Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2013) **83**, 1094–1111
doi:10.1111/jfb.12181, available online at wileyonlinelibrary.com

Spatial and temporal variation in the diet of the Pacific sand lance *Ammodytes hexapterus* in waters off the coast of British Columbia, Canada

J. M. Hipfner*† and M. Galbraith‡

**Wildlife Research Division, Environment Canada, RR#1 5421 Robertson Road, Delta, BC, V4K 3N2 Canada and ‡Institute of Ocean Sciences, Ocean Sciences Division, 9860 West Saanich Road, Sidney, BC, V8L 4B2 Canada*

(Received 22 March 2013, Accepted 17 May 2013)

Variation in the diet of the Pacific sand lance *Ammodytes hexapterus* was examined in three years (2009–2011) at four sites in British Columbia, Canada. There were 12 major taxa of prey in diets, eight of which were Crustacea, with copepods being by far the dominant taxon in all 12 site-years. Of the 22 copepod taxa recorded, only *Calanus marshallae* and *Pseudocalanus* spp. occurred in all collections, and these two calanoid species dominated diets in terms of frequency of occurrence and total numbers of prey (*Pseudocalanus* spp. in most collections), and total prey biomass (*C. marshallae* in all collections). Based on an index of relative importance, *C. marshallae* was the primary prey at the two southerly sampling sites (Pine and Triangle Islands) and *Pseudocalanus* spp. at the two northerly sites (Lucy Island and S’G̲ang Gwaay). Based on an index of dietary overlap, the species composition of the copepod component of *A. hexapterus* diets overlapped very strongly at the northerly and the southerly pairs of sites in both a cold-water La Niña year (2009) and a warm-water El Niño year (2010), but overall there was more homogeneity amongst all four sites in the La Niña year.

Key words: copepods; forage fishes; interannual variation; oceanography conditions; prey types.

INTRODUCTION

With environmental changes altering fundamental trophic relationships, there is need for a better understanding of food-web dynamics in marine ecosystems (Edwards & Richardson, 2004). In marine systems of the temperate northern hemisphere, the six species of sand lances *Ammodytes* (Robards & Piatt, 1999) often act as key trophic links between zooplankton and the broad suite of predators that feed on small forage fishes (Wanless *et al.*, 2005). *Ammodytes* figure prominently in the diets of many economically valuable fishes, including salmonids (Beacham, 1986; Haugland *et al.*, 2006), gadids (Link & Garrison, 2002; Temming *et al.*, 2004) and flatfishes (Pitt, 1973; Westrheim & Harling, 1983). They are also important prey for many marine mammals, including phocids (Beck *et al.*, 1993; Hammond *et al.*, 1994), otariids

---

†Author to whom correspondence should be addressed. Tel.: +1 604 350 1976; email: mark.hipfner@ec.gc.ca

(Wilke & Kenyon, 1957; McKenzie & Wynne, 2008) and cetaceans (Overholtz & Nicholas, 1979; Friedlaender *et al.*, 2009). The importance of *Ammodytes* to colonial seabirds is especially well documented (Springer *et al.*, 1984; Rindorf *et al.*, 2000; Parrish & Zador, 2003; Williams *et al.*, 2008; Ito *et al.*, 2009). In the north-eastern Pacific Ocean, for example, the breeding success of two colonial auks, the rhinoceros auklet *Cerorhinca monocerata* (Borstad *et al.*, 2011) and tufted puffin *Fratercula cirrhata* (Gjerdrum *et al.*, 2003), is closely tied to the availability of Pacific sand lance *Ammodytes hexapterus* Pallas 1814. *Ammodytes hexapterus* is the only species of sand lance in the region.

Despite its importance in food webs, there is little information on the diet of *A. hexapterus* and on the causes and extent of variation in its diet. Given that the energy density, growth rate and fecundity of *Ammodytes* all exhibit strong spatial and temporal variation (Robards *et al.*, 2002; Wanless *et al.*, 2005), it can be expected that feeding conditions for *Ammodytes* are also highly variable. In the north-eastern Pacific Ocean, the abundance, phenology and community composition of zooplankton all vary strongly among years in response to large-scale oceanographic processes, and with consequences for predators (Mackas *et al.*, 2007).

The diet of *A. hexapterus* in waters off the coast of British Columbia, Canada, was quantified by examining the contents of 291 stomachs of fresh, whole fish collected from a regionally abundant seabird, *C. monocerata*, in each of three years at four breeding colonies. *Cerorhinca monocerata* forages mainly within *c.* 90 km of the colony (McFarlane-Tranquilla *et al.*, 2005) and in the upper 10 m of the water column (Burger *et al.*, 1993). The birds dive actively in the early evening (Kato *et al.*, 2003), pursuing small forage fishes feeding on zooplankton near the ocean's surface (Davoren & Burger, 1999). Just after dusk, each parent then delivers a food load consisting of up to 30 whole fish to its single offspring, and it is a simple matter to collect and enumerate these prey (Bertram *et al.*, 2002).

The main objective of this study was to determine the extent to which the diet of *A. hexapterus* varies from region to region, and whether the extent of regional concordance varies from year to year in response to prevailing environmental conditions. To do this, an index of relative importance (I_{RI}; Pinkas *et al.*, 1971) was calculated to gauge the contribution of all prey types to *A. hexapterus* diets, which was then used to derive an index of dietary overlap (Schoener, 1970) that quantified the temporal and spatial similarity and dissimilarity in diets. The four sampling sites (Fig. 1) span the transition zone between the California Current and Alaska Current systems, while the three-year study included a cold-water La Niña event (2009), a warm-water El Niño event (2010) and a year of moderate ocean temperatures (2011). Effects of the interannual variation were strongly manifested in the growth rates of nestlings of a locally abundant, zooplanktivorous seabird, Cassin's auklet *Ptychoramphus aleuticus*, which were highest in 2009 and lowest in 2010 (Irving & Crawford, 2012). Zooplankton community composition differs across the bifurcation between the California Current and Alaska Current systems (Batten & Freeland, 2007), and responds rapidly to the El Niño–Southern Oscillation (ENSO) events (Batten & Welch, 2004; Zamon & Welch, 2005). ENSO events also have stronger effects on food webs within the California Current system than the Alaska Current system (Trudel *et al.*, 2007; Bertram *et al.*, 2009). Thus, the protocol followed in this study is likely to have captured a wide range of variation in feeding conditions for *A. hexapterus*.

FIG. 1. Map of the coast of British Columbia, Canada, showing the locations of the four *Cerorhinca monocerata* colonies at which stomachs of *Ammodytes hexapterus* were collected.

MATERIALS AND METHODS

FIELD SAMPLING PROTOCOLS

Whole specimens of *A. hexapterus* were collected in mid-summer of 2009–2011 on brief visits to four *C. monocerata* breeding colonies in British Columbia, Canada: Lucy Island (54° 17′ N; 130° 37′ W) along the north coast, Pine Island (50° 35′ N; 127° 26′ W) along the central coast, S'Gang Gwaay (52° 05′ N; 131° 13′ W) in the Haida Gwaii Archipelago and Triangle Island (51° 52′ N; 129° 05′ W) in the Scott Islands archipelago (Fig. 1). All four colonies are situated on the continental shelf. Information on foraging habitats of provisioning *C. monocerata* are available only for Triangle Island, where the birds foraged mainly in shallow waters (<100 m) over sand-bottomed habitat on Cook Bank to the north-east of the island (McFarlane-Tranquilla *et al.*, 2005).

