Trophic niche of the invasive red king crab *Paralithodes camtschaticus* in a benthic food web

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ABSTRACT: Understanding the trophic ecology of an invasive species is important for risk assessment. The red king crab *Paralithodes camtschaticus* is both a valuable fishery resource and a potential threat to native biota in the Barents Sea. We combined gut content analysis and stable carbon and nitrogen isotope analysis to study feeding strategy, variation in resource use and niche overlap within the benthic food web of Porsangerfjord (70.1° to 70.9° N, 25° to 26.5° E) on the northern Norwegian coast. This fjord has experienced recent invasion by the red king crab. Sediment-dwelling bivalves and polychaetes dominated gut contents of the red king crab with respect to occurrence, and the wide range of prey from multiple trophic levels revealed a generalist, opportunistic feeding strategy. There were differences in diet related to crab size and foraging location, reflecting habitat choice and depth distribution of crabs during their life cycle. Small crabs, feeding in shallow water, relied to a larger extent on littoral species such as sea urchins and gastropods. The estimated mean trophic level for red king crab in Porsangerfjord was 3.1 (range 2.7–3.5). There was no evidence of a pronounced ontogenetic niche shift in stable isotopes, with local effects concealing possible overall size effects. Competition may arise with native anomuran species (e.g. *Lithodes maja*), large predatory asteroids and gastropods, all of which overlapped with red king crab in isotopic niche. A low overlap in isotopic niche between red king crab and fish suggests that they exploit different major food resources and that predatory fish occupy a higher trophic position than the red king crab in Porsangerfjord.

KEY WORDS: Decapod · Diet · Stable isotopes · Trophic ecology · Trophic level · Introduced species · North Atlantic

INTRODUCTION

The introduction of the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) to the Barents Sea in the 1960s resulted in establishment along the Kola Peninsula (Orlov & Ivanov 1978) and later along the northern Norwegian coast (Windsland et al. 2014). Although the red king crab is now a highly valuable commercial resource, effects of this benthic predator on native biota are of major concern (Falk-Petersen et al. 2011, Oug et al. 2011, Mikkelsen & Pedersen 2012). The red king crab, one of the largest marine decapods, feeds on a variety of benthic epifauna and infauna (reviewed by Falk-Petersen et al. 2011). It is often referred to as being a generalist and oppor-

tunistic feeder, and this probably facilitates competitiveness of the red king crab in the Barents Sea. Nevertheless, size-dependent prey selection and individual preferences have been documented in laboratory experiments (Jørgensen & Primicerio 2007), and there may be changes in diet related to seasonal feeding migrations, sexual segregation and mating/ molting (Sundet et al. 2000).

Depending on prey selection, trophic position and available niches in the benthic system, invasion can have several direct and indirect effects, so diet studies are crucial for assessment of the potential impact of an invading predator. Observed effects of the red king crab in invaded areas include changes in benthic species composition and loss of benthic biodiver-

sity, density and biomass (Britayev et al. 2010, Oug et al. 2011). Invasive species also have the potential to cause niche displacements of community members (Vander Zanden et al. 1999, Fanelli et al. 2015) and outcompete native species that occupy the same trophic niche (Weis 2011). Introduced marine crustaceans can have strong top-down effects, indirectly affecting non-prey species through competition and cascading effects (Grosholz et al. 2000, Snyder & Evans 2006). Interaction with other species and competition for resources are poorly understood for red king crabs in the Barents Sea. In its native area of distribution, the Bering Sea, red king crabs share resources with a number of bottom-dwelling invertebrates and flatfish (see Falk-Petersen et al. 2011 and references therein). It has been suggested that in its new distribution range, the crab may pose a threat to commercial fish, with haddock *Melanogrammus aeglefinus*, saithe *Pollachius virens* and cod *Gadus morhua* being possible competitors for food resources (Falk-Petersen et al. 2011). Others claim that competition for food with red king crab is of no importance for commercial fish stock fluctuations in the Barents Sea (Dvoretsky & Dvoretsky 2015). Little attention has been given to the investigation of trophic niche overlap with fish, including species of minor commercial value, e.g. bottom-dwelling flatfish, and native crustaceans such as the stone crab *Lithodes maja*.

Stable isotope signatures have been used in ecological studies to investigate trophic relationships and food web structure (e.g. Hobson & Welch 1992, Layman et al. 2012). Based on enrichment of the heavier isotope from consumer to consumer, stable isotope ratios of nitrogen (expressed as $\delta^{15}N$) can give information about diet and trophic position (Minagawa & Wada 1984, Post 2002), and stable carbon isotopes (expressed as $\delta^{13}C$) are used to trace the sources of dietary carbon derived from primary producers (Cherel & Hobson 2007). Major advantages of stable isotope analysis over traditional stomach analysis are less invasive sampling and the integration of diet information over long time periods (in selected tissues). The stable isotope method is especially applicable to species, such as crabs, that crush prey items and make prey identification and quantification difficult. One of the major disadvantages of the method is that isotopic signatures do not give information about specific prey items, and prey sampling is needed to qualify diet composition (Layman et al. 2012). A combination of stable isotope and stomach content analysis is therefore a powerful tool to investigate a species' feeding habits.

The isotopic niche (Newsome et al. 2007) is defined as the space occupied by individual signatures of a sampled population in the 2-dimensional isotopic space of $\delta^{13}C$ and $\delta^{15}N$, and isotopic niche width can be quantified by a number of dispersion metrics (see Layman et al. 2007, Jackson et al. 2011). The isotopic niche concept has been applied to investigate inter- and intraspecific diet variation and resource partitioning, e.g. ontogenetic niche shifts, seasonal changes in feeding patterns (Abrantes et al. 2014) and individual specialization (Vander Zanden et al. 2010). Stable isotope analysis contributes to the investigation of impacts of invasive species via elucidation of their role in the food web (e.g. Rudnick & Resh 2005, Kadye & Booth 2012), niche overlap with native species (Layman & Allgeier 2012) and cascading effects on food web structure (Vander Zanden et al. 1999, 2003, Jackson et al. 2012, Fanelli et al. 2015).

The present study considers the northern Norwegian Porsangerfjord, which was invaded by the red king crab around 2000. We highlight the trophic role of the crab by combining stable isotope analysis and stomach content analysis to investigate (1) feeding strategy, (2) trophic position and variation in resource use with crab size and sex and (3) isotopic niche overlap with other predators in the system.

MATERIALS AND METHODS

Study area

With an area of 1877 km², the subarctic Porsangerfjord is the largest fjord on the coast of Finnmark. Initial catches of red king crab in 2002 were followed by establishment of the species in the fjord north of the sill to the inner part (Fig. 1), and a commercial fishery started in 2008. Subzero temperatures in the inner Porsangerfjord may have hindered the red king crab from rapid establishment in this area, but dense pods of juveniles (Video S1 at www.int-res.com/articles/suppl/m565p113_supp/) as well as large adults have recently been seen in the inner fjord, including the deeper basins to the east, which have year-round cold bottom temperatures. The entire fjord area now supports a quota-regulated fishery for red king crabs, yielding around 450 tons annually. Following the decline of the local coastal cod *Gadus morhua* stock in the 1990s, the red king crab fishery is the most lucrative fishery in the fjord.

Similar to other areas along the northern Norwegian coast, macroalgae have been exposed to heavy grazing by sea urchins in parts of the fjord (Sivertsen
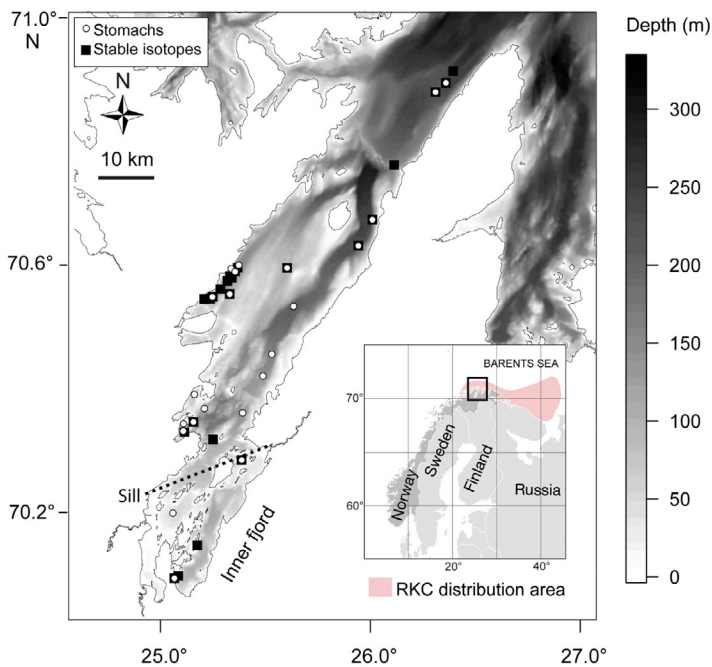
Fig. 1. Study area in Porsangerfjord, northern Norway. Shades of grey indicate depth (m). Main sampling locations of red king crabs and approximate distribution of the red king crab stock in the Barents Sea (pink). Source: Institute of Marine Research

& Bjørge 2015). Benthic biomass in Porsangerfjord is higher in the inner than in the outer areas of the fjord (Fuhrmann et al. 2015), and long-lived species dominate the macrofaunal community. The inner fjord can be considered a pristine benthic habitat, and declaring it a marine protected area has been proposed (Miljødirektorat 2004).

