

Feeding ecology of silver hake larvae on the Western Bank, Scotian Shelf, and comparison with Atlantic Cod

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The feeding ecology of the larvae of silver hake *Merluccius bilinearis* was examined during two time periods (October 1998 and December 1992) on the Western Bank, Scotian Shelf, north-west Atlantic, and compared with the feeding ecology of Atlantic cod *Gadus morhua* larvae collected in the same samples in December 1992. During both time periods silver hake exhibited strong selection for late stage copepodids and adult copepods at a small size (>3.5 mm total length, L_T). The niche width measured as the diet breadth index (I_{DB}) of silver hake declined rapidly as they increased in size and remained relatively constant from 3 to 11 mm L_T , during each time period. Atlantic cod larvae exhibited a broader niche width that was curvilinear over the same L_T . Atlantic cod were also less selective than silver hake, incorporating both naupliar and early stage copepodids in their diets throughout the length classes examined. Simple isometric relationships did not explain the differences in diet, as Atlantic cod larvae continued to feed on early stages of copepods at large size, while silver hake larvae quickly switched to large prey items. The strong selection and narrow I_{DB} observed for silver hake probably reflects adaptation to spawning during the periods between major secondary production peaks in temperate waters. © 2005 The Fisheries Society of the British Isles (No claim to original US government works)

Key words: Atlantic cod; feeding ecology; Scotian shelf; selectivity; silver hake.

INTRODUCTION

The understanding of the feeding ecology of larval fishes is critical to assessing the mechanisms responsible for the success or failure of cohorts, and potentially year class strength of marine fish populations (Cushing, 1990). Given the prevailing view that larval fishes in marine environments are food-limited (Hunt von Herbing & Gallager, 2000; Hinrichsen *et al.*, 2003), larval fishes should exhibit feeding patterns that maximize energy intake (Werner & Hall, 1974). Fish larvae are visual predators, so the number and types of prey consumed will also reflect the ease of capture (McLaren & Avendaño, 1995), the apparent size (Luo *et al.*, 1996) or presentation of food items (Fiksen *et al.*, 1998; Reiss *et al.*, 2002) to the individual, thereby describing the selectivity for

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prey by a species. Pearre (1986) has suggested that the niche width of a species (measured as the s.d. of the \log_{10} of prey size) should remain constant with length, as smaller food items are replaced by larger items during growth and development, thereby maximizing energy intake. Additionally, the selectivity exhibited by an individual should change given the prey concentration, distribution and abundance by declining in predictable or food-rich environments (Mayer & Wahl, 1997; Munk, 1997).

Many early life-history studies have focused on testing the generality of the hypothesis that the feeding-niche width remains constant with increasing fish size (jaw or body length) in order to maximize energy gain (Pearre, 1986; Hilgruber *et al.*, 1997; Munk, 1997; Pepin & Penney, 1997, 2000; Gonzalez-Quiros & Anadon, 2001). Yet the results of these studies are mixed, and authors have found increasing, constant or non-linear relationships between feeding-niche width and fish size. Fewer studies have examined whether perceived selectivity changes under different prey concentrations and distributions.

In this study, the feeding ecology of the larvae of silver hake *Merluccius bilinearis* (Mitchill) on the Western Bank, Scotian Shelf was examined and the results related to predictions from feeding theory (Shirota, 1970; Pearre, 1986; Pepin & Penney, 1997) by comparing and contrasting the feeding ecologies of larval silver hake and larval Atlantic cod *Gadus morhua* L., which occurred with the silver hake, during two time periods, October 1998 and December 1992. The hypothesis was also tested that temporal patterns of prey ingestion and niche width reflected differences in relative abundance of prey taxa and sizes available before (October) and after (December) the autumn plankton bloom, and that selectivity decreased at the end of the spawning season of silver hake (Werner & Hall, 1974; Bartell, 1982; Jeffrey & Taggart, 2000).

MATERIALS AND METHODS

PLANKTON COLLECTIONS

Zooplankton and larval fishes used in the present study were derived from three series of collections on and around the Western Bank, Scotian Shelf (Fig. 1). One series was collected during cruise 9858 from 29 September to 15 October 1998 as part of the Canadian GLOBEC (Global Ecosystem Dynamics) programme. The second series of collections was obtained during cruises conducted in support of the Ocean Production Enhancement Network (OPEN) programme conducted over and around the Western Bank between 1991 and 1993. In particular, samples were collected during the OPEN cruise 9231 in November and December 1992. Some of the Atlantic cod data used here were previously used in a different form by McLaren *et al.* (1997) to relate feeding success to oceanographic features. In the present study the data underwent a new analysis, as they specifically related to selectivity and niche width of silver hake. Finally, some measurements (120) of the lower jaw length of Atlantic cod larvae were from samples collected during the OPEN cruise 9103 conducted in May 1991 on the Western Bank.

Details of the sampling strategies for each cruise are given elsewhere (Taggart *et al.*, 1996; McLaren *et al.*, 1997; Reiss *et al.*, 2002, 2003). Briefly, larval fishes were collected at vertically discrete depths using a 1 m² BIONESS net equipped with nine nets of 333 μ m mesh. Samples were collected at *c.* 3 h intervals over a 23 day period (OPEN cruises 9231; 9103); and at a variety of times of the day and night over a 20 day period, as well as over a 36 h period during the Canadian GLOBEC cruise 9858. Larval fish abundance estimates were expressed as a concentration (number 100 m⁻³).

