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Structural and functional changes of soft-bottom ecosystems in northern fjords invaded by the red king crab (*Paralithodes camtschaticus*)

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ABSTRACT

The red king crab invaded Norwegian coastal waters in the early 1990s after having been introduced from the northern Pacific to the Russian Barents Sea coast. The crab stock increased rapidly in NE northern Norway in the latter half of the 1990s, and since 2002 there has been a commercial fishery in the eastern invaded areas. The crab is an active predator on benthic fauna especially feeding in deep soft-bottom environments. The present study is a follow-up of previous studies (2007–09) to assess the effects of the king crab predation on soft bottom species composition, ecological functioning and sediment quality. Macroinfauna (>1 mm) was investigated in three fjord areas in the Varanger region with low, moderate and very high crab abundances, respectively. Compared with data from 1994, most benthic species were markedly reduced in abundance, in particular non-moving burrowing and tube-dwelling polychaetes, bivalves and echinoderms. However, a few species appeared to recover from 2007–09 to 2012. Changes in ecological functioning were assessed using 'biological traits analysis (BTA)'. Following the crab invasion there was a relative reduction of suspension and surface deposit feeding species, an increase in mobile and predatory organisms and an increase in those with planktotrophic larval development. From low to high crab abundances functioning changed from tube-building, deep deposit feeding and fairly large size to free-living, shallow burrowing and rather small size. With regard to sediment reworking, downward and upward conveyors were reduced whereas surficial modifiers increased. The changes imply that sediment biomixing and bioirrigation were reduced leading to a degraded sedimentary environment. It is suggested that establishing relationships between ecosystem functioning and crab abundances may form the basis for estimating ecological costs of the crab invasion. Such knowledge is important for managing the crab in the Barents Sea area being both a non-indigenous species affecting native ecosystems as well as a valuable resource for commercial fishery.

1. Introduction

The red king crab (*Paralithodes camtschaticus*) is a non-indigenous species in the Barents Sea area. It was introduced from the northern Pacific to the Russian Murman coast by Russian scientists during the 1960s and 1970s, with the intention of becoming a resource for commercial fishery (Orlov and Ivanov, 1978; Sundet, 2014). Over the subsequent decades the crab has spread westwards into Norwegian waters and to the north-east into the Barents Sea (Falk-Petersen et al., 2011; Sundet, 2014; Christiansen et al., 2015). The crab became established in the Varangerfjord area close to the Russian border in the 1990s. During the late 1990s, a rapid increase took place in adult crab abundance from an estimated 0.5 million individuals (1998) to >2 million individuals (2001). The crab is now firmly established in several fjords in northern Norway (Hjelset et al., 2009; Fuhrmann et al., 2015). A commercial fishery for the crab commenced in Norwegian coastal waters in 2002. Management of the red king crab in Norwegian waters currently has two main objectives; to secure an economically viable fishery within a defined geographical area in Eastern Finnmark (Quota Regulated Area, QRA), and to limit further spread of the crab outside this area through a free fishery legislation and subsidising an eradication fishery (Sundet and Hoel, 2016). Annual scientific cruises are carried out to monitor the development of the crab stock both inside and outside the QRA, which forms the basis for advice on fishery quota to the management authorities. The Norwegian management policy is in dispute (see Falk-Petersen and Armstrong, 2013).

The red king crab is an active predator feeding on a wide range of benthic organisms (Takeuchi, 1967; Feder and Paul, 1980; Fuhrmann et al., 2017). Generally, large benthic decapod crustaceans have the potential to exert significant impacts on the benthic

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ecosystems, both as predators at various trophic levels, and by physically structuring the seabed due to their feeding activities (Boudreau and Worm, 2012). Initial studies of the king crab in the Varangerfjord demonstrated that bivalves, polychaetes, gastropods and echinoderms comprised the most frequently occurring prey items found in the stomachs of the crab (Sundet et al., 2000) At the same time, native populations of large prey species were reduced (Haugan, 2004). Russian studies from the Kola Peninsula and the Barents Sea have showed that the crab preys heavily on molluscs, echinoderms and polychaetes in these areas (Anisimova et al., 2005; Britayev et al., 2010; Falk-Petersen et al., 2011). Several impacts on benthic species assemblages in the Barents Sea area have been reported, notably loss of large specimens of prey species and changes in community composition (Falk-Petersen et al., 2011). Fuhrmann et al. (2015) reported in a recent study from the Porsangerfjord fjord that both benthic biomass and production were reduced in crab-invaded areas. In the Varanger area foraging mainly seems to take place on soft-bottom substrata (Sundet and Hjelset, 2009). Adult specimens mostly inhabit deep soft-bottom areas (100–400 m), but in late autumn and spring mature specimens migrate into more shallow waters (<50 m) for moulting and mating (Sundet and Hjelset, 2009).

The present study deals with effects on structure and function of soft bottom fauna in the Varanger area, located within the quota regulated area (QRA) of Norwegian management of the red king crab. It is a follow-up of previous studies of sediment infauna, epifauna and in situ sediment profile imagery (SPI) carried out in 2007–09 to assess the effects of the king crab on species composition and sediment quality (Oug et al., 2011). In the previous studies, changes in infaunal species assemblages were evaluated using quantitative data from samples collected in 1994 as a baseline. The crab stock at this time was low hence allowing a comparison of benthic fauna before and after the area became inhabited by dense crab populations. The study demonstrated that most dominant species had strongly reduced abundances in 2007–09 compared with 1994. The SPI indicated that sediment quality was degraded at several localities. It was suggested that organisms performing key ecological functions such as bio-irrigation and sediment reworking had been removed by the crab predation. The data from 1994 originally were obtained as part of a broad-based environmental assessment of the deposition of mine tailings in a localized part of the area (Skei et al., 1995). New data for infauna are presented here to investigate further development of the species assemblages in the crab-invaded areas.

Falk-Petersen et al. (2011) pointed out that despite clear documentation of effects of the king crab from impact studies, the ecosystem effects in the invaded areas are largely unknown. In the present study, functional changes are described and analysed along with the structural changes in the species assemblages. The study aims to describe changes in functional features following the species reductions and assessing what the possible effects on ecological processes in soft bottom ecosystems are. Including functional aspects in the study of ecosystems has come more into focus in recent years in order to provide a better basis for management of marine systems (Frid et al., 2008). The analyses were performed using the technique of 'biological traits analysis' (BTA), in which structural data for species assemblages are combined with functional features of each species (Bremner et al., 2003, 2006; Frid et al., 2008). In addition, the analyses include an assessment of the sediment reworking potential of the species assemblages, i.e. how the species may shape their environment through their activity. Sediment reworking is described based on a classification of soft bottom species with regard to bioturbation potential presented by Queirós et al. (2013). Data for bottom fauna from several other fjords in northern Norway without king crab were used as references for assessing the pattern and direction of changes in the Varangerfjord area.

