



## Contribution to the Themed Section: 'Marine Harvesting in the Arctic' Original Article

# Could the planktonic stages of polar cod and Pacific sand lance compete for food in the warming Beaufort Sea?

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The boreal Pacific sand lance (*Ammodytes hexapterus*) was recently detected in southeastern Beaufort Sea (Canadian Arctic), numbering as the second most abundant ichthyoplankton species after the polar cod (*Boreogadus saida*) in 2011. We contrast the hatching periods, growth, prey selectivity, and feeding success of the planktonic stages of the two species. Polar cod hatched from January to mid-July and sand lance from mid-July to early September, precluding any competition among the larval stages. By weight, sand lance larvae grew 3.7 times faster than polar cod larvae. The co-occurring juveniles of both species fed primarily on copepods and to a lesser extent on bivalve larvae, shifting to larger prey with growth. The feeding success of both species appeared limited by the availability of their preferred prey. A significant diet overlap in juveniles >25 mm suggested potential competition for *Pseudocalanus* spp., *Calanus* spp., and bivalve larvae. However, sand lance strongly selected for nauplii while the more diversified diet of polar cod comprised mainly the copepodites of these species. Interspecific competition for food is unlikely at this time but is predicted to amplify with a climate-related reduction in the size of zooplankton prey and an increase in the abundance of sand lance.

**Keywords:** *Ammodytes hexapterus*, *Boreogadus saida*, Canadian Arctic, diet overlap, feeding success, larval fish, northward expansion, prey selectivity, species displacement, trophic ecology.

## Introduction

Over the past two decades, the extent and thickness of the Arctic sea ice cover have plummeted. Some climate models predict that the Arctic Ocean will be mostly free of ice during summer by the 2030s (Wang and Overland, 2012). Increased surface temperature and the loss of a permanent ice cover will likely impact Arctic endemic species that are well adapted to subzero temperatures and often depend directly on the ice cover during at least a portion of their life cycle (e.g. ACIA, 2005).

In the Arctic marine foodweb, polar cod *Boreogadus saida* is a key species that dominates the fish community and channels up to 75% of the energy flow from zooplankton to higher trophic levels (Welch *et al.*, 1992). One of the predicted impacts of climate change is the northward expansion of the distribution of temperate and boreal fish species into Arctic regions (e.g. Perry *et al.*, 2005). Already, Atlantic cod *Gadus morhua* and haddock *Melanogrammus*

*aeglefinus* have expanded their range well into the Barents Sea (Renaud *et al.*, 2012). Capelin *Mallotus villosus* and Atlantic sand lance *Ammodytes* spp. have spread to Hudson Bay, displacing polar cod in the diet of seabirds (e.g. Gaston *et al.*, 2012). The invasion of Arctic seas by boreal fish could affect polar cod through competition, leading to habitat segregation or displacement. The complete or partial replacement of polar cod as the dominant forage fish could substantially modify the energy fluxes within Arctic pelagic ecosystems, resulting in persistent changes in their structure or functioning (Brierley and Kingsford, 2009).

The Network of Centres of Excellence ArcticNet has conducted annual zooplankton surveys in late summer in southeastern Beaufort Sea since 2002. Polar cod invariably dominates the ichthyoplankton, typically representing >90% of the assemblage. Sand lance (*Ammodytes* sp.) appeared in the collections for the first time in 2010 and was the second most abundant

ichthyoplankton species in 2011. Juvenile sand lance were also found in the

stomachs of several fish species sampled in Darnley Bay in 2012 (J. Johnson, Fisheries and Oceans Canada, pers. comm.). Prior reports of sand lance in the area are few and anecdotal (Bond and Erickson, 1993). Hence, these recent observations could be symptomatic of a significant change in the Beaufort Sea fish assemblage.

Under the ice of Hudson Bay in spring, the first-feeding success of co-occurring sand lance and polar cod larvae was limited by the availability of copepod nauplii (e.g. Fortier *et al.*, 1996), suggesting potential competition for food. In the present study, we assess the hatching season, growth, diet, and prey selectivity of the co-occurring planktonic stages (10–60 mm in length) of polar cod and sand lance in the Beaufort Sea. To detect potential food limitation, feeding success is correlated with the availability of preferred prey (e.g. Robert *et al.*, 2009). Diet overlap is measured with sufficient taxonomical resolution to assess potential interspecific competition for food.

**Material and methods**

**Study area**

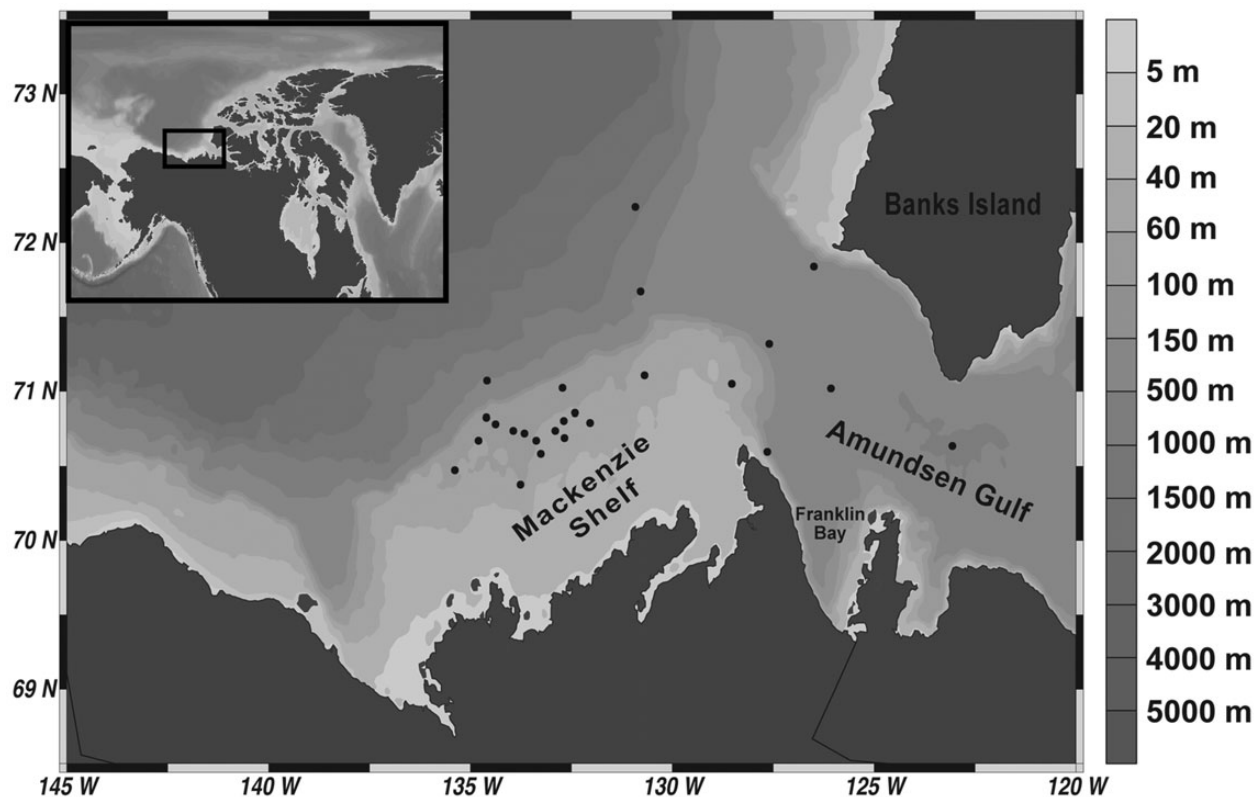
The southeastern Beaufort Sea is bordered by the Mackenzie Shelf to the south and the Amundsen Gulf to the east (Figure 1). Soft sediments and sand characterize the seafloor of the shallow (<100 m) Mackenzie Shelf. The Amundsen Gulf is a 400-km long and 170-km large channel that connects the Beaufort Sea to the Canadian Archipelago. Water masses in the region include the cold polar mixed layer (0–50 m), the Pacific halocline (50–200 m), and the Atlantic layer (>200 m; Benoit *et al.*, 2008).

