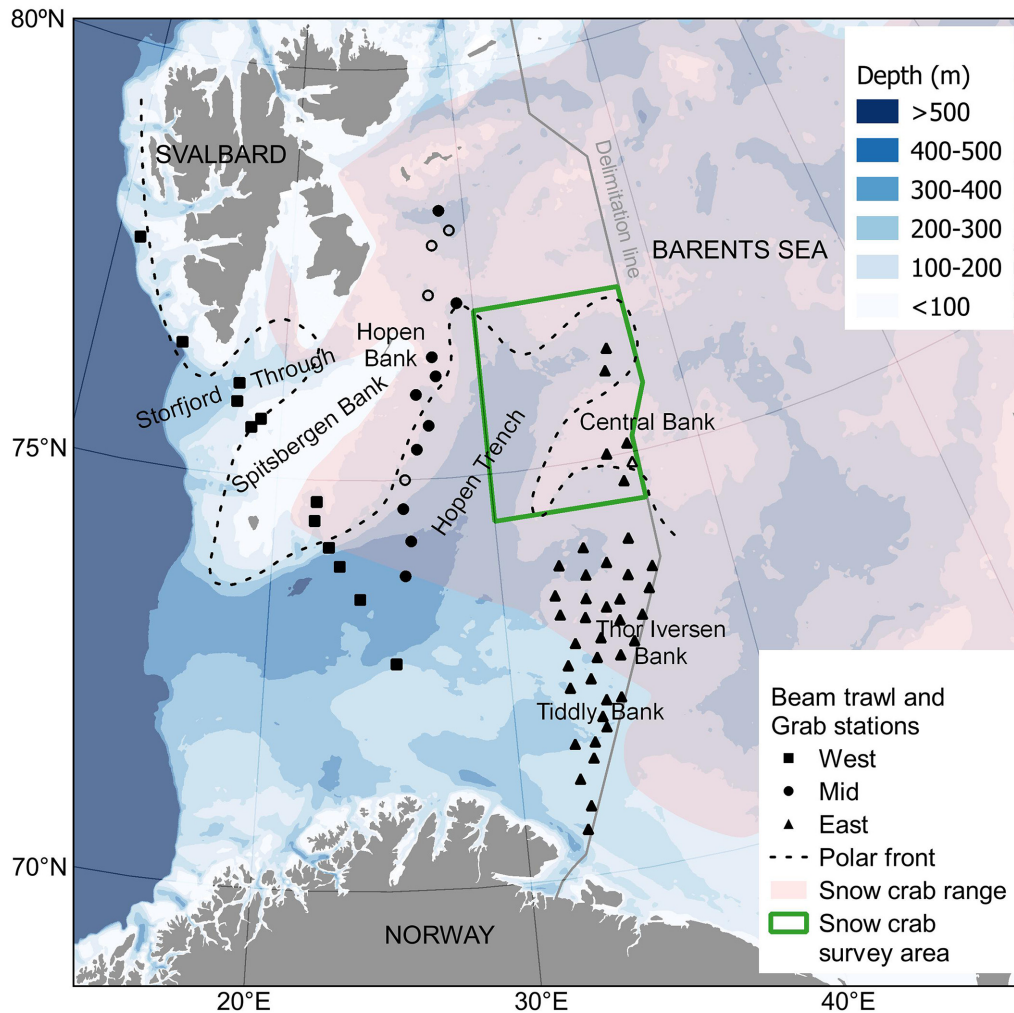


Figure 1. Study area with the 66 sampling stations obtained in three sub-areas (named west, mid, and east; see Table 1) during the period 2013–2017. The five stations with open symbols were sampled using grab solely (no beam trawl samples). The shown snow crab range is based on observations obtained from various surveys conducted by the Institute of Marine Research (IMR) and the Polar branch of the Russian Federal Research Institute of Marine Fisheries and Oceanography (VNIRO). The green polygon shows the area where annual snow crab surveys (IMR) are undertaken and where the Norwegian crab fishery mainly takes place. The snow crab densities calculated in the present study are based on survey data from this area (2020/21). Outside of this area, snow crab densities are low.

measured 10 m above the seafloor using a Seabird 911 CTD sampler.

Data on primary production and sea ice cover were retrieved from the NORWECOM model (Skogen and Søiland, 1998; Samuelson *et al.*, 2015). Values represent the net primary production (in gram carbon $\text{m}^{-2} \text{yr}^{-1}$) and the number of days with >10% ice-cover averaged for the period 2013–2017.

Benthic secondary production

Benthic invertebrate secondary production (P) was estimated from annual Production-to-Biomass ratios (P/B) obtained from the Artificial Neural Network model (ANN) by Brey (2012). This empirical model uses individual biomass as the major input variable. Environmental variables (sampling depth and mean estimated annual bottom temperature), taxonomic identity, and habit (motility, feeding mode, habitat) served as additional predictors in the model. Taxon-specific conversion factors compiled in Brey (2001) were used to convert biomass records (wet weight) into energy (J), where hard

shells were excluded from conversion. If a taxon was not listed in the database, the conversion factor was obtained from the next higher taxonomic level available. Colonial taxa were excluded from production calculations.

Macrobenthic production (kJ or $\text{g ww m}^{-2} \text{yr}^{-1}$) for each taxon at each sampling station was then estimated by multiplying P/B (yr^{-1}) with biomass (B). Total P/B values per station were calculated by summing total production over total biomass based on energy converted values (J). Taxa estimated from beam trawl samples comprised mainly epifaunal species (compare Jennings *et al.*, 1999; Reiss *et al.*, 2006) and grab samples were dominated by infauna. Because the used sampling gears have different efficiencies and for consistency, we present results separately for each gear and refer below to epifauna (beam trawl sampled) and infauna (grab sampled).

Snow crab consumption

Snow crab prey taxa (Supplementary Table S1) were identified using available published studies from northwest Atlantic Canada (Wieczorek and Hooper, 1995; Lovrich and

Table 1. Sampling periods for the three sub-areas studied (Figure 1), their geographical range, ranges of depth, sediment silt + clay content and total organic carbon content (TOC). Mean annual bottom water temperature, salinity, bottom water current velocity, mean net primary production, and mean number of ice-days with >10% ice cover are modelled data based on monthly average values over the period 2012–2017 (ice-cover and netPP: 2013–2017).

Sub-area (Figure 1)	Sampling period	Regional position	Depth m	Silt + Clay %	TOC %	Modeled data				
						Temp., °C	Salinity	Velocity cm s ⁻¹	NetPP g cm ⁻² yr ⁻¹	*Ice-days yr ⁻¹
West ■ 12 stns	2017, 28.03–07.04 2017, 18.08–20.08 2017, 12.11–15.11	N: 72° 48'–77° 42' E: 11° 14'–25° 23'	85–451	64–97	0.9–2.9	–2.0–5.6	34.3–35.5	<1–55	57–88	4–96
Mid ● 14 stns	2016, 13.09–04.10 2017, 18.08	N: 73° 50'–78° 16' E: 25° 53'–28° 32'	128–458	37–98	1.2–2.9	–2.0–2.8	34.5–35.3	<1–43	39–74	1–188
East ▲ 40 stns	2013, 31.07–17.08 2014, 25.08–04.09 2015, 05.06–18.06 2017, 23.10–23.10	N: 70° 35'–76° 18' E: 32° 15'–36° 36'	161–334	39–98	0.5–3.6	–1.5–5.2	34.7–35.0	<1–56	45–70	2–30

*There were zero ice-days for the three, two, and thirtyfour southernmost stations in the west, mid, and east sub-areas, respectively (see Figure 1).

Sainte-Marie, 1997; Squires and Dawe, 2003), the Chukchi Sea, the Beaufort Sea (Divine *et al.*, 2017), the Bering Sea (Kolts *et al.*, 2013), the Barents Sea (Pavlov, 2007; Hansen, 2015; Zakharov *et al.*, 2020), and the Sea of Japan (Chuchukalo *et al.*, 2011). Most stomach content studies do not identify prey to the lowest taxonomic level due to food organisms being crushed and/or highly digested. In this study, all organisms were included as either prey or non-prey based on information available for their higher taxonomic rank. Exceptions were made for taxa which were consistently not classified as diet items in the available literature (see above) and which also exhibit high motility and therefore may escape snow crab predation. Large species with thick shelled armour may not be available as prey to smaller crabs. However, we did not distinguish between prey size classes as we assumed juveniles are equally exposed to predation by snow crab. Colonial taxa were not considered to be a major diet item for snow crabs (e.g. Squires and Dawe, 2003; Chuchukalo *et al.*, 2011; Zakharov *et al.*, 2020).

To assess consumption by the snow crab, we estimated the annual Q/B ratio for the snow crab population biomass. The consumption to biomass ratio (Q/B) represents the number of times a population eats its own weight during a chosen period of time (usually one year) and is often used in food web modelling (e.g. Ecopath) as a standardized population estimate (see Pauly, 1986; Christensen *et al.*, 2005). Based on theory in mass-balance ecosystem modelling, the annual consumption to biomass ratio ($Q/B \text{ yr}^{-1}$) of a population can be calculated according to $Q/B = \frac{P/B}{P/Q}$ (Christensen *et al.*, 2005) and an estimate for overall consumption (Q) can then be obtained from $Q = Q/B \times B$. We chose this approach because laboratory studies obtaining rations for snow crabs are scarce (but see Foyle *et al.*, 1989; Siikavuopio *et al.*, 2018) and do not reflect *in vivo* temperatures and/or take different crab sizes into account. Holistic methods, such as empirical relationships of Q/B to characteristics such as body proportions in fish (e.g. Palomares and Pauly, 1998), have not been established for crabs. We obtained an average production to consumption ratio (P/Q) of 0.24 for snow crab from an experimental study by Paul and Fuji (1989), who studied energy budgets of Tanner crabs (*Chionoecetes bairdi*) (ranging from 10 to 82 mm CW). $P/B \text{ yr}^{-1}$ values were calculated using the ANN by Brey (2012) (see above, Supplementary Figure S2) with the exploitation parameter set to 1.

