

Abstract.— Early juvenile (Stages V–IX) American lobsters *Homarus americanus* were fed diets of mesoplankton in filtered seawater, meso/microplankton combination in filtered seawater, and frozen brine shrimp in both filtered and unfiltered seawater to determine if mesoplankton diets could sustain survival and growth throughout most of the first year of molts and if smaller zooplankters and phytoplankton in the meso/microplankton diet could be utilized as food and could sustain survival in periods of low food supply. At the beginning of the experiment, there were no significant differences in either carapace length or weight between the groups of sibling lobsters. Lobsters fed mesoplankton had high survival (80%) and significant increases in both carapace length and weight, although they weighed less at Stage IX than those fed frozen brine shrimp in unfiltered seawater. Lobsters fed frozen brine shrimp in filtered seawater had low survival (15%), but did not differ significantly at Stage IX from those fed mesoplankton in terms of both carapace length and weight. Lobsters fed brine shrimp in unfiltered seawater had high survival rates (95%) and weighed nearly twice as much at Stage IX than both the brine shrimp-fed lobsters in filtered seawater and the mesoplankton-fed lobsters; however, none of these three surviving groups differed significantly in carapace length at Stage IX. Intermolt periods for the three surviving groups were not significantly different until the molt between Stage VIII and IX when the mesoplankton-fed lobsters took nearly twice as long to molt as either of the brine shrimp-fed groups. Lobsters fed meso/microplankton did not molt out of Stage V and died within 36 days of the 107-day experiment. These results indicate that mesoplankton diets promote growth and survival of lobsters throughout most of their first season of molting and that larger planktonic organisms may contain essential nutritional requirements not met by brine shrimp alone. However, the meso/microplankton diet, consisting mostly of diatoms, does not provide sufficient nutrition for survival during periods of starvation.

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Survival and Growth of Early-Juvenile American Lobsters *Homarus americanus* Through Their First Season While Fed Diets of Mesoplankton, Microplankton, and Frozen Brine Shrimp

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Little is known of the natural foraging activities of the settled postlarvae (Stage IV) and early-juvenile (<1 year-old) stages of the American lobster *Homarus americanus*, presumably due to the inability of past investigators to locate them in the benthic environment. Recently, Barshaw and Bryant-Rich (1988) examined the behavior of the early-juvenile American lobster in naturalistic settings in the laboratory and found that they spent a considerable amount of time pleopod fanning (15% of the time) and antennule flicking (15–40% of the time) at the entrance of their burrows. During their 8-month investigation, Barshaw and Bryant-Rich never observed an early-juvenile lobster leave its burrow; of the several instances where lobsters were seen feeding, they captured amphipods near the entrance of the burrow twice while other observations indicated that the lobsters were capturing planktonic organisms via self-generated currents which drew the organisms toward the burrow entrance. Their observations are corroborated by field cage studies of Gregory Roach (Nova Scotia Dep. Fish., Halifax, N.S., Canada B3J 3C4, pers. commun., Nov. 1989) where he, too, never observed early-juvenile American lobsters leave their burrows during one year of observations.

While little is known about the natural diet of recently settled American lobsters, Cobb et al. (1983) observed presettlement Stage-IV American lobsters capturing crab megalopae and insects in the field. Stomach content analyses indicate that the Stage-IV diet is similar to that of the larvae, consisting of copepods, decapod larvae, amphipods, algae, and diatoms (Williams 1907, Herrick 1911, Templeman and Tibbo 1945). Although most laboratory investigations have used artificial feeds which wild early-juvenile lobsters would never encounter, some studies have provided information on naturalistic diets. Emmel (1908) found that Stage-IV American lobsters were capable of surviving on planktonic organisms obtained from the water alone. The intermolt period for this group of lobsters was significantly longer than that for groups fed on beef, soft-shelled clam, lobster muscle, or shredded fish, but this result was probably due to differences in the overall amount of food available to the groups, as unequal weights of food were used. More recently, Andrea (1975), D'Agostino (1980), and Good et al. (1982) found that when amphipods were used as a food source, growth rates of larval, post-larval, and early-juvenile American lobsters improved significantly over brine shrimp diets (both live and

frozen) and artificially prepared compound diets. Daniel et al. (1985) demonstrated that Stage-IV and early-juvenile American lobsters were capable of surviving and growing on a frozen filtrate diet consisting of 99% barnacle larvae and 1% calanoid copepods; however, these filtrate-fed lobsters were significantly smaller (by 17%) than lobsters fed on frozen adult brine shrimp. Similarly, Barshaw (1989) found that Stage-IV American lobsters were also capable of surviving and growing through two molts on a diet of live, unidentified plankton (size 152–1000 μm), although the plankton-fed lobsters were smaller and had a greater intermolt period from Stage V to VI than those fed on frozen brine shrimp. In all of the above studies, there were no differences in mortality between the different groups of fed lobsters.

