Seasonal changes in diet and lipid content of northern sand lance *Ammodytes dubius* on Fyllas Bank, West Greenland

Nathalie S. T. Danielsen[1], Rasmus B. Hedeholm[2], Peter Grønkjær[1,3,*]

[1]Aquatic biology, Department of Bioscience, Aarhus University, building 1135, Ole Worms Allé 1, 8000 Aarhus C, Denmark
[2]Greenland Institute of Natural Resources, PO Box 570, 3900 Nuuk, Greenland
[3]Arctic Research Centre, Department of Bioscience, Aarhus University, Aarhus, Denmark

ABSTRACT: Sandeel (*Ammodytes* spp.) are forage fishes and form a crucial link in the flow of energy from phytoplankton to marine top predators in the North Atlantic. The nutritional value of the sandeel is linked to the presence of lipid-rich zooplankton species, which makes their trophic role vulnerable to climate-induced changes in the zooplankton community. We provide the first description of diet and lipid accumulation of the northern sand lance *Ammodytes dubius* Reinhardt, 1837 in southwest Greenland (64° N) during a growing season. Sampling occurred in May, August and September 2013, and differences in diet and lipid content were found in relation to season, gender and ontogeny. In terms of numbers and biomass, nauplii constituted the vast majority of prey in May, whereas copepods (primarily large *Calanus* spp.) dominated in August and September. Groups of larger prey (euphausiids and amphipods) were only found late in the season and primarily in sandeel larger than 16 cm. Mean lipid content (% DW) was at a minimum in May for both mature (males: 5.6%, females: 6.4%) and immature sandeel (3.9%), and peaked in August for mature individuals (males: 21.7%, females: 24.2%) and in September for juveniles (19.8%). Sandeel condition responds quickly to changes in prey availability and can be used as an indicator sensitive to of productivity and environmental change on the banks in West Greenland. In the light of rapid climate changes in Arctic marine ecosystems, the present findings may serve as a baseline for future monitoring of the productivity of pelagic ecosystems in West Greenland.

KEY WORDS: Sandeel · Forage fish · Feeding ecology · Energy accumulation · Condition · Nutritional value

INTRODUCTION

Highly productive marine ecosystems are often characterized by a distinctive trophic structure, where the intermediate levels are dominated by a few, but abundant species of forage fish, also known as wasp–waist species or small pelagics (Rice 1995, Cury et al. 2000). Forage fish form a functional group of plankton-feeding, fast-growing, short-lived and school-forming fish and represent a crucial node in many food webs by channeling energy from primary producers and primary consumers to larger marine predators (Cury et al. 2000, Frederiksen et al. 2006).

Sandeel (*Ammodytes* spp.) are a widespread group of forage fish found in temperate and boreo-Arctic regions of the Northern Hemisphere. Although they share the general features of forage fish, sandeel display a unique adaptation to a seasonally changing environment. They alternate between a pelagic schooling phase during the summer feeding period and an overwintering phase, during which they lie buried in the seabed with metabolism reduced to a

minimum (Behrens et al. 2007, van Deurs et al. 2011). This unusual burrowing behavior allows them to save energy in a period of food shortage and reduces their risk of predation (van Deurs et al. 2010). Even during the active period in summer, sandeel remain buried in the seabed at night and only emerge during the day to forage in the water column.

Sandeel are both ecologically and commercially important components of many North Atlantic ecosystems. They exert heavy grazing on zooplankton and efficiently convert secondary production into fish tissue (Gilman 1994, van Deurs et al. 2013), thus facilitating an almost instantaneous transfer of energy from plankton to higher trophic levels (Eliasen et al. 2011). A wide range of predatory fishes, marine mammals and seabirds are known to feed on sandeel (reviewed by Willson et al. 1999), and some species are directly dependent on the availability of sandeel for survival and successful reproduction (Rindorf et al. 2000, Davis et al. 2005).

The key role of sandeel as prey is largely attributable to their high lipid content and high energy density (Anthony & Roby 1997, van Pelt et al. 1997). However, nutritional condition (e.g. lipid content) of sandeel varies in relation to size, gender, reproductive status, location and season (Hislop et al. 1991, Robards et al. 1999a, Anthony et al. 2000), and consequently, their value as prey for top predators varies markedly. Consideration of energy content in addition to abundance of sandeel is therefore critical in order to understand changes in the productivity of sandeel predators (Wanless et al. 2005).

Variations in growth, condition and reproduction of marine fishes (e.g. Yaragina & Marshall 2000, Bergstad et al. 2002), birds (Cairns 1988, Österblom et al. 2008) and mammals (Øigård et al. 2013) are typically linked to seasonal fluctuations in prey availability and quality. Lipid content of sandeel and other forage fish such as capelin *Mallotus villosus* and herring *Clupea harengus* is known to increase during intense summer feeding on lipid-rich zooplankton species in preparation for energetically expensive events such as migration, spawning and overwintering (Montevecchi & Piatt 1984, Henderson & Almatar 1989, Robards et al. 1999a). However, climate-driven changes in zooplankton composition and distribution have recently become apparent in North Atlantic regions (Beaugrand et al. 2002, Beaugrand 2004), with potential implications for fish dependent on zooplankton (Pitois & Fox 2006).

In West Greenland, in particular, the climate impact on distribution and phenology of the 3 large *Calanus* species (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) has attracted attention due to their importance for a range of planktivorous marine species (Kjellerup et al. 2012, Jung-Madsen et al. 2013). The 3 species differ in their latitudinal distribution, with *C. finmarchicus* being the most temperate and *C. hyperboreus* the most Arctic species (Falk-Petersen et al. 2009, Swalethorp et al. 2011). They also show species-specific reproductive adaptations to the onset of spring bloom. In West Greenland waters, *C. finmarchicus* spawn in the surface during and after the spring bloom, and their reproduction is primarily fueled by energy obtained from the spring bloom. In contrast, *C. glacialis* and *C. hyperboreus* commence spawning before the bloom and utilize stored lipid reserves, which in the case of *C. glacialis*, is supplemented by energy from the spring bloom (Madsen et al. 2001, Swalethorp et al. 2011). It has been hypothesized that ongoing changes in temperatures and sea ice extent along West Greenland will change the relative abundance of these 3 species in favor of the smaller, less lipid-rich *C. finmarchicus* and potentially cause a temporal mismatch between sandeel feeding and the production of their zooplankton prey (Kjellerup et al. 2012). In this case, the feeding and energy accumulation of sandeel may be compromised with repercussions for the higher trophic levels on the West Greenland shelf.

While the ecology, physiology and population dynamics of sandeel in the North Sea and Faroe shelf area are well known, little is known about the West Greenlandic sandeel. Sandeel are not commercially exploited in West Greenland, but the few preliminary assessments suggest that they are very abundant on the banks (Andersen 1985) and may play an important role in the food web in these areas. Here, we provide the first description of the ecology of sandeel from Fyllas Bank in southwest Greenland and investigate their diet, gonadal development and lipid accumulation during a growing season. The overall aim of the present study was to document how sandeel diet and condition changes seasonally, thus allowing us to evaluate the importance of sandeel in the Fyllas Bank ecosystem and the potential impact of climate change on the feeding, growth and nutritional value of this key species.

MATERIALS AND METHODS

Study area and data collection

Sandeel were collected aboard the RV 'Sanna', operated by the Greenland Institute of Natural

Resources. Sampling took place on Fyllas Bank in May, August and September 2013, using a bottom-trawl with a small mesh codend and 30 min tow duration (Fig. 1). There are 2 recorded sandeel species on the west coast of Greenland: the northern sand lance *Ammodytes dubius* and the lesser sandeel *A. marinus*. Although the 2 species are similar in morphology and no genetic analyses were performed in the present study, their distribution and abundance in West Greenland (Froese & Pauly 2015) indicate a high probability that all sampled individuals were northern sand lance.

Size distribution was determined from all sampled sandeel or a subsample of at least 100 individuals. A subsample of approximately 50 ind. station^{-1} was sorted in 2 cm size intervals and frozen in seawater for later analysis of lipid and water content. Stomachs and guts from another subsample of approximately 15 fish per 2 cm size interval were dissected out and stored in formalin (6%) saltwater. Stomachs from each size interval were preserved together.

Stomach content analysis

The stomachs were rinsed in water and examined under a dissecting microscope. Prey items in the stomachs were identified to the lowest possible taxonomic level, but identification was often restricted to class or order (e.g. Euphausiacea, Copepoda and Amphipoda) due to digestion. When possible, the total length was measured for all prey groups. Prey items were categorized into 1 of 7 major groups, each containing various taxonomic levels: 'Amphipoda' (*Themisto abyssorum*, *T. compressa*, *T. libellula*, *Themisto* sp., Gammaridae and unknown), '*Calanus* spp.' (*C. finmarchicus*, *C. glacialis* and *Calanus* sp.), 'other copepods' (copepodites, Harpacticoida, *Metridia longa*, *Oithona similis*, *Paracalanus parvus*, *Paraeuchaeta norvegica*, *Pseudocalanus* sp. and unknown), 'Euphausiacea' (*Thysanoessa raschii*, *Thysanoessa* sp. and unknown), 'young crustacean stages' (copepod eggs, nauplii, zoea and cyprids), 'Gastropoda' (pteropods; *Clione limacina*, *Limacina* sp.), and 'other' (unidentified prey items, Polychaeta and fish eggs).