An estimate of snow crab biomass density (B) in a high-density area was obtained based on data from dedicated snow crab research surveys conducted by the Institute of Marine Research (IMR) in 2020 and 2021 (Figure 1, snow crab survey area). These surveys used multiple sampling gears within the same area: video transect, to provide density estimates; trawl and traps, to study size composition and length–weight relationships. Snow crab density (D) was estimated based on count data obtained from video transects. A benthic sledge equipped with two cameras and lasers was towed at 1 knot for 30 to 45 min to produce a total of 85 transects. The estimated number of crabs per km² registered for video transects was skewed (skewness 2.05) and included more zeros than can be fitted by standard distributions. The distribution of the density of individuals (y) in a transect may be approximated by a mixed probability function consisting of a binary discrete distribution for zero/non-zero and a continuous lognormal distribution, $g(y)$, for the non-zero

values

$$f(y) = \begin{cases} 1 - \pi & y = 0 \\ \pi \cdot g(y) & y > 0 \end{cases} \int_{>0}^{\infty} g(y) dt = 1,$$

where π is the probability of a positive count. The probability of getting a positive count times the mean catch in the positive hauls is the survey index of mean density for which an estimate is sought; Bayesian methods were used for fitting the model and to generate *CI* for the estimates (for further details on this approach, see Hvingel *et al.* 2012). The density estimate was then converted to biomass by applying (1) the average size composition recorded from trawl hauls and trap caught crabs and (2) the estimated length–weight relationship. Density estimates based on video transects are likely to underestimate smaller snow crabs often burrowed in sediment (Dionne *et al.*, 2003), as well as crabs hidden beneath topographic structures. However, compared to alternative sampling gear like trawls and traps, video surveys are considered to provide reliable estimates of crab densities in their habitat (Zalota *et al.*, 2019).

Data analysis

All calculations and statistical analyses were performed in R version 3.6.0 (R Core Team, 2019). Mean abundance, biomass, and production estimates are given with 95% *CI* generated by bootstrap replicates and calculated using the adjusted non-parametric bootstrap intervals percentile method using the R package *boot* (Davison and Hinkley, 1997; Canty and Ripley, 2020). The relationship of macrobenthic production to community composition was investigated by non-metric MDS (nMDS) plots using Bray–Curtis dissimilarity for genus abundances (square root transformed) in the R package *vegan* (Oksanen *et al.*, 2019). Environmental parameters were fitted using the *enfit* procedure. Environmental variables and correlations among variables were explored using the non-parametric rank-based Kendall's Tau coefficient, suitable for handling tied ranks. The computed *p*-value was scaled to zero mean and unit variance and is approximately normally distributed. Data were suspected to exhibit spatial autocorrelation, especially because temperature and depth were used as input variables to the production model. The presence of strong spatial autocorrelation may affect conventional hypothesis testing because it violates the assumption of independence between samples (Legendre, 1993). Therefore, the significance level was set to $\alpha = 0.01$.

Results

Mean benthic biomass and production

A total of 718 and 787 taxa were registered in grab (below referred to as *infauna*) and beam trawl (*epifauna*) samples, respectively, of which ~70% of the taxa were identified to species level. The mean abundance was 1877 ind. m⁻² and 20 ind. m⁻², respectively, with a mean biomass of 105.4 g ww m⁻² and 9.1 g ww m⁻² (Table 2). Colonial taxa contributed 2.9 g ww m⁻² to the grab samples and 2.2 g ww m⁻² to the beam trawl samples (Figure 2).

The infaunal production ranged from 26 to 736 kJ m⁻² yr⁻¹ across stations, with a mean of 104 kJ m⁻² yr⁻¹ (Table 2; Figure 3). The epifaunal production was considerably lower, with a mean of 6.8 kJ m⁻² yr⁻¹. In terms of wet weight, the mean production corresponded to 38.4 and 2.5 g m⁻²

yr⁻¹, respectively. Due to the generally smaller infaunal individuals with higher turnover rates, mean community productivity (*P/B*) was higher for infauna (0.43 yr⁻¹) than for epifauna (0.29 yr⁻¹) (Table 2; Figure 4).

While the production increased with abundance and biomass for both epi- and infauna ($\tau \geq 0.4$), the infaunal *P/B* ratios were negatively correlated to biomass ($\tau = -0.4$), meaning that high (infaunal) biomass was attributed to organisms with low turnover rates (low *P/B*)—often long-lived species with higher individual biomass. This correlation was not found for the epifauna. In the grab samples, polychaetes were the most abundant and productive class, contributing 42% of mean infaunal production (Table 2). In this group, the most frequent species belonged to the small burrowing genera *Galathowenia* and *Spiochaetopterus*. Bivalves (e.g. *Astarte* sp., *Bathycarca* sp., *Yoldiella glacialis*, *Hiatella* sp.) were the next productive group, and together with sipunculids, these contributed significantly to benthic production. Epifaunal biomass was dominated by bivalves and asteroids, contributing 34% of the total beam trawl production.

Spatial variability and environmental drivers

Infaunal biomass and production were negatively correlated to depth ($\tau \leq -0.29$) and temperature ($\tau \leq -0.30$), and positively correlated to TOC ($\tau \geq 0.31$) and net primary production ($\tau \geq 0.28$) (Supplementary Figure S3). By contrast, epifaunal biomass and production showed no relationship to environmental variables even though patterns of production followed community composition (Figure 5) that most likely is influenced by abiotic habitat conditions. For both sampling gears, the spatial variation in *P/B* ratios correlated positively with bottom temperatures ($\tau \geq 0.28$) and negatively with the number of ice days ($\tau \leq -0.28$).

In general, infaunal production was high at stations associated with the Polar Front. Communities with high production values were dominated by bivalves and sipunculids. Specifically, the stations at or close to the southern Spitsbergen Bank, Hopen Bank, Central Bank, and Tiddley Bank, but also the deepest part of the Storfjorden Trough (298 m), exhibited high infaunal production (Figure 3). In contrast to the other areas, the region at and around the Thor Iversen Bank, which is not geographically associated with the Polar Front, showed generally low benthic and pelagic primary production (Supplementary Figure S4). However, epifaunal production was relatively high in this region, yet five to tenfold lower than the infaunal community production.

The nMDS stress ≤ 0.16 analysis showed that depth, modelled bottom temperature, net primary production, TOC, and clay + silt content correlated significantly to community composition in the ordination analyses for both sampling gears ($p \leq 0.032$) (Figure 5). Salinity ($p = 0.001$) showed a relationship to infaunal composition only, whereas bottom water velocity was related to epifaunal composition ($p = 0.017$). Geographically, relatively close stations tended to group together without forming distinct clusters. For example, northern/eastern stations were separated from southern stations as temperature, depth, and velocity gradients varied along a latitudinal gradient. Benthic invertebrate production was related to community composition, since similar communities generally displayed similar production values (Figure 5). When fitted as a vector to the ordination, the relationship between

Table 2. Macrobenthic abundance, wet weight biomass, production and P/B ratios for taxonomic classes, the entire community, and the snow crab prey fraction. Values represent means averaged over 66 grab stations (upper table) and 62 beam trawl stations (lower table) with standard deviation (SD) and 95% confidence intervals (CI). P/B was calculated as $\text{sum}(P)/\text{sum}(B)$ over all stations, based on energy.

Phylum	Class	Abundance (ind. m ⁻²)			Biomass (g WW m ⁻²)			Production (kJ m ⁻² yr ⁻¹)			Production (g WW m ⁻² yr ⁻¹)			P/B (yr ⁻¹)				
		SD	Lower CI	Upper CI	SD	Lower CI	Upper CI	SD	Lower CI	Upper CI	SD	Lower CI	Upper CI					
Grab																		
Annelida	Polychaeta	1341	1124	1096	1631	12.6	12.0	10.0	15.8	44.1	39.9	35.5	54.3	12.1	11.0	9.7	14.9	0.94
Arthropoda	Hexanauplia (Cirripedia)	0	3	0	1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.24
	Malacostraca	98	129	72	132	0.8	0.6	0.6	0.9	3.9	3.1	3.2	4.7	0.7	0.5	0.6	0.9	0.91
Brachiopoda	Pycnogonida	1	4	0	2	0.1	0.5	0.0	0.2	0.1	0.3	0.0	0.1	0.0	0.1	0.0	0.1	1.04
	Asciacea	2	6	1	4	0.1	0.3	0.0	0.2	0.1	0.2	0.0	0.1	0.1	0.2	0.0	0.1	0.41
Chordata	Anthozoa	16	21	11	21	2.2	3.0	1.5	2.9	1.8	2.3	1.3	2.4	1.0	1.4	0.7	1.4	0.72
Cnidaria	Asterozoa	10	12	7	13	17.5	70.5	6.9	36.2	9.2	17.0	5.9	13.9	3.3	5.9	2.1	4.9	0.46
	Crinoidea	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.18
Echinodermata	Echinoidea	2	4	1	3	2.7	11.1	0.3	5.7	0.3	1.3	0.1	0.7	0.3	1.3	0.1	0.7	1.02
	Holothuroidea	8	11	5	10	6.4	22.3	2.1	12.5	1.2	3.6	0.5	2.2	0.9	2.1	0.4	1.4	0.13
Enteropneusta	Ophiuroidea	74	211	36	133	4.6	19.5	1.6	9.9	3.4	12.5	1.4	6.8	1.6	6.4	0.6	3.4	0.12
	Graptolithoidea	0	1	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.35
Hemichordata	Aplacophora (paraphyletic)	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00
	Caudofoveata	1	3	0	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.17
Mollusca	Solenogastres	2	6	1	4	0.0	0.1	0.0	0.0	0.1	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.83
	Bivalvia	4	9	2	6	0.0	0.1	0.0	0.1	0.1	0.3	0.1	0.2	0.0	0.1	0.0	0.0	0.80
Nemertea	Gastropoda	254	295	188	330	48.0	161.4	16.0	92.1	20.5	54.3	10.5	35.1	10.7	31.4	4.8	19.2	0.23
	Polyplacophora	18	30	11	25	1.4	3.8	0.7	2.4	1.4	2.8	0.8	2.2	0.6	1.1	0.3	0.9	0.41
Priapulida	Scaphopoda	0	2	0	1	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.77
	Sipuncula	9	8	7	11	0.3	0.2	0.2	0.3	0.2	0.2	0.2	0.3	0.2	0.2	0.2	0.3	0.91
Sipuncula		13	14	9	16	0.8	3.5	0.2	1.7	1.8	6.8	0.7	3.8	0.5	1.8	0.2	1.0	0.62
		0	1	0	1	0.1	0.5	0.0	0.2	0.2	1.1	0.0	0.4	0.0	0.3	0.0	0.1	0.73
Community		24	26	18	31	7.8	21.2	3.7	13.7	15.3	42.5	7.1	27.2	6.2	17.1	2.9	11.0	0.79
		1383	1573	2241	105.4	199.2	64.6	159.6	104.0	109.3	80.9	132.0	38.4	49.0	28.5	51.5	0.43	0.43
Prey		1382	1550	2214	103.2	198.6	62.5	155.6	102.0	108.6	78.8	130.8	37.3	48.7	27.4	50.3	0.43	0.43