This study examined the survival and growth of early-juvenile (Stages V–IX) American lobsters fed on diets of mesoplankton (95–1000 μm) and a meso/microplankton combination (25–95 μm) while using frozen brine shrimp diets for reference. Studies with other crustaceans indicate that phytoplankton may be used as a supplement when zooplankton abundance is low and its presence may extend the period of survival over that observed for starved animals (McConaughy 1985). However, the nutritional value of phytoplankton is highly dependent on its content of essential fatty acids which can vary in response to temperature, dissolved nutrients, light, and age (Castell and Kean 1986). While American lobsters have not been classified as algal feeders (Lebour 1922), stomach content analyses of the larvae and postlarvae indicate that diatoms and other algae form part of their diet (Herrick 1895, Williams 1907, Herrick 1911). Recently, Lavalli and Barshaw (1989) have shown that Stage-IV and -V American lobsters are capable of removing particles from the water column to at least a size of 70 μm , indicating that early-juvenile lobsters may be able to utilize small organisms in the mesoplankton and microplankton. This study was designed, in particular, to determine two things: (1) Whether early juveniles could utilize an already-proven diet (mesoplankton) for Stage-IV and -V lobsters throughout much of their first season of molting activity, and (2) whether early juveniles could extend survival by utilizing the organisms found in the smaller range of mesoplankton and in the microplankton.

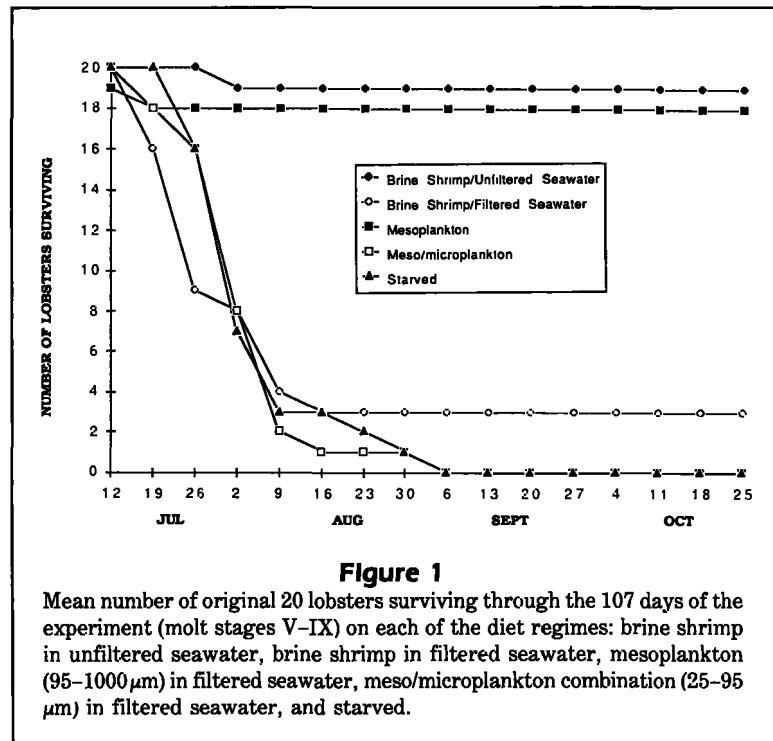


Figure 1
Mean number of original 20 lobsters surviving through the 107 days of the experiment (molt stages V–IX) on each of the diet regimes: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination (25–95 μm) in filtered seawater, and starved.

