

Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound*

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ABSTRACT: Sand lance larvae consumed phytoplankton and various developmental stages of the copepods *Temora longicornis*, *Acartia hudsonica* and *Pseudocalanus* sp. Their diet changed with ontogeny: small larvae consumed phytoplankton and larger larvae ate copepods of increasingly older developmental stages. Samples taken during daylight indicated that the larvae have a gut capacity of approximately 0.56 % of their body dry weight. Laboratory studies conducted with live larvae indicated non-selective feeding on copepod nauplii, but in the field, Ivlev indices indicated selection for *T. longicornis* nauplii and against *A. hudsonica* nauplii. Larger larvae selected for *T. longicornis* copepodites and against *A. hudsonica* copepodites and females, but as they approach metamorphosis, they began to select for *A. hudsonica* females. The feeding behavior of small larvae is passive, but becomes more aggressive as the larvae mature. Biomass consumed increased with increased prey density and water temperature. Clearance rates for larvae at 7 °C in the laboratory were 0.02, 0.05, 0.48 and 3.2 l d⁻¹ for 4.5 to 5.0, 6 to 7.0, 10 to 11.0, and 21 mm larvae, respectively. Calculations of the predatory impact of sand lance larvae on copepod nauplii indicate that they are insignificant consumers taking a maximum of 13.4 % of the copepod production per day.

INTRODUCTION

There is an important predator-prey relation between larval fish and zooplankton. In order to fully understand this interaction it is important to determine the species composition of the larval diet, the availability of the prey, and the feeding rate of the larvae in relation to prey density and environmental conditions. Combining this information with field estimates of larval and prey density, one can estimate the impact larvae have on the population dynamics of the prey species.

This paper describes the feeding ecology of larvae of the American sand lance *Ammodytes americanus* in relation to its food supply in Long Island Sound. This species was chosen because it is the most abundant fish larva in the Sound during the winter, comprising over 85 % of the ichthyoplankton (Monteleone 1984). Sand lance larvae are present in the Sound from late November through May, during which period the water temperature ranges from -1 to 10 °C (Mon-

teleone 1984). Larvae are 3 to 4 mm at hatching (Richards 1965) and complete metamorphosis by 30 to 40 mm (Reay 1970). During their larval history in Long Island Sound, prey availability ranges from low density conditions in December through a time of maximum zooplankton densities during February through April.

In this paper we discuss various aspects of the feeding ecology of sand lance larvae including a description of their diets, feeding environment, density and growth. Feeding selectivity, feeding behavior and ingestion rates were also examined in the laboratory. Finally, estimates were made of their potential impact on the zooplankton population in Long Island Sound.

MATERIALS AND METHODS

Sand lance larvae were collected during daylight at 2 stations in central Long Island Sound (Fig. 1). Water depth at Stn A was 20 m, and at Stn B, 37 m. Samples were taken at Stn A from March through May 1982, and at B from March 1982 through May 1983. One tow

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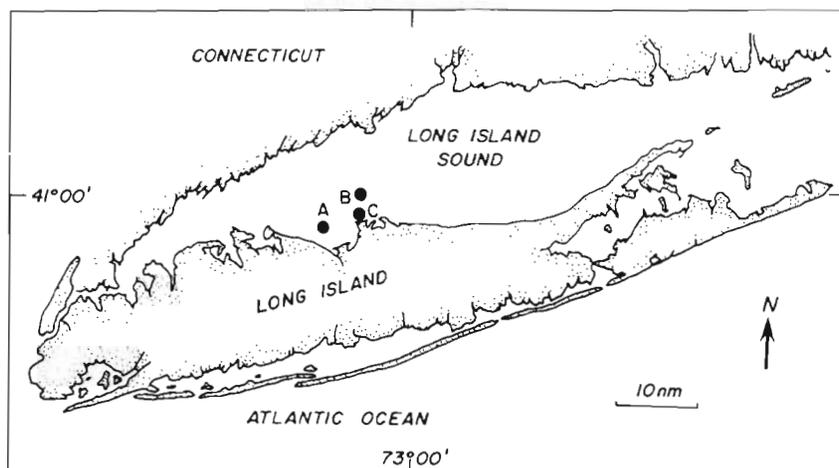


Fig. 1. Map of Long Island Sound. Stns A and B were sampled during 1982-83 and Stn C in 1985

was also taken at dawn on 8 May 1985 at Stn C. The larvae were collected with 0.75 and 1.0 m diameter plankton nets with 505 and 363 μm mesh, respectively. Towing speed was 2 to 3 knots. TSK flow meters were employed to measure the volume of water filtered. In 1982, step oblique tows were taken at A and B by lowering the net to 10 m and then towing for 1 min at 1 m intervals to the surface. Tows were taken for 5 min at discrete depths of 0 to 1, 5, and 15 m at Stn B in 1983. All samples were preserved in 5 to 10 % buffered formalin.

Temperature and salinity were measured at discrete depths of 1, 3, 5, 10, 15, 20, 30, and 37 m at Stn B with a Beckman RS-5 Induction Salinometer. Water samples were taken at the same depths with a Jabsco Water Puppy pump and a 1.9 cm i.d. hose. From each depth 100 ml was filtered through a GF/C filter for chlorophyll analysis, and 3 to 6 l were filtered through a 64 μm Nitex screen and preserved in 5 to 10 % buffered formalin for enumeration of copepod life stages.

All sand lance larvae were removed from the samples and densities estimated. The notochord length of prolarvae and standard length of postlarvae (both will be referred to as length) was measured to the nearest 0.1 mm under a dissecting microscope at 10 \times . Fifty larvae (or the entire sample, whichever was smaller) were measured.