Table 2. Continued

Phylum	Class	Abundance (ind. m ⁻²)			Biomass (g WW m ⁻²)			Production (kJ m ⁻² yr ⁻¹)			Production (g WW m ⁻² yr ⁻¹)			Upper CI	Lower CI	P/B (yr ⁻¹)			
		SD	Lower CI	Upper CI	SD	Lower CI	Upper CI	SD	Lower CI	Upper CI	SD	Lower CI	Upper CI						
Beam trawl																			
Annelida	Polychaeta	6.7	12.0	4.2	10.2	0.4	0.8	0.2	0.6	1.2	2.6	0.7	1.9	0.3	0.6	0.2	0.5	0.75	
Arthropoda	Hexanauplia (Cirripedia)	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.47
	Malacostraca	1.1	1.8	0.7	1.6	0.5	0.7	0.4	0.7	0.7	0.8	0.5	0.9	0.2	0.2	0.2	0.1	0.2	0.31
Brachiopoda	Pycnogonida	0.2	0.6	0.1	0.4	0.0	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.77
	Asciacea	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.37
Chordata	Anthozoa	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.38
	Stauzoza	0.1	0.2	0.1	0.2	0.5	0.7	0.3	0.6	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.14
Echinodermata	Asterozoa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.47
	Asterozoa	1.0	1.2	0.8	1.4	2.7	5.2	1.6	4.2	1.4	1.7	1.0	1.9	0.5	0.5	0.6	0.4	0.7	0.18
Hemichordata	Crinoidea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.29
	Echinozoa	0.3	0.9	0.1	0.5	0.5	1.7	0.2	1.0	0.1	0.3	0.0	0.2	0.1	0.1	0.2	0.0	0.1	0.14
Mollusca	Holothuroidea	0.2	0.4	0.1	0.3	0.3	0.6	0.1	0.4	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.18
	Ophiuroidea	4.1	6.1	2.7	5.8	0.9	1.4	0.6	1.2	0.6	0.9	0.4	0.9	0.3	0.3	0.4	0.2	0.4	0.34
Hemichordata	Graptolithoidea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.40
	Aplacophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.88
Mollusca	Caudofoveata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.87
	Solenogastres	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.18
Nemertea	Bivalvia	3.3	3.8	2.4	4.3	2.8	4.5	1.8	4.0	1.9	2.9	1.2	2.7	0.8	0.8	1.1	0.5	1.1	0.28
	Cephalopoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.18
Platyhelminthes	Gastropoda	0.3	0.4	0.2	0.4	0.3	0.6	0.2	0.5	0.2	0.4	0.1	0.3	0.1	0.1	0.2	0.1	0.1	0.29
	Polyplacophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.57
Priapulida	Scaphopoda	0.2	0.4	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.80
	Turbellaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.71
Sipuncula	Priapulida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.63
	Sipunculidea	2.2	3.0	1.5	3.1	0.1	0.2	0.1	0.2	0.4	0.5	0.3	0.5	0.1	0.1	0.2	0.1	0.2	0.74
Community	20.0	21.8	15.0	25.7	9.1	10.5	6.7	11.9	6.8	7.1	5.2	8.7	2.5	2.5	1.9	3.2	0.29	0.29	0.29
Prey	19.5	21.4	14.5	25.3	8.6	10.5	6.3	11.4	6.6	7.0	5.0	8.5	2.4	2.4	1.8	3.0	0.29	0.29	0.29

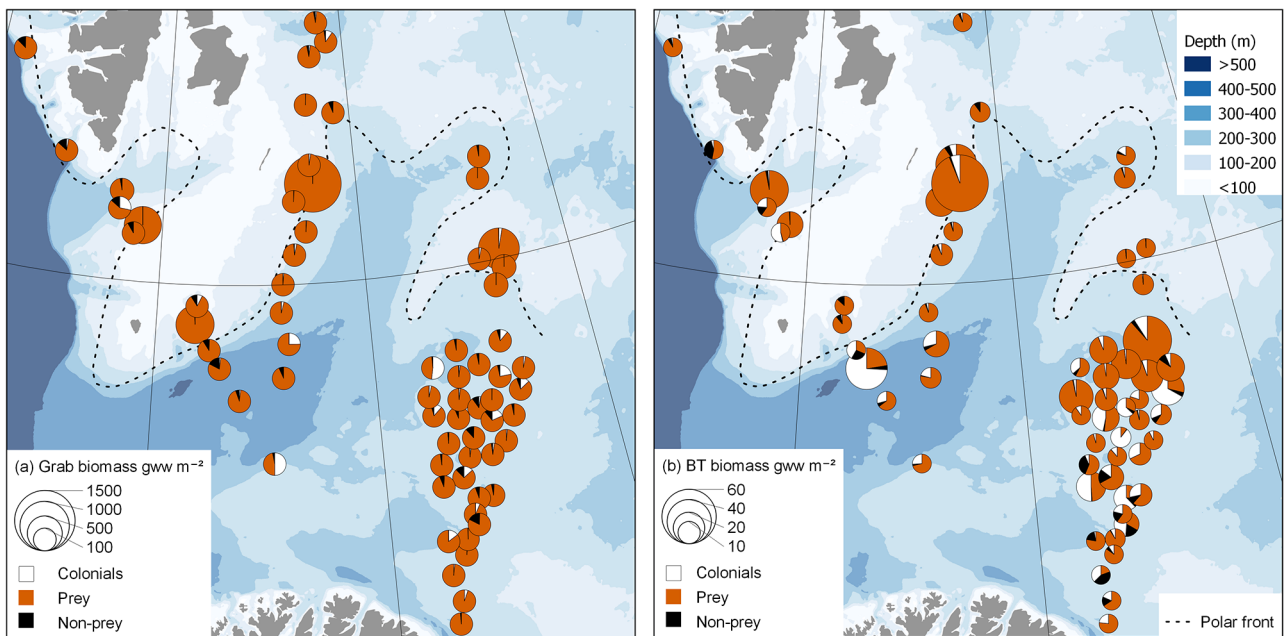


Figure 2. Benthic biomass for grab (left) and beam trawl stations (right). The pie charts represent the proportion of snow crab prey taxa (coloured), non-prey taxa (black), and colonial taxa (white). Note the scale difference between the grab and beam trawl (BT).

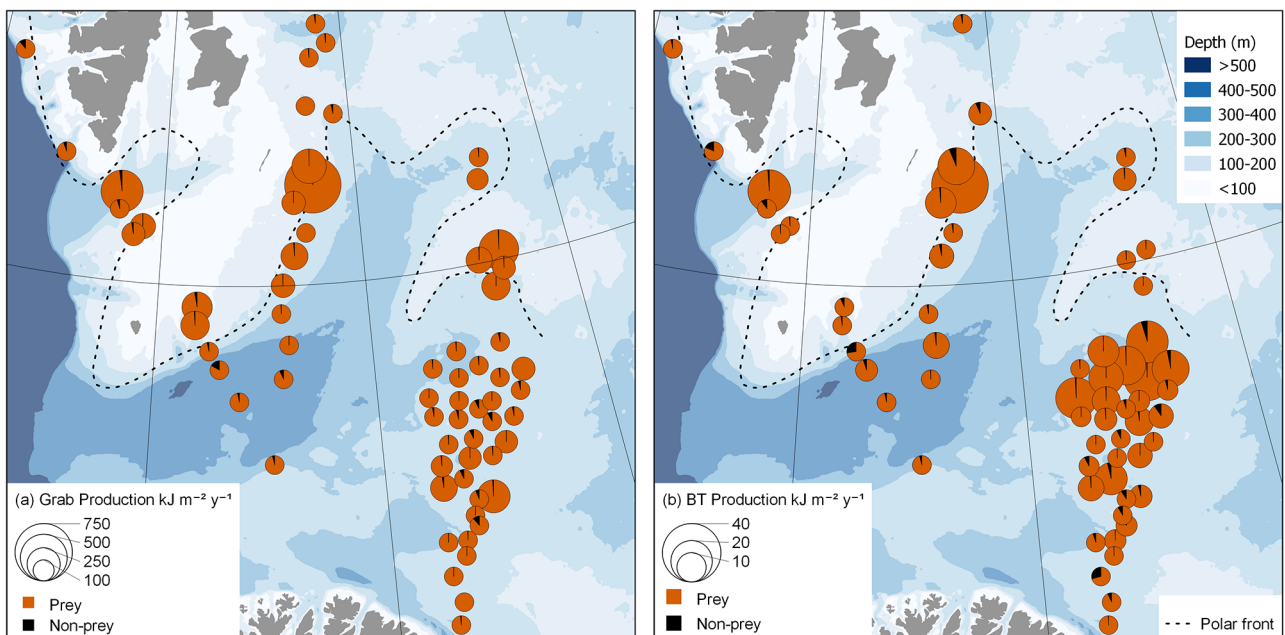


Figure 3. Annual benthic production for grab (left) and beam trawl stations (right). The pie charts represent the proportion of prey taxa (coloured) and non-prey taxa (black). Colonial taxa were excluded from production calculations. Note the scale difference between the grab and beam trawl (BT).

benthic invertebrate production and the ordination was also significant ($p \leq 0.001$).

