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SHORT NOTE

First records of Pacific sand lance (*Ammodytes hexapterus*) in the Canadian Arctic Archipelago

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Abstract An increasing number of boreal marine species are expected to invade the warming Arctic Ocean with the potential to displace endemic species. We provide first evidence that Pacific sand lance (*Ammodytes hexapterus*) is expanding its range in the Canadian Arctic Archipelago, a region far outside the species temperate-boreal traditional range south of the Bering Strait. To the best of our knowledge, supported by local Inuit knowledge, the species was not present in the area until the present decade. We observed an increasing density of larval Pacific sand lance with time over the 2011–2016 period, suggesting that environmental conditions are becoming increasingly favorable for the species to reproduce in the Central Canadian Arctic. The northward distribution change of Pacific sand lance is occurring earlier than predicted by current models and could trigger abrupt shifts in Arctic marine food webs if the boreal invader displaces polar cod, a key prey species for top predators in Arctic marine ecosystems.

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Introduction

Northward invasions into rapidly warming Arctic marine ecosystems by southern species are occurring at a higher rate than the global average (Cheung et al. 2009; Hollowed et al. 2013; Renaud et al. 2015). Invading species belong to all trophic levels of the marine food web, ranging from secondary producers (Kraft et al. 2013) to cephalopods (Golikov et al. 2013), fish (Mackenzie et al. 2014; Yoon et al. 2015) and marine mammals (Ferguson et al. 2010). In the Barents Sea, fish communities, once dominated by species endemic to the Arctic, are undergoing a "borealization" process as sub-Arctic species rapidly expand their distribution northward, outcompeting Arctic fish assemblages (Fossheim et al. 2015). The same trend is observed in the Chukchi and Beaufort Seas, where North Pacific benthic and pelagic species are increasingly reported north of the Bering Strait, including commercially important gadid and salmonid fishes (Rand and Logerwell 2011; Grebmeier 2012; Logerwell et al. 2015).

In Arctic pelagic food webs, the polar cod (*Boreogadus saida*) is a key forage fish transferring the bulk of energy from lower trophic levels to large vertebrate predators (Welch et al. 1992). Rapid temperature increases in several sectors of the Arctic, including southern Hudson Bay and the Barents Sea, have resulted in the displacement of polar cod by capelin (*Mallotus villosus*) and sand lance (*Ammodytes* sp.) with major changes in these ecosystems (Gaston et al. 2003, 2012; Provencher et al. 2012; Chambellant et al. 2013; Young and Ferguson 2014; Watt and Ferguson 2015). In 2011, Pacific sand lance (*Ammodytes* *hexapterus*) was reported for the first time reproducing in the southeastern Beaufort Sea (Falardeau et al. 2014; Suzuki et al. 2015), far from the species' traditional range. Pacific sand lance is one of the most abundant forage fish species in the North Pacific (e.g., Gladics et al. 2015; Greene et al. 2015). It is distributed along the East coast of the Pacific Ocean, from 32°N in southern California, up to the Bering Strait and the Chukchi Sea (Robards et al. 1999b; Tokranov 2007; Logerwell et al. 2015). In the present study, we provide the first evidence that Pacific sand lance are expanding their distribution eastward and now spawn into the Canadian Arctic Archipelago, as far east as the Queen Maud Gulf.

Materials and methods

Sampling of larval and early juvenile sand lance was conducted in a region ranging from the Amundsen Gulf to the west, to the Queen Maud Gulf to the east (Fig. 1) from the scientific icebreaker CCGS *Amundsen* as part of the annual ArcticNet expeditions in the period of July–September in 2011, 2014, 2015, and 2016 (no expeditions were carried out in the region in 2012 and 2013). The ichthyoplankton was sampled with a frame carrying two square-conical nets with a 1 m^2 mouth aperture and mesh size of 750 µm and 500 µm. Oblique tows were carried out to a maximum depth of 90 m and a ship-speed of 2 knots. One fish was also sampled with a beam trawl carrying a 10-m-long net with a 3 m^2 aperture and a cod end of mesh 9.5 mm, dragged near the bottom at a speed of 3 knots.