Sampling

Samples were collected from May to October in 2011 and 2012 during annual survey cruises with the RV 'Johan Ruud' by the Institute of Marine Research. Red king crabs were sampled by trawls, baited traps (both described in Hjelset et al. 2009) and scuba divers at depths of 17 to 247 m from 36 sampling stations (Fig. 1). Samples contained juvenile and adult crabs with carapace lengths (CLs) ranging from 21 to 177 mm in males and 24 to 148 mm in females and body masses ranging from 6.1 to 4768 g. Sexual maturity in red king crabs occurs when crabs reach a CL of ca. 110 mm (Hjelset et al. 2009), and most females over 110 mm CL bore roe. Samples stratified for 3 CL classes were attempted (juveniles <70 mm,

juveniles from 71 to 110 mm and adults >110 mm CL), but aggregations by sex and size were observed, and this resulted in unbalanced sampling within locality and crab size. In addition, crab size correlated with sampling depth (rho = 0.52, p < 0.001, Spearman's rank test). In particular, juvenile crabs <50 mm CL were only taken in shallow trawl hauls in the inner eastern part of the fjord, larger juveniles and adult crabs (>110 mm) extended to deeper waters (>200 m) and large adult crabs were rarely caught in the shallows of the inner fjord. Where abundant, we sampled a variety of crab prey species and possible food competitors together with red king crabs (Fig. S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m565p113_supp/). Fish were sampled by trawls. Zoobenthos was sampled by van Veen grab, epibenthic trawl (soft bottom) and triangular dredge (hard bottom). Zooplankton was sampled using a plankton net (WP2, 180 µm mesh size); jellyfish and chaetognaths were removed, leaving mainly calanoid copepods. Sediment samples were collected with a spoon from the surface (0–1.5 cm) of the grab samples and frozen.

Stomach analysis

Stomachs of 139 red king crabs were obtained from crabs caught by trawls and divers, following immediate removal and freezing on liquid nitrogen. Stomach fullness was assessed on a scale from 1 to 5, ranging from empty (1) to completely filled (5). Stomach contents of red king crabs were rinsed using a 180 µm sieve to get rid of excess stomach fluid and then identified under a stereomicroscope to the lowest possible taxon.

Assessment of sample sizes required for prey detection was made using a cumulative prey curve constructed from the collected data (Cortés 1997). For this purpose, prey items were assigned to 1 of 32 exclusive groups (including unidentified), and the order of stomachs analyzed was randomized by permutations (999) to give mean numbers of new prey types for each consecutive stomach ± SD.

Prey composition was assessed from presence and absence by calculating the percentage frequency of occurrence (F_i) is given as

$$F_i = \frac{n_i}{n} \times 100 \qquad (1)$$

where n_i equals the number of stomachs containing prey item i and n equals the total number of stomachs analyzed (139), excluding empty stomachs.

Prey items in crab stomachs were usually crushed into small fragments and were difficult to count. Consequently, a relative importance index was established to quantify contribution of a prey item relative to other stomach contents. Based on visual analysis, estimates were made of the percentage of volume for each prey item, which was then assigned to category 1 (1–20 %), 2 (21–50 %) or 3 (>50 %).

Stable isotope analysis

Muscle samples of ca. 1 cm^2 were taken from king crabs (fourth pereiopod) and fish (dorsal side) and frozen at −20°C for later analysis. Other animals were rinsed in seawater and frozen whole at −20°C for stable isotope analysis. Benthic animals were later dissected to obtain muscle tissue for isotopic analysis; if no muscle could be obtained, gonads or whole animals were used (zooplankton and echinoderms). Samples were rinsed in distilled water (except sediment samples), dried at 60°C for 48 h and then ground to a fine powder. Stable isotope analysis was conducted at Sinlab, University of New Brunswick, Canada, where samples were combusted in either a Carlo Erba NC2500 or Costech 4010 Elemental Analyzer and analyzed for $\delta^{13}C$ and $\delta^{15}N$, using either a Thermo-Finnigan Delta Plus or Delta XP isotope-ratio mass spectrometer interfaced to an Elemental Analyzer via the ConfloII or Conflo III. Samples from zooplankton, pelagic fish and gonad tissue were lipid extracted before analysis by soaking and multiple rinsing with 2:1 chloroform:methanol. Since lipid removal may affect nitrogen signatures (Sweeting et al. 2006), $\delta^{15}N$ was read from untreated samples. C:N ratios of red king crabs varied between 2.95 and 5.23 (mean 3.47 ± 0.32 SD). Lipid removal from 10 randomly selected crab samples did not result in a significant change in $\delta^{13}C$ (paired t-test, p = 0.49), but nitrogen signatures significantly increased (paired t-test, p = 0.0072). Therefore, king crab samples were not routinely treated for lipid removal. Carbonates were removed from sediments and samples containing exoskeletons (zooplankton, whole brittle stars; where $\delta^{15}N$ was read from untreated samples) by treatment with 2 N HCl prior to spectrometry.

A total of 162 red king crabs, 9 fish, 7 decapod and 38 invertebrate prey species were analyzed, aiming at 3 replicates per species (Table S1 in the Supplement). Isotopic fractionation from prey to predator was assumed to be 3.4‰ and 0.8‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (Minagawa & Wada 1984, Post 2002). Trophic levels were calculated from mean $\delta^{15}N$ sig-

natures. We considered the suspension feeding scallop *Chlamys islandica* a baseline. This bivalve is common at shallower depths in Porsangerfjord and represents a primary consumer in the benthic food web. The species is long-lived and therefore suitable as a baseline (Vander Zanden et al. 1999, Post 2002, Fukumori et al. 2008). Previous work has confirmed the suitability of using filter-feeding bivalves as baselines in marine stable isotope studies (Jennings & Warr 2003, Barnes et al. 2009). Scallops were sampled in shallow water (ca. 30 m) at 2 locations in the inner and middle fjord and signatures were compared to sediments and other bivalves found at different locations and depths (Fig. S1, Table S1 in the Supplement). Suspension feeding bivalves were rare at deeper stations in the outer fjord and could not be retained in samples. The trophic level (TL) of consumers (red king crab) was calculated as

$$TL_{consumer} = TL_{base} + (\delta^{15}N_{consumer} - \delta^{15}N_{base}) / \Delta_n$$

where $TL_{base} = 2$ and Δ_n is the enrichment factor per trophic level (Post 2002).

Statistical analysis

All numerical and statistical analyses were performed in R (R Core Team 2013). Normality of data was tested using Shapiro Wilk tests and graphical inspection (Zuur et al. 2007). Correlations were tested using Spearman's rank tests. In order to investigate whether diet composition (presence/absence of prey in stomachs) differed between crab sexes and size classes, we applied permutational multivariate analysis of variance (PERMANOVA in R *vegan*) using Jaccard distances with the given assumption of similar dispersion among groups. Multivariate diet composition was further explored using non-metric multidimensional scaling [NMDS] based on prey presence/absence in stomachs; R package *vegan*. Goodness of fit was assessed using stress plots. Crab CL, depth of capture and, where available, stable isotope signatures were fitted to the NMDS ordination as vectors (*envfit* procedure in R package *vegan*), and significance was assessed by permutation tests (10 000).

We applied general linear models to test for differences in $\delta^{13}C$ and $\delta^{15}N$ with crab size and sex. We used parsimonious stepwise model simplification. Interaction terms were included in the initial model and removed if not significant. Homogeneity of variance and model fit were evaluated by box plots, quantile−quantile plots and residual plots. Spatial structure (autocorrelation) in stable isotopes was

investigated using Moran's I test (R package *lctools*) and empirical variograms (R package *geoR*).

As a measure of isotopic niche width, we calculated the sample size-corrected standard ellipse area (SEA$_c$) available in the *Stable Isotope Bayesian Ellipses in R* (*SIBER*) package (Jackson et al. 2011). In contrast to the convex hull, which represents the total isotopic niche space occupied (Layman et al. 2007, 2012), the standard ellipse area (SEA) represents the isotopic niche of the average member of the community and contains around 40% of the data. SEA provides Bayesian estimates of uncertainty and is less sensitive to bias produced by small sample size (SEA$_c$). SEA$_c$ was used to visualize and calculate the degree of core isotopic niche overlap of red king crab size classes and potential competitors in isotopic space, provided in *SIBER* (R package). As a measure of uncertainty, credible intervals around standard ellipses were obtained from 10 000 solutions, and niche widths were compared between groups using Bayesian inference (Jackson et al. 2011).

RESULTS

Stomachs

Of the 139 crab stomachs analyzed, 7 (5%) were empty, and these were excluded from further analysis. Full stomachs (index 4–5 out of 1–5) made up 28% of the total. Mean stomach fullness was 2.9, and the fullness index was negatively correlated with crab CL (rho = −0.29, p = 0.0004). The cumulative prey curve for the major taxonomic groups approximated an asymptotic relationship, so sampling was considered sufficient to encompass major prey items and describe trophic diversity at the population level (Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m565p113_supp/).

Stomach contents comprised a wide range of prey, including soft-bottom infaunal and epifaunal species. In total, 69 taxa were identified (Table 1), and 57% of stomachs contained at least 1 unidentified prey item. Soft tissue was often separated from hard parts of ingested items, making it difficult to allocate soft tissues to specific taxa. Bivalves and polychaetes were important prey (Fig. 2); both had a frequency of occurrence over 85%. Bivalves also had a higher mean importance index than polychaetes (2.0). Small bivalves (such as *Bathyarca* sp. and *Yoldiella* sp.) were frequently encountered in all crab size classes (Table 1). The tube-building polychaetes Maldanidae, Oweniidae and *Pectinaria* sp. are common

taxa of soft-bottom macrofauna in Porsangerfjord (Fuhrmann et al. 2015) and were also frequently consumed by king crabs (Table 1). *Spiochaetopterus typicus* was mostly encountered in medium and large crabs (Table 1). *Ctenodiscus crispatus*, the mud sea star, was mainly eaten by large crabs (Table 1) and, when encountered, almost filled the entire stomach, resulting in a high mean importance index (3.0) (Fig. 2). Sea urchins *Strongylocentrotus droebachienses* were consumed by both small and large crabs (27.3% of all crabs) but were on average less important than bivalves as prey (Fig. 2). Crustacean prey consisted mostly of small Amphipoda, which were encountered in all size classes of crabs (Table 1). Analysis showed that 56.8% of the crabs had algae in their stomachs, and at shallow stations, algae would make up a large proportion of stomach content. Despite this, algae had a low mean importance index (1.2) (Fig. 2). Plastic, mostly fibers, was found in 37.9% of crab stomachs analyzed.

