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LIFE HISTORY, ECOLOGY, AND BEHAVIOR OF *LIPARIS INQUILINUS* (PISCES: CYCLOPTERIDAE) ASSOCIATED WITH THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*¹

K. W. ABLE² AND J. A. MUSICK³

ABSTRACT

In the Mid-Atlantic Bight, spawning of *Liparis inquilinus* peaked near shore, away from sea scallop beds, in March and April. In the laboratory, females appeared to initiate spawning activity and each female probably spawned more than once. The eggs are adhesive and demersal and have been found attached to hydroids in nature. The larvae were most abundant in plankton collections inshore in May and averaged 5 mm total length at that time. Larger larvae were found in deeper water, and by 12-13 mm total length they had undergone metamorphosis and descended to the bottom where they became associated with the sea scallop, *Placopecten magellanicus*. They maintained this association from August through December. The population comprises a single year class which leaves the scallops and migrates inshore to spawn as the fish are entering their second year.

Laboratory and field observations indicated that fish were more abundant in the scallops and more scallops contained fish during the day. At night, fish left the scallops to feed on small crustaceans. *Liparis inquilinus* observed in aquaria used the fin rays of the lower lobe of the pectoral fin to detect food. These fin rays have taste buds on the surface of each ray.

Liparis inquilinus is probably protected from predation while inside sea scallops since there are few predators on the scallops of the size usually occupied. Predation while outside the scallop may be minimized by feeding only at night and then returning as soon as the fish becomes satiated. Sea scallops seem to suffer no ill effects from the association and they do not compete for food with *L. inquilinus* since *P. magellanicus* is a microplanktonic filter feeder and the former feeds on small crustaceans.

Little is known of the life history of most species of *Liparis*. Most of the meager information available for North Atlantic *Liparis* is included in Bigelow and Schroeder (1953), Andriyashev (1954), Leim and Scott (1966), and Wheeler (1969). Unfortunately, taxonomic problems remain and some published life history information may be incorrect because of misidentification. Recently, Detwyler (1963) studied the life history and reproductive biology of *L. atlanticus* from New Hampshire and Maine, and Able (in press) commented on the life history of a new species of *Liparis* from the Gulf of Maine. Elsewhere, Nizortsev et al. (1963) noted the stomach contents of *L. koefoedi*, *L. liparis*, and *L. laptevi* in the Barents Sea; Johnson (1969, 1970) reported on food habits and age and growth of *L. pulchellus* off California; Kosaka (1971) described the food habits and seasonal distribution of *L. tanakae* from Japan; Gibson (1972) mentioned the vertical

distribution and feeding of *L. montagui*; and Quast (1968) described the food habits of *L. mucosus* off California.

The association between *Liparis* (= *L. inquilinus*, see Able 1973) and the sea scallop, *Placopecten magellanicus*, has been reported by several authors (Bean 1884; Goode 1884; Garman 1892; Goode and Bean 1895; Jordan and Evermann 1898; Welsh 1915; Burke 1930; Bigelow and Schroeder 1953; Leim and Scott 1966) but information is lacking on most aspects of the association. The purpose of this paper is to report on the life history, ecology, and behavior of *L. inquilinus*.

MATERIALS AND METHODS

The life history stages, although often overlapping, are defined as follows: larvae—planktonic individuals usually 3-13 mm total length (TL), which have not transformed to adult coloration; juveniles—sexually immature benthic individuals with adult coloration, often associated with the sea scallop, approximately 14-45 mm TL; and adults—sexually mature individuals greater than 33 mm TL. The latter can be distinguished by the presence of prickles on the body of males

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and by the enlarged abdomen of females. Scallop anatomical terminology follows Bourne (1964).

Larval *Liparis* were examined from monthly collections of the National Marine Fisheries Service (NMFS) laboratory at Sandy Hook in the Mid-Atlantic Bight during 1966-67 (Clarke et al. 1969) and from routine plankton sampling on the Woods Hole NMFS RV *Albatross IV* cruises 69-5 and 72-3 off southern New England, in the Gulf of Maine, and on Georges Bank. The larvae of *L. inquilinus* can be distinguished from those of other *Liparis* which occur in the Mid-Atlantic Bight and the Gulf of Maine by differences in pigmentation pattern in combination with size at hatching, disc formation, and notochord flexion (Able 1974). The eggs were identified on the basis of their similarity, in size of the egg and melanophore pattern of the embryo, to eggs deposited by the laboratory population of *L. inquilinus*.

Juvenile *L. inquilinus* were collected from sea scallops which were taken in otter trawls during cruises of the *Sea Breeze* while on charter to the Virginia Institute of Marine Science, and *Albatross IV* cruises 69-11 and 70-6. Other *L. inquilinus* were collected from sea scallops on *Albatross IV* cruises 68-14 and 69-8 with a 3-m scallop dredge with a 5.1-cm ring bag which was towed for 10 min at each station. On *Albatross IV* cruise 68-14, bottom substrate type and amount were estimated from the scallop dredge catch. Size and number of scallops and regular hydrographic data were also recorded. On *Albatross IV* cruise 69-8, scallop dredge tows were replicated every 2 h during a 24-h period on 4-5 August 1969. The same general area was maintained during sampling by using information from depth recorders and loran navigation. The scallop catch at each station was divided into 5-cm height classes and a representative number of scallops were examined for *L. inquilinus* from each size class.

A large series of adult *L. inquilinus* collected off the New Jersey coast in the 1930's was examined from uncatalogued material of the Academy of Natural Sciences of Philadelphia. Other small collections were obtained from a variety of sources that are too numerous to mention here.

Liparis inquilinus and sea scallops were collected between lat. 39°30' and 40°10'N near Hudson Canyon in depths of 36-95 m and maintained in 10 to 25 gallon aerated aquaria with sand substrates for 15 mo. The aquaria were held in a cold

room at 10°-11°C. Winter temperatures in aquaria dropped as low as 4°C because of the absence of heating facilities. Salinity varied from 23 to 42‰. Illumination was provided by a 60-W bulb in one corner of the room. This provided approximately 86 to 280-lx illumination for the aquaria, depending on their location in the room. The light cycle was controlled automatically and approximated that in nature. Occasional power failures caused irregular variation in photoperiod and temperature.

