THE ECOLOGY OF *STOMOLOPHUS MELEAGRIS*,

THE CANNON BALL JELLYFISH, AND ITS SYMBIONTS,

WITH SPECIAL EMPHASIS ON BEHAVIOR

BY

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A paper submitted in partial fulfillment of the requirements of the Honors Program in the Department of Biological Sciences.

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April, 1983

Acknowledgements

A number of people provided assistance to me during this project. Thanks go to Dr. David G. Lindquist and Dr. Anne B. McCrary for their advice and help. Special thanks are extended to Ginger Ogburn for putting up with all the hours of counting jellyfish this summer. This research was supported by a North Carolina Academy of Science Undergraduate Research Grant and by a University of North Carolina at Wilmington Research Fellowship.

Abstract

Population dynamics and seasonal movements of *Stomolophus meleagris*, the cannon ball jellyfish, are described and used to better understand fish-medusa associations. The associations of seven species of symbionts, including the crab *Libina dubia* and six fish species are described. The occurrence of these associations are shown to be dependent on the population dynamics of both the consorts and the host. The number of consorts per medusa is a function of the season, and the population size of the host jellyfish, and not of a carrying capacity of the host. The size of the symbionts is dependent on their growth and not of the size of the host jellyfish.

INTRODUCTION

The importance of coelenterates in marine ecology is just now beginning to be recognized. Many animals make use of coelenterates as an alternative food source or as shelter and protection. Many of these organisms are known to have symbiotic relationships with cnidarians, but little is known of the importance of these relationships. Most often it is assumed to be a form of commensalism bordering on parasitism or predation on the part of the fish. Attempts have been made, with limited success, to correlate the number and or the size of the fish associates to the size of the jellyfish (Mansueti, 1963). It has been generally accepted that there is a weak correlation between the size of the jellyfish and the size or number of symbionts (Mansueti, 1963; Philips et al., 1969). This can be thought of as reflecting a carrying capacity of the host. Previous studies of fish-medusa associations have not, however, taken into consideration the population biology or seasonality of either the host or its symbionts. For this reason the seasonality of the host population and the symbiotic relationships are examined and used to provide a better understanding of the symbiosis.

Literature Review

Fish associations with jellyfish are well known and documented world wide. Many species of fishes are involved, often associating with more than one jellyfish species. However, little attention has been paid to the biology of these associations. Records of the relationships have been known for many years (Peach, 1855; Smith, 1907; Mortensn, 1917; Gunter, 1935 and Miner, 1936), but little has been written on their nature. Sars (1879a; 1879b), examined the association of cods with Cyanea capillata. He indicated that young cod probaly feed on zooplankton captured by the medusae. He further suggested that they aid the medusae by feeding on parasitic crustaceans (Hyperia). Sars was one of the first to recognize the role of the jellyfish as a host to the pelagic young of a fish species which spends its adult life in a benthic environment (Sars, 1879a; 1879b: 623). Another important early study was carried out by Scheuring (1915), who described the association as a parasitic relationship based on his experiments. More recently the association of young whiting, Gadus merlangus, with the jellyfish, Cyanea capillata, was reviewed (Dahl, 1961).

Investigations into the possibility of immunity to jellyfish toxins by some of the associates (Lane, 1960; 1963), and mechanical avoidance of nematocysts by means of a heavy mucous coating by other associates (Rees, 1961; Miner, 1936; Dahl, 1961), have been made. However, the most important review on the associations of fishes is by Mansueti (1963) who reported 57 species of fishes asociating with 27 species of jellyfish. He reviewed the literature and examined theories on the nature of the symbiosis of fishes and jellyfish, in particular with Peprilus triacanthus and P. paru. Records of fish medusa associations since the work of Mansueti are compiled in Table 1 and include two unreported by him (Hargitt, 1905; and Sumner et al., 1913).

A less known but important study by McKenny (1965), discusses the association of stromateoid fishes with jellyfishes and classified the hosts into three general groups according to tentacle size, complexity of shape (size of bell cavity for example) and virulence of its nematocysts. He suggests that the strength of the fish-medusae relationship increases somewhat with the complexity of the medusae (more places to hide), but that it is more strongly influenced by the nematocyst virulence. As evidence, he cites the strong association of Nomeus (p. 104-108). He further suggests that morphological changes in other fish symbionts with growth may make them less capable of the relationship (p. 108). This idea is supported by a study on the function of the swimbladder and its relationship to the behavior and mode of life in stromateoid fishes (Horn, 1975), where the presence of a swimbladder only in juveniles is suggested to allow the fish to manaeuver with sufficient agility to avoid the jellyfish's tentacles. In the revision of the stromateiod fishes (Haedrich, 1967) and the genus Peprilus (Horn, 1970), symbiosis with jellyfish was also discussed.

A significant study on the nature of the fish associations with jellyfish is that of Phillips et al. (1969). Here the interrelationship of jellyfish and other organisms in the Mississippi Bay was studied. Visual observations of the behavior of fishes and jellyfishes were made in the field and in the laboratory. Tests were made on the immunity of associate fishes, and it was found that nematocysts adhered strongly to symbiotic fish, contradicting Dahl (1961).

Table 1

Records of the associations of fishes with jellyfish since Mansueti (1963), including those unreported by him.

Family Gadidae		
Gadus merlangus	Cyanea lamarcki	Rees (1966: 285)
Theragra chalogramma	Cyanea sp.	Van Hyning and Cooney (1974)
Family Carangidae		
Caranx fusus	Unidentified	Bohlke and Chaplin (1968: 331)
Caranx kalla	Cyanea nozakii	Morton (1972)
Caranx malabaricus	Chrysaora quinquecirrha	Morton (1972)
Caranx trachurus	Rhizostoma octopus	Rees (1966: 285)
Caranx sp.	Chrysaora quinquecirrha	Phillips et al. (1969)
Chloroscombrus chrysurus	Unidentified	Hastings (1972: 213-14)
"	Aurelia aurita	McKenny (1965: 104); Zann (1980); Franks (1970: 55-56)
"	Chrysaora quinquecirrha	Phillips et al. (1969)
"	Stomolophus meleagris	Phillips et al. (1969)
Trachurus lathami	Unidentified	Hastings (1972: 226)
Family Stromateidae		
Ictius pellucidus	Pelagia notiluca	McKenny (1965: 85)
Mupus ovalis	Physalia	Maul (1964)
Nomeus gronovii	Physalia	Sumner et al. (1913: 754)
Peprilus alepidotus	Jellyfish	Cooley (1978)
Peprilus burti	Stomolophus meleagris	Horn (1970); Phillips et al. (1969)
"	Chrysaora quinquecirrha	Phillips et al. (1969)
"	Cyanea capillata	Phillips et al. (1969)
"	Beroe ovata	Phillips et al. (1969)
"	Jellyfish	Hastings (1972: 410); Franks et al. (1972)
"	Ctenophore	Hastings (1972)
Peprilus simillimus	Aurelia	Horn (1970)
Peprilus triacanthus	Cyanea capillata	Milstein (1974: 58); Cooley (1978); Hoese et al. (1964)
"	Chrysaora quinquecirrha	Hargitt (1905: 25)
"	Stomolophus meleagris	Hoese et al. (1964)
"	Unidentified	Sumner et al. (1913)
Psenes cyanophrys	Unidentified	Parin (1958: 66) and Besedonov (1960: 184) as cited in McKenny (1965)
Psenes maculatus	Pelagia noctiluca	McKenny (1965: 85)
Psenes pellucidus	Dactylometra pacifica	Adler (1975: 120); Zann (1980)
Psenopsis sp.	Unidentified	Haedrich (1967)
Psenopsis anomala	Unidentified	Masuda et al. (1975: 246)
Family Balistidae		
Monacanthus hispidus	Stomolophus meleagris	Phillips et al. (1969); Phillips (1971)
"	Cyanea	Phillips (1971)
"	Chrysaora	Phillips (1971)

