Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab

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A B S T R A C T

We studied the macrobenthic fauna and their production potential in Porsangerfjord, Northern Norway, in relation to environmental gradients and the recent invasion by the predatory red king crab into the outer fjord. The study area is characterized by a distinct along-fjord temperature gradient, with the influence of warmer Atlantic water in the outer fjord and year-round bottom temperatures around zero in the inner fjord. Benthic organisms can play a crucial role in ecosystem energy flow. Despite this, our knowledge of factors regulating benthic secondary production in high latitude ecosystems is limited. Macrobenthic abundance, biomass (B), production (P) and production-to-biomass ratio (P/B) were estimated from grab samples collected in 2010. Annual P/B ratios were calculated using a multi-parameter artificial neural network (ANN) model by Brey (2012). The mean abundance, biomass, production and P/B were 4611 ind. m^{-2} (95% CI = 3994, 5316), 65 g ww m^{-2} (95% CI = 51, 82), 174 kJ m^{-2} y^{-1} (95% CI = 151, 201) and 1.02 y^{-1}, respectively. Benthic biomass and production in the fjord were dominated by polychaetes. Spatial variability in P/B and production was mainly driven by community structure and differences in environmental habitat conditions. The inner basins of the fjord were characterized by high total production (439 kJ m^{-2} y^{-1}), attributable to high standing stock biomass and community structure, despite cold bottom temperatures. In the middle and outer fjord, smaller taxa with low individual body masses increased the P/B ratios, but they did not compensate for the low biomass, thereby resulting in lower total production in these areas. The low biomass and the sparseness of large taxa in the outer and middle fjord may already be a result of predation by the invasive red king crab resulting in an overall lower macrobenthic production regime.

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1. Introduction

Benthic invertebrates perform numerous important functions in marine ecosystems, which range from their involvement in nutrient recycling (Welsh, 2003) to their roles as significant links among multiple trophic levels in and beyond the benthos (Commitol and Ambrose, 1985, Snelgrove, 1998). Regions with high benthic production such as the Northern Bering and Chukchi Sea support large amounts of bottom-feeding fish, mammals, and birds (Bax and Eliassen, 1990, Grebmeier et al., 2006). Ecosystem models from the coastal Northeast Atlantic suggest that a significant amount of energy is channeled via the benthos, which supports commercial fish species such as cod (*Gadus morhua*) (Kanapathippillai et al., 1994, Pedersen et al., 2008). Therefore, benthic secondary production comprises a crucial component of the energy flow in ecosystems, particularly at high latitudes (Petersen and Curtis, 1980, Nilsen et al., 2006, Blicher et al., 2009). Despite this, quantitative approaches investigating the role of benthic macrofauna as producers and consumers are limited due to the scarcity of

data from these regions (but see Brey and Gerdes, 1998, Nilsen et al., 2006 and Kędra et al., 2013). Dolbeth et al. (2012) emphasize the additional value in providing production estimates along with static community measurements, such as faunal density and biomass, in environmental monitoring studies. Not the least because secondary production integrates dynamic population processes such as growth, recruitment and mortality, as well as biotic and abiotic interactions in a population (e.g., Valentine-Rose et al., 2011, Dolbeth et al., 2012). Therefore, macrobenthic production has been studied as an indicator of ecosystem functioning (Buffagni and Comin, 2000, Valentine-Rose et al., 2011, Dolbeth et al., 2012) to assess human-induced disturbances such as trawling (Jennings et al., 2001, Hiddink et al., 2006, Reiss et al., 2009) and pollution (Steimle, 1985; Lange et al., 2004) and has great potential for the evaluation of impacts by non-indigenous species (Dolbeth et al., 2012).

The production-to-biomass ratio (P/B), or productivity, for a species was first reported by Sanders (1956) as the turnover time of an organism and lifespan has been recognized as its main predictor (Robertson, 1979). Environmental factors such as temperature and depth have indirect impacts on production processes by influencing a species' life history, as well as direct effects, e.g., on the metabolic rate. In addition to regional food supply, these factors have been recognized as major

determinants for the global patterns of macrobenthic productivity, which generally exhibit lower P/B ratios with increasing latitude (Brey and Clarke, 1993, Brey and Gerdes, 1998, Cusson and Bourget, 2005). Empirical estimates of benthic productivity that use the mean annual body mass over the lifespan as a predictor have been shown to be equally adequate and extremely useful because the body mass is easily obtained from biomass records (Banse and Mosher, 1980, Schwinghamer et al., 1986, Edgar, 1990, Tumbiolo and Downing, 1994). The multi-parameter regression model by Brey (1999 and 2001), which also incorporates taxonomic identity, temperature and depth, was shown to perform best at predicting benthic community production from P/B ∗ B (Cusson and Bourget, 2005, Dolbeth et al., 2005) and it has been applied in various marine studies (Brey and Gerdes, 1998, Nilsen et al., 2006, Bolam et al., 2010). The recent artificial neural network (ANN) proposed by Brey (2012) further requires feeding mode and motility as input and provides better predictions of secondary production compared with empirical models based on multiple linear regression (Brey et al., 1996), allowing reasonable estimation of benthic production at the scarcely studied Arctic habitats.

The studied Porsangerfjord is located on the Finnmark coast of Northern Norway and is characterized by heterogeneous environmental conditions with along-fjord gradients in depth, temperature, and salinity. The outer part is influenced by warmer and saline coastal water and depths >300 m, whereas the inner part is isolated with shallow depths in the west and two basins in the east (ca 100 m), maintaining subzero bottom temperatures throughout half of the year and ice coverage during late winter and spring. This area is believed to hold a special benthic community, including species that are usually known from the Arctic and isolated populations from the coast and Barents Sea (Soot-Ryen, 1951, Oug and Fuhrmann, 2011). Human impact in Porsangerfjord is considered to be low and there has been no commercial bottom trawling in the fjord since 1984. Porsangerfjord is however close to the present western distribution limit of the invasive red king crab (*Paralithodes camtschaticus*, Tilesius, 1815), which was introduced to the Barents Sea in the 1960s in order to establish a commercial stock (Orlov and Ivanov, 1978). At the time of study, red king crabs were present in densely populated patches in the outer and middle fjord, but had not entered the inner area (personal observations, 2010. See also video from Porsangerfjord, S1). The red king crab is one of the world's largest decapods; feeding on epi- and infaunal organisms it has the potential to reduce local benthic abundance and biomass in invaded areas (reviewed in Falk-Petersen et al., 2011, Oug et al., 2011). Stock size in Porsangerfjord was estimated to 531,773 crabs in 2010 (>70 mm carapace length, pers. communication A.M. Hjelset, 2012), which compares to values reported from Varangerfjord, the first invaded area in Norway, where benthic fauna has declined because of high predation pressure (Oug et al., 2011).

The present study investigated the macrobenthic fauna in a high latitude fjord with the main objective to examine how the abundance, biomass (B), production (P) and production-to-biomass ratios (P/B) were related to the along-fjord environmental gradients, community structure and red king crab distribution. It is part of a monitoring program of the Porsangerfjord ecosystem aiming to assess benthic invertebrate production and to follow the development and effects of the recent invasion by the red king crab. With this study we hope to contribute to our knowledge about macrobenthic production in high latitude habitats and provide a baseline for future impacts of crab predation in the inner Porsangerfjord.

2. Materials and methods

2.1. Study area

The subarctic Porsangerfjord is one of Norway's largest fjords, covering an area of ca 1877 km^{-2} (Fig. 1). It is considered to be an open fjord, with depths of ca 300 m in the outer part facing the Barents Sea toward

the north and a deep sill at ca 200 m at the fjord entrance. The inner part of the fjord is separated by a narrowing of the fjord and a sill at approximately 60 m. Small islands and skerries characterize this inner shallow area, which comprises two deeper basins (ca. 100 m depth) toward the east (Roddenessjøen and Austerbotn) (Fig. 1). Because of its high latitude, the average temperature is generally low in Porsanger, but the temperature and salinity are highest toward the mouth of the fjord due to the influence of warmer Atlantic water. The middle and outer fjord have mean annual bottom temperatures of 3.9 °C (mean ± 2.0) and 4.5 °C (±1.5), respectively. Local cooling in the winter leads to ice coverage in the inner area, approximately between January and May. Roddenessjøen and Austerbotn exhibit year-round cold bottom temperatures of 0.2 °C (±1.2) due to limited exchange with the outer fjord (Mankettikkara, 2013). Freshwater discharge is comparably low in Porsanger and it occurs mainly during the melting season from three rivers in the inner fjord (see Myksvoll et al., 2012). The mean annual bottom salinities decline from 34.7‰ (±0.2) in the outer fjord to 33.8‰ (±0.1) in the inner fjord, seasonal variation rarely exceeds 1–2‰ (Mankettikkara, 2013, data provided by the Sea monitoring Program UiT for the time period of 2006–2010). The circulation patterns and mixing in Porsangerfjord are mostly wind driven (Svendsen, 1995, Myksvoll et al., 2012) and stratification in the middle and outer parts is generally low compared to other north Norwegian fjords (Svendsen, 1995, Mankettikkara, 2013). Porsangerfjord is characterized mostly by soft bottoms, but mixed bottom types with calcareous red algae are common at shallow depths (personal observations, see video in S1).

2.2. Sampling of macrofauna

In total, 40 grab samples were collected from Porsangerfjord during a cruise in the RV *Johan Ruud* from the University of Tromsø during June 2010. The sampling depths ranged from 40 to 285 m, and due to mixed bottoms at shallow habitats, most samples were collected from depths >50 m. The sampling regime followed a stratified random design with three areas (inner fjord n = 12, middle fjord n = 16, outer fjord n = 12) under consideration of bottom substrate and topography (Fig. 1). Given the low availability of prior knowledge about the bottom types, the aim was to obtain a large spread over the area for a given amount of effort, thereby representing the spatial patterns in the benthos, rather than achieving precise estimates of the species at one locality. The inner eastern basins had a higher number of stations per unit area because prior information indicated that there was high benthic biomass, which usually results in higher variance of estimates and requires a larger number of samples. Macrofauna sampling was performed using a 0.1 m^2 van Veen grab. The samples were sieved through a 1 mm round mesh sieve and fixed with 4% buffered formaldehyde solution (1:9 dilution of 40% formaldehyde solution with seawater), and later transferred to 70% ethanol. Mesh size was chosen based on cost efficiency (see e.g., Thompson et al., 2003) and to assure comparability with the study by Nilsen et al. (2006) in the north Norwegian Ullsfjord. Identifications were made mostly to the family level; in large individuals or abundant taxa, identification to the species level was often possible (see also Table 1). The ethanol stored specimens were counted and their wet weights (ww) were recorded to the nearest 0.001 g. The specimens were blotted dry prior to weighing. Wet weight loss due to fixation was not accounted for, but since fixation is a standard procedure applied prior to biomass estimates in the need of fine scales and taxonomic identification, we assume our results are comparable to most other macrobenthic studies. In general, the tubes were removed from polychaetes, but a conversion factor was established based on a linear regression for *Spiochaetopterus typicus*, because tube removal was difficult and time consuming (Fig. S2, supplementary material). Colonial animals such as bryozoans as well as unidentified material were excluded from P/B and production estimates because their individual abundances and body masses could not be calculated.
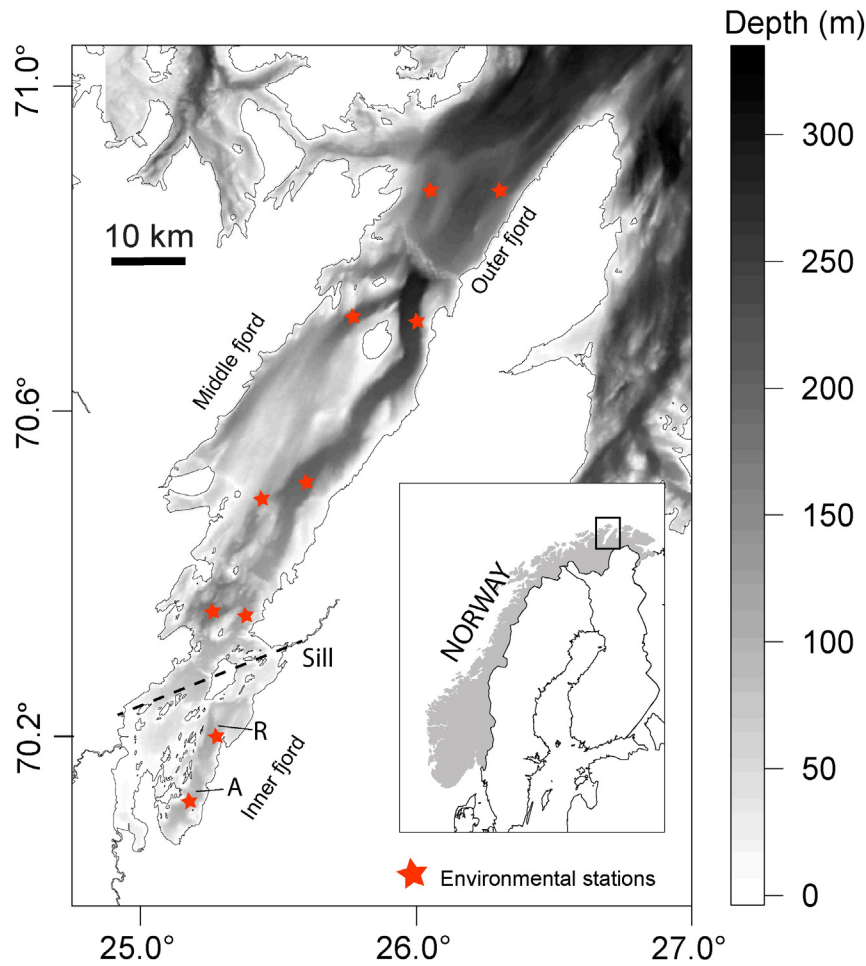
Fig. 1. Overview of the study area in Porsangerfjord, Northern Norway. Depths are indicated by shades of gray. (R) Roddenessjøen (A) Austerbotn. The subareas are indicated by names.