To evaluate the importance of specific prey groups in different months and sandeel size groups, 2 methods for quantifying the diet composition were applied. The 7 prey groups were expressed as the percentage composition by number in fish that contained that prey group, i.e. prey-specific abundance (*A*) as described by Amundsen et al. (1996):

$$A = 100(\sum S_i)(\sum S_{ti})^{-1} \quad (1)$$

where S_i is the number of prey, *i*, and S_{ti} is the total number of prey in stomachs containing prey *i*. For each prey group, frequency of occurrence (*F*) was calculated as described by Hyslop (1980):

$$F = N_i N_t^{-1} \quad (2)$$

where N_i is the number of stomachs containing prey *i*, and N_t is the total number of stomachs containing prey. Occurrence of a particular prey species or prey group was defined as the presence of at least one individual of a taxonomic group in the sandeel stomach. *A* was then plotted against *F* (Amundsen et al. 1996).

Prey biomass in terms of carbon content was estimated using literature based length–weight relationships and dry weight to carbon conversion factors (Table 1). The subgroup of unidentified prey items was omitted from biomass calculations.

Prey diversity based on the 7 prey groups was determined for each month (without regard to sandeel size) using the Shannon-Wiener index (*H'*):

$$H' = -\sum (p_i \ln p_i) \quad (3)$$

where p_i is the proportion of prey in prey group *i* of the total number of prey.

Diatoms were present in sandeel stomachs in May and September, but generally in low to moderate numbers and predominantly in small (juvenile)
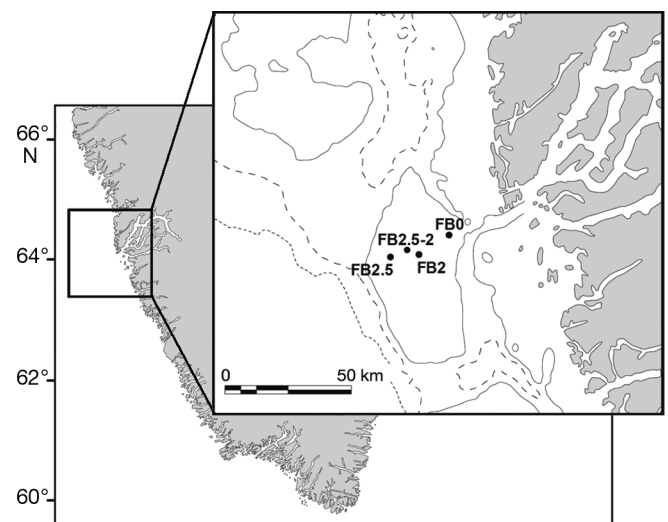

Fig. 1. Study area in southwest Greenland. Fyllas Bank is highlighted in the box, and locations of the main sampling stations are indicated. Depth ranges at the different stations were: FB0: 88–110 m; FB2: 44–47 m; FB2.5-2: 40–48 m; FB2.5: 55–63 m. Depth curves are indicated at 150 m (solid line), 400 m (dashed line), and 1000 m (dotted line)

Table 1. Algorithms used to convert body length (µm or mm) to body carbon content (C, µg). DW: dry weight; L: prosome length for copepods and total length for all other zooplankton groups; CL: carapace length

Taxon	Develop. stage	Equation (DW)	Equation (carbon)	Reference
Calanus finmarchicus	Nauplius		$C(µg) = 4.168E^{-6}L(µm)^{2.03}$	Hygum et al. (2000)
	Copepodite		$C(µg) = 2.101E^{-8}L(µm)^{2.88}$	
C. glacialis	Copepodite		as for *C. finmarchicus*	Hygum et al. (2000)
Metridia longa	Copepodite		$C(µg) = 5.39E^{-9}L(µm)^{3.0167}$	Hirche & Mumm (1992)
Oithona sp.	Copepodite		$C(µg) = 9.4676E^{-7}L(µm)^{2.16}$	Sabatini & Kiørboe (1994)
Pseudocalanus sp.	Copepodite		$C(µg) = 6.21E^{-11}L(µm)^{3.745}$	Cohen & Lough (1981)
Microsetella sp.	Copepodite		$C(µg) = 4.14E^{-4}L(µm)^{1.15}$	Satapoomin (1999)
Paraeuchaeta sp.	Adult		$C(µg) = 1.15E^{-23}L(µm)^{6.92}$	Tönnesson et al. (2006)
Paracalanus parvus	Adult	$DW(µg) = 0.0191E^{3}L(mm)^{2.74}$		Hay et al. (1991)
			C = approx. 40% of DW(µg)	T. G. Nielsen pers. comm.
Copepod egg			$C(µg) = 1.1E^{-7}(4/3)\pi[L(µm)/2]^{3}$	Swalethorp et al. (2011)
Unid. Copepoda			<1.2 mm as for *Pseudocalanus* sp.	Hay et al. (1991)
			>1.2 mm as for *Calanus* (CI–V)	
Cirripedia	Cyprid		11 µg C ind.$^{-1}$	Rodhouse & Roden (1987)
Thysanoessa raschii	Adult		$C(µg) = 1.31E^{-1}L(mm)^{3.549}$	Agersted & Nielsen (2014)
Themisto libellula	Adult	$DW(µg) = 4.5L(mm)^{2.7071}$		Pinchuk et al. (2013)
			C = approx. 40% of DW(µg)	Noyon et al. (2009)
Limacina helicina	Adult	L (mm) = 0.48, DW(µg) = 10.210		Hay et al. (1991)
			C = 37.12% of DW(µg)	Ikeda & Skjoldal (1989)
Clione limacina	Adult	$DW(µg) = 33.9L(mm)^{2.2393}$		Derived from data in Mizdalski (1988)
		if DW < 50 mg	C = 23.39% of DW(µg)	Ikeda & Skjoldal (1989)
		if DW > 50 mg	C = 33.66% of DW(µg)	
Polychaete larvae			$C(µg) = 1.58E^{-4}L(µm)^{1.38}$	Pedersen et al. (2010)
Branchyuran zoea		logDW(µg) = 2.58 × LN(CL in mm) + 2.04	C = 34.9% of DW(µg)	Lindley (1998)
Fish egg (cod)			43 µg C egg^{-1}	Jørgensen (1985)

sandeel. Phytoplankton has previously been recorded as part of sandeel diet, particularly in sandeel larvae (Trumble 1973). However, diatoms were markedly smaller compared to the dominant prey items in this study, and their volumetric contribution was negligible. Furthermore, they appeared to pass incompletely digested through the gastrointestinal tract. Diatoms were therefore omitted from the analysis of prey composition.

Lipid and water content analysis

We analyzed whole-body lipid content (% dry weight, DW) of freeze-dried sandeel. The method was modified from the procedure for Atlantic salmon produced by NIFES (NS 9402.E; Anonymous 1994), where wet muscle tissue was sampled.

The frozen sandeel were thawed in a fridge at 5°C for 1 to 2 d, rinsed briefly in tap water and blotted dry with paper towels. Total length (TL) was measured (truncated to the nearest mm). Wet weight (WW; 0.001 g) was measured both before and after removal of sagittal otoliths and stomach contents. Stomach and gut contents were removed to avoid the influence of prey lipid content and variations in stomach fullness on the analysis of sandeel lipid content. The empty guts were placed back into the fish, and the otoliths were kept dry in separate Eppendorf tubes. If possible, sex and maturity stage were determined (otherwise designated juvenile and immature) before each individual was placed in a pre-weighed (3 decimals) zip-lock bag and re-frozen (−22°C). The frozen fish were then freeze-dried. Small fish only required approximately 24 h, while bigger fish (>16 cm) required 48 h. The DW of each individual was subsequently determined, and the dried fish were kept in a desiccator until further analysis.

Each freeze-dried individual was homogenized with a stick blender in a 90 ml plastic vial with a flat bottom, and 30 ml of ethyl acetate admixed 30% isopropanol was added. When the sandeel were too

Table 2. Number of samples (lipid content) and individuals (water and stomach content) used for analysis in different sandeel size groups (6 to 22 cm) and months (May, August and September 2013)

Size group (cm)	May			Aug			Sep		
	N_{lipid}	N_{water}	$N_{stomach}$	N_{lipid}	N_{water}	$N_{stomach}$	N_{lipid}	N_{water}	$N_{stomach}$
6–8	–	–	–	–	–	–	–	3	5
8–10	3	6	15	–	–	–	9	18	10
10–12	3	10	19	12	12	4	2	2	1
12–14	3	4	8	10	10	27	10	10	23
14–16	6	6	9	22	39	51	11	11	25
16–18	6	5	9	9	11	58	10	10	21
18–20	–	1	2	11	11	33	10	10	27
20–22	–	–	–	–	–	6	–	–	3
Total	21	32	62	64	83	179	52	64	115

small to obtain sufficient material (<14 cm in May and <10 cm in September), 2 or more sandeel of the same size were pooled. Vials were sealed with an airtight lid and whirled for 10 min using a rotator drive (Stuart STR4), then left to rest overnight. The next day, the solution was whirled again for 10 min and filtered through a 1.2 µm glass fiber filter into a 500 ml glass bottle using a vacuum pump (~10 KPa). Another 20 ml of solvent was added to ensure that the filter did not retain any lipids. The solution was then poured through a glass funnel into a pre-weighed (4 decimals) glass beaker. The filtrate was left to evaporate in a fume cupboard overnight. If the solvent had not fully evaporated the next day, the glass beaker was left in the fume cupboard another night. The glass beaker was then placed in an incubator at 60°C for 1 h. If the solvent had still not evaporated, the glass beaker was left in the incubator overnight. Afterwards, the glass beaker was cooled to room temperature in a desiccator and weighed to the precision of 4 decimals. Lipid content could then be determined using the following formula:

$$\text{Lipid content (\% DW)} = 100(W_{Li}/W_{Fi}) \qquad (4)$$

where W_{Li} is the weight (g) of lipid in the glass beaker, and W_{Fi} is the weight (g) of dry fish homogenate used in the analysis.