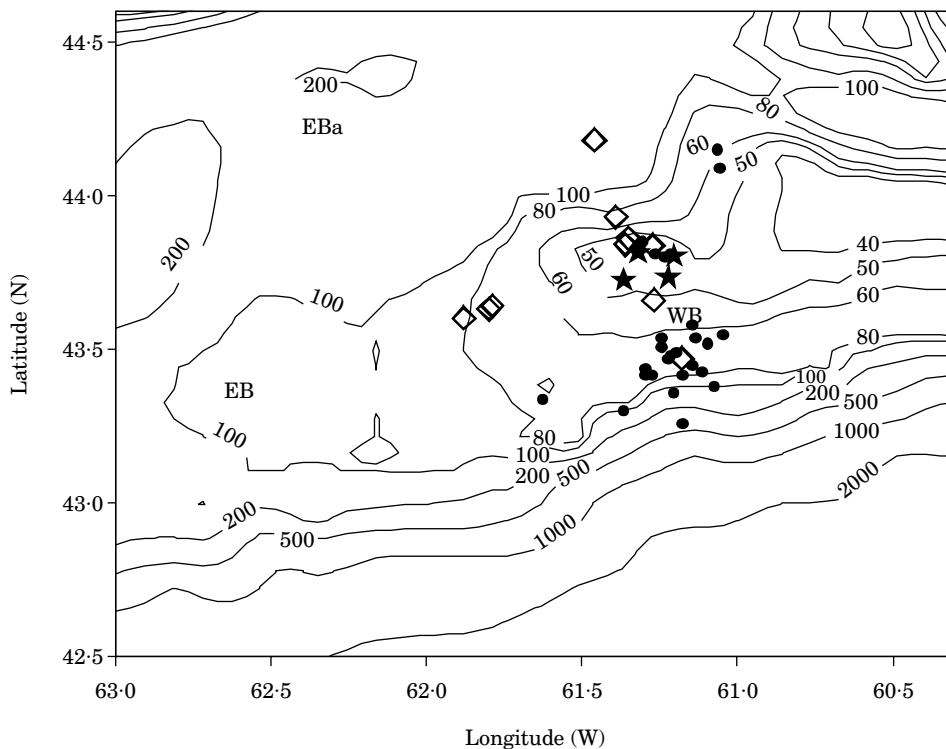


FIG. 1. Bathymetric chart of the Western Bank showing locations of BIONESS and vertical net samples collected during cruise 9858 in October 1998 (\diamond) and cruise 9231 in December 1992 (\star , \bullet). WB, Western Bank; EB, Emerald Bank; EBa, Emerald Basin.

The vertical distribution of zooplankton was also determined during these two cruise periods. During November 1998, a closing ring-net, 50 cm in diameter with 64 μ m mesh equipped with a mechanical flowmeter was used to sample three to six depth strata at each station, including the mixed layer, a pycnocline layer and sub-pycnocline waters. At some stations, samples were collected from five nominal depth strata 0–7, 7–14, 14–21, 21–28 and 28–35 m, at *c.* 3 h intervals using the closing 64 μ m plankton net. Further, smaller zooplankton size classes were sampled concurrently with the bongo samples using an attached 25 cm diameter net with 64 μ m mesh. During November 1992, the vertical distribution of zooplankton was determined at four stations near the crest of the Western Bank (McLaren & Avendaño, 1995) and four discrete depths (5, 15, 25 and 35 m) using a 25 cm Clarke-Bumpus sampler equipped with 64 μ m mesh nets. Because depth, or other associated variables may contribute to perceptions of feeding selectivity and niche width, the zooplankton and larval fish data were pooled into four depth zones (0–10, 10–20, 20–30 and >30 m) in order to ensure adequate numbers of fishes of a variety of sizes were available for subsequent analyses. Preliminary analyses of the depth discrete samples as described below did not show any large differences as compared to the pooled data, so niche widths and selectivity indices are shown for the overall pooled data.

LABORATORY ANALYSIS

Fish larvae were removed from all plankton samples, identified to species, enumerated and measured (total length, L_T , to the nearest 0.1 mm) under magnification using a video

camera and SigmaScan Pro (Ver 5.0.0, SPSS, Inc. 1999) or using an ocular micrometer under magnification. No correction for shrinkage was made.

Samples preserved in formalin (37% formaldehyde) from the 64 µm mesh nets were used to enumerate copepod eggs, nauplii, copepodids and adults, as well as other invertebrate taxa. The fine-mesh (64 µm) samples were sub-sampled by a Folsom plankton splitter, and eggs, nauplii, copepodid and adult copepods were identified and enumerated to species and developmental stage mainly from Lawson & Grice (1970), Diaz & Evans (1983), Sazhina (1985) and Frost (1989), or to lowest possible taxonomic category. Other well-known planktonic taxa were identified to genera from a variety of sources. Abundance of copepods and other zooplankton was expressed as concentration (number m⁻³).

FEEDING SUCCESS

Larval fishes used for gut content analysis were randomly selected from each of the formalin-preserved BIONESS samples in proportion to their concentration among collections (as many as 30 fish per sample) for a total of 837 silver hake larvae in 1998. On average, 16 fish were examined (range one to 30) per sample. Historical gut content data for 683 Atlantic cod larvae collected during November to December 1992 were obtained from databases, and 227 silver hake larvae were removed from preserved samples collected at the same stations, and their guts examined for prey items. The samples were restricted to those collected between 0800 and 2400 hours. Stomach contents of all larval fishes were examined under magnification, identified and enumerated according to the method of McLaren & Avendaño (1995). The gut was excised and opened using PrecisionGlide[®] 27G ½ needle or a 2.5 Mrad. Feather[®] scalpel. Each food item was identified to the lowest possible taxonomic level and developmental stage and the item was measured. Where possible, the length and width of both the prosome and metasome of late stage copepods was measured. The shape of nauplii, however, differs, so a third measurement was made corresponding to the narrowest part of the body that in copepodid stages would form the posterior portion of the metasome and urosome. Lengths and widths of individual prey items were determined to 0.1 mm using a calibrated ocular micrometer.