**Sampling of fish larvae and their zooplankton prey**

Sampling was conducted in the southeastern Beaufort Sea from 22 September to 29 October, 2011 aboard the scientific Canadian Coast Guard icebreaker *Amundsen* as part of the annual ArcticNet survey. The ichthyoplankton assemblage was sampled at 25 stations to a maximum depth of 100 m with a Double Square Net sampler which consists of a rectangular metal frame carrying two 6-m long nets, with 750- $\mu$ m and 500- $\mu$ m mesh and 1-m<sup>2</sup> mouth aperture, towed in a double-oblique cast at a speed of 1 m s<sup>-1</sup>. The zooplankton assemblage integrated over the entire water column was sampled at every station with the 5-Net Vertical Sampler, a structure carrying four 1-m<sup>2</sup> aperture nets (three with 200- $\mu$ m mesh and one 500- $\mu$ m) and one 50- $\mu$ m mesh tow with 0.1-m diameter aperture, retrieved from 10 m above bottom to the surface at a speed of 0.5 m s<sup>-1</sup>. The volume of water filtered by nets was measured with KC Denmark® flowmeters mounted in the centre of each 1-m<sup>2</sup> aperture nets. In all, 509 polar cod and 110 sand lance larvae and juveniles were measured [standard length (SL) and body height at anus] directly after capture. Fish larvae were preserved in 95% ethanol while zooplankton was preserved in a 4% buffered formaldehyde seawater solution.

**Genetic analysis**

Ammodytidae larvae are nearly impossible to identify to species using morphological characters. The CO1 region of the mitochondrial genome of all (110) sand lance larvae collected was sequenced to determine species. For each larva, DNA was extracted from a tissue sample from the tail using a standard 5% Chelex extraction method and amplified using primers and PCR conditions. Amplicons were sequenced on an ABI 3730 Capillary Sequencer (Applied Biosystems, Inc.) and resulting sequences were edited



**Figure 1.** Bathymetric map of SE Beaufort Sea with the position of stations sampled from 22 September to 29 October 2011.

and aligned using Genious 6.1.5 (Biomatters Ltd). Species was determined by searching the NCBI GENBANK database with the resulting sequences.

### Morphometric, growth, and age analysis

The wet weight ( $W$ ) of individual fish was estimated from its SL using  $\ln W = 3.095 \ln SL - 5.4$  for polar cod after Ponomarenko (2000). For sand lance, the SL was first converted into dry weight using  $\ln DW = -2.9721 + 3.5764 \ln SL$  (McGurk and Warburton, 1992). Dry weight was then converted into wet weight assuming a moisture content of 77.68% for sand lance < 100 mm (Payne et al., 1999).

Subsets of 48 sand lance and 191 polar cod were aged by enumerating otolith growth increments (Wright, 1993; Bouchard and Fortier, 2011). Fish were dissected and their left and right lapilli were mounted on glass slides using Crystal Bond<sup>®</sup> thermoplastic glue. For each polar cod, one side of a lapillus was polished with 5  $\mu\text{m}$  sandpaper and analysed at  $\times 1000$  using a microscope linked to an image analysing system (Image-Pro Plus<sup>®</sup> software) with a Leica<sup>®</sup> digital camera. For sand lance, both sides of a lapillus were polished with 1  $\mu\text{m}$  sandpaper and with an aluminium suspension (0.3  $\mu\text{m}$ ), then covered again with thermoplastic glue. The sand lance lapilli were analysed at  $\times 400$  or  $\times 630$  magnification. Age was linearly related to SL (polar cod: age = 4.000 SL + 16.617,  $r^2 = 0.79$ ,  $n = 191$ ; sand lance: age = 35.284 ln SL - 72.861,  $r^2 = 0.81$ ,  $n = 48$ ), enabling us to estimate the age of all remaining fish (318 polar cod and 62 sand lance) from their SL. The hatch date of each individual fish was calculated by subtracting age from date of capture.

### Stomach contents analysis

For each species, the entire gut content of a larval subsample was examined under a dissecting microscope and prey were identified to the lowest taxonomical level possible, measured (length and width), and enumerated. The carbon content of each prey was estimated from taxa-specific carbon-length regressions (Table 1).

To assess the potential prey field of fish larvae and juveniles, zooplankton collected in the 50- $\mu\text{m}$  mesh net was identified to the lowest taxonomical level possible under the microscope. For each station, successive known aliquots of the net sample were analysed until a minimum of 300 organisms were identified. The large copepodite and adult stages were enumerated in the 200- $\mu\text{m}$  mesh net collections due to potential undersampling in the 50- $\mu\text{m}$  mesh nets.