Water content was determined as the difference between WW (after removal of otoliths and stomach contents) and DW.

Statistical analysis

All statistical analyses were performed in SPSS. The level of statistical significance was $\alpha = 0.05$ for all tests. Data on lipid and water content are presented as size group means in figures for clarity, but the

ANCOVA was performed with individual length as covariate. Sample sizes in all analyses are summarized in Table 2.

RESULTS

Trawling for sandeel on Fyllas Bank was successful in all months, indicating that sandeel were present in the water column from at least early May to late September. May sampling yielded fewer sandeel and the size distribution was skewed towards smaller individuals (<12 cm in length) compared to August and September. With few exceptions, sandeel >12 cm in length were mature. Visual inspection showed that gonads from mature sandeel collected in May were small and had only recently started developing, but most mature sandeel were ripe in August and started spawning in September. Thus, gonadal development occurred over a period of 3 to 4 mo.

Sandeel diet

A total of 356 sandeel stomachs were analyzed from Fyllas Bank sampled in May, August and September 2013; and 46% of the stomachs were empty. Abundance data on all prey groups are provided in Tables 3 & 4. Copepods constituted the most diverse prey group, and a total of 7 species were identified: *Calanus finmarchicus*, *C. glacialis*, *Metridia longa*, *Oithona similis*, *Paracalanus parvus*, *Paraeuchaeta norvegica* and *Pseudocalanus* sp. The remaining identifiable specimens were classified as copepodites or belonged to the order Harpacticoida. Copepods were numerically dominated by the genus *Calanus* (70%), and most of these were *C. finmarchicus* (46%). Three species of amphipods were identified:

Table 3. Percentage number of prey species found in stomachs of sandeel size 6 to 14 cm sampled in May, August and September

Prey group species	6–8 cm	—8–10 cm—		———10–12 cm———			———12–14 cm———		
	Sep	May	Sep	May	Aug	Sep	May	Aug	Sep
Amphipoda									
Themisto abyssorum	–	–	0.2	–	–	–	–	–	–
Themisto compressa	–	–	–	–	–	–	–	–	0.3
Themisto libellula	–	–	–	–	–	–	–	–	–
Themisto sp.	–	–	–	–	2.1	–	–	–	0.3
Gammaridae	–	–	–	–	–	–	–	0.2	–
Unknown	–	–	–	–	–	–	–	–	0.3
Copepoda									
Calanus spp.									
C. finmarchicus	21.3	–	47.5	–	18.8	72.8	–	19.0	57.1
C. glacialis	1.1	–	1.6	–	–	6.2	–	–	5.9
Calanus sp.	21.3	–	5.7	–	–	–	–	55.7	11.7
Other copepods									
Copepodite	18.0	6.1	5.3	3.4	18.8	–	1.6	9.6	–
Harpacticoida	20.2	0.2	2.1	0.2	–	–	–	0.2	1.9
Metridia longa	–	–	–	–	–	1.2	–	–	2.5
Oithona similis	–	0.2	1.0	0.1	–	–	0.8	0.7	0.9
Paracalanus parvus	–	–	0.8	–	–	–	–	–	–
Paraeuchaeta norvegica	–	–	–	–	–	–	–	–	0.6
Pseudocalanus sp.	–	–	0.6	–	–	2.5	–	0.5	0.6
Unknown	15.7	–	1.0	6.8	14.6	13.6	1.0	4.8	4.0
Euphausiacea									
Thysanoessa raschii	–	–	1.0	–	–	–	–	–	0.6
Unknown	1.1	–	–	–	–	–	–	–	–
Young crustacean stages									
Copepod egg	–	5.2	0.2	5.2	10.4	–	2.1	–	–
Zoea	–	–	–	1.3	–	–	1.8	–	–
Nauplius	1.1	88.0	0.8	82.9	35.4	–	92.7	8.9	0.3
Cypris	–	–	–	–	–	1.2	–	–	1.5
Gastropoda									
Clione limacina	–	–	–	–	–	–	–	–	–
Limacina sp.	–	0.2	–	–	–	2.5	–	0.2	1.2
Other									
Fish egg	–	–	–	–	–	–	–	–	–
Polychaeta	–	–	–	–	–	–	–	–	–
Unknown	–	–	32.4	0.1	–	–	–	–	10.2
Number of prey	89	424	512	1348	48	81	382	415	324
Number of stomachs	5	15	10	19	4	1	8	27	23
Empty stomachs (%)	0	46.7	0	47.4	0	0	75	14.8	30.4

Themisto abyssorum, *T. compressa* and *T. libellula*, where *T. compressa* was numerically the most abundant of amphipods (42%). In general, euphausiids were highly digested and therefore difficult to identify, but all identifiable specimens were *Thysanoessa raschii*. Euphausiids only occurred in sandeel stomachs in August and September and primarily in sandeel >14 cm. Similarly, gastropods were only found in August and September and were often highly digested, but 2 species were identified as *Clione limacina* and *Limacina* sp. (pteropods). The group of young crustacean stages included nauplii, branchyuran zoea larvae, cyprids and copepod eggs,

but nauplii accounted for the majority of individuals (94%).

Considering prey from all size groups, there were clear seasonal differences in prey composition between May and August/September (Fig. 2). In May, the number of different prey species found in sandeel stomachs was low for all size groups (H' = 0.26), and young crustacean stages (primarily nauplii) dominated the total number of prey (93%). The remaining prey items were copepods (mainly copepodites), and none of the stomachs contained adult calanoids. Sandeel diet was more diverse in August (H' = 1.24) compared to May, and the overall propor-

Table 4. Percentage number of prey species found in the stomach of sandeel size 14 to 22 cm sampled in May, August and September

Prey group species	14–16 cm			16–18 cm			18–20 cm			20–22 cm	
	May	Aug	Sep	May	Aug	Sep	May	Aug	Sep	Aug	Sep
Amphipoda											
Themisto abyssorum	–	0.8	–	–	1.1	–	–	4.5	–	–	–
Themisto compressa	–	0.3	3.5	–	1.3	28.1	–	27.3	22.7	–	–
Themisto libellula	–	–	–	–	0.4	–	–	–	–	5.3	–
Themisto sp.	–	–	–	–	1.1	–	–	18.2	–	5.3	100.0
Gammaridae	–	–	–	–	–	–	–	–	–	–	–
Unknown	–	0.8	–	–	1.8	–	–	18.2	–	10.5	–
Copepoda											
Calanus spp.											
C. finmarchicus	–	14.3	51.2	–	8.0	21.9	–	11.4	27.3	–	–
C. glacialis	–	–	4.1	–	0.1	6.3	–	–	–	–	–
Calanus sp.	–	52.7	8.7	–	45.3	6.3	–	–	–	–	–
Other copepods											
Copepodite	0.2	0.5	2.3	–	0.2	–	–	–	4.5	–	–
Harpacticoida	0.2	–	2.9	–	–	1.6	–	–	–	–	–
Metridia longa	–	–	0.6	–	–	–	–	–	–	–	–
Oithona similis	–	0.3	–	–	–	1.6	–	2.3	–	–	–
Paracalanus parvus	–	0.3	–	–	–	–	–	–	–	–	–
Paraeuchaeta norvegica	–	–	0.6	–	–	1.6	–	–	–	–	–
Pseudocalanus sp.	–	3.8	2.9	–	–	1.6	–	–	–	–	–
Unknown	1.1	4.1	6.4	–	29.5	21.9	–	11.4	4.5	–	–
Euphausiacea											
Thysanoessa raschii	–	–	2.3	–	0.1	3.1	–	–	4.5	–	–
Unknown	–	2.5	–	–	0.9	–	–	2.3	4.5	–	–
Young crustacean stages											
Copepod egg	0.9	–	–	–	0.1	1.6	–	–	–	–	–
Zoea	2.6	–	–	–	–	1.6	–	–	–	–	–
Nauplius	95.0	19.5	–	100.0	–	–	–	–	–	–	–
Cypris	–	–	1.7	–	–	–	–	–	–	–	–
Gastropoda											
Clione limacina	–	–	–	–	0.7	–	–	–	–	78.9	–
Limacina sp.	–	–	–	–	–	1.6	–	–	–	–	–
Other											
Fish egg	–	–	–	–	–	–	–	–	27.3	–	–
Polychaeta	–	–	–	–	–	–	–	2.3	–	–	–
Unknown	–	–	12.8	–	9.3	1.6	–	2.3	4.5	–	–
Number of prey	543	364	172	6	907	64	0	44	22	19	2
Number of stomachs	9	51	25	9	58	21	2	33	27	6	3
Empty stomachs (%)	66.7	47.1	40	88.9	46.6	66.7	100	66.7	59.3	16.7	66.7

tion of young crustacean stages in the stomachs was considerably lower (7%). Instead, prey composition was dominated by copepods (80%), and most of these were *Calanus* spp. Amphipods were also part of the diet (5%), whereas euphausiids and gastropods occurred in low numbers (1%). However, 20 to 22 cm sandeel stomachs contained a large proportion of the gastropod *Clione limacina* (79%), but this prey species was only found in August and only in sandeel >16 cm (Table 4). The September diet resembled that of August, with relatively high prey diversity (H' = 1.15) and with copepods dominating numerically (76%). There was a relatively large pro-

portion of 'other' (18%), reflecting a high number of unknown prey items that were impossible to identify due to digestion.