2.3. Estimation of P/B and production

The annual somatic production-to-biomass ratios (P/B) and total production (P) were estimated from raw data using the following step-wise approach. Biomass records (in g wet weight m^{-2}) were converted into energy values ($J\,m^{-2}$) using the established conversion factors compiled in Brey (2001) and Brey et al. (2010), which are available as a MS Excel worksheet (version 04–2012). Tubes and hard shells were excluded from conversion into energy, meaning factors correcting for shell weights were used. In general, taxa were compiled into families because conversion factors were available widely at this level. If no factors could be obtained or if they were unavailable for wet weights, a factor was selected from the next highest taxonomic level, which broadly applied to most mollusks. We found conversion factors to vary slightly, depending on which option for functional feeding mode, habit and motility was chosen in the quest of the database. We made the choice to our best knowledge for higher taxa (which could include multiple functional modes) and accepted conversion factors available at species level, with the functional mode given in the database. Annual somatic P/B ratios were then computed for each taxa at each station using the ANN model proposed by Brey (2012), which is available as an MS Excel data entry worksheet (version 01–2012). Individual *body mass* (J), *temperature* (°C), and *depth* (m) were used as the input variables for the ANN. Other factors were included as dummy variables, which comprised *motility* (infauna, sessile, crawler, and facultative swimmer), *feeding* (herbivore, omnivore, and carnivore), *habitat* (lake, river, marine, subtidal, and exploited), and *taxon* (Mollusca, Annelida, Crustacea, Echinodermata, and Insecta). For other recorded taxa (e.g., Echiura), *taxon* was set to the most similar category (e.g., Annelida). The bottom temperatures were based on long-term environmental data provided by the Sea monitoring Program at UiT (2006–2010, Fig. 1). The frequency of measurements varied from once per month to once per quarter. In order to obtain mean annual temperatures and salinities, we incorporated measurements from several years, yielding at least one measurement per month, to avoid data being biased toward certain seasons. The values for the sampling stations were extracted according to the depths of the nearest environmental station. Production was then estimated from P/B multiplied by the biomass of the respective taxon at a station (as g ww m^{-2} or kJ m^{-2}).

The P/B ratios for each station and subarea were calculated by dividing the sum of production by the sum of the biomass (in kJ or g ww). Discrepancy between energy and wet weight retrieved values for community P/B arose from conversion. Community P/B will be higher than the corresponding wet weight estimate, if groups with low energy per unit wet weight also have low P/B values (often the case in large, long lived organisms). In other words, community P/B ratios based on wet weight, are biased toward large organisms with high wet mass, but comparably low energy and P/B. Since sampling effort per unit area was slightly higher in the inner fjord, all mean values reported for the whole fjord were calculated as stratified means, weighted by the proportion of each subarea to the total fjord area. The P/B stated for the whole fjord was calculated from mean (weighted) production divided by mean (weighted) biomass.

Table 1
Most important macrobenthic taxa in Porsangerfjord. The 20 most predominant taxa for each variable are marked in bold. In case an identified family contained only one definite genus or species, its name is given instead. The values represent the weighted means from all sampling stations. P/B ratios were calculated from mean production divided by mean biomass (in kJ) in the fjord.

Phylum	Class	Taxon	Abundance (ind. m^{-2})	S.D.	Lower 95% CI	Upper 95% CI	Biomass (g ww m^{-2})	S.D.	Lower 95% CI	Upper 95% CI	Production (kJ m^{-2} y^{-1})	S.D.	Lower 95% CI	Upper 95% CI	P/B (y^{-1})
Annelida	Polychaeta	Ampharetidae	**37**	38	25	50	**0.6**	1.1	0.3	1.0	**2.2**	3.9	1.2	3.9	1.59
		Amphinomidae	**52**	120	30	102	0.1	0.1	0.0	0.1	0.3	0.7	0.2	0.7	1.37
		Capitellidae	**120**	111	88	162	0.1	0.1	0.1	0.2	**1.0**	0.9	0.7	1.3	1.67
		Cirratulidae	**120**	111	88	162	0.1	0.1	0.1	0.2	**1.0**	0.9	0.7	1.3	3.59
		Lumbrineridae	**220**	194	171	285	**1.1**	2.0	0.7	2.4	**5.1**	6.8	3.6	9.4	0.88
		Maldanidae	**1312**	1655	829	1908	**11.0**	12.4	7.5	15.0	**48.1**	53.9	33.0	66.4	1.62
		Nepthyidae	**44**	30	35	54	**2.7**	2.5	2.0	3.5	**9.4**	8.4	7.0	12.2	0.90
		Opheliidae	19	36	13	26	**1.1**	2.8	0.6	1.7	**4.7**	12.0	2.8	7.2	0.88
		Orbiniidae	**77**	69	59	105	0.2	0.2	0.1	0.3	**1.4**	1.5	1.0	2.0	1.50
		Oweniidae	**1030**	918	806	1393	**4.1**	3.9	3.3	5.4	**14.4**	12.8	11.4	18.8	1.54
		Paraonidae	**79**	154	46	190	0.0	0.1	0.0	0.1	0.4	0.8	0.2	0.9	1.93
		Pectinariidae	8	11	5	12	**0.6**	1.7	0.2	1.3	**1.5**	4.2	0.7	3.5	0.98
		Spiochaetopterus typicus	**283**	754	193	388	**12.2**	41.8	6.6	21.1	**59.2**	140.7	45.1	75.6	1.16
		Spionidae	**95**	139	72	130	**0.6**	1.2	0.3	1.1	**1.8**	2.9	1.1	3.1	1.25
		Syllidae	**61**	134	34	95	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.1	1.95
		Terebellidae	**65**	105	42	105	**0.3**	0.6	0.2	0.5	**1.2**	1.9	0.7	1.8	1.48
		Trichobranchidae	**50**	90	37	66	0.3	0.7	0.2	0.5	**1.0**	1.8	0.7	1.4	1.35
Chordata	Ascidiacea		2	7	1	4	**1.5**	7.8	0.3	4.1	0.3	1.5	0.1	0.8	0.23
Cnidaria	Anthozoa	Edwarsiidae	8	14	5	14	**0.7**	1.6	0.3	1.5	**1.0**	2.2	0.4	2.1	0.72
Echinodermata	Asteroidea	Ctenodiscus crispatus	9	36	3	31	**3.7**	13.3	1.6	6.9	**1.6**	5.1	0.8	2.9	0.16
	Echinoidea	Brissopsis lyrifera	0	2	0	1	**2.4**	14.9	0.0	9.5	0.3	1.5	0.0	1.0	0.25
Mollusca	Bivalvia	Astarte sp.	20	43	11	43	**6.6**	21.0	2.1	18.2	**1.3**	3.4	0.5	2.8	0.24
		Cardiidae	10	20	6	17	**4.6**	28.6	0.2	16.4	**0.9**	4.2	0.3	2.4	0.12
		Mya sp.	0	1	0	0	**0.9**	7.6	0.0	2.7	0.1	1.1	0.0	0.4	0.10
		Mytilidae	**58**	113	30	111	0.3	1.1	0.1	0.7	0.6	1.2	0.3	1.1	0.81
		Thracia sp.	7	34	0	33	0.4	2.9	0.0	1.7	0.2	1.0	0.0	0.8	0.35
		Thyasiridae	**109**	106	82	159	0.2	0.3	0.2	0.4	0.5	0.5	0.3	0.7	1.38
		Yoldia hyperborea	2	9	0	5	**2.5**	12.8	0.6	6.4	0.6	2.9	0.2	1.4	0.10
		Yoldiella sp.	**292**	239	219	0	**1.7**	2.4	1.2	2.2	**3.6**	3.6	2.6	4.6	0.93
Nemertea			**45**	49	32	63	**0.5**	1.4	0.2	1.1	**2.2**	6.0	1.0	5.2	0.91
Sipunculida			**55**	105	32	86	0.1	0.2	0.0	0.1	0.3	0.6	0.2	0.5	1.69
Community			4611	2008	3994	5316	64.6	82.5	51.3	82.2	174.1	151.2	151.3	200.9	1.02

2.4. Numerical analysis

All of the numerical and statistical analyses were performed in R (R Core Team, 2013, version 2.15.2). Nonparametric 95% confidence intervals (CIs) given for means of the fjords and subareas, were generated by bootstrap replicates (10,000) of the station data and calculated using the adjusted nonparametric bootstrap intervals percentile method (Efron, 1987). Stratified resampling was performed for fjord means, where importance weights were specified according to the proportion of each subarea to the total fjord area (*boot* package). Non-parametric Kruskal–Wallis tests were used to test for similarity among multiple groups (i.e., subareas), followed by Dunn's test of multiple comparisons (Dunn, 1964) with Bonferroni correction of *p*-values. A non-parametric Mann–Whitney U test (MW) was used to compare two groups, i.e., east and west side of the fjord. The null hypothesis was rejected at $\alpha = 0.05$ ($p < 0.05$).

We used principal components analysis (PCA) on the standardized biological variables (macrobenthic biomass, P/B ratios and production) to investigate and visualize their relationships with each other and the environmental gradients (in temperature, depth and salinity), as well as estimated king crab densities along the fjord (see below). The multivariate community structure and its relationship with biological and abiotic environmental variables was analyzed by correspondence analysis (CA) based on untransformed family abundances. Explanatory variables were fitted to the ordinations as linear vectors by the R envfit procedure (*vegan* package). The significance of fits was determined by permutation tests (number of permutations = 1000).

We also used a bivariate approach to test for correlations between macrobenthic estimates, environmental variables and red king crab abundances using Spearman's rank correlation coefficient (r_s) because the data were not normally distributed (Shapiro–Wilk tests, $p < 0.05$). The data were suspected to include some spatial autocorrelation because of the method used to assign temperature and depth and the sampling approach utilized. The presence of strong spatial autocorrelation (i.e., the variables obtained from nearby stations are more likely to have similar values) can affect conventional hypothesis testing because it violates the assumption of independence (Legendre, 1993). Therefore, the data were tested for spatial autocorrelation using the ranked Mantel test, which correlates two dissimilarity matrices (see Goslee and Urban, 2007), where Euclidean distances were employed to represent space, as well as biological data. In the process, we used piecewise correlograms to evaluate the presence of autocorrelation (Goslee and Urban, 2007). The *p*-values for the Spearman's rank correlation coefficients (p_{corr}) were calculated based on a two-tailed *t*-test.