A number of measurements (all in mm) were made on each larva, including body depth, gut length, depth and height (these measurements were necessary to properly calculate the gut volume), and the length of the lower jaw, an index of maximum mouth gape. Previous feeding studies on silver hake and Atlantic cod have shown that body length was highly correlated ($r^2 > 0.9$) with mouth width (Sumida & Moser, 1980; Kane, 1984). Additionally, maxillary length (lower jaw) was also highly correlated with L_T . Given these findings, in this study the lower jaw length was used as an index of mouth gape, and therefore as an index of the ability of each species to feed on prey of a given size.

DATA ANALYSES

The feeding-niche width was calculated for each species and time period using Pearre's (1986) diet breadth index, I_{DB} , which is defined here as the s.d. of the log₁₀ of the prey length in individual guts. Only larvae with three or more prey items in their gut were used. Pearre (1986) has suggested that this index is independent of prey size, and has suggested that the diet breadth should be independent of size. Chesson's (1978) index of prey selection was also used to determine the relative selectivity of prey types by Atlantic cod and silver hake larvae collected in the same samples during 1992 and the patterns were compared to those observed for silver hake (Atlantic cod were not found in 1998) during 1998, by size class (<3, 3–5, 5–7, 7–9, 9–11 and >11 mm L_T). Chesson's (1978) index was calculated as: $P_i = (a_i n_i^{-1}) / [\sum a_i n_i^{-1}] (i = 1..m)^{-1}$, where a_i and n_i are the proportions of prey items of each type (i) in the stomachs and in the environment, and m are the number of prey types (Chesson, 1978). Selection for 16 developmental classes of prey that roughly corresponded to size [eggs, nauplii 1–6, copepodids 1–5 and adults (males

and females) of the copepods, and for *Limacina* spp., and *Placopecten* sp.] was examined. Chesson's (1978) index is lower-bounded, and neutral selection is defined as m^{-1} of developmental or size classes considered.

Previous studies on the Western Bank have shown that time of day is an important factor contributing to variability in the gut contents of Atlantic cod (McLaren & Avendaño, 1995; McLaren *et al.*, 1997) and silver hake (Coates-Markle, 1982), potentially complicating inferences about feeding preference. To directly compare the diel patterns in feeding between silver hake and Atlantic cod, data from the 1992 cruises were pooled into six 4 h periods between 0800 and 0000 hours. The mean prey per gut and mean prey size by time of day pooled across size for each species were pooled for comparison.

RESULTS

BODY AND MOUTH SIZE RELATIONSHIPS

Silver hake larvae collected during 1992 and 1998 ranged from 2.5 to 35.0 and 2.5 to 20.0 mm L_T , respectively. Atlantic cod larvae ranged from 2.1 to 25.0 mm L_T . Linear regressions explained between 95 and 97% of the variability in jaw length, and the relationships between lower jaw and L_T differed between silver hake and Atlantic cod (Table I). No difference in this isometric relationship was found between years for silver hake. Atlantic cod had smaller jaws at a given size than silver hake. In addition, the jaw length of silver hake larvae increased at a faster rate than Atlantic cod. Thus, at any given size silver hake larvae could potentially consume larger prey items than Atlantic cod larvae of a similar L_T . For example, Atlantic cod larvae would need to be between 5 and 7 mm L_T to have the lower jaw length of 3 to 5 mm L_T silver hake larvae.

WATER COLUMN PREY ABUNDANCE

Considerable differences in the average prey abundances were observed between the two cruise periods (Table II). For example, *Pseudocalanus parvus* abundances were lower in December 1992 than in October 1998. Nauplii of *P. parvus* ranged from 17 to 294 m⁻³ in 1998 and copepodids ranged from 3 to 573 m⁻³. In December 1992, the mean abundance of naupliar stages of *P. parvus* ranged from 0 to 25 m⁻³, while copepodids ranged 6 to 107 m⁻³.

TABLE I. Relationship between lower jaw length (y , mm) and total length (x , mm) of silver hake collected in October 1998 and November 1992 and Atlantic cod collected in November 1992 on and around Western Bank, Scotian Shelf. Values in parentheses are S.E. of the coefficient estimates

	n	Equation	r^2
Silver hake 1992	227	$y = 0.026(0.020) + 0.1822(0.002)x$	0.95
Silver hake 1998	877	$y = -0.062(0.008) + 0.1878(0.001)x$	0.96
Atlantic cod 1992	120	$y = 0.004(0.03) + 0.1318(0.002)x$	0.97

TABLE II. Mean abundance of zooplankton taxa collected on and around the Western Bank during cruises 9231 and 9858 conducted in October 1998 and December 1992 respectively. Stage represents developmental stage of copepods from eggs and naupliar stage (n1–n6) to copepodids (c1–c5) and adults (c6) of each sex (F and M). The sample size for 1998 was 92 and the sample size for 1992 was 14. Samples were pooled across locations and over depths

Species	Pooled	eggs	Mean abundance (number m ⁻³)												
			n1	n2	n3	n4	n5	n6	Stage						c6m
Cruise 9231															
<i>Oithona similis</i>		448.3	1.8	18.2	91.4	215.0	348.0	231.6	203.5	218.1	197.2	278.3	276.0	173.7	39.1
<i>Pseudocalanus</i> spp.		97.2	51.8	114.4	78.7	59.5	20.3	8.4	12.1	11.0	11.3	12.9	25.2	4.7	4.7
<i>Centropages typicus</i>		64.5	41.9	231.3	504.5	237.1	104.8	171.7	183.9	167.2	95.7	78.8	65.0		
<i>Paracalanus parvus</i>		20.8	0	2.5	17.1	24.7	11.6	43.4	6.0	23.2	43.4	64.9	107.1	96.6	15.4
<i>Clausocalanus</i> spp.		0	0	0	0	0	0	0	0.0	0.3	2.1	7.3	26.5	39.7	3.4
<i>Temora longicornis</i>		0	9.8	12.2	9.8	3.6	0	0	0.8	3.4	6.4	5.6	8.0	7.1	14.9
<i>Metridia lucens</i>		0	0	0	0	1.0	1.3	0	1.7	2.3	3.5	3.8	2.2	1.3	0.2
<i>Microcalanus pusillus</i>		0	0	0	0	0	0	0	0	0	0.1	0	0.5	1.1	2.5
<i>Limacina</i> spp.	3065.0														
<i>Placoepecten</i> spp.	255.0														
<i>Sagitta elegans</i>	1.7														
<i>Oncaea</i> spp.	0.8														
Unknown cyclopoid	0.6														
Unknown harpacticoid	0.8														
Unknown calanoid	3.8														
<i>Oikopleura</i>	0.5														