Permutational multivariate analysis of variance revealed differences in diet composition between crab size classes (pseudo-$F_{2,131}$ = 3.29, p = 0.001), but sex and interaction terms were not significant (p ≥ 0.905). Multivariate diet composition was further investigated using NMDS (Fig. 3). The ordination had a stress of 0.168, providing a moderate representation of variance in the data. CL and depth gave significant fits to the ordination (R^2 = 0.15 and 0.12, p ≤ 0.002), indicating that crabs of similar size fed on similar prey and showing the effect of foraging at different depths (Fig. 3). Small crabs from the shallow sill location towards the inner fjord ate littoral species, such as Bryozoa, sea urchins, littoral gastropods, Polyplacophora and Isopoda (Fig. 3, Table 1), whereas Sipuncula, Ascidiacea, Bryozoa and the small crustacea Cumacea and Tanaidacea were more characteristic prey for crabs caught at deeper middle and outer fjord locations (Fig. 3).

Stable isotopes

Mean stable isotope values of crabs were −17.5 ± 0.53‰ for δ^{13}C and 10.9 ± 0.65‰ for δ^{15}N. The SEA$_c$ of crab size classes overlapped (Fig. 4), but niche width based on SEA simulations (Fig. S3 in the Supplement) was larger for the smallest crab size class compared to the largest crab size class (probability = 0.99) and also tended to be larger compared to the medium size class (probability = 0.90). There was no significant difference in δ^{15}N between crab size classes ($F_{2,157}$ = 0.85, p = 0.429) or sexes ($F_{1,157}$ = 3.78, p = 0.054).

Table 1. Frequency of occurrence (%) of prey items found in red king crab stomachs by size class. Prey categories are presented to their lowest level of identification. The 10 most frequent stomach items for each size class are marked in **bold**

Phylum/ item	Subphylum	Class	Prey item	Frequency of occurrence (%)		
				0–70 mm	71–110 mm	111–147 mm
Algae				**62.5**	**53.3**	**53.8**
Annelida		Polychaeta	Polychaeta (unid.)	16.7	6.7	2.6
			Lumbrineridae	4.2	2.2	2.6
			Maldanidae	**52.1**	**48.9**	**66.7**
			Nothria conchylega	0.0	2.2	2.6
			Oweniidae	**31.3**	**53.3**	**51.3**
			***Pectinaria* sp.**	25.0	**35.6**	**56.4**
			Pholoe sp.	2.1	0.0	0.0
			Polynoidae	16.7	13.3	17.9
			Phyllodocidae	2.1	0.0	0.0
			Serpulidae	0.0	0.0	2.6
			Spiochaetopterus typicus	14.6	**31.1**	**33.3**
			Syllidae	6.3	11.1	20.5
Arthropoda	Chelicerata	Arachnida	Acarina (Mites)	8.3	0.0	0.0
		Pycnogonida	*Pycnogonum* sp.	0.0	0.0	2.6
	Crustacea	Crustacea (unid.)		14.6	8.9	12.8
		Malacostraca	Amphipoda	20.8	28.9	30.8
			Cumacea	12.5	6.7	7.7
			Decapoda (unid.)	6.3	4.4	2.6
			Munida sp.	0.0	0.0	7.7
			Isopoda	4.2	2.2	0.0
			Tanaidacea	0.0	2.2	0.0
		Maxillopoda	Copepoda	14.6	20.0	5.1
			Sessilia (Cirripedia)	0.0	2.2	0.0
		Ostracoda		18.8	0.0	0.0
Brachiopoda				0.0	2.2	0.0
Bryozoa			**Bryozoa (unid.)**	**35.4**	4.4	7.7
			Porella sp.	0.0	2.2	0.0
Chordata	Tunicata	Ascidiacea	Ascidiacea	27.1	11.1	0.0
	Vertebrata	Actinopterygii	Actinopterygii	2.1	2.2	2.6
Cnidaria		Hydrozoa	Hydrozoa	22.9	6.7	15.4
Echinodermata			Echinodermata (unid.)	16.7	13.3	2.6
		Asteroidea	*Ctenodiscus crispatus*	0.0	4.4	20.5
		Echinoidea	***Strongylocentrotus droebachiensis***	**35.4**	13.3	**33.3**
		Holothuroidea	Holothuroidea	4.2	0.0	2.6
		Ophiurida	*Ophiopholis aculeata*	10.4	2.2	0.0
			Ophiura albida	2.1	0.0	0.0
			Ophiura sp.	0.0	2.2	0.0
			Ophiuroidea (unid.)	25.0	13.3	12.8
Eggs				4.2	2.2	10.3
Foraminifera				**54.2**	**42.2**	**53.8**
Mollusca		Bivalvia	Bivalvia (unid.)	16.7	8.9	12.8
			Anomiidae	18.8	13.3	12.8
			Astarte sp.	25.0	15.6	5.1
			***Bathyarca* sp.**	20.8	**31.1**	**33.3**
			Cardiidae (unid.)	8.3	8.9	7.7
			Crenella decussata	10.4	8.9	0.0
			Hiatella arctica	6.3	0.0	0.0

Table 1 (continued)

| Phylum/ item	Subphylum	Class	Prey item	Frequency of occurrence (%)		
				0–70 mm	71–110 mm	111–147 mm
			Musculus niger	0.0	2.2	0.0
			Mya truncata	0.0	0.0	7.7
			Mytilidae (unid.)	12.5	6.7	10.3
			Mytilus sp.	2.1	4.4	0.0
			Nucula sp.	18.8	26.7	17.9
			Nuculana sp.	22.9	13.3	7.7
			Parvicardium minimum	10.4	6.7	15.4
			Tellinidae	4.2	6.7	15.4
			Thyasiridae	0.0	4.4	0.0
			Yoldia hyperborea	2.1	2.2	2.6
			***Yoldiella* sp.**	**52.1**	**51.1**	**48.7**
		Gastropoda	**Gastropoda (unid.)**	**29.2**	24.4	7.7
			Buccinum sp.	2.1	2.2	0.0
			Margaritidae	25.0	20.0	5.1
			Naticidae	20.8	11.1	23.1
			Testudinalia testudinalis	2.1	0.0	0.0
		Polyplacophora	Polyplacophora (unid.)	18.8	0.0	5.1
			Tonicella sp.	16.7	0.0	0.0
		Scaphopoda	Dentaliidae	0.0	4.4	2.6
Plastic				**35.4**	**37.8**	**41.0**
Porifera				12.5	6.7	0.0
Sipuncula				10.4	4.4	12.8
Unidentified				**58.3**	**48.9**	**64.1**
Wood/plants				10.4	13.3	15.4
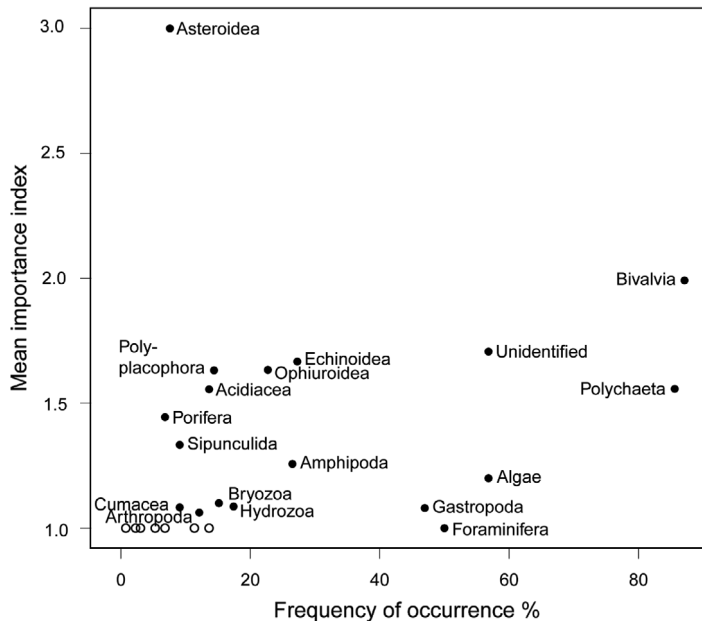
Fig. 2. Prey importance in red king crab (RKC) diet. Open circles (○, from left to right) represent (1) Brachiopoda, Cirripedia, Pycnogonida, Tanaidacea; (2) Actinopterygii, Holothuroidea, Isopoda, Scaphopoda; (3) Acarina; (4) eggs; (5) Decapoda, Ostracoda; (6) Echinodermata (unid.); (7) Copepoda

