Natural diet and feeding habits of the postlarval lobster *Homarus americanus*

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ABSTRACT: Postlarval *Homarus americanus* were collected from Block Island Sound, Rhode Island, USA, during 5 diel neuston sampling periods in summer 1988 and 1989. The foregut contents of the postlarvae were determined and compared with the relative abundances of potential prey groups in the plankton. Nine taxonomic prey groups were identified in the gut contents (N = 802). The composition of the prey groups and their relative frequencies of occurrence in the guts did not differ with time of day or sampling period. The frequent occurrence of copepods, decapod larvae, fish eggs and insect parts indicates a predominantly carnivorous feeding habit. Furthermore, the disproportionate frequency of occurrence of large copepod species and decapod larvae in the guts relative to their densities in the plankton suggests a preference for larger sized prey. Contrary to expectations, the mean gut fullness and condition of gut contents of individuals at different molt stages were not significantly different. Likewise, there was no significant difference in the incidence of guts with newly ingested prey between postlarvae in the premolt stages and those in the post and intermolt stages. Completely empty guts were rare. In addition, the variability in gut fullness and the condition of gut contents among individuals was high during all sampling periods. These indicate that postlarvae in the field forage successfully throughout the day. However, the significantly higher incidence of newly ingested prey in the guts of postlarval lobsters at night indicates a higher feeding activity during this time.

INTRODUCTION

The American lobster *Homarus americanus* passes through 4 planktonic instars before settling to the bottom as juveniles. The first 3 larvae are in a mysis form. Metamorphosis into the adult form occurs at the molt from the third to the fourth instar which is called the postlarval stage. Although it resembles the adult, the postlarva swims on the upper meter of the water column before it becomes bottom-seeking (e.g. Herrick 1911, Harding et al. 1987, Cobb et al. 1989). As with the postlarvae of other marine invertebrates with complex life histories, the postlarval period of *H. americanus* is thought to be a period at which benthic recruitment is determined (Caddy & Campbell 1986, Fogarty & Idione 1986, Scheltema 1986). Interannual variability in postlarval abundance has been documented for various localities (Scarratt 1973,

review in Fogarty 1983, Cobb unpubl. data) but the mechanisms contributing to the observed variability in postlarval recruitment are not well understood. Food limitation has been suggested to be an important source of mortality during the early planktonic life stages of the American lobster (Phillips & Sastry 1980, Harding et al. 1983, Castell & Kean 1986). Basic to an understanding of the importance of food limitation to postlarval recruitment is a knowledge of their feeding ecology.

In contrast to juveniles and adults (see review in Elner & Campbell 1987), very little is known about the natural diet and feeding habits of postlarval *Homarus americanus* especially during the planktonic period. Most of the information on the diet of the early planktonic life stages is from laboratory studies undertaken to find suitable diets for the culture of lobster larvae (e.g. Hughes & Mathiessen 1962, Carlberg & Van Olst 1976, Eagles et al. 1986). Williams (1907) examined the foreguts of 25 postlarval lobsters held in hatching bags suspended at a dock at Wickford, Rhode Island, USA.

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He found that more guts contained copepods and diatoms than clam meat which was provided as food for these lobsters. The earliest report on the gut content of postlarval lobsters from the wild was by Herrick (1911) who reported echinoderm and mollusk larvae, worms, fish eggs and sand in the gut of 2 'lobsterlings' collected from Vineyard Sound (Massachusetts, USA). From observations in the laboratory, he noted that the early pelagic life stages feed raptorially but seemed to lack precise discrimination for their food. In contrast, Harding et al. (1983) examined the foreguts of 16 postlarvae from St. Georges Bay (Newfoundland, Canada) and reported that postlarvae, as well as the third stage, 'preferentially prey on adult female *Centropages,* large gastropod larvae and zoea and megalops (sic) larvae of *Cancer irroratus*' relative to the first and second stages. Anectodal accounts in the laboratory and field suggest that while in the plankton, postlarvae are visual predators actively pursuing prey (Williams 1907, Cobb et al. 1983). However, Lavalli & Barshaw (1989) demonstrated that newly settled postlarvae living in burrows are capable of suspension feeding. It is therefore likely that the postlarval lobster is capable of various feeding mechanisms in both the pelagic and benthic environment.

In this study, the foregut contents of postlarval lobsters collected from Block Island Sound (Rhode Island) during diel neuston sampling were analyzed and compared with the relative abundances of potential prey groups in the plankton. The questions addressed in the present paper are: (1) What is the natural diet of postlarval lobsters in the area, (2) Is there any evidence of preference for any prey group, (3) Is there any periodicity in the feeding activity, and (4) Are there differences in the feeding activity of individuals at different molt stages?