2. Material and methods

2.1. Study area and location of sampling stations

The Varanger area constitutes the easternmost part of Norway adjacent to the Russian border and facing the Barents Sea (Fig. 1). The main fjord (Varangerfjord) has depths of 300–400 m at the mouth. At the southern side of the fjord there are several small bays and relatively narrow side-inlets, with depths to 100–300 m. The majority of the study area comprises silty to sandy sediments. Bottom water temperatures are between 4 and 6 °C and the salinity approximately 34 psu. The oxygen conditions are generally good. This geographical part of Norway has a sparse human population and industrial activity is mostly low, but in the inner part of Bøkfjord, fine-grained tailings from an iron mining industry were deposited until 1997 and later from 2008 to 2015. During environmental studies, no biological effects from tailings have been recorded in the outer fjord outside of the deposition area (Skei et al., 1995). The king crab is found throughout the area, but it seems that the bays and inlets at the southern side of Varangerfjord may be preferred areas. These small fjords and inlets were the major fishing areas at the onset of the commercial king crab fishery in Norway, and are still important for fishery in the Varanger area. Traps are used in commercial crab fishing. There is no fishing activity with bottom trawls in the fjords.

The sampling stations were located in the Varangerfjord (stn 21), the side-inlet Bøkfjord (stns 14–20) and Kobbholmfjord (stn 01) (Fig. 1). The stations in Varangerfjord and Bøkfjord were established in 1994 as part of the mine tailings environmental study (Skei et al., 1995), but were all found to be uninfluenced by the tailings. At this time the king crab had reached the area, but the population was low and the stations are therefore considered to represent the faunal status before the king crab invasion. The station in Kobbholmfjord was established in 2009. Kobbholmfjord is a small semi-enclosed inlet close to the Russian border. High densities of king crabs have been recorded every year since crab surveys commenced in 1993.

Data from fjords used for reference were taken from Bergsfjord, Balsfjord, Kaldfjord, Olderfjord, Byluft and inner Porsangerfjord (Roddenes) (Fig. 1). The data from Balsfjord are from a monitoring station (Oug, 2000) and Porsangerfjord from a study conducted to obtain king crab pre-invasion data (Oug and Fuhrmann, 2013). The data from Bergsfjord and Kaldfjord are from environmental assessment studies (Berge et al., 1994; Witte, 1991), where stations found to be unaffected by human influence were selected. Bergsfjord, in particular, was subjected to discharges of mining deposits, and is in this context comparable to the Bøkfjord stations. The data from Olderfjord and Byluft are from a study of faunal diversity in fjords unaffected by human activities (Holte et al., 2004).

2.2. Sampling and sample processing

Samples were collected in June 2012 using a 0.1 m^2 van Veen grab. Four replicate samples were taken at stn 21 in Varangerfjord, and two samples at the other stations. In the previous studies, four samples were taken at each station using a 0.1 m^2 day grab (1994) or 0.1 m^2 van Veen grab (2007, 2009). The samples were sieved through 5 and 1 mm mesh screens and fixed in a buffered 4–6% formaldehyde-seawater solution. Subsamples of surface sediment (0–1 cm) for analysis of silt-clay fraction (% < 0.063 mm) and organic content (total organic carbon – TOC) were taken at each station.

All specimens were identified to the lowest possible taxonomic unit, generally to species. Community structure was described using the Shannon-Wiener H′ diversity index (log 2 base). Faunal composition was assessed using correspondence analysis (CA). Before analysis, the species lists from 1994 and later samplings were compared and harmonized by amalgamating synonyms and taxa identified to different levels.

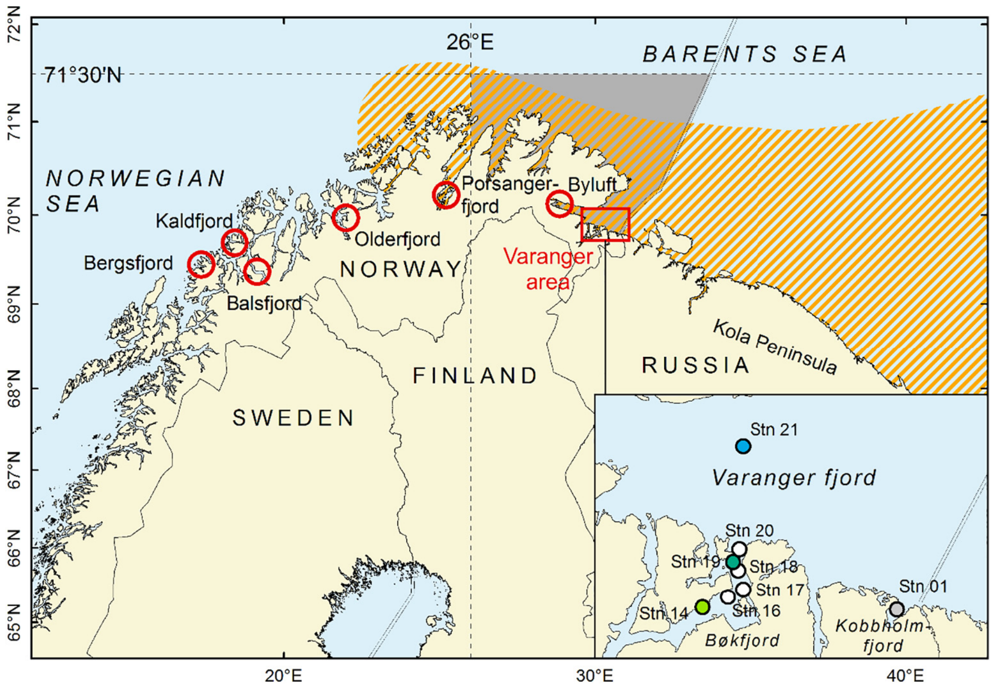

Fig. 1. Study area (rectangle) and location of fjords with data of soft bottom fauna used for reference (red circles) in northern Norway. Inset shows location of sampling stations in the Varanger area, colour-coded stations were revisited in 2007–2008 and 2012. Approximate present distribution of red king crab in northern Norway and the Barents Sea is indicated by hatching. Double shaded area indicates the quota regulated area (QRA).

Data were normalised by log-transformation ($\log_{10}(n + 1)$) prior to analysis.