Liparis inquilinus were fed live amphipods, usually *Orchestia platenis* and *Gammarus mucronatus*, and the mysid shrimp *Neomysis americana* and various other small crustaceans. Sea scallops were fed a mixture of algae, *Monochrysis lutheri*, *Isochrysis galbana*, and *Phaeodactylum triconutum*, that was added to the unfiltered aquarium water.

Pectoral fins of *L. inquilinus* were sectioned and stained with Harris' hematoxylin and eosin Y following fixation in 10% Formalin.⁴

LIFE HISTORY OF *LIPARIS INQUILINUS*

In the Mid-Atlantic Bight, spawning of *L. inquilinus* occurs near shore and away from scallop beds in the winter. In the early 1930's, over 700 adult, sexually mature and maturing *L. inquilinus* were collected from mid-December through April (Figure 1) off the coast of New Jersey and Delaware. This species was found from the Brigantine Can Buoy north of Atlantic City, N.J., to near the mouth of Delaware Bay and inside the bay at Old Bare Shoal and in deep holes off Brandywine (Shoal?) and Lewes, Del. Most of the collections were in 7-14 m; however, part of this series was from depths as shallow as 3-4 m "off New England Creek (near Cape May Co.)." Unfortunately, we have been unable to locate this area in New Jersey. Recently (January-March 1971 and January-February 1973) other mature adults were found off New Jersey, especially off Little Egg Inlet in depths from 4 to 7 m. Sea scallops were never taken in the vicinity of these collections (D. Thomas pers. commun.).

The average total length of *L. inquilinus* increases from December through April (Figure 1). Detwyler (1963) attributed an increase in total

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

length of *L. atlanticus* during the winter to the replacement of smaller adults by larger adults as the spawning season progressed. This may occur for *L. inquilinus*, but it seems more likely that sexually immature fish moving inshore in November, December, and January may continue to grow as they become sexually mature. In the laboratory, fish continued to feed during spawning periods. Although the range in total length for collections for each month is large, the variation about and between the means is small (Figure 1). This probably indicates that a single year class is present in each sample.

Spawning in *L. inquilinus* probably peaks in March and April. A single collection of *L. inquilinus* eggs was made on 9 March 1973, approximately 3.5 nautical miles off Holgate, Long Beach Island, N.J. Also, the adult fish represented in Figure 1 were examined for sexual maturity. The percentage of sexually mature fish increased from 12% in January, to 44% in February, and to 67% in March, but decreased to 33% in April, although this last sample was small. Hatching times for other *Liparis* vary from 22-30 days for *L. atlanticus* (Detwyler 1963) to 6-8 wk for *L. liparis* (Breder and Rosen 1966). Therefore, the occurrence of *L. inquilinus* larvae averaging 5 mm in May (Figure 1) infers that spawning probably takes place in March and April, and this is in agreement with the time of occurrence of sexually mature adults in inshore waters.

In the laboratory, reproductive activity and egg laying occurred over many months. During 1969, females distended with eggs and performing prespawning behavior (see below) were present from January through August. Eggs with eyed larvae were first found in late April and egg masses were found through June. Successful hatching occurred only in May. The extensive period of egg deposition and reproductive behavior observed in the laboratory does not agree with the limited reproductive period inferred from field collections. These differences may be attributable to the occasional power failures which affected photoperiod, water temperature, and water quality in the laboratory aquaria or simply to laboratory confinement.

It is likely that the average size of sexually mature males and females is similar and that the sex ratio is 1:1. A single collection of 143 *L. inquilinus* (off New England Creek, 7 m, 22 February 1933) contained 75 mature and maturing males (mean 55.3 mm TL, range 37.1-69.6 mm

TL) and 68 females (mean 54.3 mm TL, range 44.3-65.7 mm TL). Neither the ratio of males to females nor the average total length was significantly different.

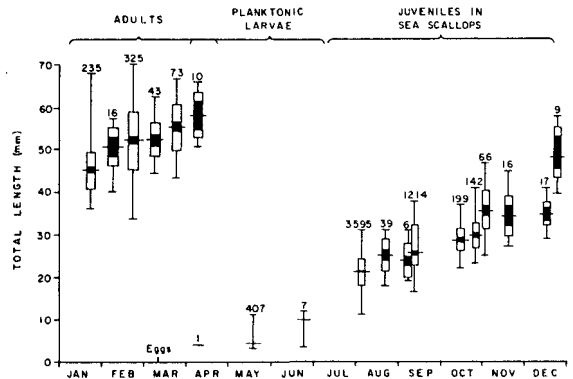


FIGURE 1.—Length-frequency distribution of *Liparis inquilinus* collected from the Mid-Atlantic Bight. For each sample, the range is represented by the vertical line, mean by the horizontal line, one standard deviation on each side of the mean by hollow rectangles and two standard errors on each side of the mean by solid rectangles. Numbers above figure are sample sizes. A single collection of *L. inquilinus* eggs is noted on the horizontal axis.

Female *L. inquilinus* may spawn more than once. In the laboratory, the abdomen of individual fish was observed to decrease in size as more egg masses were found in aquaria and increase again later. Also the egg diameters in ovaries of females from 16 March 1932 and 1933 usually had two well-defined modes. Fourteen ovaries were examined and most eggs were either 1.00-1.30 or 0.01-0.50 mm in diameter. The largest eggs were clear and contained several oil globules and these were more abundant in the center of the ovary. When egg diameter modes in the ovary were not well-defined, egg distribution by size was often random. Counts for the larger eggs ranged from 105 to 1,135 (mean 447) in seven ovaries from females raised in the laboratory and from 231 to 563 (mean 342) for females collected off New Jersey. The high count for females raised in the laboratory may have been due to the failure of the female to spawn and continued development and accumulation of the eggs in the ovary because of disturbances in the laboratory. There seemed to be no correlation between fish size and egg numbers. The average number of eggs is less than the 475 to 700 eggs reported for *L. atlanticus* (Detwyler 1963), a larger species.