Auklet parents delivering food loads to their nestlings were caught on the ground with long-handled nets just after sunset. The species composition of all food loads was enumerated, and *A. hexapterus* were then separated from other prey types and placed in Whirl-Pak bags(http://www.enasco.com/c/whirlpak/Whirl-Pak%26%23174%3B+Bags/). The remaining prey items were tossed into burrows near the site of capture for nestlings to consume. Within *c.* 2 h, the *A. hexapterus* were measured (fork length, L_F, ±1 mm with a ruler) and weighed (±0·1 g on an electronic balance). For stomach content analysis, generally only the single largest *A. hexapterus* in a food load was selected; all had $L_F \geq 100$ and and on the basis of the studies by Blackburn & Anderson (1997) and Robards *et al.* (2002) are assumed to be age 1+ year fish by mid-summer. The gastrointestinal tracts of these fish were excised with scalpel and forceps, and placed in vials filled with 15% buffered formalin.

The dates of sampling at the four colonies in the three years, the number of food loads collected from *C. monocerata* and the number of *A. hexapterus* stomachs preserved are listed in Table I. Note that sample sizes were small in some colony-years, due to one or more of several factors: infrequent sampling due to inclement weather (Triangle Island in 2011); a shortage of *A. hexapterus* in diets (S'G̱ang Gwaay in 2009); or an abundance of juvenile *A. hexapterus*, but shortage of adults in diets (S'G̱ang Gwaay in 2010 and 2011).

IDENTIFICATION OF PREY IN *A. HEXAPTERUS* STOMACHS

Excised gastrointestinal tracts, preserved in buffered formalin in individual vials, were returned to the laboratory for analysis and washed over a 0·063 mm mesh to remove the formalin, which was captured for neutralization treatment and disposal. The stomach was then separated out, transferred to a 1 mm gridded Petri dish, slit longitudinally and gauged for apparent fullness under a Wild M420 dissecting microscope (www.leica-microsystems.com) with ×20 oculars and 6·3–32 zoom capability. The contents were removed from the stomach using water from a squeeze bottle, then counted, life stage was determined and identified to the lowest taxonomic level possible. Some stomachs' contents were fresh (prey items

TABLE I. Information on sampling for *Cerorhinca monocerata* food loads, and the contents of *Ammodytes hexapterus* stomachs, in three years at four auklet breeding colonies in waters off British Columbia, Canada

Colony	Year	Sampling dates	Number of loads (number with *A. hexapterus*)	Number of fishes (number with *A. hexapterus*)	Number of *A. hexapterus* stomachs examined (number empty)
Lucy Island	2009	30 July–2 August	42 (12)	101 (32)	38 (9)
	2010	12–15 July	84 (48)	275 (165)	35 (2)
	2011	12–15 July	26 (13)	80 (50)	27 (4)
Pine Island	2009	24–27 July	65 (36)	223 (149)	50 (19)
	2010	6–9 July	65 (49)	223 (171)	40 (3)
	2011	5–9 July	43 (31)	319 (275)	28 (9)
S'G̱ang Gwaay	2009	6–9 August	48 (12)	228 (27)	7 (1)
	2010	21–23 July	44 (30)	372 (178)	11 (6)
	2011	18–20 July	19 (17)	240 (232)	14 (1)
Triangle Island	2009	23 June–10 July	27 (17)	113 (57)	23 (8)
	2010	25 June	11 (11)	50 (45)	15 (1)
	2011	23–28 June	10 (10)	102 (100)	3 (0)

recently eaten) and in condition that allowed the prey to be identified to species; the majority of stomach contents, however, were at least partly digested. As a result, the representation in diets of soft-bodied prey types, such as larvaceans, could have been underestimated. Dry mass estimates were assigned to each species and stage based on mass *v*. length regressions from Fulton (1968) and McCauley (1984), as well as from direct laboratory measurements. Total length (L_T) was used for most prey items, the only exception being copepods, for which prosome length was used.

DATA ANALYSES

Variation in L_F of *A. hexapterus* whose stomachs were collected was examined using two-way ANOVA, with colony and year as predictor variables. Three measures of feeding intensity were examined: (1) whether the stomach was empty or full (vacuity rate), and (2) the number and (3) dry mass of prey items present, with year, colony and the L_F as predictor variables using logistic regression (vacuity rate) and ANCOVA (number and mass of prey). Empty stomachs were excluded in the last two analyses. All analyses were run with the Fit Model function of programme JMP (SAS Institute; www.sas.com).

An index of relative importance (Pinkas *et al.*, 1971) was calculated to quantify the contribution of each prey type to *A. hexapterus* diets in each colony-year. The formula for the index is: I_{RI} = the proportion of all non-empty stomachs that contained prey type (i) × (the proportion by number of prey type (i) item relative to all prey types + the proportion by dry mass of prey type (i) relative to all prey types). Following Santic *et al.* (2012), I_{RI} values for each prey type were standardized to a scale of 0–100 using: $\%I_{RI} = 100\left[I_{RI}\left(\sum I_{RI}^{-1}\right)\right]$. Again following Santic *et al.* (2012), these $\%I_{RI}$ values were used to calculate Schoener's (1970) index of dietary overlap in order to quantify the extent of dietary overlap in each of the three years among all six colony-pairs (Lucy *v*. Pine, Lucy *v*. S'G̲ang Gwaay, Lucy *v*. Triangle, Pine *v*. S'G̲ang Gwaay, Pine *v*. Triangle and S'G̲ang Gwaay *v*. Triangle). The formula for the index is: $C_{xy} = 1 - 0{\cdot}5|p_{xi} - p_{yi}|$, where p_{xi} and p_{yi} are the proportions of prey type (i) in *A. hexapterus* diets at colonies x and y. Values of Schoener's (1970) index range from 0 (no overlap in prey types) to 1 (all prey types present in equal proportions). Following Wallace (1981), values of Schoener's index $>0{\cdot}6$ were considered to indicate significant overlap in diets.

Means and parameter estimates are reported as ±95% C.I.

RESULTS

SPECIES COMPOSITION OF SEABIRD FOOD LOADS

Ammodytes hexapterus was the numerically dominant (48–97% of all items) prey species fed to *C. monocerata* nestlings in 10 of the 12 site-years of sampling. Both exceptions occurred in 2009, when Pacific herring *Clupea pallasii pallasii* (Vallenciennes 1847) was more common than *A. hexapterus* at Lucy Island (35 *v*. 32% of prey items) and at S'G̲ang Gwaay (78 *v*. 12%). No other prey species made up as much as 25% of the diet in any site-year.

INTENSITY OF FEEDING BY *A. HEXAPTERUS*

Ammodytes hexapterus that had their stomachs excised ranged from 100 to 188 mm L_F. Based on two-way ANOVA, L_F varied among colonies ($F_{3,284} = 3{\cdot}95$, $P < 0{\cdot}01$) and years ($F_{2,284} = 19{\cdot}30$, $P < 0{\cdot}001$). Fish were smaller at S'G̲ang Gwaay ($124{\cdot}2 \pm 5{\cdot}2$ mm) than at Lucy ($134{\cdot}1 \pm 4{\cdot}3$ mm), Pine ($134{\cdot}9 \pm 3{\cdot}0$ mm) or

Triangle (136·9 ± 5·2 mm) Islands, and were smaller in 2009 (122·8 ± 3·5 mm) than in 2010 (138·0 ± 3·6 mm) or 2011 (133·5 ± 4·3 mm).