The prey composition in terms of carbon biomass was a similar to that based on count (Fig. 2). However, 2 prey groups differed from the general trend and showed a markedly higher importance by means of their carbon biomass compared to their numbers. Gastropods constituted 25% of the total carbon biomass in August, and euphausiids constituted 19% of the total carbon biomass in September, whereas both groups only accounted for approximately 1% of the total prey count in the respective months.
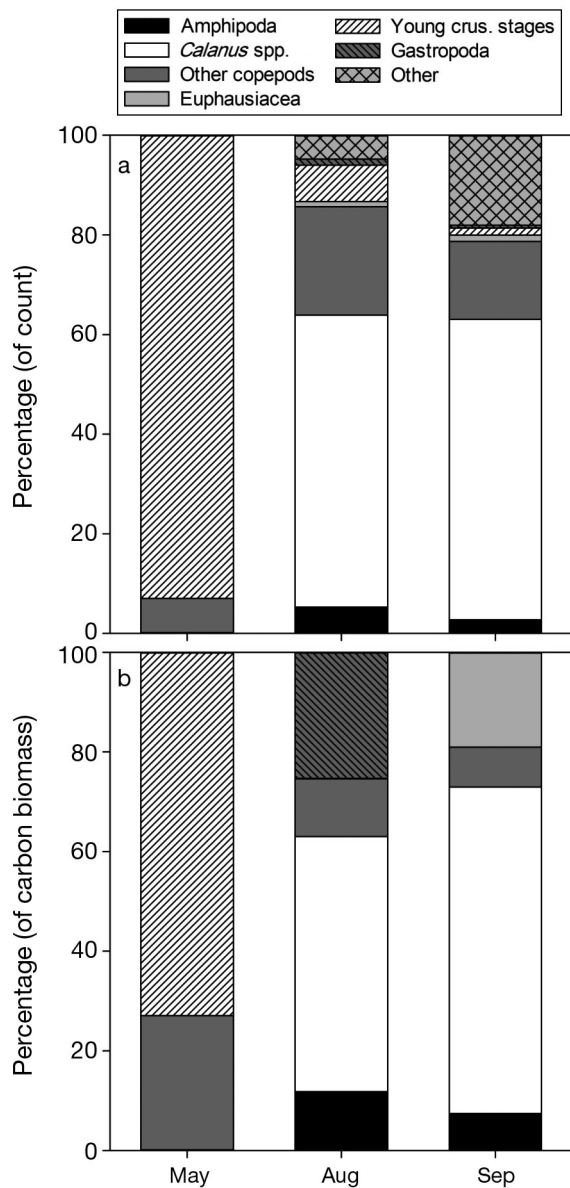
Fig. 2. Composition of stomach content based on (a) count and (b) weight (μg C) in sandeel collected in 2013 in May (n = 62), August (n = 179) and September (n = 115) from Fyllas Bank, West Greenland

In addition to the seasonal differences in sandeel feeding patterns, the plots of prey-specific abundance versus frequency of occurrence of the different prey categories indicated a marked difference between size groups in August and September (Fig. 3). In May, the diet was homogenous across size groups, with young crustacean stages (primarily nauplii) as the single dominant prey. In contrast, sandeel diet was more heterogeneous in August and September and consisted of at least 4 prey groups in each

sandeel size group. In August, most small sandeel (10 to 12 cm) consumed young crustacean stages in moderate numbers (high *F*, medium *A*), other copepods occasionally and *Calanus* spp. in low numbers. The diet of larger sandeel (12 to 18 cm) was dominated by *Calanus* spp., which were consumed often by most individuals (high *F*, high *A*). Other copepods, amphipods and young crustacean stages varied in importance between size groups. For example, amphipods were consumed in high numbers by a few individuals (low *F*, high *A*) in size group 12 to 14 cm, whereas in size group 16 to 18 cm, amphipods occurred in many stomachs in low numbers (high *F*, low *A*). Although amphipods and euphausiids in general had low *A* and *F*, they often accounted for a large proportion of total stomach content due to large individual biomass. In September, *Calanus* spp. were the dominant prey in all size groups (high *F*, high *A*), but otherwise prey composition resembled that of August.

Lipid and water content

Sandeel collected in May were visibly leaner than individuals collected in late summer, having little or almost no observable abdominal lipid. In contrast, abdominal lipid reserves were large and easily distinguished in August and September. The analysis of whole-body lipid content (% DW) confirmed these observations, and mean lipid content varied significantly in response to month, sex and size (Fig. 4, Table 5).

For both sexes across size groups, mean lipid content was lowest in May (5.6% in males, 6.4% in females) and peaked in August (21.7% in males, 24.2% in females). Compared to September values, the mean lipid content of mature sandeel was 15% lower in May and 2% higher in August. The decline in lipid content observed from August to September paralleled gonad maturation and the onset of spawning. The ANCOVA (Table 5) showed that females had significantly higher lipid content than males in all months, and there was a significant decrease in mean lipid content with increasing length for both sexes. Similarly, mean lipid content in juvenile sandeel varied significantly in response to month and length (Table 6), with the lowest values in May (3.9%). However, mean lipid content peaked in September (19.8%), and in contrast to mature sandeel, the ANCOVA showed a significant increase in mean lipid content with increasing size for juveniles.
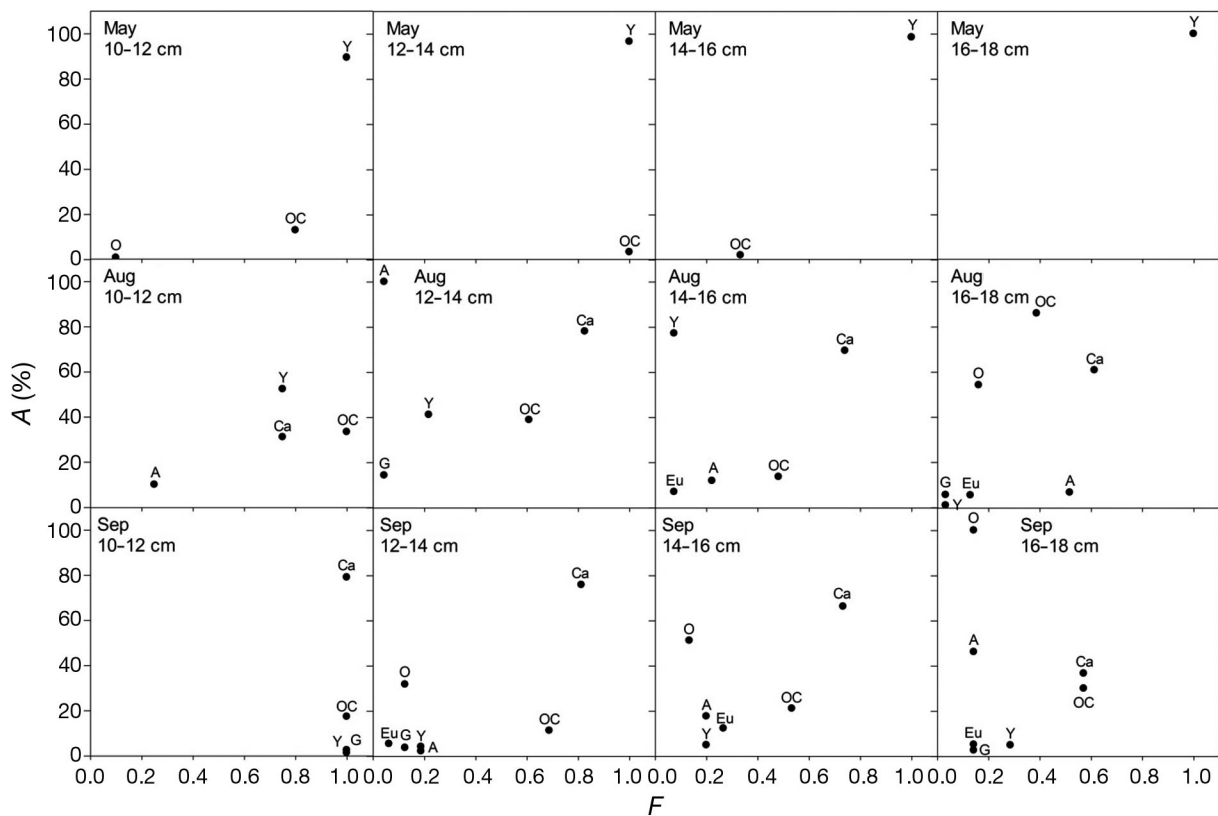
Fig. 3. Plots of prey-specific abundance (*A*, %), against frequency of occurrence (*F*) for sandeel collected on Fyllas Bank, West Greenland in May, August and September 2013, showing the relative importance of major prey groups (A: Amphipoda; Ca: *Calanus* spp.; OC: other copepods; Eu: Euphausiacea; Y: young crustacean stages; G: Gastropoda; O: other)

Mean water content (% WW) also varied according to month, sex and size (Fig. 5, Table 7), but showed the opposite pattern of lipid content: water content peaked in May (80.9% in males, 81.4% in females) and was at a minimum in August for both sexes (77.2% in males, 75% in females). The ANCOVA (Table 7) showed that females had significantly higher water content than males in May, but was at its lowest in August and September. There was a significant decrease in mean water content with increasing length. Similarly, mean water content in juvenile sandeel varied in response to month and length (Table 8), with minimum values occurring in May and a significant decrease in mean water content with increasing length.