Spawning Behavior

Female *L. inquilinus* may initiate spawning activity. In laboratory aquaria females with distended abdomens were the most active. They often swam in quick dashes around the sides of the aquarium then up to the surface and down again. During these dashes, the snout came out of the water and there was considerable splashing. Similar behavior has been reported for *L. atlanticus* females (Detwyler 1963). This activity often lasted several minutes and on one occasion 7 min and 20 s. Occasionally during these excited dashes the females would bump into other fish, both males and females. In a few instances, this activity seemed to excite other females and they also became active. In one instance, a ripe female repeatedly nudged with her snout a fish of unknown sex that was attached to the side of the aquarium. Soon a prominent bulge appeared just posterior to the genital papilla of the female. This has been observed just before spawning in *L. atlanticus* (Detwyler 1963) and *Cyclopterus lumpus* (Cowan 1929). In this instance, the nudged fish did not respond and the female swam away. The bulge receded after about 5 min. Sexually mature males are covered with numerous prickles while the females usually lack these or have only a few. Thus, the female may be able to recognize males by making contact with them. Breeding tubercles and contact organs in fishes may function in maintenance of body contact between the sexes during spawning and stimulation during breeding (Wiley and Collette 1970). The prickles on *L. inquilinus* males may function in these ways also. Spawning was not observed but is probably similar to that in *L. atlanticus* (Detwyler 1963). In the laboratory, *L. inquilinus* deposited small clumps of 20-80 eggs on the bottom of the aquaria and did not guard them. The eggs collected on 9 March 1973 off New Jersey were attached to hydroids as has been reported for *L. liparis* (Ehrenbaum 1905). The larvae that hatched in the laboratory did not survive beyond yolk sac absorption.

Larvae

In the Mid-Atlantic Bight, larvae of *L. inquilinus* are planktonic during the spring. During monthly larval fish surveys in 1966-67 by the Sandy Hook Laboratory, 98% of the *L. inquilinus* larvae were collected in May (Figure 1) from deep and shallow tows. These averaged 5.1 mm TL

(range 3.2-12.0 mm TL). Larvae were most abundant in samples collected nearest to shore (Figure 2). Other larvae of the same average size have been collected during May from inshore waters in the Gulf of Maine and on Georges Bank (Table 1, Fig. 3). Larvae larger than 13 mm TL were usually not found in the plankton.

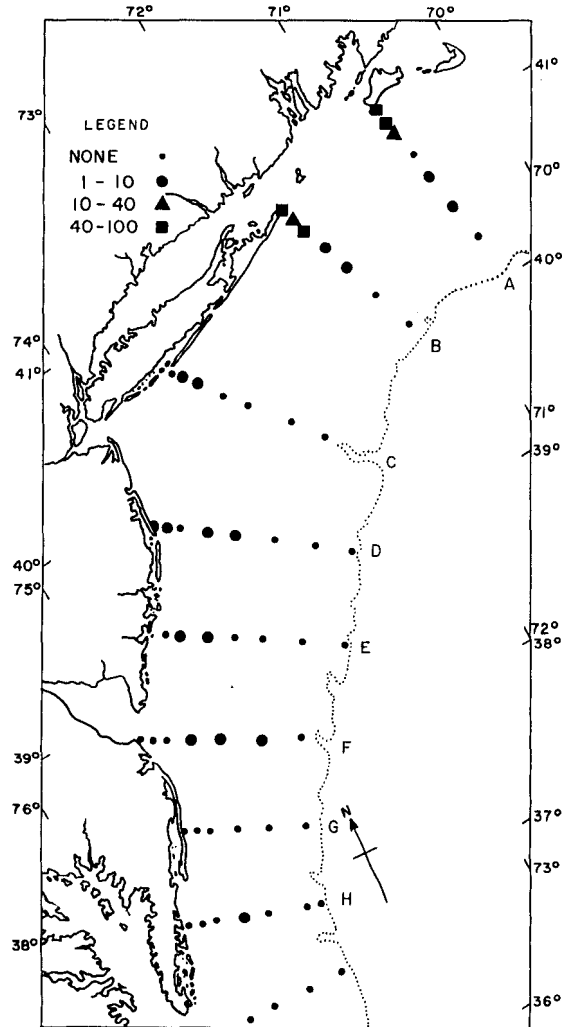


FIGURE 2.—Distribution and abundance of larval *Liparis inquilinus* from Dolphin cruise D-66-5 during May 1966.

Juveniles

In the Mid-Atlantic Bight, juvenile *L. inquilinus* are associated with sea scallops from August through December. Stevenson⁵ reported

⁵Stevenson, J. A. Fish. Res. Board Can., St. Andrews, New Brunswick, Manuscr. Rep. 373.

TABLE 1.—Collections of larval *Liparis inquilinus* from plankton sampling cruises. Mean followed by range in parentheses.

Item	Dolphin 66-3	Dolphin 66-5	Dolphin 66-7	Albatross IV 69-5	Albatross IV 72-3
Locality	Mid-Atlantic Bight	Mid-Atlantic Bight	Mid-Atlantic Bight	Georges Bank	Southern New England Gulf of Maine Georges Bank
Date	8 April 1966	12-20 May 1966	18-27 June 1966	22-26 May 1969	6-16 May 1972
Water depth (m)	—	—	—	73.0(65-88)	65.8(36-96)
Number collected	1	414	7	28	73
Number measured	1	269	7	26	32
Total length (mm)	3.8	5.0(4.0-11.0)	9.4(3.4-11.5)	5.8(3.5-15.7)	4.6(3.7-10.0)

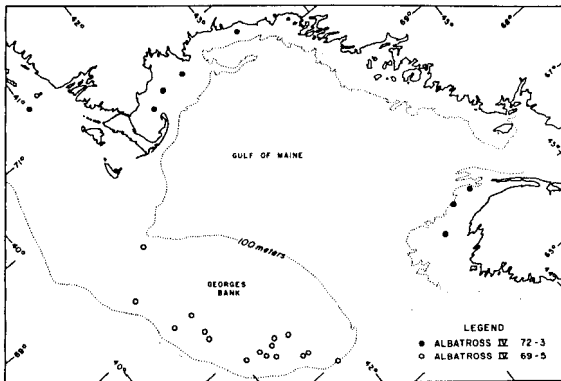


FIGURE 3.—Locations of collections of larval *Liparis inquilinus* from Albatross IV cruises 69-5 and 72-3.