METHODS

Field collection. Postlarval lobsters were collected from Block Island Sound off Point Judith, Rhode Island (41° 21' N, 71° 31' W) using neuston nets (0.5 × 1.0 m, 500 µm mesh) towed for 10 min at 1.5 knots. As much as possible, diel sampling was conducted at 3 h intervals starting at 09:00 h and continuing to 06:00 h the following day (i.e. 8 sampling times) for 3 periods during summer 1988 (June 29–30, July 5–6, July 14–15) and twice in 1989 (June 20–21, June 28–29). In 1989, diel sampling was conducted from 09:00 h to 09:00 h of the next day. Each of the 09:00 h samples were treated as separate sampling times. Altogether 37 sampling times were conducted during the 5 sampling periods.

Postlarvae were removed immediately from the neuston samples and held in chilled seawater until return to the laboratory. After each neuston tow, a 5 min surface water (top 0.5 m of the water column) bongo tow was made using 33 cm diameter paired nets (333 µm mesh) which were fitted with mechanical flowmeters (General Oceanics). In addition, postlarvae were collected from neuston tows made at 09:00 h on 2 days in 1988 and 4 days in 1989. Postlarvae from these additional tows and those collected at 09:00 h during the diel sampling periods (a total of 12 sampling dates) were used to evaluate if there were significant differences in the relative gut fullness and condition of the gut contents among individuals at different molt stages.

In the laboratory, the molt stage of each postlarva was determined by examination of the tissues of the uropod, telson and setae (following the criteria of Sasaki 1984) under the stereomicroscope (60 ×). Individuals from each tow were sorted with respect to molt stage. Both postlarvae and zooplankton samples were initially preserved in 5 % formaldehyde for at least 1 wk and transferred to 70 % isopropyl alcohol prior to storage.

Gut analyses. The foregut of each postlarva was dissected and the contents were examined under the stereomicroscope. Percent gut fullness was visually estimated (empty, <25 %, 26–50 %, 51–75 % and 76–100 %) and scored 0 to 4 respectively, prior to gut dissection. The prey groups found in each gut were recorded and the prey items were identified to the lowest taxonomic level possible. Prey occurrence in the foregut were recorded on a present or absent basis for each gut. The identity of newly ingested prey items (defined below) was noted. The general condition of the gut contents was scored using the following criteria based on preliminary gut analyses and laboratory experiments. (1) Advanced state of digestion: predominantly fine unrecognizable particles and/or fragments which were not tissue-filled; (2) intermediate state of digestion: presence of almost whole copepods and/or predominantly coarse, recognizable parts (i.e. >0.5 mm along the longest axis) with some tissue; (3) newly ingested: presence of whole and intact prey (e.g. copepods, zoea, fish eggs) and recognizable parts (e.g. whole decapod appendages) that were tissue-filled.

Determination of relative abundance of prey groups in the field. Debris, juvenile fish and gelatinous plankton were removed from the bongo tow samples. The sample from each net was split into 2 size fractions: 333 to 1000 µm and >1000 µm by washing the samples through a 1000 µm mesh sieve. The total wet weight of each size fraction was determined using a Sartorius top-loading balance (± 0.1 g) after the sample was drained and blotted dry. Immediately after weighing, the sample was rinsed into a beaker with clean seawater and split to ca 200 to 600 individuals using a Folsom plankton splitter. The copepods, decapod larvae and fish eggs in the subsample were counted. The mean densities (ind. m^{-3})

of these prey groups in each of the size fractions were estimated for each bongo tow using the paired nets as replicates. These data were used to infer the general patterns of abundance of these potential prey groups in the plankton.

RESULTS

Foregut contents

There were 9 taxonomic groups identified in the guts of 802 postlarvae examined during each sampling period (Table 1). In addition, unidentified fibrous bundles and tissue clumps were included as prey groups. Although some guts contained plant material (e.g. filamentous algae and in a few cases diatoms), remains of animal prey items were always found. The composition of the prey groups based on their frequencies of occurrence in the guts was similar among the sampling times (Kendall's coefficients of concordance, $W = 0.7$ to 0.9, $p < 0.005$) during each diel sampling period . When all of the samples for each sampling period were pooled (Table 1), the ranking of the prey groups during the 5 sampling periods was also highly similar ($W = 0.70$, $p = 0.0001$). These results show that overall, the most common prey groups in the guts of postlarval lobsters were decapod larvae and copepods, followed by fish eggs and insect parts. In comparison, other prey groups were rare and encountered only during 1 or 2 sampling periods (e.g. cladocerans, larvaceans, mysids).