Schoener's index was used to quantify the diet overlap between polar cod and sand lance (Schoener, 1970). The selectivity of each species for its prey was quantified with Chesson's  $\alpha$  index (Chesson, 1978). For both species, prey selectivity was first computed for each fish then averaged over the length classes and the overall population for the calculation of feeding success indices. A length-independent index of feeding success was calculated for each fish as the weight of the preferred prey in the gut ( $\mu\text{g}$  carbon) divided by SL. The dependence of feeding success ( $F$ ) on the *in situ* density of the preferred prey ( $P$ ) was tested by fitting an Ivlev (1961) function  $F = a(1 - e^{-bP})$  to the data.

## Results

### Sand lance species identification

Based on the determination of the CO1 locus, all sand lance larvae and juveniles captured in southeast Beaufort Sea were Pacific sand lance *Ammodytes hexapterus*.

### Length, weight, and growth

The stocky polar cod and the slender Pacific sand lance larvae presented similar length frequency distributions but different weight frequency distributions. Polar cod and sand lance ranged from 12.1 to 60.0 mm and 12.1 to 53.0 mm respectively, with essentially the same modal length (26.3 vs. 27.0 mm) and length frequency distribution except for a slightly larger proportion of sand lance (10%) than polar cod (4.5%) in the 40- and 55-mm interval (Figure 2). In contrast, 78.2% of the sand lance weighed between 10 and 100 mg, whereas 63.5% of the polar cod weighed between 100 and 1000 mg (Figure 3). By weight, the growth of Pacific sand lance was 3.7 times faster than that of polar cod (Figure 4).

### Hatch date frequency distributions of polar cod and Pacific sand lance

Polar cod ranged in age from 60 to 237 d and Pacific sand lance from 9 to 70 d. There was no overlap in the hatching seasons of the two species (Figure 5). Polar cod hatched over a 185-d period from January to mid-July, with a peak in May and most hatching occurring under the ice. Pacific sand lance hatched during 41 d from mid-July to early September in ice-free waters, with peak hatching in early August.

### Diet composition of polar cod and Pacific sand lance

The two species preyed primarily on the developmental stages of copepods, with polar cod, and to a lesser extent sand lance, shifting from nauplii to copepodites with increasing length (Table 2). Copepods eggs, nauplii, and copepodites represented from 52 to 65% of the prey of polar cod by number and from 69 to 92% of their carbon intake depending on length-class. Pooling nauplii and copepodites, important carbon sources, were the large *Calanus* spp. (27.8% C) and cyclopoid copepods (*Oithona similis*, *Triconia borealis*, and *Cyclopina* sp., 16.9% C) for polar cod < 25 mm and *Pseudocalanus* spp. (13.5% C), *Calanus* spp. (43.7% C), and *Metridia longa* (27.5% C) for polar cod > 25 mm. Among other taxonomic groups, bivalve larvae (15.3% C in fish < 25 mm) and appendicularians were also frequent in the diet of polar cod (Table 2).

In Pacific sand lance, copepods contributed 59–70% of the prey by number and 63–78% of the carbon intake depending on length class (Table 2). The main carbon sources (nauplii and copepodites pooled) were *Calanus* spp. nauplii (24.3% C), *Pseudocalanus* spp. (15.5% C), and cyclopoids (12.0% C) for sand lance < 25 mm, and appendicularians (18.7% C), mainly of the genus *Oikopleura*, *Calanus* spp. (14.8% C), and *Pseudocalanus* spp. (14.8% C) for sand lance > 25 mm. Bivalve larvae were frequent in the diet of larger Pacific sand lance and contributed 10% of the carbon intake (Table 2).

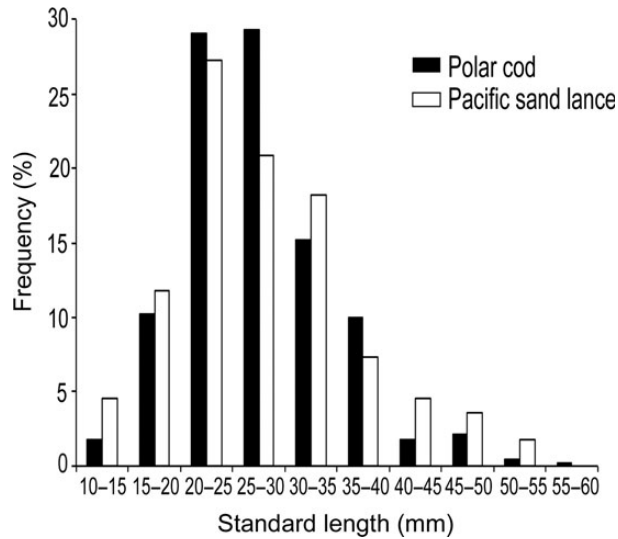
Both species consumed more prey and larger prey with increasing size (ANOVA,  $p < 0.05$ ), with the heavier polar cod ingesting bigger and carbon-richer prey than sand lance of the same length ( $p < 0.0001$ ). Sand lance > 25 mm captured a larger number of smaller prey on average than polar cod of the same length class (Table 2). The diet of the two species overlapped less for larvae < 25 mm (Schoener index = 0.46) than for larvae > 25 mm (Schoener index = 0.64).

### Prey selectivity

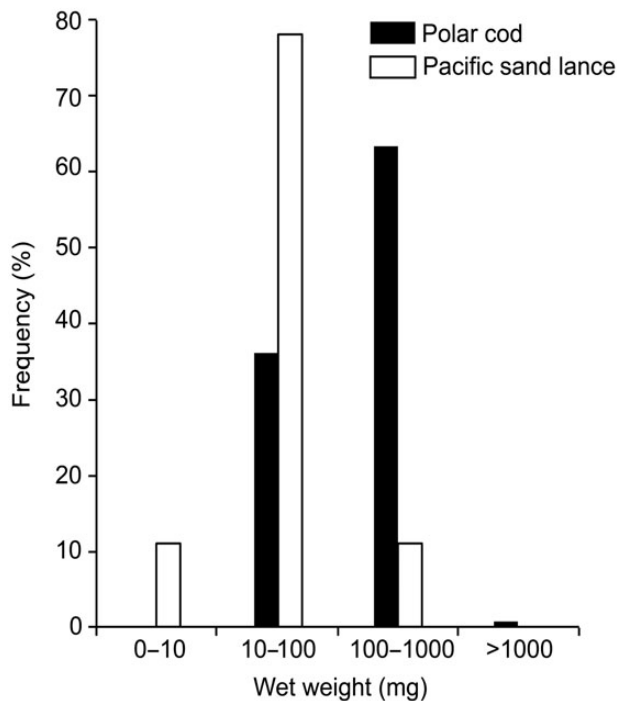
In general, selection for or against prey was weaker in polar cod than in Pacific sand lance (Figure 6). Polar cod < 25 mm selected for

**Table 1.** Relationships between carbon content (C, in  $\mu\text{g}$ ), dry weight (DW, in  $\mu\text{g}$ ), and prosome (PL, in  $\mu\text{m}$ ) or total length (L, in  $\mu\text{m}$ ) used to calculate the carbon contribution of zooplankton prey to the diet of polar cod *B. saida* and Pacific sand lance *A. hexapterus* early life stages.