Dry weights of 35 randomly chosen, measured larvae were taken to obtain a length-weight relation. Larvae were placed on pre-weighed aluminum foil, and dried for a minimum of 24 h at 60°C, then weighed on a Cahn Electrobalance to the nearest 0.1 μg .

Ten larvae from each sample (or the whole sample, whichever was smaller) were dissected for gut content analysis using a technique similar to Last's (1978). A total of 175 larvae were examined. The entire gut was separated from the larva by teasing it free with a dissecting pin, the gut was placed in glycerin, opened,

and the contents identified and counted to species and stage of development. The total amount of food consumed was converted to dry weight by using dry weights of various developmental stages of prey items reported in Harris & Paffenhöfer (1976), Durbin & Durbin (1978), and Peterson (unpubl.). The gut contents were also compared to the prey items in the field and Ivlev (1961) electivity indices were calculated.

For laboratory studies of feeding rates, behavior, and feeding selectivity, larvae were collected with a 0.75 m diameter, 363 μm plankton net and transported to the laboratory in an insulated container. Live zooplankton was collected with a 0.5 m diameter, 64 μm mesh net and transported in a similar manner. The larvae were fed copepod nauplii and copepodites while maintained in 6 l battery jars at temperatures of 2 and 7°C on a 10:14 light:dark cycle. During the feeding experiments, the larvae were kept individually in 200 to 1000 ml glass containers with 64 μm filtered seawater. The containers were covered on the sides and bottom with green or brown paper to simulate the dark background of their natural environment.

Selective feeding experiments were conducted in the laboratory by offering known numbers of *Temora longicornis* and *Acartia hudsonica* (formerly *Acartia clausii*) nauplii to individual larvae ranging from 7 to 11.5 mm. After feeding for 24 h, the larvae were removed from the containers, the remaining nauplii filtered from the water, preserved in 5 % formalin and counted.

Feeding rates for larvae 4.5 to 21 mm long were determined in the laboratory. Larvae of size groups 4.5 to 5.0, 6.0 to 7.0 and 10.0 to 11.0 mm were placed individually into 200 and 1000 ml containers with known numbers of a mixture of *Temora longicornis* and *Acartia hudsonica* nauplii (results showed neutral selection between species in the laboratory). A larger larva of 21 mm was fed known amounts of a mixture of nauplii, copepodites and adults of *T. longicornis* and

A. hudsonica in 5 l glass containers. After feeding for 24 h, the larvae were removed, the remaining prey items filtered from the water, preserved in 5 % formalin, and counted. The dry weight of food consumed was calculated.

The predatory impact sand lance larvae have on copepod populations was calculated from the formula:

$$I = \sum_{i = \min}^{i = \max} V_i N_i D_i \quad (1)$$

where I = the total number of nauplii consumed each day by the sand lance larval population; V = the volume cleared by a larva ($l d^{-1}$); N = the concentration of nauplii in the field (nauplii l^{-1}); D = the density of the larvae in the field (no. m^{-3}); $i = 1$ mm intervals from the minimum to maximum length larva present.

RESULTS

Density and growth of larvae

Sand lance larvae were present in the water column from March 1982 when sampling began, through May 1982 and again from December 1982 through April 1983. The larvae were more abundant at 5 and 15 m and least abundant at the surface (Table 1). The monthly mean and range of standard lengths of sand lance larvae increased as the season progressed (Fig. 2). In December 1982 the larvae had a mean length of 5.8 mm (range 3 to 8 mm). By April 1983, the mean length had increased to 18.6 mm (range 8 to 35 mm). Small larvae were present from December through March, indicating that egg hatching occurs for several months.

Even though the hatching season is prolonged, most of the prolarvae were collected in December. A well defined cohort of larvae was evident during the 1982–83 growth season. Growth of the larvae was esti-

Table 1. *Ammodytes americanus*. Number of larvae per m^3 at 3 depths during Jan, Mar and Apr 1983 at Stn B. * Densities $< 0.005 m^{-3}$

Date	Depth		
	1 m	5 m	15 m
12 Jan 83	1.20	3.58	3.41
26 Jan 83	*	3.80	2.76
3 Mar 83	*	0.60	0.30
16 Mar 83	0.00	1.63	0.33
24 Mar 83	*	0.82	0.30
7 Apr 83	0.03	0.77	0.03
11 Apr 83	0.57	0.02	0.05
21 Apr 83	0.03	0.44	0.04

mated from this cohort (Fig. 3). Because of prolonged hatching, monthly means were calculated using only the largest 25 % of the larvae collected on a given date. This modification eliminated recently-hatched larvae, thus giving a more accurate measurement of growth rate. From December to January, the larvae grew 2.65 mm; from January to March, 5.22 mm (or an average of 2.61 $mm mo^{-1}$); and from March to April, 6.88 mm.