Of the 291 *A. hexapterus* stomachs examined, 63 (21·6%) were empty (Table I). A logistic model that included year, colony and L_F weakly ($R^2 = 0{\cdot}07$) but significantly ($\chi^2 = 23{\cdot}94$, $P < 0{\cdot}001$) predicted whether or not a stomach was empty. The effects of year and L_F were statistically significant (both $P < 0{\cdot}05$), but the effect of colony was not ($P > 0{\cdot}05$). Empty stomachs occurred with greater frequency in 2009 (31%) than in 2010 (12%) or 2011 (19%), and the probability of a stomach being empty declined with L_F (in the full model, parameter estimate $-0{\cdot}025 \pm 0{\cdot}019\ \text{mm}^{-1}$).

Non-empty *A. hexapterus* stomachs contained two to 812 prey items. An ANCOVA that included year, colony and L_F weakly ($R^2 = 0{\cdot}16$) but significantly ($F_{6,221} = 6{\cdot}89$, $P < 0{\cdot}001$) predicted the number of prey items present. Effects of year and colony were significant (both $P < 0{\cdot}01$), that of L_F was not ($P > 0{\cdot}05$). Across all years, *A. hexapterus* stomachs collected on Lucy Island had the most prey items (233·1 ± 41·3), while those collected on Pine Island had the fewest (142·8 ± 25·8); numbers for S'G̲ang Gwaay (175·1 ± 70·8) and Triangle Island (198·9 ± 68·9) were intermediate and did not differ significantly from those for Lucy or Pine Islands. Stomachs contained more prey items in 2010 (254·0 ± 40·5) than in 2009 (153·0 ± 29·6) or 2011 (134·6 ± 38·4).

The dry mass of all prey items found in non-empty stomachs ranged from 0·073 to 201·1 mg. An ANCOVA that included year, colony and L_F weakly ($R^2 = 0{\cdot}15$) but significantly ($F_{6,221} = 6{\cdot}46$, $P < 0{\cdot}001$) predicted the mass of prey. Neither year nor colony had significant effects (both $P > 0{\cdot}5$), while L_F did ($P < 0{\cdot}001$; in the full model, the parameter estimate $= 0{\cdot}49\ \text{mg} \pm 0{\cdot}18\ \text{mm}^{-1}$). Across all colonies and years, dry mass of prey in non-empty stomachs was 14·1 ± 3·0 mg.

DIET COMPOSITION: MAJOR TAXONOMIC PREY GROUPS

Prey items present in *A. hexapterus* stomachs belonged to 12 major taxonomic groups (Appendix): (1) Mollusca, (2) Cirripedia, (3) Cladocera, (4) Copepoda, (5) Hyperiidea, (6) Cumacea, (7) Mysidacea, (8) Euphausidacea, (9) Decapoda, (10) Chaetognatha, (11) Larvacea and (12) Teleostei. Eight of the 12 groups [(2)–(9)] were Crustacea. Of the 12, 11 were recorded on Lucy Island in one or more years (all but molluscs), and two, cumaceans and mysids, occurred only at Lucy Island in 2011; all the 10 remaining taxa were recorded on Pine and Triangle Islands; but only eight were recorded on S'G̲ang Gwaay (cladocerans and teleosts absent) (Appendix).

Copepods were by far the dominant prey group, with indices of relative importance ($\%I_{RI}$) values ranging from 62·8% (at Triangle in 2010) to 95·3% (at Lucy in 2010), and averaging 79·0% across all colony-years (Fig. 2). There was little consistency in the choice of secondary prey types. Molluscs (at S'G̲ang Gwaay in 2011), cirripeds (Pine and Triangle in 2010), mysids (Lucy in 2011), euphausiids (Pine in 2011 and Triangle in 2010), decapods (S'G̲ang Gwaay in 2010) and larvaceans (Pine in 2009) each contributed at least 10% of the $\%I_{RI}$ values in any single colony-year (Fig. 2).

There was little consistency in the degree or pattern of dietary overlap of the 12 major prey taxa relative to years or colonies (Table II). There was no significant

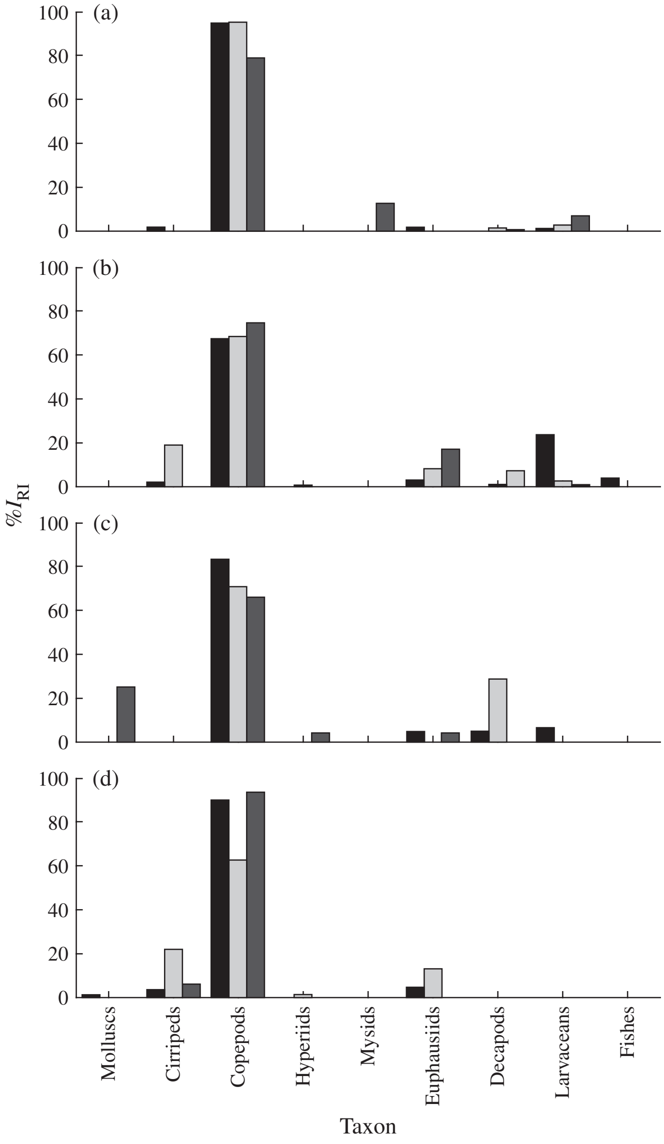

FIG. 2. Indices of relative importance (%I_{RI}) for major prey taxa of *Ammodytes hexapterus* collected at four *Cerorhinca monocerata* colonies in British Columbia, Canada, (a) Lucy Island, (b) Pine Island, (c) S'G̲ang Gwaay and (d) Triangle Island, in three years [2009 (■), 2010 (□) and 2011 (■)]. Three other prey taxa (cladocerans, cumaceans and chaetognaths) occurred in very small amounts (all %$I_{RI} < 0{\cdot}5\%$). Copepods were by far the most important prey of *A. hexapterus* in all 12 colony-years.

dietary overlap between any of the six colony-pairs in 2009, significant overlap in three of the six colony-pairs in 2010 and in two of the six colony-pairs in 2011. Notably, there was little indication of a latitudinal pattern: diets overlapped significantly in only 1 year at the northerly pair of sites, Lucy Island and S'G̲ang Gwaay, and not in any year at the southerly pair, Pine and Triangle Islands (Table II).