Gut contents taxa	Equation taxa	Equation	Reference
<i>Acartia</i> spp.	<i>Acartia longiremis</i>	$C = 1.023 \times 10^{-8} \times \text{PL}^{2.906}$	Hansen <i>et al.</i> (1999), Figure 9
<i>Calanus glacialis</i>	<i>Calanus glacialis</i>	$C = 4.742 \times \text{PL}^{3.452}$	Forest <i>et al.</i> (2011), Figure 4b (summer)
<i>Calanus hyperboreus</i>	<i>Calanus hyperboreus</i>	$C = 7.263 \times \text{PL}^{3.106}$	Forest <i>et al.</i> (2011), Figure 4a (summer)
<i>Calanus</i> spp. nauplii	<i>Calanus finmarchicus</i> nauplii	$C = 4.29 \times 10^{-6} \times L^{2.05}$	Hygum <i>et al.</i> (2000), Figure 4 (high food resources)
Cyclopoid nauplii	<i>Oithona similis</i> nauplii	$C = 5.545 \times 10^{-8} \times \text{PL}^{2.71}$	Sabatini and Kjørboe (1994), Figure 1
<i>Eurytemora</i> spp.	<i>Eurytemora herdmani</i>	$C = (10^{2.960 \times \log \text{PL} - 7.604}) \times 0.447$	Middlebrook and Roff (1986), Equation 8
<i>Centropages harmatus</i>	<i>Centropages harmatus</i>	$C = (10^{2.970 \times \log \text{PL} - 6.098}) \times 0.447$ $+ (10^{2.970 \times \log \text{PL} - 6.098}) \times 0.07$	Klein Breteler (1982), Table 1
<i>Centropages typicus</i>	<i>Centropages typicus</i>	$C = (10^{2.452 \times \log \text{PL} - 6.103}) \times 0.447$	Hay <i>et al.</i> (1991), Table 2
<i>Limnocalanus</i> spp.	Copepoda	$C = 10^{3.07 \times \log \text{PL} - 8.37}$	Uye (1982), Table 1
<i>Metridia longa</i>	<i>Metridia longa</i>	$C = 7.498 (\text{PL} \times 0.001)^{3.225}$	Forest <i>et al.</i> (2011), Figure 4c (summer)
<i>Metridia</i> spp. nauplii	<i>Calanus finmarchicus</i> nauplii	$C = 4.29 \times 10^{-6} \times L^{2.05}$	Hygum <i>et al.</i> (2000), Figure 4 (high food resources)
<i>Microcalanus</i> spp.	Copepoda	$C = 10^{3.07 \times \log \text{PL} - 8.37}$	Uye (1982), Table 1
<i>Microcalanus</i> spp. nauplii	<i>Pseudocalanus</i> spp. nauplii	$C = (10^{2.269 \times \log \text{PL} - 5.570}) \times 0.447$ $+ (10^{2.269 \times \log \text{PL} - 5.570}) \times 0.07$	Klein Breteler (1982), Table 1
<i>Oithona similis</i>	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times \text{PL}^{2.16}$	Sabatini and Kjørboe (1994), Figure 1
<i>Oncaea parila</i>	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times \text{PL}^{2.16}$	Sabatini and Kjørboe (1994), Figure 1
<i>Pseudocalanus</i> spp.	<i>Pseudocalanus</i> spp.	$C = (10^{2.85 \times \log \text{PL} - 7.62}) \times 0.447$	Liu and Hopcroft (2008), Figure 1
<i>Pseudocalanus</i> spp. nauplii	<i>Pseudocalanus</i> spp. nauplii	$C = (10^{2.269 \times \log \text{PL} - 5.570}) \times 0.447 + (10^{2.269 \times \log \text{PL} - 5.570}) \times 0.07$	Klein Breteler (1982), Table 1
<i>Temora</i> spp.	<i>Temora longicornis</i>	$C = (10^{3.064 \times \log \text{PL} - 7.696}) \times 0.447 + (10^{3.064 \times \log \text{PL} - 7.696}) \times 0.07$	Klein Breteler (1982), Table 1
<i>Triconia borealis</i>	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times \text{PL}^{2.16}$	Sabatini and Kjørboe (1994), Figure 1
Unidentified copepod	Copepoda	$C = 10^{3.07 \times \log \text{PL} - 8.37}$	Uye (1982), Table 1
Unidentified copepod nauplii	<i>Calanus finmarchicus</i> nauplii	$C = 4.29 \times 10^{-6} \times L^{2.05}$	Hygum <i>et al.</i> (2000), Figure 4 (high food resources)
Unidentified cyclopoid	<i>Oithona similis</i>	$C = 9.4676 \times 10^{-7} \times \text{PL}^{2.16}$	Sabatini and Kjørboe (1994), Figure 1
Appendicularia	<i>Oikopleura rufescens</i> (synonym: <i>Oikopleura vanhoeffeni</i> )	$C = 8.20 \times 10^{-8} \times (L_{\text{TR}})^{2.70}$ (where $L_{\text{TR}}$ = trunk length)	Sato <i>et al.</i> (2003), Equation 7
Frittilaria	<i>Frittilaria pellicuda</i>	$C = 10^{-9.450} \times L^{3.241}$	López-Urrutia <i>et al.</i> (2003), Table 3
Bivalvia	<i>Mytilus edulis</i>	$C = 3.06 \times 10^{-8} \times L^{2.88}$	Fotel <i>et al.</i> (1999), Section 3.4
Cirripeda	<i>Mytilus edulis</i>	$C = 3.06 \times 10^{-8} \times L^{2.88}$	Fotel <i>et al.</i> (1999), Section 3.4
Eggs	Seven copepod species ( <i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> , <i>Temora longicornis</i> , <i>Acartia longiremis</i> , <i>A. tonsa</i> , <i>Centropages hamatus</i> and <i>Pseudocalanus</i> spp.)	$C = 0.14 \times 10^{-6} \times (4/3\pi(L/2)^3)$	Kjørboe <i>et al.</i> (1985)
Gastropoda	<i>Spiratella retroversa</i>	$C = 10^{3.102 \times \log(D \times 0.001) + 1.469}$ ( $D$ = diameter)	Conover and Lalli (1974), Figure 1
Cladocera	<i>Podon leuckarti</i>	$C = 10^{4.15 \times \log L - 11.15}$	Uye (1982), Table 1
Polychaeta	<i>Neanthes succinea</i>	$1.42 \times 10^{-4} \times L^{1.47}$	Hansen (1999), Table 1
Protists	Protists	$C = (10^{-0.665 + 0.939 \log V}) \times 10^{-6}$	Menden-Deuer and Lessard (2000), Table 4, $V$ ( $\mu\text{m}^3$ ) = volume of a sphere, cylinder or ellipsoid
Algal cells	Diatoms	$C = (10^{-0.541 + 0.811 \log V}) \times 10^{-6}$	Menden-Deuer and Lessard (2000), Table 4, $V$ ( $\mu\text{m}^3$ ) = volume of a sphere, cylinder or ellipsoid
Digested and unidentified material	Digested and unidentified material	$C = (109.08 \times (\pi \times ((W \times 0.001)/2)^2 \times (L \times 0.001))^{0.9591}) \times 0.4$ (where $W$ = width)	Sirois (1999)
(1)	Copepoda	$C = 44.7\% \text{ DW}$	Mauchline (1998)
(2)	Zooplankton	$C = 40\% \text{ DW}$	Legendre and Michaud (1998)