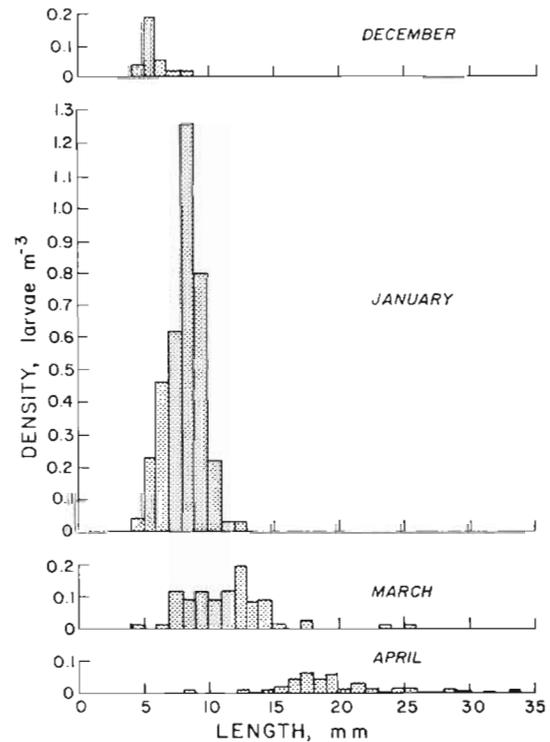


Fig. 2. *Ammodytes americanus*. Length-frequency distribution of larvae collected in oblique tows from 1 to 10 m during Dec 1982 and in horizontal tows at 5 m during Jan, Mar and Apr 1983 at Stn B

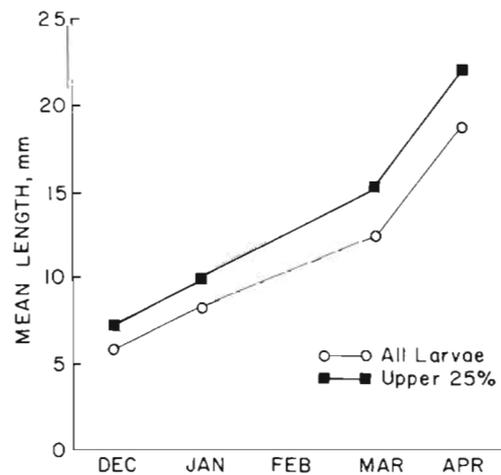


Fig. 3. *Ammodytes americanus*. Growth of larvae in length during winter and spring 1982–83

The growth rate in terms of length was converted to dry weight using a length-weight formula derived from the length-weight relation illustrated in Fig. 4. The resulting formula was expressed as:

$$\text{Log } W = 2.91 \text{Log } L - 0.245 \quad (2)$$

where W = dry weight of the larvae in μg ; L = length of the larvae in mm. The growth of the largest 25% larvae, in $\mu\text{g d}^{-1}$, was 0.31 for December to January, 0.56 for January to March, and 5.20 for March to April. The instantaneous specific growth rates in terms of dry weight for these time periods were 0.03, 0.02 and 0.04 d^{-1} .

Feeding environment

During the larval season, the water temperature ranges from approximately 10°C to probably a minimum of 0°C during February. The water column in Long Island Sound is isothermal from October through April (Peterson 1986). At the onset of the larval season in December, the larvae were abundant but their food environment was poor, containing limited amounts of both phytoplankton and zooplankton (Fig. 5). The spring bloom in Long Island Sound does not start until mid-February to mid-March (Fig. 5; Riley 1956, 1967, Riley & Conover 1956, Vishniac & Riley 1961, Peterson 1985). This bloom is followed approximately 1 mo later by a significant increase in

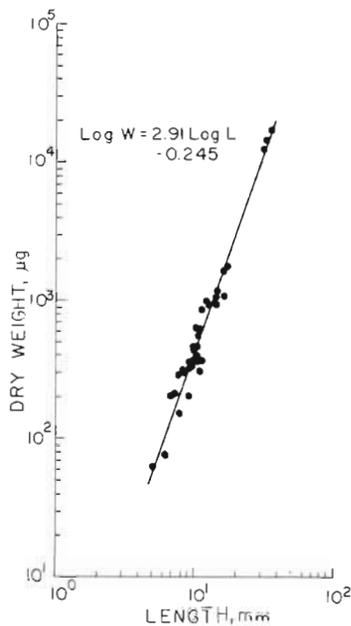


Fig. 4. *Ammodytes americanus*. Length(L)-dry weight(W) relation. $N = 35$

copepod biomass. The 3 most common species in the Sound during that time of year are *Temora longicornis*, *Acartia hudsonica* and *Pseudocalanus* sp., which were most abundant between 5 and 15 m (Peterson 1985).

Gut content analyses

The major food items of sand lance larvae consisted of phytoplankton and various developmental stages of copepods (Table 2). Larvae < 8 mm were either empty or contained only phytoplankton. Larvae 8 to 11.9 mm consumed copepod nauplii of *Temora longicornis*, *Acartia hudsonica* and *Pseudocalanus* sp. Larvae 12 to 18.9 mm consumed both nauplii and copepodites,

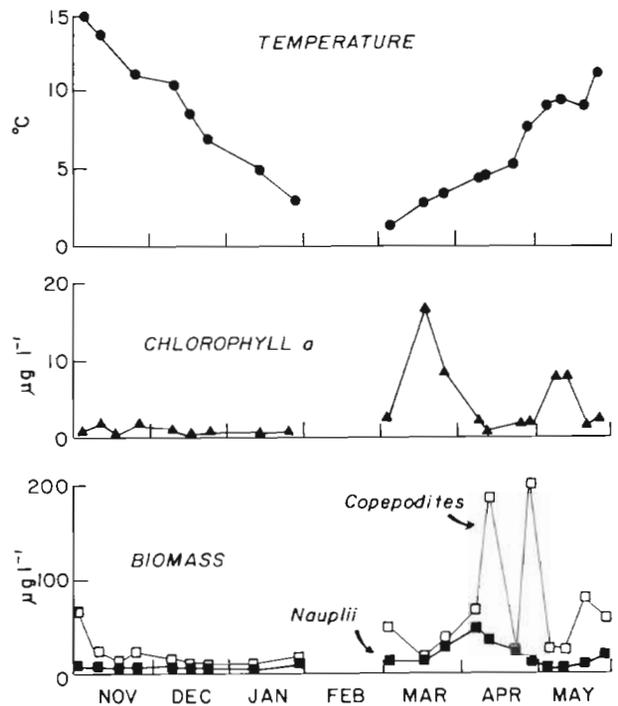


Fig. 5. Temperature, chlorophyll a concentrations and biomass (dry weight) of all species of copepod nauplii and copepodites during winter and spring 1982-83 at depth 5 m at Stn B