Relative abundances of red king crabs at benthic stations were obtained using ordinary kriging (R package *gstat*, see S3 for details) from crab trawl surveys by the Institute of Marine Research (Fig. S4). Ordinary kriging creates synthetic data from a weighted linear estimator, using distances between sampling stations with an assumed level of autocorrelation. These crab beam trawls (see Hvingel et al., 2012) do not usually catch smaller crabs <70 mm carapace length, and little information is available on the distribution and behavior of these size classes. However, juvenile crabs usually stay in shallower water (Jørgensen and Nilssen, 2011), not covered by benthic macrofauna sampling. We pooled the years 2007 to 2010 in order get spatial coverage over the entire fjord. This assumes that distribution did not vary with time. The purpose of the procedure was purely spatial interpolation and we did not attempt to address any temporal dynamics associated with king crab migration. We would suspect recovery of benthic animals via recruitment from the early years of invasion, given that the impact does not persist. Despite this, any impact by crabs in 2007 could be relevant for benthic animals older than 3 years. The general tendency of crabs to occur in aggregations, resulted in high variability between catches and many zeros in crab trawl data. We compared kriging results to pot catches (CPUE) available from the same time period and evaluated uncertainty in predictions for benthic grab stations from sequential Gaussian simulation (see S3), where the variability of the different realizations is a measure of uncertainty in crab abundances at grab locations.

3. Results

3.1. Means and group contributions

The mean abundance, biomass (B), and production (P) (95% CI) for the whole fjord (n = 40) were 4611 ind. m^{-2} (3994, 5316), 65 g ww m^{-2} (51, 82), and 57 g ww m^{-2} y^{-1} (47, 71), respectively. This corresponded to a biomass of 171 kJ m^{-2} (157, 194) and a production of 174 kJ m^{-2} y^{-1} (151, 201) (Fig. 2). The community production-to-biomass ratio (P/B) was 0.88 y^{-1} based on wet weight (ww) and 1.02 y^{-1} based on energy (kJ) (Table 1 and Fig. 2). In the following, we refer to the P/B ratios obtained from the energy-converted values, since they allow comparison with other studies using carbon values and are more relevant with regard to energy flow.

Polychaeta was the most abundant taxonomic group in Porsangerfjord (Fig. 2a) and this group contributed greatly to the biomass despite the low individual weights (Fig. 2c). This was also the most productive group (Fig. 2e) with a P/B ratio of 1.26 y^{-1}. The most abundant families within this group were Maldanidae and Oweniidae (Table 1). The tube-dwelling, deposit-feeding *Spiochaetopterus typicus* had a high biomass in the inner fjord and it dominated the overall mean production (Table 1). Large bivalves such as *Yoldia hyperborea* and *Ciliatocardium ciliatum* were limited to the inner eastern basins and the inner western part, respectively, and contributed greatly to benthic biomass in these areas (Fig. 2c) because of their high individual weights. The small and abundant genus *Yoldiella sp.* had a comparably high P/B ratio of 0.93 y^{-1} (Table 1) and was present in most of the samples. Echinodermata mainly comprised small ophiuroids in the outer fjord, but the mud star *Ctenodiscus crispatus* was responsible for higher echinoderm biomass in the inner fjord (Fig. 2c) and had a low P/B of 0.16 y^{-1} (Table 1). Echinodermata were generally absent from stations in the middle fjord. Malacostraca (mainly Amphipoda and Cumacea) had the highest P/B ratios (1.61 y^{-1}), but they contributed little to total production due to their low biomass. High variation among stations (0.99 to 4.34 y^{-1}) reflected the large interspecific differences in this group. Colonial organisms comprised Porifera, Bryozoa, Hydrozoa and Alcyonacea. In total, colonials contributed with an additional 3.0 g ww m^{-2} (95% CI = 0.3, 13.6) to benthic biomass, which converts to 6.4 kJ m^{-2} (95% CI = 0.1, 18.6). A few heavily calcified Bryozoans in the outer part of the fjord strongly influenced mean biomass values. Mean abundance of colonies was estimated to 8 ind. m^{-2} (95% CI = 4, 13).

3.2. Spatial variability

We compared the subareas of the fjord by grouping the stations from the inner fjord (n = 12), the middle fjord beyond the sill (n = 16) and the outer fjord (n = 12), and detected significant differences in biomass, body mass, production and P/B (Kruskal–Wallis, $p < 0.001$). Pairwise comparisons revealed higher macrofaunal biomass (means = 191, 41 and 38 g ww m^{-2}), body mass (means = 41, 12 and 7 mg ww m^{-2}), and production (means = 439, 131 and 104 kJ m^{-2} y^{-1}) in the inner area compared with both the middle and outer fjord (Dunn's test with Bonferroni correction, $p < 0.001$, Fig. 2a–c). By contrast, the P/B ratios were lower in the inner fjord compared with the other two subareas (0.81, 1.29 and 1.20 y^{-1}, Fig. 2. g). The macrobenthic abundance did not differ significantly between the three subareas (Kruskal–Wallis, $p = 0.55$) (Fig. 2a) and showed no clear spatial pattern (Fig. 3a). The abundance varied from 1580 to 9460 ind. m^{-2} and the biomass ranged between 10 and 434 g ww m^{-2} (Fig. 3b). The estimated production ranged from 45 to 780 kJ m^{-2} y^{-1}. Despite the low P/B ratios in the inner part (Fig. 3c),
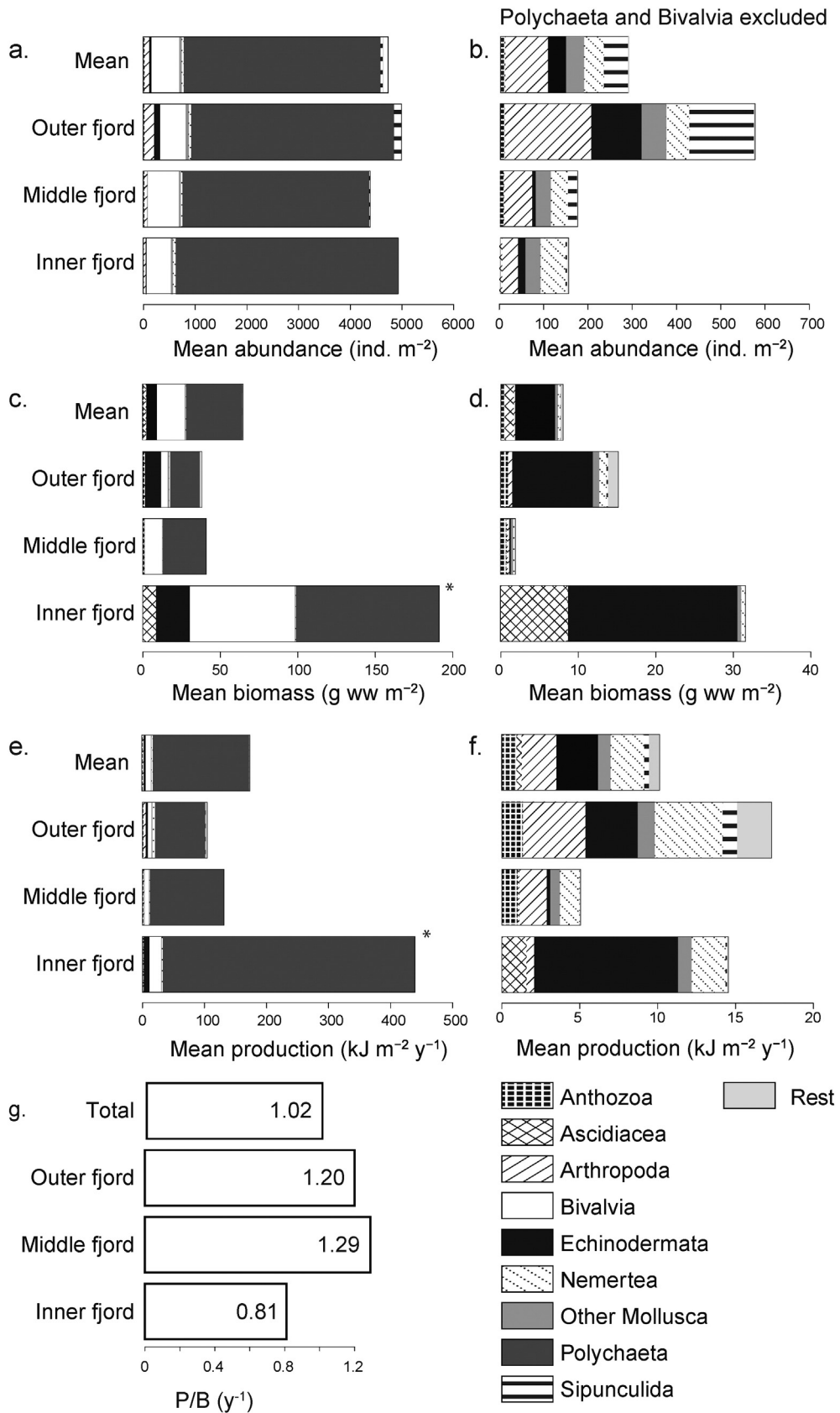
Fig. 2. (a, b) Macrobenthic abundance (ind. m^{-2}), (c, d) wet weight biomass (g ww m^{-2}), (e, f) production (kJ m^{-2} y^{-1}) and (g) P/B values. (a–f) The data are presented as means for each subarea. (b, d, f) Polychaeta and Bivalvia excluded. * Statistically different from the other two regions (Mann–Whitney U test, $p < 0.05$).
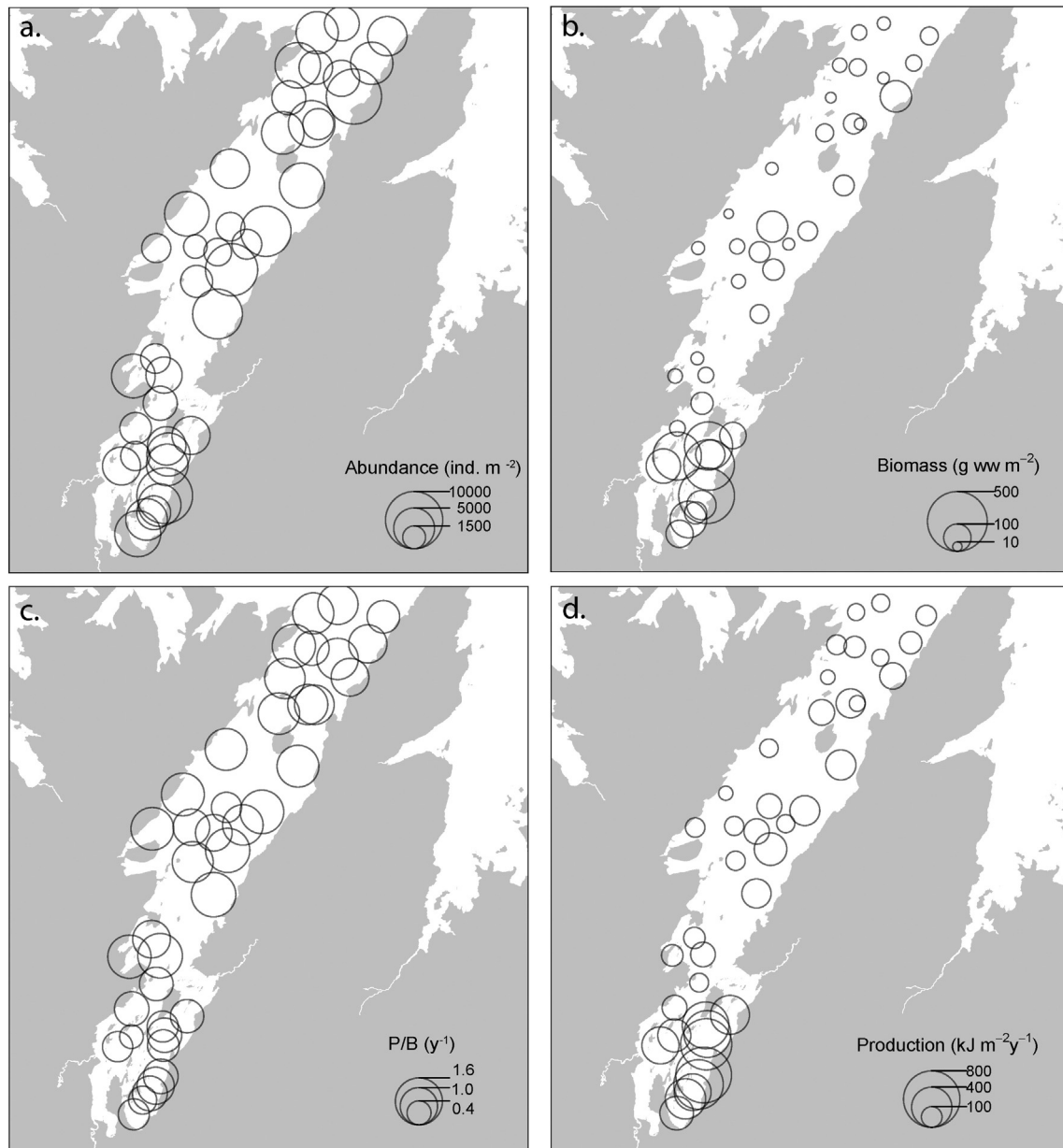
Fig. 3. Map of Porsangerfjord showing the totals for all sampling stations. (a) Abundance (m^{-2}), (b) biomass (g m^{-2}), (c) production-to-biomass ratio (P/B, y^{-1}), and (d) production ($kJ\ m^{-2}\ y^{-1}$). The areas of the circles are scaled to the values.

production was highest in this area, especially in Austerbotn and Roddenessjøen (Fig. 3d). In addition to the general trend toward high biomass and production at the inner stations, there was a cross-fjord trend in the middle and outer parts of the fjord (Fig. 3b and d). Comparisons of stations in these areas showed that biomass and production were significantly higher at stations located toward the eastern coastline (n = 12) than those toward the west (n = 15) (MW, $p < 0.047$).