Neoliparis (Liparis) atlanticus from sea scallops as early as July in the Bay of Fundy off Digby, Nova Scotia. Specimens we have from sea scallops in that area are all *L. inquilinus*. Juvenile *L. inquilinus* have also been collected from scallops from Georges Bank in July and may be present in sea scallops during July in the Mid-Atlantic Bight as well. The fish found in the scallops during August (Figure 1) corresponded in size with that expected from the earlier collection of planktonic larvae (Figure 1) and represented the same year class. The average total length of fish from scallops increased steadily from August through November (Figure 1). The small variation in each collection indicated that there was a single year class inhabiting sea scallops during a single year. *Liparis inquilinus* have been collected from sea scallops as late as mid-December (17 Dec. 1967, lat. 38°20'N, long. 73°59'W, 66 m and lat. 38°18'N, long. 74°23'W, 42 m) (Figure 1). The absence of fish in the scallops collected in January (18 Jan. 1968, lat. 38°34.5'N, long. 73°36'W, 62 m; 26 Jan. 1968, lat. 38°05'N, long. 74°13'W, 66 m) corresponds with the appearance of *L. inquilinus* inshore off Delaware and New Jersey during the same periods. These mature and maturing fish

represent the same year class as the juveniles that were associated with sea scallops. Therefore, *L. inquilinus* reproduces when 1 yr old in the Mid-Atlantic Bight.

Adults may not survive to spawn the following year. Specimens larger than 50 mm have never been taken from May through December. The life history of *L. inquilinus* in the Mid-Atlantic Bight is summarized in Figure 4.

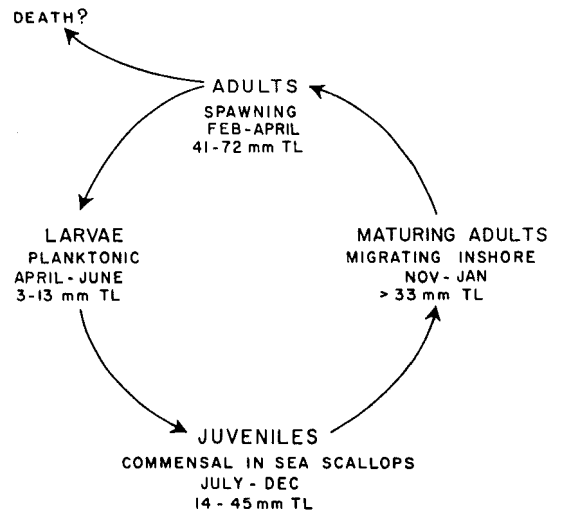


FIGURE 4.—Schematic presentation of the life history of *Liparis inquilinus* in the Mid-Atlantic Bight.

ECOLOGY AND BEHAVIOR OF *LIPARIS INQUILINUS* ASSOCIATED WITH SCALLOP

Resting

In aquaria, *L. inquilinus* preferred an inverted resting position with the disc attached to any smooth substrate such as the side of the aquarium, the interior of mollusk shells, rocks, or glass containers. Once attached, the fish flexed its

tail so that the caudal fin was alongside the head. From 13 November to 20 December 1968, observations were made on the position of fish attached to four hinged sea scallop shells or "clappers." These were positioned on the bottom of an aquarium, with one of each of these pairs placed with the right valve (flat valve) up and the left valve down. One valve rested on the bottom and the other was at an angle of approximately 30°-40°. Of 40 observations, 95% of the fish in shells were attached upside-down to the top valve of the clapper with as many as eight attached to the same valve. The inverted resting position was also the most commonly observed during the remainder of the time fish were maintained in the laboratory.

Feeding

Liparis inquilinus has several morphological and behavioral adaptations which may allow it to feed at night. In aquaria, fish swimming over the bottom appeared to depend on reception of tactile and/or gustatory stimuli received by the head and pectoral fins. Swimming resulted from the combined action of the tail and the upper lobe of the pectoral fins. The eight or nine filaments in the lower lobe of the pectoral fins were extended vertically toward and often touched the bottom. When amphipods were placed in aquaria, fish did not appear to respond to visual cues but feeding usually occurred when the head or the lower lobe of the pectoral fin touched an amphipod. If food touched the head, it was immediately ingested. If food touched the pectoral fin, the fish quickly backed up or arched its body to the side and sucked in the prey. The rays in the lower lobe of the pectoral fin of *L. inquilinus* contain dark staining buds along the surface of each ray (Figure 5A) which are most abundant at the tips (Figure 5B). They are identified as taste buds on the basis of their similarity to the figures presented by Bardach and Case (1965). They described the sensitivity of the pelvic fins in *Urophycis chuss* and the pectoral fins in *Prionotus carolinus* and *P. evolans* to gustatory stimuli. Freihofner (1963) suggested that the particular pattern of the ramus lateralis accessorius nerve to the pectoral and pelvic fins in the Liparidae allows the development of these fins as "sensory, locomotor and support appendages." The well-developed cephalic lateralis system of *L. inquilinus* may also function in detecting moving

prey. Occasionally fish sucked in amphipods which passed within less than 1 inch of the head.

Liparis inquilinus feeds on benthic prey. Stomachs of fish collected in nature contain almost exclusively small crustaceans and small numbers of sand grains. In the laboratory, sand from the bottom was frequently sucked in with food items and then discharged from the gill opening. A round mouth, as in *L. inquilinus*, is well-adapted to sucking in prey (Alexander 1967).

Behavior of Fish Associated with Sea Scallops

The association between *L. inquilinus* and sea scallops is well-developed and both partners show definite behavioral adaptations. Fish collected from sea scallops were isolated from them for several weeks. Upon reintroduction of fish into aquaria containing acclimated sea scallops, many of the fish swam around and over the scallops but concentrated most of their activity along the scallops' mantles. Most fish alternated between swimming parallel to the mantle with the lower lobe of the pectoral fin extended toward it or swimming with the head oriented directly toward the mantle. The tentacles on the mantle often contracted but the valves did not close. On one occasion a fish "mouthed" a tentacle, an action similar to the acclimatization behavior of some pomacentrid fishes associated with anemones (Mariscal 1966). On two occasions, fish attached to the mantle, and in one of these instances the tentacles of the scallop mantle moved over the body of the fish and depressed the anterior portion of the dorsal fin. There was no reaction by either partner and eventually the fish attempted unsuccessfully to enter the scallop.

The tentacles of the sea scallop are tactile and chemical receptors (Bourne 1964) and may be able to discriminate between *L. inquilinus* and other fishes. In aquaria, sea scallops exposed to individuals of *Gobiosoma bosci* and *Gobiosox strumosus* reacted negatively, when the mantle of the scallop was brushed by either species, by closing the valves. Similar results were observed when *Fundulus heteroclitus* and *Tautogolabrus adspersus*, were exposed to sea scallops (Musick 1969).