Cruise 9858	1998-4	15-9	222-6	1093-8	1935-8	1752-6	545-2	1412-1	1325-2	1460-6	1530-8	1516-2	1110-0	1610-1	199-4
<i>Oithona similis</i>	1862-0	17-6	43-1	291-4	294-4	170-0	109-2	113-6	108-8	220-0	572-8	525-5	281-5	3-4	0
<i>Paracalanus parvus</i>	349-9	10-2	0	1-7	2-2	1-6	1-1	0	1-6	104-1	416-4	455-4	1553-9	573-0	392-2
<i>Microsetella norvegica</i>	260-1	34-0	173-6	219-4	134-6	119-9	128-2	200-5	202-3	312-3	1032-1	930-3	994-2	1108-8	0
<i>Centropages typicus</i>	131-9	45-4	14-2	101-6	21-0	15-5	1-4	40-8	52-4	205-5	305-9	338-1	118-6	9-9	0
<i>Pseudocalanus</i> spp.	2-4	0-0	2-5	31-9	37-8	6-0	3-7	5-7	8-1	23-1	131-1	146-4	158-0	2-1	0
<i>Clausocalanus</i> spp.	1-0	1-3	1-4	2-7	0-9	0-5	0-2	0-1	0	0-2	2-7	1-3	1-2	00	0
<i>Metridia lucens</i>	0	0-1	4-8	5-6	2-4	4-0	4-6	11-1	3-8	6-8	6-1	5-8	13-9	11-9	0
<i>Temora longicornis</i>	0	0	0	1-2	2-5	3-4	5-1	18-7	7-0	10-1	25-4	25-0	23-9	0-6	0
<i>Microcalanus pusillus</i>	0-3	0	0	0	0	0	0-4	2-7	2-9	7-2	9-4	3-3	0-3	0	0
<i>Calanus finmarchicus</i>	0	0	0	0	0	0	0	0-6	0-6	1-0	0-0	0-0	0	0	0
<i>Calanus glacialis</i>	0	0	0	0	0	0	0	2-4	2-2	1-5	1-5	0-1	0	0	0
<i>Calanus hyperboreus</i>	0-1	0	0	1-1	0	0	0	0	0	0-1	0-1	0	0	0	0
<i>Calanus</i> spp.	4-7	0	0-4	2-7	1-7	0-4	1-2	0	0	0	0	0	0	0	0
Unknown calanoid	7-1														
<i>Placoepecten</i> spp.	334-6														
<i>Limacina</i> spp.	219-1														
<i>Oncaea</i> spp.	7-8														
Unknown	6-8														
harpacticoid															
<i>Oikopleura</i> spp.	6-3														
Ctenophora	5-9														
Cladocera	0-7														
Salps	0-1														
Isopoda	6-3														
<i>Meganythipines</i> spp.	1-2														
<i>Parathemisto</i> spp.	6-7														
<i>Thysanoessa</i> spp.	6-5														
Echinoderma	1-2														
<i>Sagitta elegans</i>	6-1														
<i>Tomopteris</i> spp.	1-4														

Such a pattern is consistent with the seasonal decline in many species following the autumn plankton bloom. In contrast, the mean abundance of naupliar stages of *Pseudocalanus* spp. ranged between 1.4 and 45 m⁻³ in October 1998, and were higher (between 20 and 97 m⁻³) in December 1992, while copepodids ranged between 90 and 338 m⁻³ in 1998 and 4 to 25 m⁻³ in 1992. The variability in mean concentration of prey items would suggest that considerable variability in the diet of silver hake should be expected between the two time periods.

The vertical distributions of developmental stages of copepods showed differences between cruises when pooled into four broad depth strata (Fig. 2.). In October 1998 copepodid and adult stages of copepods increased from the surface with depth, while nauplii exhibited a more uniform distribution across depth zones. In December 1992, all stages had essentially uniform vertical distributions, although there was some variability that reflected low sample sizes ($n < 4$).

PREY COMPOSITION IN DIETS

For both Atlantic cod and silver hake, four prey taxa comprised >90% of the items in the diets (Table III). *Pseudocalanus* spp. and *Centropages typicus* made up most items in the diets of Atlantic cod (>80%), with fewer *Limacina* spp. and *Oithona similis*. *Paracalanus parvus* was a minor component of the diet (>1%). The same four copepod taxa dominated the diet of silver hake. During autumn 1998, silver hake ate mostly *P. parvus* and *C. typicus* (>75%), with smaller contributions of *Clausocalanus* spp. (12%), and *Pseudocalanus* spp.