Thiel (1979), recently reviewed the types of symbiosis between fish and jellyfish and discussed some of the parameters affecting the relationship. The most recent treatment of the subject is found in Zann (1980), an excellent review of fish symbiosis in general. It includes a good summary of current knowledge on the behavior of the fish symbionts and groups them into temporary and permanent consorts. He further discusses the evolution of the association and possible immunity to stings by the fish.

Records of the association of non-fish organisms with jellyfish, except for amphipod parasites (interested readers are referred to Rice and Powell, 1970; Dahl, 1959; and Bowman et al., 1963) have been reviewed and compiled in Table 2. Phillips and Levin (1973), describe the occurrence of cestode larvae in schyphozoans and review the literature. Phyllosoma larva associations with jellyfish are discussed by Thomas (1963) and later by Herrnkind and Kanciruk (1976). Various crabs are known to associate with medusa. The association of Cancer gracilis with jellyfish is described by Weymouth (1910) and Corrington (1927). Corrington (1927) reports that megalops larvae of Cancer gracilis were found in association with the medusae and speculated that the association of Libinia dubia with Stomolophus as first reported by him, also extends to the megalops stage. Gutsell (1928) also reported the association of L. dubia with Stomolophus. The most important review of the association of L. dubia with jellyfish was produced by Phillips et al. (1969). They carried out laboratory and field experiments which showed that Libinia will eat medusae tissue and that they would associate with any medusa placed with them in an aquarium. They cite evidence supporting the belief that the young crabs begin associating with jellyfish when the medusae brushes or rests on the bottom and not as a megalops larvae. In the study, they collected specimens 4-18 mm in carapace width with Chrysaora and Stomolophus, the percent association with jellyfish varing from 0-100% with different swarms. Libinia dubia has also been reported as

Table 2

Records of organisms other than fishes and amphipods, associating with jellyfish.

Cidaria		
Peachia parasitica	*Cyanea capillata*	McDermott et al. (1982)
Cestode larvae	*Periphylla periphylla*	Phillips and Levin (1973)
	Stomolophus meleagris	Phillips (1971); Phillips and Levin (1973)
Arthropoda		
Phylosoma larva	*Pelagia panopyra*	Thomas (1963)
Ibacus	Seaestome medusae	Thomas (1963)
"	*Catostylus mosancus*	Thomas (1963)
Scyllarus	*Aurelia aurita*	Herrnkind et al. (1976)
Brachyura		
Cancer gracilis	Unidentified	Weymouth (1910); Corrington (1927)
Cancer jordani	Unidentified	Corrington (1927)
Charybdis feriatus	*Cyanea?*	Trott (1972)
"	*Ropilema esculenta*	Trott (1972)
"	*Stomolophus nomurai*	Trott (1972)
Callinectes sapidus	*Chrysaora quinquecirrha*	Phillips et al. (1969)
Libinia dubia	*Stomolophus meleagris*	Corrington (1927); Gutsell (1928); Hyman (1940); Hildebrand (1954); Phillips et al. (1969); Whitten et al. (1950)
"	*Aurelia aurita*	Jachowski (1963)
"	*Chrysaora quinquecirrha*	Phillips et al. (1969); Heck and Orth (1980)
Libinia emarginata	*Stomolophus meleagris*	Hildebrand (1954)
Ophiuroids	*Rhopilema hispidum*	Panikkar and Prasad (1952)

associating with Aurelia (Jachowski, 1963) on which it was found to feed and burrow its way into the medusae.

Literature concerning the ecological importance of jellyfish are extremely scarce. Phillips et al. (1969) discussed the trophic significance of jellyfish in Mississippi Sound as did Phillips (1971). The ecological impact of Chrysaora has been discussed primarily by Cargo and Schultz (1966; 1967), while Miller and Williams (1972) studied its energy requirements and effect on zooplankton populations. Most recently, Larson (1978), has made an extensive study of the feeding of schyphozoans. For the readers convenience the following indispensable general references are given: Medusae of the World (Mayer, 1910), Some Medusae and Siphonophorae from the Western Atlantic (Bigelow, 1918), The Invertebrates: Protozoa through Ctenophora (Hyman, 1940), Synopsis of the Medusae of the World (Kramp, 1961), The Meduasae of the British Isles. I. II. (Russell, 1970), Bibliography on the Scyphozoa, with selected references on Hydrozoa and Anthozoa (Calder et al.1971), Marine Flora and Fauna of the Northwestern United States (Larson, 1976), and finally references for the identification of marine invertebrates of the southern Atlantic coast of the United States (Douds, 1979). To my knowledge, there are only two studies on coelenterates in North Carolina waters. Brooks (1882), compiled a list of medusae from Beaufort, North Carolina and Schwartz and Chestnut (1974) investigated the seasonal abundance and occurrence of coelenterates and ctenophores in North Carolina. The three species of jellyfish captured in this study will be review separately.

Chrysaora quinquecirrha

This is perhaps the best studied of the scyphozoans. Calder (1972a; b) compiled an outline of the knowledge and biology of the species and of cnidarians of the Chesapeake Bay. The life history of Chrysaora (sea nettle) has been studied by Cargo and Schultz (1966; 1967). It is usually considered a brackish water form (Agassiz and Mayer, 1898; Hedgpeth, 1954; Calder and Hester, 1978; Gunter, 1950; Wass, 1972). Although the medusa is capable of living under a wide range of salinities (Burke, 1976), the distribution of the polyp stage is thought to be limited by a low tolerance to high salinity (Cargo and Schultz, 1966;1967; Kraeuter and Setzler, 1975). It first appears in estuarine creeks as very young medusae in the late spring and early summer (Agassiz and Mayer, 1898; Calder, 1972b; Cargo and Schultz, 1966), and moves into more saline waters as it grows (Copeland, 1965; Kraeuter and Setzler, 1975; Schwartz and Chestnut, 1974). Chrysaora is usually noted as occurring in the warm months (Sumner et al., 1913; Burke, 1975; Kraeuter and Setzler, 1975; Mansueti, 1955; Christmas, 1973), but is killed off by the onset of cold weather (Calder, 1972b; Cargo and Schultz, 1966;1967). Variations in abundance from year to year have been suggested to be caused by fluxuations of salinity in estuaries, with increased runoff being blamed for decreases in the population (Mansueti, 1959). The growth rate of the jellyfish has been studied by Cargo and Schultz (1966; 1967) and energy requirements by Miller and Williams (1972).