2.3. King crab abundance

Red king crabs were sampled at the annual cruises for monitoring of the crab stock using an enlarged version of an Agassiz trawl (6 m wide) and by traps (Stiansen et al., 2008; Hjelset et al., 2009). A number of regular sampling stations were established in the quota regulated area (QRA) in 2001, and since visited every year with minor modifications. Based on monitoring data for sex, size and fecundity, annual quotas have been set for the commercial crab fishery within the QRA (Hjelset et al., 2009; Sundet and Hoel, 2016).

The number of trawl samples in each of the fjords here studied varied from one per year in Kobbholmfjord to about 12 in Varangerfjord. The samples from Varangerfjord were taken outside the mouth of Bøkfjord in the vicinity of faunal station 21. Crab abundances were estimated as catch per unit effort (CPUE) from the trawl data for each of the fjord areas. CPUE was calculated as number of crabs captured per 30 min trawling.

2.4. Traits analyses

Biological traits analysis (BTA) was carried out using eight traits representing features such as life habit, degree of attachment, mobility, size, body form, sediment dwelling depth, feeding mode, and larvae type. Each trait is divided in a number of categories that expresses different states of the trait (Table 1). Each species is scored for the traits according to the 'fuzzy coding' procedure (Chevenet et al., 1994). This procedure implies that a species may be given values in more than one category for a trait. A four-stage scale was used: 0 = no affinity, 1 = low importance, 2 = moderately high importance, 3 = dominant. In cases where more than one category was relevant, the values 1 and 2 were used according to the relative importance of each. Traits information for the species was extracted from the traits database at the Norwegian Institute for Water Research (NIVA) that presently comprises data for >500 species. Further information on the traits database and the principles for character scoring is given by Oug et al. (2012).

In addition to the traits, a measure of sediment reworking (bioturbation in the wide sense, see Kristensen et al., 2012) was entered in the analyses. This measure includes four categories for the present fauna: surficial modifiers, upward conveyors, downward conveyors and biodiffusors (Table 1). The categories were defined by Solan (2000) in the following way; surficial modifiers being species whose activities are restricted to the surficial layer (0–2 cm) of the sediment profile, upward conveyors being head-down feeders that actively transport sediment to the sediment surface, downward conveyers being species that actively bring sediment downwards from the sediment surface, and biodiffusors being species that mediate a random diffusive transport of particles over short distances in the sediment. Queirós et al. (2013) presented a classification of the most common benthic invertebrates from European coastal waters that are here used. Kristensen et al. (2012) reviewed in more detail the importance of the various categories for sediment transport, water irrigation and biogeochemical cycling in the sediments.

The analyses were carried out in a multi-step approach. First, affinity scores for trait categories within each trait were standardised to sum = 1 for each species. Then the species-by-station matrix (transposed) was multiplied with the species-by-traits matrix to obtain a station-by-traits matrix giving 'trait profiles' for the sampling stations. Trait profiles hence represent the 'abundances' of the traits at the stations and thus reflect the main functional features of the species assemblages. Species abundances were log-transformed ($\log(n + 1)$) before the calculations to balance the abundance values between abundant and rare species.

Trait profiles were subjected to principal component analysis (PCA) to examine patterns and assess associations between functional features. Sediment reworking categories were entered as passive in the analysis, i.e. correlated to the traits relationships. Data for depth and sediment parameters at the sampling stations (% silt-clay, TOC), sampling time (year) and king crab abundance were used as explanatory variables that were correlated to the traits patterns. In addition, fjord area and time period before and after the king crab invasion were

Table 1
Overview of traits used in the present study. Sediment reworking was added passively in the analyses to indicate the bioturbatory potential of the fauna.

Trait	Features/categories
Adult life habit	Sessile
	Permanent tube
	Semi-permanent tube
	Burrower
	Surface crawler
	Swimmer
Degree of attachment	None
	Temporary
	Permanent
Adult mobility (relative)	None
	Low
	Medium
	High
Sediment dwelling depth	0 cm (surface)
	0–1 cm
	1–5 cm
	5–15 cm
	>15 cm
Body form	Short cylindric
	Flattened dorsally
	Flattened laterally
	Ball-shaped
	Long, thin threadlike
	Irregular
Normal adult size	<0.5 cm
	0.5–1 cm
	1–3 cm
	3–6 cm
	6–10 cm
	>10 cm
Feeding	Suspension/filter feeder
	Surface deposit feeder
	Subsurface deposit feeder
	Deep deposit feeder
	Dissolved matter/symbionts
	Sandlicker/large detritus/scraper
	Scavenger
	Carnivore/omnivore
	Parasite/commensal
Larvae type	Planktotroph (feeding larvae)
	Lecitotroph (non-feeding larvae)
Sediment reworking	Surface living/epifauna
	Surficial modifier
	Upward conveyor
	Downward conveyor
	Biodiffusor
	Regenerator

entered as categorical variables with classes for fjords (Bøkfjord, Kobbholmfjord, Varangerfjord) and time period (before, after), respectively. All multivariate analyses were performed using Canoco 4.5 software (ter Braak and Smilauer, 2002).

3. Results

3.1. Diversity and composition of soft bottom species assemblages

The fauna in the three fjords was dominated by mostly small (polychaetes typically 0.5–5 cm in length, bivalves 0.2–0.5 cm in diameter), burrowing species. The number of species per station varied from 27 to 91, with the highest number of species recorded in 1994 (Table 2). The abundances were generally between 1500 and 5000 ind m^{-2} (Fig. 2), but in Kobbholmfjord even higher densities (6500 ind m^{-2}) were found. Polychaetes and bivalves constituted the most important groups, whereas crustaceans and echinoderms were rather poorly represented. Faunal diversity (Shannon-Wiener H′) decreased from 1994 to 2007–09, but increased slightly in 2012 (Table 2).

The abundances of most of the common species changed notably from 1994 to 2007–09 and 2012 (Table 3). Several species were strongly reduced in 2007–09, among them shallow or deep living deposit feeding polychaetes (*Leitoscoloplos*, *Spiophanes*, *Chaetozone*, *Laphania*), the maldanids *Chirimia*, *Praxillella*, *Nicomache*, and deposit feeding bivalves (*Yoldiella* spp). For some of the species the reduction was >90% in Bøkfjord (Oug et al., 2011). A few species increased in abundance and dominated the fauna in 2007–09, in particular oweniid polychaetes (*Galathowenia*, *Myriochele*) and small bivalves (*Nuculoma*, *Thyasira* spp), whereas one dominant species, the maldanid polychaete *Maldane sarsi*, did not change significantly (Fig. 2). From 2007 to 09 to 2012 there were fewer species changes, but some species recovered, such as *Spiophanes*, *Chaetozone*, nemerteans, caudofoveates and predatory polychaetes (*Eteone*, *Lumbrineris*). A few species that increased in 2007–09, continued to increase (*Paramphinome*, *Cossura*, *Nuculoma*), but largely the fauna was characterized by the same dominant species as in 2007–09. One species that is often among the dominants in terms of biomass in northern Norwegian fjords, the mud star *Ctenodiscus crispatus* (Nilsen et al., 2006; Oug et al., 2011; Fuhrmann et al., 2015), was present in most grab samples in 1994, but were not found in 2007–09 and 2012.