Prey production and consumption

The mean infaunal prey biomass and production available as prey to the snow crab (hereafter called “prey”) were estimated to be 103.2 and 37.3 g m⁻² yr⁻¹, respectively (Table 2). The corresponding epifauna values were: 8.6 g m⁻² and 2.4 g m⁻² yr⁻¹. Thereby, prey production constituted 98 and

96% (range: 71–100%) of the total average in- and epifaunal production, respectively. Slightly, higher proportions of prey compared to the total biomass and production were found at the northern stations (Figure 2; Figure 3), where there was a higher proportion of bivalves and sipunculids and fewer colonial epifauna.

The mean density of snow crab (D) estimated from the video surveys was 12800 ind. km⁻² (95% CI: 8791 to 18000). This corresponded to a biomass density (B) of 2349 kg km⁻². The mean P/B -ratio for snow crab was calculated to be 0.15

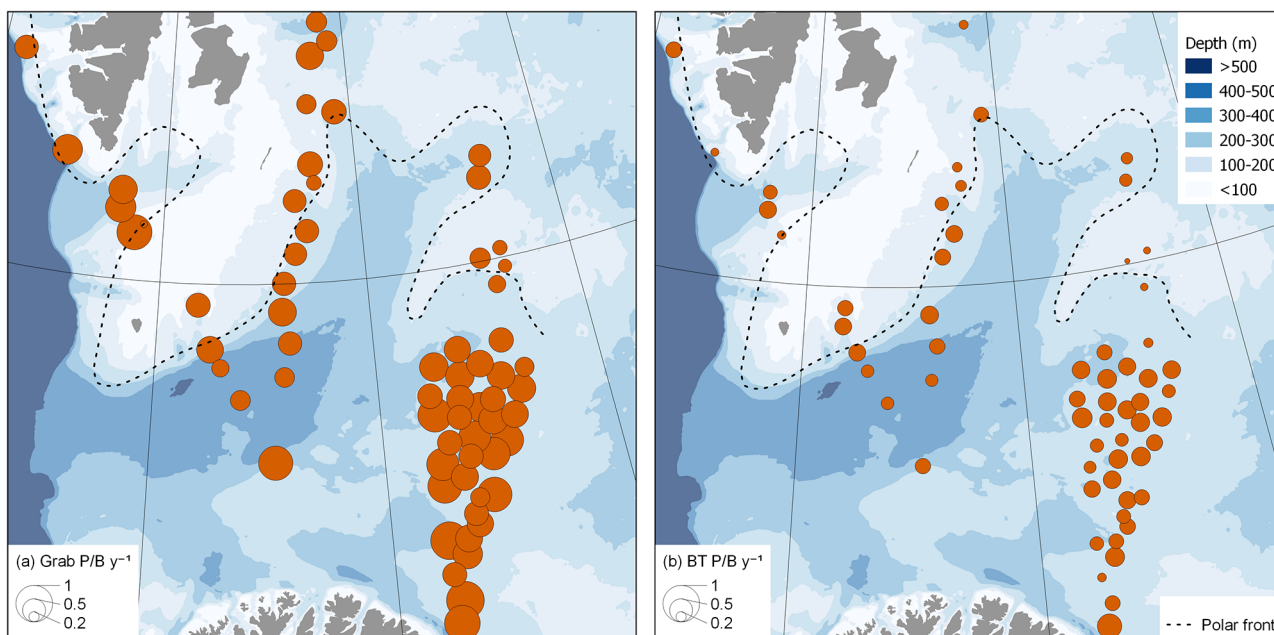


Figure 4. Annual benthic $P/B \text{ yr}^{-1}$ ratios for grab (left) and beam trawl stations (right). Colonial taxa were excluded.

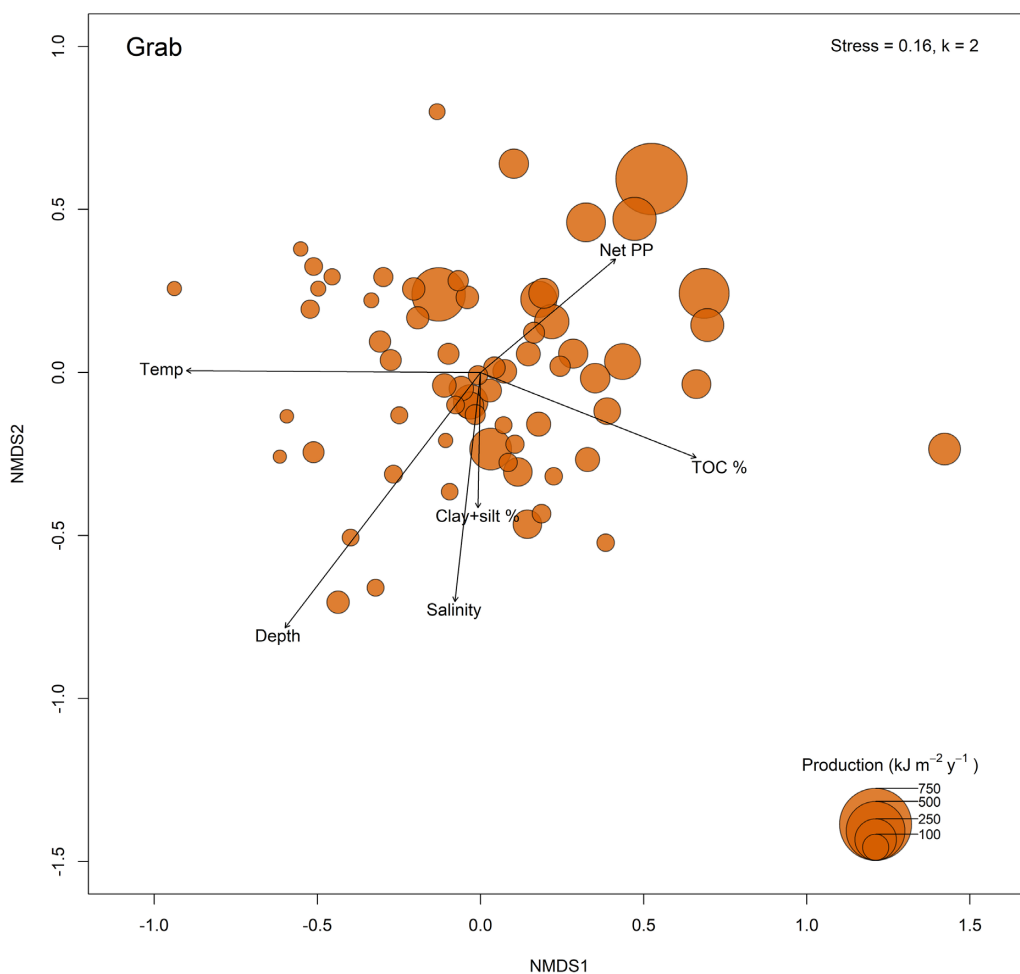


Figure 5. Non-metric multidimensional scaling (nMDS) based on Bray–Curtis dissimilarity (square root transformed genus abundances) for grab (above) and beam trawl (below) collected fauna (stress = 0.17/0.15; 1000 permutations). The size of each circle is relatively scaled to benthic production at the respective sites. Vectors indicate statistically significant ($p \leq 0.05$) relations of environmental parameters; the length of a vector is proportional to its correlation strength ($\sqrt{\text{R}^2}$). Species coordinates are not shown.

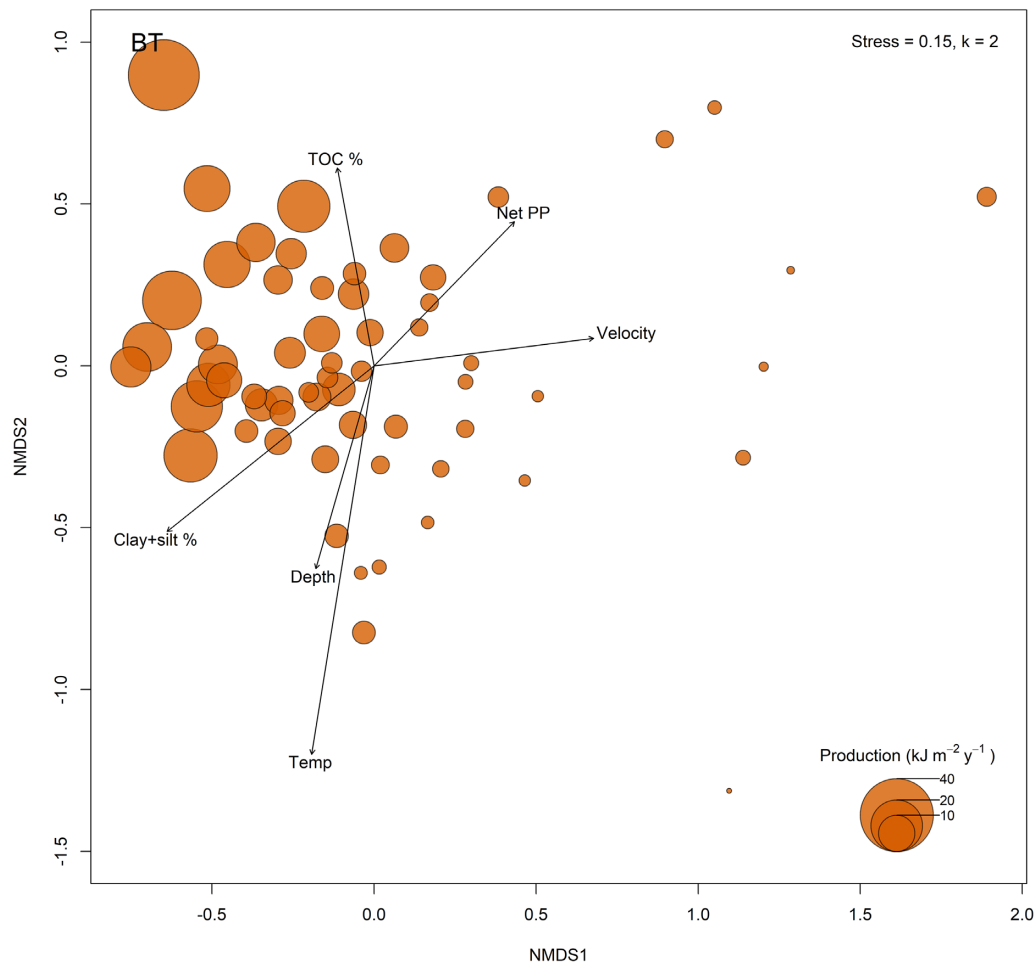


Figure 5—*continued*. See text in Figure 5 grab.

yr^{-1} and the Q/B was 0.64 yr^{-1} ($P/Q = 0.2$, Paul and Fuji, 1989), giving an annual consumption (Q) of $1.5 \text{ g m}^{-2} \text{ yr}^{-1}$ (1.0 to $2.1 \text{ g m}^{-2} \text{ yr}^{-1}$; 95% CI). Applying these consumption estimates to the estimates of benthic prey production, snow crab at densities comparable to those found in the surveyed area will consume 4% (3–6%, CI) of the infaunal prey production. At stations with relatively low benthic production, e.g. east and west of Svalbard and some of the southernmost stations ($8\text{--}20 \text{ g m}^{-2} \text{ yr}^{-1}$), the consumption of available prey would amount to 8–19%.