Aurelia aurita

The literature on the seasonality and distribution of *Aurelia* is confusing. In the Gulf of Mexico it is considered a winter form (Burke, 1975; 1976), but it has been described as a late summer-early fall species there also (Franks et al., 1972; Haertel and Osterberg, 1967; Cooley, 1978). *Aurelia* is usually considered a marine form (Haertel and Osterberg, 1967; Franks et al., 1972; Cooley, 1978; Hedgpeth, 1954; Gunter, 1950), but has also been occasionally abundant in protected sounds and bays (Gunter, 1950; Cooley, 1978). It is interesting that the occurrences of *Aurelia* in lower salinity waters were in the warmer months. Gunter(1950), collected them in Aransas Bay in August and October, while Cooley (1978) collected them in the late summer and early fall in the Pensacola Bay, Florida estuary. In Georgia, Kraeuter and Setzler (1975), report *Aurelia* as rare and recorded only a few young medusae in July from Hudson Creek. Calder and Hester (1978), recorded it as rare in South Carolina and Brooks (1882) does not include it in his list of medusae from Beaufort, North Carolina. Schwartz and Chestnut (1974), however, report *Aurelia* as occasional in August and September in the Newport River and the Atlantic ocean from Cape Lookout to Cape Fear North Carolina, but they indicate that the species was never abundant. Wass (1972), reports it as common to abundant in the Chesapeake Bay area, indicating that ephyrae occur in late May to June while the medusa occurs up to November. It is considered common around Woods Hole in the spring and summer and Sumner et al. (1913) suggest it may sexually reproduce at that time.

Stomolophus meleagris

Calder (1982) recently described the life history of Stomolophus and reviewed the literature on the life stages of rhizostomes. Reports of the occurrence of Stomolophus and its abundance are numerous and varied. Mayer (1910), reports that Stomolophus is abundant in the winter and spring off the coast from Florida to South Carolina and that it is not usually found in brackish waters. He described a 3 mm specimen from Charleston harbor South Carolina. In North Carolina it has been reported as very abundant in June in the sounds and in the ocean and common through the summer (Brooks, 1882). Gutsell (1928) reported it as abundant in 1927 inside and outside the Beaufort bar. It became abundant in June, very abundant in July, but its abundance decreased in August, with most specimens being less than 150 mm in diameter. More recently Schwartz and Chestnut (1974) reported it as uncommon during their study, collecting only a few specimens in the mouth of the Cape Fear River in September and one offshore in August, but they indicate that the medusa became very abundant after their study, in the sounds and ocean from April to November 1973. In South Carolina, it was reported as the most common schyphomedusae by Calder and Hester (1978), occurring sporadically year round.

In the Gulf of Mexico, it has been discussed in a number of studies. Cooley (1978), found it to occur in low abundance in the Pensacola Florida estuary. Gunter (1950), also reported it as rare in his study, but noted that it was reported to be extremely abundant at times. Stomolophus is usually described, however, as the most abundant scyphozoan in the Gulf, particularly in the late summer and fall (Hedgpeth, 1954; Hoese et al., 1964) when it "swarms" around inlet passes. Hedgpeth estimated that during one such swarm in September, approximately two million jellyfish per hour moved through Port Aransas Pass Inlet. It is considered most abundant in the winter in the Gulf (Burke, 1975; 1976; Copeland, 1965).

Copeland (1965), reported Stomolophus as the most abundant organism collected in tide traps from Aransas Pass Inlet, Texas, occuring in all months except July, August and September. He cites figures of 1 gm/m^3 from late December through February, 10 gm/m^3 in March, April, November and December. Peaks of 10-100 gm/m^3 occurred in May and October which he suggested may correspond to a mass movement into the pass with a drop in water temperature to 25^{o} C in October and out of the pass with the rise of the temperature to 25^{o} C in early June.

The most important study of the occurrence and seasonality of Stomolophus is that of Kraeuter and Setzler (1975). They report it as the most abundant scyphomedusae in Georgia waters, occurring sporatically year round. They collected young individuals in abundance from Hudson Creek and Duplin River in July, and indicate that the population decreased by August and moved toward the mouth of the sound until occurring at the sea buoy in September. By mid-October they disappeared and did not return until March. They noted a drop in size and weight in August and September. Large individuals appear in March and move inshore in May and June. They report large numbers taken by shrimpers off the Georgia coast in October and November, disappearing by December at which time they were reported as occurring in large numbers in the Florida shrimp grounds. They suggest that this may indicate a southern migration in the winter. Stomolophus is discribed as "outflowing" from estuarine waters to more saline water with growth, but indicate that they could not determine if large individuals arriving in the spring were releasing planulae which form scyphistomae or if overwintering stages occur in the estuaries.

Larson (1978), described the feeding and functional morphology of scyphomedusae including Stomolophus. He indicates that water flow which is directed over the arm cylinder (formed by the fusion of eight oral arms) stabilizes the medusae in swimming. The method of feeding employed by Stomolophus is described in the following manner (Figure 1). Water is sucked into spaces between the sixteen scapulets during the contraction of the bell and is channeled along their length until forced out of the subumbrellar space. The bell margin is suggested to act as a valve during diastole to insure that the water flows through the scapulet spaces before exiting. He also states that most prey capture occurs in these scapulets during diastole and not by secretions of mucous strands as suggested by Phillips et al. (1969). Larson further indicates that the mucous secretions are a behavioral response to handling or confinement. Stomolophus was found to feed on macrocrustanceans, veligers and fish ova (Larson, 1978; Phillips et al., 1969).

Stomolophus has been the subject of numerous studies on its toxicity and biochemistry (Bodanski and Rose, 1922; Burnett and Calton, 1977; Toom and Chan, 1972; Toom et al., 1975; Toom and Phillips, 1975; Toom et al., 1976; and Yasuda, 1974).