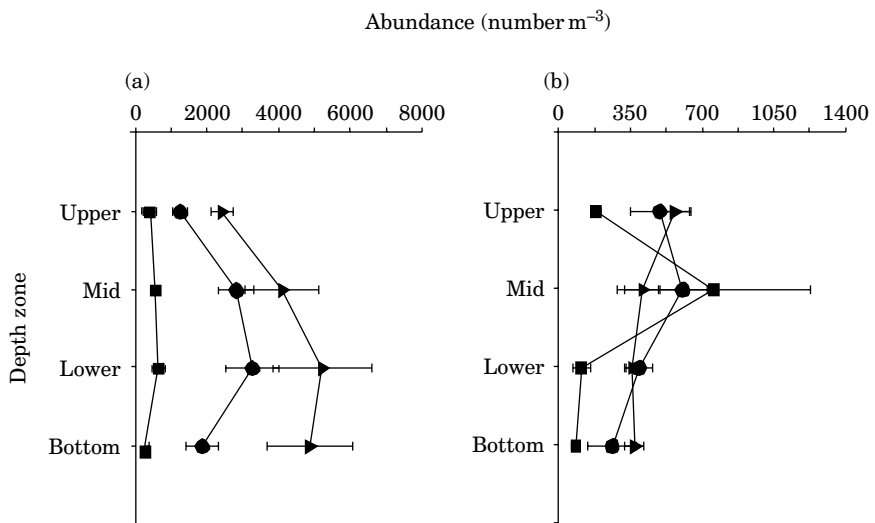


FIG. 2. Mean \pm 2 S.E. vertical distribution of the abundance for three developmental stages [n2 (■), c3 (●) and c6f (▲), see Table II] of copepods collected during (a) 1992 and (b) 1998. Note the difference in the x axis between (a) and (b).

TABLE III. Number and per cent occurrence of prey species in the diets of silver hake in 1992 and 1998 and Atlantic cod collected during 1992

Prey species	Silver hake 1992		Silver hake 1998		Atlantic cod 1992	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Amphipod	0	0	6	<1	0	0
<i>Calanus</i> spp.	18	1	89	2	30	<1
<i>Clausocalanus</i> spp.	621	43	497	12	14	<1
<i>Centropages typicus</i>	102	7	848	20	2346	25
Decapoda	0	0	0	0	1	<1
Euphausiid	0	0	4	<1	0	0
<i>Eurytemora</i>	0	0	4	<1	0	0
Fish larvae	1	<1	1	<1	0	0
<i>Limacina</i>	0	0	1	<1	690	7
<i>Microcalanus pusillus</i>	0	0	0	0	1	<1
<i>Microsetella norvegica</i>	0	0	0	0	9	<1
<i>Metridia longa</i>	0	0	0	0	2	<1
<i>Metridia lucens</i>	1	<1	0	0	125	1
<i>Oithona similis</i>	42	3	57	1	511	6
<i>Paracalanus parvus</i>	380	27	2233	54	118	1
<i>Placopecten magellanicus</i>	0	0	0	0	30	<1
Polychaete	0	0	1	<1	0	0
<i>Pseudocalanus</i> spp.	239	17	220	5	5305	58
<i>Temora</i>	5	<1	2	<1	21	<1
Tintinid	0	0	5	<1	0	0
Calanoidea	4	<1	3	<1	5	<1
Unknown	0	0	1	<1	3	<1
Empty guts	9	1	0	0	9	<1
Debris	0	0	11	<1	0	0

(5%). In winter 1992, *Clausocalanus* sp. (>45%) was the dominant food item followed by *P. parvus* (>25%) and while *Pseudocalanus* spp. formed a larger percentage (c. 17%) of the diets of silver hake, *C. typicus* declined in occurrence from 20% in October to just 7% in December. During autumn and winter *Limacina* sp. was also prominent in the diet of silver hake.

DIEL FEEDING PATTERNS

The number of prey per gut varied by time of day, and silver hake larvae had fewer prey in their guts than Atlantic cod at all hours of the day (Fig. 3). During 1992, both Atlantic cod and silver hake larvae had the most prey items in their guts during the crepuscular period between 1600 and 2000 hours. In 1998 silver hake had the highest numbers of prey items in guts between 2000 and 0000 hours.

On average, Atlantic cod and silver hake consumed prey of different sizes, and silver hake consumed larger prey than Atlantic cod. Mean size of prey of

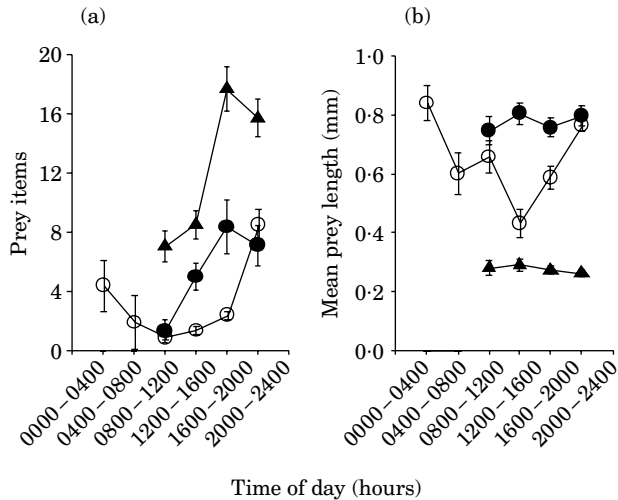


FIG. 3. Diel variability in (a) the number and (b) size of prey in the guts of silver hake in 1992 (●) and 1998 (○) and Atlantic cod in 1992 (▲). All sizes of larvae were combined and samples were pooled into six 4 h groups between 0800 and 0000 hours over the course of each cruise. Values are means \pm 2 S.E.

both silver hake and Atlantic cod larvae in 1992 increased during the afternoon period. In 1998, silver hake showed the opposite pattern, with a substantial decrease in mean prey size in the afternoon. Overall, however, the mean size of prey consumed by silver hake was much larger than that of Atlantic cod. Thus, while there was some evidence of changes in the size of prey eaten with time of day in 1998, the patterns were not consistent between time periods.