Discussion

Based on grab (infauna) and beam trawl (epifauna) samples taken in the central and western parts of the Barents Sea, annual macrobenthic production was estimated to assess the total prey production available for snow crab consumption. Infaunal production estimates were considerably higher than for epifauna (104 versus $6.8 \text{ kJ m}^{-2} \text{ yr}^{-1}$), especially in bank areas close to the Polar Front, likely driven by high primary production. Due to the wide dietary niche of the snow crab, a major part of the benthic invertebrate production was estimated to be available as prey for snow crabs. At snow crab densities high enough to support commercial fisheries, it was estimated that snow crabs consume 4% (3–6% CI) of annual macrobenthic production (supported by infaunal taxa mainly), which is higher than previous estimates (Zakharov *et al.*, 2020), but

supports the assumption that snow crabs generally were not limited by food supply in the areas and times investigated.

Macrobenthic production and environmental drivers

Few studies assessing both infauna and epifauna at the same location and time in the Barents Sea are available, although Jørgensen *et al.* (2011) found profoundly higher biomass in fauna collected using grab than retrieved using beam trawl, supporting results in this study. The presented infaunal biomass and production values are, albeit with clear spatial variations, largely at a similar order of magnitude as estimated in other comparable Barents Sea studies (Carroll *et al.*, 2008; Cochrane *et al.*, 2012; Zakharov *et al.*, 2020). However, studies from northern Norwegian fjord systems (Nilsen *et al.*, 2006; Fuhrmann *et al.*, 2015; sampled in June and January, respectively) found higher mean infaunal production (174 and $185 \text{ kJ yr}^{-1} \text{ m}^{-2}$, respectively), than the present study ($104 \text{ kJ m}^{-2} \text{ yr}^{-1}$), reflecting different prevailing depth conditions, lower predation pressure, and higher input of macroalgal detritus to these inner fjords (Nilsen *et al.*, 2006; Pedersen *et al.*, 2018). The relatively low mean P/B ratio reported in this study (0.43 yr^{-1}) is similar to previous estimates for the Barents Sea (0.3 yr^{-1} , Denisenko and Titov, 2003) and the northern Norwegian Sørkjord (0.42 yr^{-1} , Nilsen *et al.*, 2006). Degen *et al.* (2016) report a mean P/B ratio of 0.15

yr^{-1} for Barents Sea megafauna collected by Campelen trawl (bycatch), which is considerably lower than our estimates for epifauna (0.29 yr^{-1}) and reflects life history traits of larger megafauna.

The estimated infaunal production was strongly correlated with pelagic net primary production and sediment TOC content, which covaried with depth and bottom water temperature. By contrast, the epifaunal production revealed no significant relationship with net primary production (or other available environmental parameters), which was also found in studies from the Chukchi Sea (Bluhm *et al.*, 2009) and the Barents Sea (Degen *et al.*, 2016). Despite cold bottom water in northern areas, it is well documented that high primary production in shallow Arctic seas fuels benthic production (e.g. Piepenburg, 2005; Reigstad *et al.*, 2011; Grebmeier *et al.*, 2015). Other surveys undertaken at the Spitsbergen Bank indicate that primary production represents a considerable carbon input (Reigstad *et al.*, 2011; Kedra *et al.*, 2013), which strongly benefits benthic communities in this region due to tight benthopelagic coupling (Carroll *et al.*, 2008; Cochrane *et al.*, 2009, 2012).

Previous studies report a dominance in echinoderms in benthic production (Kedra *et al.*, 2013; Degen *et al.*, 2016) while annelids, sipunculids, and bivalves were found to be major contributors to production in this study (compare also Zakharov *et al.*, 2020), again revealing the importance of infaunal taxa. These are especially important on slopes and in deeper areas, whereas epifaunal suspension feeders (molluscs, cnidarians, and the echinoderm *Cucumaria frondosa*) are major contributors to the high benthic production on the shallow Svalbard Bank (syn. Spitsbergen Bank; Kedra *et al.*, 2013), where coarse substrate dominates.

As for most production studies at high latitudes (e.g. expensive surveys, seasonal ice cover, sampling challenges), our production estimates were based on single sampling events (between March and November). Hence, potential seasonality in production patterns in the Barents Sea was not accounted for in the annual estimates. Driven by seasonal differences in biomass due to relatively high recruitment and individual growth, benthic secondary production tends to be substantially higher in the spring and summer months than in late winter (Beukema and Dekker, 2013; Saulnier *et al.*, 2018). Beukema and Dekker (2013) emphasize the constraints of the Brey model (2001 version) for predicting production of (individual species) populations, which is why the model should only be applied to communities with multiple species contributing to biomass (Brey, 2001; Beukema and Dekker, 2013). Seasonality in macrobenthic production, or even biomass, at polar latitudes has received little attention and may vary substantially compared with data from shallow, temperate coastal habitats (see the studies by Beukema and Dekker, 2013 and Saulnier *et al.*, 2018). On the other hand, a few studies from Svalbard fjords indicate that benthic communities may maintain their abundance and biomass over the year (Włodarska-Kowalczyk *et al.*, 2016; reviewed in Renaud *et al.*, 2020; Morata *et al.*, 2021) despite high seasonality in nutrient flux. This is partly explained by food storage within the sediments throughout the year after the spring pulse of primary production (Smith *et al.*, 2006). This may particularly benefit infauna, while less beneficial to epifaunal/megafaunal communities that are often numerically dominated by suspension feeders. To some degree, seasonality in production patterns might

be influenced by temperature, and we accounted for this by choosing modelled annual means as input to the Brey (2012) model. We found no obvious differences in production estimates among sampled stations (i.e. higher production at stations sampled during a supposed biomass maximum in the summer/autumn). Fauna was not sampled in winter months (see Table 1), and any seasonality in the presented data may be masked by confounding environmental factors. It is therefore important to treat values from single stations with caution.

Our study estimated roughly a 15-fold higher production for infauna than for epifauna. This difference may be due partly to a relatively low beam trawl sampling efficiency, which may underestimate biomass by up to 50% (Reiss *et al.*, 2006). In the present study, however, where (grab collected) infauna is included in the total snow crab prey production, this bias is likely to be small. There are currently few alternatives to the 2 m beam trawl, while larger trawl gears targeting megafauna (e.g. Campelen trawl, see Jørgensen *et al.*, 2019) are inappropriate in assessing snow crab prey (Jennings *et al.*, 1999). Hence, in the muddy habitats of the Barents Sea, we suggest that infaunal sampling alone is sufficient in future snow crab prey studies.

Snow crab consumption

Our estimates of consumption by the snow crab ($1.0\text{--}2.1 \text{ g m}^{-2} \text{ yr}^{-1}$) lie within previous estimates by Jørgensen *et al.*, 2019 (and see references therein), which state an annual consumption of $<5 \text{ g ww m}^{-2}$, although which snow crab densities these estimates relate to are unclear. Zakharov *et al.* (2020) found high infaunal biomass and high snow crab density (up to ca. $12000 \text{ ind. m}^{-2}$) in the eastern part of the Russian Barents Sea shelf and concluded that the snow crab consumes $<0.5\%$ of the average benthic biomass available in the Barents Sea. These estimates of consumption may not be entirely comparable to ours due to a different approach used in estimating crab consumption, but they seem low, at least in areas with commercial snow crab densities.

Estimating Q/B for a population is a difficult task because natural populations are exposed to variable mortality (e.g. from fishing), and age structure has to be taken into account. The snow crab consumption estimates given in this study are not representative for small size classes ($<ca. 25 \text{ mm CW}$, see above) and the population P/B (0.15 yr^{-1}) for snow crab, therefore, is likely underestimated. Since younger individuals allocate more energy to growth, a population dominated by younger individuals will exhibit a higher P/B . In addition, confidence for P/B estimation of a single population is low (Brey, 2012). Krylov (2000) estimated the annual production of Pacific snow crab of marketable size to be equal to $\sim 1/10^{\text{th}}$ of the total standing stock biomass (i.e. $P/B = 0.1 \text{ yr}^{-1}$) which is similar to our estimates. Pedersen *et al.* (2021), on the other hand, assumed $P/B = 0.5 \text{ yr}^{-1}$ for the Barents Sea snow crab, giving a $Q/B = 2.08 \text{ yr}^{-1}$. This is >3 times the Q/B estimated in this study (0.64 yr^{-1}) and is due to the difference in estimated P/B . Savenkoff *et al.* (2004) used a Q/B of $1.3\text{--}1.5 \text{ yr}^{-1}$ for Pacific snow crabs as input to an ecosystem model (Morissette *et al.*, 2009), providing another example that literature values for the Q/B of large cold-water crustaceans vary considerably. In general, there is little information on the feeding rates of the snow crab, and laboratory experiments are needed to inform consumption estimates. During

a feeding experiment by Siikavuopio *et al.* (2018), the daily ration of large adult males (ca. 650 g) was estimated to be 7 g week⁻¹ at around 5°C, giving a Q/B closer to this study's (0.56 yr⁻¹). In light of uncertainties connected to a population estimate for small juvenile crabs and Q/B ratios, our consumption value at the given densities likely presents a minimum estimate.