The proportion of lipid in dry matter increased with increasing percentage dry matter (Fig. 6), meaning that a weight increase was to a large extent caused by lipid accumulation. A 1-way ANCOVA showed a significant effect of % DW ($F_{1,33}$ = 98.4, p ≤ 0.001) on lipid content with no significant effect of sex and no significant interaction.

DISCUSSION

This study documented pronounced seasonal variation in sandeel diet as well as seasonal, gender-related and ontogenetic differences in lipid content in a sandeel population on Fyllas Bank in Southwest Greenland during the summer feeding period. These variations are likely driven by changes in the availability of prey and the need to accumulate lipid energy in preparation for spawning and winter hibernation. Future climate-related changes in the distribution, phenology and abundance of lower trophic levels in West Greenland waters are likely to have a pronounced impact on the productivity of the local sand lance populations.

Sandeel diet

The northern sand lance (*Ammodytes dubius*, hereafter sandeel) was present and feeding in the water column during the day from early May to late
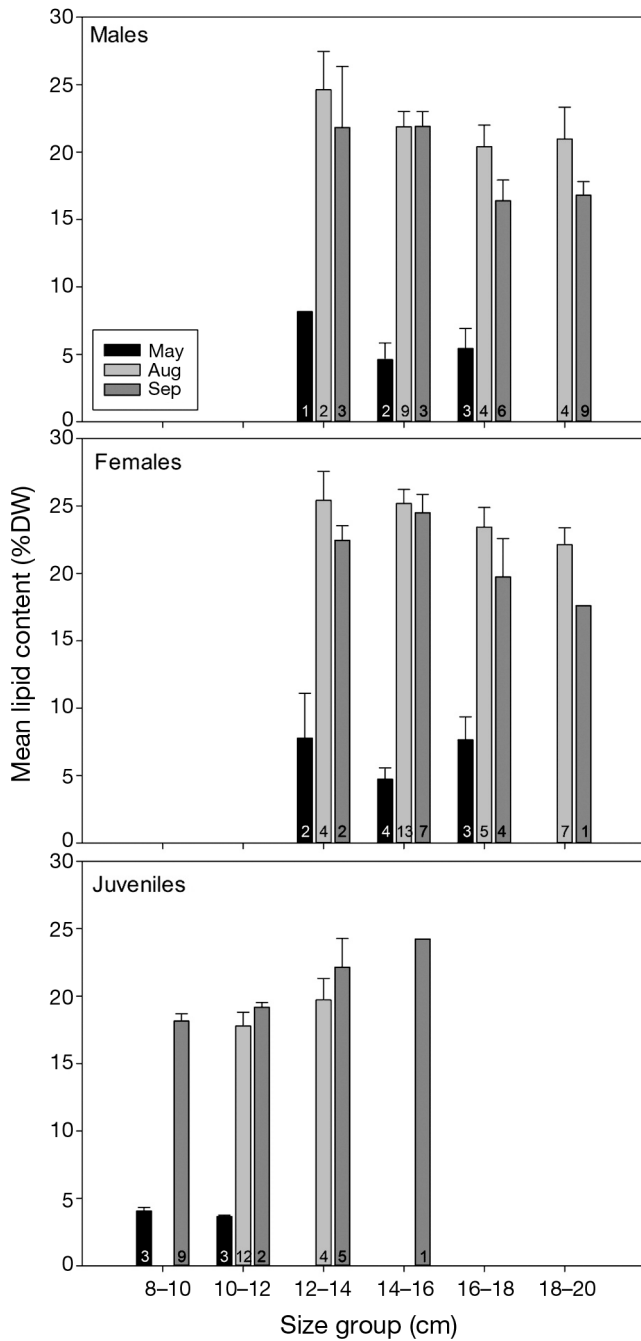
Fig. 4. Mean (±SE) lipid content (% dry weight, DW) of male, female and juvenile sandeel. Numbers in bars represent numbers of samples

Table 5. Results of 2-way, fixed factor ANCOVA for the mean lipid content of mature sandeel, testing the effect of month (May, August and September) and sex (male and female) with total length (cm) as covariate. Parameter estimates (B) are shown with standard error (SE[B]) and p-value. B(Males) = 0; B(September) = 0

Source	MS	df	F	p
Intercept	950.303	1	72.331	≤0.001
Sex	144.928	1	11.031	0.001
Month	1758.349	2	133.834	≤0.001
Length	165.547	1	12.600	0.001
Error	13.138	93		

Parameter	B	SE(B)	p
Intercept	30.769	3.473	≤0.001
Females	2.506	0.755	0.001
Aug	2.353	0.829	0.006
May	−15.166	1.153	≤0.001
Length	−0.724	0.204	0.001

Table 6. Results of the 1-way, fixed factor ANCOVA for the mean lipid content of juvenile sandeel, testing the effect of month (May, August and September) with total length (cm) as covariate. Parameter estimates (B) are shown with standard error (SE[B]) and p-value. B(September) = 0

Source	MS	df	F	p
Intercept	31.015	1	3.723	0.062
Month	529.382	2	63.551	≤0.001
Length	68.531	1	8.227	0.007
Error	8.330	35		

Parameter	B	SE(B)	p
Intercept	11.608	2.943	≤0.001
Aug	−2.331	1.043	0.032
May	−15.469	1.381	≤0.001
Length	0.780	0.272	0.007

September. The duration of the feeding season may extend even further, but there are no available samples to document this. Trawl hauls conducted on the same station on Fyllas Bank in December 2014 did not catch any sandeel, which indicates that the winter hibernation had commenced (R. B. Hedeholm pers. obs.). These recordings are consistent with ob-

servations made during sandeel exploratory fisheries in 1978 (Andersen 1985). In accordance with a pelagic feeding behavior, stomachs contained mostly crustacean zooplankton similar in composition to the other dominant pelagic fish, capelin, in the same area (Hedeholm et al. 2012). However, benthic prey (mostly harpacticoids) was also identified, probably reflecting the fact that sandeel are associated with the sea bottom at certain times during the diurnal cycle. The diet resembled that of sandeel reported elsewhere (Macer 1966, Reay 1970, Meyer et al. 1979, O'Connell & Fives 1995, Hipfner & Galbraith 2014), with copepods as the principal constituent.
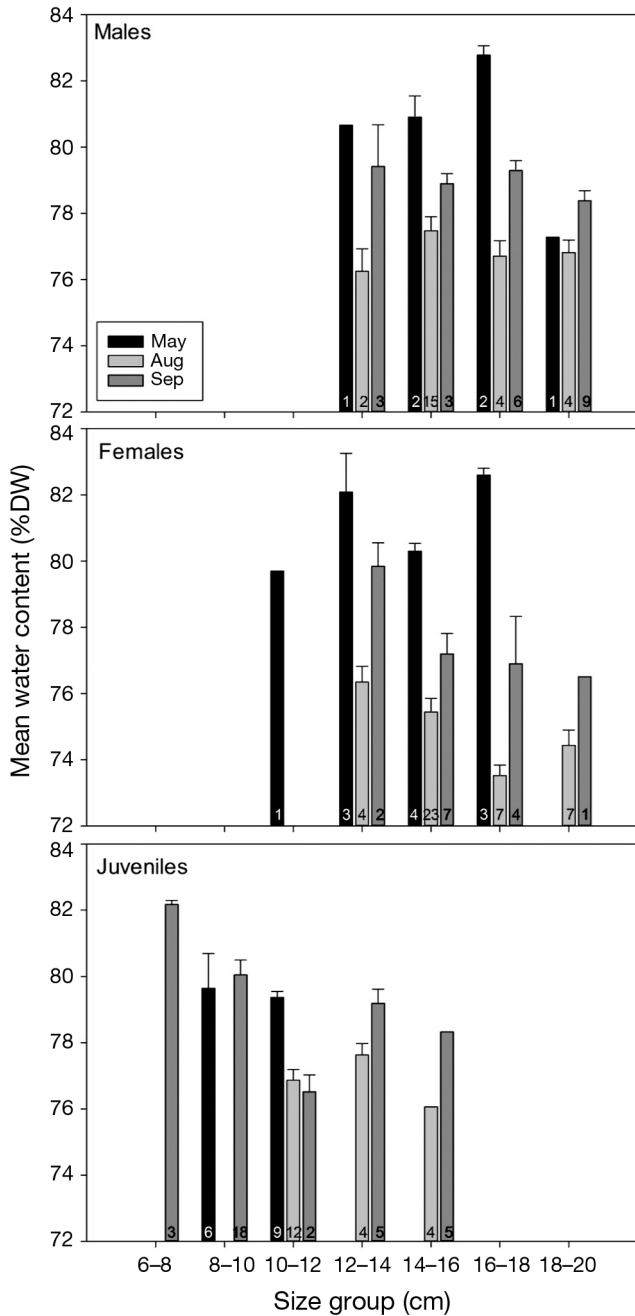
Fig. 5. Mean (±SE) water content (% wet weight, WW) of male, female and juvenile sandeel. Numbers in bars represent numbers of individuals