The main patterns in species composition and changes are illustrated in the correspondence analysis (CA) on the fauna (Fig. 3). The analysis indicates that the strongest pattern (axis 1) is represented by the differences between the three areas, the open Varangerfjord (stn 21), the Bøkfjord (stns 14–20) and the Kobbholmfjord (stn 01), whereas the second-most important pattern (axis 2) is a time gradient that separates the 1994 samples (lower part of diagram) from the later samples (upper part of diagram). The plot of species illustrates several of the main trends for species. Generally, decreasing species are located at the bottom of the plot (most abundant in 1994), whereas increasing species are located at the top and towards the right of the plot.

The patterns in the Varanger area were compared with faunal data from other fjords in northern Norway without king crabs in subsequent correspondence analyses to assess the extent of the changes related to uninfluenced areas (Fig. 4). The species assemblages differed between the fjords, but generally were similar to the Varangerfjord and Bøkfjord with respect to composition and abundances of the dominant species groups. It appears that the stations in the Bøkfjord showed a high similarity to sites in several fjords, with the samples from 1994 most close to the Balsfjord and Porsangerfjord sites, whereas the 2007 and 2012 samples were more similar to the Kaldfjord and Bergsfjord sites. All these sites had high abundances of oweniid polychaetes. Consequently, the faunal changes in Bøkfjord from 1994 to 2012 appear to be within the range of faunal variation among fjords in northern Norway. Most other fjords, however, had more dissimilar fauna that were less suited for comparison (among them Olderfjord and Byluft 1994; analyses not shown). None of the fjords were similar to Kobbholmfjord (stn 01) indicating that this fjord had a faunal assemblage that was not generally found elsewhere in fjords in northern Norway.

Table 2
Species richness and diversity (Shannon-Wiener H′, log base 2, average ± SD) at the sampling stations in 1994, 2007–2009 and 2012. Diversity H′ is calculated for samples (0.1 m^2) in order to estimate replicate variability, pooled SD across stations is 0.19 and 95% confidence interval for stations with four samples is ±0.30.

Stn	Depth m	Number of species			Diversity H'_{log2}		
		1994	2007–09	2012	1994	2007–09	2012
14	195	64	45	27	4.39 ± 0.25	3.45 ± 0.30	3.52 ± 0.32
16	222	85			4.27 ± 0.11		
17	224	69			4.40 ± 0.16		
18	235	72			4.31 ± 0.09		
19	260	83	58	69	4.36 ± 0.20	3.15 ± 0.09	3.72 ± 0.04
20	265	83			4.43 ± 0.11		
21	375	91	69	47	4.35 ± 0.30	4.39 ± 0.11	3.86 ± 0.01
01	140	–	50	37	–	3.18 ± 0.25	3.52 ± 0.10

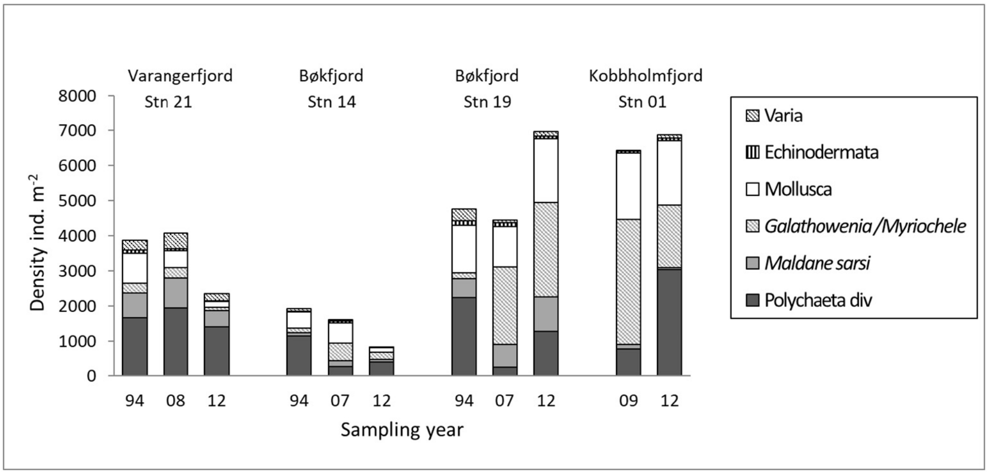

Fig. 2. Abundances of major species groups at the revisited stations in the Varanger area. Oweniid polychaetes (*Galathowenia*, *Myriochele*) and the maldanid *Maldane sarsi* are shown separately.

Table 3
Mean densities (ind. m^{-2}) and changes from 1994 to 2007–09 and from 2007–09 to 2012 for the most abundant species. Mean densities are calculated across all years from stations that were revisited (stns. 21, 14, 19, 01). Density changes of >50% decrease (−) or increase (+) is indicated.

	Densities ind. m^{-2}	>50% change	
		1994 to 2007-09	2007-09 to 2012
Edwardsiidae indet	12		
Nemertinea indet	30	−	+
Polychaeta			
Paramphinome jeffreysii	21	+	+
Eteone sp/cf *longa*	45		+
Aglaophamus malmgreni	25	−	
Nephtys ciliata	22	+	
Lumbrineris mixochaeta	323		+
Leitoscoloplos mammosus	58	−	
Spiophanes kroeyeri	121	−	+
Spiochaetopterus typicus	12		−
Aphelochaeta sp	70		−
Chaetozone setosa	88	−	+
Cossura longocirrata	85	+	+
Heteromastus filiformis	46	+	
Chirimia biceps	35	−	
Praxillella/Euclymene spp	96	−	
Maldane sarsi	430		
Nicomache sp	8	−	−
Galathowenia oculata	717	+	
Myriochele olgae/sp	308	+	
Melythasides laubieri	18	−	−
Laphania boecki	70	−	+
Polycirrus arcticus	15		
Proclea malmgreni	10	−	
Terebellides sp	12		−
Mollusca			
Caudofoveata indet	41	−	+
Nuculoma tenuis	112	+	+
Yoldiella fraterna/sp	120		−
Yoldiella lenticula	33	−	
Yoldiella lucida	15	−	−
Dacrydium vitreum	12		−
Thyasira equalis/dunbari	308	+	
Thyasira pygmaea/sp	237	−	
Thyasira sarsi	40	+	
Sipunculida			
Golfingia minuta	65		
Echinodermata			
Ctenodiscus crispatus	4	−	
Ophiura spp	41		