Materials and methods

Prior to the beginning of the experiment, Stage-IV American lobster siblings *Homarus americanus* were held collectively in a seawater table supplied with ambient, unfiltered seawater and were fed *ad libitum* on frozen adult *Artemia* (San Francisco Bay type). Siblings were used for the experiment, since genetic differences between females can produce significant differences in weight among similarly raised juvenile lobsters (Conklin et al. 1975, Hedgecock and Nelson 1978). The lobsters were then randomly assigned to one of four groups of 20 animals: a mesoplankton-fed group (95–1000 μm), a meso/microplankton combination-fed group (25–95 μm), a frozen brine shrimp-fed group, and a starved group. Upon assignment, individual lobsters were placed into plastic trays (Rubbermaid Drawer Organizers, No. 2915) with dimensions 224 mm long \times 75 mm wide \times 50 mm deep, and volume of \sim 750 mL. Each tray was modified to include a sidewall screen for water flow and a dark-grey PVC tube (10 mm diameter) glued to the bottom which could act as a shelter. The trays were provided with ambient seawater which was filtered with a dual-cartridge filtering system (a 50- μm honeycomb filter followed by a 5- μm nominal filter). They were arranged in a Latin square design to intersperse the treatments and were kept in darkness, except during cleaning and feeding periods, as previous investigations demonstrated that juvenile lobsters

grew more quickly and were more active in a nearly constant dark regime (Bordner and Conklin 1981). The water flow to the trays was turned off for 1 hour after the introduction of food to allow the lobsters to more easily capture the food. Filters were replaced during these feeding periods if they were clogged.

Lobsters were fed according to group; excess food and other debris were removed daily with a kitchen baster. All trays were thoroughly scrubbed each week to remove algal growth from the sidewalls and bottom. During cleaning the lobsters were held in a moist, small-mesh fish net. Every attempt was made to feed equal wet weights of food, and representative portions of each diet were weighed each week. For the plankton diets, representative portions were also photographed using the technique of silhouette photography (Edger-ton 1977, Ortner et al. 1979) so that identification of the planktonic organisms could be made without the aid of a microscope.

Plankton was collected three to four times per week by towing with a #10 plankton net (152 μ m) and a phytoplankton net (25 μ m) in the Waquoit Bay/Nantucket Sound areas. After collection it was sieved to remove objects >1000 μ m and to divide the plankton into each size group. Half of the plankton was used immediately while the other half was refrigerated overnight and used the following day.

Carapace lengths of Stage-V lobsters were measured to the nearest 0.1 mm using calipers, and their weights were recorded on a Brainweigh B300D scale to the nearest 0.001 g. The lobsters were blotted with absorbent paper to remove excess water prior to weighing. The experiment ran until all surviving lobsters attained Stage IX. During this time, the dates for all molts (for the determination of intermolt periods) and deaths were recorded. Although no post-mortems were performed, it was noted whether lobsters died in the process of molting or of unknown causes. Coloration of the lobsters was also noted. After achieving Stage IX, the lobsters were once again measured and weighed.

During the time of this experiment, a fifth group of lobsters (also siblings of the other four groups of lobsters) was raised in seawater tables for another experiment. The lobsters in this fifth group were placed individually into separate circular containers (85 mm diameter; 200 mm high) consisting of a black plastic bottom glued to a cylinder made of screening (1-mm mesh). These lobsters were fed the same amount of brine shrimp as the brine shrimp group of lobsters above, but lived in unfiltered, ambient seawater and were subject to ambient daylight plus overhead fluorescent lighting. Organic debris was cleaned out of the seawater table and containers at least once per month. While data on the initial (Stage V) weights and cara-

pace lengths are unavailable for this fifth group of lobsters, their final (Stage IX) weight and carapace length were recorded. Intermolt periods were recorded except for the period between Stages V and VI, since this group was held communally until after they had molted into Stage V.

Data for each of the measurements taken (intermolt period, initial (Stage V) and final (Stage IX) carapace lengths and weights) were analyzed using the Student's *t*-test when comparisons between two groups or two measurements within a group (i.e., initial and final weights or carapace lengths) were made, and by 1-way ANOVA tests when more than two groups were compared. Where ANOVA tests indicated significant differences were present, the groups were compared to determine which groups were different by using the Tukey test with unequal sample sizes. Differences in survival rates were tested with a 2 \times 2 chi-square contingency table. This experiment was conducted at the Marine Biological Laboratory in Woods Hole, MA from 13 July to 27 October 1987. The ambient seawater temperature ranged from 23 to 14.5°C and averaged 19.6°C.

