GROWTH AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, ON A DIET OF PLANKTON

Larval American lobsters, *Homarus americanus*, are planktonic and are known to feed raptorially on zooplankton (Herrick 1895; Williams 1907; Templeman 1936). However, the benthic, postlarval stages of the American lobster are not routinely found in the field, and their natural habitat and feeding behavior are not known. Consequently, the natural diet of these stages is unknown. Stomach content analyses of larger juveniles and adult lobsters show that they feed on a great variety of benthic animals, including polychaetes, molluscs, macroalgae, and other crustaceans (Leavitt et al. 1979; Carter and Steele 1982).

Older juvenile and adult American lobsters, however, seem to have fundamental differences in their behavior compared with the early juvenile stages used in this study. Laboratory studies and field observations indicate that early juveniles are more (perhaps exclusively) shelter bound (as Cooper unpublished data in Cooper and Uzmann 1980; Lawton 1987; Barshaw and Bryant-Rich 1988). If the early juveniles do not forage for food outside of their burrows, they must feed in a different manner and on a different diet than that of older lobsters. During behavioral observations in naturalistic substrates, early juvenile lobsters were seen to generate a current through their U-shaped burrows by pleopod fanning (Barshaw and Bryant-Rich 1988). They appeared to catch and feed on the plankton that was carried in by this current. These observations form the basis for the hypothesis that early juvenile lobsters can feed upon plankton.

Materials and Methods

Stage IV lobster siblings from the Department of Fisheries and Oceans Laboratory, St. Andrews, New Brunswick, Canada were held in plankton "kreisels" (Hughes et al. 1972) for one day after being transported to Woods Hole, MA. These lobsters had all molted into Stage IV approximately two days before they were transported and were all fed on frozen brine shrimp until the experiment started. At the start of the experiment, individual lobsters were placed into 72 trays (22 cm long × 6.4 cm wide × 5 cm deep; water volume = 750 mL). Each tray was provided with filtered, ambient, running seawater, kept on a natural light/dark regime, and had an artificial lobster shelter made of black tubing glued to the bottom. The lobsters were allowed four days to acclimate to the trays before the experiment began. During this time, all of the lobsters were fed once on frozen brine shrimp (*Artemia*), and any dead lobster was replaced by another sibling. The 72 lobsters were then randomly divided into three groups of 24; one group was starved, one group was fed daily on five frozen brine shrimp per lobster, and the last group was fed daily on plankton. Dead, settled plankton was not used; only plankton which appeared living was presented to the lobsters. The trays were cleaned daily and any uneaten shrimp or plankton were removed.

The plankton was collected every other day by plankton tows in the Woods Hole area. After collection, the plankton was sieved through a 1 mm mesh. Half of the plankton was kept alive for 24 hours, while the rest was fed to the lobsters immediately. Representative subsamples from the daily portions were rinsed with distilled water, filtered, dried, and weighed; the same was done with the daily portion of frozen brine shrimp.

For one hour at the onset of feeding, the flow of seawater through all the trays was stopped so that the plankton-fed lobsters had a chance to feed before the plankton was flushed out of the trays. During this hour, informal observations were made on the behavior of the feeding lobsters. Movements of the lobsters in the trays, pleopod-fanning and mouth part activity were observed.

The experiment continued until all surviving lobsters had completed two molts; this took 65 days, from 14 October to 17 December 1984. During that time, all molts and deaths were recorded. The lobsters' weight and carapace length (CL) were taken after 40 days and at the end of the experiment. To make these measurements, each lobster was carefully removed from its tray and placed on absorbent paper to remove excess water. The lobster was then weighed to 0.01 mg on a Mettler balance; CL was measured to the nearest 0.1 mm using calipers. This procedure took less than two minutes and did not appear to adversely affect the lobsters.

Results

There was no significant difference in American lobster survival between the group fed brine shrimp (75% survival) and the group fed plankton (83% survival). All of the starved lobsters died by day 39 of the experiment (Fig. 1). This group is significantly different from the other two (χ^2, $P < 0.001$).