The volume of filtered water was measured with flow meters (KC Denmark) installed in the centre of each net except for the beam trawl. All fish were measured (standard length and body width) immediately after capture. Fish larvae and juveniles were preserved in 95% ethanol.

For each fish, genomic DNA was extracted from a muscle tissue sample using a salt-extraction protocol (Al-janabi and Martinez 1997) and amplified in PCR reactions. The reaction solution comprised 10–20 ng of genomic DNA, 5 U of GoTaq Flexi DNA Polymerase (Promega; Ivanova et al. 2007), 10 µM of each forward and reverse primer (Ward et al. 2005), 2 µL of 5 × PCR buffer, 10 mM dNTPs and 25 mM $MgCl_2$ and was brought to a

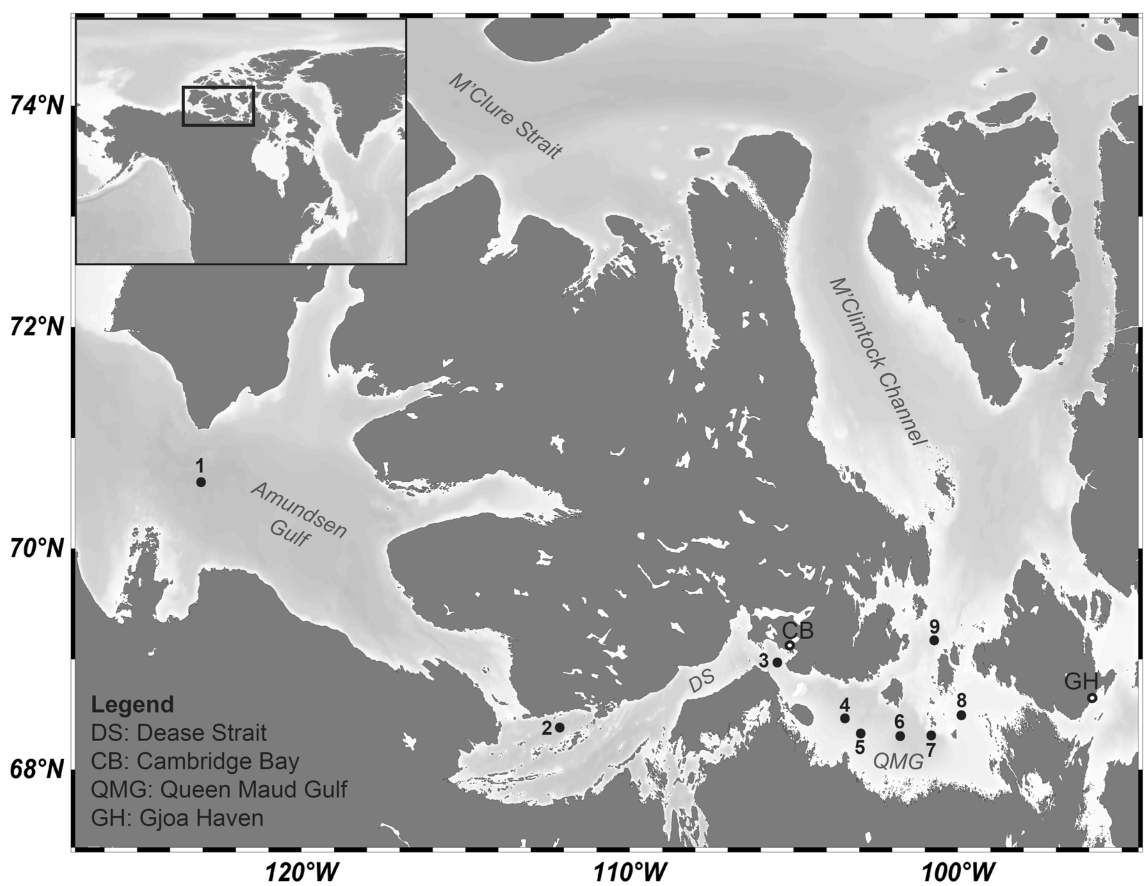

Fig. 1 Map of study area in the Canadian Arctic. *Black dots* represent the stations where the occurrence of Pacific sand lance (*Ammodytes hexapterus*) was monitored in 2011, 2014, 2015 and 2016. *Open dots* represent the two communities of interviewed harvesters: Cambridge Bay (CB) and Gjoa Haven (GH)

10 μL volume with Milli-Q water. PCR amplification parameters included an initial denaturation at 95 °C for 5 min followed by 32 cycles of denaturation, annealing, and extension fixed at, respectively, 94 °C for 45 s, 52 °C for 45 s, and 72 °C for 45 s and a final extension at 72 °C for 10 min. PCR product sequencing was performed using the Big Dye terminator sequencing kit v3.1 (Thermo Fisher Scientific) with the Applied Biosystem 3130 xl genetic analyser (Thermo Fisher Scientific) at the Institute for Integrative and Systems Biology (Université Laval). Species was determined by searching the NCBI GENBANK database with the resulting sequences.

The values of densities were not normally distributed (Shapiro–Wilk normality test; $W = 0.59$, $p < 0.0001$). Thus, non-parametric tests (Kruskal–Wallis and Wilcoxon rank-sum tests) were used to compare fish densities between years. Statistical analysis was performed in R version 3.1.1 (R Core Team 2014).

Results

A total of 69 sand lance larvae and juveniles were sampled in 2011, 2015 and 2016 in the Amundsen Gulf and Northwest Passage (Fig. 1, Table 1). A total of 68 sand lance were successfully identified as *Ammodytes hexapterus* based on DNA sequencing. The remaining sample was in a state of degradation which prohibited genetic analysis. Five sand lance were sampled in 2011, seven in 2015, and 57 in 2016. Fish size averaged 10.7 mm in August 2011, 36.1 mm in September 2015, 16.0 mm in August 2016, and 26.1 mm in September 2016.