Liparis inquilinus occasionally may enter an alternate host species. Hoff (1968) reported a specimen of *L. atlanticus* from the bay scallop, *Aequipecten irradians*, in Buzzards Bay, Mass.

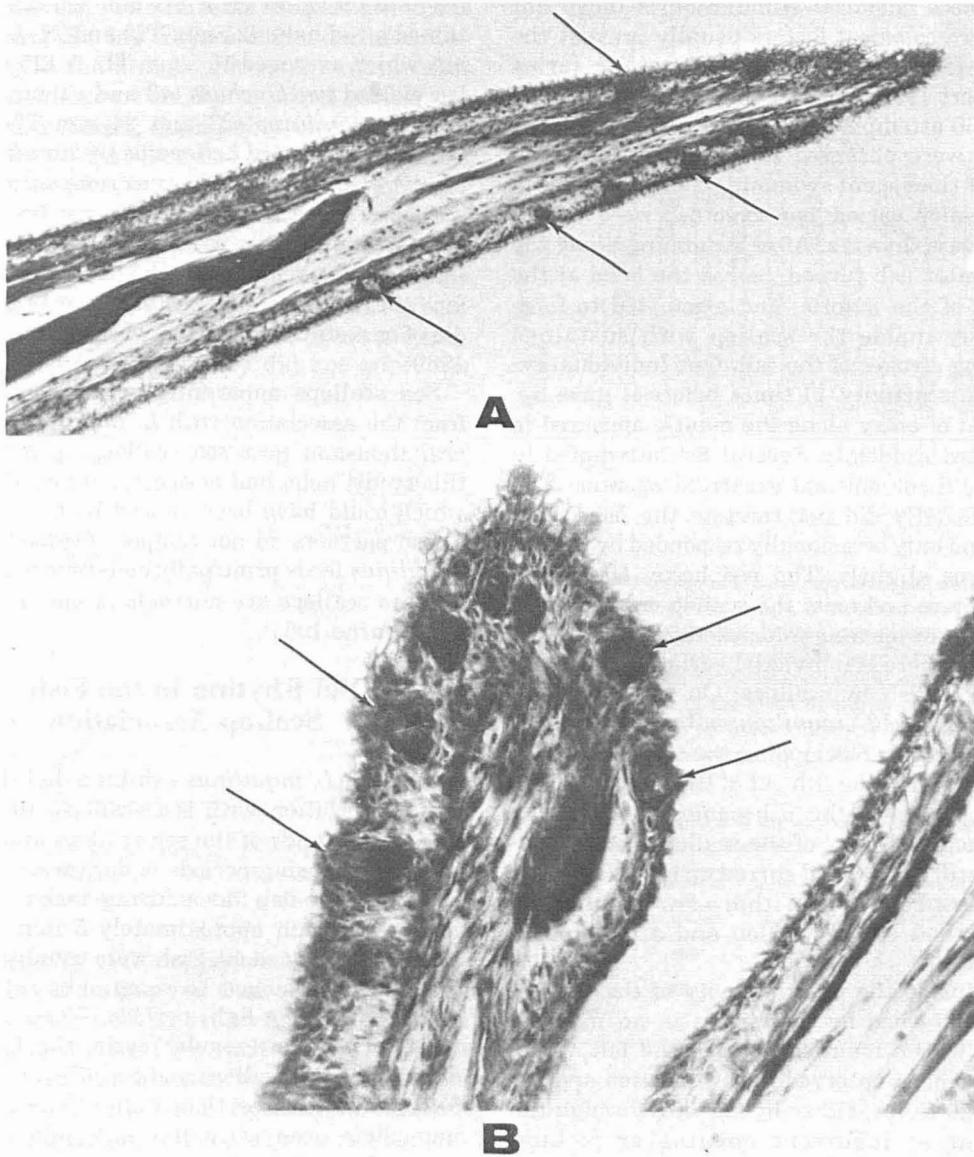


FIGURE 5.—Section through a fin ray from the lower lobe of the pectoral fin of *Liparis inquilinus* stained with hematoxylineosin. Arrows indicate taste buds. A. Taste buds on margin of fleshy portion of fin ray. B. Numerous taste buds at the tips of the fin rays.

We identified a specimen provided by him as *L. inquilinus*. Since that initial occurrence he has collected several other *Liparis*, which are probably also *L. inquilinus*, from bay scallops (pers. commun.). *Liparis inquilinus* originally collected from sea scallops were placed in aquaria with bay scallops to determine if they would attempt to enter the scallops. These scallops were completely ignored and the fish made no attempt to enter or

attach to them. When brushed by *L. inquilinus*, the bay scallops either showed no response or closed the valves slightly. Bay scallops are found in much shallower water than the sea scallops, and the occurrence of *L. inquilinus* in depths frequented by bay scallops is unusual. These fish which occur in shallower water may attempt to associate with bay scallops in the absence of their regular host. Confusion in host recognition may

occur where chemical stimulation is important but other ecological factors usually prevent the animal from associating with other forms (Davenport 1955).

Over 30 attempts by *L. inquilinus* to enter sea scallops were observed in the laboratory. The length of time spent swimming along the mantle of the scallop varied, but some fish were able to enter in less than 3 s. After swimming along the mantle most fish turned, placed the head at the margins of the mantle, and attempted to force their way inside the scallop with sustained swimming strokes of the tail. One individual repeated this activity 10 times before it gave up. The point of entry along the mantle appeared to be selected randomly. Several fish attempted to enter the incurrent and excurrent opening. The scallop usually did not react to the fishes' entrance and only occasionally responded by closing the valves slightly. The red hake, *Urophycis chuss*, enters and exits the scallop only through the excurrent opening (Musick 1969).

Perhaps there is individual variation in the acceptance of fish by scallops. On two occasions, scallops rejected *L. inquilinus* after they had entered the scallop by clapping the valves together and thus forcing the fish out of the mantle cavity. In each instance, the fish came to rest a few inches from the edge of the scallop. The fish remained still as the sand stirred up by the scallop's activity settled over it. Within a few minutes, the fish returned to the scallop and attempted to enter again.

Once inside the mantle cavity of the scallop, the fish attached by their discs in an inverted position to the mantle tissue of the left valve. Fish have been observed in this position approximately 20 times, either by viewing through the excurrent or incurrent opening or picking the scallop out of the water and looking in as it clapped. Often several fish were observed in the same scallop simultaneously. This position in the scallop is the same as that preferred by fish attached to clam shells and other smooth substrates. In approximately 100 other instances, *L. inquilinus* presence in sea scallops was confirmed by their absence elsewhere in the aquaria.