ONTOGENETIC CHANGES IN DIET

Both silver hake and Atlantic cod larvae exhibited significant positive relationships between body size and both the number and mean size of prey items ingested (Fig. 4 and Table IV). Overall there was considerable scatter in the data, and strong relationships were not observed when data collected over all times of the day were pooled. The correlation between prey size and L_T , however, increased for both species when the data were restricted to the evening hours, when guts should have been fullest, but the increase was smaller for Atlantic cod than for silver hake. The correlation between the number of prey items in the gut and L_T increased substantially for silver hake larvae in the evening hours. In contrast, the correlation remained very low for Atlantic cod larvae at all times of night and day. Overall feeding success (number of fish with at least one prey item) was high for both species, with food present in guts of between 95 and 100% for larvae of all sizes and for each species, between 0800 and 0000 hours.

As they grew, silver hake larvae switched from small to large prey at a relatively small size during both 1992 and 1998 (Fig. 4). In October 1998, prey

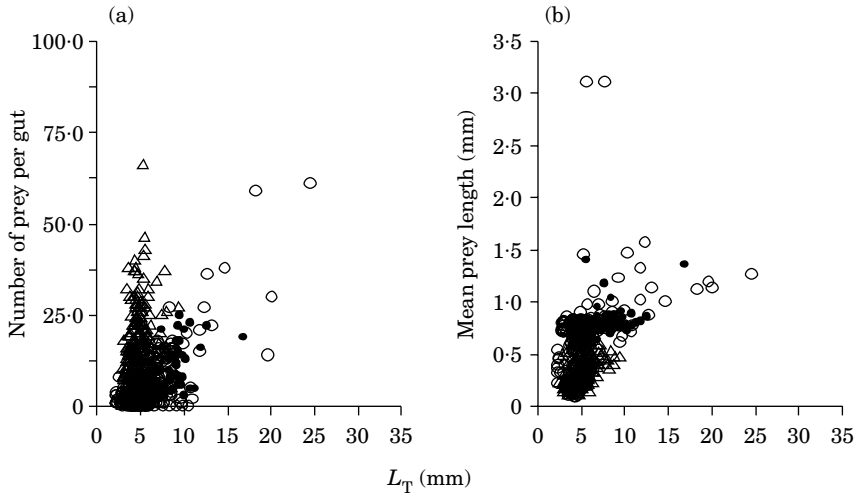


FIG. 4. Scatter plots of (a) the number and (b) mean size of prey in the guts in relation to total length of silver hake during 1992 (●) and 1998 (○) and Atlantic cod (△) in 1992, collected between 0800 and 0000 hours. A random selection of 50% of the data is presented.

consumed by the smallest silver hake larvae (<3.5 mm) were bi-modally distributed with regard to size, and ranged from 0.1 to 0.15 and 0.4 to 0.6 mm. When silver hake larvae were *c.* 7 mm L_T , >80% of the food items in their guts were >0.6 mm. In contrast, prey size increased more gradually with L_T for Atlantic cod larvae. For example, between 3 and 5 mm 60% of the numbers of items in their guts were 0.15–0.25 mm long. Likewise, while small prey items gradually diminished in importance in the diets of Atlantic cod larvae with increasing L_T , even at the largest sizes larvae continued to feed on a broad range of developmental stages of copepods. In contrast, small prey items (<0.4 mm) virtually disappeared from the diet of silver hake by 5 mm L_T .

NICHE WIDTH AND SELECTIVITY

During November and December of 1992, silver hake and Atlantic cod larvae exhibited very different patterns in their feeding-niche widths (I_{DB}) with size, while the I_{DB} patterns for silver hake were generally similar during 1992 and 1998 (Fig. 5). During both years, the I_{DB} of silver hake larvae declined with L_T , although the I_{DB} in 1998 was on average broader in 1992, but did not differ significantly between 3 and 11 mm L_T where data overlapped. In 1998, I_{DB} declined from 0.30 at 2–3 mm to 0.05 at 6 mm L_T , and remained relatively constant and narrow until 10–11 mm L_T . The I_{DB} of silver hake in 1992 declined more rapidly from *c.* 0.24 at 3 mm (the smallest size class captured) to <0.05 at 4 mm L_T . From 4 to 13 mm L_T , I_{DB} remained narrow. There was a larger increase at 10–11 mm for silver hake examined from 1998 than from 1992. In contrast to the pattern of relatively narrow I_{DB} in silver hake (between 0.03 and 0.08), the I_{DB} of Atlantic cod was on average broader (0.12 to 0.16), but the

TABLE IV. Relationships between prey size (y , mm) and number of prey in the gut (y) and total length (x , mm) of silver hake and Atlantic cod larvae collected at the Western Bank in November 1992 and October 1998. Relationships are based on mean prey size for fishes with more than three items in their gut. Restricted regressions are based on fishes sampled between 2000 and 2359 hours EST. Values in parentheses are s.e. of the coefficient estimates

	Full data	n	r^2	Restricted data	n	r^2
Prey size						
Silver hake 1992	$y = 0.620 (0.028) + 0.023(0.004)x$	209	0.14	$y = 0.60(0.036) + 0.027(0.005)x$	73	0.31
Atlantic cod 1992	$y = 0.049 (0.013) + 0.046 (0.003)x$	668	0.33	$y = -0.024(0.02) + 0.061(0.004)x$	231	0.48
Silver hake 1998	$y = 0.423(0.019) + 0.045(0.003)x$	752	0.25	$y = 0.53(0.016) + 0.039 (0.002)x$	308	0.50
Prey items						
Silver hake 1992	$y = -4.71(0.852) + 1.59(0.117)x$	227	0.45	$y = -4.50(1.14) + 1.66 (0.15)x$	75	0.62
Atlantic cod 1992	$y = 5.59(1.360) + 1.63(0.272)x$	683	0.04	$y = 9.43(2.55) + 1.34(0.527)x$	234	0.02
Silver hake 1998	$y = -6.10 (0.369) + 1.81 (0.058)x$	877	0.54	$y = -7.30(0.49) + 2.53(0.069)x$	314	0.81