Nine of the starved lobsters molted to Stage V before dying. All of the surviving lobsters in the two
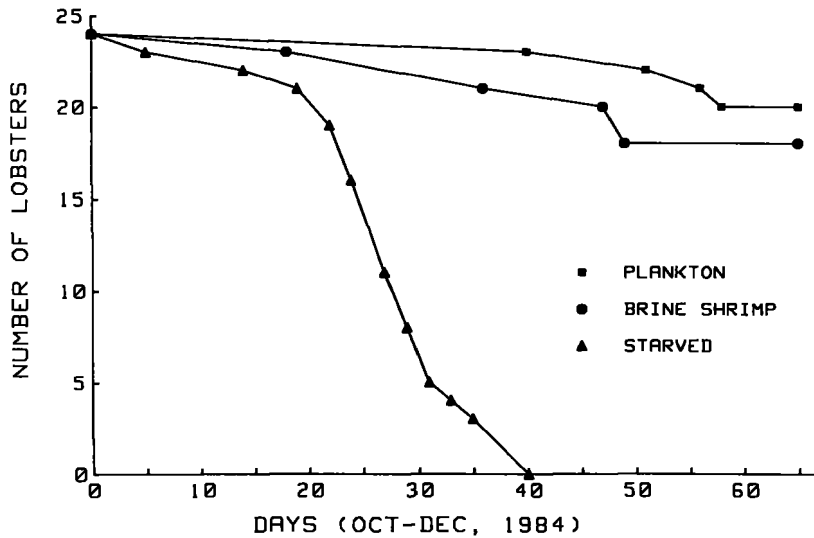
FIGURE 1.—The number of lobsters surviving in each treatment over the time course of the experiment.

fed groups molted twice during the experiment ending at Stage VI. There was no significant difference between the two fed groups in the number of days from Stage IV to Stage V. However, the plankton-fed group took an average of 34 days to molt from Stage V to Stage VI, significantly longer than the brine shrimp-fed group which took 23 days (Students t-test, $P < 0.001$; Fig. 2).

Both fed groups showed significant increase in CL and weight (Students t-test, $P < 0.001$). The group fed brine shrimp grew more; they were significantly larger (Students t-test, $P < 0.05$)
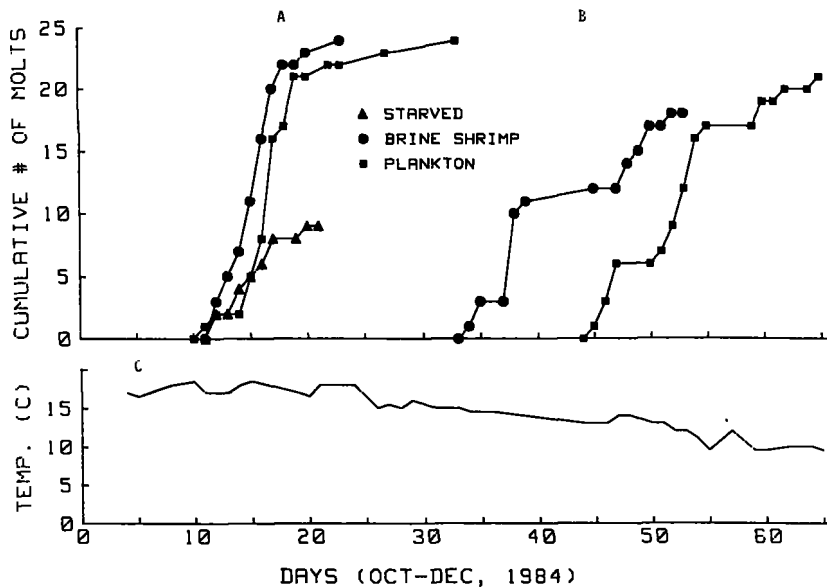

FIGURE 2.—The cumulative number of lobsters in each treatment molting from (A) Stage IV to Stage V and (B) Stage V to Stage VI.

and heavier (Students *t*-test, *P* < 0.001) at the end of the experiment than the group fed plankton (Fig. 3).

The brine shrimp-fed lobsters were observed to routinely leave their burrow in order to obtain the brine shrimp which was fed to them daily. They would then return and eat inside of their shelters. The plankton-fed lobsters behaved differently. After the plankton was placed in their tray, they would begin vigorous pleopod-fanning while remaining in their shelters. Plankton was seen being drawn into their shelters by this fanning.

The average dry weight of the plankton fed to the lobsters daily was 2.6 ± 1.4 mg, while the average dry weight of the brine shrimp fed to the lobsters daily was 5.0 ± 4.7 mg. The water temperature ranged from 18.5° to 10°C, averaging at 14.7°C.