Results

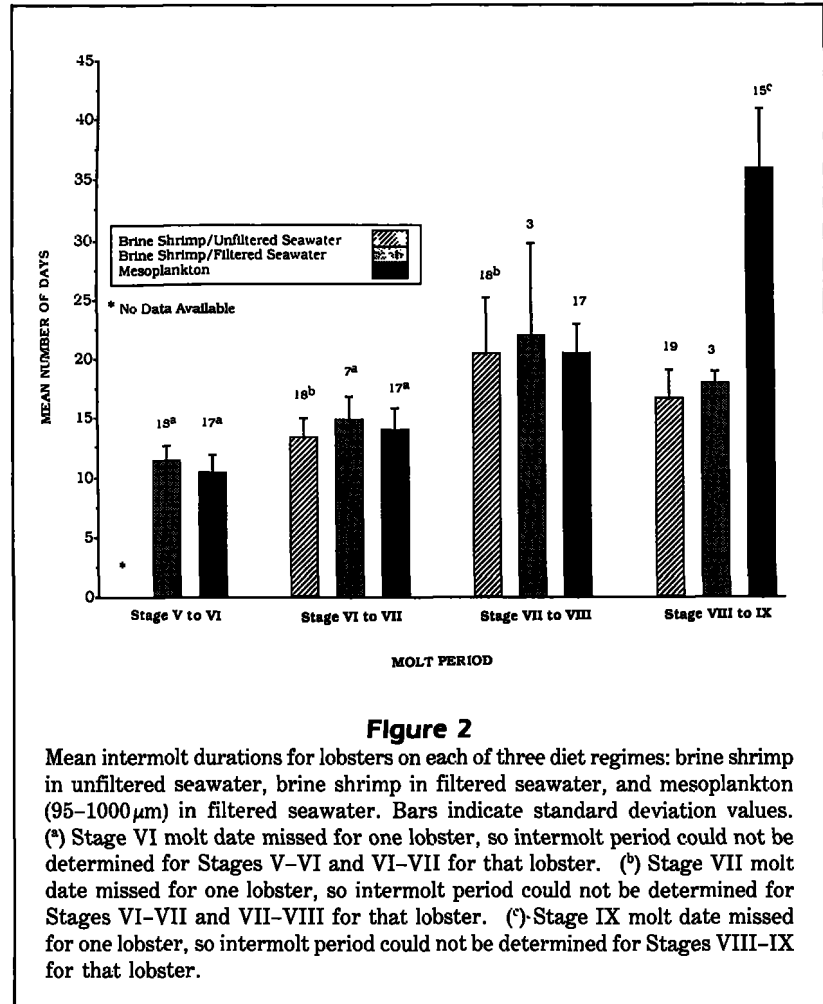
Survival was high in the groups fed brine shrimp in unfiltered seawater (95% survival), brine shrimp in filtered seawater (95% survival), and mesoplankton (90% survival) for the molt between Stage V and VI. During the subsequent molts, however, the group fed brine shrimp in filtered seawater had significantly higher mortality (χ^2 , $P < 0.001$; Fig. 1), with only 15% survival by the end of the experiment. The survival of the brine shrimp-fed group in unfiltered seawater remained unchanged, while that of the mesoplankton-fed group fell to 80% by the end of the experiment. However, there was no significant difference in survival between these two groups. Of the deaths noted for each of the groups, one lobster fed brine shrimp in unfiltered seawater and one fed mesoplankton died during its molt; of the 17 lobsters which died on the brine shrimp diet in filtered seawater, 14 died while in the process of molting. Coloration of the surviving groups differed, with the brine shrimp-fed group in filtered seawater being pale blue, typical of brine shrimp-fed lobsters, and the mesoplankton-fed group and brine shrimp-fed group in unfiltered seawater being the wild-type coloration.

None of the starved or meso/microplankton combination-fed lobsters molted beyond Stage V. All of the lobsters in these two groups died within 36 days of the 107-day experiment, and although the lobsters fed the meso/microplankton combination diet took slightly

longer to die (23.842 ± 10.035 (SD) days vs. 21.75 ± 7.063 days), this difference was not significant.