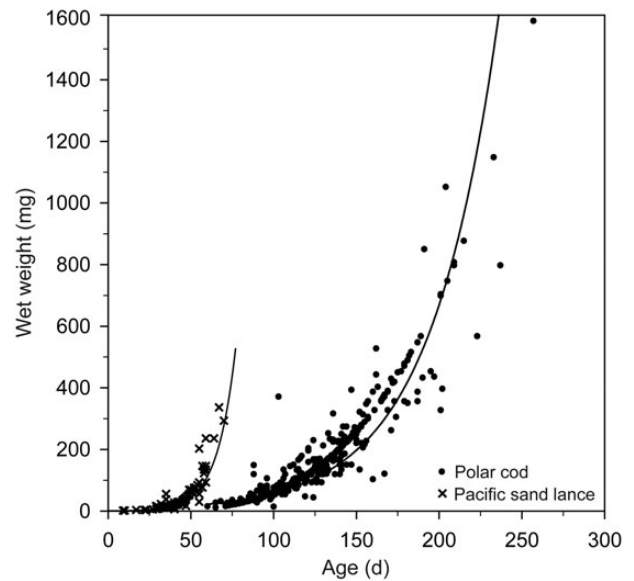


**Figure 2.** Length frequency distributions of polar cod ( $n = 509$ ) and Pacific sand lance ( $n = 110$ ) larvae and juveniles sampled in the Beaufort Sea in September and October 2011.



**Figure 3.** Weight frequency distributions of polar cod ( $n = 509$ ) and Pacific sand lance ( $n = 110$ ) larvae and juveniles sampled in the Beaufort Sea in September and October 2011.

nauplii of *Pseudocalanus* spp. and *Calanus* spp. and copepodites of *Pseudocalanus* spp. and *T. borealis* and selected against large calanoid copepodites such as *Calanus hyperboreus* and *M. longa*. Beyond 25 mm in length, polar cod shifted preferences to the copepodite stages of the medium and large calanoid copepods *M. longa*, *Pseudocalanus* spp., *C. hyperboreus*, and *C. glacialis*. Polar cod larvae of all lengths also selected for bivalve larvae. Pacific sand lance larvae <25 mm strongly selected for *Pseudocalanus* spp. nauplii, shifting



**Figure 4.** Non-linear regressions of wet weight ( $W$ ) against age for polar cod and Pacific sand lance larvae and juveniles sampled in the Beaufort Sea in September and October 2011. Polar cod:  $W = 5.08 e^{0.0244x}$ ,  $r^2 = 0.79$ ,  $n = 509$ ; Pacific sand lance:  $W = 0.48 e^{0.0909x}$ ,  $r^2 = 0.81$ ,  $n = 110$ .

to *Calanus* spp. nauplii and bivalve larvae as they grew beyond 25 mm (Figure 6).

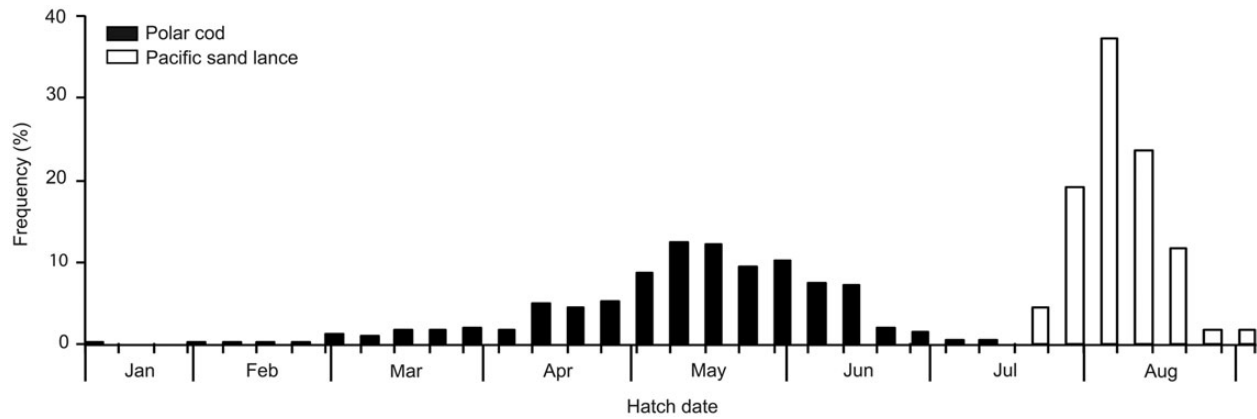
#### Feeding success in relation to preferred prey density

For both species, feeding success increased exponentially at a decreasing rate with increasing *in situ* density of the preferred prey, a process captured by the Ivlev function despite the low sample size of 13 stations (Figure 7). The density of preferred prey *Pseudocalanus* spp. copepodites and bivalve larvae explained 62% of the variance in the feeding success of polar cod. The density of *Pseudocalanus* spp. and *Calanus* spp. nauplii accounted for 44% of the variance in the feeding success of Pacific sand lance. Based on the Ivlev model, polar cod and sand lance reached ~50% of their optimal feeding success at preferred prey densities of  $32 \times 10^3$  and  $11 \times 10^3 \text{ m}^{-2}$ , respectively.