The overall proportions of lobster guts with decapod larvae (range: 42 to 75 %) and copepods (range: 28 to 72 %) during the 8 diel sampling times were not significantly different (arcsine-transformed proportions, paired t-test, $p = 0.31$). However, copepods were encountered as newly ingested prey more frequently than decapod larvae (arcsine-transformed overall proportions per sampling time, paired t-test, $p = 0.03$). The condition of these prey items in the guts indicates that copepods are commonly ingested whole while larger decapod larvae are torn apart prior to ingestion. Although the incidence of insect parts was fairly high (i.e. 26 % of the guts examined), only in 2 guts were insect appendages found filled with tissue. Most of the insect parts were small fragments of various appendages and portions of wings. Likewise, fish eggs (commonly 2 to 4 in a gut) with some tissue (i.e. newly ingested) were rare. In most cases only empty egg cases were found.

The list of crustacean prey items that were identified from the gut contents are shown in Table 2. Among the decapod larvae, crab megalopae were by far the most frequently found. In many cases, megalopae were identified by the presence of a whole cheliped and/or telson. Although it was often impossible to determine the taxa to the species, megalopae and zoea of *Cancer* spp. were identified in a total of 33 guts. In addition, intact zoea of *Ovalipes ocellatus, Pagurus* sp. and *Callianassa* sp. were found. Notably, the remains of more than 2 copepods were found in about 80 % of the total number of guts found to have copepods. In many guts, as many as 6 to 12 individual copepods were found. Calanoid copepods were the most frequently encountered copepod group. The most common species identified were *Centropages hamatus* and *C. typicus* followed by *Acartia* spp. and *Tortanus discaudatus*. As in the case of crab megalopae, calanoid copepods were frequently present during all sampling times and periods. Harpacticoid and cyclopoid copepods and the smaller calanoid copepods (e.g. *Paracalanus* sp., copepodites) were rare.

Table 1. Frequency of occurrence of the major prey groups found in the guts of postlarval *Homarus americanus*, sampled during each diel sampling period. The mean ranks (from Kendall's coefficient of concordance) of the prey groups and overall % frequency of occurrence are also shown (N = total number of samples)

Prey groups	1988			1989		Mean rank	Overall frequency %
	June 29–30 (N = 49)	July 5–6 (N = 145)	July 14–15 (N = 168)	June 20–21 (N = 248)	June 28–29 (N = 192)		(N = 802)
Decapod larvae	36	100	108	147	107	10.6	62.1
Copepods	31	88	77	176	60	10.0	53.9
Insect parts	0	13	17	64	116	7.6	26.2
Fish eggs	6	38	43	7	37	8.2	16.3
Plant matter	2	1	1	18	11	5.4	4.1
Chaetognaths	0	2	5	0	1	4.0	1.0
Larvaceans	7	0	9	0	0	4.4	2.0
Cladocerans	5	0	0	0	0	2.8	0.6
Mysids	0	1	1	0	0	2.6	0.2
Fibrous bundles	2	1	5	3	10	5.0	2.6
Tissue clumps	1	5	4	1	9	5.4	2.5

Table 2. Crustacean prey items and the total number of guts in which they were found (N = 302) collected during the 5 diel sampling periods in 1988 and 1989. (N = no. of sampling periods in which the prey item was identified)

Crustacean prey items	N	No. of guts
Cladoceran	1	5
Mysid		
Neomysis americana	2	2
Copepods		
Cyclopoid copepod		
Oithona sp.	2	2
Harpacticoid copepod		
Microsetella norvegicus	1	1
Calanoid copepod		
Paracalanus sp.	1	1
Pseudocalanus sp.	4	13
Acartia spp.	5	69
Centropages spp.	4	11
C. hamatus	5	139
C. typicus	5	147
Tortanus discaudatus	4	62
Labidocera aestiva	3	9
Temora longicornis	4	33
Calanus sp.	4	6
Unidentified copepodite	4	17
Decapod larvae		
Brachyuran larvae		
Cancer spp.		
Zoea	3	8
Megalopa	4	25
Ovalipes ocellatus zoea	2	6
Unidentified zoea	3	25
Unidentified megalopa	5	124
Anomuran larvae		
Pagurus sp. zoea	1	1
Macruran larvae		
Callianassa sp. zoea	3	5
Unidentified, shrimp-like	3	10

Gut fullness and condition of gut contents

Of the 822 postlarval lobsters collected during the 5 diel sampling periods in 1988 and 1989, only 20 individuals had empty guts. Of these, 9 were in molt stage A (early postmolt) ; the remaining were in molt stages B (postmolt) to D_1 (premolt). Furthermore, lobsters with empty guts were collected during different sampling times. Generally, the mean gut fullness during each sampling time was at least 50 % (i.e. scored > 2.0, Table 3).