Discussion

Emmel (1908) found that Stage IV lobsters could molt to Stage V without being fed when they were kept in flowing unfiltered water. Daniel et al. (1985) showed that early juveniles can survive and grow on a diet of frozen barnacle larvae. Budd et al. (1978) showed that the young crayfish, *Orconectes immunis*, can filter feed on algae by creating a feeding current and catching the algae in a filter formed by the first maxillipeds and their maxillae. Factor (1978) suggested that the mouthparts of larval lobsters have enough setae placed appropriately to make filter feeding a possibility. Upon close examination of Factors's data on Stage IV lobsters, it is seen that this stage has even more setae than the three previous stages. Recently, Kari Lavalli[1] has extended Factor's study, finding that lobsters, at least up to Stage VI, continue to have appropriately placed setae for catching plankton. Thus, morphologically, postlarval lobsters seem to be capable of catching plankton.

This experiment has shown that while the unfed postlarval lobsters all died, lobsters fed plankton survived as well as lobsters fed brine shrimp. The lobsters fed plankton also showed a significant increase in carapace length and weight. Therefore, these lobsters were able to catch and consume live plankton resulting in a net energy gain. Templeman (1936) found that lobsters held at 13°C took 29 to 30 days between their fifth and sixth molt; therefore, the rate of molting in the brine shrimp-fed group fell well within the rate of normal, nonfood limited molting at a temperature of 15°C.
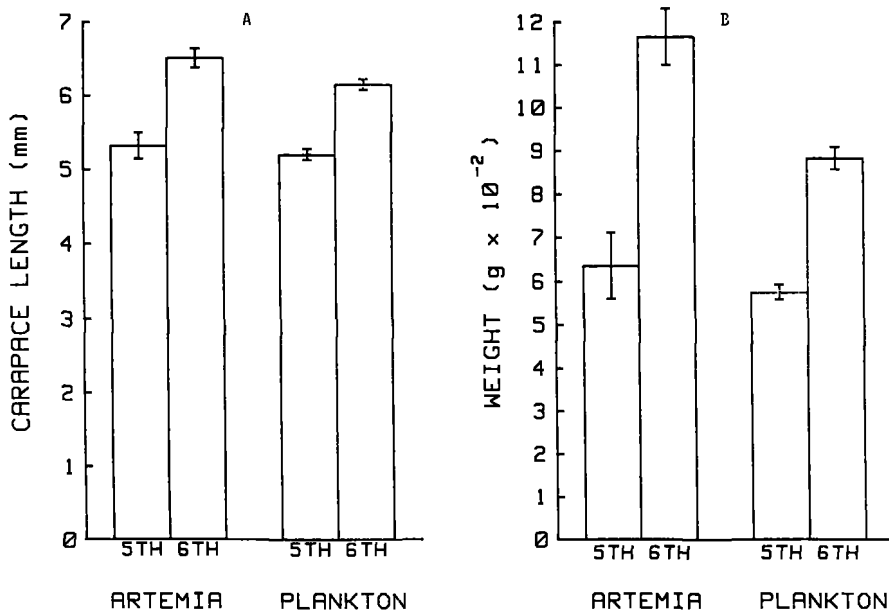
FIGURE 3.—The (A) carapace length and (B) weight of the *Artemia* (brine shrimp) fed lobsters and plankton-fed lobsters at Stage V and Stage VI, (C) water temperature over the time course of the experiment.

The amount of plankton that was given to the lobsters fell within the upper range of natural plankton densities found in Narragansett Bay, RI (Durbin and Durbin 1981). Juveniles living in deeper water would, of course, be unable to feed on algae and upper water plankton. However, suprabenthic plankton and swarming epiplankton are also plentiful (Cornet et al. 1983; Sainte-Marie and Brunel 1985) and could be caught in the same manner as the upper water plankton. I fed the lobsters in this experiment upper water plankton because evidence to date shows early juveniles to settle in shallow subtidal areas (as Cooper unpublished data in Cooper and Uzmann 1980; MacKay 1926; Hudon et al. 1986; Able et al. 1988). I do not wish to suggest that early juveniles feed exclusively on plankton; they also eat small benthic organisms in the vicinity of their burrows (Berrill 1974; Barshaw and Bryant-Rich 1988).