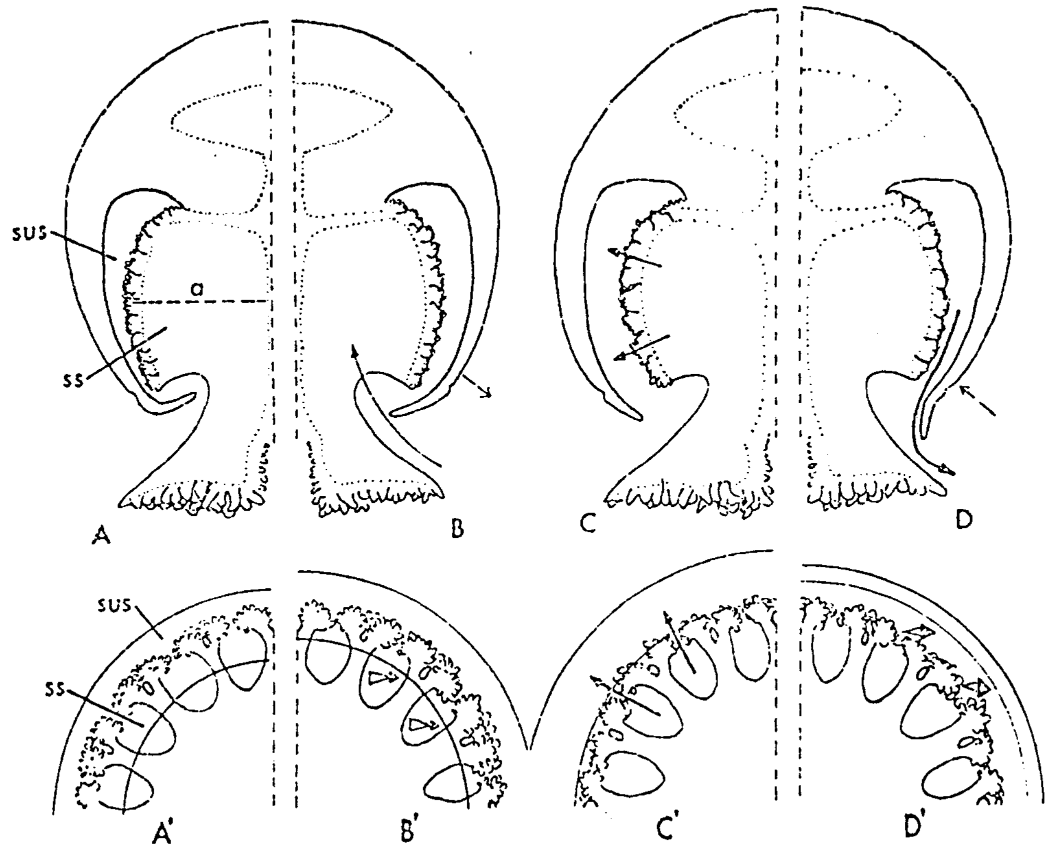

Figure 1. <u>Stomolophus meleagris</u>: Movement of umbrella and water during swimming (speculation based on observation of swimming and morphology)

A - D - diagrammatic longitudinal 1/2 sections

A'- D'- diagrammatic 1/4 cross-sections at level of dashed line (a) as viewed from below; outer semicircle in lower figures indicates approx. position of umbrella; inner semicircle, position of umbrellar margin in reference to longitudinal section above each 1/4 cross-section

A, A'- systole completed; no water flow except that around umbrella and distal portion of oral arms due to momentum

B, B'- diastole beginning; water flows into scapular spaces; (arrow indicates flow away from observer); position of margin prevents water from flowing into subumbrellar space

C, C'- diastole continuing; water flows from scapular spaces through the digitata, where filtration occurs, and into subumbrellar space

D, D'- diastole completed and systole beginning; water flows from subumbrellar space (arrow in D' pointing toward observer); digitata probably prevent backflow of water into scapular spaces

ss - scapular space

sus - subumbrellar space

(Figure from Larson, 1978)

MATERIALS AND METHODS

Jellyfish were observed and collected from the south shore of Wrightsville Beach and in the vicinity of Masonboro Inlet North Carolina (Figure 2),from May to December 1982. A transect was established which paralleled the shore at about one hundred meters for approximately one kilometer (0.6 miles), using easily recognized permanent landmarks. The transect was usually sampled twice, once along a northern direction and second returning along the same transect in a southern direction. Occasionlly the return leg was completed farther off shore at 1.2 and 1.6 kilometers.

Other transects were selected randomly along five degree compass headings from a fixed point 0.8 km out on the Wrightsville Beach Jetty (Figure 2). Each of these transect headings were followed for a randomly determined period of time. Underwater observations of behavior were made in the general area near the end of the jetty.

Before beginning a transect, a data sheet recording information such as location, dates, air and water temperature was filled out. A parallel heading from shore was held as constant as possible with the engine at low throttle. Counts of jellyfish or sargassum were made as they passed through an area extending about fifteen meters on either side of the boat. Subsamples were captured in a large fifty by seventy centimeter fine mesh net. Only those jellyfish which passed close to the boat were sampled so that only minor adjustments in the boat heading were made. The jellyfish were allowed to drift into the net (with the boat in neutral or reverse to further slow it down), so that the fish were not frightened by the net. The fish were separated from the jellyfish and immediately placed in small jars of seawater and put on ice. Crabs were left with the jellyfish which were bagged and