3.3. Environmental gradients and predation

A PCA was performed using the biological variables obtained for the 40 sampling stations (Fig. 4), where the first and second axes explained 60.5% and 27.4% of the total variation in the data, respectively. Mean body mass, biomass, production, and P/B corresponded to the first component (PC 1) and, in agreement with the results from above, separated stations located in the inner fjord from the outer and middle fjord. P/B had an inverse relationship with body mass, which may be expected

because body mass was used as an input variable for the ANN model and it is the major predictor of P/B. Vectors for biomass and production pointed in the same direction, indicating a positive correlation between these, which can also be expected with production estimates deriving from P/B ∗ B. Interestingly however, the P/B vector points in the opposite direction, showing that stations with higher production tended to have lower P/B values. The second axis (PC 2) was related mainly to faunal abundance and it separated a group of stations with high abundances located toward the eastern middle and outer fjord. All fitted explanatory variables were significantly correlated to the ordination ($R^2 > 0.23$, $p < 0.008$). Red king crab densities and the abiotic environmental variables (temperature, depth and salinity) were mostly associated with variation along the first axis (PC 1), where the annual mean bottom temperature was most important ($R^2 = 0.59$, $p < 0.001$). Here it may also be pointed out, that temperature showed an inverse relationship to production. Depth was closely related to P/B, showing a positive interaction with increasing water depth and hence, an opposite relation with mean body mass.
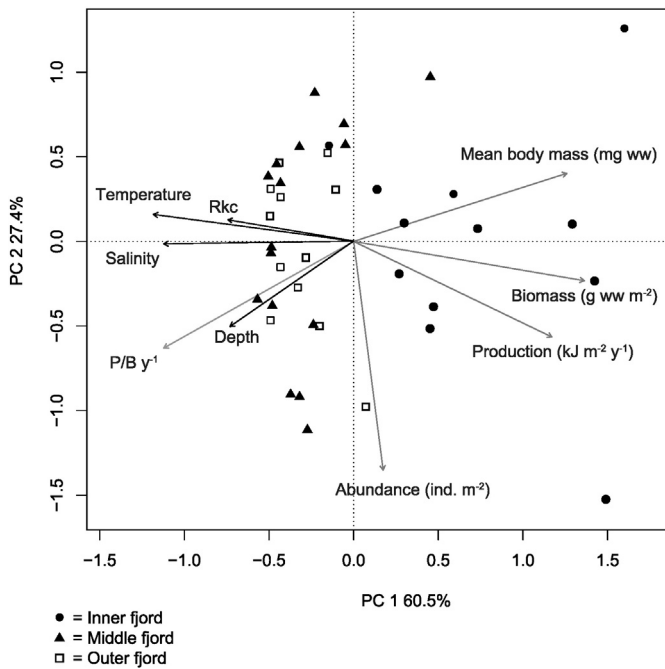
Fig. 4. Principal components analysis (PCA) of the sampling stations according to their biological variables (mean body mass, abundance, biomass, P/B ratio and production) and fitted environmental variables (depth, temperature and salinity).The stations are coded by the subarea of the fjord (see Fig. 1). Rck = Red king crab density estimated from kriging interpolation (see S5).

Spearman's rank correlation coefficient tests were performed to assess the correlations among variables (Table 2). Please note that temperature, depth and mean individual body mass were used as input variables for the modeling of P/B, and P derived from P/B ∗ B, constituting dependency among variables and thus, could contribute to significant correlations. By contrast, the mean body mass was positively correlated with biomass and production (Table 2). As expected, high spatial autocorrelation was detected in all abiotic environmental variables and to a certain extent in the biological estimates (S5), requiring a cautious causal interpretation. The high auto-, and intercorrelation of temperature, salinity and depth are caused by the fact that they follow some of the same spatial gradients along the fjord. They were negatively correlated to biomass and production and positively with P/B values (Table 2). Biomass was positively correlated with mean individual body mass ($r_s = 0.86$, $p < 0.001$), indicating that total biomass increased because of larger animals. Confirming results from the PCA, biomass was significant positively correlated with production ($r_s = 0.88$, $p < 0.001$), while production was negatively correlated to P/B ($r_s = -0.43$, $p = 0.005$).

Relative red king crab abundances at grab stations predicted from ordinary kriging correlated significantly negative with benthic biomass

and production, and positively with benthic P/B ratios (Table 2). The distribution of crabs in the fjord predicted from kriging (Fig. S6) was similar when using pot data (Fig. S7), indicating that crab trawl data provided a reliable estimate. Interpolated densities were especially uncertain in shallow areas at the slope and where crab trawl (and pot) stations were scarce (Figs. S6b and S7b). Very low crab density was predicted in the far outer fjord, while densities in the inner fjord were probably overestimated, since video observations did not show larger crabs in this area before 2011 (pers. observation, 2011). Variability between the different realizations from sequential Gaussian simulation was large (Figs. S8 and S9), reflecting the variation in original data, with numerous 0 catches in close proximity to stations with high numbers of crabs (Fig. S8).

3.4. Community structure

A correspondence analysis (CA) was used to separate the stations based on their family abundances (Fig. 5). Abundance count data represented community patterns best, while biomass data was extremely skewed and single large specimens would contribute largely to the ordination solution, not realistically reflecting taxonomic composition and resulting in low variance explained. Taxa contributing greatly to the ordination usually had high frequencies at the respective stations. The first and second axes of the ordination accounted for 24.6 and 17.2% of the total variation in the data, respectively. Temperature, salinity, and depth were correlated with the first two components ($R^2 = 0.89$, 0.72, and 0.44, respectively, $p < 0.001$), thereby indicating their significant roles in explaining the community structure. Three main communities were identified based on the ordination plot, but stations did not group strictly according to areas defined (Figs. 5 and S10). Stations from the inner cold basins (Austerbotn and Roddenessjøen) were however separated clearly from the middle and outer subarea and they were dominated by the polychaete family Chaetopteridae (*Spiochaetopterus typicus*) (Figs. 5 and S10). The second community was characterized by the polychaete family Maldanidae, which mainly dominated stations in the deeper middle and outer fjord (Figs. 5 and S10). The third community was characterized by the abundant Oweniidae and Yoldiidae (Fig. 5) and it included shallower stations from the inner western part as well as outer fjord stations (Fig. S10). Syllidae and Spionidae were mainly responsible for further separation of outer fjord stations (Fig. 5). In order to relate P/B ratios and production to the community structure, their values were projected onto stations in the ordination plot (Fig. 5b and c). With a few exceptions, the observed trends in P/B and production were well reflected by the differences among communities. The highest production was observed in the *Spiochaetopterus* community in the inner area, which had at the same time low P/B ratios. Low production was linked to the community in the outer part, which was dominated by small polychaetes. The Maldanidae community at deeper stations was associated with moderate production values and generally high P/B ratios.

Table 2
Spearman's rank correlation coefficients between variables. Values in bold derive from variable pairs which did not observe spatial autocorrelations. Whereas spatial autocorrelation was present in the other variables (ranked mantel test, p < 0.05), requiring p-levels given for correlation coefficients to be interpreted with care. See text for further explanation.

Spearman's rank correlation coefficient (r_s)	Depth	Temperature	Salinity	Biomass	Production	Abundance	P/B
Temperature (°C)	0.35*						
Salinity (‰)	0.83*	0.77*					
Biomass (g ww m^{-2})	−0.36*	−0.69*	−0.56*				
Production (kJ m^{-2} y^{-1})	**−0.28**	−0.82*	−0.60*	0.88*			
Abundance (ind. m^{-2})	0.33*	−0.19	0.15	0.28	**0.38***		
P/B (y^{-1})	0.52*	0.43*	0.53*	−0.63*	−0.43*	**0.31**	
Mean bodymass (mg ww)	−0.54*	−0.67*	−0.69*	0.86*	0.74*	−0.18	−0.80*
Red king crab density[a]	**−0.04**	**0.15**	**0.00**	−0.42*	−0.36*	**−0.18**	0.45*

[a] Estimated from kriging interpolation (see S5).
* Statistically significant at α < 0.05.
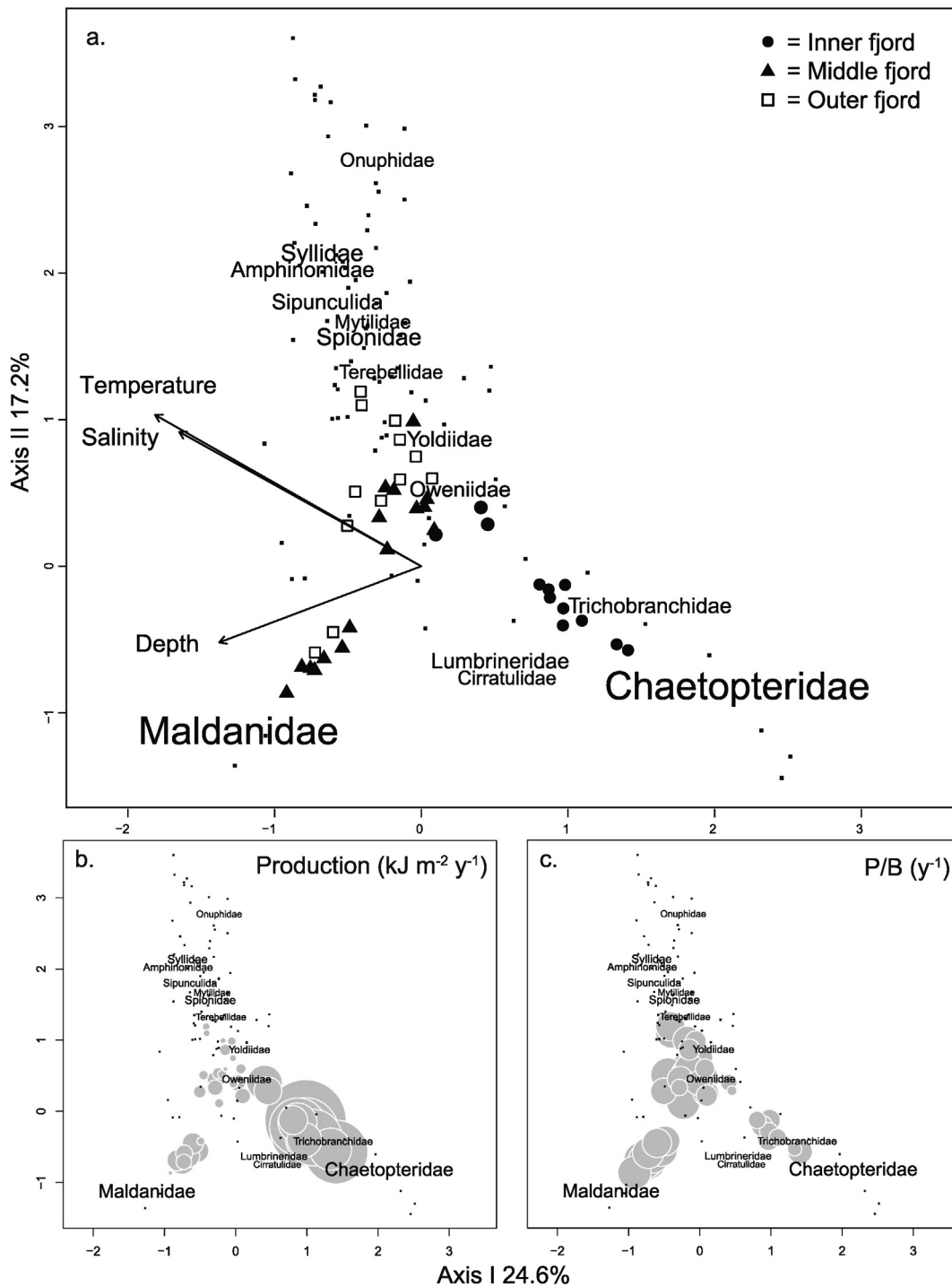
Fig. 5. Correspondence analysis (CA) of stations and families. The percentage eigenvalues are given for dimensions I and II. Families that contributed >1% to the total variation are labeled and scaled by font size to their contributions, whereas others are represented by points. (a) The environmental variables are indicated by vectors. The stations are coded by the subareas of the fjord (see Fig. 1). (b) Production (kJ m^{-2} y^{-1}) and (c) P/B ratios (y^{-1}) superimposed on the CA, where the circle radius is scaled to the value for the respective station.