3.2. Abundance of the king crab in the Varanger area

The king crab appears to be unevenly distributed in the Varanger fjord system. The highest crab densities have generally been found in side-fjords at the southern range of the main fjord. For the three areas studied here, estimates of the crab stock (CPUE-estimates) indicated clear differences among the areas (Fig. 5). The estimates are calculated as mean values for a four-year period previous to the soft bottom sampling to facilitate comparison with the faunal data. Generally, the catches showed a high variation (high SD). In Kobbholmfjord usually 100–300 specimens were caught per 30 min tows, which was clearly higher than the catches in Bøkfjord and Varangerfjord. The catches in Bøkfjord were higher than in Varangerfjord in 2005–08, but decreased in 2009–12 to about the same level as in Varangerfjord. However, over a longer time period (2002 − 2012) since the establishment of a commercial crab fishery in 2002, the average catch estimate for Bøkfjord (65 crabs, 31 samples) was significantly higher than in Varangerfjord (5 crabs, 75 samples).

3.3. Functioning of soft bottom species assemblages

The main functional patterns in the species assemblages are illustrated in the principal component analysis (PCA) of trait profiles for sampling stations. The plot of stations (Fig. 6) was rather similar to the plot from the faunal analysis (Fig. 3), suggesting that the functioning of the species assemblages changed in parallel with the species changes. The two first axes represented the geographical difference between the areas (axis 1) and a time gradient (axis 2), respectively, as in the faunal analysis, but the inner Bøkfjord station (stn 14) was more similar to Kobbholmfjord, and the outer station (stn 19) was more close to the Varangerfjord station. The differences between the Varangerfjord samples (1994, 2008, 2012) appeared to be less with regard to traits than for faunal composition.

The plot of trait categories (variables) (Fig. 7) showed that the main gradient (axis 1) was represented in features such as adult life habit, degree of attachment, normal adult size and to a certain degree also in sediment dwelling depth and feeding habit. Whereas Kobbholmfjord was characterized by small-sized, burrowing, non-attached, shallow-digging subsurface deposit feeders, Varangerfjord (stn 21) was characterized by relatively large, tube-building, less mobile, generally deep-digging suspension and deep deposit feeders. The change with time in Bøkfjord stations was characterized by a loss of surface deposit feeders and an increase in motile predatory forms. There was also a change in

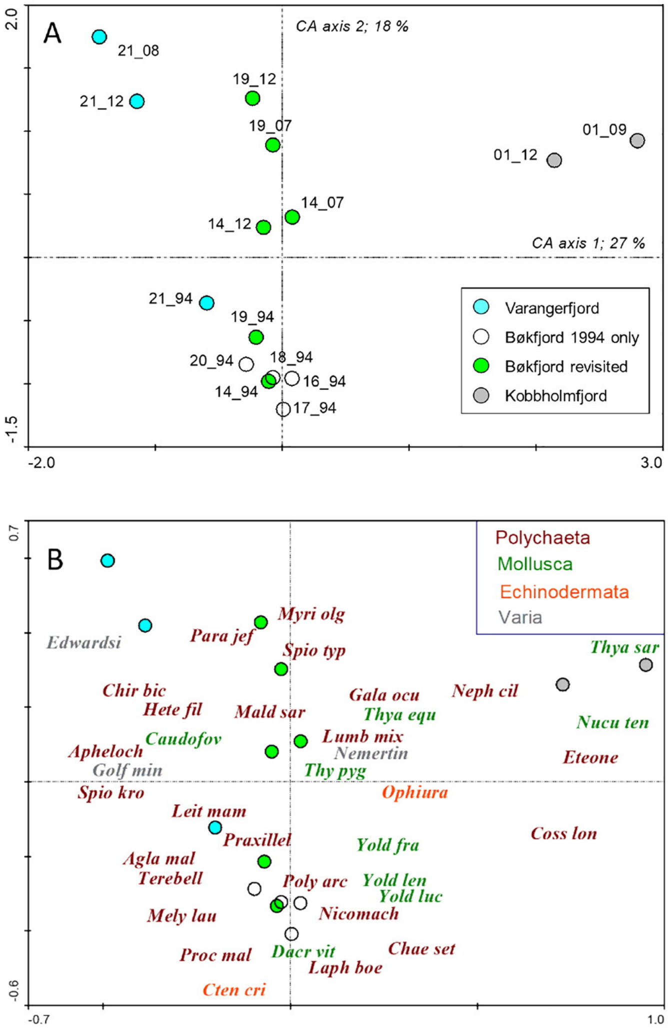

Fig. 3. Correspondence analysis (CA) of species composition at sampling stations in the Varanger area. A: plot of stations; revisited stations are colour-coded. Labels show station number and sampling year. B: plot of most important species (abundance-dominants). See Table 3 for full species names.

the type of larvae of the species, with a relative decrease in lecitotrophic non-feeding larvae and a relative increase in planktotrophic larvae.

With regard to the sediment reworking ability, the main gradient (axis 1) distinguished between a relative abundance of surficial modifiers in Kobbholmfjord (stn 01) and a relative abundance of upward conveyors in Varangerfjord (stn 21). The second axis illustrated that the time change at the Varangerfjord and Bøkfjord stations was characterized by a reduction of downward conveyors and an increase of biodiffusors.

The explanatory variables of crab abundance and depth were highly correlated with the first axis, whereas the variable year was highly correlated with the second axis (Fig. 7). The sediment parameters (% silt-clay, total organic carbon - TOC) were poorly correlated and could not explain the main patterns in traits distribution. The categorical variable for crab invasion (before, after) not surprisingly overlapped with the year variable, whereas the categorical variable for fjord areas illustrated the differences between the three fjords. Depth and crab abundance were inter-correlated (negative) since Kobbholmfjord (depths 120–140 m) is the shallowest area, whereas Varangerfjord (depths 300–400 m) is the deepest. Both factors may contribute to explain the functional changes along the main gradient (axis 1), but crab abundance is assumed to be the most influential because of the direct effect on the fauna from predation. It may be of significance that crab abundances in Bøkfjord were lower during the period 2009–12 than in 2005–08, coinciding with the observed functional changes at the stations, notably an increased abundance of upward conveyers.

The functional patterns in the Varanger area were further compared with fjords elsewhere in northern Norway without king crabs. Most sites were similar to the Varangerfjord (stn 21) and the 2012 samples in Bøkfjord, but Porsangerfjord were similar to the 1994 samples in Bøkfjord (Fig. 8). Generally, however, it seems that fjords in northern Norway are characterized by a relative importance of upward conveyors and some also by downward conveyors. These features had been reduced in the Varanger area, particularly in Kobbholmfjord.