TABLE II. Schoener's (1970) indices of dietary overlap, based on the per cent index of relative importance (%I_{RI}) values, for the 12 major prey taxa included in the diets of *Ammodytes hexapterus* in waters off the coast of British Columbia. Values >0·6 (in bold) indicate significant overlap (Wallace, 1981)

		Colony 1		
Year	Colony 2	Lucy Island	Pine Island	S'Gang Gwaay
2009	Pine Island	0·559	–	–
	S'Gang Gwaay	0·270	0·458	–
	Triangle Island	0·128	0·548	0·235
2010	Pine Island	0·553	–	–
	S'Gang Gwaay	0·545	**0·609**	–
	Triangle Island	**0·729**	0·177	**0·736**
2011	Pine Island	0·474	–	–
	S'Gang Gwaay	**0·667**	0·588	–
	Triangle Island	0·417	0·501	**0·672**

DIET COMPOSITION: COPEPOD COMPONENT

Two calanoid copepods, *Calanus marshallae* and *Pseudocalanus* spp., were the only prey taxa to appear in *A. hexapterus* diets in all the 12 colony-years (Appendix). Eight other copepods were present in at least one year at all four colonies: *Acartia longiremis, Calanus pacificus*, *Centropagus abdominalis*, *Eucalanus bungii*, *Metridia pacifica*, *Neocalanus cristatus, Neocalanus plumchrus* and *Tortanus discaudatus*. Other copepod taxa recorded only rarely and in trace amounts (%$I_{RI} < 0·5$%) were *Aetideus divergens* at Lucy Island, *Acartia hudsonica*, Harpacticoids, *Microsetella rosea*, *Oithona atlantica*, *Corycaeus anglicus* and *Paracalanus indicans* at Pine Island, *Epilabidocera longipedata* and *Paracalanus* spp. at Pine Island and S'Gang Gwaay and *Oithona similis* at Pine, S'Gang Gwaay and Triangle Islands (Appendix). Noteworthy among the rarer copepods were the southerly, warm-water species, *P. indicans* and *C. anglicus*, at Pine Island in the El Niño year of 2010.

The smaller *Pseudocalanus* spp. was the primary prey of *A. hexapterus* in terms of frequency of occurrence and number of prey items in most samples, while the larger *C. marshallae* was in all samples the most important prey in terms of biomass; late stage copepodites (stages iii–v in *C. marshallae* and iv–v in *Pseudocalanus* spp.) and adults of both sexes were consumed (Table III). Based on %I_{RI}, *C. marshallae* was the more important of the two at the southerly sites, Pine and Triangle Islands, in all three years, whereas *Pseudocalanus* spp. was more important at Lucy Island in all three years and at S'Gang Gwaay in 2 of the three years. Diets deviated from this latitudinal pattern only in 2011, when *C. marshallae* was more important than *Pseudocalanus* spp. at S'Gang Gwaay (Fig. 3). Interestingly, after controlling for effects of year and colony, the mass of *C. marshallae* found in a fish's stomach increased with its L_F ($0·15 \pm 0·08$ mg mm^{-1}), while the mass of *Pseudocalanus* spp. tended very weakly to decline ($-0·0086 \pm 0·0109$ mg mm^{-1}).

Compared with the major prey taxa, there were clearer patterns of dietary overlap in the copepod component of diets across years and colonies (Table IV). Diets at the four colonies overlapped more strongly in the La Niña year of 2009 (five of the

TABLE III. Per cent frequency of occurrence, number and biomass of prey comprising the two primary copepods [*Calanus marshallae* (Cm) and *Pseudocalanus* spp. (Ps)] found in stomachs of *Ammodytes hexapterus* at four *Cerorhinca monocerata* breeding colonies in British Columbia in three years. Copepodite life stages and adult sex (f, female; m, male) are indicated

		Cm				Ps			
Colony	Year	%Frequency (%)	%Number	%Mass	Stage (sex)	%Frequency	%Number	%Mass	Stage (sex)
Lucy Island	2009	58·6	13·4	61·2	iv, v (f, m)	96·5	82·6	24·8	iv, v (f, m)
	2010	78·8	6·8	56·5	iv, v (f, m)	97·0	92·4	41·8	v (f, m)
	2011	21·7	6·1	57·5	v (f)	70·0	78·9	37·0	v (f, m)
Pine Island	2009	83·9	28·9	85·1	iii, iv, v (f, m)	64·5	54·3	8·2	iv, v (f, m)
	2010	83·8	45·8	82·5	iii, iv, v (f, m)	67·6	46·5	4·3	v (f, m)
	2011	78·9	32·8	72·5	v (f, m)	84·2	52·7	6·0	v (f, m)
S’G̲ang Gwaay	2009	83·3	12·3	63·7	v (f)	100	80·2	22·4	iv, v (f)
	2010	60·0	3·6	43·7	v (f)	100	71·7	43·4	iv, v (f, m)
	2011	92·3	45·8	91·9	v (f)	76·9	49·1	5·4	v (f)
Triangle Island	2009	66·7	30·5	60·1	iii, iv, v (f, m)	80·0	48·5	6·4	iv, v (f, m)
	2010	85·7	56·7	94·2	iv, v (f, m)	92·9	39·9	3·1	v (f, m)
	2011	66·7	92·0	99·5	v (f, m)	66·7	4·9	0·2	v (f)