whereas larvae 19 to 23.9 mm consumed a greater weight of copepodites and *A. hudsonica* adults than of nauplii. Those ≥ 24 mm fed almost exclusively on adult *A. hudsonica*. Minor items in the diet of sand lance larvae include copepod, invertebrate and fish eggs, and barnacle cyprids. The larvae collected at dawn on 8 May 1985 were empty and were not included in Table 2.

Average total dry weight of the gut contents for larvae of different lengths was calculated for those larvae whose guts were not empty (Fig. 6). The aver-

age dry weight of the gut contents in μg (W_g), vs the length of the larvae in mm (L) followed a logarithmic function:

$$\text{Log } W_g = 4.51 \text{Log } L - 4.64 \quad (3)$$

Using the length-weight relation and the weight of the gut contents vs the length of the larvae, the percent of the larval body weight consisting of gut contents was calculated for 1 mm size classes of larvae. They ranged from 0.05 to 2.64 % with an average of 0.56 %. There were no obvious trends in the relation of percent larval body weight consisting of gut contents versus the total dry weight of the larvae.

Feeding selectivity

Feeding selectivities on different species of copepods were calculated using the Ivlev index. The electivity indices for nauplii showed that in 1983, the larvae selected for *Temora longicornis* and against *Acartia hudsonica* (Table 3a). In general, the larvae selected for *T. longicornis* copepodites (Table 3b). During March and early April, *A. hudsonica* adult females were strongly selected against, but were positively selected for by the end of April. In selective feeding studies conducted in the laboratory, using copepod nauplii, the larvae did not show a preference for either *T. longicornis* or *A. hudsonica* nauplii (Fig. 7).

Table 2. *Ammodytes americanus*. Gut contents of 165 larvae collected in Long Island Sound. Larvae with empty guts were not included in the calculations. Data are average dry weight (μg) of prey items for each size group. * Weights < 0.005 μg ; ** unknown weights. N = naupliar stage and C = copepodite stage of copepods. 'Acartia adults' are not differentiated by sex so dry weight is an average. Weights for prey items were taken from Harris & Paffenhöfer (1976), Durbin & Durbin (1978) and Peterson (unpubl.)

Size in mm	< 8.0	8-11.9	12-18.9	19-23.9	≥ 24
Number of larvae examined	15	37	84	16	13
% with phytoplankton	80	22	0	0	0
% empty	20	13	2	0	0
<hr/>					
<i>Temora</i> egg (0.1 μg)			0.23	0.05	*
<i>Temora</i> N1-5 (0.25)		0.52	0.90	0.47	
<i>Temora</i> N6 (0.7)		0.15	0.31	0.76	0.03
<i>Temora</i> C1 (1.2)			0.57	1.08	
<i>Temora</i> C2 (2.3)			0.46	1.36	
<i>Temora</i> C3 (4.2)			0.30	1.34	
<i>Temora</i> C4 (7.7)					
<i>Temora</i> C5 (13.2)				1.76	0.94
<i>Temora</i> adult (28.0)					4.00
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<i>Acartia</i> egg (0.1)				0.05	*
<i>Acartia</i> N1-5 (0.25)		0.07	0.13	0.06	
<i>Acartia</i> N6 (0.3)		0.01	0.01		
<i>Acartia</i> C1 (0.6)			0.07		0.17
<i>Acartia</i> C2 (0.9)			0.04	0.02	
<i>Acartia</i> C3 (1.5)			*	0.60	0.13
<i>Acartia</i> C4 (2.4)			0.75	0.48	
<i>Acartia</i> C5 (4.3)			1.35		2.10
<i>Acartia</i> male (5.8)			0.50	0.77	
<i>Acartia</i> female (9.6)			1.65	10.88	51.20
<i>Acartia</i> adult (7.7)			2.50	3.22	29.23
<hr/>					
<i>Pseudocalanus</i> N1-5 (0.25)		0.02	0.03	0.10	
<i>Pseudocalanus</i> N6 (0.3)				0.02	
<i>Pseudocalanus</i> C3 (4.6)			0.04		
<i>Pseudocalanus</i> adult (16.7)			0.48		
<hr/>					
<i>Centropages</i> C4 (7.7)				0.17	
<i>Centropages</i> male (20.0)					0.71
<hr/>					
Unidentified N1-5 (0.25)				0.02	
Unidentified C1-5 (**)			**	**	
Unknown copepod egg (0.1)		0.01	0.01		
Invertebrate egg (**)		**	**		
Fish egg (**)			**		**
Barnacle cyprid (10.0)					0.71