The average relative gut fullness and condition of gut contents of postlarvae at different molt stages [B = 9 individuals, C (intermolt) = 49, premolt stages D_0 = 29, and D_1 = 35], sampled at 09:00 h, during 12 dates in 1988 and 1989, were not significantly different (Kruskal-Wallis 1-way ANOVA, p > 0.05). Mean gut fullness was not correlated with the mean condition of the gut contents (Table 3) (Spearman's rank correlation

coefficient, p = 0.65). Moreover, the variability of these 2 indices was high during each sampling time. The co-efficients of variation ranged from 10 to 50 % for gut fullness and 29 to 67 % for the condition of the gut contents. However, there was a significant difference in the mean relative gut fullness among the 8 sampling times (Kruskal-Wallis 1-way ANOVA, p = 0.03). The mean ranks indicate that the mean gut fullness of post-larval lobsters to be lowest during midnight and early morning (24:00 and 03:00 h). Similar analysis on the mean condition of gut contents showed no significant differences with respect to time. In addition, the prey items in each gut were at different states of digestion. This suggests that the gut is not completely evacuated and feeding occurs at different times of the day.

The overall proportion of guts with newly ingested prey was not significantly different between individuals at molt stages B to C and D_0 to D_1 during the 8 sampling times (paired t-test on arcsine transformed proportions, p = 0.73). Pooling all individuals regardless of molt stage, the proportion of guts with newly ingested prey was not significantly different among the 8 time periods. However, when the sampling times were grouped into night (21:00, 24:00, 03:00 h), day (09:00, 12:00, 15:00 h), and dawn/dusk (06:00, 18:00 h), there was a significant difference among these time categories (1-way ANOVA on arcsine transformed proportions, p = 0.02) (Fig. 1). The proportion of guts examined with newly ingested prey was significantly higher at night and dawn/dusk than during the day (Scheffe's t-test, p < 0.05). Similarly, the proportion of guts with newly ingested copepods was significantly higher at night. In contrast, there was no significant difference in the proportion of guts with newly ingested decapod larvae among these time categories.

Abundance of potential prey groups

The most common potential prey groups in the plankton were decapod larvae, copepods and fish eggs. Of these, decapod larvae accounted for most of the total zooplankton biomass. As such, the general trend in total zooplankton biomass (Fig. 2) mirrored the diel pattern of the densities of decapod larvae (Fig. 3a). However, in general, copepods were an order of magnitude more abundant than decapod larvae and fish eggs (Fig. 3). Notably, a significant positive correlation between the total prey density and their frequency of occurrence in the gut was found only for copepods during the sampling period July 5–6, 1988 (Spearman's rank correlation, p = 0.01). Furthermore, there was no significant difference in the total densities of decapod larvae and fish eggs during the day, night and dawn/dusk. On the other hand, copepods

Table 3. Mean fullness of guts (F, scale: 1 to 4) and condition of gut contents (CG, scale: 1 to 3) for each sampling time during each sampling period. The total number of samples for each sampling time is shown in parentheses

| Time (h) | 1988 | | | | | | 1989 | | | |
| | June 29–30 | | July 5–6 | | July 14–15 | | June 20–21 | | June 28–29 | |
	F	CG	F	CG	F	CG	F	CG	F	CG
09:00	3.6 (13)	1.9	2.7 (12)	1.6	–	–	3.2 (20)	2.2	3.0 (19)	1.3
12:00	2.9 (9)	1.9	3.0 (29)	1.7	2.7 (27)	1.5	3.5 (26)	1.8	3.6 (11)	1.9
15:00	–	–	3.9 (22)	1.6	2.8 (17)	1.8	2.7 (13)	2.1	3.6 (29)	1.4
18:00	3.5 (20)	2.2	3.5 (14)	1.9	3.5 (27)	1.5	3.8 (4)	1.5	3.6 (25)	1.7
21:00	–	–	3.3 (14)	2.2	3.6 (30)	1.8	3.3 (51)	1.6	3.2 (27)	1.5
24:00	–	–	3.2 (26)	2.1	2.6 (31)	1.9	1.9 (37)	1.4	2.7 (31)	1.9
03:00	–	–	3.2 (15)	2.4	2.7 (22)	1.9	1.8 (47)	1.8	2.2 (23)	2.0
06:00	3.0 (7)	2.3	2.9 (13)	2.1	3.6 (14)	1.9	2.4 (17)	1.5	2.9 (19)	2.1
09:00[a]	–	–	–	–	–	–	3.0 (33)	1.6	3.1 (8)	1.5

[a] Last sampling time during sampling periods in 1989, see 'Methods'

were significantly more abundant at night than during the day or the crepuscular period (Scheffe's t-test, $p < 0.05$). As earlier mentioned, the incidence of newly ingested copepods were also higher during the night.