The filter-feeding scallop *Chlamys islandica*, which served as the baseline for trophic level (TL) estimation, had higher average $\delta^{15}N$ in the inner station than in the outer fjord (7.9 vs. 7.0, see Fig. S4b in the Supplement). A relative $\delta^{15}N$ enrichment in primary consumers from the inner fjord compared to the outer fjord was also indicated for other bivalves (Fig. S4b) and zooplankton (sampled at 4 stations in the middle and inner fjord). This was underpinned by sediment $\delta^{15}N$, which increased towards the inner fjord (in the range of approximately 1‰; Fig. S5 in the Supplement). There seemed, therefore, to be a baseline shift in $\delta^{15}N$ values as a function of sampling location along the fjord and/or with depth (Figs. S4 & S5). Consequently, we applied different baseline values in TL calculation to crabs caught in the inner and outer areas of the fjord. The average TL of the red king crab in Porsangerfjord was estimated to be 3.1 (range 2.7–3.5, n = 161). Crabs in the smallest size class (<70 mm) had a marginally but significantly lower TL than those in the larger size classes (2.96 vs. 3.12, $F_{2,157} = 17.55$, p < 0.001) (Fig. 5), and there was a small difference between sexes ($F_{1,157} = 4.0$, p = 0.047). There was no significant shift in $\delta^{13}C$ within
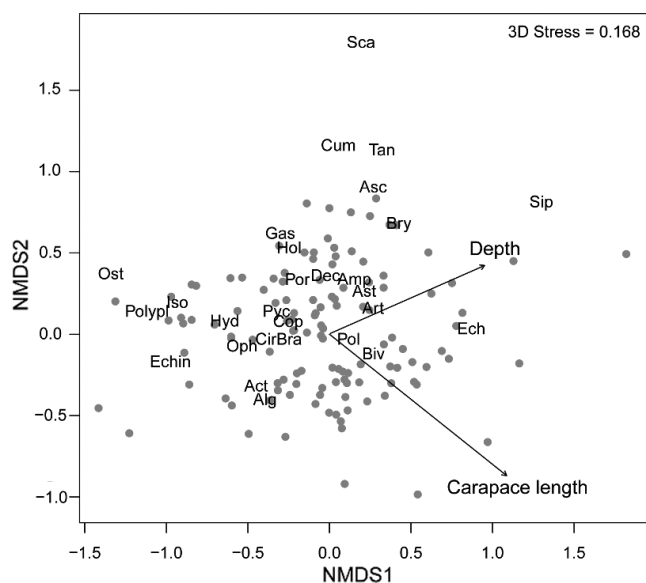
Fig. 3. Non-metrical multidimensional scaling (NMDS) (axes 1 and 2) of diet composition in red king crabs from stomach content analysis. Crab carapace length and depth were fitted to the ordination and are indicated by the vector. Act: Actinopterygii; Amp: Amphipoda; Asc: Ascidiacea; Art: Arthropoda (unid.); Ast: Asteroidea; Biv: Bivalvia; Bra: Brachiopoda; Bry: Bryozoa; Cir: Cirripedia; Cop: Copepoda; Cum: Cumacea; Dec: Decapoda; Echin: Echinoidea; Ech: Echinodermata (unid.); Gas: Gastropoda; Hol: Holothuroidea; Hyd: Hydroida; Iso: Isopoda; Oph: Ophiurida; Ost: Ostracoda; Pol: Polychaeta; Polypl: Polyplacophora; Por: Porifera; Pyc: Pycnogonida; Sca: Scaphopoda; Sip: Sipunculida; Tan: Tanaidacea
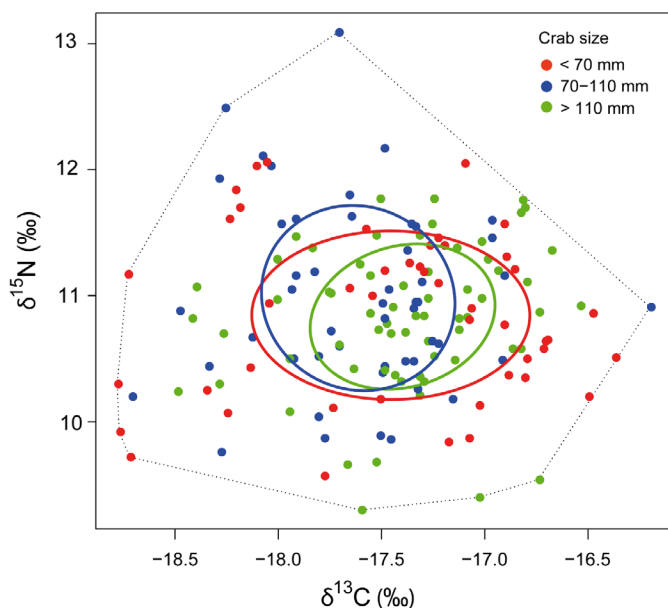

Fig. 4. Isotopic niche of red king crab size classes. The convex hull is depicted by the dotted line. Ellipses are sample size corrected standard ellipses after Jackson et al. (2011). δ^{13}C: stable carbon isotope; δ^{15}N: stable nitrogen isotope
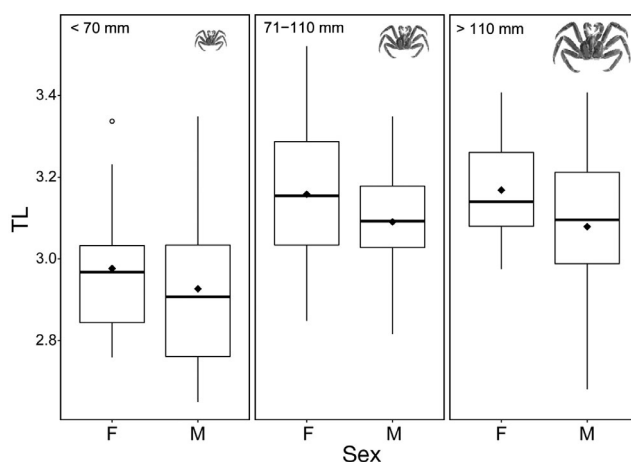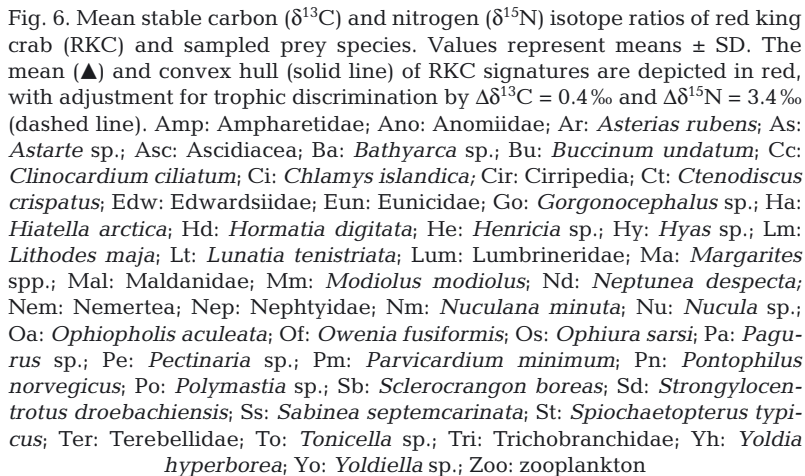

Fig. 5. Trophic level (TL) for size classes of red king crab in Porsangerfjord. Boxplots show median (solid line), mean (◆), 25th and 75th percentiles (box), 1.5 × interquartile range (whiskers) and outliers (O)

crab size classes ($F_{1,158} = 0.027$, p = 0.871) or between sexes ($F_{1,158} = 0.876$, p = 0.351).

Sampling depth was not included in the models because depth and crab size were interrelated and small crabs were only present at shallow stations.

Mean δ^{15}N slightly decreased with depth (rho = −0.189, p = 0.016), while there was no depth relation for δ^{13}C (rho = −0.08, p = 0.311). Moran's I index for both δ^{13}C and δ^{15}N indicated significant spatial autocorrelation (Table S2 in the Supplement), and the variogram for δ^{15}N showed a clear increase in semivariance with distance (Fig. S6 in the Supplement). This means that crabs sampled in close distance to each other were more similar in their isotopic composition. Despite having high δ^{15}N, crabs from the innermost shallow stations also had low δ^{13}C. Next to these local effects, we found that in crabs where both stable isotope signatures and stomach data were available (n = 57), δ^{13}C (but not δ^{15}N) was significantly related to multivariate diet composition ($R^2 = 0.28$, p < 0.001, Fig. S7 in the Supplement). Crabs feeding on littoral taxa such as Echinoidea and Polyplacophora, most of which were caught at the shallow sill location, were also more enriched in ^{13}C.

Isotopic compositions of potential prey species ranged over approximately 2 TLs (Fig. 6, Table S1 in the Supplement). We inspected probable prey resources by plotting fractionation-adjusted red king crab signatures together with prey signatures (Fig. 6). Commonly, exploited food resources are expected to fall within the adjusted convex hull of the red king crab. The filter-feeding bivalves *Chlamys islandica*, *Yoldia hyperborea* and *Nuculana minuta*

Fig. 6. Mean stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of red king crab (RKC) and sampled prey species. Values represent means ± SD. The mean (▲) and convex hull (solid line) of RKC signatures are depicted in red, with adjustment for trophic discrimination by $\Delta\delta^{13}C = 0.4‰$ and $\Delta\delta^{15}N = 3.4‰$ (dashed line). Amp: Ampharetidae; Ano: Anomiidae; Ar: *Asterias rubens*; As: *Astarte* sp.; Asc: Ascidiacea; Ba: *Bathyarca* sp.; Bu: *Buccinum undatum*; Cc: *Clinocardium ciliatum*; Ci: *Chlamys islandica*; Cir: Cirripedia; Ct: *Ctenodiscus crispatus*; Edw: Edwardsiidae; Eun: Eunicidae; Go: *Gorgonocephalus* sp.; Ha: *Hiatella arctica*; Hd: *Hormatia digitata*; He: *Henricia* sp.; Hy: *Hyas* sp.; Lm: *Lithodes maja*; Lt: *Lunatia tenistriata*; Lum: Lumbrineridae; Ma: *Margarites* spp.; Mal: Maldanidae; Mm: *Modiolus modiolus*; Nd: *Neptunea despecta;* Nem: Nemertea; Nep: Nephtyidae; Nm: *Nuculana minuta*; Nu: *Nucula* sp.; Oa: *Ophiopholis aculeata*; Of: *Owenia fusiformis*; Os: *Ophiura sarsi*; Pa: *Pagurus* sp.; Pe: *Pectinaria* sp.; Pm: *Parvicardium minimum*; Pn: *Pontophilus norvegicus*; Po: *Polymastia* sp.; Sb: *Sclerocrangon boreas*; Sd: *Strongylocentrotus droebachiensis*; Ss: *Sabinea septemcarinata*; St: *Spiochaetopterus typicus*; Ter: Terebellidae; To: *Tonicella* sp.; Tri: Trichobranchidae; Yh: *Yoldia hyperborea*; Yo: *Yoldiella* sp.; Zoo: zooplankton

and the sea urchin *Strongylocentrotus droebachiensis* were centered close to the crab mean. Filter feeders such as Ascidiacea, Porifera and *Gorgonocephalus* sp. were more depleted in carbon (Fig. 6, Table S1 in the Supplement). Small infaunal ascidians were frequently found in stomachs of small crabs (Table 1), but the ascidians analyzed for stable isotopes were mostly larger species with similar signatures to other predatory suspension feeders (e.g. *Gorgonocephalus* sp., Edwardsiidae) (Fig. 6, Table S1). The detritivorous polychaetes Maldaniidae, *Pectinaria* sp. and *Spiochaetopterus typicus* and the mud

sea star *Ctenodiscus crispatus* were enriched in ^{15}N (Fig. 6, Table S1 in the Supplement) and fell outside the convex hull of the red king crab. Therefore, these prey were indicated to be of minor relevance in the crab′s diet, despite their importance in stomachs.