4. Discussion

The studies in the Varanger area in 2007–09 showed that the soft-bottom fauna in areas which were invaded by the red king crab during the 1990s was reduced in both faunal abundances and diversity. In particular, echinoderms, larger molluscs and deep burrowing polychaetes with low motility were sparse and poorly represented. Compared to samples from 1994, the densities of most sedentary burrowing and tube-living forms had decreased, for several dominants as much as 70–90%, whereas some few small forms had increased and dominated the species assemblages (Oug et al., 2011). The follow-up studies of macroinfauna in 2012 presented here showed that the faunal composition in the Varanger area was relatively unchanged since 2007–09, but some species that previously were reduced, had recovered or had increased in abundance. The faunal changes in Varangerfjord and Bøkfjord, however, were within the range of variation of macroinfauna species communities in fjords in northern Norway. Kobbholmfjord, only sampled after the invasion of the king crab differed considerably from the other areas, especially with regard to the samples in Bøkfjord and Varangerfjord from 1994, before the main invasion of the king crab.

The faunal differences between the three fjord areas and the species changes with time appear to be well correlated to the estimated crab abundances in the fjords. This is consistent with the view that the king crab significantly influences the composition of the species assemblages. Oug et al. (2011) showed that the species that had decreased in abundance between 2007 and 09 are among the favorite prey items of the king crab. The red king crab is commonly patchily distributed along the coast of northern Norway. Regular surveys in the quota-regulated area have indicated that the density generally is higher in small side-fjords such as Bøkfjord and Kobbholmfjord than in the main fjord systems. This may be due to preferable temperatures or depths in the side-fjords, or better food availability than in the deeper main fjord areas. The red king crab in Norwegian waters seems to display a high site-fidelity; groups of crabs in small local fjords and inlets appear to be very isolated with little immigration and emigration (Windsland et al., 2014). In addition to depth, this behavior seems to be regulated by temperature which is crucial threshold for movement and spread of the crab (Windsland et al., 2014; Christiansen et al., 2015). In the Varanger area the king crab seems to encounter both preferable depths and bottom temperatures in the main fjord as well as in the small side fjords. Considering the seasonal migrations for reproduction between different depths, the distance between preferred shallow and deep areas is very small in the side fjords. Presuming no food limitation, there is no need for the crabs to move out of the area. The lower crab abundance in Bøkfjord during 2009–2012 compared to 2005–2008 (Fig. 5) may be due to an unusually high fishing effort in 2009. During this year, the fishing quotas were exceptionally high due to a change in the management regime (Anonymous, 2007). In 2010, the overall fishing quota was reduced to less than half of that in 2009, and remained stable until 2016 when the total extraction quota was raised to 2000 metric tonnes.

The alteration in species composition of the benthic fauna resulted in notable changes in the functioning of the sediment communities. The changes from 1994 to 2007–12 resulted in a relative reduction in

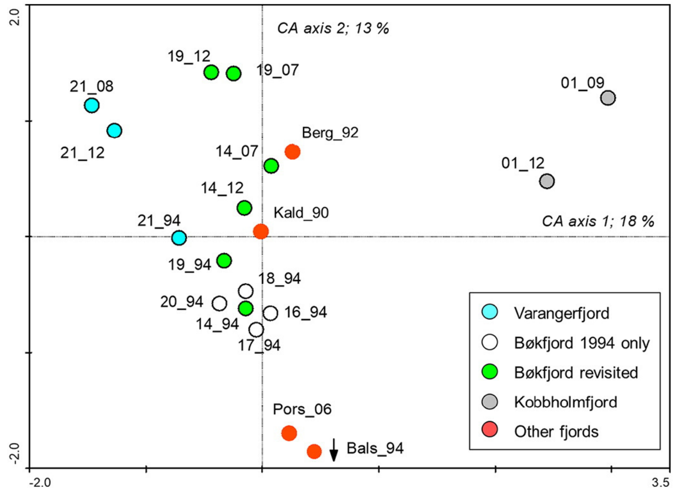

Fig. 4. Correspondence analysis (CA) of species composition at sampling stations in the Varanger area and other fjord basins in northern Norway (red symbols). Labels show station number/fjord basin and sampling year.

suspension and surface deposit feeding activities and an increase in motility and predatory feeding. The faunal differences between the Varangerfjord which had low densities of the king crab and Kobbholmfjord with high densities, involved a change from tube-building, deep deposit feeding forms of fairly large size to free-living, shallow burrowing forms of rather small size. With regard to sediment reworking it appears that downward and upward conveyors were reduced after the crab invasion and with increasing crab densities, whereas surficial modifiers increased. In other north Norwegian fjords without the king crab, upward conveyors generally seem to be well represented, whereas the importance of downward conveyors varies. The Bøkfjord samples from 1994 were relatively similar to the sample from Porsangerfjord in terms of the importance of downward conveyors. This is the site geographically closest to Varanger, which possibly could indicate that there are regional differences in the functioning of species communities in northern fjords. Fuhrmann et al. (2017) showed that the red king crab during recent invasion of Porsangerfjord had a generally opportunistic feeding strategy catching a wide range of prey organisms across multiple trophic levels, but with some differences related to crab size and foraging locations. The functional changes in the benthos demonstrated in the present study may thus represent a

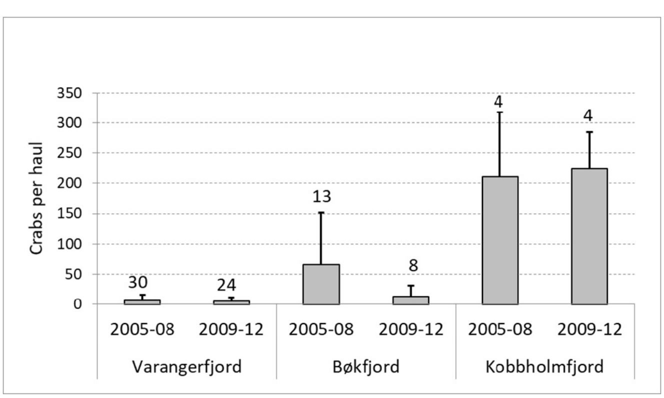

Fig. 5. Mean number of specimens of red king crabs (+SD) in trawl hauls from Varangerfjord, Bøkfjord and Kobbholmfjord in the periods 2005–2008 and 2009–2012. Trawl data were standardised to 30 min tow duration. Number of hauls for each period and fjord is indicated. The differences between areas are statistically significant ($p < 0.01$; two-tailed *t*-tests, log-transformed data) within each time-period, except for Varangerfjord and Bøkfjord in 2009–12 ($p > 0.6$).

scenario following the loss of the most easily accessible prey organisms in the Varanger area.