Two-way analysis of variance on the densities of decapod larvae with respect to the size fractions and sampling time showed significant differences only due to size fraction ($p = 0.03$). Decapod larvae > 1000 μm during all sampling times were significantly more abundant than those 333 to 1000 μm in size ($p = 0.02$,

Fig. 4a). On the other hand, both the size fraction ($p = 0.109$) and the time of day ($p = 0.011$) contributed significantly to the variability in copepod densities. In contrast to decapod larvae, smaller copepods were significantly more abundant than copepods > 1000 μm in size. In addition, both smaller decapod larvae and copepods were generally more abundant at night (Fig. 4). There was no significant differences with
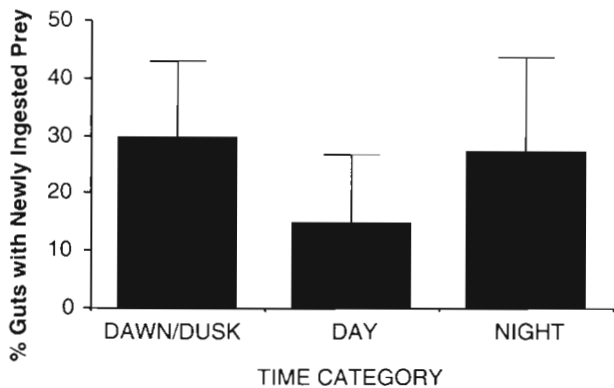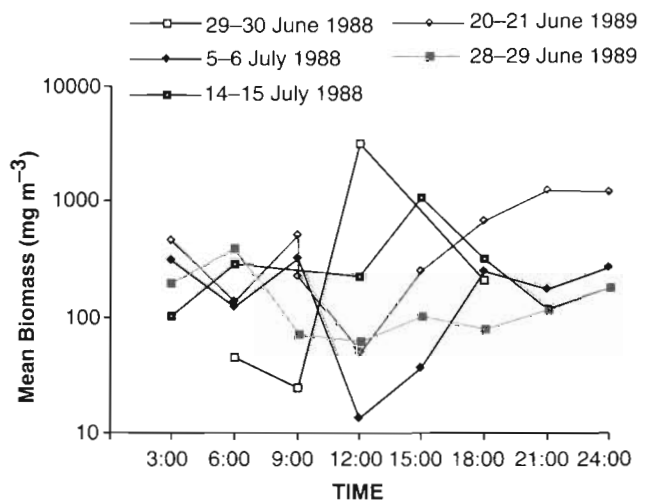

Fig. 1. *Homarus americanus.* Average frequency of guts with newly ingested prey during dawn/dusk (06:00, 18:00 h), day (09:00, 12:00, 15:00 h) and night (21:00, 24:00, 03:00 h). Standard error bars are shown