SEAc overlap with other species

The isotopic niche of red king crab, defined as the SEA_c, was found to overlap with that of predatory sea stars *Asterias rubens* and *Henrica* sp. and, to some extent, with that of the native stone crab *Lithodes maja*, hermit crabs *Pagurus* sp. and large predatory snails *Neptunea despecta* and *Buccinum undatum* (Fig. 7, Table S3 in the Supplement). The single data points available for the sea star *Henricia* sp., spider crab *Hyas* sp. and mud shrimp *Pontophilus norvegicus* all lay within the SEA_c of red king crab, indicating some resource overlap (Fig. 7). There was no overlap between the crab SEA_c and the demersal fish species investigated, although the convex hull area of red king crab (Fig. 7) overlapped with the SEA_c of the European plaice *Pleuronectes platessa* and the long rough dab *Hippoglossoides platessoides* and that of the predatory snail *Lunatia tenistriata* and the deep-water shrimp *Pontophilus borealis* (Fig. S8 in the Supplement).

Uncertainty around Bayesian SEA estimated for the competitor species was largely due to relatively small sample sizes (Fig. S9 in the Supplement).

DISCUSSION

We studied the trophic niche of red king crabs that have recently invaded Porsangerfjord, northern Norway. Diet composition indicated that the crab has a generalist, opportunistic feeding strategy and that major prey items were polychaetes, small bivalves and sea urchins. Variation in resource use was
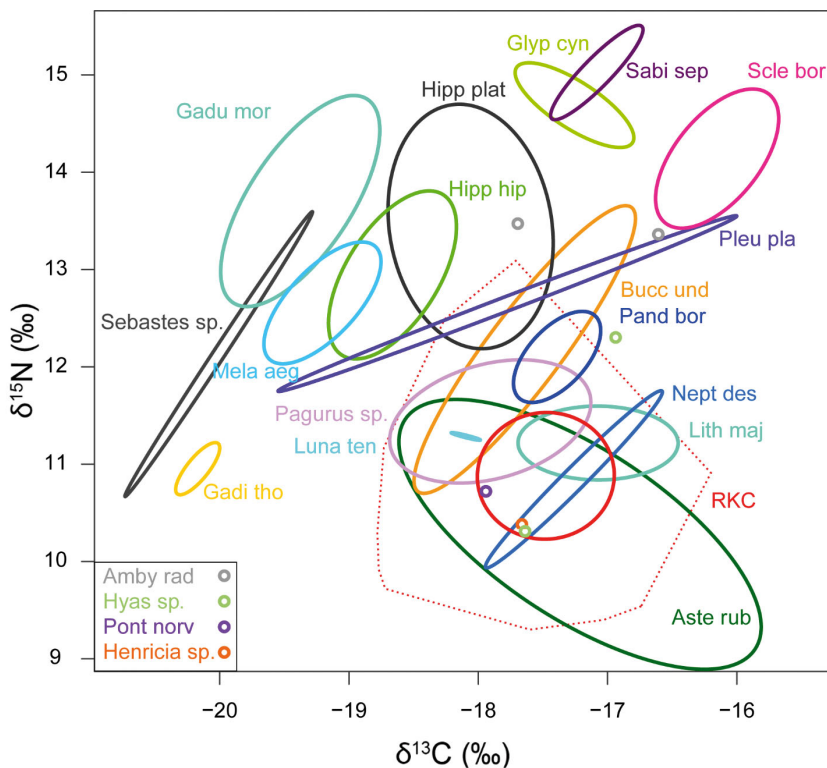
Fig. 7. Isotopic niche of red king crab and possible competitors in the benthic food web of Porsangerfjord. Data are represented by sample-size corrected standard ellipses, after Jackson et al. (2011). Red king crab convex hull is depicted by the dotted line (solid hull in Fig. 6). Single data points are represented by dots. δ^{13}C: stable carbon isotope; δ^{15}N: stable nitrogen isotope; Amby rad: *Amblyraja radiata* (thorny skate); Aste rub: *Asterias rubens*; Bucc und: *Buccinum undatum*; Gadi tho: *Gadiculus thori* (silvery cod); Gadu mor: *Gadus morhua* (cod); Glyp cyn: *Glyptocephalus cynoglossus* (witch flounder); Hipp pla: *Hippoglossoides platessoides* (long rough dab); Hipp hip; *Hippoglossus hippoglossus* (halibut); RKC: *Paralithodes camtschaticus* (red king crab); Lith maj: *Lithodes maja* (stone crab); Luna ten: *Lunatia tenistriata*; Mela aeg: *Melanogrammus aeglefinus* (haddock); Nept des: *Neptunea despecta*; Pand bor: *Pandalus borealis*; Pleu plat: *Pleuronectes platessa* (European plaice); Pont norv: *Pontophilus norvegicus*; Sab sep: *Sabinea septemcarinata*; Scle bor: *Sclerocrangon boreas*

mainly due to foraging in different areas at different depths, evident from isotopic signatures and stomach contents. We did not find pronounced evidence for an ontogenetic niche shift, but TL increased slightly with crab size. Stable isotope analysis indicated resource overlap with other benthic predatory invertebrates, mainly crabs, asteroids and predatory gastropods.

Feeding strategy

Sampled red king crabs seemed to have been generally well fed, with few empty stomachs being

found. Feeding activity is typically higher in small than in large crabs (Jewett & Feder 1982, Zhou et al. 1998), and stomach fullness was found to decrease with increasing crab size. A wide range of invertebrate prey items was discovered in stomachs, supporting the hypothesis that the red king crab is an opportunistic generalist predator, in both invaded (Sundet et al. 2000, Britayev et al. 2010) and its native areas (Jewett & Feder 1982). Feeding plasticity has proven to be a successful strategy in invasive fish (Kadye & Booth 2012) and is also likely to be beneficial for crustaceans in a new environment (Snyder & Evans 2006). In laboratory experiments, red king crabs are highly adaptable at handling offered prey (N. Mikkelsen pers. comm.), and their ability to scoop sediment for infaunal prey (Jørgensen 2005, Mikkelsen & Pedersen 2012) means they can effectively feed on tubiculous polychaetes that are inaccessible to most fish. Small infaunal bivalves were frequent prey items (see also Jewett & Feder 1982) and are some of the most abundant taxa in soft-bottom environments in Porsangerfjord (Fuhrmann et al. 2015). Remains of larger bivalves were rarely found in stomachs, but the crabs may have been able to extract soft tissue using the chela and leave identifiable hard parts behind (Jørgensen 2005). Stable isotope analysis identified *Chlamys islandica* and *Modiolus modiolus* as potential prey for crabs in Porsangerfjord, and field observations made during August 2012 and July 2014 showed crabs fed on mussel beds in shallow water (Video S1 at www.int-res.com/articles/suppl/m565p113_supp/). Stomach contents and stable isotope analysis pointed to sea urchins *Strongylocentrotus droebachiensis* as being an important part of the diet of both large and small crabs. Predation on sea urchins was probably opportunistic, because occurrence in crab stomachs was high at a few shallow stations where sea urchins were common. Consumption of sea urchins may depend on the availability of other prey because crabs may prefer mollusks over echinoids (Jørgensen & Primicerio 2007).

Accurate assessment of dietary contribution using stable isotope analysis is difficult for predators that have multiple possible sources of prey (Phillips & Gregg 2003, Newsome et al. 2012). One way to circumvent this problem is to group prey species and apply mixing models, but the combining of sources introduces additional uncertainty (Ward et al. 2011). A visual analysis seems to reveal a lack of prey species towards the right of the adjusted convex hull of the crab (Fig. 6), with most possible prey species more enriched in ^{15}N (and depleted in ^{13}C) than expected. This could be an artefact caused by a deviance from assumed fractionation factors or because some prey sources were not included in the analysis. Tube-building polychaetes in particular fell outside the convex hull of crabs, despite being a frequent prey found in stomachs. Depending on species, tissue, food type and quality, values for isotopic fractionation may deviate from the accepted values of 0.8‰ for $\Delta\delta^{13}C$ and 3.4‰ for $\Delta\delta^{15}N$ (Pinnegar & Polunin 1999, Vander Zanden & Rasmussen 2001, Yokoyama et al. 2005), and fractionation in anomuran crab tissues is largely unknown. High enrichment factors, especially in $\delta^{13}C$, have been observed in some decapod crustaceans (Rudnick & Resh 2005, Yokoyama et al. 2005) and could explain why adjusted red king crab signatures corresponded little with common prey such as polychaetes. Most of the prey species found in stomachs were also sampled for stable isotope analysis. However, we did not include algae as a potential food source. Macroalgae are of low energetic value (Griffen et al. 2015) but may occasionally supplement the crab's diet and could contribute to higher $\delta^{13}C$ values in crabs. Despite high frequency of occurrence in crab stomachs, algae rarely dominated stomach contents and were likely not a targeted prey item but were probably ingested by crabs while sieving the sediment for other prey. Similar findings were reported by Jewett & Feder (1982). Algae have been shown to vary considerably in isotopic composition (Fredriksen 2003), which makes tracing them as a food resource more difficult (Nilsen et al. 2008).