The main functional patterns may be summarised as reflecting basically two gradients; one related to the timing of the crab invasion and one related to the crab abundances, as a proxy for the predation pressure which is affecting the benthic fauna (Fig. 9). The functional features of the fauna in Kobbholmfjord are markedly similar to faunal communities in physically disturbed environments, for instance from bottom trawling (Tillin et al., 2006; Olsgard et al., 2008; van Denderen et al., 2015), the latter study also showing parallels with natural tidal-driven sediment disturbance, organic enrichment (Villnäs et al., 2011), toxic contaminants (Oug et al., 2012), glacial sedimentation (Wlodarska-Kowalczuk et al., 2005) or deposition of mine tailings (Brooks et al., 2015). The changes in faunal composition related to crab abundance may therefore be interpreted as a disturbance gradient. The most typical changes are loss of large permanent tube dwelling forms and increase of small surface living and shallow burrowing forms. The changes for several of the traits, however, may differ with different stress factors and the fauna's ability to cope with the type of stress (Brooks et al., 2015). In the case of the king crab predation, it may seem that the decrease of suspension and surface deposit feeders is a typical response, which implies that downward conveyors are reduced.

With regard to sediment reworking, the reduction of upward and downward conveyors implies that the physical mixing of sediments and advection of pore water and solutes are reduced. Large tube-building or burrowing forms also contribute significantly to water exchange by ventilation of the burrows (Kristensen et al., 2012). These processes influence levels of oxygen, pH, redox gradients and nutrient cycling (Queirós et al., 2013) in the sediment. Sediment profile imagery (SPI) from Kobbholmfjord in 2009 indicated that the sedimentary environment was degraded, having a rather shallow oxidized surface layer (about 3 cm) and a sharp boundary to the underlying chemically reduced sediment (Oug et al., 2011). The effects on ecosystem functioning here estimated from the functional analyses hence corroborate the previous observations of sediment structure in areas with high crab densities.

The functional analyses also indicated that the relative occurrence of species with lecitotrophic larval development, i.e. short or no pelagic phase, decreased after the invasion of the king crab. This change may be of consequence for maintaining and developing the species assemblages. Species with lecitotrophic larvae will most probably have lower ability to recruit from outside populations than species with a long pelagic phase. Several studies have shown that species with pelagic larvae and the potential for wide dispersal may rapidly colonize sediments after severe disturbances (Rosenberg, 1976; Whitlatch et al., 1998; Villnäs et al., 2011). Possibly the constant removal of specimens by crab predation may drive the faunal composition towards species that have the highest recruitment potential. Such changes may also be of consequence for community recovery if the king crab stock is reduced. Species with lecitotrophic larvae may be expected to take long time to build up populations after having been depleted. The recovery process, however, will depend on a number of biotic and habitat-related factors, natural variation, and the degree of faunal patchiness caused by the disturbance (Whitlatch et al., 1998; Villnäs et al., 2011), and may be impossible to predict.

The apparent close relationship between crab abundances and functional changes in the benthos may suggest that the ecological consequences of invasion of king crab to new areas can be forecasted from data on native faunal composition and estimates of crab abundances. More data are needed, however, to substantiate these relationships and to indicate more specifically the most affected benthic traits. If relationships can be firmly established, it may further be suggested that the ecosystem costs of the king crab can be estimated. A question of interest for management is to evaluate the ecological costs of maintaining a crab stock for a long-term commercial fishery. Effects of the red king crab on the native ecosystems and the consequences for valuable ecosystem

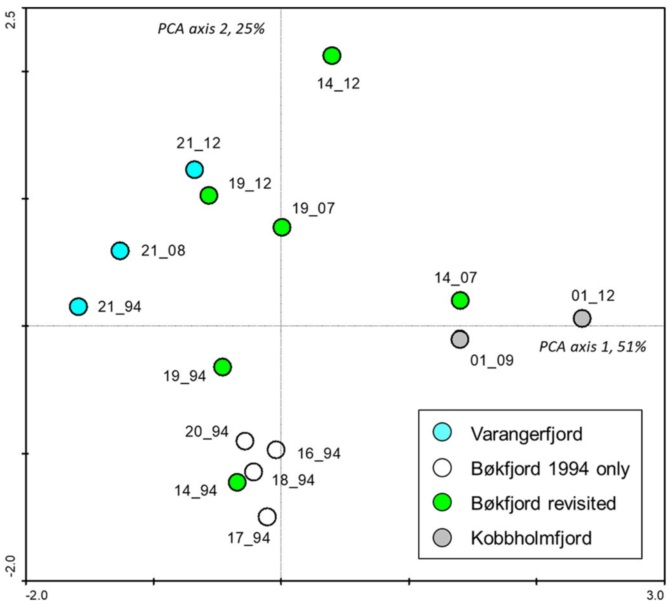

Fig. 6. Station diagram from principal components analysis (PCA) of species traits at sampling stations in the Varanger area. Labels show station number and sampling year.

services are important issues in judging how the crab should be managed inside the quota regulated area (QRA) (Anonymous, 2015). Falk-Petersen and Armstrong (2013) made an attempt using bio-economic models to estimate the optimal crab stock giving an economic yield without causing unwanted changes in ecosystem structure and services. They pointed out, however, that the analyses were severely limited by the poorly-known relationship between crab population size and ecosystem impacts. The relationship could be of linear, exponential or threshold (abrupt change) form. Establishing the relationship ('damage function') as well as the carrying capacity of the invaded ecosystems is essential to determine the socially optimal crab stock size (Falk-Petersen and Armstrong, 2013). In any case, further knowledge on the relationship would provide a better basis for management of the king crab as both a non-indigenous species and a resource in the Barents Sea area.

The technique of BTA appears to be well suited for the present functional analyses. Theoretical functional analyses, however, are rather recently developed techniques that need to be further developed and refined. Several methodological aspects, for instance with regard to the range of traits used, scoring of functional features in trait categories, quality of the species-specific information, weighing of species in the analyses (e.g. by abundance or biomass; transformations), should be further assessed (see for example Cochrane et al., 2012; Oug et al., 2012; van Son et al., 2013). Further applications of the techniques in different environmental conditions and in different bio-geographical areas would benefit future research on the functionality of benthic systems.