Fig. 2. Mean total biomass (mg wet wt m^{-3}) of zooplankton sampled from the bongo tows per sampling time during the diel sampling periods in 1988 and 1989
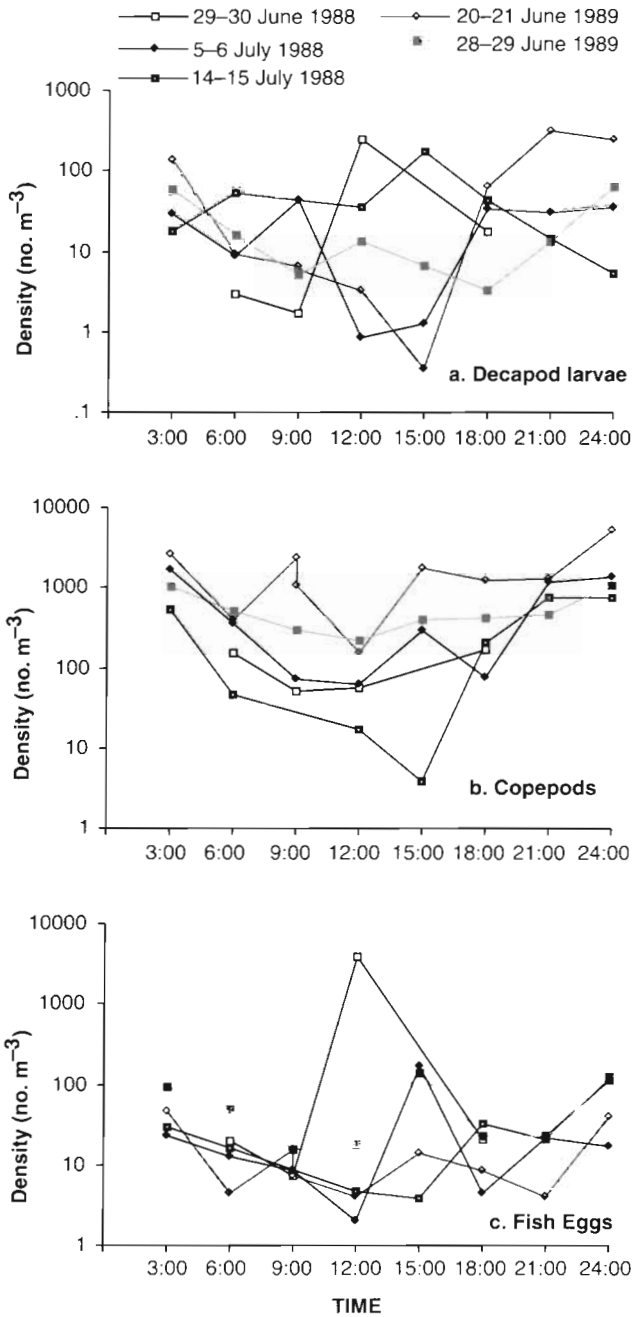
Fig. 3. Mean total densities (ind. m^{-3}) of (a) decapod larvae, (b) copepods and (c) fish eggs from the bongo tows per sampling time during the diel sampling periods in 1988 and 1989
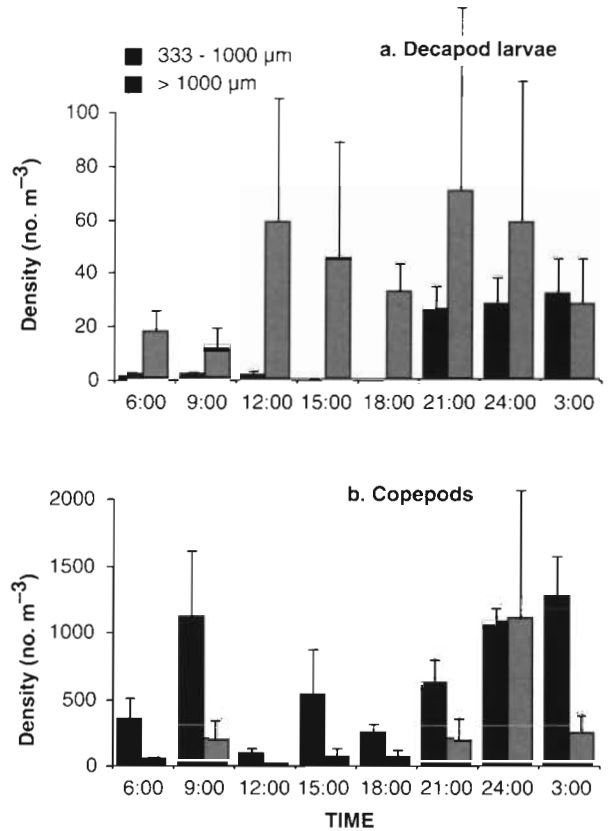

Fig. 4. Mean densities (ind. m^{-3}) of (a) decapod larvae and (b) copepods in the >1000 μm and 333–1000 μm size fractions from the bongo tows per sampling time during the 5 diel sampling periods in 1988 and 1989. Standard error bars are shown

respect to either size fraction or sampling time for fish eggs. Interestingly, large decapod larvae, particularly crab megalopae (1.2 to 1.5 mm total body length) were very frequently found in the gut contents (Table 2). Moreover, despite the greater abundance of smaller copepods especially at night, adult and larger calanoid copepods like *Centropages* spp. (0.9 to 1.35 mm body length) and *Tortanus discaudatus* (1.75 to 2.25 mm

body length) were the predominant calanoid copepods identified in the guts. These results strongly indicate preference of postlarval lobsters for larger sized prey.