Liparis inquilinus and *U. chuss* apparently cooccur in sea scallops frequently and in considerable numbers. We have collected these fishes together in sea scallops from Georges Bank in September, November, and December. In the Mid-Atlantic Bight (4 August 1969, lat. 39°40'N,

long. 73°09'W, 40 m) a 141-mm sea scallop contained a red hake (21 mm TL) and 21 *L. inquilinus* which averaged 16.5 mm TL. A 125-mm scallop yielded two *U. chuss* (43 and 47 mm TL) and two *L. inquilinus* (23 and 24 mm TL). Goode (1884) also reported *L. lineatus* (= *inquilinus*) and *Phycis* (= *Urophycis*) *chuss* as companions in sea scallops. These two fishes may not be in direct competition for this particular habitat since the *L. inquilinus* remain attached to the upper surface of the cavity and *U. chuss* swims in the middle of or rests on the bottom of the cavity (Musick 1969).

Sea scallops apparently suffer no ill effects from the association with *L. inquilinus*. Of several thousand host sea scallops opened during this study, none had noticeable internal damage which could have been caused by *L. inquilinus*. These partners do not compete for food since *L. inquilinus* feeds principally on larger crustaceans and sea scallops are microplanktonic filter feeders (Bourne 1964).

Diel Rhythm in the Fish— Scallop Association

Juvenile *L. inquilinus* exhibit a diel rhythm in their association with sea scallops. In aquaria, fish were outside of the sea scallops and actively swimming during periods of darkness. The color pattern of the fish faded during dark periods but returned within approximately 5 min after the lights were turned on. Fish were usually inside of scallops or attached to some substrate in the aquarium during light periods. When the lights went off on their regular cycle, the fish would often leave the scallops and become active within 5-10 min. These reactions to light and dark were immediate even when the dark-light cycle was changed drastically during a single day. *Liparis inquilinus* which were collected from sea scallops during a 24-h period on 4-5 August 1969 near Hudson Canyon (Figure 6) exhibited the same pattern (Figure 7). During this period, 3,595 *L. inquilinus*, averaging 21.0 mm TL, were collected from 616 of the 841 scallops examined. In one instance, 32 fish were found inside a 139-mm scallop. Fish were more abundant in scallops and more scallops contained fish during the day than at night (Table 2). However, some fish were present in scallops during every sampling period. The greatest increase and decrease in the number of fish per scallop occurred around sunrise and sun-

set respectively. The number of fish per scallop was high during the day (Figure 7) and declined substantially in the first sample after sunset. After the initial decrease in the numbers of fish per scallop after sunset, the number increased regularly up to daytime levels as sunrise approached. The number of fish in scallops was slightly greater than presented in Figure 7. Fish found outside of scallops (122 or 3% of the total) in the collecting buckets or on the deck were not included in the averages. However, these fish were more abundant at stations where the number of fish per scallop was greater so that they did not affect the comparative data.

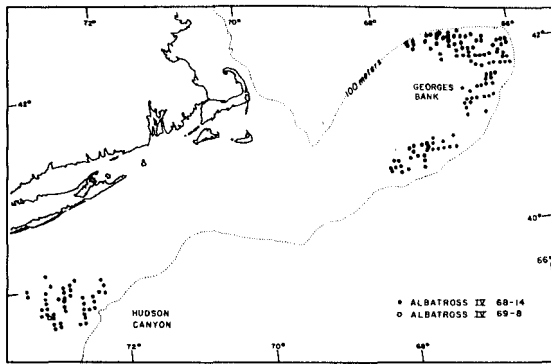


FIGURE 6.—Locations of sampling sites for fish-scallop association on 5-17 September 1968, *Albatross IV* cruise 68-14 and on 4-5 August 1969, *Albatross IV* cruise 69-8.

The majority of *L. inquilinus* leave scallops to feed during the night and then return near sunrise or as they become satiated. Sixty stomachs were examined (five from each sampling period) and were assigned a separate value for relative fullness (0-4) and state of digestion of contents (1-3) with the highest numbers given to stomachs with the most food and the least degree of digestion. When added together, these give a relative value referred to as the stomach analysis index. The maximum value possible is 7, the minimum is 1. The higher values should be from fish which had recently fed, and digestion had not begun or had not progressed very far. The stomach analysis index values increased from 2200 h, with highest values occurring just before and after sunrise (Figure 8). The lowest values were found just before and after sunset (Figure 8). Whole undigested amphipods were found in stomachs of fish taken at night, but after 0800 h stomach contents were in increasingly advanced stages of

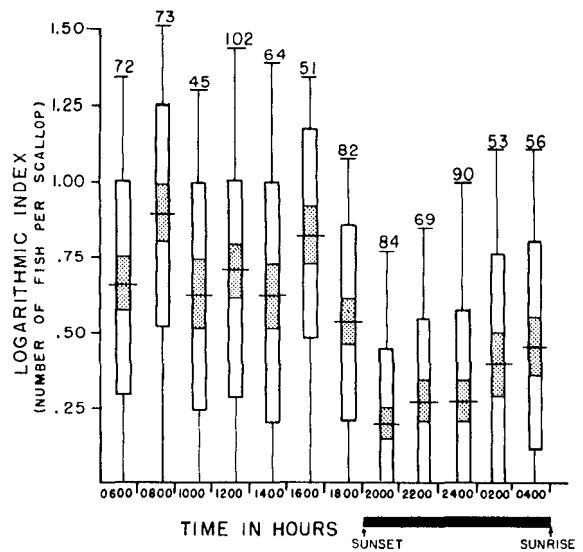


FIGURE 7.—Number of *Liparis inquilinus* per scallop from the combined total of two 10-min tows taken every 2 h over a 24-h period on 4-5 August 1969 at approximately lat. 39°39'N, long. 73°08'W. For each sample, the range is represented by the vertical line, mean by the horizontal line, one standard deviation on each side of the mean by hollow rectangles and two standard errors on each side of the mean by solid rectangles. Numbers above each figure represent the number of scallops sampled.

TABLE 2.—Comparison of the number of *Liparis inquilinus* in sea scallops during the day and night for a 24-h period.