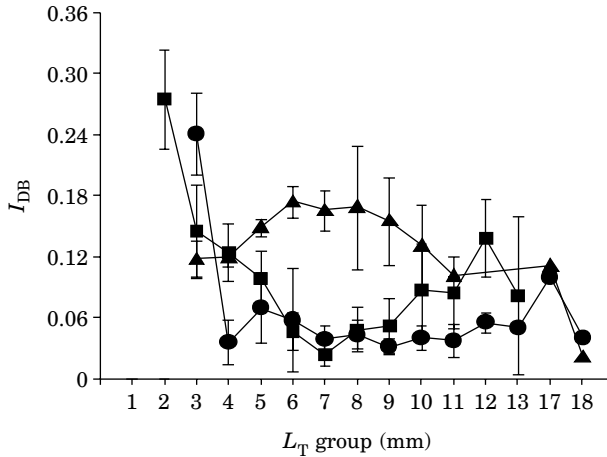


FIG. 5. Diet breadth index (niche width) over 1 mm total length groups from 1 to 18 mm, estimated as the s.d. of the \log_{10} of prey lengths (Pearre, 1986) for silver hake larvae collected in 1992 (■) and 1998 (●) and Atlantic cod (▲) collected in 1992. Only individuals of the given L_T class with three or more items in their guts were used in the analysis.

pattern was non-linear increasing in larvae from 3 to 6 mm before declining at larger L_T (Fig. 5).

Changes in larval feeding ecology could also be assessed using cumulative frequency distributions of developmental stages of copepod prey items [Fig. 6(a), (c), (e)] in diets, which showed large differences between the two fish species. In both years, silver hake larvae initially fed on small, early developmental stages of copepods, but also on later stages of copepods. With increasing L_T , small prey items 'dropped out' of the diet and silver hake switched almost exclusively to larger prey, maintaining a narrow niche width. In contrast, Atlantic cod larvae exhibited the commonly assumed pattern of slowly replacing small items for large items with increasing body size. The cumulative frequency distributions clearly showed how the niche width could be a non-linear function of L_T . As larvae began to feed both on large and small items, the variance in the mean size increased, and then declined as the switch to larger prey was completed.

The relative concentration of prey items in the water column revealed more about the difference in the feeding ecology of these two species. Values of P_i [Fig. 6(b), (d), (f)] illustrated considerable ontogenetic and temporal variability by silver hake larvae. During autumn 1998, silver hake were less selective than in winter 1992. In autumn, small silver hake larvae selected nauplii, but rapidly shifted at 5 mm L_T to selecting copepodids. In the winter of 1992, silver hake were more selective, feeding mostly on adult copepods and late stage copepodids. In contrast, developing Atlantic cod larvae showed a gradual shift in selectivity from small nauplii to copepodids. The increase in selectivity by silver hake larvae, presumably following the autumn plankton bloom (McLaren & Avendaño 1995), suggested that both the size-frequency distribution and species composition affected the diets of silver hake larvae.

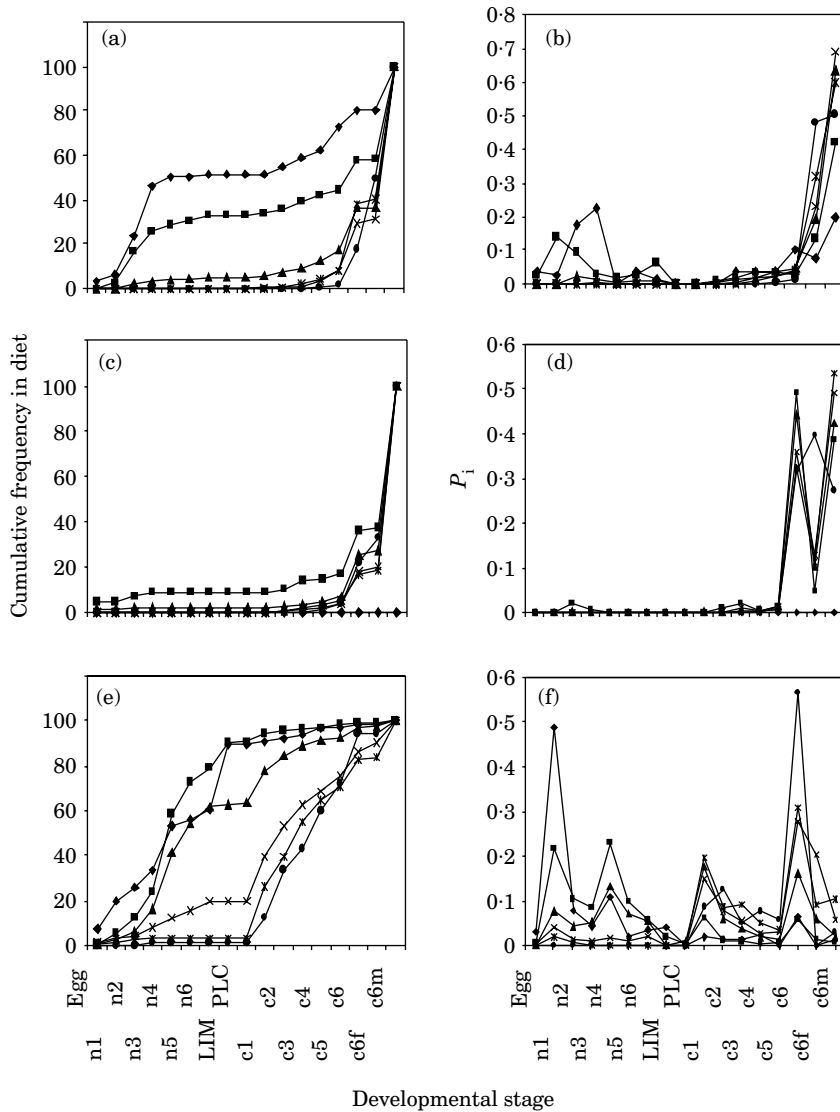


FIG. 6. Cumulative frequency distribution of prey items in the diets of silver hake in (a) 1998 and (c) 1992 and (e) Atlantic cod in 1992, and Chesson's (1978) index of prey selectivity (P_i) for silver hake in (b) 1998 and (d) 1992 and (f) Atlantic cod in 1992 for 16 prey types of nominal size order (see Table II), in relation to fish total length [<3 (\blacklozenge), 3 to 5 (\blacksquare), 5 to 7 (\blacktriangle), 7 to 9 (\blacktriangledown), 9 to 11 (\ast) and >11 (\bullet) mm].