4. Discussion

In the present study, we estimated the abundance, biomass (B), production (P) and production-to-biomass ratio (P/B) of the macrobenthic fauna in Porsangerfjord. The spatial variability in these estimates was mainly related to community structure along environmental gradients. The stations in the inner subarea accounted for the highest total production because of their high standing stock biomass, despite cold temperatures and low P/B values. An impact of predation by the red king crab was indicated by significant negative correlation of macrobenthic biomass and production with crab density.

4.1. Benthic P/B ratios and production in perspective

The annual somatic P/B ratio estimated for whole Porsangerfjord (1.02 y^{-1}) exceeds the values reported by Nilsen et al. (2006) and Ramsvatn (2013) for the north Norwegian Ullsfjord and Sørfjord (Table 3), mainly because of the greater contribution of large, long-

Table 3
Literature values for macrobenthic biomass (B), production (P) and P/B ratios from temperate and high latitude habitats. Data are reported as means ± S.D. if available. For a comparison of values in a global context see Cusson and Bourget (2005) and Burd et al. (2012).

Area	Latitude	Depth (m)	B (g ww m^{-2})	P (kJ m^{-2} y^{-1})	P/B y^{-1}	Mesh size (mm)	Reference
Porsanger fjord, northern Norway	70°N–71°N	40–285	28 (±32)–191 (±132)	104 (±49)–439 (±187)	0.81–1.29	1	This study
Svalbard bank, Barents Sea	75°N–76°N	40–150	80–275	50–197[a]	–	0.5	Kędra et al., 2013
Tromsøflaket, Barents Sea	71°N	90–450	5 (±3)–22 (±17)	8 (±4)–35 (±17)	0.67–0.92[b]	1	Buhl-Mortensen et al., 2012
Barents Sea	68°N–78°N	ca. 50–450	59.5	–	0.3	–	Denisenko and Titov, 2003
Ullsfjord, northern Norway	69°N–70°N	<270	115.6	130[a]	0.49[c]	1	Ramsvatn, 2013
Sørfjord, northern Norway	69°N	18–128	307 (±595)	185	0.42	1	Nilsen et al., 2006
UK shelf	49.5°N–59°N	14–138	61 (±11)	103.3 (±23.3)	1.4 (±0.1)	1	Bolam et al., 2010
Strait of Georgia, coastal Canada	48°N–51°N	0–678	10–2530 kJ m^{-2}	1.7–820	0.23–2.08[d]	1	Burd et al., 2012
Livingston Island, Antarctica	62°S	32–421	520–2130	502.7[a]	0.57–0.08	1	Saiz-Salinas and Ramos, 1999
Weddel, Lazarev Sea	68°S–78°S	100–300	1226 kJ m^{-2a}	219[a]	0.18	0.5	Brey and Gerdes, 1998

[a] Converted from Salonen et al., 1976.
[b] Pers. communication J. Dannheim, 2014.
[c] Calculated from biomass and production values.
[d] Calculated from production and biomass values.

lived bivalves (with low P/B values) to biomass and production in these fjords. Our results were considerably higher than previous estimates for the Barents Sea (0.3 y^{-1}, Denisenko and Titov, 2003) and the Antarctic (Brey and Gerdes, 1998, Saiz-Salinas and Ramos, 1999) (Table 3). Because higher P/B ratios in Porsangerfjord were often accompanied by a low biomass, they did not tend to result in high production, despite the fact that production was derived from P/B ∗ B. The production in inner Porsangerfjord (439 kJ m^{-2} y^{-1}) was mostly higher than the values reported previously for similar latitudes (Table 3). By contrast, the production in the middle (131 kJ m^{-2} y^{-1}) and outer Porsangerfjord (104 kJ m^{-2} y^{-1}) were below the values reported for Sørfjord (Nilsen et al., 2006), but comparable to the UK shelf (Bolam et al., 2010) and the Svalbard bank in the Barents Sea (Kędra et al., 2013) (Table 3). The estimates obtained from a deeper offshore bank (Tromsøflaket) in north Norway (Table 3, Buhl-Mortensen et al., 2012) were considerably lower than those reported from north Norwegian fjords (including this study), which may indicate a trend toward higher macrobenthic biomass and production in fjords and bays than offshore locations (see also Carroll et al., 2008).

4.2. Evaluation of estimates

In our study, macrofauna was sampled in June and the estimates of biotic variables did not reflect seasonal variations. However, since the mean turnover time was estimated to be approximately 0.7 to 1.2 years, the macrofaunal biomass would have varied moderately during the time period considered (1 year). The community P/B may vary due to seasonal changes in environmental factors and the relative contribution of juveniles (with small body size and higher P/B ratios). Time of sampling was before the settling of juveniles for most macrofaunal organisms. We did observe some juveniles in our samples, but would expect variation in the juvenile fraction to be largest in a lower size fraction (<1 mm), not sampled in this study. Consequently, estimates given here are probably not subject to large seasonal changes because of small juveniles. We accounted for seasonal differences in temperatures by using annual average temperatures as an input to the model. According to data from Mankettikkara (2013), inter-annual variation in temperatures in Porsangerfjord are highest in summer, but seem to fall within the range of <3 °C at 100 m. Hence, we believe inter-annual variation in bottom temperatures is less important than the spatial variation in environmental conditions controlling average benthic productivity in our study area.

The chosen mesh size (1 mm) on the other hand may underestimate juveniles (temporary meiofauna) and other small taxa in our samples. While Cartes et al. (2002) did not find sieve mesh size important in community P/B estimations, it is likely that juveniles contribute to production especially in spring and summer. Cusson and Bourget (2005) compared mesh sizes from a variety of studies and found a weak effect on the P/B ratio (comparing <0.5 and > = 0.5 mm), except on muddy substrate, where it explained a small part (2%) of the variance. Burd et al. (2012) noted that small organisms (<1 mm) were especially important in shallow/sandy habitats and P/B ratios were higher in those habitats, where small fauna contributed most to biomass values. Community estimates of production given in this study would be affected in case smaller fauna contributed not only with higher P/B ratios but also to biomass. Piepenburg et al. (1995) found meiofaunal biomass to be 25 to 600 times lower than macrobenthic endo- and megafaunal biomass in the Barents Sea, while meiofaunal respiration was similar or slightly lower, indicating high consumption and high metabolism of these size classes. Unfortunately, production estimates of small benthic size fractions are still lacking for Arctic and fjord habitats. The comparison of studies on macrobenthic production remains therefore somewhat challenging. Where feasible, a mesh size of 0.5 mm may however better capture contribution of juveniles and small taxa.

4.3. Spatial variability and environmental gradients

The observed benthic production patterns were driven mainly by spatial variability in biomass. The finding that benthic biomass (B) was an important factor in determining benthic production (P) is consistent with other studies (Tumbiolo and Downing, 1994, Cusson and Bourget, 2005), but it is obviously also due to the calculation of P based on P/B ∗ B. The macrobenthic biomass in the inner subarea of Porsangerfjord was significantly higher than that in the middle and outer fjord. The mean biomass estimates from the inner Porsangerfjord (191 g ww m^{-2}) are within the range of values reported for the north Norwegian Ullsfjord and Sørfjord (Table 3; Ramsvatn, 2013 and Nilsen et al., 2006), whereas the values for the middle and outer Porsangerfjord are significantly below that range. Benthic biomass may vary because of food availability (Carroll and Ambrose, 2012). The Southeast Barents Sea and the Svalbard bank have high benthic standing stocks supported by high primary productivity in the overlying water column and/or enhanced vertical particle flux (Grebmeier and Barry, 1991, Cochrane et al., 2012, Kędra et al., 2013). Blicher et al. (2009) suggested that primary production is highly important for regulating the benthic carbon demand, and Burd et al. (2012) report organic flux as the main predictor for macrobenthic production in the Strait of Georgia, West Canada. A previous study of the phytoplankton biomass in Porsangerfjord did not determine higher values for the inner part of the fjord (Eilertsen and Frantzen, 2007), but the low temperatures in this area likely reduce bacterial degradation (see Pomeroy and Wiebe, 2001), possibly fueling the benthic food web. The benthic community in Austerbotn and Roddenessjøen consisted mostly of detritivores, suggesting detritus to be a major food source. Intertidal kelp associations are common in the

inner Porsangerfjord (Sivertsen and Bjørge, 2015) and provide detritus to the area. Low competition with bacteria for this resource (Van Nugteren et al., 2009) may therefore enhance macrobenthic production in this area. Variation in the hydrographic conditions could explain why biomass and production were higher at the eastern stations than at the western stations in the middle and outer fjord. During summer, the prevailing winds cause upwelling at the eastern side of the fjord (Svendsen, 1991, Myksvoll et al., 2012), which may increase the food supply available to the benthos in this area. Another cause has to be taken into consideration regarding these differences though. When looking at the early phase of invasion and current distribution of the red king crab (Figs. S5 and S7), one can see that crabs tended to accumulate at the western side of the fjord, where they possibly impacted macrobenthic fauna by foraging.

The most important descriptors of P/B ratios were the mean body mass, and with that, associated taxonomic identity. Body mass was the main predictor variable for P/B, thus the variation in P/B was (inversely) related to the variation in mean body mass at the sampling stations. Consequently, the inner fjord had lower P/B ratios than the middle and outer fjord, where small-sized species or individuals dominated. Environmental variables influence community composition and community P/B is largely a function of the intrinsic characteristics of its members, rather than a direct result of environmental conditions (Cusson and Bourget, 2005). That the lowest P/B values were found in the inner, cold area of Porsangerfjord, supports the general assumption that temperature affects growth and metabolic activity (e.g., Cusson and Bourget, 2005 and the references therein, Tagliapietra et al., 2007), which may be reflected at the population level as well as the community level (Brey and Gerdes, 1998). Globally, a general positive relationship between temperature and P/B can be expected, which has also been established for polar benthos (Brey and Clarke, 1993). It is questionable however, whether temperature differences in Porsangerfjord cause differences in P/B. Since lower P/B ratios were related to community composition and higher average body mass, the elevated standing stock biomass in the inner fjord is likely due to a combination of a higher contribution of large and long-lived species (e.g., large bivalves and asteroids) as well as low mortality at cold temperatures (Brey and Clarke, 1993, Tumbiolo and Downing, 1994). The salinity measurements in Porsangerfjord were strongly correlated with temperature (see Figs. 4 and 5 and Table 2), although, the differences in salinity were small and we considered them to have little direct impact on P/B and production, which agrees with the findings of Cusson and Bourget (2005).

In our study, the community P/B ratios increased with depth, although the ANN model predicted decreasing P/B ratios with increasing depths when the other variables remained constant. This was caused by a higher proportion of Polychaeta at deeper stations, decreasing mean body mass and thus increasing P/B ratios. Despite this, the overall biomass and production decreased with depth in Porsangerfjord, which has been demonstrated for other benthic communities and could be expected since food availability usually decreases with depth (Tumbiolo and Downing, 1994, Rosenberg, 1995, Brey and Gerdes, 1998).