Time	Number of scallops examined	Mean number of fish per scallop	Percent of scallops with fish	Number of replicated stations
Day (0503-1908 h)	489	6.1	86.3	7
Night (1909-0502 h)	352	1.7	57.3	5
Total	841	4.2	73.2	12

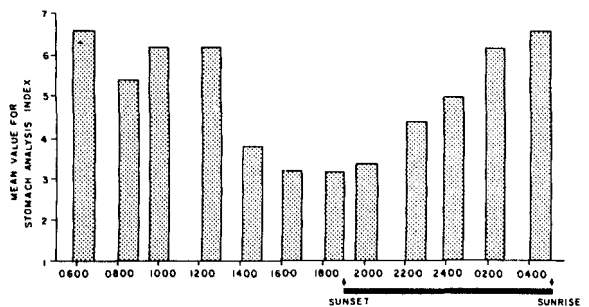


FIGURE 8.—Results of stomach analysis of *Liparis inquilinus* taken from scallops over a 24-h period on 4-5 August 1969. Stomach analysis index value for each stomach was derived from ranking relative fullness (0-4) which is added to the state of digestion of the contents (1-3), with the highest numbers given to stomachs having the most food and the least degree of digestion.

digestion until only unidentifiable material remained in stomachs collected just before and after sunset. Fish with full stomachs and undigested contents were first collected at 2200 and 2400 h. These were probably returning to scallops as they became satiated. All fish do not leave the scallops at sunset (Figure 7). Some may remain if they still have food in their stomachs. Those fish examined around 2000 h did not have completely empty stomachs (Figure 8). None of the fish examined at 0200 and 0400 h had empty stomachs.

The number of *L. inquilinus* occupying sea scallops probably decreases through the fall and early winter. During September 1968, 43 collections near Hudson Canyon (Figure 6), which overlapped the collecting area in August 1969 (Figure 6), yielded fewer fish per scallop (Table 3) than in August. These differences could be due to relative year-class strength or may reflect an actual change in the number of fish occupying scallops later in the year. Mortality of *L. inquilinus* owing to predation or a breakdown in the association as the fish grow larger could explain a decrease of this magnitude. Small numbers of sea scallops collected during the fall and early winter of several years did not yield as many *L. inquilinus* as were collected earlier in the year.

Size of individual sea scallops may be a factor in their selection by fish. In one instance, a 60-mm scallop contained a 21-mm TL fish, but it is the larger scallops which contain the largest number of fish (Figure 9).

TABLE 3.—Abundance and average total length of *Liparis inquilinus* in sea scallops from August 1969 and September 1968.

Collecting dates	Number of scallops examined	Mean number of fish per scallop	Maximum number in single scallop	Average TL of fish (mm)
4-5 Aug. 1969	841	4.2	32	21.0
14-17 Sept. 1968	717	1.7	18	26.1

Geographic Variation in Abundance of Fish in Scallops

The abundance of fish in scallops varies with geographic location (Figure 10). On *Albatross IV* cruise 68-14, 155 10-min scallop dredge tows were made as part of a sea scallop survey on Georges Bank and in the Mid-Atlantic Bight near Hudson Canyon (Figure 6). From these, 2,274 *L. inquilinus* were collected from 1,228 of the 5,905 sea scallops examined. The mean number of fish per scallop (Figure 10) and the mean number of

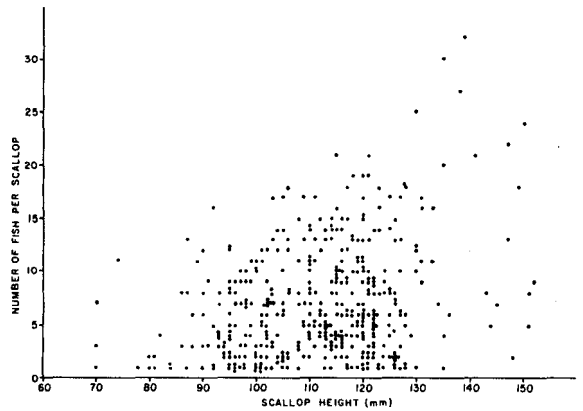


FIGURE 9.—Plot of mean number of fish per scallop versus scallop height (mm) from daytime collections from *Albatross IV* cruise 69-8.

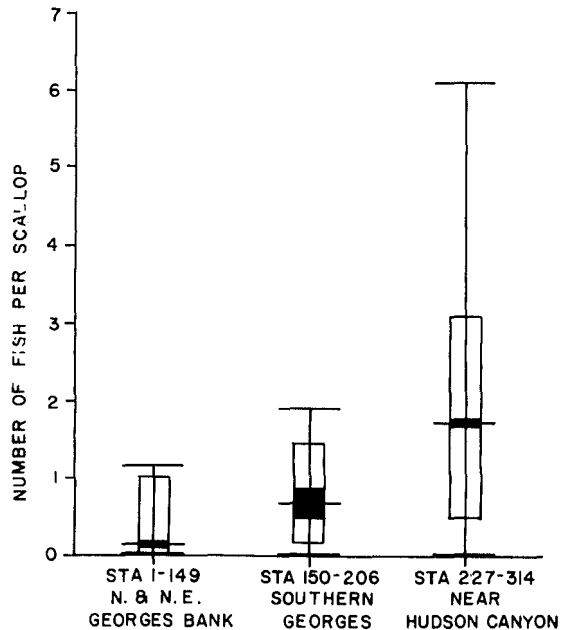


FIGURE 10.—Plot of mean number of fish per scallop at different localities from collections of 5-17 September 1968.

fish per station (Table 4) were highest north of Hudson Canyon, lowest on the north and northwest edges of Georges Bank, and intermediate on southern Georges Bank. Although the greatest abundance of fish in sea scallops occurred near Hudson Canyon, where the average depth and bottom temperature were lowest (Table 4), these parameters did not seem to be related to abundance in this area (Figures 11, 12). The average

TABLE 4.—Comparison of the possible parameters affecting *Liparis inquilinus* abundance in sea scallops over a wide geographic area. Given as mean followed by range in parentheses.