DISCUSSION

Natural diet

The prey groups found in the foregut of postlarval lobsters indicate a predominantly carnivorous food habit. This is consistent with earlier reports of other workers (i.e. Williams 1907, Herrick 1911, Harding et al. 1983). The large number of postlarvae examined in this study allowed a quantitative assessment of the relative importance of different prey groups in the diet of lobster postlarvae. We recognize that the frequency of occurrence by itself is by no means an adequate indicator of the relative importance of a prey item (see Hyslop 1980 for a general review of the inherent limitations of gut content analyses). Because it is based on the presence or absence of prey groups in each gut, the frequency of occurrence does not take into account

the number of individuals for each prey group. Unfortunately, the number of individuals could not always be estimated. This is especially true for decapod larvae of which only the remains of appendages were often recognized. Another measure commonly used together with the frequency of occurrence to evaluate the relative importance of the prey found in the stomachs of crustaceans is the volumetric contribution of the various prey groups in each gut (e.g. Carter & Steele 1982, Elner & Campbell 1987 – juvenile and adult lobsters; Haefer 1990 – crabs). Because of the small size of the foregut of postlarval lobsters, approximating relative volumes of various prey groups was impractical. Due to these limitations it was not possible to assess whether copepods are more important than decapod larvae in the diet of postlarval lobsters. Despite the generally higher densities of copepods in the plankton, the overall frequency of occurrence of copepods and decapod larvae in the guts examined was not significantly different. However, the frequency of guts examined with copepods as newly ingested prey was greater than those with newly ingested decapod larvae. It is possible that the gut residency period of decapod larvae (e.g. appendages) may be greater than that for whole copepods. Evidently, a study of the feeding behavior of postlarval lobsters together with determination of the nutritional value and gut retention periods is needed to better elucidate the relative importance of these prey items. Nonetheless, results unequivocally show that while in the plankton, decapod larvae and copepods are major food items of postlarval *Homarus americanus* during all times of the day.

The fairly high incidence of fish eggs (commonly 2 to 4) and insect parts in the gut contents, compared to other prey groups, also suggests that these are regular prey items in the diet of postlarval lobsters. However, it was rare that these prey items were found as newly ingested. It is possible that insect parts and fish egg cases have long residence times in the gut of postlarval lobsters. If this were the case, the frequencies with which these prey groups were found probably overestimate their relative importance as prey items.

The high incidence of the most common and regular members of the plankton (i.e. copepods and decapod larvae) in the guts of postlarval lobsters suggests that postlarvae are opportunistic feeders. Likewise, the wide variety of prey groups including larvaceans, mysids and chaetognaths also suggest a non-selective feeding mode. However, the disproportionate frequency of occurrence of some prey groups in the gut contents relative to their abundance in the plankton suggests some degree of prey selectivity. For example, despite densities in the plankton comparable to decapod larvae, fish eggs were not as frequently found in the guts of postlarval lobsters. Furthermore, the higher incidence of adult and larger copepod species in the guts despite the generally much higher abundances of small copepods (<1000 μm) particularly at night, strongly indicate preference for larger sized prey. The predominant species of calanoid copepods identified in the gut were adult *Centropages* spp., *Acartia* spp., *Tortanus discaudatus* and *Temora longicornis* which are among the largest copepod species in the area (Wilson 1932). Although species densities were not estimated in this study, visual assessment of the zooplankton samples (while counting the copepods from the bongo tow samples) suggested that the dominant species were the same as those previously reported by Deevey (1952a, b) and Frolander (1955). In view of this, *Tortanus discaudatus* presents an interesting case, since it is not one of the most abundant larger species in the area. Furthermore, most of the times that *T. discaudatus* was identified in the gut contents it was also newly ingested. Assuming that the gut residency period of copepod species are similar, the disproportionately high incidence of *T. discaudatus* despite its relative low abundance in the plankton, suggests that when present, this species may be selectively preyed upon by postlarval lobsters. Preference for crab megalopae which are large compared to most members of the plankton was even more evident from our observations in the laboratory that megalopae aggressively fend off postlarvae attacking them. Despite this, megalopae were the most common decapod larvae found in the guts examined. It is interesting to note that the genus *Cancer* was also found to be a frequently ingested prey item of benthic juvenile and adult *Homarus americanus* (Weiss 1970). Harding et al. (1983) also found larger plankton such as *Cancer* spp. zoea and megalopae, adult *Centropages* spp. and large gastropod larvae to be most frequently present in the guts of postlarval lobsters (N = 16) collected from St. Georges Bay. This evident preference for larger prey would suggest that while in the plankton, lobster postlarvae generally feed raptorially. This is in contrast to other feeding modes, such as suspension feeding, which has been suggested to be important for newly settled postlarvae (Lavalli & Barshaw 1989).