Based on our results, we suggest that snow crab predation can be supported by highly productive infaunal taxa such as polychaetes, which have a higher turnover ($P/B > 0.9$ yr⁻¹) compared to the average benthic community. The snow crab thrives in soft bottom areas, and it is reported that they have adapted to silty habitats (Pavlov and Sokolov, 2016; Zakharov *et al.*, 2020) using an effective feeding technique to search the sediment for burrowing prey items (Wieczorek and Hooper, 1995; Author's video observations). There is evidence that the snow crab also occupies hard bottom habitats (e.g. Bluhm *et al.*, 2009), and that females and juveniles reside in habitats with different bottom substrates in the Barents Sea (Zakharov *et al.*, 2020), where data on benthic invertebrate production is deficient (but see Kedra *et al.*, 2013).

The variety of taxa considered to be diet items of snow crab in this study is likely overestimated. Stomach content studies in crabs often have low taxonomic resolution, resulting in entire groups of organisms assigned as diet. For example, studies show that crustaceans are a frequent diet group for snow crabs (e.g. Divine *et al.*, 2017; Gebruk *et al.*, 2020), while predation is likely limited to smaller and less mobile species. A broad diet may enhance a species' plasticity when a resource becomes limited, being able to switch prey to another group. Diet studies show that crabs also ingest a considerable amount of plant material (Wieczorek and Hooper, 1995; Divine *et al.*, 2019). Also, the occurrence of cannibalism is well documented (e.g. Lovrich and Sainte-Marie, 1997; Kolts *et al.*, 2013; Divine *et al.*, 2017), albeit not known from the Barents Sea. High-resolution diet studies in the Barents Sea are therefore needed to better understand the snow crab's trophic niche and impact on particular prey groups. The gross predation impact on the benthic community will largely depend on competitors in the system and also on consumption by the snow crab on these competitors, potentially resulting in a subsequent increased availability of prey organisms. There are a few studies looking at resource overlap between snow crab and other benthic predators. A recent stable isotope study by Gebruk *et al.* (2020) found that the crab displays an overlapping trophic niche with *Hyas araneus* and *Pagurus pubescens*, species present at comparatively low numbers and biomass in our study area. Other large decapods in northern Norwegian waters are *Lithodes maja* and the red king crab *Paralithodes camtschaticus*, the latter occupying coastal waters (not found in our study). Limited habitat overlap between these species and snow crab suggests low competition. There is little evidence that the snow crab targets larger predatory taxa (such as other large crabs, buccinid snails, or large asteroids). Instead, the snow crab prefers smaller epifauna and infauna, such as bivalves and polychaetes (Gebruk *et al.*, 2020). A trophic overlap with benthic-feeding fish such as flatfish and cottids may be present, but this needs further investigation. We suggest that low competition for abundant small infauna may have facilitated the establishment of the snow crab in the Barents Sea. However, the potential future increase in the snow crab population should inspire both researchers

and the snow crab management agencies to contribute to food web studies looking at energy flow (see Pedersen *et al.*, 2021).

We show that snow crab consumption would in theory exceed epifauna production in most areas, and that possible selective feeding on epifaunal taxa may therefore have a greater impact. Infaunal bivalves are one of the preferred prey groups for snow crabs in the Barents Sea (Gebruk *et al.*, 2020; Zakharov *et al.*, 2020), and we found a low P/B for this group (0.23–0.28 yr⁻¹), which makes them potentially more vulnerable to predation effects despite a relatively high standing stock biomass. Changes in community composition have been suggested as a consequence of predation from the invasive red king crab (*Paralithodes camtschaticus*), resulting in a decrease of slow-growing species and a raise in community P/B (Fuhrmann *et al.*, 2015; Pedersen *et al.*, 2018). A Barents Sea ecosystem model, however, indicates that increasing snow crab biomass had a small impact on total ecosystem energy flow in the simulated time period from 2000 to 2013 (Pedersen *et al.*, 2021). Reliable impact studies and time series are needed to evaluate the effects of predation in colonized areas as compared to pre-established states. This present study may also serve as a pre-invasive baseline for areas exposed to any future increased snow crab abundance.

The most suitable snow crab foraging areas

The Polar Front area of the Barents Sea seems to meet two of the most important criteria for the possible establishment of commercially exploitable snow crab densities, namely high benthic secondary production and a bottom water temperature regime suitable for its growth. Results from several papers indicate an optimum temperature for snow crab of <4°C (Chabot *et al.*, 2008; Avlsvåg *et al.*, 2009; Siikavuopio *et al.*, 2019) and a maximum temperature of 4–6°C (Dawe *et al.*, 2002; Siikavuopio *et al.*, 2017; Fedewa *et al.*, 2020). Foyle *et al.* (1989) found that snow crab total metabolic costs exceeded caloric intake at temperatures <1°C and >7°C, whereas the caloric intake decreased when passing 5°C. These temperature data in general coincide with the bottom water temperatures extracted from the SVIM model around and somewhat south of the Polar Front, which, in combination with our production estimates, presumably facilitates a substantial growth of the snow crab population in soft-bottom areas close to the Polar Front. However, in addition to high food availability (Kolts *et al.*, 2013; Zakharov *et al.*, 2020) and suitable climatic conditions, other factors such as larvae dispersal, stock dynamics, and ecological interactions presumably will play a major role in a future quantitative expansion of the snow crab population in the Barents Sea. It is noted that the coarse substrate and high bottom water velocity on the shallowest parts of the Spitsbergen Bank (see e.g. Carroll *et al.*, 2008; Kedra *et al.*, 2013; Lepland *et al.*, 2014) may not be a suitable snow crab habitat. The ongoing climatic development in the central parts of the Barents Sea, with a predicted increase in water temperature of one degree over the next 50 yr (Anon., 2020; Ellingsen *et al.*, 2008; Sandø *et al.*, 2014) and no significant change in the geographical position of the Polar Front (Ellingsen *et al.*, 2008), are unlikely to impact a possible westward expansion of the snow crab population over the upcoming decades.

Conclusions

This study estimates snow crab consumption, under high (i.e. commercially exploitable) densities, equalling 4% of mean annual infaunal prey production in the central and western parts of the Barents Sea. Thus, there is little evidence of resource limitation impeding further expansion of this newly established predator. It is suggested that the expected future geographical dispersion and subsequent increase in snow crab density will primarily take place in areas where the infaunal prey production is highest and where other environmental conditions are suitable for its growth, i.e. in most bank areas and their slopes located close to the Polar Front. Our study shows that estimating benthic invertebrate production based on epifaunal sampling alone underestimates total production substantially for prey resources available to generalist predators such as crabs. As the Barents Sea snow crab expansion continues, investigations should be conducted into the structural impacts on benthic communities caused by snow crab foraging activities.

Acknowledgements

We thank our Mareano/IMR colleagues for their accurate and systematic field sampling and sample preparations, and we are grateful for the helpful cooperation given by the crew of RV G.O. Sars. We also thank all involved experts/taxonomists for their dedicated identifications of invertebrates: our colleagues at IMR/Mareano programme, and Akvaplan-niva (Polychaeta/Amphipoda), the Norwegian Institute for Water Research/NIVA (Polychaeta/Amphipoda), STIM miljø (Amphipoda), and Taxonomicum, Finland (Isopoda). We greatly appreciate the help from the following colleagues: Fabian Zimmermann (analysis advice), Karen Assmann (advice on climate projections), Rebecca Ross (English corrections; text advice), Vidar Lien, and Morten Skogen for taking out modelled values on, respectively, bottom water temperature and pelagic primary production. Last but not least, we are thankful for the valuable comments on the manuscript given by the ICESJ Editor and an anonymous referee.

Supplementary data

Supplementary material is available at the ICESJMS online.

Conflict of interest

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

Funding

This study was supported by the governmental Mareano seafloor mapping programme (Norway) and the Snowman project (project number 14862, Institute of Marine Research, Norway).

Author contributions

BH: Conceptualization, data collection, project administration, raw data preparation, writing, incl. original draft. MMF: Conceptualization, formal analysis, raw data preparation, vi-

sualization, writing, incl. original draft. AHST: Raw data preparation, data collection, writing. CH: Formal analyses and writing. AMH: Snow crab raw data preparation, incl. SC field sampling/methods, and writing.

Data availability statement

Benthic fauna data are available through the EMODnet.eu portal, and the Mareano's search engine for single taxa: http://mareano.no/marbunn_web/viewspecies.