4.4. Community structure

Our results indicated that the macrobenthic production in Porsangerfjord was associated with taxonomic identity because the three communities identified reflected the major trends in the P/B ratios and production. The multivariate community analysis (CA) showed that the inner eastern basins were distinctly different from middle and outer stations. Environmental habitat conditions typically structure benthic communities (see e.g., Gray and Elliott, 2009), which was also evident in Porsangerfjord where depth, temperature and salinity all significantly related to multivariate community structure. Observed production patterns were therefore more likely a result of community type at prevailing abiotic conditions, rather than being directly regulated by those factors.

The major phyla contributed little to the spatial variation in observed production because production was dominated mostly by Polychaeta. In the inner eastern basins (Austerbotn and Roddenessjøen), the detritivore polychaete Spiochaetopterus typicus accounted for most of the production. This species is common in deeper offshore areas of the Barents Sea (Carroll et al., 2008), where it is related to sediments with a high organic carbon content (Denisenko et al., 2003). The second community was dominated by small detritivore Maldanidae, especially common at deeper stations in Porsangerfjord. Previously, Maldanidae have also been reported as highly abundant in the shallow inner western area of Porsangerfjord (Holte, 2001), which was not part of this study. The stations from the inner western area clustered with outer stations but they had higher production and lower P/B values than outer stations because a few larger bivalves (e.g., C.ciliatum) contributed little in terms of abundance. Larger bivalves and echinoderms were limited mostly to the inner part of the fjord. The high dominance of Polychaeta and low abundance of Echinodermata have been discussed as a common characteristic of soft sediments from north Norwegian sill fjords (Larsen, 1997, Oug, 2000, Holte et al., 2004), but to the best of our knowledge these are not typical features of open fjords. Mobile and patchy epifauna can contribute significantly to macrofaunal production (Cartes et al., 2002), but were underestimated in this study due to the chosen sampling gear. Surveys in Porsangerfjord using an epibenthic sledge (5 mm mesh size) between 2007 and 2010 detected a mean biomass of ca 14 g ww m^{-2} and a production of ca 5 kJ m^{-2} y^{-1} (L. Jørgensen, unpublished data), which is comparably low to our estimates based on grabs. Echinoids (Strongylocentrotus droebachiensis) and ophiurids made up a major proportion of the biomass in shallow waters above 50 m, whereas shrimps were dominant epifaunal producers below these depths. The scallop Chlamys islandica has been observed locally in high densities at shallow depths, but contributed only little to mean production of epifauna.

The observed spatial patterns in biomass and production were not reflected well by the total density of macrofauna, which agrees with the findings of Bolam et al. (2010). In general, the abundances were within the range recorded in other north Norwegian fjords (Larsen, 1997, Oug, 2000, Holte et al., 2004), but they were higher compared with Sørfjord (Nilsen et al., 2006).

4.5. Predation by the red king crab

Our results demonstrate that benthic production does not follow a single gradient, but that a combination of biotic and abiotic variables are responsible for the observed variability.

Numerous studies have shown that the impact of predation can also shape benthic communities and may affect biomass as well as production processes (Virnstein, 1977; Wilson, 1990, Grosholz et al., 2000). The invasive red king crab is a major benthic predator in the outer and middle Porsangerfjord and it has been shown to affect prey density, biomass and community composition in other invaded areas (Pavlova, 2008, Britayev et al., 2010, Falk-Petersen et al., 2011, Oug et al., 2011). Large epifaunal taxa are often believed to be at higher risk of predation by adult crabs (Jørgensen and Primicerio, 2007, Falk-Petersen et al., 2011). The comparably low biomass of macrofauna in the middle area, coupled with the dominance of small individuals and the absence of larger bivalves and echinoderms, may be a first indication of an impact of predation (see Oug et al., 2011) in Porsangerfjord. In other ecosystems, long-term bottom trawling causes similar shifts in size structure, thereby leading benthic systems toward high turnover and lower biomass systems (Jennings et al., 2001), which also modifies the energy flow (Dannheim et al., 2014). A community dominated by taxa that exhibit high renewal rates may be more resilient to perturbations (Tumbiolo and Downing, 1994) and the increased production of opportunistic species or young individuals is seen in such systems (Dolbeth et al., 2011). However, community production depends greatly on the total biomass, thus an increase in the community P/B does not

necessarily compensate for the loss in community biomass (Jennings et al., 2001, Reiss et al., 2009). The significant correlation between red king crab density and benthic biomass, production and P/B leads us to conclude that a predation impact in Porsangerfjord is likely. Obtaining precise information on king crab distribution in light of aggregative behavior and high mobility was a major challenge, but telemetry studies on king crabs in Porsangerfjord have shown that movements were restricted to local areas (pers. comm. Jan. Sundet, 2015). This leads us to believe that our kriged estimates for the fjord reflect the distribution of crabs well on a large spatial scale. Few crabs were predicted in the outer fjord, and while this presents a reliable reproduction of the original catches, crabs must have passed this area making their way into the fjord, not captured by the first official survey in 2006.

Based on our results, we assume that the lower renewal rates make the macrofauna in the inner fjord more susceptible to predation and changes in the community structure are likely to result in different production regimes. Time series are needed in order to estimate and quantify predation effects on the benthic community in Porsangerfjord, and we believe this study can serve as a valuable baseline for the inner, just recently invaded area.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.seares.2015.09.003.

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Supplementary material

Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab.

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J Sea Res 106:1-13

S 1 Video

Video of bottom survey in Porsangerfjord, 2012. By courtesy of Norges geologiske undersøkelse.
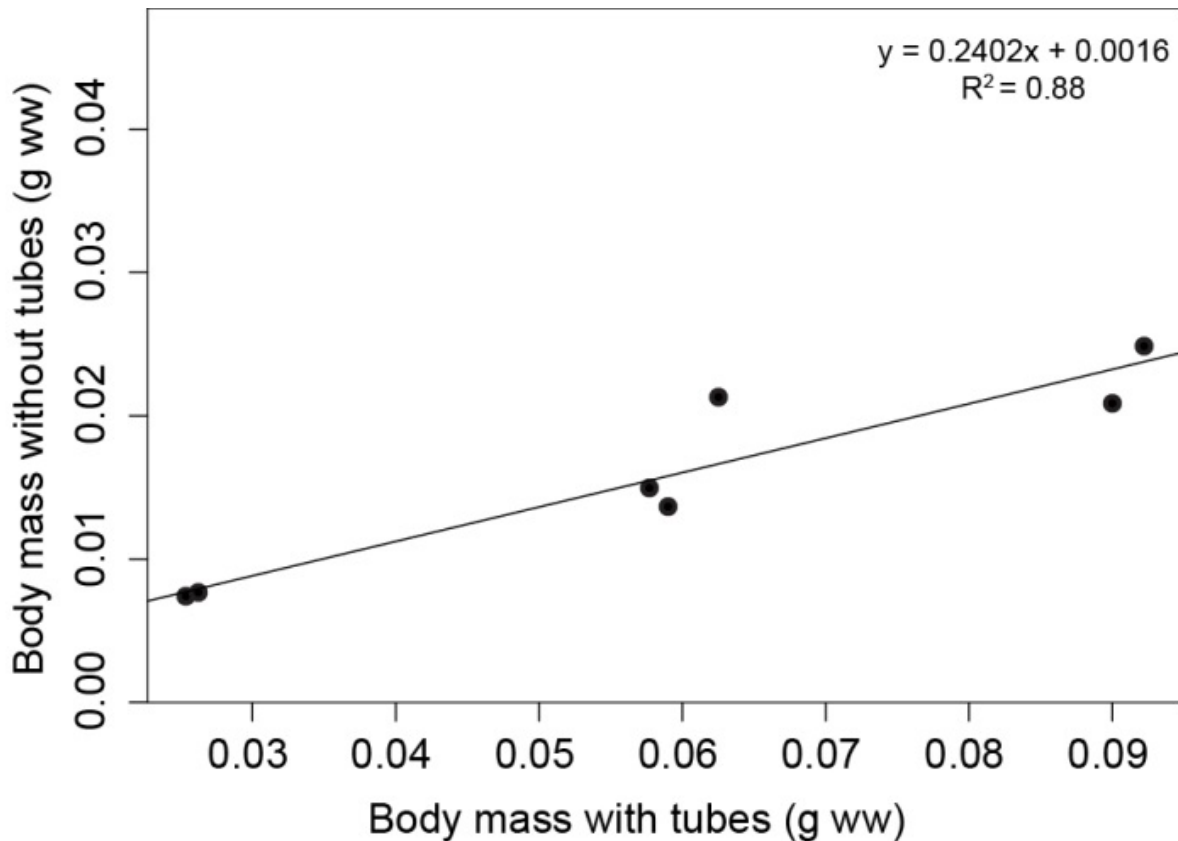
S 2 Tube conversion for *Spiochaetopterus typicus*

Fig. S 2. Conversion factor for the wet weight biomass of the polychaete *Spiochaetopterus typicus*. The data represent the mean body masses obtained from bulk weighed individuals (3–10 individuals per bulk weighing, n = 7).

S 3 Kriging procedure for the prediction of relative red king crab densities

In order to estimate relative red king crab densities at benthic stations, we performed spatial prediction by kriging (package *gstat* in R, Pebesma 2004) from crab trawl and pot surveys by

the Institute of Marine Research between the years 2007 to 2010. Ordinary kriging predicts values in space using distances between sampling stations with an assumed level of spatial autocorrelation (Diggle & Ribeiro 2007). The spatial correlation decreasing with distance is modeled through a variogram. It is widely used to address terrestrial resource distributions and has also been applied in marine studies including stock estimation of king crabs (Vining & Watson 1996). Sequential Gaussian simulations were used to provide a measure of uncertainty at points in space.

Since catchability of crab trawls and pots differed, we analyzed these methods separately and compared the results. Crab trawls catches were standardized according to towing time and speed and total catches varied from 0 to 451 crabs per haul (8334 m^2 effective catch area). Baited pot catches were standardized to catch per unit effort (CPUE) by equal soak times of 24 h. Each set consisted of a 3 separate square traps. Exact catchability is unknown for pots of this type, but for relative comparison this is irrelevant. Catches per set of pots varied from 0 to 504 crabs.

Trawl and pots stations provided good coverage, except for the inner western area (see Fig. S 5). Ordinary kriging assumes stationarity in the data. However, variance in catches from the outer and inner fjord was larger compared to the middle fjord, indicating minor non-stationarity. Ordinary kriging is generally robust towards minor non-stationarity (Yost et al. 1982). We investigated the relationship between catches and bottom temperature and found no obvious relationships, indicating that a more complex procedure, such as regression kriging with such covariates, would not account for additional spatial variation.