Item	Northern and northeastern Georges Bank	Southern Georges Bank	Near Hudson Canyon
No. of stations	83	29	43
Date, 1968	5-10 Sept.	10-12 Sept.	14-17 Sept.
No. of fish per scallop	0.11(0.0-1.1)	0.65(0.0-1.8)	1.74(0.0-6.1)
Scallops with fish (%)	10.1(0.0-90.9)	41.0(0.0-78.9)	59.2(0.0-100.0)
No. of fish per station	4.8(0-31)	20.6(0-64)	27.1(0-82)
TL (mm) of fish in scallops	29.4(14-47)	28.2(16-43)	26.1(17-38)
Depth (m)	77(47-95)	77(62-90)	57(37-77)
Bottom temp (°C)	10.0(4.0-14.5)	9.7(8.2-13.3)	7.8(6.5-10.1)
Clapper shells (bushels)	3.4(1-7)	5.8(2-9)	4.0(2-8)
No. scallops >60 mm per station	152(3-456)	38(10-79)	68(3-311)

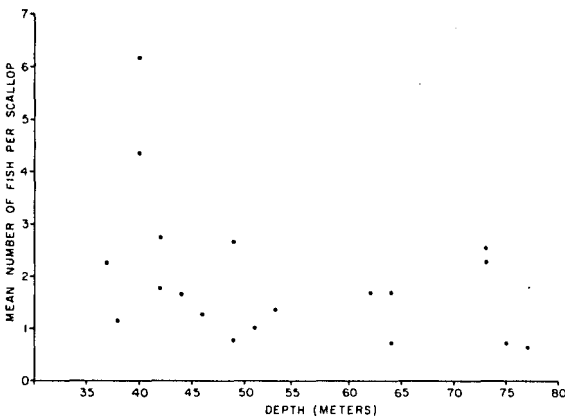


FIGURE 11.—Plot of mean number of fish per scallop versus water depth from daytime collections of 14-17 September 1968 near Hudson Canyon.

number of scallops per station for each area was not related to increased abundance of fish in scallops (Table 4). Clapper shell abundance, regardless of species, was originally hypothesized to be important in *L. inquilinus* survival and abundance since *L. inquilinus* readily occupied shells in the laboratory, and this habit may offer protection from predators. A plot of this possible relationship did not suggest a correlation (Figure 13). The similarity of abundance estimates for southern Georges Bank and the area near Hudson Canyon could be attributed to a similarity in bottom types. Both of these areas have smooth bottoms and are quite different from the rough topography of northern Georges Bank (Uchupi 1968). Fish living on smooth bottom would have less chance of concealment and evasion of predators,

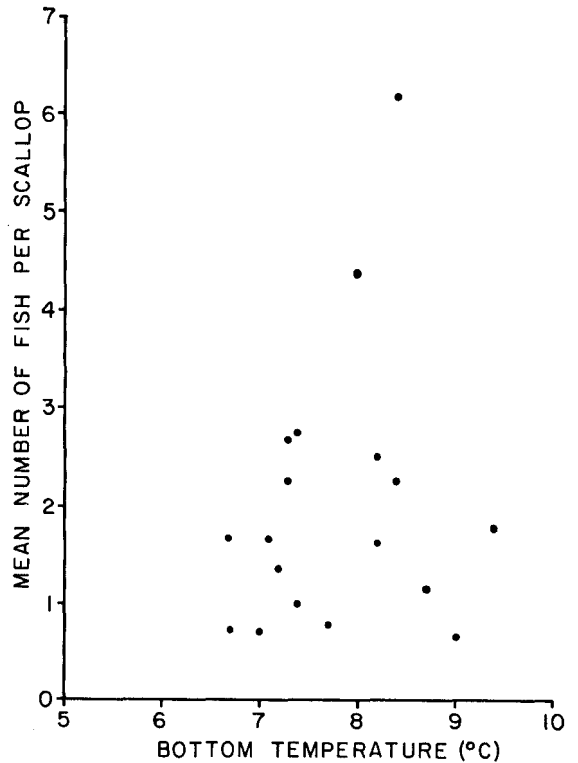


FIGURE 12.—Plot of mean number of fish per scallop versus bottom temperature from daytime collections of 14-17 September 1968 near Hudson Canyon.

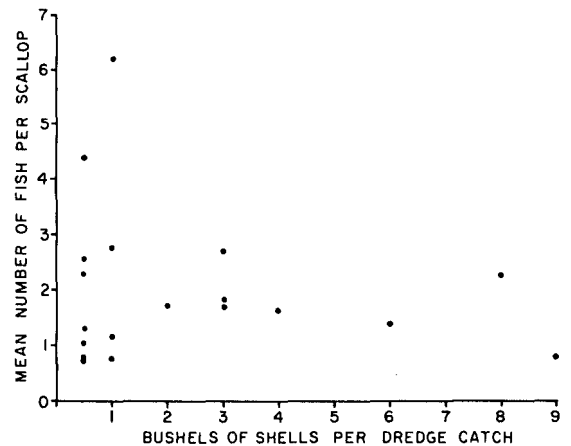


FIGURE 13.—Plot of mean number of fish per scallop from daytime collections versus clapper shell abundance from collections of 14-17 September 1968 near Hudson Canyon.

which would place a greater selective advantage on association with scallops. The simplest explanations for observed differences in abundance are

differences in the year-class strength and differences in actual abundance among different *L. inquilinus* populations.

Possible Advantages of the Association

Liparis inquilinus probably is protected from predation by its association with sea scallops. The only known predators of larger sea scallops which might also ingest *L. inquilinus* are Atlantic wolfish, *Anarhichas lupus*, and Atlantic cod, *Gadus morhua* (Bourne 1964). Wolfish and cod only feed occasionally on scallops and they are rare or only winter inhabitants of the Mid-Atlantic Bight. Also, *L. inquilinus* is not associated with scallops during most of the winter.

Individuals of *L. inquilinus* maximize the period of protection by associating with sea scallops for most of their demersal life. In the Mid-Atlantic Bight, *L. inquilinus* remains associated with sea scallops from the time they leave the plankton until they begin to move inshore to spawn. Also, individuals only leave sea scallops to feed and then return as soon as they become satiated. Nocturnal feeding may also decrease the possibility of detection by predators.

The relative number of scallops may not be a limiting factor for survival of juvenile *L. inquilinus*. In every sample, at any time of the year in which *L. inquilinus* have been taken with sea scallops, some scallops were always empty. However, this assumes that all sea scallops will accept fish. This remains to be proven.

The symbiosis between *L. inquilinus* and *P. magellanicus* should be referred to as a commensal association. Such an association is one in which the population of the commensal benefits and the host is unaffected (Odum 1971).

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