Cannibalism among red king crabs has been documented under laboratory conditions (Borisov et al. 2007, Stoner et al. 2010) and is assumed to be one of the major causes for failure in hatchery grow-out in native areas (Epelbaum et al. 2006). We did not find any evidence of cannibalism, and cannibalism may not be an important source of mortality of red king crabs in Porsangerfjord at the time of this study.

The relative high frequency of plastic in the stomachs of red king crab highlights the problem of contamination and accumulation of microplastics in marine sediments (Thompson et al. 2004). There is evidence that other species that feed on benthos, such as the Norway lobster (Murray & Cowie 2011) and Atlantic cod (Bråte et al. 2016), also ingest plastic. Crabs likely ingest plastic when filtering sediment searching for prey; consequences of ingestion, toxicity and biotransfer of plastic to higher TLs are largely unknown (Wright et al. 2013).

Isotopic niche width and variation in resource use

Prey selectivity and niche width might be expected to change with crab size, because a larger range of prey becomes available as crabs increase in size (Jørgensen 2005, Jørgensen & Primicerio 2007). Ontogenetic diet shifts related to an increase of chela size and handling capacity occur in other decapods, such as the American lobster (Sainte-Marie & Chabot 2002, Hanson 2009). However, in our study, isotopic niches largely overlapped between crab size classes, and the size of the ellipse area (SEA_c) was actually smallest in adult crabs. Data from a few at shallow-water sampling stations added to the variation in isotopic composition of juvenile crabs, whereas large adult crabs were rarely caught at these stations. Stable isotope and diet composition did not differ between males and females. A difference found by a previous study was mainly ascribed to sexual aggregation in foraging areas (Sundet et al. 2000) rather than a size-related difference caused by larger males. Differences in stable isotope signatures of red king crabs between sampling areas were generally more distinct than differences between size classes, and this was indicated by spatial correlation of stable isotope signatures (Moran's *I*; Table S2 in the Supplement). Thus, the variation in diet and stable isotope signatures found in our study are probably less a reflection of size difference than habitat choice throughout the life cycle and aggregation at certain depths and in specific foraging areas. Following larval settlement, small crabs remain in shallow waters for 2 to 3 yr (Jørgensen & Nilssen 2011), sometimes forming dense aggregations or pods (Dew 1990), and simultaneous feeding activity can be observed (Video S1). In their native areas, mature crabs generally remain below 100 m depth during the summer and autumn and migrate into shallower waters in late winter, followed by mating and breeding in springtime (Stone et al. 1992). At this time, juvenile and adult red king crabs may share similar food resources. Periodic returns to specific foraging areas

have been documented for female crabs in Alaska (Stone et al. 1992). Whether red king crabs present in Norwegian fjords follow pronounced migrations is not known and may depend on time of invasion. Larger crabs (>70 mm) in this study were caught slightly deeper in the autumn (October), and since depth was related to δ^{15}N and diet composition in stomachs, this may indicate a diet shift related to seasonal migration. There are, however, indications for high individual differences, and movement patterns of red king crabs in Norwegian waters may be more restricted due to higher complexity in bottom topography (Jørgensen et al. 2007, Windsland et al. 2014).

An ontogenetic change in diet due to a habitat shift may be reflected in δ^{13}C (Hammerschlag-Peyer et al. 2011). In our study, carbon isotopes seemed to show very local patterns related to foraging site, possibly concealing overall effects across size classes. δ^{13}C was significantly related to diet composition in stomachs, indicating that individual differences in diet persisted over time, which could be due to site fidelity or individual prey specialization. The fact that large crabs, despite great motility, had spatial similarity in isotopic composition points towards the former. However, experimental work has shown that crabs show differences in handling and prey preference (Michelsen 2011), and individual specialization would result in variation among individuals and increase isotopic niche width (Bearhop et al. 2004, Vander Zanden et al. 2010).

Relative enrichment in δ^{15}N and low δ^{13}C in crabs sampled in the inner fjord could have arisen from a shift in baseline (see 'Discussion: Baseline shift') or due to the consumption of fish not detected by stomach content analysis. Dead post-spawned capelin make up a part of the diet of crabs close to capelin spawning areas along the Finnmark coast (Mikkelsen & Pederson 2017). It is not known whether the innermost Porsangerfjord is a spawning site for capelin and would give crabs access to dead fish.

Trophic position

We estimated the TL of red king crabs in Porsangerfjord to be 3.1, which represents the trophic position of a secondary consumer or first-order predator. Differences in the range of δ^{15}N in the red king crabs examined in our study corresponded to roughly 1 TL. To our knowledge, no studies have addressed the trophic position of red king crabs in the Barents Sea, whereas a food web model for the Bering Sea gave a slightly higher trophic position of 3.4 for adult

king crabs *Paralithodes* spp. (Aydin et al. 2007). The trophic position of an organism has implications for biomass, production, fishery yield and, in the case of invasive species, its potential impact. It has been suggested that the red king crab's omnivorous feeding habits result in lower impacts on a native community than might be expected from a specialized predator (Britayev et al. 2010). This may be true regarding single-species extinctions but can probably not be generalized with respect to ecosystem effects that include changes in production processes, competition with native species and trophic cascades (see Vander Zanden et al. 1999). In feeding across multiple TLs, the red king crab's effects on the food web may be widespread and difficult to predict (Snyder & Evans 2006, Boudreau & Worm 2012). Considered alone, trophic position may be a low predictor of impact (Ricciardi et al. 2013), and decapod predators can play key roles in ecosystems, structuring benthic habitats via top-down effects (Snyder & Evans 2006), e.g. by suppressing herbivory (Lafferty 2004, Boudreau & Worm 2012, Jackson et al. 2014). Local consumption of sea urchins by red king crabs in Porsangerfjord might suppress herbivory to the extent that it facilitates algal regrowth (see Steneck et al. 2013, Fagerli et al. 2014).

We found a small increase of TL with size, probably of low ecological significance. However, in benthic generalist predators, size-related diet shifts may not necessarily be reflected in isotopic composition. For example, large crabs are able to use their claws to crush large bivalves and sea urchins, both of which occupy a low TL and are relatively low in δ^{15}N. Size-related increases in δ^{15}N in benthic invertebrates (serving as prey for crabs in this case) are mostly a result of intraspecific increase in TL rather than differences between large and small species (Jennings et al. 2002) and may therefore not reflect the selection of large vs. small prey species in size classes of red king crab. Consequently, most studies on decapod crabs fail to detect clear increases in TL with size but emphasize the importance of foraging area for differences in diet (Bodin et al. 2007, Divine et al. 2017).

Baseline shift

Accurate estimation of TL depends on correct increment factors and a reliable baseline (Post 2002, Barnes et al. 2009, Layman et al. 2012, Jennings & van der Molen 2015). Average trophic fractionation used in our study for the calculation of crab TL (3.4‰

for $\Delta\delta^{15}N$; Post 2002) is a generalization, and several studies have shown deviations from this (Hussey et al. 2014). Variation in baselines is often a result of different water mass properties (Jennings & Warr 2003, Barnes et al. 2009, Hedeholm et al. 2012) and/or depth (Jennings & Warr 2003, Iken et al. 2005, Bergmann et al. 2009). We found that $\delta^{15}N$ in filter-feeding bivalve species varied considerably in our study area (see also Xu et al. 2011) possibly as a result of variation along the fjord and not only depth, which was supported by sediment signatures becoming more enriched in ^{15}N towards the inner fjord. Even though our study area is relatively small, different water masses influence the fjord: warm Atlantic coastal water in the outer fjord and cold Arctic water in the inner areas. The taxonomic composition of the phytoplankton in Porsangerfjord changes with time (Eilertsen & Frantzen 2007) and space (Hegseth et al. 1995), and these changes would act as a source of variation in the baseline (Søreide et al. 2006). In addition, terrigenous material brought to the innermost fjord by rivers could influence isotopic composition of primary producers, resulting in high $\delta^{15}N$ (Iken et al. 2010) and low $\delta^{13}C$ (Feder et al. 2011). Sampling size did not allow us to account for uncertainty in $\delta^{13}C_{base}$ and $\delta^{15}N_{base}$, and future studies may consider a more extended baseline sampling, with particulate organic matter (POM) as a plausible alternative to bivalves, which were scarce at deep outer fjord stations.

Trophic pathways and overlap in isotopic niche

The isotopic signatures of benthic consumers indicated a high diversity in feeding types and a complex food web with various food sources available. Stable isotope signatures of king crabs in Porsangerfjord indicated a benthic/littoral carbon source, and crabs likely rely on carbon originating from benthic detritus or reworked material, because typical pelagic POM consumers (zooplankton, Porifera and Ascidiacea) were more depleted in ^{13}C. The high $\delta^{15}N$ recorded in some deposit feeders (e.g. Maldanidae, *Ctenodiscus crispatus*), the suspension-feeding bivalve *Bathyarca* sp. and predatory shrimps *Sabinea septemcarinata* and *Sclerocrangon boreas* suggests a reliance on detritus pathways (Caraco et al. 1998, Iken et al. 2005, Mintenbeck et al. 2007) or selective feeding at higher TLs (e.g. Birkely & Gulliksen 2003). Subsurface deposit feeders may be enriched in ^{15}N and ^{13}C due to the use of refractory and degraded organic matter (Carlier et al. 2007). Benthic carbon can be important for cod and other demersal fish

(Nilsen et al. 2008) that prey on both planktivores and benthivores (Pedersen et al. 2016). In our study, cod and haddock were more depleted in carbon than, for example, flatfish and seemed more reliant on pelagic pathways. As they are known to feed on benthic invertebrates (Jiang & Jørgensen 1996, Pedersen et al. 2008), haddock and cod have been proposed as being possible competitors to the Barents Sea red king crab (Falk-Petersen et al. 2011). Cod, which has been a major predator in Porsangerfjord, occupied a high TL (ca. 4), and the isotopic niches (defined as SEA_c) of cod and haddock did not overlap with red king crab. However, haddock is known to feed on detritivorous polychaetes in Porsangerfjord (T. Pedersen unpubl. data) and probably shares this resource with the red king crab. There was little evidence of isotopic niche overlap between crabs and other investigated fish, likely due to the capability of the fish to capture mobile prey and consume high TL predatory benthos and pelagic species.