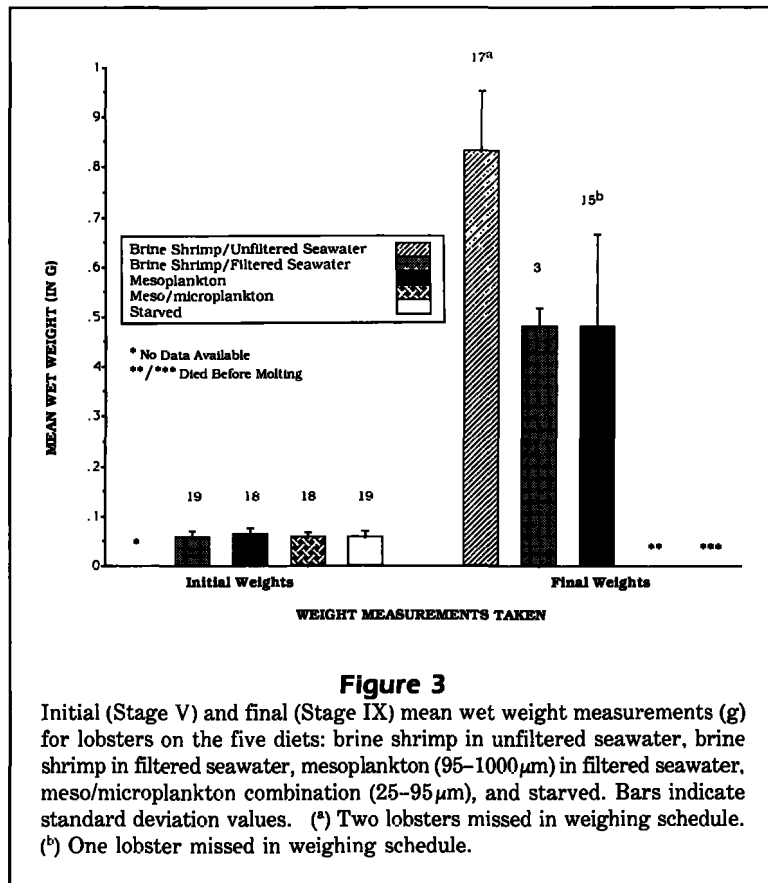
Intermolt duration data (Fig. 2) showed that the brine shrimp-fed group in filtered seawater took significantly longer to molt (by 1 day) into Stage VI than the mesoplankton-fed group (10.412 ± 1.502 days vs. 11.389 ± 1.243 days; Student's *t*-test, $P < 0.025$). Data are not available on the intermolt period between Stages V and VI for the brine shrimp-fed group in unfiltered seawater. There was no significant difference between the groups brine shrimp-fed in filtered seawater, brine shrimp-fed in unfiltered seawater, and mesoplankton-fed for the intermolt periods between Stages VI and VII (14.857 ± 2.035 vs. 13.444 ± 1.653 vs. 14.059 ± 1.853 days) and Stages VII and VIII (22.0 ± 7.810 vs. 20.556 ± 4.681 vs. 20.529 ± 2.528 days). However, the intermolt periods of both brine shrimp-fed groups were significantly different (18.0 ± 1 and 16.842 ± 2.292 days; 1-way ANOVA, $P < 0.001$; Tukey test, $P < 0.001$) from those of the mesoplankton-fed group (36 ± 5.057 days) for the molt between Stages VIII and IX, with the two brine shrimp-fed groups taking nearly half the time of the mesoplankton-fed group to molt into Stage IX.

There was no significant difference between any of the groups brine shrimp-fed in filtered seawater, mesoplankton-fed, meso/microplankton combination-fed, and starved lobsters at the beginning of the experiment in either weight (0.06 ± 0.011 vs. 0.066 ± 0.011 vs. 0.059 ± 0.009 vs. 0.061 ± 0.011 g, respectively; Fig. 3) or carapace length (4.66 ± 0.214 vs. 4.761 ± 0.214 vs. 4.739 ± 0.236 vs. 4.716 ± 0.236 mm respectively; Fig. 4). Although measurements are not available for the brine shrimp-fed group in unfiltered seawater, they probably did not differ significantly from the other groups since they were maintained in conditions identical to their siblings until immediately before the molt to Stage V. Each of the surviving groups of lobsters fed brine shrimp in filtered seawater, brine shrimp in unfiltered seawater, and mesoplankton showed significant growth (Student's *t*-test, $P < 0.001$) in terms of both increased weight and carapace length (Figs. 3 and 4). However, final (Stage IX) weights did differ between groups (1-way ANOVA, $P < 0.001$). The weight of the brine shrimp-fed group in unfiltered seawater (0.837 ± 0.117 g) was significantly greater (Tukey test, $P < 0.001$) than that of both the



brine shrimp-fed group in filtered seawater (0.484 ± 0.183 g) and the mesoplankton-fed group (0.484 ± 0.037 g). However, there was no significant difference between the latter two groups. Final (Stage IX) carapace lengths did not differ between the three surviving groups (brine shrimp-fed in filtered seawater, 9.9 ± 1.353 mm; brine shrimp-fed in unfiltered seawater, 10.459 ± 0.564 mm; mesoplankton-fed, 9.907 ± 0.732 mm).