Table 7. Results of 2-way, fixed factor ANCOVA for the mean water content of mature sandeel, testing the effect of month (May, August and September) and sex (male and female) with total length (cm) as covariate. Parameter estimates (B) are shown with standard error (SE[B]) and p-value. B(Males) = 0; B(September) = 0

Source	MS	df	F	p
Intercept	9307.542	1	3694.260	≤0.001
Sex	23.755	1	9.429	0.003
Length	21.349	1	8.473	0.004
Month	170.897	2	67.831	≤0.001
Sex × Month	10.264	2	4.074	0.020
Error	2.519	110		

Parameter	B	SE(B)	p
Intercept	83.099	1.496	≤0.001
Females	−1.723	0.557	0.003
Aug	−2.085	0.487	≤0.001
May	1.618	0.748	0.033
Length	−0.250	0.086	0.004
F × Aug	−0.365	0.690	0.597
F × May	2.237	0.988	0.025

Table 8. Results of the 1-way, fixed factor ANCOVA for the mean water content of juvenile sandeel, testing the effect of month (May, August and September) with total length (cm) as covariate. Parameter estimates (B) are shown with standard error (SE[B]) and p-value. B(September) = 0

Source	MS	df	F	p
Intercept	10398.578	1	4335.519	≤0.001
Length	22.655	1	9.446	0.003
Month	18.760	2	7.822	0.001
Error	2.398	58		

Parameter	B	SE(B)	p
Intercept	83.285	1.164	0.000
August	−2.023	0.540	0.000
May	−0.123	0.487	0.802
Length	SGH0.365	0.119	0.003

However, there were marked seasonal differences in prey composition and diversity. Sandeel fed almost exclusively on nauplii in May, whereas adult copepods of the genus *Calanus* were the most important prey among a broader variety of prey taxa in August and September. Pedersen et al. (2005) examined plankton community composition on the banks of the Southwest Greenland shelf and found that early life stages of zooplankton, in particular large (>200 μm) copepod nauplii, dominated in terms of abundance following the onset of the spring phytoplankton bloom in April–May. They also found that adult *Calanus* spp., particularly *C. finmarchicus*, became increasingly dominant in terms of biomass during the post-bloom period. Thus, the diet of sandeel in this study appears to match the production cycle closely, reflecting the availability of different prey taxa and developmental stages during the feeding period.

In both August and September, ontogenetic differences in prey composition were apparent. Although
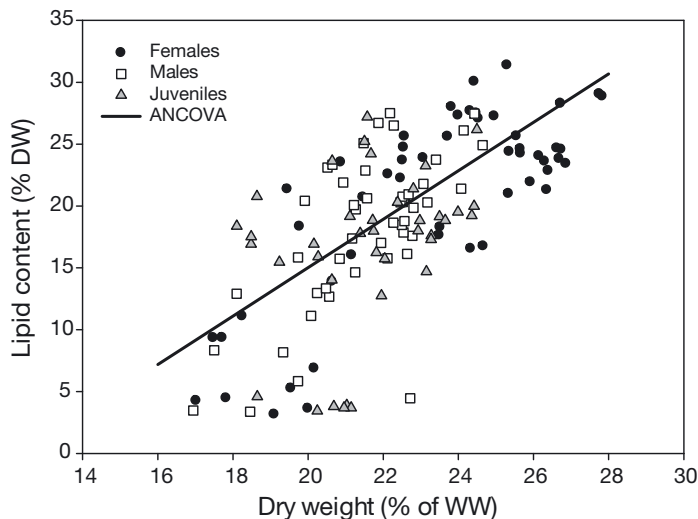
Fig. 6. Lipid content (% DW) plotted against dry weight (% WW) for mature and immature sandeel. The regression line is indicated for all sandeel ($y = 1.96x − 24.14$, SE[b] = 4.31)

copepods generally remained the most important prey, amphipods and euphausiids constituted an increasingly larger proportion of prey numbers and carbon biomass with increasing fish length. This size-related shift in feeding patterns could be biased by a relatively small sample size in August and September for sandeel <12 cm. However, ontogenetic shifts in diet from smaller to larger prey groups are well-known for sandeel (reviewed by Robards et al. 1999b) as well as other forage fishes feeding in Arctic waters (e.g. capelin; Hedeholm et al. 2012).

Planktonic crustaceans in the Arctic are known to contain very high lipid amounts, e.g. up to 76% DW in *C. finmarchicus* (Jónasdóttir 1999), 42% in *Themisto libellula* and *T. abyssorum* (Auel et al. 2002) and 40 to 54% in *Thysanoessa* sp. (Falk-Petersen 1981). Although hyperiid amphipods and euphausiids generally exhibited low frequency of occurrence and low species-specific abundance, these prey groups often accounted for a large proportion of the prey biomass when present. Given their large size and consequently large energy content, it is likely that they contribute significantly to the energy budget of the sandeel that feed on them.

Energy accumulation

The lipid content values found in this study are similar to those reported for Pacific sand lance *A. hexapterus* (Van Pelt et al. 1997, Robards et al. 1999a, Anthony et al. 2000) and lesser sandeel *A. tobianus*

(Reay 1970, Spitz et al. 2010). A dramatic increase in lipid content was observed in parallel to gonadal development in mature individuals from May to August, illustrating that adult sandeel spend the summer months feeding vigorously on zooplankton to build up sufficient energetic reserves to spawn in autumn and survive the winter. This resembles the energy accumulation cycle reported for lesser sandeel *A. marinus* (Hislop et al. 1991), where total body energy reaches a maximum in August after the summer feeding period and a minimum in April following overwintering. Spawning on Fyllas Bank was initiated in September, similar to other northern sand lance *A. dubius* populations off the eastern coast of the USA, where spawning occurs from mid-autumn to early-winter (Nelson & Ross 1991).

Rapid increases in energetic reserves have also been documented in Japanese sandeel *A. personatus* prior to summer estivation (Sekiguchi 1977). Robards et al. (1999a) found lipid content increased in Alaskan *A. hexapterus* from a minimum in February to peak levels in July. It is possible that the lipid content in West Greenland sandeel peaks earlier than August, but our data do not cover the period between May and August. However, the minimum and maximum values we report are similar to those observed in same-sized *A. hexapterus*, suggesting a temporal difference in development between the 2 species. The proportion of lipid increased with increasing percentage dry mass, indicating the importance of lipids as energy storage during the feeding period.

In agreement with other studies (Anthony & Roby 1997, Robards et al. 1999a, Anthony et al. 2000), females had larger lipid reserves than males in all months. Production of large demersal eggs places higher demands on female energy reserves than sperm production in males (Wootton 1998), and consequently, females need to develop larger reserves to accommodate this reproductive effort. However, lipids constitute only 20% (DW) of sandeel eggs (Tocher & Sargent 1984), and gonad maturation therefore depends on other sources of energy in addition to lipids. For example, Bradford (1993) found that protein was the primary energy source for gonadal development in northwest Atlantic herring, whereas lipids were utilized primarily in routine and active metabolism. Similarly, protein levels in mature *A. hexapterus* declined to 60% of peak levels during spawning (Robards et al. 1999a). Protein content was not quantified in the present study, and it is therefore impossible to infer whether West Greenland sandeel depend on protein during spawning as well. However, water content is negatively correlated with

protein content in some fishes (Siddique et al. 2012), and we found a significant increase in water content from August to September, suggesting that mature sandeel utilize stored muscle protein for gonadal development.

Similar to adults, juveniles exhibited a rapid increase in lipid content from May to August. Juveniles continued to gain lipid reserves during September, whereas mature sandeel exhibited a relatively small but consistent decline in lipid content across sex and size from August to September, corresponding with the onset of spawning. Robards et al. (1999a) found that lipid content in *A. hexapterus* decreased prior to, rather than during spawning, and argued that mature sandeel may reduce feeding in the final stage of maturation due to gonads filling the entire body cavity. However, we found no evidence that mature sandeel reduce feeding during spawning as there was no obvious increase in the proportion of empty stomachs in September compared to May and August.

Juvenile *A. marinus* have been observed to continue feeding for several months after the adults have started overwintering (van Deurs et al. 2011). Similarly, Brêthes et al. (1992) documented a longer period of otolith growth (indicative of continued growth in fish length) in immature *A. americanus* compared to mature individuals. They suggested that adults allocate a large proportion of energy to gonad production, whereas juveniles focus energy into somatic growth. Observations on continued growth and lipid accumulation in juveniles can be explained in relation to the energetic costs of overwintering. Smaller absolute size of energetic reserves in young (small) sandeel combined with higher mass-specific metabolism results in faster depletion of stored lipids compared to older (large) fish. This may lead to increased winter starvation mortality or force juveniles to emerge and feed in the water column in a time of low food availability, thus increasing the risk of predation mortality. Evidence exists from laboratory experiments that *A. marinus* displays winter feeding activity to support metabolism, if the individuals fail to reach a critical threshold size of 9.5 cm before entering the overwintering phase (van Deurs et al. 2011). This also applies to adult sandeel, where size at maturation must exceed the critical threshold size to accommodate the metabolic demands of both reproduction and overwintering. Tomiyama & Yanagibashi (2004) found that larger individuals of *A. personatus* entered summer estivation earlier, adding further evidence to the notion that the size of lipid reserves is an important factor in controlling initiation of dormancy.