The core isotopic niche (SEA_c) of red king crab in Porsangerfjord was found to overlap with that of other decapod crustaceans, such as the native stone crab *Lithodes maja*, which has previously been suggested as a probable competitor (see Falk-Petersen et al. 2011). We also found an overlap in crab SEA_c with predatory sea stars (e.g. *Asterias rubens*) and, to a smaller degree, large predatory snails (e.g. *Buccinum undatum* and *Neptunea despecta*). These species feed mostly on bivalves but may also consume polychaetes (Pearce & Thorson 1967, Allen 1983). Being both putative prey for and competitors of the crab, all of these species can be expected to be affected by the invasion. Supporting this, data from yearly whelk-trap samples in Porsangerfjord from 2005 to 2008 indicated a decrease in abundance of *Buccinum undatum* (E. M. Nilssen unpubl. data). Competition could also arise with small benthic fishes, such as sculpins, that are present in inner area of Porsangerfjord. The sculpins *Artediellus atlanticus* and *Myoxocephalus scorpius* feed on small benthic invertebrates, mostly polychaetes (Källgren et al. 2015). However, their isotopic niche shows marginal overlap with that of the red king crab, and their TL was estimated to be slightly higher due to consumption of predatory invertebrates.

Low sample size in possible competitors and high diversity of food sources with sometimes similar isotopic signatures demands care when interpreting SEA overlap. The SEA represents the core trophic niche of a population (Jackson et al. 2011), but low sample sizes introduce uncertainty into estimated standard ellipses (Fig. S9 in the Supplement) even

when sample size corrected (SEA$_c$) (Syväranta et al. 2013). An increase in sample size would be desirable to reveal more about how local factors influence variation in isotopic niches of benthic invertebrate predators. Competition with the king crab could, for example, arise in areas of co-occurrence not covered by our sampling or may arise under limitation of food. Overlap with the convex hull area of red king crabs indicated this could be the case for the deep-water shrimp *Pandalus borealis,* the European plaice and the long rough dab. The SEA method suffers from weaknesses arising from possibly uneven distributions of individuals within the calculated niche space, meaning that despite considerable overlap, only a few individuals may actually share a common core isotopic niche (Swanson et al. 2015). On the other hand, small differences in prey resource proportions may result in isotopic niches failing to overlap when sample sizes are small.

We have analyzed only a small proportion of the species that contribute to the benthic food web of Porsangerfjord (disregarding, for example, bottom-feeding sea birds). One also has to keep in mind that this study represents a time point of invasion where the outer fjord has held a high red king stock since the middle 2000s, and whether isotopic niches of competitors present their original trophic niche remains unknown.

The ability of the red king crab to consume a wide range of taxa with different body sizes, including large bivalves and echinoderms, suggests that it occupies a niche that was not extensively used by any fish predator. Before the invasion of the red king crab into Porsangerfjord, only large asteroids, predatory gastropods, the stone crab *Lithodes maja* and the relatively rare Atlantic wolffish *Anarhicas lupus* (Falk-Petersen et al. 2010) may have preyed on large hard-shelled benthic invertebrates. Red king crab forages in several habitats, from the littoral to deeper coastal waters, and its prey species were from at least 3 TLs, including macroalgae, detritivores, grazers and epibenthic predators. Thus, effects of the red king crab on the ecosystem are likely complex and challenging to predict.

LITERATURE CITED

Abrantes KG, Barnett A, Bouillon S (2014) Stable isotope-based community metrics as a tool to identify patterns in food web structure in east African estuaries. Funct Ecol 28:270–282

Allen PL (1983) Feeding behaviour of *Asterias rubens* (L.) on soft bottom bivalves: a study in selective predation. J Exp Mar Biol Ecol 70:79–90

Aydin K, Gaichas S, Ortiz I, Kinzey D, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. NOAA Tech Memo NMFS-AFSC-178, US Dept of Commerce. https://core.ac.uk/download/files/542/14512136.pdf (accessed on 1 January 2016)

Barnes C, Jennings S, Barry JT (2009) Environmental correlates of large-scale spatial variation in the δ^{13}C of marine animals. Estuar Coast Shelf Sci 81:368–374

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012

Bergmann M, Dannheim J, Bauerfeind E, Klages M (2009) Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. Deep-Sea Res I 56:408–424

Birkely SR, Gulliksen B (2003) Feeding ecology in five shrimp species (Decapoda, Caridea) from an Arctic fjord (Isfjorden, Svalbard), with emphasis on *Sclerocrangon boreas* (Phipps, 1774). Crustaceana 76:699–715

Bodin N, Le Loc'h F, Hily C, Caisey X, Latrouite D, Le Guellec AM (2007) Variability of stable isotope signatures (δ^{13}C and δ^{15}N) in two spider crab populations (*Maja brachydactyla*) in western Europe. J Exp Mar Biol Ecol 343:149–157

Borisov RR, Epelbaum AB, Kryakhova NV, Tertitskaya AG, Kovatcheva NP (2007) Cannibalistic behavior in red king crabs reared under artificial conditions. Russ J Mar Biol 33:227–231

Boudreau SA, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. Mar Ecol Prog Ser 469:195–213

Bråte ILN, Eidsvoll DP, Steindal CC, Thomas KV (2016) Plastic ingestion by Atlantic cod (*Gadus morhua*) from the Norwegian coast. Mar Pollut Bull 112:105–110

Britayev TA, Rzhavsky AV, Pavlova LV, Dvoretskij AG (2010) Studies on impact of the alien red king crab (*Paralithodes camtschaticus*) on the shallow water benthic communities of the Barents Sea. J Appl Ichthyol 26:66–73

Caraco NF, Lampman G, Cole JJ, Limburg KE, Pace ML, Fischer D (1998) Microbial assimilation of DIN in a nitrogen rich estuary: implications for food quality and isotope studies. Mar Ecol Prog Ser 167:59–71

Carlier A, Riera P, Amouroux JM, Bodiou JY, Grémare A (2007) Benthic trophic network in the Bay of Banyuls-sur-Mer (northwest Mediterranean, France): an assessment based on stable carbon and nitrogen isotopes analysis. Estuar Coast Shelf Sci 72:1–15

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool

to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci 54: 726–738

Dew CB (1990) Behavioral ecology of podding red king crab, *Paralithodes camtschatica.* Can J Fish Aquat Sci 47: 1944–1958

Divine LM, Bluhm BA, Mueter FJ, Iken K (2017) Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and δ^{13}C and δ^{15}N stable isotopes. Deep-Sea Res II 135:124–136

Dvoretsky A, Dvoretsky V (2015) Commercial fish and shellfish in the Barents Sea: Have introduced crab species affected the population trajectories of commercial fish? Rev Fish Biol Fish 25:297–322

Eilertsen HC, Frantzen S (2007) Phytoplankton from two sub-Arctic fjords in northern Norway 2002–2004: I. Seasonal variations in chlorophyll *a* and bloom dynamics. Mar Biol Res 3:319–332

Epelbaum AB, Borisov RR, Kovatcheva NP (2006) Early development of the red king crab *Paralithodes camtschaticus* from the Barents Sea reared under laboratory conditions: morphology and behaviour. J Mar Biol Assoc UK 86:317–333

Fagerli CW, Norderhaug KM, Christie H, Pedersen MF, Fredriksen S (2014) Predators of the destructive sea urchin *Strongylocentrotus droebachiensis* on the Norwegian coast. Mar Ecol Prog Ser 502:207–218

Falk-Petersen IB, Kanapathippilai P, Primicerio R, Hansen TK (2010) Size, locality and seasonally related feeding preferences of common wolffish (*Anarhichas lupus* L.) from north-Norwegian waters. Mar Biol Res 6:201–212

Falk-Petersen J, Renaud P, Anisimova N (2011) Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea — a review. ICES J Mar Sci 68:479–488

Fanelli E, Azzurro E, Bariche M, Cartes JE, Maynou F (2015) Depicting the novel eastern Mediterranean food web: a stable isotopes study following Lessepsian fish invasion. Biol Invasions 17:2163–2178

Feder HM, Iken K, Blanchard AL, Jewett SC, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: an assessment using δ^{13}C and δ^{15}N analyses. Polar Biol 34:521–532

Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope (δ^{13}C and δ^{15}N) analysis. Mar Ecol Prog Ser 260:71–81

Fuhrmann MM, Pedersen T, Ramasco V, Nilssen EM (2015) Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. J Sea Res 106:1–13

Fukumori K, Oi M, Doi H, Takahashi D and others (2008) Bivalve tissue as a carbon and nitrogen isotope baseline indicator in coastal ecosystems. Estuar Coast Shelf Sci 79:45–50

Griffen BD, Vogel M, Goulding L, Hartman R (2015) Energetic effects of diet choice by invasive Asian shore crabs: implications for persistence when prey are scarce. Mar Ecol Prog Ser 522:181–192

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224

Hammerschlag-Peyer CM, Yeager LA, Araújo MS, Layman CA (2011) A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. PLOS ONE 6:e27104

Hanson JM (2009) Predator–prey interactions of American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence, Canada. NZ J Mar Freshw Res 43:69–88

Hedeholm R, Grønkjær P, Rysgaard S (2012) Feeding ecology of capelin (*Mallotus villosus* Müller) in West Greenland waters. Polar Biol 35:1533–1543

Hegseth E, Svendsen H, von Quillfeldt CH (1995) Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of fjords and coastal waters. Elsevier Science, Amsterdam, p 45–72