In this experiment, lobsters in the brine shrimp treatment were seen to routinely leave their shelters. While in a long-term experiment, lobsters never were seen out of their burrows (Barshaw and Bryant-Rich 1988). Perhaps these observations indicate that early juvenile lobsters more readily leave an artificial shelter than a burrow they construct themselves in a relatively natural habitat. Also, in this experiment, if the lobsters in the brine shrimp treatment had not left their shelters, they would have been unable to eat.

Many investigators have suggested that early juvenile lobsters do not leave their burrows in nature (e.g., Cooper unpublished data in Cooper and Uzmann, 1980; Atema et al. 1982; Barshaw and Bryant-Rich 1988), but this idea poses the problem of how the lobsters then forage for food. The results from this experiment indicate a mechanism by which settled lobsters can fulfill all of their energy and nutritional requirements while remaining in their burrows.

Acknowledgments

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BEHAVIORAL OBSERVATIONS ON FIN WHALE, *BALAENOPTERA PHYSALUS*, IN THE PRESENCE OF KILLER WHALE, *ORCINUS ORCA*

Detailed observations of baleen whales attacked by killer whales, *Orcinus orca*, are scarce. Most of these records involve attacks on gray whales, *Eschrichtius robustus* (e.g., Scammon 1874; Gilmore 1961; Morejohn 1968; Pike and MacAskie 1969; Rice and Wolman 1971; Baldridge 1972). Although reports exist of killer whale tooth marks on different body parts of fin whales, *Balaenoptera physalus*, sei whales, *B. borealis* (Hoyt 1981), minke whales, *B. acutorostrata* (Jonsgård 1968), and bowhead whales, *Balaena mysticetus* (Tomilin 1967); and although remains of some of these species (fin, sei, and minke whales) have been found in stomachs of killer whales (Nishiwaki and Handa 1958; Tomilin 1967; Rice 1968; Hoyt 1981; International Whaling Commission 1982), we know of only a few reports of direct observations of killer whales attacking mysticetes besides gray whales. These include attacks on 1) southern right whales, *Eubalaena australis* [= *glacialis*] (Cummings et al. 1972); 2) a humpback whale, *Megaptera novaeangliae* (Martinez and Klinghammer 1970); 3) a minke whale (Hancock 1965);

4) a female sei whale with a calf (Gaskin 1982); 5) a fin whale (Pike and MacAskie 1969); and 6) an immature blue whale, *Balaenoptera musculus* (Tarpy 1979). Of these authors, only Hancock (1965) and Cummings et al. (1972) provided some detailed behavioral observations.

In this paper, we describe the behavior of a group of fin whales in the presence of three killer whales and discuss these observations with regard to the available literature.

Field Observations

While searching for gray whales on 2 March 1982 (0850 h), we headed offshore from Tojahui (lat. 26°37′N, long. 109°23′W), a small fishing camp approximately 9 km SE of Yavaros, Sonora, in the Gulf of California, México, in a 5 m dory powered by a 75 hp outboard motor. Sea conditions were excellent with a calm and glassy water surface, no wind, and visibility about 6 km. Twelve km from shore, over a water depth of 50 m, we encountered a large group of 20 fin whales, judged to be adults (estimated total lengths ca. 18–20 m). We stopped the boat and motor within 40–300 m of the whales, and began observing their behavior. The whales formed closely spaced pairs or triplets within <5 m of each other and were lunge-feeding at the surface on dense patches of fish larvae and other macroplankton. The whales continued in this activity for 20 minutes, while forming a large semicircle off the stern of the boat at distances ranging from ca. 50 to 500 m (Fig. 1). None of the whales appeared to be moving in any definite direction.

While we were photographing a pair of fin whales swimming slowly north, 50 m from the boat and parallel to it, we sighted several killer whales ca. 200 m from us and heading in the direction of the pair. The killer whales were moving extremely fast and disturbing the water surface. The pair of fin whales continued swimming in their original direction for 30 m and then abruptly changed direction, by about 65°, increased their speed notably, and moved towards the boat (Fig. 1). At that time the killer whales were 60 m behind the fin whales, and the two sets of whales and the boat were all in straight line. As the killer whales moved to 20 m from the boat, the fin whales disappeared just below the surface, and at that instant, a killer whale's head protruded above the water with its mouth open and teeth visible. There were two other killer whales slightly behind the first one. Judging by the size and shape of their dorsal fins, all three individuals were females or immature males. The pair of fin whales