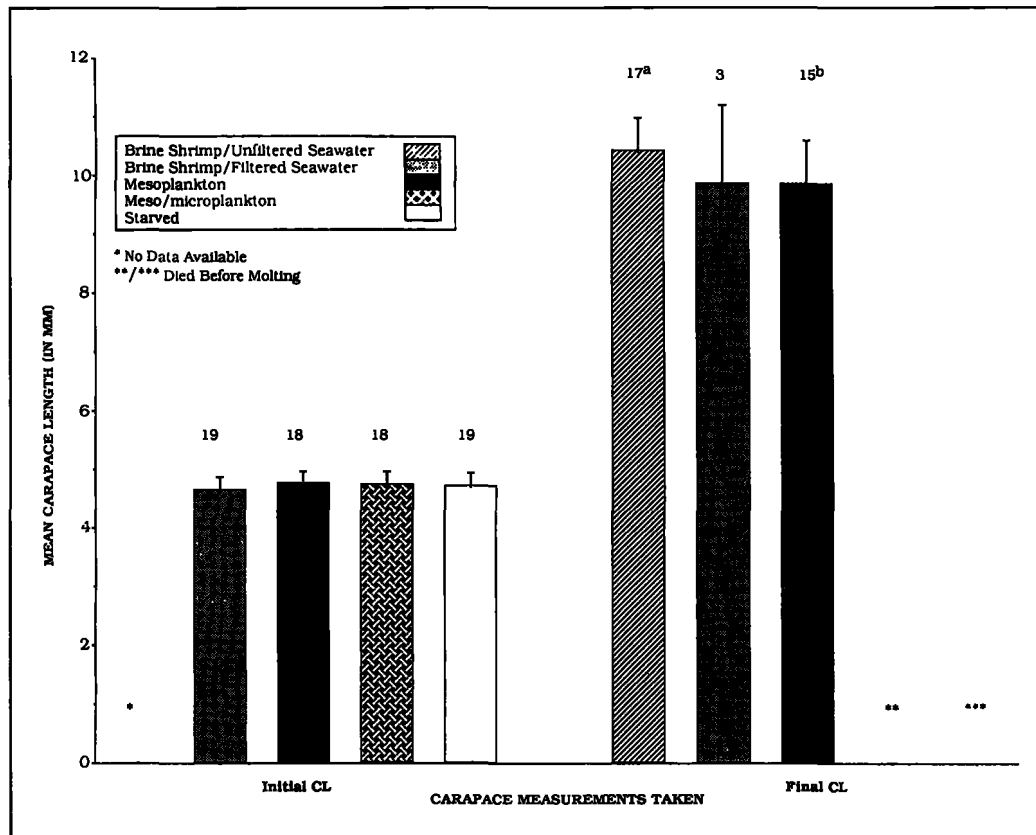
There was no significant difference in the wet weights of each diet fed the lobsters. The average wet weights of the diets were 0.408 ± 0.095 g for the mesoplankton; 0.364 ± 0.108 g for the meso/microplankton combination diet; and 0.391 ± 0.072 g for the brine shrimp diets. The mesoplankton diet consisted predominantly of *Acartia* copepods, barnacle nauplii, pagurid shrimp zoea, invertebrate eggs, brachyuran crab zoea, foraminifera, centric and pennate diatoms, and marine algae, with occasional instances of ascidian tadpoles, barnacle exoskeletons, fish eggs and young, amphipods, hydroids, brachyuran crab prezoa,



caridean shrimp zoea, *Centropages* and *Calanus* copepods, dinoflagellates, and juvenile nemertea. The meso/microplankton combination diet typically consisted of centric and pennate diatoms with occasional instances of fragments of marine algae and crustaceans.