Hjelset AM, Sundet JH, Nilssen EM (2009) Size at sexual maturity in the female red king crab (*Paralithodes camtschaticus*) in a newly settled population in the Barents Sea, Norway. J Northwest Atl Fish Sci 41:173–182

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Mar Ecol Prog Ser 84:9–18

Hussey NE, MacNeil MA, McMeans BC, Olin JA and others (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17:239–250

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: evidence from δ^{13}C and δ^{15}N analysis. Polar Biol 28:238–249

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep-Sea Res II 57:71–85

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLOS ONE 7:e31757

Jackson MC, Jones T, Milligan M, Sheath D and others (2014) Niche differentiation among invasive crayfish and their impacts on ecosystem structure and functioning. Freshw Biol 59:1123–1135

Jennings S, van der Molen J (2015) Trophic levels of marine consumers from nitrogen stable isotope analysis: estimation and uncertainty. ICES J Mar Sci 72:2289–2300

Jennings S, Warr KJ (2003) Environmental correlates of large-scale spatial variation in the δ^{15}N of marine animals. Mar Biol 142:1131–1140

Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2002) Linking size-based and trophic analyses of benthic community structure. Mar Ecol Prog Ser 226:77–85

Jewett SC, Feder HM (1982) Food and feeding habits of the king crab *Paralithodes Camtschatica* near Kodiak Island, Alaska. Mar Biol 66:243–250

Jiang W, Jørgensen T (1996) The diet of haddock (*Melanogrammus aeglefinus* L.) in the Barents Sea during the period 1984–1991. ICES J Mar Sci 53:11–21

Jørgensen LL (2005) Impact scenario for an introduced decapod on Arctic epibenthic communities. Biol Invasions 7: 949–957

Jørgensen LL, Nilssen EM (2011) The invasive history, impact and management of the red king crab *Paralithodes camtschaticus* off the coast of Norway. In: Galil BS, Clark PF, Carlton JT (eds) In the wrong place — alien

marine crustaceans: distribution, biology and impacts. Springer, Dordrecht, p 521–536

Jørgensen LL, Primicerio R (2007) Impact scenario for the invasive red king crab Paralithodes camtschaticus (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian, native, epibenthic prey. Hydrobiologia 590:47–54

Jørgensen T, Løkkeborg S, Fernö A, Hufthammer M (2007) Walking speed and area utilization of red king crab (Paralithodes camtschaticus) introduced to the Barents Sea coastal ecosystem. Hydrobiologia 582:17–24

Kadye WT, Booth AJ (2012) Integrating stomach content and stable isotope analyses to elucidate the feeding habits of non-native sharptooth catfish Clarias gariepinus. Biol Invasions 14:779–795

Källgren EK, Pedersen T, Nilssen EM (2015) Food resource partitioning between three sympatric fish species in Porsangerfjord, Norway. Polar Biol 38:583–589

Lafferty KD (2004) Fishing for lobsters indirectly increases epidemics in sea urchins. Ecol Appl 14:1566–1573

Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Mar Ecol Prog Ser 448:131–141

Layman CA, Arrington DA, Montana CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM and others (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol Rev Camb Philos Soc 87:545–562

Michelsen HK (2011) Prey selection of the red king crab (Paralithodes camtschaticus) preying on lumpfish eggs (Cyclopterus lumpus), sea urchins (Strongylocentrotus droebachiensis) and scallops (Chlamys islandica). MS thesis, University of Tromsø. http://hdl.handle.net/10037/3392

Mikkelsen N, Pedersen T (2012) Invasive red king crab affects lumpsucker recruitment by egg consumption. Mar Ecol Prog Ser 469:87–99

Mikkelsen N, Pedersen T (2017) Invasive red king crabs feed on both spawned-out capelin and their eggs. Mar Ecol Prog Ser 563:139–155

Miljødirektoratet (2004) Råd til utforming av marin verneplan for marine beskyttede områder i Norge. Rådgivende utvalg for marin verneplan 30. juni 2004. (In Norwegian) www.miljodirektoratet.no/old/dirnat/multimedia/1831/Endelig_tilradning.pdf

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48:1135–1140

Mintenbeck K, Jacob U, Knust R, Arntz WE, Brey T (2007) Depth-dependence in stable isotope ratio δ^{15}N of benthic POM consumers: the role of particle dynamics and organism trophic guild. Deep-Sea Res I 54:1015–1023

Murray F, Cowie PR (2011) Plastic contamination in the decapod crustacean Nephrops norvegicus (Linnaeus, 1758). Mar Pollut Bull 62:1207–1217

Newsome SD, del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Newsome SD, Yeakel JD, Wheatley PV, Tinker MT (2012) Tools for quantifying isotopic niche space and dietary variation at the individual and population level. J Mammal 93:329–341

Nilsen M, Pedersen T, Nilssen EM, Fredriksen S (2008) Trophic studies in a high-latitude fjord ecosystem—a

comparison of stable isotope analyses (δ^{13}C and δ^{15}N) and trophic-level estimates from a mass-balance model. Can J Fish Aquat Sci 65:2791–2806

Orlov YI, Ivanov BG (1978) On the introduction of the Kamchatka king crab Paralithodes camtschatica (Decapoda: Anomura: Lithodidae) into the Barents Sea. Mar Biol 48:373–375

Oug E, Cochrane S, Sundet J, Norling K, Nilsson H (2011) Effects of the invasive red king crab (Paralithodes camtschaticus) on soft-bottom fauna in Varangerfjorden, northern Norway. Mar Biodiv 41:467–479

Pearce JB, Thorson G (1967) The feeding and reproductive biology of the red whelk, Neptunea antiqua (L.) (Gastropoda, Prosobranchia). Ophelia 4:277–314

Pedersen T, Ramsvatn S, Nilssen EM, Nilsen M and others (2016) Species diversity affects ecosystem structure and mass flows in fjords. Reg Stud Mar Sci 3:205–215

Pedersen T, Nilsen M, Nilssen EM, Berg E, Reigstad M (2008) Trophic model of a lightly exploited cod-dominated ecosystem. Ecol Model 214:95–111

Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269

Pinnegar JK, Polunin NVC (1999) Differential fractionation of δ^{13}C and δ^{15}N among fish tissues: implications for the study of trophic interactions. Funct Ecol 13:225–231

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org (accessed on 1 January 2016)

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282

Rudnick D, Resh V (2005) Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod crustacea. Freshw Biol 50:1323–1336

Sainte-Marie B, Chabot D (2002) Ontogenetic shifts in natural diet during benthic stages of American lobster (Homarus americanus), off the Magdalen Islands. Fish Bull 100:106–116

Sivertsen K, Bjørge A (2015) On the brink of the Arctic: unusual intertidal sub-Arctic kelp associations in the Porsangerfjord, north Norway. Mar Biol Res 11:405–413

Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. Annu Rev Ecol Evol Syst 37:95–122

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59–87

Steneck RS, Leland A, McNaught DC, Vavrinec J (2013) Ecosystem flips, locks, and feedbacks: the lasting effects of fisheries on Maine's kelp forest ecosystem. Bull Mar Sci 89:31–55

Stone RP, O'Clair CE, Shirley TC (1992) Seasonal migration and distribution of female red king crabs in a southeast Alaskan estuary. J Crustac Biol 12:546–560

Stoner AW, Ottmar ML, Haines SA (2010) Temperature and habitat complexity mediate cannibalism in red king crab: observations on activity, feeding, and prey defense mechanisms. J Shellfish Res 29:1005–1012

Sundet JH, Rafter EE, Nilssen EM (2000) Sex and seasonal variation in the stomach content of the red king crab (*Paralithodes camtchaticus*) in the southern Barents Sea. Crustac Issues 12:193–201

Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD (2015) A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. Ecology 96:318–324

Sweeting CJ, Polunin NVC, Jennings S (2006) Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Commun Mass Spectrom 20:595–601

Syväranta J, Lensu A, Marjomäki TJ, Oksanen S, Jones RI (2013) An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. PLOS ONE 8: e56094

Thompson RC, Olsen Y, Mitchell RC, Davis A and others (2004) Lost at sea: Where is all the plastic? Science 304: 838

Vander Zanden HB, Bjorndal KA, Reich KJ, Bolten AB (2010) Individual specialists in a generalist population: results from a long-term stable isotope series. Biol Lett 6: 711–714

Vander Zanden MJ, Rasmussen JB (2001) Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46:2061–2066

Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467

Vander Zanden MJ, Chandra S, Allen BC, Reuter JE, Goldman CR (2003) Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California−Nevada) basin. Ecosystems 6:274–288

Ward EJ, Semmens BX, Phillips DL, Moore JW, Bouwes N (2011) A quantitative approach to combine sources in stable isotope mixing models. Ecosphere 2:art19

Weis JS (2011) Invasion and predation in aquatic ecosystems. Curr Zool 57:613–624

Windsland K, Hvingel C, Nilssen EM, Sundet JH (2014) Dispersal of the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters: a tag-recapture study. ICES J Mar Sci 71:1966–1976

Wright SL, Thompson RC, Galloway TS (2013) The physical impacts of microplastics on marine organisms: a review. Environ Pollut 178:483–492

Xu J, Zhang M, Xie P (2011) Sympatric variability of isotopic baselines influences modeling of fish trophic patterns. Limnology 12:107–115

Yokoyama H, Tamaki A, Harada K, Shimoda K, Koyama K, Ishihi Y (2005) Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. Mar Ecol Prog Ser 296: 115–128

Zhou SJ, Shirley TC, Kruse GH (1998) Feeding and growth of the red king crab *Paralithodes camtschaticus* under laboratory conditions. J Crustac Biol 18:337–345

Zuur A, Ieno EN, Smith GM (2007) Analysing ecological data. In: Gail M, Krickeberg K, Sarnet J, Tsiatis A, Wong W (eds) Statistics for biology and health. Springer, New York, NY, p 24−48