The highest number of sand lance was captured in Queen Maud Gulf in 2016 ($n = 51$; Fig. 1). Sand lance density captured in 2016 (median = 1.2 fish 10^3 m^{-3}) was significantly higher than in 2015 (median = 0 fish 10^3 m^{-3}; Wilcoxon rank-sum test, $W = 11$, $p = 0.001$). On 21 August 2016, 26 sand lance were captured at station 6. In 2016, most fish were captured in August ($n = 45$) and fewer in September ($n = 12$).

We interviewed eight active Inuit harvesters (six from Cambridge Bay and two from Gjoa Haven; Fig. 1) as well as the board members of the Ekaluktutiak Hunters and Trappers Organization (EHTO; eight board members) about the presence of sand lance in the area. They only started to observe sand lance in the area in recent years. Some harvesters indicated that frequency of sand lance occurrence increased since their first observations, which date back two to five years depending on the respondent. Fish observed were juveniles and/or adults.

Over the summer of 2016, the species was observed by local fishers at Gravel Pit in Cambridge Bay area—an important Arctic char fishing area characterized by a gravelly and sandy substrate. Furthermore, one harvester (C. Kaiyogana) observed significant amount of sand lance at his cabin near Gravel pit in the past two years. In 2016, he observed more than 50–100 sand lance at this location, and, for the first time, he found several sand lance in the stomachs of Arctic char.

Discussion

We provide the first evidence that Pacific sand lance have expanded their distribution and spawning grounds eastward into the central Canadian Arctic Archipelago. The observed trend of increasing larval density over the years suggests that the population is rapidly expanding in its new environment. In support to our results, two additional sand lance specimens were captured during a zooplankton survey carried out by the *R/V Martin Bergmann* in the Cambridge Bay area in July 2015 (M. Falardeau, unpublished data). Moreover, the recent sand lance invasion of the Queen Maud Gulf region that we revealed based on ichthyoplankton sampling is consistent with local Inuit knowledge.