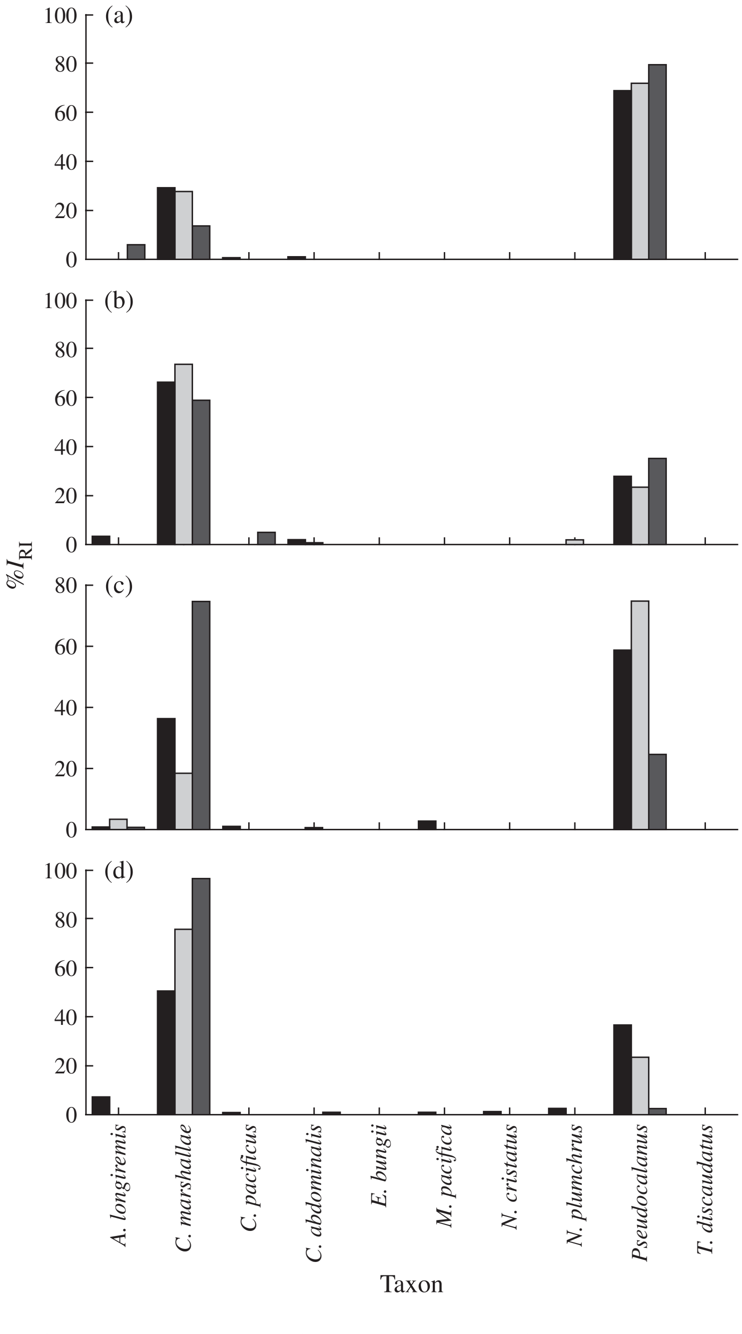

FIG. 3. Indices of relative importance (%I_{RI}) for copepod component of diets (see Appendix) of *Ammodytes hexapterus* collected at four *Cerorhinca monocerata* colonies in British Columbia, Canada, (a) Lucy Island, (b) Pine Island, (c) S'Gang Gwaay and (d) Triangle Island, in three years [2009 (■), 2010 (□) and 2011 (▨)]. Only copepods with %$I_{RI} > 0{\cdot}5$ in at least one colony-year are included. *Calanus marshallae* tended to dominate *A. hexapterus* diets at Pine and Triangle Islands, the two southerly sites, while *Pseudocalanus* spp. tended to dominate at Lucy Island and S'Gang Gwaay, the two northerly sites.

TABLE IV. Schoener's (1970) indices of overlap, based on the per cent index of relative importance (%I_{RI}) values, for the copepod component of the diets of *Ammodytes hexapterus* in waters off the coast of British Columbia. Values >0·6 (in bold) indicate significant overlap (Wallace, 1981)

		Colony 1		
Year	Colony 2	Lucy Island	Pine Island	S'G̲ang Gwaay
2009	Pine Island	0·582	–	–
	S'G̲ang Gwaay	**0·887**	**0·654**	–
	Triangle Island	**0·669**	**0·822**	**0·758**
2010	Pine Island	0·513	–	–
	S'G̲ang Gwaay	**0·906**	0·425	–
	Triangle Island	0·512	**0·975**	0·421
2011	Pine Island	0·491	–	–
	S'G̲ang Gwaay	0·388	**0·838**	–
	Triangle Island	0·166	**0·620**	**0·772**

six pairwise comparisons were significant) than in the El Niño year of 2010 (two of the six) or in 2011 (three of the six). There was significant dietary overlap at the southerly pair of colonies, Pine and Triangle Islands, in all three years, and at the northerly pair of colonies, Lucy Island and S'G̲ang Gwaay, in two of the three years. Latitudinal pattern of congruence was, however, strongest in the El Niño year of 2010, when Schoener's index exceeded 0·9 between both the northerly and southerly pairs of colonies (Table IV).

DISCUSSION

AMMODYTES HEXAPTERUS IN SEABIRD FOOD LOADS

Ammodytes hexapterus is an important prey species for many piscivores in the north-east Pacific Ocean (Beacham, 1986), so there is need for a thorough understanding of its trophic relationships. In this study, specimens were collected from provisioning parents of an abundant seabird, *C. monocerata*, in order to quantify the diet of *A. hexapterus*. At all four of the large auklet colonies in British Columbia, Canada, at which sampling occurred, *A. hexapterus* was the most common prey species in nestling diets in most years. In this region, the amount of juvenile (age 0+ year) *A. hexapterus* fed to auklet nestlings by their parents gauges the strength of *A. hexapterus* recruitment in that year (Bertram & Kaiser, 1993), is higher in years with an early and strong spring bloom (Borstad *et al.*, 2011) and closely predicts breeding success in *C. monocerata* and other species of seabirds (Gjerdrum *et al.*, 2003; Hedd *et al.*, 2006).

INTENSITY OF FEEDING BY *A. HEXAPTERUS*

While provisioning, *C. monocerata* catches prey feeding near the ocean's surface late in the day (Davoren & Burger, 1999). As a result, it was expected that few

A. hexapterus stomachs would be empty. Yet compared to studies that used other methods to collect specimens in summer, the per cent stomachs that were empty (22%) was higher than in *A. hexapterus* off Kodiak Island, Alaska (8%; Blackburn & Anderson, 1997), similar to that of *Ammodytes tobianus* L. 1758 off the west coast of Ireland (19%; O'Connell & Fives, 1995), and lower than that of *Ammodytes americanus* Dekay 1842 in the Gulf of Maine (36%; Meyer *et al.*, 1979). In addition, there was extreme variation in both the number (two to 812 items), and dry mass (0·073 to 201·100 mg) of prey items in non-empty *A. hexapterus* stomachs. For comparison, the maximum number of prey items found in a single *Ammodytes personatus* Girard 1856 stomach was 1523 (Sekiguchi, 1977).

Some of the variation in feeding intensity by *A. hexapterus* might be attributable to the year, based on effects of oceanography on feeding conditions for other fishes in the north-east Pacific Ocean (Perry *et al.*, 1996), and on the body condition of *A. hexapterus* (Robards *et al.*, 2002; Wanless *et al.*, 2005). It might have been expected that feeding intensity by *A. hexapterus* would be reduced in 2010, an El Niño year, compared with 2009, a La Niña year. The vacuity rate was lower in 2010 than in 2009, however, and the number of prey items in stomachs is higher in 2010 than in 2009. Collected *A. hexapterus* were larger in 2010 than 2009, but size did not affect the number of prey items in stomachs. Individuals might have spent more time feeding in 2010, and if so, that strategy appears to have been successful in that the mass of stomach contents did not vary among years. A trade-off between foraging effort and predation risk, however, is probable (McNamara & Houston, 1987).

As for spatial variation in feeding intensity, as in *A. americanus* (Richards, 1982), there was no significant variation among colonies in the vacuity rate of *A. hexapterus*, whereas stomachs contained more prey items on average at Lucy Island than at Pine Island. That difference probably reflects increased consumption of the smaller *Pseudocalanus* spp. off Lucy Island, but more of the larger *C. marshallae* off Pine Island. Accordingly, the mean mass of prey found in stomachs did not vary among colonies.

Not unexpectedly, smaller *A. hexapterus* were more likely than larger individuals to have empty stomachs, and the mass of stomach contents increased with size, as in *A. personatus* (Sekiguchi, 1977). Because there was no effect of fish size on the number of prey items in stomachs, it appears that larger *A. hexapterus* take larger prey. Indeed, the mass of the larger *C. marshallae* found in stomachs tended to increase with L_F, while that of the smaller *Pseudocalanus* spp. declined weakly. Likewise, O'Connell & Fives (1995) suggested that only the largest *A. hexapterus* take the largest of available prey types, and in this study, only two individual *A. hexapterus* had >100 mg of dry mass of prey in their stomach (183 and 201 mg), both were large fish ($L_F = 154$ and 178 mm), and both had consumed only a large prey type, the mysid *Neomysis kadiakensis*.