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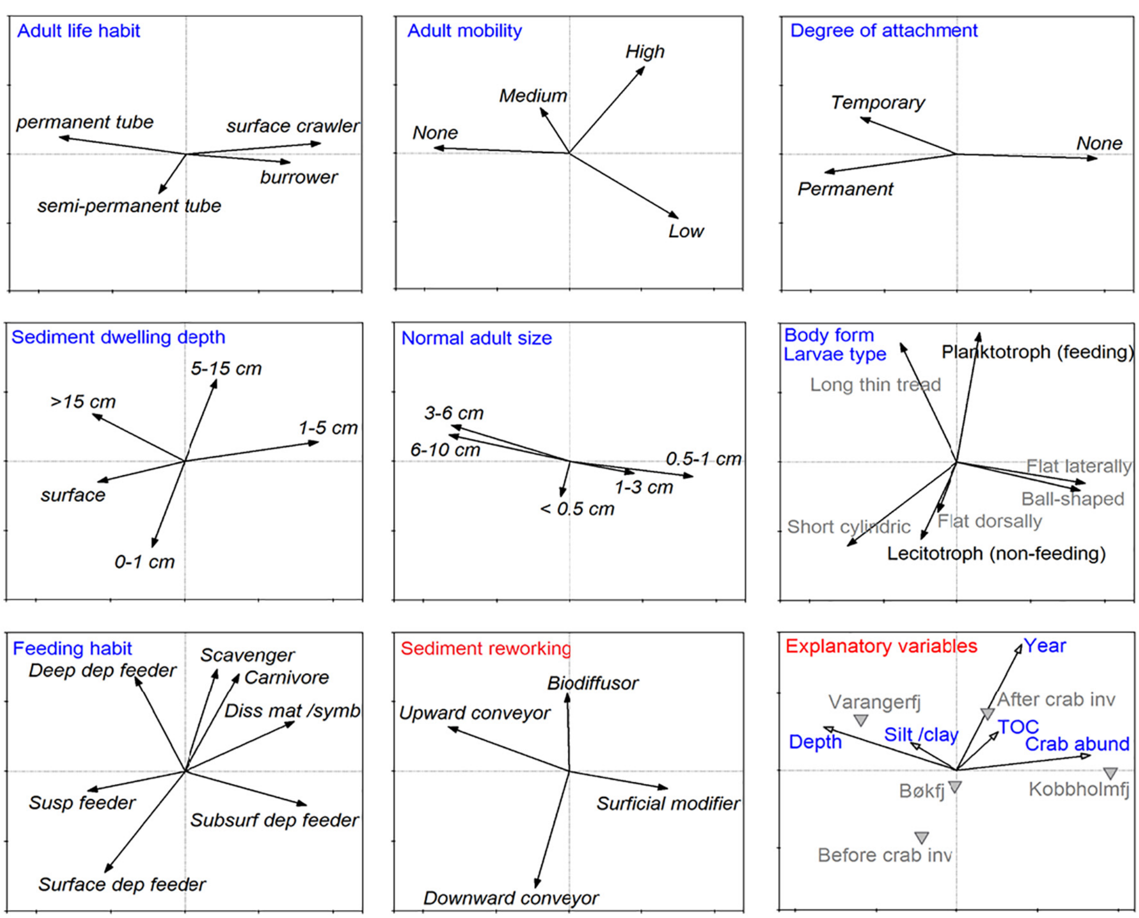

Fig. 7. Trait category diagrams from principal components analysis (PCA) of species traits at sampling stations in the Varanger area. Vectors point in the direction of maximum increase of the trait category. Long vectors indicate strong trends. Poorly represented trait categories ('abundance' < 3%) have been omitted. Sediment reworking categories and explanatory variables were passively fitted in the analysis. The explanatory variables of crab abundance, depth and year are significantly correlated to axis 1 and axis 2, respectively (p < 0.01). Triangles mark centroids of categorical variables for area (Varangerfjord, Bøkfjord, Kobbholmfjord) and crab invasion (before, after).

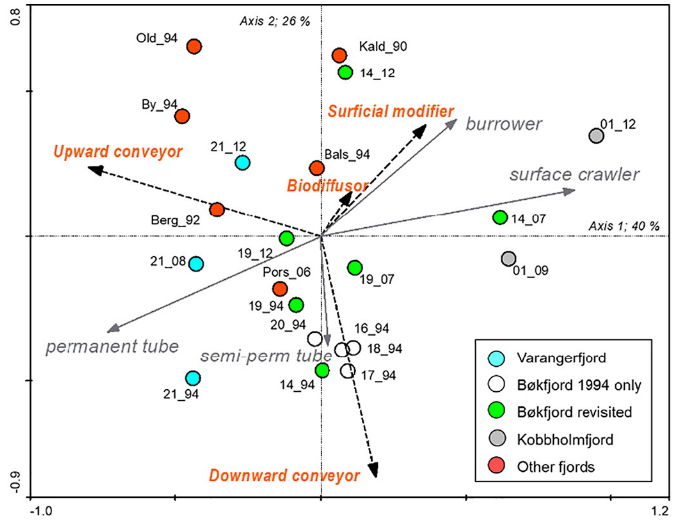

Fig. 8. Station diagram of principal components analysis (PCA) of species traits at sampling stations in the Varanger area and in other fjord basins in northern Norway. Trait category vectors of adult life habit (solid line) and sediment reworking (stippled) have been entered to illustrate the main functional gradients.

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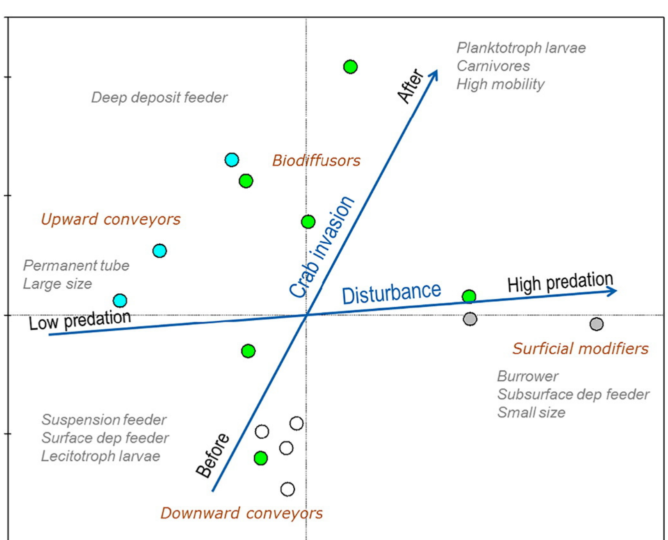

Fig. 9. Main patterns in functional features and sediment reworking in soft bottom species communities in the Varanger area in relation to gradients in time (king crab invasion) and crab predation pressure (disturbance). The two gradients are fitted on the explanatory variables for crab abundance and year (see Fig. 7). Sampling stations are indicated by points (blue - Varangerfjord; open - Bøkfjord 1994 only; green - Bøkfjord revisited; grey - Kobbholmfjord).

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