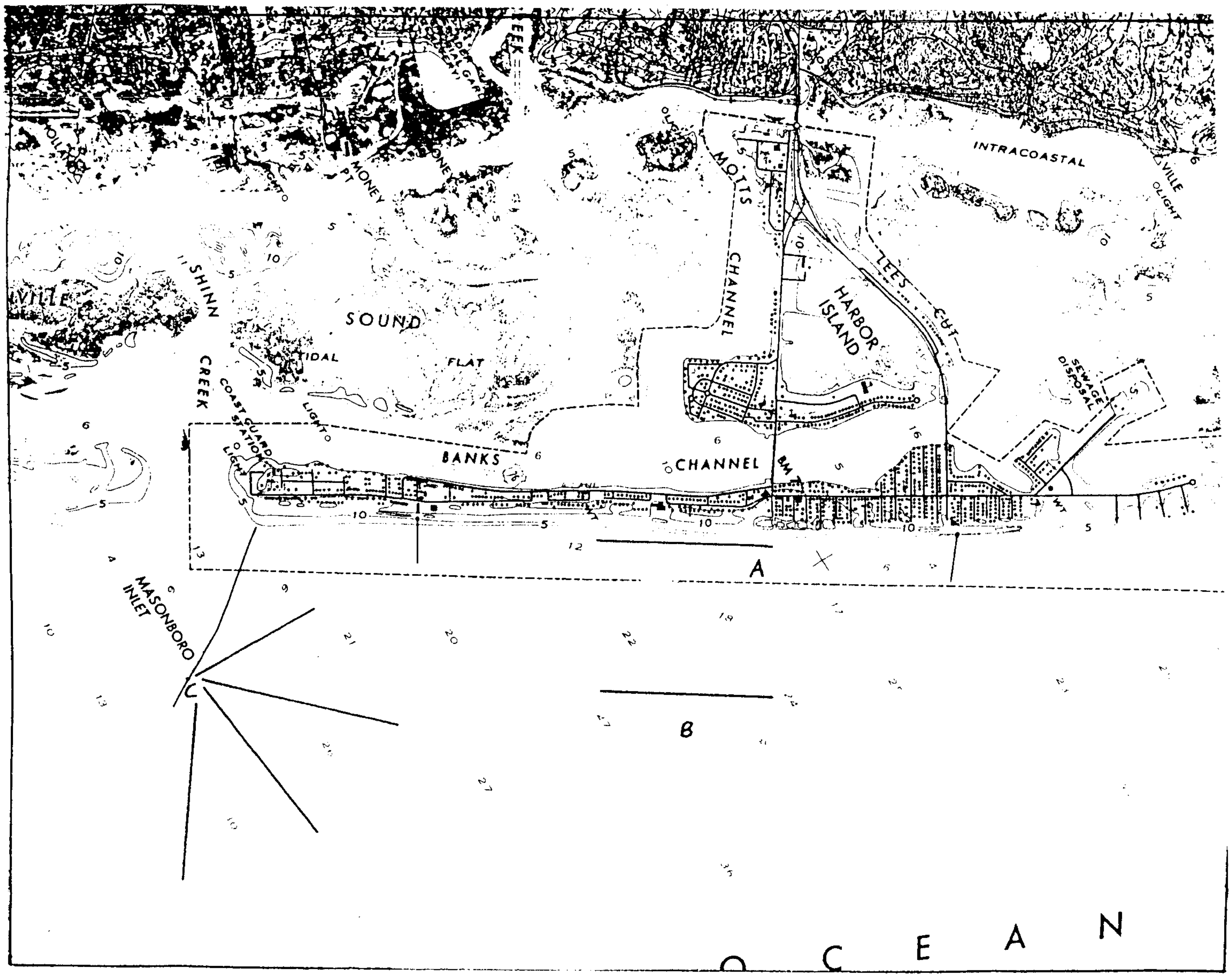

Figure 2. Study area showing jellyfish collectinn locations off Wrightsville Beach, North Carolina. Shoreline transects: 100 meters at A; 0.8 km at B; random heading transects from jetty at C.

put on ice if possible. Preprepaired tags with date, local and specimen numbers were placed in the bag and in the specimen jars so that the fish symbionts could be paired with their specific host in the laboratory.

All specimens were examined in the laboratory the same day of capture. The fish were identified and preserved in ten percent formalin. The jellyfish were carefully examined for crabs, any other symbionts and fish which had been missed in the field. Crabs were preserved or placed in aquaria for observation. The examination was made while constantly rinsing the jellyfish with fresh water. The runoff was seived and examined for organisms. After all symbionts were removed from the medusa, it was carefully rinsed again and measurements of bell height and diameter were recorded (Figure 3). Bell height measurments were made to the nearest millimeter from one rhopalium to what was judged to be the apex of the manubrium (although Stomolophus is a particulary solid and dense jellyfish, after several hours it becomes deformed by its own weight). For Stomolophus the bell diameter was measured to the nearest centimeter from one rhopalium to an opposite rhopalium on a line through the center of the medusa. The wet weight in grams was then taken after shaking off any excess water. Finally, the jellyfish were sectioned and the genital chamber examined for the presence of symbionts.

Changes in the jellyfish populations by month were examined, as were the number of associates per jellyfish and the percent frequency of the association. The size and weight of the jellyfish and the size of its symbionts were examined for trends. Populations of symbionts associating with Stomolophus were compared to populations collected with sargassum weed.

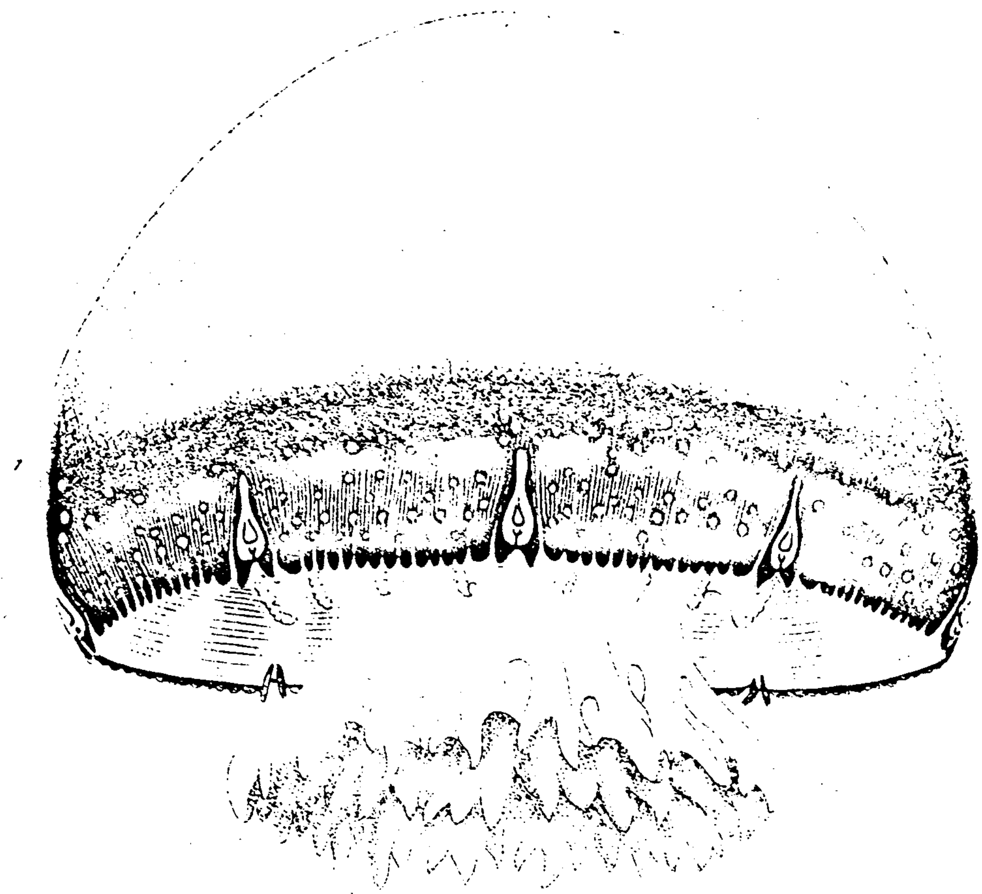

Figure 3. Explanation of measurments used in this study.
Bell diameter (A) was measured from opposite rhopalia which lie on a line through the center of the circle formed by the bell margin. This measurement is subject to large error due to the flexibility of the margin. Bell height (B) is measured from the proximal notch of a rhopalium to the apex of the bell dome. This measurement is best made on capture of the jellyfish as the medusaoid tissue is greatly deformed with time. (Figure adapted from Mayer, 1910).

RESULTS

Aggregations of large cannon ball jellyfish (Stomolophus) were first reported several miles offshore during the late spring (April-May). By the end of May, small numbers of jellyfish were seen in the nearshore (0-1.6km) waters. The population density, as expressed in numbers of jellyfish sighted per hour, increased through out the season. The mean density was eight per hour in June and had increased to twenty-eight in July. By the end of July and through August numerous small jellyfish began to appear (200-300 grams as opposed to 1000-1200 grams). Through this time the average weight dropped from about 950 grams in June to about 500 grams in August. In August, Stomolophus appeared in Masonboro Inlet in large numbers for the first time. Although no data are available for September, many jellyfish were reported inside the protected waterways behind Wrightsville Beach Island (Figure 2). Masses of dead jellyfish were reported washed up in salt marshes behind Wrightsville Beach in October, and I noted frequent specimens of Stomolophus in the Atlantic Intracoastal Waterway. From general observations the population density of Stomolophus appeared to have declined in October and November except for a tremendous influx of Stomolophus in the second and third weeks of November when 200-300% higher counts were made (peak of 630 per hour). A large percentage of the population was comprised of small individuals and at this time the smallest and largest specimens were obtained (143-1378 grams, respectively). After this two week period the numbers of jellyfish declined drastically so that by December very few specimens were seen. Trips were made on a number of occasions in December, January and Febuary but no jellyfish were sighted. (No reqular collections were made at this time, however, and these data were not incorporated in the data analysis).