DIET COMPOSITION OF *A. HEXAPTERUS*

In waters off the coast of British Columbia, *A. hexapterus* included 12 major prey taxa in its diet: eight crustacean groups, as well as molluscs, chaetognaths, larvaceans and teleosts. That suite of prey taxa is generally similar to that of other species of sand lances: *Ammodytes dubius* (Scott, 1973), *A. americanus* (Meyer *et al.*, 1979; Richards, 1982) and *A. personatus* (Sekiguchi, 1977), and in *A. hexapterus* at other locations (Field 1988; Blackburn & Anderson, 1997). The overall representation of the 12 taxa varied from site to site (11 of the 12 were recorded at Lucy Island, 10 at Pine and Triangle Islands, but only eight at S'G̱ang Gwaay), and there was no obvious latitudinal pattern of dietary overlap of the major prey groups in *A. hexapterus* diets.

Copepods, represented by 22 taxa, were by far the most important prey types for *A. hexapterus*. Other species of *Ammodytes* (Robards & Piatt, 1999), and *A. hexapterus* at other locations (Field 1988; Blackburn & Anderson, 1997), also feed mainly on copepods in summer; one exception was *A. tobianus*, which fed mainly on mysids in summer off the west coast of Ireland (O'Connell & Fives, 1995). There was a strong overlap in the copepod component of the diets between the northerly pair of colonies (Lucy Island and S'G̱ang Gwaay) and the southerly pair of colonies (Pine and Triangle Islands) in both the La Niña year of 2009 and the El Niño year of 2010. There was also evidence of an effect of yearly oceanographic variation, in that there was greater homogeneity in diets amongst all four sites in the La Niña year compared to the El Niño year. Further, several southerly, warm-water copepods, notably *P. indicans* and *C. anglicus*, appeared in *A. hexapterus* diets only at Pine Island, the most southerly of the four colonies, during the 2010 El Niño event. That concurs with results of Zamon & Welch (2005), who collected those two copepods on shipboard surveys running from the vicinity of Pine Island to the vicinity of Triangle Island during the strong El Niño event of 1998, whereas both were absent during the strong La Niña event of 1999.

The only prey taxa recorded in *A. hexapterus* diets in all 12 site-years were two calanoid copepods, *C. marshallae* and *Pseudocalanus* spp., which dominated diets in terms of frequency of occurrence and total numbers (the smaller *Pseudocalanus* spp. in most collections), and of biomass (the larger *C. marshallae* in all collections). *Calanus marshallae* and *Pseudocalanus* spp., especially *Pseudocalanus mimus*, are the dominant taxa in continental shelf waters off the British Columbia coast (Mackas, 1992). In fact, these two plus a third calanoid species, *A. longiremis*, which was absent in *A. hexapterus* diets only at Triangle Island in 2011 (where the sample size was very small), are very abundant along the continental margin of the north-east Pacific Ocean from southern Oregon to the Bering Sea (Mackas & Coyle, 2005).

There was, however, a signal of regional variation. Relative importance values showed that *C. marshallae* was the more important prey type at Pine and Triangle Islands, the two southerly sites, while *Pseudocalanus* spp. was more important at the two northerly sites, Lucy Island and S'G̱ang Gwaay. That result too is consistent with results of zooplankton surveys: Zamon & Welch (2005) reported that *Pseudocalanus* spp. was more abundant along a transect at 54° N, to the west of Lucy Island, than on a transect at 51° N near Pine and Triangle Islands in both a La Niña and an El Niño year; Perry & Waddell (1997) reported that *Pseudocalanus* sp., but not *C. marshallae*, was abundant in spring and summer in waters off both the east and west sides of Haida Gwaii and Mackas & Galbraith (2002) reported that *P. mimus* was abundant, but *C. marshallae* rare, in seaward-propagating anticyclonic eddies in the vicinity of S'G̱ang Gwaay.

In summary, *A. hexapterus*, similar to other species of *Ammodytes*, was found to rely heavily on calanoid copepods as prey; off the coast of British Columbia, Canada, the primary prey were *C. marshallae* (especially in the south) and *Pseudocalanus* spp. (especially in the north). In this region, the diets of *A. hexapterus* appear to reflect not only primary latitudinal levels of copepod community structure, but also secondary levels that result from oceanographic variation such as ENSO events. As with those of the zooplanktivorous seabird *P. aleuticus* (Bertram *et al.*, 2009; Hipfner, 2009), *Ammodytes* diets thus could be a useful means to track long-term patterns of zooplankton community structure that result from environmental change. It should be noted, however, that the Pacific Decadal Oscillation was in the negative phase throughout the three-year period of this study, and it is therefore probable that the extent of oceanographically driven variation in diets is actually greater than reported here.

The authors gratefully acknowledge all those who assisted with the field work, especially G. Keddie, who participated in all three years. The Canadian Coast Guard, Moresby Explorers, Parks Canada and West Coast Helicopters provided safe transport to and from field sites. M. Court, M. Lemon and C. Smith provided logistical support. The major funding for this research was provided by Environment Canada and the Centre for Wildlife Ecology at Simon Fraser University.

References

Batten, S. D. & Freeland H. J. (2007). Plankton populations at the bifurcation of the North Pacific Current. *Fisheries Oceanography* **16,** 536–546.

Batten, S. D. & Welch, D. W. (2004). Changes in oceanic zooplankton populations in the North-east Pacific associated with the possible climatic regime shift of 1998/1999. *Deep-Sea Research II* **51,** 863–873.

Beacham, T. D. (1986). Type, quantity and size of food of Pacific salmon *Oncorhynchus* in Strait of Juan-de-Fuca, British Columbia, Canada. *Fishery Bulletin* **84,** 77–90.

Beck, G. G., Hammill, M. O. & Smith, T. G. (1993). Seasonal variation in the diet of harp seals (*Phoca groenlandica*) from the Gulf of St Lawrence and western Hudson Bay. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1363–1371.

Bertram, D. F. & Kaiser, G. W. (1993). Rhinoceros auklet *(Cerorhinca monocerata*) nestling diet may gauge Pacific sand lance (*Ammodytes hexapterus*) recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1908–1915.

Bertram, D. F., Golumbia, T., Davoren, G. K., Harfenist, A. & Brown, J. (2002). Short visits reveal consistent patterns of interyear and intercolony variation in seabird nestling diet and performance. *Canadian Journal of Zoology* **80,** 2190–2199.

Bertram, D. F., Harfenist, A. & Hedd, A. (2009). Seabird nestling diets reflect latitudinal temperature-dependent variation in availability of key zooplankton prey populations. *Marine Ecology Progress Series* **393,** 199–210.

Blackburn, J. E. & Anderson, P. J. (1997). Pacific sand lance growth, seasonal availability, movements, catch variability, and food in the Kodiak–Cook Inlet area of Alaska. *University of Alaska Sea Grant College Program Report 97-01*, pp. 409–426. Anchorage, AK: University of Alaska.