In summary, this study suggests a close coupling between the diet of sandeel and seasonal changes in plankton production and community structure in West Greenland, which in turn determines the size of energetic reserves available for spawning and overwintering. We demonstrated that lipid content of West Greenland sandeel is strongly dependent on time of year, adding to the growing body of literature on seasonal cycles in lipid content of forage fishes in general.

Perspectives

Given that sandeel function as a vital component of several North Atlantic ecosystems (e.g. Wanless et al. 2005, Eliasen et al. 2011) and that the diet and energy content of sandeel in this study resembled that of other sandeel populations, it is very likely that sandeel serve the same key role in the food web on offshore banks along West Greenland. Fyllas Bank provides feeding grounds for a wide range of marine mammals, sea birds and commercially important fish species (Mosbech et al. 1996), many of which are known to prey on sandeel. Our findings indicate that sandeel have maximum energy density in late summer and early autumn, consistent with important feeding periods for some of these top predators (e.g. humpback whales; Heide-Jørgensen & Laidre 2007).

What impact will increasing temperatures have on the feeding ecology of sandeel along West Greenland? Interannual variability in diet composition of Pacific sand lance *A. hexapterus* between La Niña and El Niño years highlight the role of variation in oceanographic conditions for the feeding of sand lances (Hipfner & Galbraith 2014). Modeling studies have shown that sandeel suffer direct fitness consequences if they fail to time the initiation of the foraging period with the zooplankton spring bloom (van Deurs et al. 2010). Climatic changes due to accelerating global warming (Cox et al. 2000) and the subsequent increased metabolism during overwintering will result in faster depletion of energetic reserves. Thus, in order to avoid starvation mortality, sandeel will be forced to engage in feeding activity earlier. This success of early feeding may be dependent on *C. glacialis*, which start to spawn earlier than *C. finmarchicus* (Swalethorp et al. 2011) and thus provide the sandeel with nauplii prey prior to the spring bloom. If *C. glacialis* is replaced by *C. finmarchicus* due to increasing temperatures, it may lead to a fatal mismatch between prey production and sandeel feeding activity. In line with these scenarios, Green-

street et al. (2010) found that even small temperature variations can partly explain changes in winter mortality of local sandeel populations in the field, and (Pedersen & Smidt 2000) documented that sandeel larvae were more abundant in West Greenland during the cold period between 1969 and 1984 than in the preceding warm period, suggesting that low temperatures are beneficial for reproduction of sandeel.

A change in zooplankton composition will also have an impact later in the season. *C. glacialis* and *C. hyperboreus*, in contrast to *C. finmarchicus*, have been shown to rebuild their lipid stores after spawning (Swalethorp et al. 2011). This means that they will continue to constitute a high-lipid prey item during the summer, when the nutritional value of *C. finmarchicus* has been shown to decrease.

Temperature effects on the population dynamics of sandeel have potential food web ramifications. If sandeel need to forage before zooplankton becomes abundant, this can result in prolonged exposure to predation (van Deurs et al. 2011). Further, *A. dubius* on the Newfoundland Grand Banks has been shown to move to deeper waters during the summer when sea surface temperature increases (Winters 1983), thereby dramatically reducing the foraging success of top predators such as puffins (Gjerdrum et al. 2003). Moreover, the poor nutritional value of sandeel has been linked to breeding failure of seabirds in the North Sea (Wanless et al. 2005), and this may also be the case in West Greenland.

As documented by Pedersen & Smidt (2000), zooplankton abundance and composition along West Greenland is related to environmental factors and has been shown to vary among the warm and cold periods. It is very likely that the present composition reflects the current warm period that started in the mid-1990s (Holland et al. 2008, Sünksen et al. 2010, Ribergaard 2014), as argued by Hansen et al. (2012). Consequently, the diet and nutritional condition of sandeel in this study may differ from the situation during the cold periods. Unfortunately, the lack of published data on sandeel condition and diet during these periods precludes a more thorough analysis.

Future research should address the influence of climatic variability on sandeel feeding patterns and energy accumulation, including indirect effects mediated by changes in zooplankton life history, ultimately leading to identification of factors that control sandeel abundance, condition and distribution in West Greenland. Elucidating the trophic role of sandeel in this area could be a key to understanding fluctuations in the populations of top predators. In the light of rapid climate change in Arctic regions, the present findings may serve as a baseline for future comparisons and monitoring of sandeel on West Greenland banks.

LITERATURE CITED

Agersted MD, Nielsen TG (2014) Krill diversity and population structure along the sub-Arctic Godthåbsfjord, SW Greenland. J Plankton Res 36:800–815

Amundsen PA, Gabler HM, Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. J Fish Biol 48:607–614

Andersen OGN (1985) Forsøgsfiskeri efter tobis i Vestgrønland 1978, biologiske resultater, del I: Tekst. Fiskeri- og miljøundersøgelser i Grønland, ser III, Greenland Fisheries and Environmental Research Institute, Copenhagen

Anonymous (1994) Norwegian standard 9402 E: Atlantic salmon colour and fat measurement. Standard Norge, Bergen

Anthony JA, Roby DD (1997) Variation in lipid content of forage fishes and its effect on energy provisioning rates to seabird nestlings. In: Forage fishes in marine ecosystems: proceedings of the international symposium on the role of forage fishes in marine ecosystems, Anchorage, AK, 13–16 November 1996. Alaska Sea Grant College Report, Vol 97, University of Alaska, Fairbanks, AK, p 725–729

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J Exp Mar Biol Ecol 248:53–78

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25: 374–383

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245–262

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694

Behrens JW, Stahl HJ, Steffensen JF, Glud RN (2007) Oxygen dynamics around buried lesser sandeels *Ammodytes tobianus* (Linnaeus 1785): mode of ventilation and oxygen requirements. J Exp Biol 210:1006–1014

Bergstad OA, Høines ÅS, Jørgensen T (2002) Growth of sandeel, *Ammodytes marinus*, in the northern North Sea and Norwegian coastal waters. Fish Res 56:9–23

Bradford RG (1993) Role of spawning condition in the determination of the reproductive traits of spring- and autumn-spawning Atlantic herring from the southern Gulf of St. Lawrence. Can J Zool 71:309–317

Brêthes JCF, Saint-Pierre R, Desrosiers G (1992) Growth and sexual maturation of the American sand lance (*Ammodytes americanus Dekay*) off the north shore of the Gulf of St. Lawrence. J Northwest Atl Fish Sci 12:41–48

Cairns DK (1988) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271

Cohen RE, Lough RG (1981) Length–weight relationships for several copepods dominant in the Georges Bank–Gulf of Maine area. J Northwest Atl Fish Sci 2:47–52

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187

Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Verheye HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in 'wasp-waist' ecosystems. ICES J Mar Sci 57: 603–618

Davis SE, Nager RG, Furness RW (2005) Food availability affects adult survival as well as breeding success of parasitic jaegers. Ecology 86:1047–1056

Eliasen K, Reinert J, Gaard E, Hansen B, Jacobsen JA, Grønkjær P, Christensen JT (2011) Sandeel as a link between primary production and higher trophic levels on the Faroe shelf. Mar Ecol Prog Ser 438:185–194

Falk-Petersen S (1981) Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: seasonal changes in body weight and the main biochemical composition of *Thysanoessa inermis* (Krøyer), *T. raschii* (M. Sars) and *Meganyctiphanes norvegica* (M. Sars) in relation to environmental parameters. J Exp Mar Biol Ecol 49:103–120

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5: 18–39

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Froese R, Pauly D (eds) (2015) FishBase. www.fishbase.org (accessed 15 Aug 2015)

Gilman SL (1994) An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977-1986. Fish Bull 92:647–654

Gjerdrum C, Vallée AMJ, St. Clair CC, Bertram DF, Ryder JL, Blackburn GS (2003) Tufted puffin reproduction reveals ocean climate variability. Proc Natl Acad Sci USA 100: 9377–9382

Greenstreet SPR, Holland GJ, Guirey EJ, Armstrong E, Fraser HM, Gibb IM (2010) Combining hydroacoustic seabed survey and grab sampling techniques to assess 'local' sandeel population abundance. ICES J Mar Sci 67: 971–984

Hansen MO, Nielsen TG, Stedmon CA, Munk P (2012) Oceanographic regime shift during 1997 in Disko Bay, Western Greenland. Limnol Oceanogr 57:634–644

Hay SJ, Kiørboe T, Matthews A (1991) Zooplankton biomass and production in the North Sea during the autumn circulation experiment, October 1987–March 1988. Cont Shelf Res 11:1453–1476

Hedeholm R, Grønkjær P, Rysgaard S (2012) Feeding ecology of capelin (*Mallotus villosus* Müller) in West Green-

land waters. Polar Biol 35:1533–1543

Heide-Jørgensen MP, Laidre KL (2007) Autumn space-use patterns of humpback whales (*Megaptera novaeangliae*) in West Greenland. J Cetacean Res Manag 9:121–126