The mean population density, mean jellyfish weight and bell diameter were calculated for arbitrarily assigned consecutive fifty day periods beginning May 1, 1982 and ending January 4, 1983 with day 250. Each period was tested for serial change using a students t-test with a corrected degrees of freedom. The population of Stomolophus is seen to rise from a low of 2.6 per hour in period one (May-June), to a peak of 139 per hour in period four (October-November) from which it declined to 6.5 per hour in period five (Figure 4). All time periods were significantly different except periods three and four which were not significantly different at an 80 % confidence level. Figure 5 shows the mean wet weight in grams and the mean bell diameter in millimeters for Stomolophus for each time period for which data are available. Both measurements show a decline in the mean size of the jellyfish through the summer and a subsequent increase in the mean size in the fall. A minimum mean size thus occurs in the late summer (August). The linear regression line for the wet weight of Stomolophus versus the bell diameter is shown in Figure 6, while Figure 7 showns the wet weight versus the bell height.

The following miscellaneous observations were also made. It was noted that the gonadal tissue of Stomolophus changed from a translucent green-blue early in the season to a gray mucosal mass in July and August. An occasional albino variation of Stomolophus was noted. The jellyfish were usually noted as occurring in very diffuse but perceptable aggregations or masses. Often when a boat (particularly a large one) approached within several yards of a jellyfish, or when one was aggresively handled while diving, a unique behavioral response was noted. (This invariably occured for those individuals which were at the immediate water surface). The jellyfish would immediatly stop its forward movement and invert (almost a pivot) so that the centrum and oral arm mass was directed upward, often breaking the surface. It would then begins to swim vigorously downward for at least a few feet.

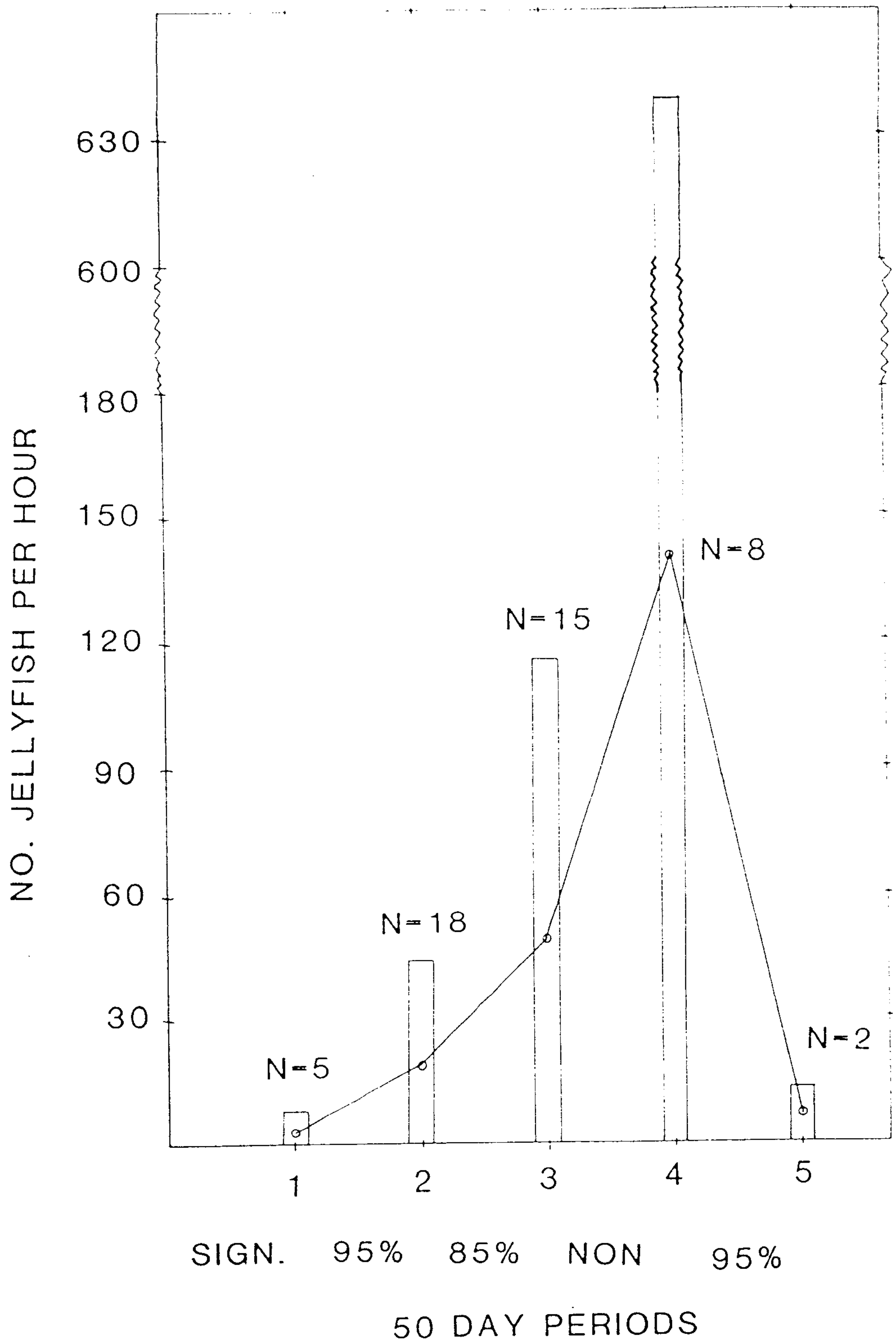

Figure 4. Mean population density of Stomolophus as expressed in numbers sighted per hour, for five fifty day period beginning May 1, 1982 and ending January 4, 1983. All populations are serially significant except three and four.