Pacific sand lance most likely expanded their range northeastward from the Chukchi Sea to the Beaufort Sea (Falardeau et al. 2014; Suzuki et al. 2015), before reaching the Northwest Passage. This contrasts with the Hudson Bay where sand lance is of Atlantic origin, belonging to the species *Ammodytes dubius* or *Ammodytes americanus* as revealed by a previous genetic analysis (M. Falardeau, unpublished data). This and the fact that the Northwest Passage is highly influenced by Pacific waters (McLaughlin et al. 2006) strongly suggest that sand lance now invading the High Canadian Arctic are of Pacific origin.

The northeastward expansion of Pacific sand lance into the Canadian Arctic was likely facilitated by the rapid warming and sea ice loss in the Beaufort Sea (e.g., Manson and Solomon 2007; Falardeau et al. 2014), a trend also observed in the Canadian Arctic Archipelago (Steiner et al. 2015). In 2016, the high densities of Pacific sand lance observed in the Northwest Passage corresponded to a year of extremely low rate of sea ice formation in the Cambridge Bay region compared to previous years (Ocean Networks Canada 2016). These relaxed climatic conditions in the Central Canadian Arctic could be responsible for increased habitat suitability for Pacific sand lance. Niche-based models run under climate change scenarios further support this assumption as they predict a shift in the range of several Pacific species, which will eventually lead to an Atlantic-Pacific interchange (Wisz et al. 2015). Among these range shifts, an expansion of Pacific sand lance into the Northwest Passage and the Northwest Atlantic Ocean is projected by 2100. The American sand lance (*A.*

Table 1 Number, average density (nb fish/10^3 m^{-3}) and mean standard length (mm) of Pacific sand lance (*Ammodytes hexapterus*) captured in the Canadian Arctic in July, August, September and October of 2011, 2014, 2015, and 2016

Year	Station number	Date	*n*	Density (nb fish/10^3 m^{-3})	Standard length (mm) Mean ± SD
2011	1	26 Sept.	0	0	NA
	3	10 Aug.	5	3.36	10.71 ± 3.13
	3	6 Oct.	0	0	NA
	9	8 Aug.	0	0	NA
	9	7 Oct.	0	0	NA
2014	1	17 Aug.	0	0	NA
	3	12 Aug.	0	0	NA
	9	11 Aug.	0	0	NA
2015	1	23 Aug.	0	0	NA
	3	18 Aug.	0	0	NA
	3	20 Sept.	0	0	NA
	4	21 Sept.	1	0.43	27.57
	5	21 Sept.	2	0.93	35.50 ± 2.12
	6	21 Sept.	0	0	NA
	7	21 Sept.	4	1.97	38.50 ± 4.21
	9	17 Aug.	0	0	NA
	9	22 Sept.	0	0	NA
2016	1	27 Aug.	2	1.40	20.50 ± 2.12
	2	23 Aug.	1	0.61	22.81
	2 (BT)	18 Sept.	1	NA	38.00
	3	23 Aug.	1	0.59	11.25
	4	23 Aug.	1	1.06	17.24
	5	22 Aug.	8	6.88	15.35 ± 2.33
	5	19 Sept.	2	1.06	27.50 ± 2.12
	6	21 Aug.	26	13.27	16.24 ± 3.90
	6	19 Sept.	2	0.94	19.00 ± 0.00
	7	21 Aug.	5	7.09	14.65 ± 3.11
	7	19 Sept.	6	4.59	27.17 ± 10.43
	8	22 Aug.	1	1.28	2.55
	9	20 Sept.	1	0.44	19.00

For each year, all the stations that were sampled are included

SD standard deviation, *BT* captured with the beam trawl, *NA* not applicable

americanus), distributed along the U.S. and Canadian East coast, is also expected to move northward over the same period, implying that the two *Ammodytes* species could meet in the Northwest Atlantic by the end of this century (Wisz et al. 2015).