#### Discussion

##### Climate change and the potential displacement of polar cod in Arctic seas

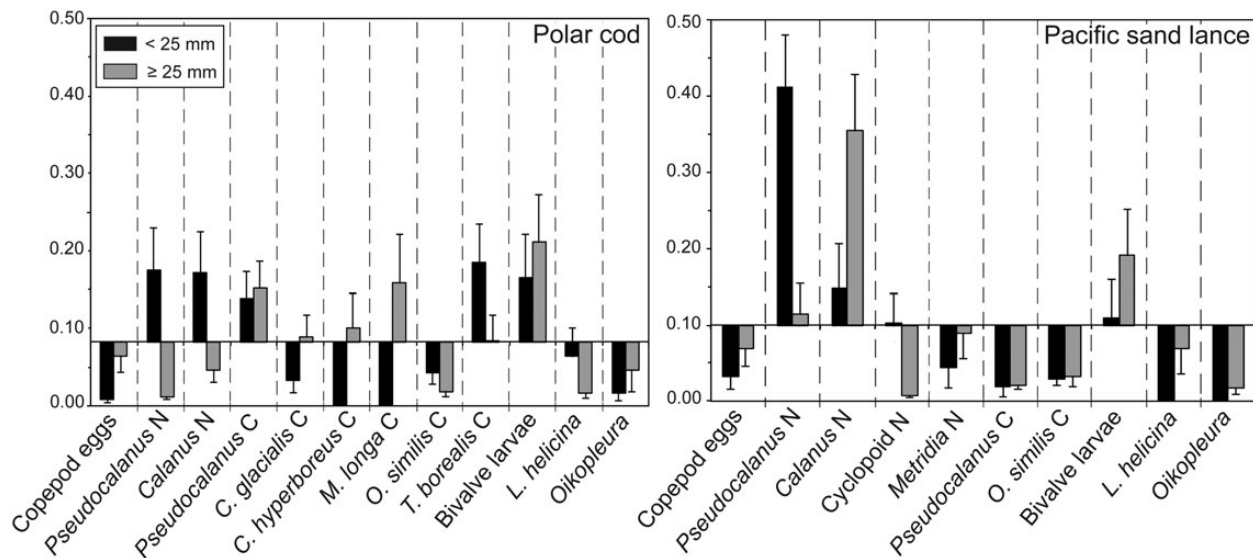
Polar cod is the dominant forage fish in Arctic seas and its replacement by one or several boreal species such as the sand lance or the capelin (*M. villosus*) could haringer a rapid shift in the Arctic pelagic ecosystem and the services it provides to local communities (e.g. ACIA, 2005). In seasonally ice covered seas at the southern limit of its distribution, polar cod often live in sympatry with large populations of sand lance and capelin that support a diversified boreal assemblage of fish and marine mammals. In recent decades, the partial replacement of polar cod by sand lance and capelin in the diet of seabirds (Gaston et al., 2012) and seals (Chambellant et al., 2013) suggest that sea ice decline may have triggered a shift of the Arctic ecosystem of Hudson Bay towards such a more diversified and productive boreal ecosystem. The assumed interspecific competition underpinning this displacement of polar cod by boreal invaders may take place during the early larval and juvenile planktonic



**Figure 5.** Hatch date frequency distributions of polar cod ( $n = 509$ ) and Pacific sand lance ( $n = 110$ ) collected in the Beaufort Sea in September and October 2011. Each bar represents a subcohort of larvae hatched in the same week.

**Table 2.** Diet composition by length classes for polar cod *B. saida* and Pacific sand lance *A. hexapterus* sampled in the Beaufort Sea in September and October 2011 expressed in per cent relative contribution to total number of preys (%N) and in relative contribution in carbon of prey (%C) of given prey taxa.

Prey taxa	<i>Boreogadus saida</i>				<i>Ammodytes hexapterus</i>			
	<25 (mm)		≥25 (mm)		<25 (mm)		≥25 (mm)	
	%N	%C	%N	%C	%N	%C	%N	%C
Copepods								
Eggs	5.1	1.5	12.0	0.5	6.0	8.9	10.5	8.8
Nauplii								
<i>Calanus</i> spp.	9.3	13.3	2.3	0.6	9.6	24.3	10.5	13.7
Cyclopoid	2.1	0.6	0.3	<0.1	15.9	8.5	7.2	2.0
<i>Pseudocalanus</i> spp.	3.1	2.1	4.3	0.6	8.9	12.9	11.7	8.7
<i>Microcalanus</i> spp.	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.3	0.2
<i>Metridia longa</i>	0.5	0.4	0.5	0.1	0.9	1.7	1.2	1.4
Others and unidentified	1.5	1.0	0.2	<0.1	5.6	7.7	0.9	0.6
Copepodites and adults								
<i>Acartia</i> sp.	<0.1	0.1	0.1	<0.1	0.4	0.9	2.9	3.7
<i>Calanus glacialis</i>	0.4	12.5	2.0	28.7	–	–	0.1	0.7
<i>Calanus hyperboreus</i>	–	–	0.2	13.2	–	–	–	–
<i>Calanus</i> spp.	0.5	2.0	0.2	1.2	–	–	<0.1	0.4
<i>Centropages</i> spp.	0.8	5.9	0.1	0.3	0.1	1.1	0.6	3.9
<i>Pseudocalanus</i> spp.	2.6	4.4	18.2	12.9	1.0	2.6	5.2	6.1
<i>Metridia longa</i>	–	–	0.5	27.5	<0.1	0.1	<0.1	0.4
<i>Microcalanus</i> spp.	1.2	2.1	0.4	0.1	0.1	0.1	0.2	0.2
<i>Temora</i> spp.	0.2	0.6	0.1	0.1	0.2	0.7	–	–
<i>Triconia borealis</i>	10.9	7.3	10.5	1.5	<0.1	0.1	0.4	0.3
<i>Oithona similis</i>	8.8	8.9	8.4	1.9	2.8	3.3	13.7	9.9
Unidentified cyclopoid	0.2	0.1	0.1	<0.1	0.1	0.1	0.2	0.1
Others and unidentified	4.8	6.4	5.0	2.5	7.2	4.9	3.8	1.5
Partial total: copepods	52.0	69.3	65.4	91.8	58.7	78.0	69.5	62.5
Gastropods	6.4	5.3	4.6	1.1	2.5	3.4	3.5	2.5
Bivalve larvae	18.7	15.3	21.3	3.2	4.0	3.4	20.7	10.0
Appendicularians	16.0	2.5	6.3	1.0	0.4	0.1	1.8	18.7
Cladocera	–	–	<0.1	0.3	–	–	0.2	4.9
Cirripeda	–	–	0.1	0.7	–	–	<0.1	<0.1
Polychaeta	0.3	0.7	<0.1	<0.1	–	–	0.1	0.4
Protists	<0.1	<0.1	<0.1	<0.1	0.2	0.1	0.2	<0.1
Algal cells	0.7	<0.1	0.1	<0.1	23.6	1.5	2.7	0.1
Others and unidentified	5.8	6.8	2.1	1.9	10.6	13.6	1.3	1.0
Number of larvae analysed	24		30		35		31	
Mean number of prey ingested	99		311		98		443	
Mean prey length (μm)	292.5		394.9		202.4		270.3	
Mean gut carbon content (μg)	45.6		704.0		17.1		187.1	