Discussion

The results clearly indicate that early juvenile American lobsters are not capable of extending survival on a diet consisting mostly of diatoms, despite their common presence in stomach content analyses (Herrick 1895, Williams 1907, Herrick 1911). Larger planktonic organisms are required for survival and growth. This result is not entirely surprising even though Lavalli and Barshaw (1989) showed that post-larval and early juvenile (Stage V) American lobsters could remove particles from the water down to a size of at least 70 μm. Other crustaceans fed on phytoplankton can gain some nutrients and extend their survival in periods of low



food abundance, but this type of diet does not support molting or growth (McConaugha 1985). Post-larval lobsters are known to contain diatoms and other algae in their guts (Herrick 1895, Williams 1907, Herrick 1911) which suggests some nutritional role for these items, but one not fully understood nor clarified by this experiment. The smaller planktonic organisms in the meso/microplankton combination diet may not have been present in sufficient numbers to make up for the small amount of nutrients derived. Because the meso/microplankton diet consisted mostly of diatoms which have a high content of silicon-based ash, it is likely that this diet had a greater percentage of non-digestible fiber or bulk than that in the mesoplankton or brine shrimp diets (John Castell, Dep. Fish. & Oceans, Halifax, N.S., Canada B3J 2S7, pers. commun., May 1990). Furthermore, these smaller organisms may have been more easily flushed out of the containers when the water flow resumed.

The results presented here also clearly support those of Barshaw (1989) and Daniel et al. (1985) in terms of postlarval and early-juvenile lobsters being capable of surviving on mesoplankton, and in demonstrating high survival among the brine shrimp-fed (in filtered seawater) and mesoplankton-fed groups through Stage VI. These studies differ, however, in that Barshaw (1989) found molt delays in her plankton-fed group between Stages V and VI, whereas no molt delays were found in this study until Stage VIII. Barshaw's lobsters also took longer to molt into Stage VI (34 days for the plankton-fed lobsters and 23 days for the brine shrimp-fed lobsters) than did the lobsters in this experiment (10 and 11 days for the same groups), indicating that they were not receiving enough food and thus took longer to build up the reserves to molt. In addition, both Daniel et al. (1985) and Barshaw (1989) found that lobsters fed on frozen brine shrimp in filtered seawater were significantly larger than the filtrate-fed or plankton-fed lobsters. This study found no such difference between the similarly treated groups.

The differences between the two groups of lobsters fed on brine shrimp diets were striking. Lobsters fed brine shrimp in the filtered seawater had pale blue coloration and poor survival, with the majority of deaths occurring during molting. However, this difference in survival was not present until after Stage VI where Barshaw's (1989) experiment ended. Similar drops in survival of brine shrimp-fed lobsters in filtered seawater after Stage VI have been observed by Colleen Boggs (Edgerton Res. Lab. [in collaboration with the Kravitz Lab., Harvard Medical School], New England Aquarium, Boston 02110, pers. commun., summer 1990). Certain strains of brine shrimp promote better growth than others (McConaugha 1985), and the success of one strain versus another is linked to its fatty

acid content (Fujita et al. 1980), the presence of which is extremely important for the survival of postlarval and early-juvenile American lobsters (D'Abramo et al. 1981). The San Francisco Bay brand used in this experiment is intermediate in lipid content (McConaugha 1985), but even different lots of the same strain of brine shrimp are known to be highly variable in quality (Eagles et al. 1984, 1986). Thus, whatever nutritional component was lacking in the lot of the brine shrimp used in this experiment was compensated by the planktonic organisms entering through the ambient water supply, since the brine shrimp-fed group of lobsters in unfiltered seawater showed high survival, a greater weight increase compared with those in filtered seawater, and wild-type coloration. What is particularly interesting, though, is that while the lobsters fed brine shrimp in unfiltered seawater were nearly twice as heavy at Stage IX as both those fed brine shrimp in filtered seawater and mesoplankton, there was no significant difference at Stage IX between any of these groups in terms of carapace lengths. Weight, therefore, might be a more important index of growth in early-juvenile lobsters. The carapace lengths achieved by the three surviving groups of lobsters at Stage IX were shorter than those predicted by calculations of Hudon (1987) from early juveniles captured in the field. This contradiction may have resulted from the lobsters used in this experiment being hatchery- and laboratory-reared and thus being typically smaller than wild lobsters at Stage V (pers. observ.).