References

- Agnalt, A.-L., Jørstad, K. E., Pavlov, V., and Olsen, E. 2010. Recent trends in distribution and abundance of the snow crab (*Chionoecetes opilio*) population in the Barents Sea. *In* Biology and Management of Exploited Crab Populations under Climate Change, pp. 81–90. Ed. by Kruse G. H., Eckert G. L., Foy R. J., Lipcius R. N., Sainte-Marie B., Stram D. L., and Woodby D.. Alaska Sea Grant, University of Alaska Fairbanks, Fairbanks, AK.
- Anon. 2011. First update of the integrated management plan for the marine environment of the Barents Sea–Lofoten area. Meld.St. (2010–2011). Report to the Storting (white paper). 144pp. <https://www.regjeringen.no/en/dokumenter/meld.-st.-10-20102011/id635591/>. (Last accessed on October 16, 2022).
- Anon. 2020. Status for miljøet i Barentshavet—Rapport fra Overvåkinggruppen 2020. (Status of the Environment of the Barents Sea—Report from The Advisory Group on Monitoring 2020). English summary. Ed. by Arneberg P., Vee I., Franzen S., and van der Meer G.. Rapport fra Havforskningen 2020-13. ISSN 1893–4536. Institute of Marine Research, Cadiz. 126pp.
- Avlsvåg, J., Agnalt, A. L., and Jørstad, K. E. 2009. Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. *Biology Invasions*, 11: 587–595.
- Beukema, J. J., and Dekker, R. 2013. Evaluation of Brey's production/biomass mode on the basis of a long-term data set on a clam population. *Marine Ecology Progress Series*, 489: 163–175.
- Blumh, B. A., Iken, K., Mincks Hardy, S., Sirenko, B. I., and Holladay, B. A. 2009. Community structure of epibenthic megafauna in the Chukchi Sea. *Aquatic Biology*, 7: 269–293.
- Bøe, R., Bjarnadóttir, L. R., Elvenes, S., Dolan, M., Bellec, V., Thorsnes, T. *et al.*. 2020. Revealing the secrets of Norway's seafloor—geological mapping within the MAREANO programme and in coastal areas. *In* From Continental Shelf to Slope: Mapping the Oceanic Realm. Ed. by Asch K., Kitazato H., and Vallius H.. Geological Society (Special Publications), Boulder, CO. 505pp.
- Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. <http://www.thomas-brey.de/science/virtualhandbook/> (last accessed Jan 2022).
- Brey, T. 2012. A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. *Limnology and Oceanography Methods*, 10: 581–589.
- Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M. F. J., and Holte, B. 2015. The MAREANO programme—a full coverage mapping of the Norwegian off-shore benthic environment and fauna. *Marine Biology Research*, 11: 4–17.
- Canty, A., and Ripley, B. 2020. Bootstrap R (S-Plus) functions. R package version 1.3-22. <https://cran.r-project.org/package=boot>. (Last accessed on July 2021).
- Carroll, M. L., Denisenko, S. G., Renaud, P. E., and Ambrose, W. G. 2008. Benthic infauna of the seasonally ice-covered western Barents Sea: patterns and relationships to environmental forcing. *Deep-Sea Research Part II*, 55: 2340–2351.
- Chabot, D., Sainte-Marie, B., Briand, K., and Hanson, J. M. 2008. Atlantic cod and snow crab predator–prey size relationship in the Gulf of St. Lawrence, Canada. *Marine Ecology Progress Series*, 363: 227–240.

- Christensen, V., Walters, C. J., and Pauly, D. 2005. Ecopath with ecosim: a user's guide. In Fisheries Centre. University of British Columbia, Vancouver. 154pp. www.ecopath.org (last accessed November 2005, edition).
- Chuchukalo, V. I., Nadtochy, V. A., Koblikov, V. N., and Boriko, O. Y. 2011. Diet and some ecological features of the most widespread commercial crab species in the northwestern Sea of Japan in early spring. Russian Journal of Marine Biology, 37: 558–569.
- Cochrane, S. K. J., Denisenko, S. G., Renaud, P. E., Emblow, C. S., Ambrose, W. G., Ellingsen, I. H., and Skardhamar, J. 2009. Benthic macrofauna and productivity regimes in the Barents Sea—ecological implications in a changing Arctic. Journal of Sea Research, 61: 222–233.
- Cochrane, S., Pearson, T., Greenacre, M., Costelloe, J., Ellingsen, I., Dahle, S., and Gulliksen, B. 2012. Benthic fauna and functional trails along a polar front transect in the Barents Sea—advancing tool for ecosystem-scale assessments. Journal of Marine Systems, 94: 204–217.
- Comeau, M., Conan, G. Y., Maynou, F., Robichaud, G., Therriault, J.-C., and Starr, M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. Canadian Journal of Fisheries and Aquatic Sciences, 55: 262–279.
- Dahle, G., Sainte-Marie, B., Mincks, S. L., Farestveit, E., Jørstad, K. E., Hjelset, A. M., and Agnalt, A. L. 2022. Genetic analysis of the exploited snow crab (*Chionoecetes opilio*) in the Barents Sea—possibilities of origin. ICES Journal of Marine Science. <https://doi.org/10.1093/icesjms/fsac172>.
- Danielsen, H. E. H., Hjelseth, A. M., Bluhm, B. A., Hvingel, C., and Agnalt, A.-L. 2019. A first fecundity study of the female snow crab *Chionoecetes opilio* Fabricius, 1788 (Decapoda: Brachyura: Oregoniidae) of the newly established population in the Barents Sea. Journal of Crustacean Biology, 39: 485–492.
- Davison, A. C., and Hinkley, D. V. 1997. Bootstrap Methods and their Applications. Cambridge University Press, Cambridge. ISBN 0-521-57391-2.
- Dawe, E. G., and Colbourne, E. B. 2002. Distribution and demography of snow crab (*Chionoecetes opilio*) males on the Newfoundland and Labrador shelf. In Crabs in Cold Water Regions: Biology, Management, and Economics, pp. 577–594. Ed. by Paul A. J., Dawe E. G., Elnor R., Jamieson G. S. *et al.* University of Alaska Sea Grant, AK-SG-02-01, Fairbanks, AK.
- Degen, R., Jørgensen, L. L., Ljubin, P., Ellingsen, I. H., Pehlke, H., and Brey, T. 2016. Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. Marine Ecology Progress Series, 546: 1–16.
- Denisenko, S. G., and Titov, O. V. 2003. Distribution of zoobenthos and primary plankton production in the Barents Sea. Oceanology, 43: 78–88.
- Dionne, M., Sainte-Marie, B., Bourget, E., and Gilbert, D. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. Marine Ecology Progress Series, 259: 117–128.
- Divine, L. M., Bluhm, B. A., Meuter, F. J., and Iken, K. 2019. Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes. Deep Sea Research Part II, 135: 124–136.
- Dolbeth, M., Cusson, M., Sousa, R., and Pardal, M. A. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences, 69: 1230–1253.
- Ellingsen, I. H., Dalpadado, P., Slagstad, D., and Loeng, H. 2008. Impact of climatic change on the biological production in the Barents Sea. Climatic Change, 87: 155–175.
- European Standard, 2012. Sludge Treated Biowaste, Soil and Waste Determination of Total Organic Carbon by Dry Combustion. EN 15936, Procedure A – Indirect Method. <https://standards.iteh.ai/catalog/standards/cen/d102db97-be7e-4014-b5f7-b9d28c3fb68e/en-15936-2012> .(last accessed October 2022).
- Fabricius, O. 1788. Beskrivelse over den store Grønlandske Krabbe. Nye Samling af Det Kongelige Danske Videnskabers Selskabs Skrifter, <https://www.marinespecies.org/aphia.php?p=sourcedetails&cid=391494>.(last accessed October 2022).
- Fedewa, E. J., Jackson, T. J., Richar, J. I., Gardner, J. L., and Litzow, M. A. 2020. Recent shifts in northern Bering Sea snow crab (*Chionoecetes opilio*) size structure and the potential role of climate-mediated range contraction. Deep-Sea Research Part II, 181–182: 104878.
- Fer, I., and Drinkwater, K. 2014. Mixing in the Barents Sea polar front near Hopen in spring. Journal of Marine Systems, 130: 206–218.
- Foyle, T. P., Odor, R. K., and Elnor, R. W. 1989. Energetically defining the thermal limits of the snow crab. Journal of Experimental Biology, 145: 371–393.
- Fuhrmann, M. M., Pedersen, T., Ramasco, V., and Nilssen, E. M. 2015. Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. Journal of Sea Research, 106: 1–13.
- Gebbruk, A., Zalota, A. K., Dgebuadze, P., Ermilova, Y., Spiridonov, V. A., Shabalin, N., Henry, L.-A. *et al.* 2020. Trophic niches of benthic crustaceans in the Pechora Sea suggest that the invasive snow crab *Chionoecetes opilio* could be an important competitor. Polar Biology, 44: 57–71.
- Grebmeier, J. M., Bluhm, B. A., Cooper, L. W., Danielson, S., Arrigo, K. R., Blanchard, A. L., Clarke, J. T. *et al.* 2015. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Progress in Oceanography, 136: 92–114.
- Hansen, H. S. B. 2015. Snow crab (*Chionoecetes opilio*) in the Barents Sea. Diet, biology and management. Master thesis in international fisheries management. Norwegian college of fishery science. The Arctic University of Norway, Tromsø. 95pp.
- Holte, B., and Buhl-Mortensen, L. 2020. Does grab size influence on macrofauna composition? A test conducted on deep-sea communities in the northeast Atlantic. Marine Environmental Research, 154: 104867.
- Hvingel, C., Kingsley, M. C. S., and Sundet, J. H. 2012. Survey estimates of king crab (*Paralithodes camtschaticus*) abundance off northern Norway using GLMs within a mixed generalized gamma-binomial model and Bayesian inference. ICES Journal of Marine Science, 69: 1416–1426.
- Hvingel, C., Sainte-Marie, B., and Kruse, G. H. 2021. Cold-water shellfish as harvestable resources and important ecosystem players. ICES Journal of Marine Science, 78: 479–490.
- Jennings, S., Lancaster, J., Woolmer, A., and Cotter, J. 1999. Distribution, diversity and abundance of epibenthic fauna in the North Sea. Journal of the Marine Biological Association of the UK, 79: 385–399.
- Jørgensen, L. L., Primicerio, P., Ingvaldsen, R. B., Fossheim, M., Strelkova, N., Thangstad, T. H., Manushin, I. *et al.* 2019. Impact of multiple stressors on sea bed fauna in a warming Arctic. Marine Ecology Progress Series, 608: 1–12.
- Jørgensen, L. L., Renaud, P. E., and Cochrane, K. J. 2011. Improving benthic monitoring by combining trawl and grab surveys. Marine Pollution Bulletin, 62: 1183–1190.
- Kedra, M., Renaud, P. E., Andrade, H., Goszczko, I., and Ambrose, W. G. 2013. Benthic community structure, diversity, and productivity in the shallow Barents Sea bank (Svalbard Bank). Marine Biology, 160: 805–819.
- Kolts, M. K., Lovvorn, J. R., North, C. A., Grebmeier, J. M., and Cooper, L. W. 2013. Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. Marine Ecology Progress Series, 483: 209–220.
- Krylov, V. V. 2000. The ratio of annual production to biomass of marketable snow crabs, *Chionoecetes opilio* (Decapoda, Brachyura). Crustaceana, 73: 1287–1289.
- Kuzmin, S. A., Akhtar, S. M., and Meni, D. T. 1999. The first findings of the snow crab *Chionoecetes opilio* (Decapoda, Majiidae) in the