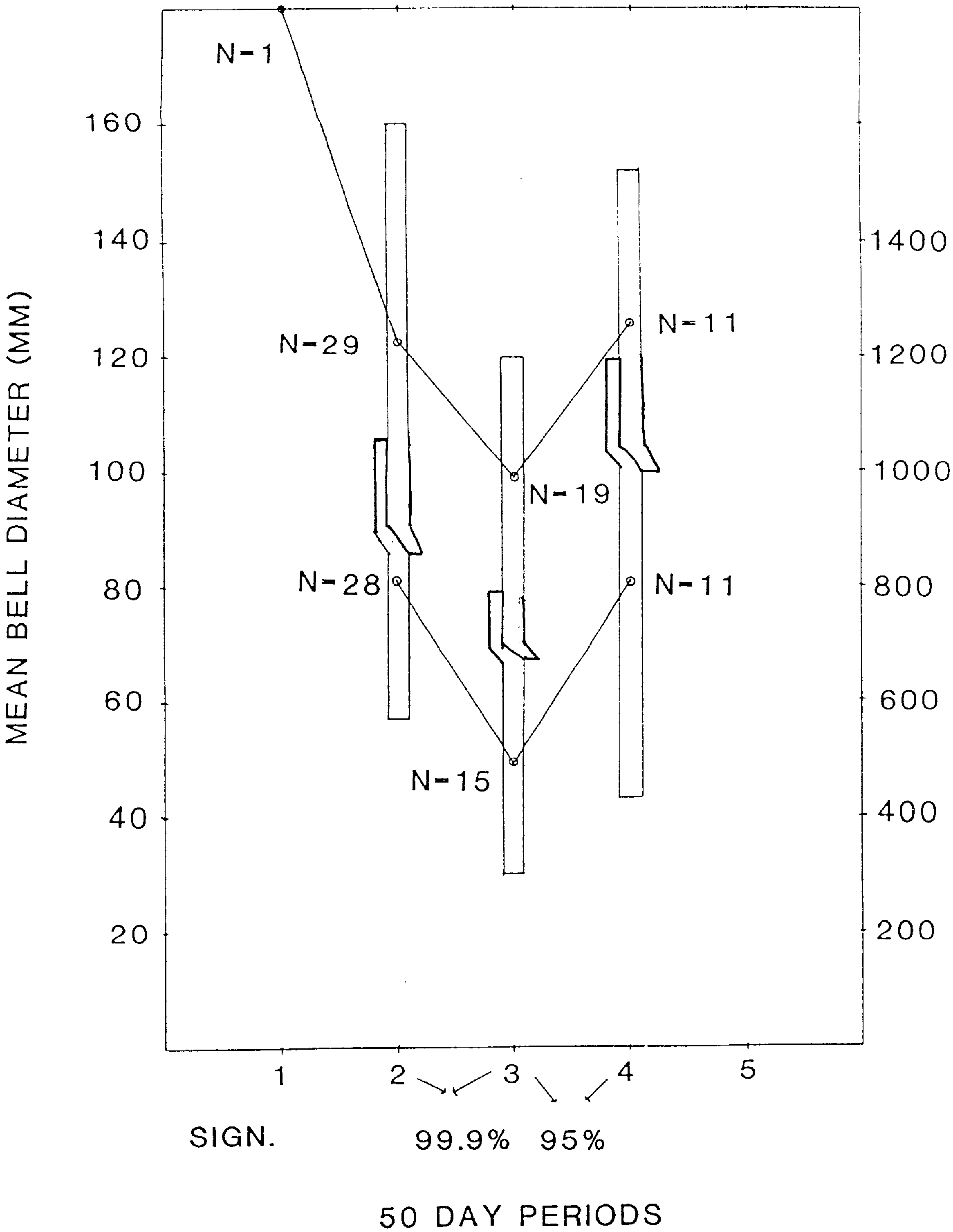

Figure 5. Mean wet weight and bell diameter of Stomolophus by fifty day time period. The mean weight of period two versus three and three versus four are highly significant.

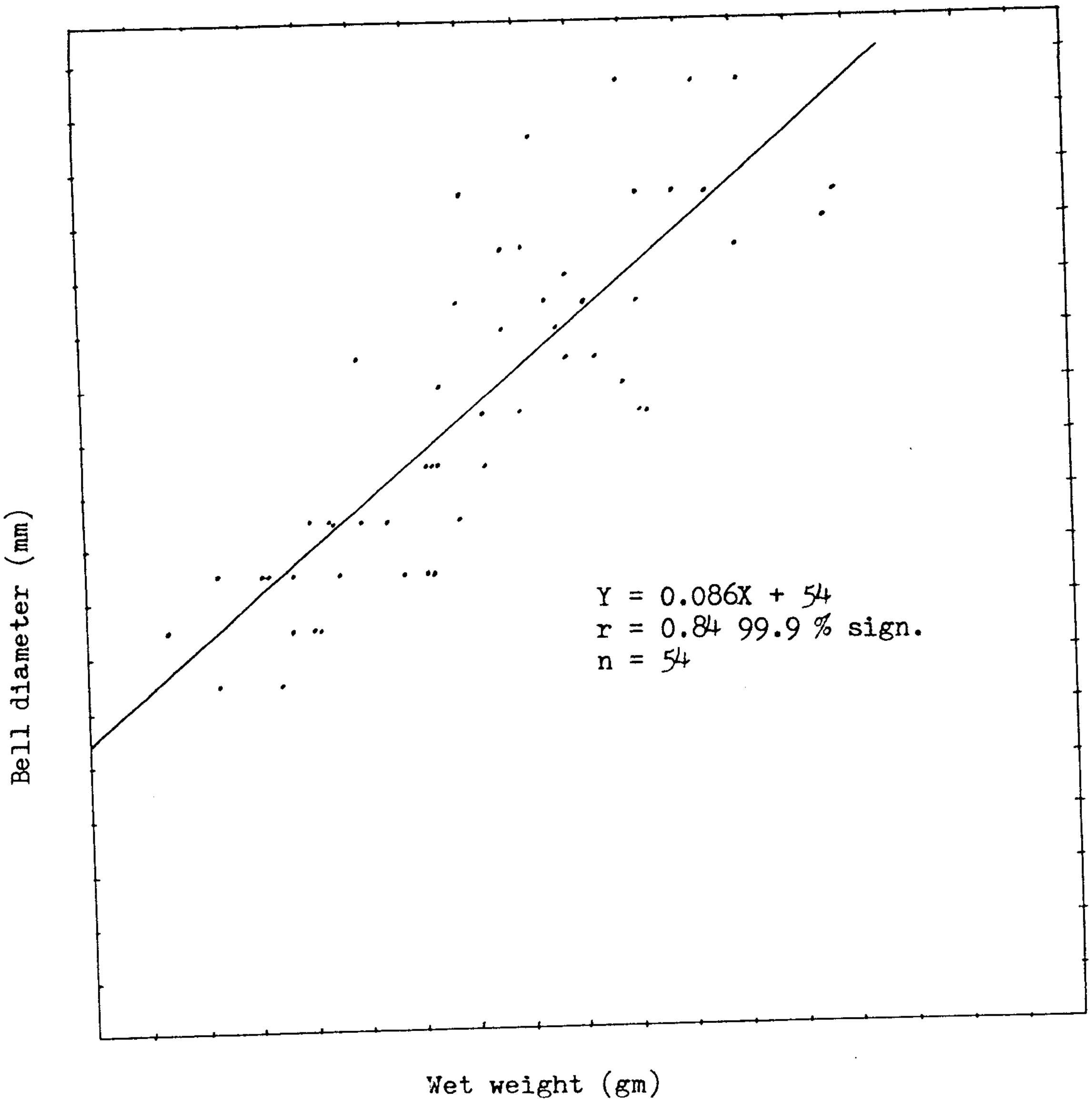

Figure 6. Bell diameter versus wet weight for Stomolophus.