Data were $\log_e$ +1 transformed before analysis. Distances between trawl and pot locations were computed based on UTM coordinates. An exponential variogram model was fitted to the data with distance lags of 5 km and 4 km, up to a maximum distance of 35 km and 40 km for trawls and pots respectively (Fig. S 3), using an automated fitting procedure implemented in the *gstat* package. Data were then kriged and king crab relative abundances were predicted for points on a 1 nm resolution grid for the entire fjord and specifically for each of the benthic sampling stations. The mean and variance obtained from 1000 realizations of sequential Gaussian simulations were computed and compared (Fig S 8 an S 10).
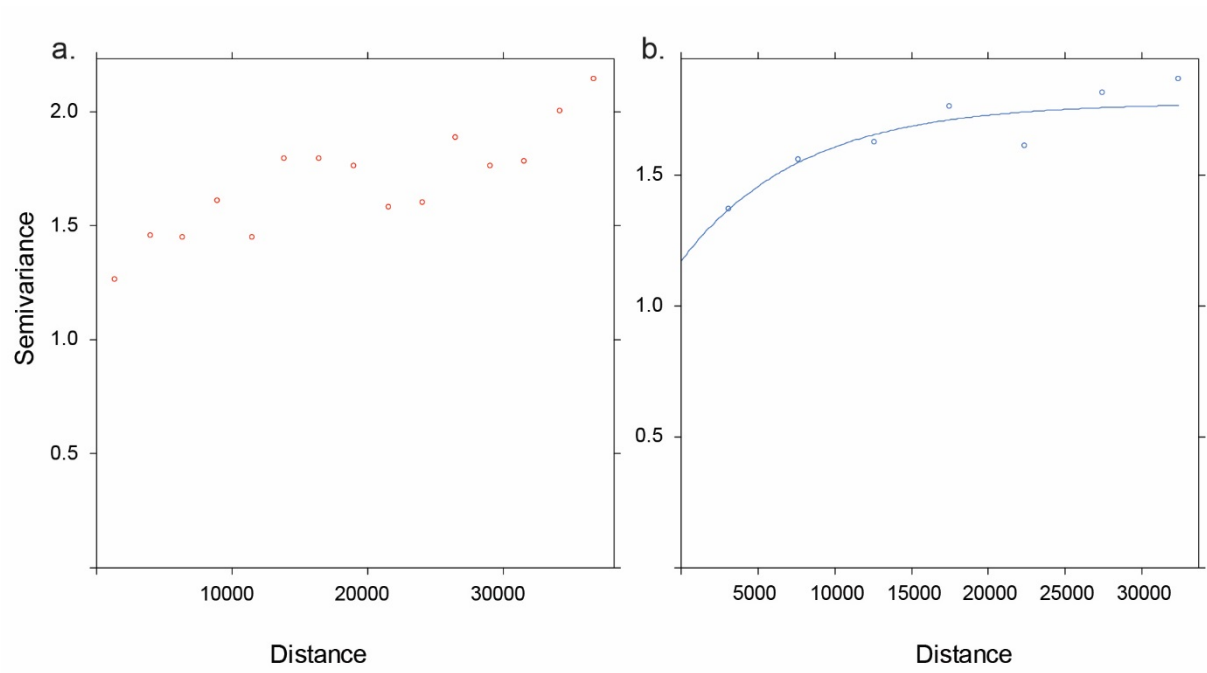
Fig. S 3 Sample variograms of red king crab catches in crab trawls. (a) Log_e+1 transformed original data (b) Fitted variogram used in kriging and sequential simulations.
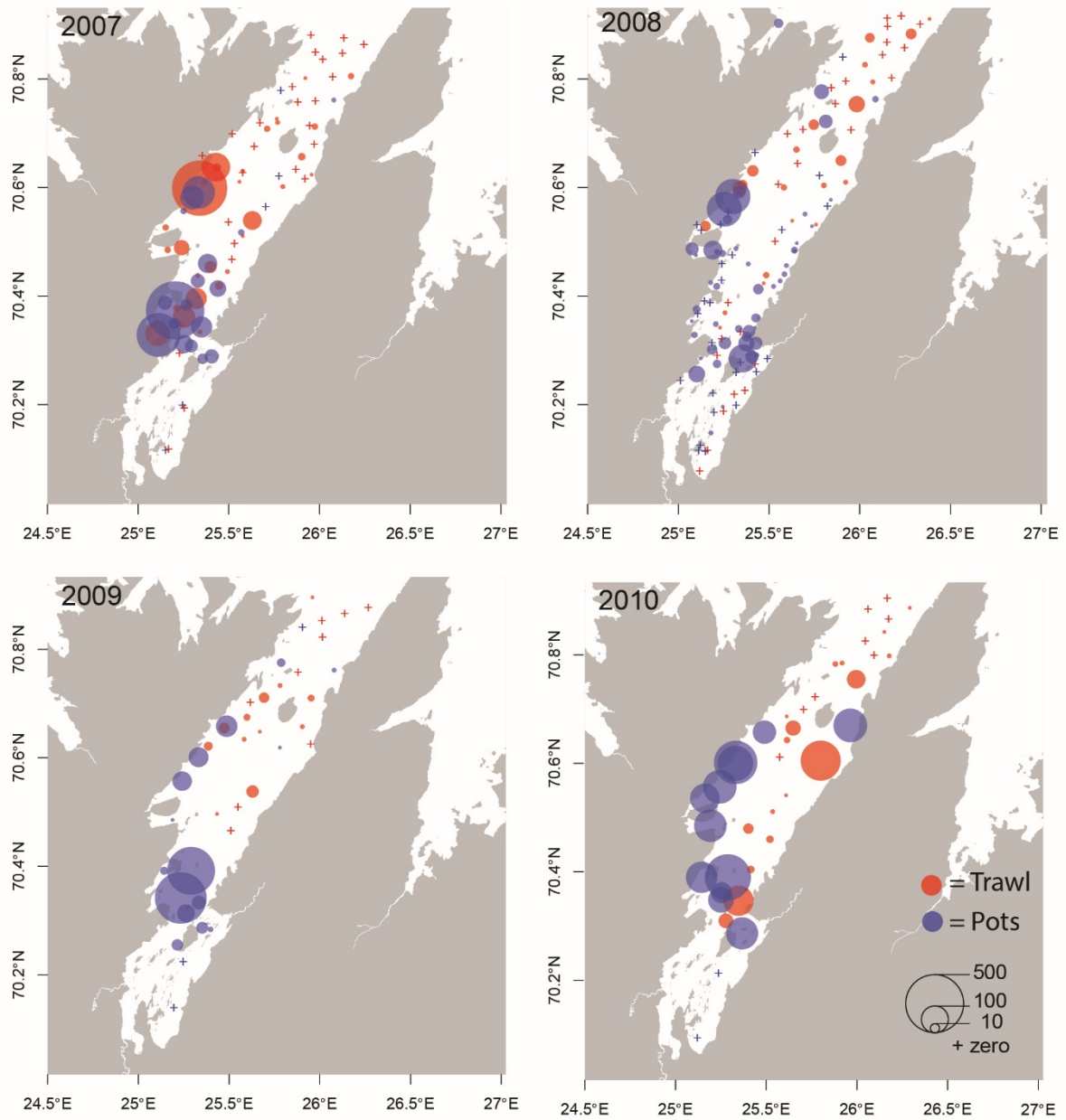
S 4 Red king crab survey data

Fig. S 4 Total numbers of red king crabs and input to kriging (sequential simulations) in survey catches between the years 2007 and 2010. Data were provided by the Institute of Marine research

S 5 Test for spatial autocorrealtion

Table S 5

Mantel coefficients (*r*) and significance levels (*p*) from the ranked Mantel test (R package *ecodist*). Significance was assessed by permutation tests (n = 10000).

V.dists ~ Station.dists	Mantel r	*p*
Depth (m)	0.3249	0.0001
Temperature (ºC)	0.6456	0.0001
Salinity (‰)	0.7849	0.0001
Biomass (g ww m^{-2})	0.1977	0.0004
Production (kJ m^{-2} y^{-1})	0.2946	0.0001
Abundance (ind. m^{-2})	-0.0469	0.8973
P/B y^{-1}	0.2648	0.0001
Mean bodymass (mg ww)	0.6456	0.0001
Red King crab density[1]	0.0773	0.0439

[1] Estimated from kriging interpolation (see S 5)
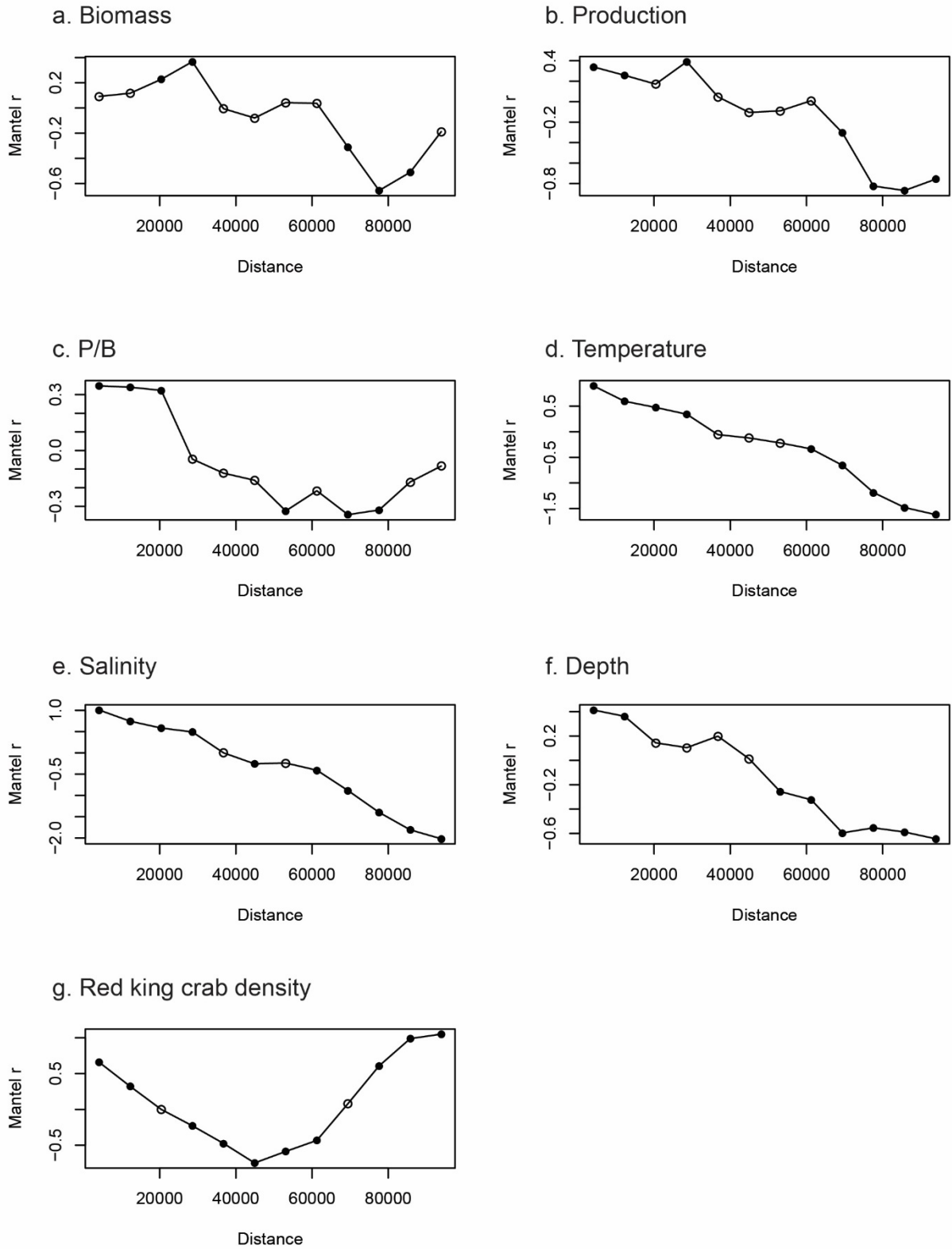
Fig. S 5 Simple piecewise correlograms (Goslee & Urban 2007) from biological variables showing spatial patterns in macrobenthic estimates (a-c), abiotic environmental variables (d-f) and predicted red king crab densities at grab stations (g). Distances are given in meters and

appropriate distance classes are determined by Sturge's rule (see Goslee & Urban 2007). Filled circles denote significant Mantel r (using permutation tests).
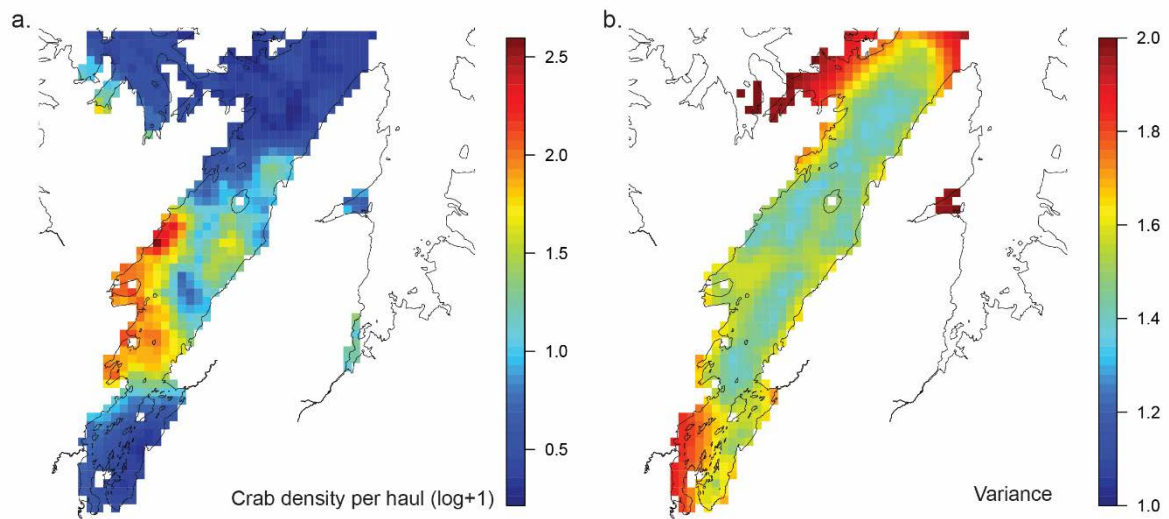
S 6 - 9 Predicted distribution of red king crabs in Porsangerfjord