Borstad, G., Crawford, W., Hipfner, J. M., Thompson, R. & Hyatt, K. (2011). Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. *Marine Ecology Progress Series* **424,** 285–302.

Burger, A. E., Wilson, R. P., Garnier, D. & Wilson, M. P. T. (1993). Diving depths, diet and underwater foraging of rhinoceros auklets in British Columbia. *Canadian Journal of Zoology* **71,** 2528–2540.

Davoren, G. K. & Burger, A. E. (1999). Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behavior* **58,** 853–863.

Edwards, M. & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430,** 881–884.

Field, L. J. (1988). Pacific sand lance, *Ammodytes hexapterus*, with notes on related *Ammodytes* species. In *Species Synopses, Life Histories, of Selected Fish and Shellfish* *of the Northeast Pacific and Bering Sea* (Wilimovsky, N. J., Lincze, L. S. & Westrheim, S. J., eds), pp. 15–33. Seattle, WA: Washington Sea Grant Program.

Friedlaender, A. S., Hazen, E. L., Nowacek, D. P., Halpin, P. N., Ware, C., Weinrich, M. T., Hurst, T. & Wiley, D. (2009). Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Marine Ecology Progress Series* **395,** 91–100.

Fulton, J. (1968). A laboratory manual for the identification of British Columbia marine zooplankton. *Fisheries Research Board of Canada Technical Report* **55**.

Gjerdrum, C., Vallée, A. M. J., St, C., Clair, C., Bertram, D. F., Ryder, J. L. & Blackburn, G. S. (2003). Tufted puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Sciences* **100,** 9377–9382.

Hammond, P. S., Hall, A. J. & Prime, J. H. (1994). The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. *Journal of Applied Ecology* **31,** 340–350.

Haugland, M., Holst, J. C., Holm, M. & Hanson, L. P. (2006). Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Sciences* **63,** 1488–1500.

Hedd, A., Bertram, D. F., Ryder, J. L. & Jones, I. L. (2006). Effects of interdecadal climate variability on marine trophic interactions: rhinoceros auklets and their fish prey. *Marine Ecology Progress Series* **309,** 263–278.

Hipfner, J. M. (2009). Euphausiids in the diet of a North Pacific seabird: seasonal and annual variation and the role of ocean climate. *Marine Ecology Progress Series* **390,** 277–289.

Irving, J. R. & Crawford, W. R. (2012). State of the physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2011. *Department of Fisheries and Oceans Canadian Scientific Advisory Secretariat Research Document* **2012/072**.

Ito, M., Minami, H., Tanaka, Y. & Watanuki, Y. (2009). Seasonal and interannual oceanographic changes induce diet switching in a piscivorous seabird. *Marine Ecology Progress Series* **393,** 273–284.

Kato, A., Watanuki, Y. & Naito, Y. (2003). Foraging behaviour of chick-rearing rhinoceros auklets *Cerorhinca monocerata* at Teuri Island, Japan, determined by acceleration-depth recording micro data loggers. *Journal of Avian Biology* **34,** 282–287.

Link, J. S. & Garrison, L. P. (2002). Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. *Marine Ecology Progress Series* **227,** 109–123.

Mackas, D. (1992). Seasonal cycle of zooplankton off southwestern British Columbia: 1979–89. *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 903–921.

Mackas, D. L. & Coyle, K. O. (2005). Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep-Sea Research II* **52,** 707–725.

Mackas, D. L. & Galbraith, M. (2002). Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: I. Transport and loss of continental margin species. *Journal of Oceanography* **58,** 725–738.

Mackas, D. L., Batten, S. & Trudel, M. (2007). Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. *Progress in Oceanography* **75,** 223–252.

McCauley, E. (1984). The estimation of the abundance and biomass of zooplankton in samples. In *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters* (Downing, J. A. & Rigler, F. H., eds), pp. 228–265. Boston, MA: Blackwell Scientific Publication.

McFarlane-Tranquilla, L., Ryder, J. L., Boyd, W. S., Shisko, S. G., Amey, K., Bertram, D. F. & Hipfner, J. M. (2005). Diurnal marine distributions of radio-tagged Cassin's Auklets and Rhinoceros Auklets breeding at Triangle Island, B.C. *Canadian Wildlife Service Technical Report Series 423*. Ottawa, ON: Environment Canada.

McKenzie, J. & Wynne, K. M. (2008). Spatial and temporal variation in the diet of Steller's sea lions in the Kodiak Archipelago, 1999 to 2005. *Marine Ecology Progress Series* **360,** 265–283.

McNamara, J. M. & Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology* **68,** 1515–1519.

Meyer, T. L., Cooper, R. A. & Langton, R. W. (1979). Relative abundance, behavior, and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. *Fishery Bulletin* **77,** 243–253.

O'Connell, M. & Fives, J. M. (1995). The biology of the lesser sand-eel *Ammodytes tobianus* L. in the Galway Bay area. *Biology and Environment* **95,** 87–98.

Overholtz, W. J. & Nicholas, J. R. (1979). Apparent feeding of the fin whale, *Balaenoptera physalus*, and humpback whale, *Megaptera novaeanglia*, on the American sand lance, *Ammodytes americanus*, in the northwest Atlantic. *Fishery Bulletin* **77,** 285–287.

Parrish, J. K. & Zador, S. G. (2003). Seabirds as indicators: an exploratory analysis of physical forcing in the Pacific northwest coastal environment. *Estuaries* **26,** 1047–1057.

Perry, R. I. & Waddell, B. J. (1997). Zooplankton in Queen Charlotte Islands waters: distribution and availability to marine birds. In *The Ecology, Status and Conservation of Marine and Shoreline Birds of the Queen Charlotte Islands* (Vermeer, K. & Morgan, K. H., eds), pp. 18–28. Ottawa, ON: Environment Canada.

Perry, R. I., Hargreaves, N. B., Waddell, B. J. & Mackas, D. L. (1996). Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. *Fisheries Oceanography* **5,** 73–88.

Pinkas, L., Oliphant, M. S. & Iverson, I. L. K. (1971). Food habits of albacore, bluefin tuna and bonito in California waters. *Fisheries Bulletin* **152,** 1–105.

Pitt, T. K. (1973). Food of American plaice *Hippoglossoides platessoides* from the Grand Bank, Newfoundland Canada. *Journal of the Fisheries Research Board of Canada* **30,** 1261–1273.

Richards, S. W. (1982). Aspects of the biology of *Ammodytes americanus* from the St. Lawrence River to Chesapeake Bay, 1972-75, including a comparison of the Long Island Sound postlarvae with *Ammodytes dubius*. *Journal of the Northwest Atlantic Fisheries Society* **3,** 93–104.

Rindorf, A., Wanless, S. & Harris, M. P. (2000). Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series* **202,** 241–252.

Robards, M. D. & Piatt, J. F. (1999). Biology of the genus *Ammodytes*, the sand lances. In *Sand Lance: A Review of Biology and Predator Relations and Annotated Bibliography* (Robards, M. D., Willson, M. F., Armstrong, R. H. & Piatt, J. F., eds), pp. 1–16. Portland, OR: U.S. Department of Agriculture.

Robards, M. D., Anthony, J., Rose, G. A. & Piatt, J. F. (2002). Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska, relative to maturity and season. *Journal of Experimental Marine Biology and Ecology* **242,** 245–258.

Santic, M., Rada, B. & Pallaoro, A. (2012). Diet and feeding strategy of thornback ray *Raja clavata*. *Journal of Fish Biology* **81,** 1070–1084.