The difference in weights at Stage IX between lobsters fed brine shrimp in unfiltered seawater and those fed mesoplankton indicates that growth (as well as survival) might be significantly enhanced if the lobsters have access to both a planktonic diet and a diet of small benthic organisms. Andrea (1975) demonstrated that lobster larvae (Stages I-IV) fed frozen copepods or frozen amphipods had significantly higher survival rates than those fed frozen brine shrimp. Furthermore, those larvae fed live copepods had higher survival than those fed both live and frozen adult brine shrimp when held under the same rearing conditions. Andrea's data also showed that the increase in carapace length and the gain in weight by lobsters fed diets of live copepods were comparable to the increases found in lobsters fed live brine shrimp.

Evidence to date indicates that early juveniles are found in shallow subtidal areas (Cooper and Uzmann 1980, Hudon 1987, Able et al. 1988, Wahle 1990) where they would have access to suprabenthic plankton and epiplankton (Wieser 1960, Cornet et al. 1983) as well as surface plankton that vertically migrate in response to light/dark conditions (Hardy 1970). They would also have access to the many benthic organisms found in subtidal areas (Orth 1973, Reise 1977). In support of

this hypothesis, postlarvae and early juveniles in laboratory settings have been observed to lunge out of their burrows to grab at food (amphipods) passing by (Berrill 1974 with *H. gammarus*; Barshaw and Bryant-Rich 1988) or to stalk swimming amphipods (Good et al. 1982). Also, Crnkovic (1968) suggested that the creation of new openings in existing *Nephrops norvegicus* burrows may be linked to searching for food within the sediment.

The intermolt periods, with the exception of that for the mesoplankton-fed group between Stages VIII and IX, were consistent with or shorter than previous studies at the same average temperature (19°C) (Templeman 1948, as reported in Wilder 1953) and were close to the values predicted by Hudon (1987) for the same stages. These results show that early-juvenile lobsters fed on mesoplankton are able to capture it effectively enough to keep pace with the brine shrimp-fed lobsters in terms of intermolt periods until Stage VIII. At that time, the mesoplankton-fed lobsters spend nearly twice as much time in intermolt than either of the brine shrimp-fed groups. This result could be indicative of one of three conditions or some combination of all of them: (1) Either the lobsters became less efficient at capturing the plankton, (2) the planktonic organisms were not present in sufficient numbers in this study to compete with a brine shrimp diet at later stages, or (3) dietary requirements change with later molt stages.

In support of the first hypothesis is the fact that the claws of the postlarvae are small and symmetrical prior to Stage VIII. The claws slowly develop into the crusher and seizer claws during the early-juvenile stages; concomitant with this gradual development is a change in the posture of the lobster from one that is completely defensive (withdrawing or tail-flipping) to one that is more aggressive (Lang et al. 1977), and a change in the muscle fiber pattern and innervation of the two types of claws (Govind 1984). At Stage VIII the claw asymmetry is well established and the fiber composition and innervation are nearly the same as that found in the adult (Govind and Pearce 1986). These changes may indicate a shift in the feeding strategies used by the lobster, where capture of small benthic organisms becomes more important than the capture of planktonic organisms at or near Stage VIII.

As for the second hypothesis, Bordner and Conklin (1981) determined that older juvenile lobsters could consume up to 10% of their body weight per day. During this entire experiment, each group of lobsters was fed more than 10% of their body weight per day. Therefore, it seems unlikely that the later stages of lobsters were underfed on the mesoplankton diet. Finally, dietary requirements might indeed change as the lobster becomes more able to defend itself and thereby forage,

and as the claws develop the ability to crush small molluscs; however, this experiment was not designed to answer such a question.

In conclusion, the results from this experiment contradict those of Barshaw (1989) and Daniel et al. (1985) in that they show no difference in growth and survival of early-juvenile lobsters (Stages V and VI) fed on a diet of mesoplankton versus a diet of frozen brine shrimp in filtered seawater. Stage VI–VIII lobsters are able to survive and grow on planktonic diets, but after Stage VIII they experience molt delays when compared with lobsters fed frozen brine shrimp diets. Despite this delay, the mesoplankton diet allows the early juveniles the opportunity to reach the predicted (Hudon 1987) winter stages of Stage VI (for late-fall settlers) to IX or X (for August settlers) without the need for other benthic food. Diets composed of smaller members of the mesoplankton plus microplankton do not provide sufficient nutrition to support survival in periods of low food abundance.

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