**Figure 6.**  $\alpha$  index of prey selectivity ( $\alpha$  index; Chesson, 1978) of polar cod and Pacific sand lance larvae and juveniles for their prey for two length classes of fish. The horizontal line represents the  $1/N$  threshold where selectivity is neutral. Selectivity for a prey taxon is positive when  $\alpha$  is higher than the threshold and negative otherwise. N indicates the nauplii and C the copepodites. Vertical bars indicate standard errors.

stages or the late juvenile and adult nektonic stages or both. In the following sections, we review the potential for interspecific competition for food between polar cod and Pacific sand lance during the successive phases of planktonic life in the offshore Beaufort Sea.

#### Hatching season and temporal segregation during the early larval stage

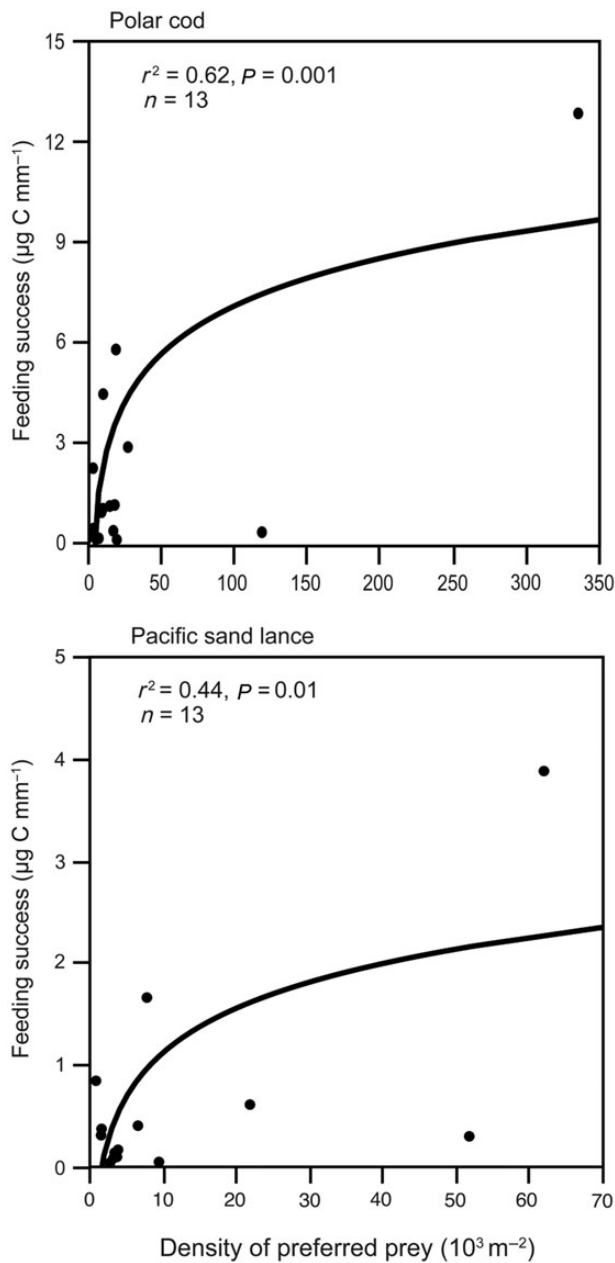
In SE Hudson Bay in spring, the recently hatched larvae of both species co-occurred under landfast ice where feeding was limited by the availability of their primary prey copepod nauplii (Fortier et al., 1996), suggesting potential competition at first feeding. Consistent with earlier reports (Bouchard and Fortier, 2011), polar cod hatched from January to early July in the Beaufort Sea with most larvae emerging before the ice breakup in June (Figure 5). The early and protracted hatching season of polar cod is interpreted as an adaptation to ensure that the juveniles reach a minimum size before their fall migration to overwinter grounds at depth (Bouchard and Fortier, 2011). By comparison, Pacific sand lance hatched in ice-free waters during a short period from late July to late August. Sand lance typically hatch over a short period with a well-defined hatching peak (e.g. Pinto, 1984; our study). In its boreal and temperate habitat, Pacific sand lance spawns in ice-free waters in autumn and winter (Robards et al., 2000). Depending on egg development rate, hatching occurs slightly before or during the spring bloom (e.g. Wright and Bailey, 1996). Egg development time in Pacific sand lance increases exponentially with decreasing temperature and can reach months at near zero temperatures (Robards et al., 1999). The demersal eggs are laid in the intertidal zone and possibly in subtidal areas (McGurk and Warburton, 1992) at maximum depths of 100 m (Garrison and Miller, 1982). In the Beaufort Sea, temperatures as cold as  $-1.6^{\circ}\text{C}$  prevail at these depths in winter (e.g. Benoit et al., 2008). Hence, the hatching of Pacific sand lance in late summer in the Beaufort Sea likely results from a combination of winter spawning and inordinately long egg incubation at subzero temperatures. The resulting temporal segregation of emerging polar cod and Pacific sand lance

larvae precludes any direct interspecific competition for food during the first-feeding and early larval stages.