Schoener, T. (1970). Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* **51,** 408–418.

Scott, J. S. (1973). Food and inferred feeding behavior of northern sand lance (*Ammodytes dubius*). *Journal of the Fisheries Research Board of Canada* **30,** 451–454.

Sekiguchi, H. (1977). Further observations on the feeding habits of planktivorous fish sand-eel in Isle Bay. *Bulletin of the Japanese Society of Scientific Fisheries* **43,** 417–422.

Springer, A. M., Roseneau, D. G., Murphy, E. C. & Springer, M. (1984). Environmental controls of marine food webs: food habits of seabirds in the eastern Chukchi Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **41,** 1202–1215.

Temming, A., Gotz, S., Mergardt, N. & Ehrich, S. (2004). Predation of whiting and haddock on sandeel: aggregative response, competition and diel periodicity. *Journal of Fish Biology* **64,** 1351–1372.

Trudel, M., Thiess, M. E., Bucer, C., Farley, E. V. Jr., Macfarlane, R. B., Casillas, E., Fisher, J., Morris, J. T. F. & Murphy, J. M. (2007). Regional variation in the marine growth and energy accumulation of juvenile Chinook salmon and coho salmon along the west coast of North America. *American Fisheries Society Symposium Series* **57,** 205–232.

Wallace, R. K. (1981). An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* **110,** 72–76.

Wanless, S., Harris, M. P., Redman, P. & Speakman, J. R. (2005). Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* **294,** 1–8.

Westrheim, S. J. & Harling, W. R. (1983). Principal prey species and periodicity of their incidence in stomachs of trawl caught Pacific cod (*Gadus macrocephalus*), rock sole (*Lepidopsetta bilineata*), and petrale sole (*Eopsetta jordani*) landed in British Columbia 1950-1980. *Canadian Manuscript Report of the Fisheries and Aquatic Sciences* **1691,** 1–38.

Wilke, F. & Kenyon, K. W. (1957). The food of fur seals in the eastern Bering Sea. *Journal of Wildlife Management* **21,** 237–238.

Williams, C. T., Iverson, S. J. & Buck, C. L. (2008). Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. *Marine Ecology Progress Series* **363,** 287–298.

Zamon, J. E. & Welch, D. W. (2005). Rapid shift in zooplankton community composition on the northeast Pacific shelf during the 1998-1999 El Niño–La Niña event. *Canadian Journal of Fisheries and Aquatic Sciences* **62,** 133–144.

APPENDIX. Prey taxa recorded in *Ammodytes hexapterus* diets at four sites in British Columbia, Canada. Numbers indicate in which of the three years of study (2009–2011) that prey was recorded at that site

		Colony			
Prey taxon	Sub-taxon–species	Lucy Island	Pine Island	S’Ga̲ng Gwaay	Triangle Island
Molluscs	Gastropod	–	–	–	2009 (v)
		–	–	–	2010 (v)
	Limacina helicina	–	All	2011	2009
	Octopus sp.	–	2010 (l)	–	–
Cirripeds	Barnacle	2009 (c, n)	2009 (c, n)	–	2009 (c, n)
		2010 (c)	2010 (c, n)	–	2010 (c, n)
		2011 (n)	2011 (c, n)	2011 (c)	2011 (c, n)
Cladocerans	*Podon* sp.	All	2009, 2010	–	–
	Evadne sp.	2011	2009	–	2009
Copepods	Copepod	2011 (e)	2009 (n)	–	2009 (n)
	Acartia hudsonica	–	2010	–	–
	Acartia longiremis	All	All	All	2009, 2010
	Aetideus divergens	2011	–	–	–
	Calanus marshallae	All	All	All	All
	Calanus pacificus	2009	All	All	2009, 2010
	Centropages abdominalis	2009, 2011	All	2009, 2010	All
	Corycaeus anglicus	–	2010	–	–
	Epilabidocera longipedata	–	All	2009	–
	Eucalanus bungii	2009	All	2009, 2011	2010
	Harpacticoids	–	2009	–	–
	Metridia pacifica	2009, 2010	All	2009	2009, 2010
	Microsetella rosea	–	2010	–	–
	Neocalanus cristatus	2009	2009, 2010	2009, 2010	2009
	Neocalanus plumchrus	2010	2010, 2011	2009, 2011	2009, 2010
	Oithona atlantica	–	2009	–	–

APPENDIX. Continued

		Colony			
Prey taxon	Sub-type/species	Lucy Island	Pine Island	S'G̱ang Gwaay	Triangle Island
	Oithona similis	–	2009	2011	2009
	Paracalanus sp.	–	2009, 2010	2011	–
	Paracalanus indicans	–	2010	–	–
	Pseudocalanus sp.	All	All	All	All
	Pseudocalanus minutus	–	2010	–	–
	Pseudocalanus moultoni	–	2010	–	–
	Tortanus discaudatus	All	2009	2010	2010
Hyperiids	Gammaridae	2009 (j)	–	–	–
	Themisto pacifica	2009, 2011	2010	2009, 2010	2010
Cumaceans	Cumacean	2011	–	–	–
Mysids	*Neomysis kadiakensis*	2011	–	–	–
Euphausids	Euphausiid	2009 (n, p, z)	2009 (n, p, z)	–	2009 (n, p, z)
		2010 (e, z)	2010 (n, p, z, j)	2010 (z)	2010 (z)
		2011 (n, p, z)	2011 (z)	2011 (e, p, z)	–
	Thysanoessa spinifera	2009	All	2009, 2011	2010
	Euphausia pacifica	2011	2009, 2011	–	2010
Decapods	Caridea	2009 (z, my)	2009 (z)	2009 (z)	–
		2010 (my)	2010 (z, my)	–	–
		2011 (my)	–	–	–
	Axiidae, *Neotrypaea* sp.	2010 (my)	–	–	–
	Galatheoidea	–	–	–	2009 (z)
	Paguroidea	2009 (z)	–	2009 (z)	–
		2010 (z)	2010 (z)	–	–
		–	2011 (z)	2011 (z)	–
	Brachyura	2009 (z)	–	2009 (z, m)	2009 (z, m)
		2010 (z)	2010 (z, m)	2010 (z)	2010 (z)
		2011 (z, m)	2011 (z, m)	2011 (z)	–
	Cancer sp.	2009 (z)	2010 (z, m)	2009 (z, m)	–
		–	–	2010 (z)	–
	Cancer magister	2010 (z)	2010 (z)	–	–
	Cancer oregonensis	–	2010 (m)	–	–
	Cancer productus	–	–	2010 (m)	2010 (m)
	Majoidea	–	2011 (m)	–	–
	Lophopanopeus sp.	–	2011 (m)	–	–
	Pinnotheroidea	2011 (z)	2010 (z)	–	–
	Porcellanoidea	–	2010 (m)	–	–
		–	2011 (z)	–	–
Chaetognaths	Chaetognath	2010	2010	–	2010
	Parasagitta elegans	2010	All	2009	2009, 2010
Larvaceans	*Oikopleura* sp.	All	All	2009	2009, 2010
Teleosti	Fish	2010	2009, 2010	–	2010
	Sebastes sp.	–	2009, 2010	–	–

Life stages (in parentheses): c, cyprid; e, eggs; j, juvenile; l, larvae; m, megalops; my, mysis; n, nauplii; v, veliger; z, zoea.