Feeding activity

It is interesting to note that only 20 postlarvae collected from the field had empty guts. Of these, nearly half (9 individuals) were in molt stage A. A total of 11 postlarvae in molt stage A were caught; the 2 that had material in their foreguts indicate that feeding during this molt stage is possible although the incidence is low. A few hours immediately after ecdysis,

postlarvae are unable to feed (pers. lab. obs.). It is therefore likely that the postlarvae in molt stage A which had empty guts were caught before they had a chance to feed. In the laboratory, we found postlarvae with completely empty guts after 6 to 12 h of food (i.e. live zooplankton) deprivation. The very low incidence of postlarvae with completely empty guts during the diel sampling periods indicate that postlarvae forage successfully throughout the day. It is therefore highly unlikely that a considerable number of postlarvae in the field die due to starvation.

Results indicate no difference in the feeding activity of postlarvae at different molt stages. This finding does not agree with the expected higher feeding activity at post-molt and intermolt inferred from the rapid accumulation of reserves in early molt stage B to early D_0 during the postlarval instar (Sasaki et al. 1986). Other studies have found that the feeding activity of crustaceans change over the molt cycle. Weiss (1970) found that the stomach fullness of juvenile *Homarus americanus* declined through the molt cycle. He noted that the stomachs of most individuals at molt stage D_2 were empty. Lipcius & Herrnkind (1982) also noted the same for subadults of the spiny lobster *Panulirus argus*. Furthermore, feeding ceased completely during ecdysis. Only 3 postlarvae at the late molt stages D_2 and D_3 were collected during this study, and all 3 had guts that were more than half full. The low number of animals at the late premolt stage may be attributed to settlement during this period (Cobb et al. 1989). It is likely that reduced feeding activity during the postlarval instar occurs after settlement to the benthos, prior to ecdysis to the fifth stage. However, while in the plankton, there was no apparent difference in feeding activity due to the molt cycle.

The very high individual variability in relative gut fullness and the condition of gut contents suggest that postlarval lobsters feed asynchronously and inter-mittently. However, despite this variability, some feeding periodicity exists at the population level. The significantly higher incidence of postlarvae with newly ingested prey in their guts during the night (21:00, 24:00 and 03:00 h) was suggestive of higher feeding activity during this time. We recognize that this index of feeding periodicity may be biased if net-feeding occurred during the 10 min neuston tows. Harding (pers. comm.) placed 10 stage 1 larvae which were starved for 1 d (to clear their guts) in the cod-end of a standard ring net which was towed at about 3 m for 30 min, and found that each had a complete fresh copepod in the foregut. In our study, we assumed that the probability of net-feeding occurring was the same during all the sampling periods and that the probability was low since the duration of the tows was only 10 min. Furthermore, it is reasonable to expect that net feeding would be less common in nature compared to

the observation of Harding (pers. comm.) since the larvae in that experiment were starved and undoubtedly ravenous. Thus, the significant difference in the incidence of newly ingested prey found among time categories was unlikely to have been an artifact of net-feeding. Conversely, gut fullness was significantly lower at midnight and at 03:00 h. Other studies have suggested that ingestion may be affected by stomach fullness (e.g. Sainsbury 1986, Penry & Jumars 1987). It is conceivable that ingestion ceases or decreases when maximum gut capacity is attained. Whether this is true for *Homarus americanus* needs further study.

The higher feeding activity at night may be attributed to the generally greater abundance of prey in the surface waters during this time. This was suggested by the significantly higher incidence of copepods as newly ingested prey during the night when this prey group was more abundant. Carlberg & Van Olst (1976) found that the consumption rates of laboratory-reared postlarval lobsters increased with increasing prey densities (i.e. live adult brine shrimp *Artemia salina*). However, there is no information on the threshold level for this feeding response. The high feeding activity during the night also indicates that detection of prey is not primarily visually mediated. This is in contrast to suggestions based on the daytime observations of Cobb et al. (1983) from the field as well as those of Herrick (1911) in the laboratory. The mechanisms by which foraging is accomplished at night is unclear. From our observations in the laboratory, frozen adult brine shrimps as well as live megalopae were generally not captured until the postlarvae 'bumped' into them. This suggests that tactile stimulation is also necessary for prey capture in postlarval lobsters. We speculate that in the absence of visual perception, swimming would increase the probability of encountering a prey at night.

In summary, this study contributed various insights into the diet and feeding habits of postlarval *Homarus americanus* in nature. Clearly, while in the plankton postlarvae are raptorial feeders preferring larger sized prey, particularly decapod larvae and calanoid copepods. Moreover, the molt cycle had no apparent effect on the feeding activity during the planktonic phase of the postlarval instar. Despite the high variability among individuals, feeding activity was highest during the night. Furthermore, the low incidence of completely empty guts indicate that postlarvae forage successfully throughout the day in the nearshore waters of Block Island Sound.

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