- Barents Sea. Canadian Translation of Fisheries and Aquatic Sciences no. 5667, pp. 1–5.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74: 1659–1673.
- Lepland, A., Rybalko, A., and Lepland, A. 2014. Seabed sediments of the Barents Sea. Scale 1:3.000.000. Geological Survey of Norway (Trondheim) and SEVMORGEO. St. Petersburg. www.Mareano.no/kart/ (last accessed Jan 2022).
- Lien, V. S., Gusdal, Y., and Vikebø, F. B. 2014. Along-shelf hydrographic anomalies in the Nordic Seas (1960–2011): locally generated or advective signals? *Ocean Dynamics*, 64: 1047–1059.
- Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*, 10: 5–18.
- Loeng, L., and Drinkwater, K. 2007. An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. *Deep-Sea Research II*, 54: 2478–2500.
- Lovrich, G. A., and Sainte-Marie, B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. *Journal of Experimental Marine Biology and Ecology*, 211: 225–245.
- Lutz-Collins, V., Cox, R., and Quijon, P. A. 2016. Habitat disruption by a coastal invader: local community change in Atlantic Canada sedimentary habitats. *Marine Biology*, 163: 177.
- Morata, N., Michaud, E., Poullaouec, M.-A., Devesa, J., Goffi, M. L., Corvaisier, R., and Renaud, P. E. 2021. Climate change and diminishing seasonality in Arctic benthic processes. *Philosophical Transactions of the Royal Society A*, 378: 20190369.
- Morissette, L., Castonguay, M., Savenkoff, C., Swain, D. P., Chabot, D., Bourdages, H., Hammill, M. O. *et al.* 2009. Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks. *Deep Sea Research Part II, Topical Studies in Oceanography*, 56: 2117–2131.
- Nilsen, M., Pedersen, T., and Nilssen, E. M. 2006. Macro-benthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. *Marine Ecology Progress Series*, 321: 67–77.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R. *et al.* 2019. Vegan: community ecology package. R Package Version 2.5-5. <https://CRAN.R-project.org/package=vegan>. (Last accessed on July 2021).
- Oug, E., Sundet, J. H., and Cochrane, S. K. J. 2018. Structural and functional changes of soft-bottom ecosystem in northern fjords invaded by the red king crab (*Paralithodes camtschaticus*). *Journal of Marine Systems*, 180: 255–264.
- Oziel, L., Sirven, J., and Gascard, J.-C. 2016. The Barents Sea frontal zones ad water masses variability (1980–2011). *Ocean Science*, 12: 169–184.
- Palomares, M. L. D., and Pauly, D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research*, 49: 447–453.
- Paul, A. J., and Fuji, A. 1989. Bioenergetics of the Alaskan crab *Chionoecetes bairdi* (Decapoda: Majidae). *Journal of Crustacean Biology*, 9: 25–36.
- Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data of food conversion experiments. *U.S. Fishery Bulletin*, 84: 827–840.
- Pavlov, V. A. 2007. Feeding of the snow crab *Chionoecetes opilio* (Fabricius, 1788) in the Barents Sea. *In Marine Shellfish and Algae: Biology and Fisheries*. Ed. by Sokolov V. I. VNIRO Press, Moscow.
- Pavlov, V. A., and Sokolov, K. M. 2016. Spatial distribution of snow crab. *In Snow Crab Chionoecetes opilio in the Barents and Kara Seas*. Ed. by Sokolov K. M., Strelkova N. A., Manushin I. E., and Sennikov A. M. PINRO Press, Murmansk. pp. 9–16.
- Pedersen, T., Fuhrmann, M. M., Lindstrøm, U., Nilssen, E. M., Ivarjord, T., Ramasco, V., Jørgensen, L. L. *et al.* 2018. Effects of the invasive red king crab on food web structure and ecosystem properties in an Atlantic fjord. *Marine Ecology Progress Series*, 596: 13–31.
- Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P. E., Nascimento, M. C., Blanchet, M.-A., Ellingsen, I. H. *et al.* 2021. Overexploitation, recovery, and warming of the Barents Sea ecosystem during 1950–2013. *Frontiers in Marine Science*, 8: 732637.
- Piepenburg, D. 2005. Recent research on Arctic benthos: common notions to be revised. *Polar Biology*, 28: 733–755.
- Quijón, P. A., and Snelgrove, P. V. R. 2005. Predation regulation of sedimentary faunal structure: potential effects of a fishery-induced switch in predators in a Newfoundland sub-Arctic fjord. *Oecologia*, 144: 125–136.
- R Core Team. 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>.
- H. L. Rees (ed.) 2009. Guidelines for the study of the epibenthos of subtidal environments. ICES techniques in marine environmental sciences. No. 42. 88pp. https://ices-library.figshare.com/articles/report/Guidelines_for_the_study_of_the_epibenthos_of_subtidal_environments/18626975. (Last accessed on October 16, 2022).
- Reigstad, M., Carroll, J., Slagstad, D., Ellingsen, I., and Wassmann, P. 2011. Intra-regional comparison of productivity, carbon flux and ecosystem composition within the northern Barents Sea. *Progress in Oceanography*, 90: 33–46.
- Reiss, H., Kröncke, I., and Ehrich, S. 2006. Estimating the catching efficiency of 2-m beam trawl for sampling epifauna by removal experiments. *ICES Journal of Marine Science*, 63: 1453–1464.
- Renaud, P. E., Ambrose, G. A., and Weslawski, J. M. 2020. Benthic communities in the polar night. *In Polar Night Marine Ecology: Life and Light in the Dead of Night*, pp. 161–179. Ed. by Berge J., Johnsen G., and Cohen J. H.. *Advances in Polar Ecology (Ser. Ed. D. Piepenburg)* ISBN 978-3-030-33207-5. doi: 10.1007/978-3-030-33.
- Samuelsen, A., Hansen, C., and Wehde, H. 2015. Tuning and assessment of the HYCOM-NORWECOM V2.1 biogeochemical modeling system for the North Atlantic and Arctic oceans. *Geosciences Model Development*, 8: 2187–2202.
- Sandø, A. B., Melsom, A., and Budgell, W. P. 2014. Downscaling IPCC control run and future scenario with focus on the Barents Sea. *Ocean Dynamics*, 64: 927–949.
- Saulnier, E., Brind'Amour, A., Tableau, A., Rufino, M. M., Dauvin, J. C., Luczak, C., and Le Bris, H. 2018. Seasonality in coastal macrobenthic biomass and its implications for estimating secondary production using empirical models. *Limnology and Oceanography*, 64: 935–949.
- Savenkoff, C., Bourdages, H., Castonguay, M., Morissette, L., Chabot, D., and Hammill, M. O. 2004. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). *Canadian Technical Report of Fisheries and Aquatic Science*, 2531. Cat. No. Fs 97-6/2531E. , 99. ISSN 0706-6457.
- Siikavuopio, S. I., Bakke, S., Sæther, B. S., Thesslund, T., and Christiansen, J. S. 2019. Temperature selection and the final thermal preference of snow crab (*Chionoecetes opilio*, Decapoda) from the Barents Sea. *Polar Biology*, 42: 1911–1914.
- Siikavuopio, S. I., Johansson, G. S., James, P., and Lorentzen, G. 2018. Effect of starvation on the survival, injury, and weight of adult snow crab, *Chionoecetes opilio*. *Aquaculture Research*, 50: 550–556.
- Siikavuopio, S. I., Whitaker, R. D., Sæther, B. S., James, P., Olsen, B. R., Thesslund, T., Hustad, A. *et al.* 2017. First observations of temperature tolerances of adult male snow crab (*Chionoecetes opilio*) from the Barents Sea population and the effects on the fisheries strategy. *Marine Biology Research*, 13(7): 744–750 doi: 10.1080/17451000.2017.1313989.
- Skogen, M., and Søliland, H. 1998. A user's guide to NORWECOM v2.0, The Norwegian ecological model system. *Fisken og havet* No. 18., Insitute og Marine Research, Bergen.
- Slizkin, A. G. 1982. Distribution of snow crabs of the genus *Chionoecetes* and their habitat in the northern part of the Pacific Ocean: population dynamics and reproductive conditions of commercial invertebrates and algae in the far Eastern Seas. *Izvestia Tikhookean Nauchno-Issled Inst Ryb Khoz Oceanogr*, 106: 26–33.

- Smith, C. R., Mincks, S., and DeMaster, D. J. 2006. A synthesis of benthic-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. *Deep Sea Research Part II*, 53: 875–894.
- Squires, H. J., and Dawe, E. G. 2003. Stomach contents of snow crab (*Chionoecetes opilio*, Decapoda, Brachiura) from the north-east Newfoundland Shelf. *Journal of Northwest Atlantic Fisheries Science*, 32: 27–38.
- Wieczorek, S. K., and Hooper, R. G. 1995. Relationship between diet and food availability in the snow crab *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. *Journal of Crustacean Biology*, 15: 235–247.
- Williams, A. B. 1984. *Shrimps, Lobster and Crabs of the Atlantic Coast and Eastern United States, Main to Florida*. Smithsonian Institution Press, Washington, DC. 550pp.
- Włodarska-Kowalczyk, M., Górska, B., Deja, K., and Morata, N. 2016. Do benthic meiofaunal and macrofaunal communities respond to seasonality in pelagic processes in an Arctic fjord (Kongsfjorden, Spitsbergen)? *Polar Biology*, 39: 2115–2129.
- Zakharov, D. V., Manushin, I. E., Nosova, T. B., Strelkova, N. A., and Pavlov, V. A. 2021. Diet of snow crab in the Barents Sea and macrozoobenthic communities in its area of distribution. *ICES Journal of Marine Science*. 78 2 545–556
- Zalota, A. K., Zimina, O. L., and Spiridonov, V. A. 2019. Combining data from different sampling methods to study the development of an alien crab *Chionoecetes opilio* invasion in the remote and pristine Arctic Kara Sea. *PeerJ*, 7: e7952.
- Zimina, O. L., 2014. Finding the snow crab *Chionoecetes opilio* (O. Fabricius, 1788) (Decapoda: Majidae) in the Kara Sea. *Russian Journal of Marine Biology*, 40: 490–492.

Handling Editor: Ivan Rodil