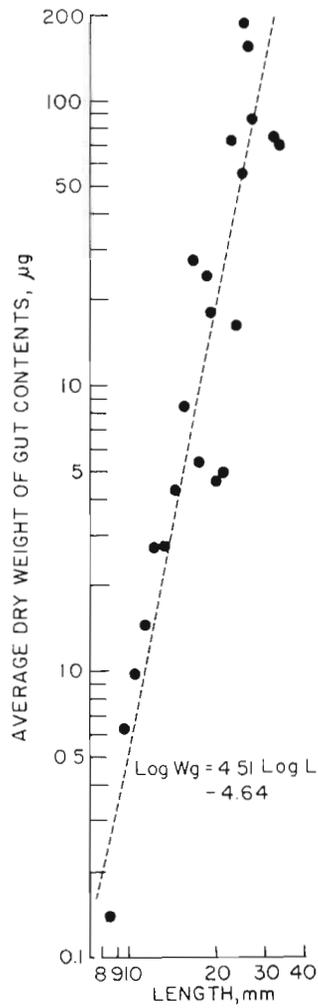


Fig. 6. *Ammodytes americanus*. Average dry weight of gut contents (W_g) vs length of larvae (L)

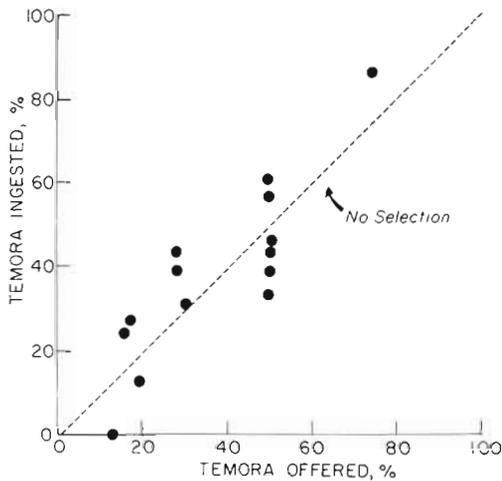


Fig. 7. *Ammodytes americanus*. Selective feeding experiment in the laboratory using nauplii of *Temora longicornis* and *Acartia hudsonica*. Larvae ranged from 7 to 11.5 mm, naupliar densities were 5 to 200 l^{-1} and temperature was 7°C. The line of slope equal to 1 is line of no selection

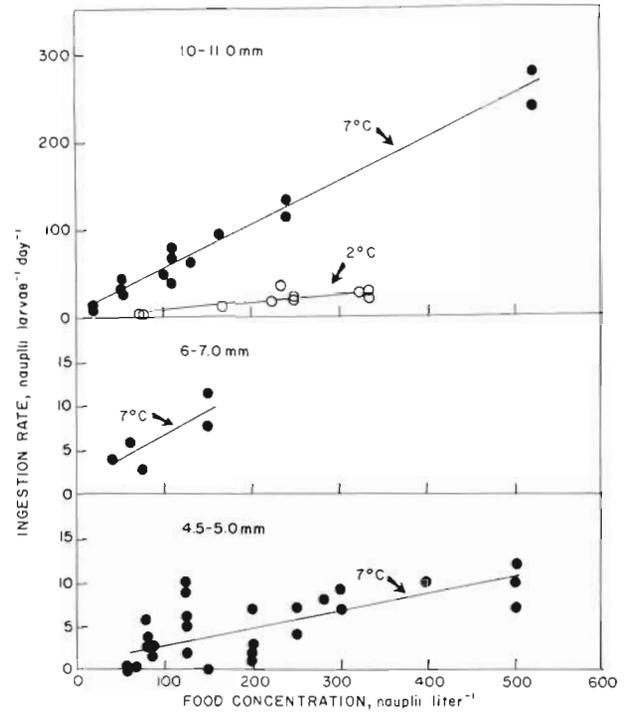


Fig. 8. *Ammodytes americanus*. Ingestion rates of individual larvae of size groups 4.5 to 5.0, 6 to 7.0, and 10 to 11.0 mm in length in the laboratory. Larvae 10 to 11.0 mm were studied at 2 temperatures. All larvae were fed a mixture of *Temora longicornis* and *Acartia hudsonica* nauplii

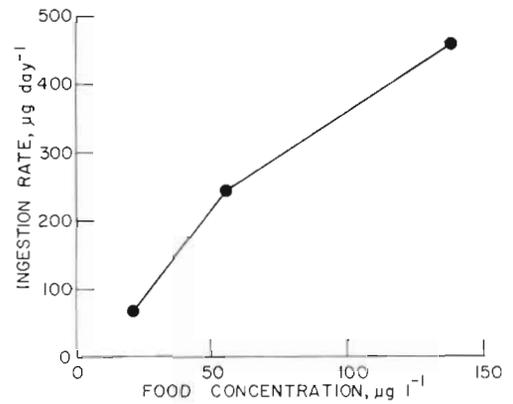


Fig. 9. *Ammodytes americanus*. Ingestion rate of 21 mm larva. The prey items consisted of naupliar through adult stages of *Temora longicornis* and *Acartia hudsonica*

Feeding behavior

Observations of live larvae in the laboratory showed that their feeding behavior changed with ontogeny. Larvae less than 9 mm remained in a head-down position most of the time, swimming only occasionally. Feeding was not observed. Larvae greater than 10 mm were more active swimmers. They assumed an S-pos-

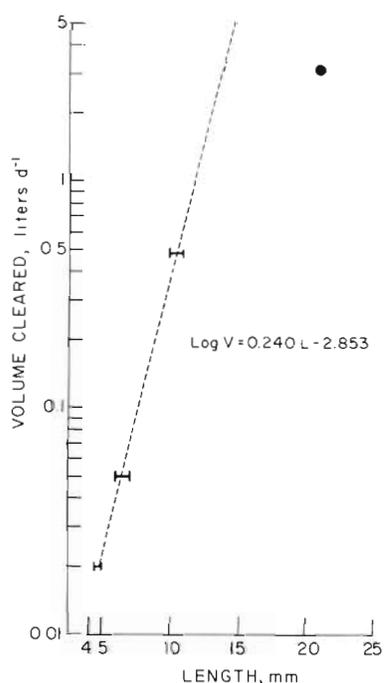


Fig. 10. *Ammodytes americanus*. Volume cleared (V) for 3 size groups 4.5 to 5.0, 6 to 7.0, and 10 to 11.0 mm larvae (L) fed copepod nauplii. Closed circle indicates volume cleared for the 21 mm larva fed naupliar through adult stages

ture while maintaining their orientation to a moving prey, never struck at a prey more than once, and often seemed only to observe a potential prey item.