#### Potential competition for food during the pre-metamorphosis and early juvenile stage

Despite hatching later, and thanks to explosive growth, Pacific sand lance soon caught up with polar cod in length. By September–October, the two species presented the same length frequency distribution (Figure 2), but not necessarily the same predatory skills as the heavier polar cod captured larger prey totalling a larger carbon content than the slender sand lance (Table 2). Polar cod completes metamorphosis between 27 and 35 mm (Ponomarenko, 2000), whereas Smigielski et al. (1984) report that *A. americanus* completes metamorphosis at 29 mm. Before metamorphosis (lengths  $<25$  mm), the overlap in diet (Schoener index = 0.46) was lower than the 0.6 threshold considered ecologically significant (Wallace and Ramsey, 1983), primarily because polar cod  $<25$  mm already captured the copepodites of small cyclopoid copepods and *Pseudocalanus* spp., which generally still escaped Pacific sand lance  $<25$  mm (Table 2). At this developmental stage, Pacific sand lance strongly selected for *Pseudocalanus* nauplii and moderately for *Calanus* nauplii, while polar cod moderately selected for several prey including *Pseudocalanus* nauplii (Figure 6). Hence, except perhaps for *Pseudocalanus* spp. nauplii, potential competition for the same prey was unlikely before metamorphosis.

During and after metamorphosis (lengths  $>25$  mm), the overlap in diet between the two species became significant (Schoener index = 0.64). The feeding success of polar cod appeared limited at combined density of *Pseudocalanus* copepodites and bivalve larvae  $<32 \times 10^3 \text{ m}^{-2}$ , and that of sand lance at combined densities of *Pseudocalanus* nauplii and *Calanus* nauplii  $<11 \times 10^3 \text{ m}^{-2}$ . Similar limitation of feeding at low density of the preferred prey has been reported for the larval stages of polar cod, sand lance, and other fish species (e.g. Fortier et al., 1996; Robert et al., 2009). Thus, all conditions for interspecific competition for food were apparently met at metamorphosis and beyond: the two species co-occurred in



**Figure 7.** Mean feeding success ( $\mu\text{g C}$  of preferred prey in the gut content) of polar cod and Pacific sand lance larvae and juveniles in relation to the density of preferred prey. Each point is the average for a sampling station. Exponential rise-to-maximum curves represent the theoretical Ivlev function linking feeding success to prey density.

time and space, shared an overlapping diet (although not exactly the same preferred prey), and feeding success was limited by prey availability. We conclude that the potential for interspecific competition for food during early life in the plankton peaked during the early juvenile stage, soon after metamorphosis. However, despite similarities in the diet of both species, polar cod preyed on larger prey than sand lance after metamorphosis, and the carbon sources of the two species differed. Metamorphosed polar cod obtained 89.9% of their carbon from copepodites, primarily *M. longa*, *Calanus glacialis*, *C. hyperboreus*, and *Pseudocalanus*, whereas sand lance relied about equally on copepod eggs and nauplii (35.4%C), copepodites (27.2%C), and

non-copepod prey (37.6%C). In addition, the heavier polar cod juveniles feeding on large prey were ca. fivefold more abundant than the slender sand lance feeding on smaller prey. Therefore, intraspecific competition for food was likely to prevail over interspecific competition among juveniles  $>25$  mm.

**Interspecific competition beyond life in the plankton**

Juvenile polar cod start their fall migration to the deep overwintering grounds at lengths of 30–35 mm (Ponomarenko, 2000). Juvenile sand lance start burying in sediments when reaching sizes of 60–70 mm (Heath et al., 2012). The scarcity of polar cod  $>40$  mm and sand lance  $>50$  mm in our epipelagic collections is consistent with these reports (Figure 2). At lengths  $>60$  mm, juvenile sand lance prey primarily on calanoid copepodites (e.g. Tokranov, 2007). Hence, by the time they migrate to their overwintering grounds, the juveniles of both species could share copepodites of calanoid copepods as their main carbon source. However, in the Beaufort Sea, polar cod juveniles are believed to overwinter in the relatively warm Atlantic layer on the slope of the continental shelf at depths of 200–400 m (Geoffroy et al., 2011), whereas sand lance invariably distribute in shallow nearshore waters (Robards et al., 2000) and are thus likely bounded to the Mackenzie Shelf. Such spatial segregation of the overwintering juvenile stages would again preclude any interspecific competition for food until the adult stage when polar cod can compete for prey with co-occurring planktivore fish species (Orlova et al., 2009).

**Conclusion**

Our comparison of the diet of the co-occurring planktonic stages indicates that the relatively rare Pacific sand lance newly detected in the offshore Beaufort Sea are unlikely to be significant competitor of polar cod for food at this time. However, this situation could rapidly evolve as seen in Hudson Bay where sand lance now dominates ichthyoplankton collections (L. Fortier, unpublished data). A striking difference in the early life strategy of the two species is the capacity of metamorphosed polar cod to capture the copepodites of large calanoid copepods such as *M. longa*, *C. glacialis*, and even *C. hyperboreus*. As the ice-free season lengthens in Arctic seas, the large *C. glacialis* and *C. hyperboreus* could be displaced by smaller copepods such as *Pseudocalanus* spp. and *C. finmarchicus* (Falk-Petersen et al., 2006). Clearly, this alteration of the copepod assemblage would favour Pacific sand lance over polar cod during life in the plankton.

In boreal marine ecosystems, Pacific sand lance is a key forage species for several vertebrate predators including seabirds and marine mammals (e.g. Robards et al., 2000), and commercially important fish species such as Pacific halibut (*Hippoglossus stenolepis*; Best and St-Pierre, 1986) and sockeye salmon (*Oncorhynchus nerka*; Farley et al., 2007). The partial or complete displacement of polar cod by Pacific sand lance as the main forage species would likely trigger major changes in the vertebrate community of the pelagic ecosystem of the Beaufort Sea (Brierley and Kingsford, 2009), raising new challenges for the management of ecosystem services, especially if the species implicated in these changes have economical value (Hoegh-Guldberg and Bruno, 2010).

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