Henderson RJ, Almatar SM (1989) Seasonal changes in the lipid composition of herring (*Clupea harengus*) in relation to gonad maturation. J Mar Biol Assoc UK 69: 323–334

Hipfner JM, Galbraith M (2014) Diet of the Pacific sand lance (*Ammodytes hexapterus*) in the Salish Sea, British Columbia, in the 1960s. Can Field Nat 128:57–62

Hirche HJ, Mumm N (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. Deep-Sea Res A Oceanogr Res Pap 39:S485–S505

Hislop JRG, Harris MP, Smith JGM (1991) Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J Zool (Lond) 224:501–517

Holland DM, Thomas RH, De Young B, Ribergaard MH, Lyberth B (2008) Acceleration of Jakobshavn Isbræ triggered by warm subsurface ocean waters. Nat Geosci 1:659–664

Hygum BH, Rey C, Hansen BW (2000) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. Mar Biol 136:1075–1085

Hyslop EJ (1980) Stomach contents analysis—a review of methods and their application. J Fish Biol 17:411–429

Ikeda T, Skjoldal HR (1989) Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. Mar Biol 100:173–183

Jónasdóttir SH (1999) Lipid content of *Calanus finmarchicus* during overwintering in the Faroe–Shetland Channel. Fish Oceanogr 8:61–72

Jørgensen L (1985) Carbon and nitrogen utilization in developing eggs and larvae of cod (*Gadus morhua*, L.) and variation among different parents. Fish Res 3:337–342

Jung-Madsen S, Nielsen TG, Grønkjær P, Hansen BW, Møller EF (2013) Early development of *Calanus hyperboreus* nauplii: response to a changing ocean. Limnol Oceanogr 58:2109–2121

Kjellerup S, Dunweber M, Swalethorp R, Nielsen TG, Moller EF, Markager S, Hansen BW (2012) Effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicus* and *C. glacialis* in Disko Bay, western Greenland. Mar Ecol Prog Ser 447:87–118

Lindley JA (1998) Dry weights, carbon and nitrogen content of decapod larvae from the plankton. J Mar Biol Assoc UK 78:341–344

Macer CT (1966) Sandeels (Ammodytidae) in the southwestern North Sea: their biology and fishery. Fishery Investigations Series II, Vol 24. Ministry of Agriculture, Fisheries and Food, HM Stationery Office, London

Madsen SD, Nielsen TG, Hansen BW (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Biol 139:75–93

Meyer TL, Cooper RA, Langton RW (1979) Relative abundance, behaviour and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. Fish Bull 77:243–254

Mizdalski E (1988) Weight and length data of zooplankton in the Weddell Sea in austral spring 1986 (ANT-V/3). Reports on Polar Research, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven

Montevecchi WA, Piatt J (1984) Composition and energy

contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comp Biochem Physiol 78:15–20

Mosbech A, Dietz R, Boertmann D, Johansen P (1996) Oil exploration in the Fylla area: an initial assessment of potential environmental impacts. NERI Tech Rep no. 156, National Environmental Research Institute, Denmark

Nelson GA, Ross MR (1991) Biology and population changes of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight. J Northwest Atl Fish Sci 11:11–27

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biol 32:1559–1570

O'Connell M, Fives JM (1995) The biology of the lesser sand-eel *Ammodytes tobianus* L. in the Galway Bay area. Biol Environ Proc R Ir Acad 95:87–98

Øigård TA, Lindstrøm U, Haug T, Nilssen KT, Smout S (2013) Functional relationship between harp seal body condition and available prey in the Barents Sea. Mar Ecol Prog Ser 484:287–301

Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. Oikos 117:967–977

Pedersen SA, Smidt ELB (2000) Zooplankton distribution and abundance in West Greenland waters, 1950–1984. J Northwest Atl Fish Sci 26:45–102

Pedersen SA, Ribergaard MH, Simonsen CS (2005) Micro- and mesozooplankton in Southwest Greenland waters in relation to environmental factors. J Mar Syst 56:85–112

Pedersen TM, Almeda R, Fotel FL, Jakobsen HH, Mariani P, Hansen BW (2010) Larval growth in the dominant polychaete *Polydora ciliata* is food-limited in a eutrophic Danish estuary (Isefjord). Mar Ecol Prog Ser 407:99–110

Pinchuk AI, Coyle KO, Farley EV, Renner HM (2013) Emergence of the Arctic *Themisto libellula* (Amphipoda: Hyperiidae) on the southeastern Bering Sea shelf as a result of the recent cooling, and its potential impact on the pelagic food web. ICES J Mar Sci 70:1244–1254

Pitois SG, Fox CJ (2006) Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from continuous plankton recorder data. ICES J Mar Sci 63:785–798

Reay PJ (1970) Synopsis of biological data on North Atlantic sandeels of the genus *Ammodytes* (*A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*). Fisheries Synopsis No. 82. FAO, Rome

Ribergaard MH (2014) Oceanographic investigations off West Greenland 2013. NAFO Scientific Council Documents, 14/001. Danish Meteorological Institute, Copenhagen

Rice J (1995) Food web theory, marine food webs, and what climate change may do to northern marine fish populations. In: Beamish RJ (ed) Climate change and northern fish populations. Canadian special publication of Fisheries and Aquatic Sciences, Vol 121. National Research Council of Canada, Ottawa, p 561–568

Rindorf A, Wanless S, Harris MP (2000) Effects of changes in sandeel availability on the reproductive output of seabirds. Mar Ecol Prog Ser 202:241–252

Robards MD, Anthony JA, Rose GA, Piatt JF (1999a) Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. J Exp Mar Biol Ecol 242:245–258

Robards MD, Willson MF, Armstrong RH, Piatt JF (eds) (1999b) Sand lance: a review of biology and predator relations and annotated bibliography. Research Paper PNW-RP-521, US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR

Rodhouse PG, Roden CM (1987) Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve molluscs. Mar Ecol Prog Ser 36:225–236

Sabatini M, Kiørboe T (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis*. J Plankton Res 16:1329–1351

Satapoomin S (1999) Carbon content of some common tropical Andaman Sea copepods. J Plankton Res 21: 2117–2123

Sekiguchi H (1977) On fat deposits of the spawners of sandeels in Ise Bay, central Japan. Bull Jpn Soc Sci Fish 43: 123–127 (in Japanese with English Abstract)

Siddique MAM, Mojumder P, Zamal H (2012) Proximate composition of three commercially available marine dry fishes (*Harpodon nehereus*, *Johnius dussumieri* and *Lepturacanthus savala*). Am J Food Technol 7:429–436

Spitz J, Mourocq E, Schoen V, Ridoux V (2010) Proximate composition and energy content of forage species from the Bay of Biscay: high- or low-quality food? ICES J Mar Sci 67:909–915

Sünksen K, Stenberg C, Grønkjær P (2010) Temperature effects on growth of juvenile Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in West Greenland waters. J Sea Res 64:125–132

Swalethorp R, Kjellerup S, Dünweber M, Nielsen TG, Møller EF, Rysgaard S, Hansen BW (2011) Grazing, egg production and biochemical evidence of differences in the life strategies of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Ecol Prog Ser 429:125–144

Tocher DR, Sargent JR (1984) Analyses of lipids and fatty acids in ripe roes of some Northwest European marine fish. Lipids 19:492–499

Tomiyama M, Yanagibashi S (2004) Effect of temperature, age class, and growth on induction of aestivation in Japanese sandeel (*Ammodytes personatus*) in Ise Bay, central Japan. Fish Oceanogr 13:81–90

Tönnesson K, Nielsen TG, Tiselius P (2006) Feeding and production of the carnivorous copepod *Pareuchaeta norvegica* in the Skagerrak. Mar Ecol Prog Ser 314: 213–225

Trumble RJ (1973) Distribution, relative abundance and general biology of selected underutilized fishery resources of the eastern North Pacific Ocean. MSc thesis, University of Washington, Seattle, WA

van Deurs M, Christensen A, Frisk C, Mosegaard H (2010) Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective. Mar Ecol Prog Ser 416:201–214

van Deurs M, Hartvig M, Steffensen JF (2011) Critical threshold size for overwintering sandeels (*Ammodytes marinus*). Mar Biol 158:2755–2764

van Deurs M, Christensen A, Rindorf A (2013) Patchy zooplankton grazing and high energy conversion efficiency: ecological implications of sandeel behavior and strategy. Mar Ecol Prog Ser 487:123–133

Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. Comp Biochem Physiol 118:1393–1398

Wanless S, Harris MP, Redman P, Speakman J (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar Ecol Prog Ser 294:1−8

Willson MF, Armstrong RH, Robards MD, Piatt JF (1999) Sand lance as cornerstone prey in predator populations. In: Robards MD, Willson MF, Armstrong RH, Piatt JF (eds) Sand lance: a review of biology and predator relations and annotated bibliography. Research Paper PNW-RP-521, US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p 18−44

Winters GH (1983) Analysis of the biological and demographic parameters of northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank. Can J Fish Aquat Sci 40:409−419

Wootton RJ (1998) Reproduction. In: Wootton RJ (ed) Ecology of teleost fishes. Kluwer Academic Publishers, Dordrecht, p 141−171

Yaragina NA, Marshall CT (2000) Trophic influences on interannual and seasonal variation in the liver condition index of northeast Arctic cod (*Gadus morhua*). ICES J Mar Sci 57:42−55