The rapid invasion of the Canadian Arctic Archipelago by Pacific sand lance might be attributable at least in part to flexible habitat requirements. Species of the family Ammodytidae can tolerate a wide range of temperatures, explaining their broad traditional distribution (Robards et al. 1999b). While they primarily forage on copepods, they exhibit a generalist diet and are not limited to specific prey species (O'Connell and Fives 1995; Robards et al. 1999b; Tokranov 2007; Falardeau et al. 2014). Diet shifts of Pacific sand lance between La Niña and El Niño years suggest that the species is resilient to rapid changes in oceanographic conditions (Hipfner and Galbraith 2014). The generalist feeding habits of Pacific sand lance might facilitate its establishment in shifting Arctic marine ecosystems characterized by high variability in zooplankton production. This life strategy differs from that of the endemic polar cod characterized by specialized diet based on the large, lipid-rich Arctic copepods, making it vulnerable to alterations of zooplankton production and phenology (Falk-Petersen et al. 2006; Bouchard et al. 2016).

Another factor facilitating the rapid expansion of sand lance distribution into the Arctic could be fast post-hatching growth rates, allowing individuals to reach a relatively large size before the onset of the first winter (Falardeau et al. 2014). At the juvenile stage, sand lance shift to a semi-demersal lifestyle and start burying themselves in sediments of intertidal and subtidal zones to hide from predators or to initiate dormancy in adverse conditions (Girsa and Danilov 1976; Hobson 1986; Heath et al. 2012). We speculate that such a strategy provides an advantage over other boreal species for settling into Arctic ecosystems by optimizing survival rate in harsh environments during the winter period. In the present study, 33% of the fish caught in September had already surpassed the size at which other *Ammodytes* species metamorphose into demersal juveniles (29 mm for *A. americanus*; Smigielski et al. 1984), confirming that growth rates achieved as far east as the Queen Maud Gulf were sufficient for juvenile settlement prior to overwintering.

The first records of Pacific sand lance in the Northwest Passage reported in this study may indicate a long-term climate-driven range shift of this boreal species into the Arctic, with expected consequences on species interactions and ecosystem functioning (Fogarty et al. 2017, Pecl et al. 2017). As sand lance keep expanding their range into the rapidly warming Arctic, areas of competition among forage fish species are expected to increase, with the predicted displacement of polar cod by boreal species, as previously documented in the Barents Sea (Fossheim et al. 2015), the Southern Hudson Bay (e.g., Gaston et al. 2003, 2012), and Cumberland Sound (Watt et al. 2016) through the shifting diet and population dynamics of apex vertebrate predators. The potential loss of the energy-rich polar cod as the main forage prey could have dramatic impacts on Arctic marine food webs (Welch et al. 1992; Whitehouse et al. 2014). In particular, the relatively low energy content of Pacific sand lance (15.7–21.1 kJ/g dw^{-1}; Van Pelt et al. 1997; Robards et al. 1999a, b; Anthony et al. 2000) compared with that of polar cod (24.2–26.1 kJ/g dw^{-1}; Weslawski et al. 1994; Hop et al. 1997) suggests that the boreal invader may not be able to meet the energy needs of some of the Arctic top predators. Moreover, the current invasion is occurring at a rate higher than that predicted by model projections (Wisz et al. 2015), potentially limiting the adaptation period over which top predators will face a new prey field. A rapid shift in forage fish species composition is expected to mediate major top-down and bottom-up effects, accelerating the borealization of marine food webs in Canadian Arctic ecosystems, and raising potential challenges for ecosystem services, human well-being and governance in the Arctic (Pecl et al. 2017).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. This article does not contain any studies with animals performed by any of the authors. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Informed consent Informed consent was obtained from all individual participants included in the study. Additional informed consent was obtained from all individual participants for whom identifying information is included in this article.

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