Feeding rates

Feeding rates were directly related to the size of the larvae, the water temperature, and the concentration of nauplii (Fig. 8). At 7°C, larvae 4.5 to 5.0 mm consumed 2 to 11 nauplii d^{-1} at prey densities of 50 to 500 l^{-1} . Larvae 6 to 7.0 mm consumed 4 to 10 nauplii d^{-1} at prey densities of 40 to 150 l^{-1} . Larvae 10 to 11.0 mm consumed 15 to 265 nauplii d^{-1} at prey densities of 20 to 525 nauplii l^{-1} . At 2°C, prey consumption by larvae 10 to 11.0 mm was reduced to 5 to 30 nauplii d^{-1} at prey densities of 65 to 325 nauplii l^{-1} . An asymptotic ingestion rate was not reached over the domain of the concentrations of nauplii used.

When offered a mixture of prey sizes, including nauplii, copepodites and adults of *Temora longicornis* and *Acartia hudsonica*, the 21 mm larva consumed organisms weighing from 0.25 to 13.2 μg dry weight. In general, the dry weight of food consumed seems to increase linearly with the concentration of food offered over the domain 20 to 140 $\mu g l^{-1}$ (Fig. 9).

Table 3. *Ammodytes americanus*. Ivlev electivity indices. Tl: *Temora longicornis*; Ah: *Acartia hudsonica*; Ps: *Pseudocalanus* sp. Positive numbers = selection for a species; negative numbers = selection against; zero = neutral selectivity. All larvae taken at Stn B. (A) Selectivity among different species of nauplii. (B) Selectivity of larger larvae among copepodites and adult females of *A. hudsonica* and *T. longicornis*

A. Nauplii													
Date	Depth (m)	Mean length (mm)	Avg nauplii in gut	% ingested			Nauplii in water (l^{-1})	% in water			Ivlev index		
				Tl	Ah	Ps		Tl	Ah	Ps	Tl	Ah	Ps
26 Jan 83	5	8.2	0.3	100			34.5	10	90		0.82	-1.00	
3 Mar 83	5	13.5	11.0	82	18		42.8	20	80		0.61	-0.63	
3 Mar 83	15	13.5	0.7	100			37.9	14	84	2	0.75	-1.00	-1.00
24 Mar 83	5	13.5	5.6	90	5	5	100.8	36	60	4	0.42	-0.85	0.11
24 Mar 83	15	13.4	8.0	91	9		123.7	43	53	4	0.35	-0.71	-1.00
21 Apr 83	5	20.3	7.2	65	11	24	105.5	10	87	3	0.73	-0.78	0.78
B. Copepodites and adult female <i>Acartia hudsonica</i>													
Date	Depth (m)	Mean length (mm)	Avg copepodite & adult in gut	% ingested			Copepodites and adults in water (l^{-1})	% in water			Ivlev index		
				Tl	Ah	Adult Ah		Tl	Ah	Adult Ah	Tl	Ah	Adult Ah
3 Mar 83	5	13.5	1.4	86	14		8.5	2	68	29	0.95	-0.66	-1.00
3 Mar 83	15	13.5	1.3	54	46		7.5	13	77	10	0.61	-0.25	-1.00
24 Mar 83	5	13.5	1.6	62	38		15.5	5	90	5	0.85	-0.41	-1.00
24 Mar 83	15	13.4	2.5	100			17.9	18	77	5	0.69	-1.00	-1.00
7 Apr 83	5	17.5	0.8	75	25		30.7	29	67	4	0.44	-0.46	-1.00
11 Apr 83	15	17.1	7.7	8	32	60	31.7	63	32	4	-0.77	0.00	0.88
21 Apr 83	5	20.3	3.1	84	13	3	5.9	34	54	12	0.42	-0.61	-0.60
21 Apr 83	10	27.1	2.2	9	23	69	34.2	35	56	9	-0.59	-0.42	0.77
29 Apr 83	1	25.5	10.4	3	6	91	2.1	0	62	38	1.00	-0.82	0.41

The slopes of the lines in Fig. 8 and 9 are equivalent to the volume of water cleared by the larvae, in units of $l d^{-1}$. For larvae 4.5 to 5.0, 6 to 7.0, 10 to 11.0, and 21 mm, the slopes at 7°C were 0.02, 0.05, 0.48, and $3.2 l d^{-1}$, respectively. Clearance rates were plotted against the length of the larvae (Fig. 10). The volume cleared for the 3 size classes of smaller larvae followed a logarithmic function:

$$\text{Log } V = 0.240L - 2.853 \quad (4)$$

where V = volume of water cleared in $l d^{-1}$; L = length of the larvae in mm. The volume cleared for the 21 mm larva fell below the predicted value.