DISCUSSION

Silver hake and Atlantic cod larvae exhibited distinctly different patterns of feeding selection and niche width. Silver hake larvae were highly selective with a relatively narrow and consistent feeding-niche width that changed sharply with increasing larval size. This differs from many studies that have shown that larval fish begin feeding on small prey items and gradually switch to larger

prey items with increasing body size (body length and jaw length), but usually continue to include small prey items in their diets (McLaren & Avendaño, 1995), resulting in a nearly constant feeding-niche width (log scale) through development (Pearre, 1986). The pattern observed for silver hake, however, is similar to that described for other merluccid hake species (de Chiechowski & Weiss, 1974; Sumida & Moser, 1980; Coates-Markle, 1982; Cass-Calay, 2003). Atlantic cod larvae exhibited the more usual feeding strategy, beginning to feed on naupliar stages and proceeding to larger and larger prey items as they grew. Over the same L_T classes as silver hake, however, the feeding niche width of Atlantic cod larvae was non-linear, inconsistent with the predictions of Pearre (1986), but similar to the findings for blue whiting *Micromesistius poutassou* (Risso) in the eastern Atlantic (Gonzalez-Quiros & Anadon, 2001).

Despite the different feeding strategies, both silver hake and Atlantic cod fed on just a few of the total number of species present on the Western Bank. Only four species dominated each of their diets. The largest differences were related to the developmental stages that made up the diets of each species. Silver hake selected for larger, later developmental stages at much smaller L_T than Atlantic cod larvae. Based on the isometric relationships for silver hake and Atlantic cod, Atlantic cod larvae 5–7 mm L_T had a jaw length of that of a 3–5 mm silver hake. Yet, the difference in jaw length at size is not entirely responsible for the differences in prey size. For example at a jaw length of 1 mm, Atlantic cod fed on prey items of *c.* 0.2 mm in width, while silver hake ate animals >0.3 mm in width. This has clear implications for the differences in feeding ecology between the two species, creating the opportunity for silver hake to take advantage of the larger prey items not consumed by Atlantic cod, or other species that are spawned on the Western Bank.

Apparent selectivity for particular size classes or species may reflect the ease of capture, the apparent size (Luo *et al.*, 1996), or energetic benefits to maximize energy intake and minimize energy expenditure (Werner & Hall, 1974). The hypothesis that the selection exhibited by silver hake larvae, and the difference in selection between silver hake and Atlantic cod are passive responses to the presentation of food items cannot be rejected. The similarity in the diets, in terms of species selected and the pattern of selectivity of silver hake given the large (order of magnitude) differences in mean prey concentration between the two time periods, however, suggests that silver hake larvae feed on a very different part of the available prey spectrum than the co-occurring Atlantic cod larvae. At the same time, the fact that Atlantic cod feed on small prey items in a variety of habitats (Kane, 1984; Thompson & Harrop 1991; Pepin & Penney, 1997) suggests that regardless of availability, resulting selection by Atlantic cod is for smaller prey items.

Feeding theory also predicts that under food-limited conditions larval fishes should increase their feeding niche by ingesting a wider range of prey sizes or less nutritionally valuable prey (Werner & Hall, 1974; Bartell, 1982). Despite an order of magnitude decline in prey abundance between October 1998 and December 1992, there was no evidence that silver hake larvae increased their feeding niche. In fact, silver hake exhibited a wider niche width over the 3–11 mm L_T classes from autumn of 1998 as compared to winter of 1992. Moreover, niche width was narrower during winter of 1992 despite the fact that other

prey species and developmental stages were available and used by Atlantic cod larvae, some of which (*Pseudocalanus* spp.) are known to store large quantities of energy rich lipids (Reiss *et al.*, 1999). For example, while *Pseudocalanus* spp. increased slightly as a percentage of the diet (from 5 to 15% of gut content), *Clausocalanus* spp. increased from 12 to 43% of the diet of silver hake between October and December. *Paracalanus parvus*, another species that is believed to be easy to capture and nutritious (McLaren & Avendaño, 1995) declined from 54 to 26% of the diet. In addition, no significant change in the mean prey size was observed between October and December as might be expected if food were limiting. One reason why an increase in the niche width may not have been observed was that two disparate time periods, with differing light or ancillary environmental conditions were compared. On the other hand, the remarkable similarity in diets of silver hake between the time periods, and the distinct and consistent pattern in feeding niche width with L_T , suggests that silver hake may not be food limited on the Western Bank, and that other factors are critical in affecting their early life history.

On the Scotian Shelf, silver hake are common in the plankton from early July to December, while Atlantic cod are primarily present in early spring and early winter (Taggart *et al.*, 1996; Jeffrey & Taggart, 2000; Reiss *et al.*, 2000). These two times represent different periods of the seasonal plankton cycle. During spring and early winter, the plankton is dominated by small copepods, either developmental stages or smaller species (McLaren *et al.*, 1989), while the summer is dominated by later stages of larger copepods and a more developed plankton community. It is interesting to speculate that the differences in feeding ecology represent different adaptations to the plankton community during the peak spawning periods of these two species. Of course it is not possible to test such an hypothesis, although the observations that in almost all systems examined *Merluccius* spp. eat very large prey at small sizes lends some credibility to this hypothesis (de Chiechowski & Weiss, 1974; Sumida & Moser, 1980; Cass-Calay, 2003).

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