Fig. S 6 Spatial maps of kriged red king crab abundances (a) and their variance (b) from crab trawl data between 2007 and 2010. Data were $\log_e+1$ transformed before analysis.
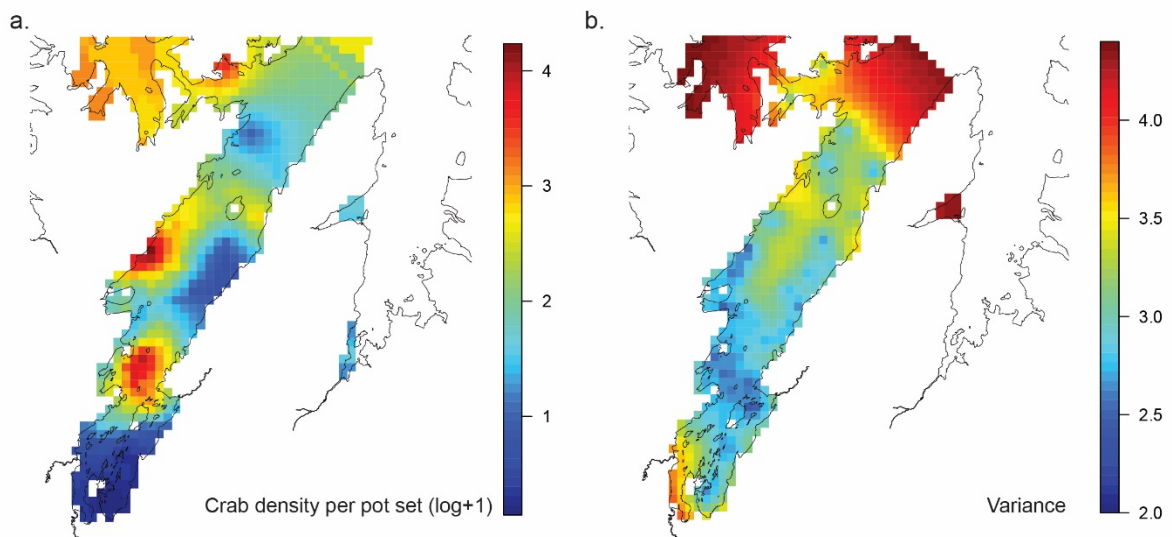

Fig. S 7 Spatial map of kriged red king crab abundance (a) and their variance (b) from pot data between the years 2007 and 2010. Data were $\log_e+1$ transformed before analysis.
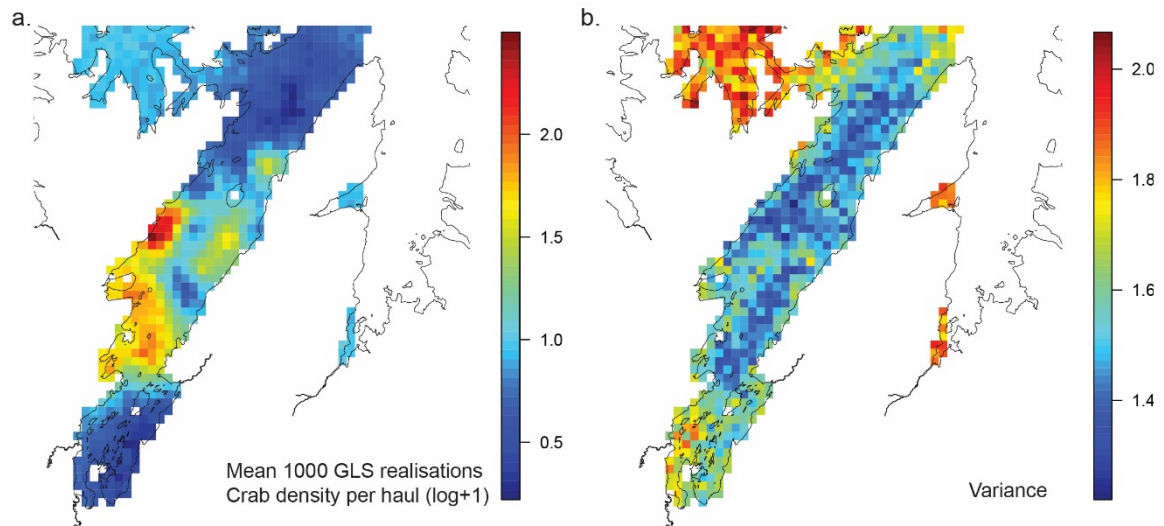
Fig. S 8 Mean red king crab abundances from crab trawls (a) and their variance (b) from 1000 sequential Gaussian realizations. Data were $\log_e+1$ transformed before analysis.
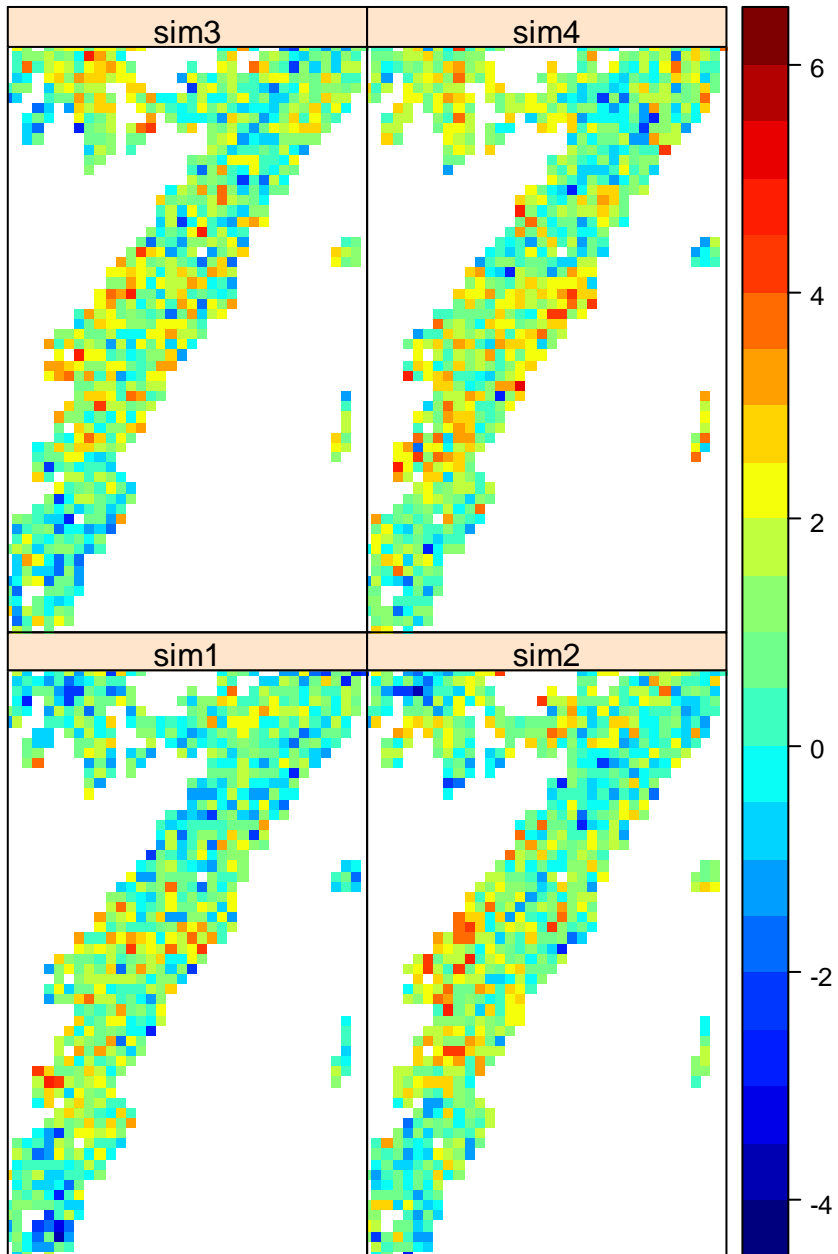
Fig. S 9 Maps of red king crab abundances from 4 of the 1000 sequential Gaussian realizations. Data were $\log_e+1$ transformed before analysis.
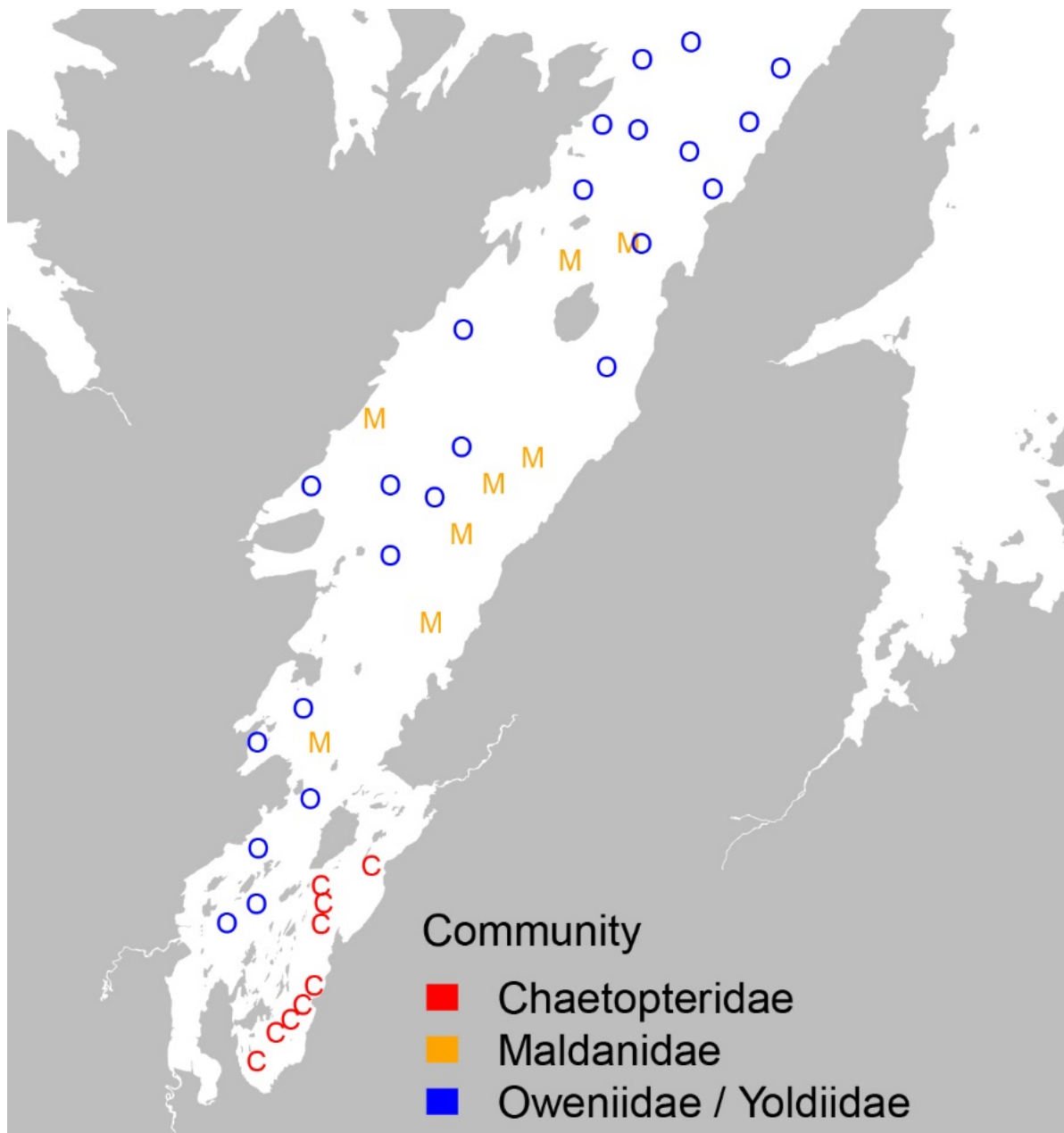
S 10 Distribution of macrobenthic communities

Fig S 10. Distribution of communities identified by the correspondence analysis (CA) in Fig. 5. Letters indicate major families responsible for the separation in the CA biplot. C = Chaetopteridae, M = Maldanidae, O = Oweniidae and Yoldiidae.

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