The frequency of gut fillings under natural conditions was estimated using the ingestion rate data from the laboratory and estimates of prey densities in the field. At prey densities of $25 \mu g$ dry weight of nauplii l^{-1} (approximately 100 nauplii l^{-1} ; typical of Long Island Sound during March-April) a 10.5 mm larva at 7°C would consume approximately $12 \mu g$ of prey biomass d^{-1} . The gut contents of field-collected larvae indicated an gut capacity of $0.92 \mu g$ (from Eq. 3). These larvae would, therefore, fill their guts 13 times d^{-1} . Ryland (1964) suggested that sand lance larvae feed only during daylight, and the present study reinforces his hypothesis. Assuming 10 to 12 h of daylight, larval gut evacuation times would range from 45 to 55 min. These times could be somewhat longer if the estimates of gut capacity is biased downward due to the possibility of some regurgitation during collection.

Impact of larvae on zooplankton populations

Variables influencing the feeding rate of sand lance larvae (size of larvae, temperature, and food concentration) were examined, and the impact that the larvae

have on copepod nauplii was calculated. Calculations were carried out for several days in March. During that month, copepod nauplii and sand lance larvae are abundant, so it is the time when the larvae are expected to have the greatest impact on the copepod nauplii. It is also a time when a majority of the larvae are within the size range which feed primarily on copepod nauplii. The calculations for 24 March 1982 (Table 4) show that approximately $380 \text{ nauplii } m^{-3}$ were consumed by larvae. Given a density of $140\,000 \text{ nauplii } m^{-3}$, and an instantaneous net growth rate of $0.02 d^{-1}$ (calculated from observed change in biomass at the time; Peterson unpubl.), $2828 \text{ nauplii } m^{-3} d^{-1}$ would be produced. The larvae, therefore, consumed 13.4 % of the total number of copepod nauplii produced per day, but only 0.27 % of the standing stock. The results of all other dates indicated that less than 10 % of the daily production of copepod nauplii was consumed. Given this estimate of production is very conservative, the actual loss due to fish larvae is probably lower.

DISCUSSION

The diet of American sand lance *Ammodytes americanus* larvae consists initially of phytoplankton, but following the spring bloom, the diet shifts to primarily nauplius through adult stages of copepods, as is typical of most marine fish larvae (Hunter 1981). The dominant copepods consumed were *Temora longicornis* and *Acartia hudsonica* which is in agreement with an earlier study of sand lance larval diets in Long Island Sound (Covill 1959). Lebour (1918, 1919) and Ryland (1964) also reported phytoplankton or 'green food remains' and various stages of copepods as the most common food items of *A. americanus*, *A. lanceolatus*, *A. marianus*, and *A. tobianus*.

Small sand lance larvae appear to be opportunistic

Table 4. *Ammodytes americanus*, 24 Mar 1982. Calculations showing impact of sand lance larvae on copepod nauplii in Long Island Sound using consumption rates obtained in the laboratory and densities of larvae in the field. Total nauplii consumed was $379 m^{-3} d^{-1}$ at a prey density of $140 \text{ nauplii } l^{-1}$

Length (mm)	Volume cleared ($l d^{-1}$)	Nauplii consumed (no. larvae $^{-1} d^{-1}$)	Density (larvae m^{-3})	Nauplii consumed (no. $m^{-3} d^{-1}$)
6.5	0.05	7.1	0.08	0.6
7.5	0.09	12.5	0.03	0.4
8.5	0.15	21.5	0.09	1.9
9.5	0.2	37.4	0.15	5.6
10.5	0.4	65.3	0.32	20.9
11.5	0.8	113.0	0.23	26.0
12.5	1.4	196.4	0.17	33.4
13.5	2.4	341.3	0.19	64.9
14.5	4.2	593.0	0.12	71.2
15.5	7.3	1030.7	0.15	154.6

feeders. In Long Island Sound, larvae < 8 mm feed primarily on phytoplankton, but in the laboratory they will readily consume copepod nauplii. Field-collected larvae probably never contained nauplii because there were few nauplii available during December and January when < 8 mm larvae occur. Covill (1959) found some copepod nauplii in the guts of larvae of this size range but noted that nauplii were found in 20 % fewer guts during winter than during spring.

An increase in size and range of size of prey items with increasing size of larvae has been noted for other species by Laurence (1977), Last (1978), Gamble et al. (1981), Hunter (1981), Cohen & Lough (1983), Govani et al. (1983), Kane (1984), and Peterson & Ausubel (1984). This means that larger larvae which require more food are able to clear additional items, including larger items, from a unit volume than smaller larvae. In the laboratory experiments a 21 mm larva consumed not only nauplii but copepodites and adult copepods. All stages were also found in the guts of field-collected larvae. Larvae ≥ 24 mm consumed adult copepods, which are the same prey items consumed by adult sand lance (McKown 1984).

For sand lance larvae, the type of prey item consumed was closely related to their swimming ability. Prolarval behavior was consistent with observations of larval anchovies *Engraulis ringens* and *E. mordax* by Hunter (1972) and Ware et al. (1981), respectively. The passive, head-down orientation is an indicator of poor swimming ability. At this stage, the larvae feed on phytoplankton and a few copepod nauplii which are small and more quiescent. Larvae > 9 mm are more active hunters adding copepodites which are much stronger swimmers than nauplii to their diet. In addition, they assume an S-posture while they observe their prey. Anatomical changes begin to take place in fish of this size. Richards (1965) reported that *Ammodytes americanus* begin to develop dorsal and anal fin rays at 9 to 12 mm in length, suggesting a change in swimming ability. Larvae of approximately 21 mm captured faster swimming prey, including older copepodites of *Temora longicornis* and older copepodites and adults of *Acartia hudsonica*, along with nauplii of both species. Dorsal fin rays develop forward of the vent in larvae ranging from 15 to 20 mm (Richards 1965), suggesting another increase in swimming ability. When larvae reach 24 mm, they begin to feed primarily on adult copepods. This is also the size range in which the vertebral column forms (Sarah W. Richards, pers. comm.). The increase in size of the prey items with larval ontogeny may also be influenced by the increase in mouth width, as discussed by Hunter (1981); however, for sand lance, ontogenetic changes in swimming ability and hunting tactics may also explain the occurrence of larger prey in their diets.

Temperature directly affected the daily ration of sand lance larvae. An increase of water temperature from 2 to 7°C resulted in a 6-fold increase in the daily ration of the 10 to 11.0 mm larvae from 7 to 48 nauplii d^{-1} at 100 nauplii l^{-1} . Other larval fish, such as Atlantic menhaden *Brevoortia tyrannus*, spot *Leiostomus xanthurus*, and pinfish *Lagodon rhomboides*, which occur at higher temperatures (15 to 17°C), have greater daily rations of 3.5 to 9.0 % of their body weight (Kjelson et al. 1975). Atlantic mackerel *Scomber scombrus* larvae, which also occur over a higher range of temperature than do sand lance, have daily rations an order of magnitude greater than those of sand lance (Peterson & Ausubel 1984). It is important, therefore, that the ingestion rates of organisms be studied over the complete range of temperatures to which they are exposed in nature. A temperature change of only a few degrees could considerably alter calculations of the feeding impact.

In feeding experiments, the ingestion rate of sand lance larvae showed a positive linear response to prey concentration. There was no evidence of an Ivlev-type response (Ivlev 1961), as was found for larvae of winter flounder *Pseudopleuronectes americanus* (Laurence 1977), bay anchovy *Anchoa mitchilli*, lined sole *Achirus lineatus*, and sea bream *Archosarus rhomboidalis* (Houde & Schekter 1980). Those larvae, however, only reached asymptotic ingestion rates at prey densities much higher both than those in this study and than natural conditions.

When the daily ration obtained in the laboratory at food concentrations that are typical of natural concentrations is calculated and compared to the ration needed to satisfy daily growth requirements, the larvae appear to be starving. As an example, a 10.5 mm sand lance larva feeding in the laboratory on 100 nauplii l^{-1} at 7°C would consume 11.6 μg dry weight of nauplii d^{-1} (from Fig. 8). At 7°C the instantaneous growth rate of larvae was 0.048 d^{-1} in the laboratory (Smigielski et al. 1984) and 0.04 d^{-1} in nature (this study, calculated from March-April). This is equivalent to growths of 25 and 21 μg dry weight d^{-1} , respectively. Assuming a gross growth efficiency of 30 % (a value similar to that found for winter flounder larvae by Laurence 1977), a 10.5 mm larva must consume 60 to 70 μg dry weight d^{-1} to fulfill metabolic requirements, far greater than the 12 μg d^{-1} measured in the laboratory. For 4.5 and 6.5 mm sand lance larvae, the discrepancy between measured and calculated daily ration was 9-fold and for a 21 mm larva, 3-fold. Laurence (1977), raising winter flounder larvae at 8°C, found that they survived less than 2 wk when supplied with 100 nauplii l^{-1} , but bay anchovy, lined sole, and sea bream grew at that prey concentration (Houde & Schekter 1981). These larvae, however, were maintained at 26 to 28°C, and

Table 5. *Ammodytes americanus*. Estimate of percent of copepod biomass removed by sand lance larvae assuming that individual larvae consume one-third of their body weight d^{-1} . Percent removed for larvae collected in Mar was calculated assuming they feed only on nauplii and those in Apr for only copepodites

Date	Depth (mm)	Larval biomass ($\mu g l^{-1}$)	Copepod biomass ($\mu g l^{-1}$)		% removed
			Nauplii	Copepodites	
3 Mar 83	5	1.7	10.6	47.2	5.30
3 Mar 83	15	0.3	9.3	59.8	1.10
24 Mar 83	5	0.8	23.3	34.8	1.10
24 Mar 83	15	0.1	12.5	84.3	0.27
7 Apr 83	5	1.8	54.8	65.9	0.90
11 Apr 83	15	0.1	17.6	148.6	0.00
21 Apr 83	5	3.0	25.2	24.0	4.10
21 Apr 83	10	0.2	18.1	59.3	0.11
29 Apr 83	1	1.7	14.3	199.5	0.28

consumed 5 times the number of prey consumed by sand lance larvae of a similar size at the same prey concentration. The difference between measured and calculated ration for small sand lance (< 8 mm) may be explained by our observation that, in nature, they feed primarily on phytoplankton which is not accounted for in our calculations. The larger larvae may encounter microscale patches of copepod nauplii and copepodites. Alternatively, feeding behavior in the laboratory may not, because of containment effects, accurately represent feeding behavior in nature.

The feeding impact that sand lance larvae have on copepod biomass seems to be small. The calculations in Table 4 indicate that in March, when the biomass of sand lance was highest, less than 1 % of the biomass of copepod nauplii was consumed. However, as suggested above, we may have underestimated the daily ration of sand lance by a factor of 5. In Table 5, we recalculate the impact that the sand lance larvae have on copepod biomass, assuming that the fish consume one-third of their body weight per day. The results show that the fish removed at most an average of 1.5 % of the copepod biomass per day in March and April. This is similar to calculations given by Cushing (1983) for larval hake and plaice, Dagg et al. (1984) for walleye pollock and Peterson & Ausubel (1984) for Atlantic mackerel larvae.

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