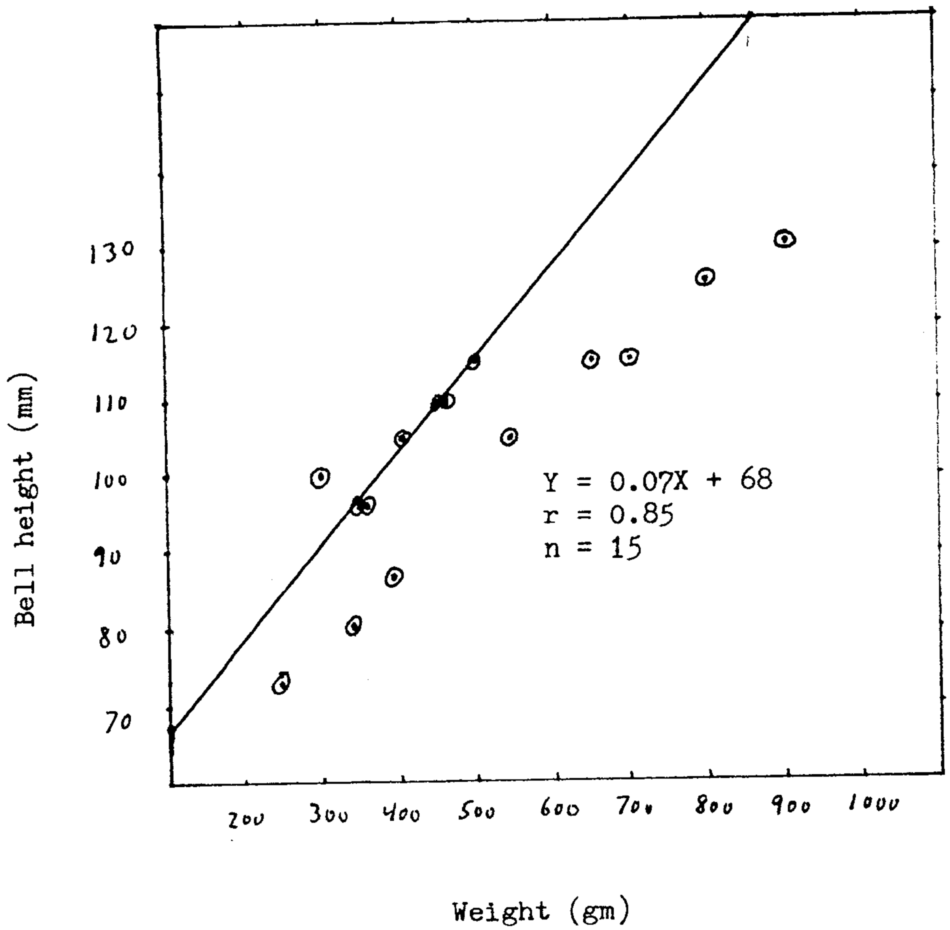

Figure 7. Bell height versus wet weight of *Stomolophus*.

The mean monthly population density of other jellyfish and sargassum weed collected during this study are shown in Table 3. Sargassum was collected only in June with a mean of 12.25 "clumps" per hour. The sea nettle Chrysaoura quinquecirrha was collected only in July and August with a mean density of 0.83 and 0.75 per hour, respectively. Aurela aurita was collected in October and November with mean densities of 27.5 and 3.5 per hour, respectively.

Table 4 lists the species of associating organisms collected with each of the jellyfish species and with sargassum. Six species of fishes and the crab Libinia dubia were captured with Stomolophus including: Peprilus triacanthus, Chloroscombrus chrysurus, Monacanthus hispidus, Aluterus schoepfi, Caranx bartholomaei and Caranx hippos. Data and observations for each of these will be described separately.

Specimens of Libinia dubia were found with Stomolophus throughout most of the study period. The mean number of crabs per jellyfish decreased from a high of two per jellyfish in June (Figure 8) with sixty-three percent of the jellyfish carrying crabs. In October and November lows of zero and 0.17 crabs per jellyfish were recorded. In July ninty five percent of the population of Stomolophus harbored symbiotic crabs. The mean carapace length of the crabs increased slightly in July from a mean of 11 mm in June, to 12.5 mm in July, but promptly fell back to 11 mm (Figure 8). Note that the size range of the crabs gradualy increased through the summer from 5-22 mm in June to 3-37 mm in August. Crabs of various sizes were sometimes found which had recently molted so that they remained quite soft. Small crabs were most often found between the scapulets of the medusa in the field, but were occasionally found wedged in the oral arm mass and rarely (three times) within the subgenital pits. Larger crabs were usually found on the under surface of the manubrium within the bell cavity and occasionally on the

Table 3

Mean population densities of jellyfish and sargassum by month as expressed in numbers per hour, including standard deviation, range and number of counts made.

		June	July	August	October	November
Stomolophus	X	8.4	27.7	49.0	77.8	136.0
	σ	13.6	41.1	69.3	107.0	250.0
	r	0-42	0-140	0-240	0-234	0-630
	n	9	15	15	4	6
Sargassum	X	12.5	0	0	0	0
	σ	19.6				
	r	0-54				
	n	8	15	15	4	6
Chrysaora	X	0	0.83	0.75	0	0
	σ		1.99	3.00		
	r		0-6	0-12		
	n	9	12	16	4	6
Aurela	X	0	0	0	27.5	3.5
	σ				30.2	5.6
	r				0-72	0-13
	n	9	12	16	4	6

Table 4

Symbiotic and associating organisms of jellyfish and sargassum collected in this study, together with mean weight and bell diameter and range of the host weight. The months each species were taken and the mean and range of the standard length for fish and carapace length for crabs, are shown. for crabs, are shown. Measurements of Libinia are of the carapace length while those of the sargassum crab are of carapace width.

Sargassum

n=14, Mean weight = 249 gm, r = 57-679 gm

Associates

Monacanthus hispidus (May-June): n = 92, x = 22.6 mm, r = 16-37 mm
Caranx hippos (June): n = 23, x = 31.8 mm,
r = 22-36 mm
Histro histro (June): 15 mm
Sargassum crab (May-June): n = 5, x = 36.8 mm, r = 12-53
r = 12-53 mm, (33 % occurrence)
Sargassum shrimp (May-June): n = 11 (42 % occurrence)

Stomolophus

n = 63, Mean weight = 737 gm, r = 143-1378 gm
Average number of associates per medusa: 4.32
Average number of fish per medusa: 5.02
Symbionts:

Libinia dubia (June-November): n = 66, x = 12 mm,
r = 3-37 mm.
Peprilus triacanthus (June): n = 31, x = 19.6 mm,
r = 16-48 mm
Chloroscombrus (June-August): n = 117, x = 14.9 mm,
r = 10-37
Monacanthus (June-November): n = 44, x = 19, r = 10-37
Caranx hippos (June): n = 9, x = 19, r = 32-35
Caranx barthomlomaei (July): 51 mm
Alutera schoepfi (July): 38 mm

Chrysaora quinquecirrha

n = 1, 119 gm, bell diameter = 0.91 mm
species:

Peprilus alepidotus (August): n = 2, x = 52.5,
r = 50-55 mm
Chloroscombrus (August): n = 41, x = 10 mm,
r = 7.5-17 mm

Aurelia aurita

weight = 119 gm, bell diameter = 91 mm species:

Chloroscombrus (October): 34 mm

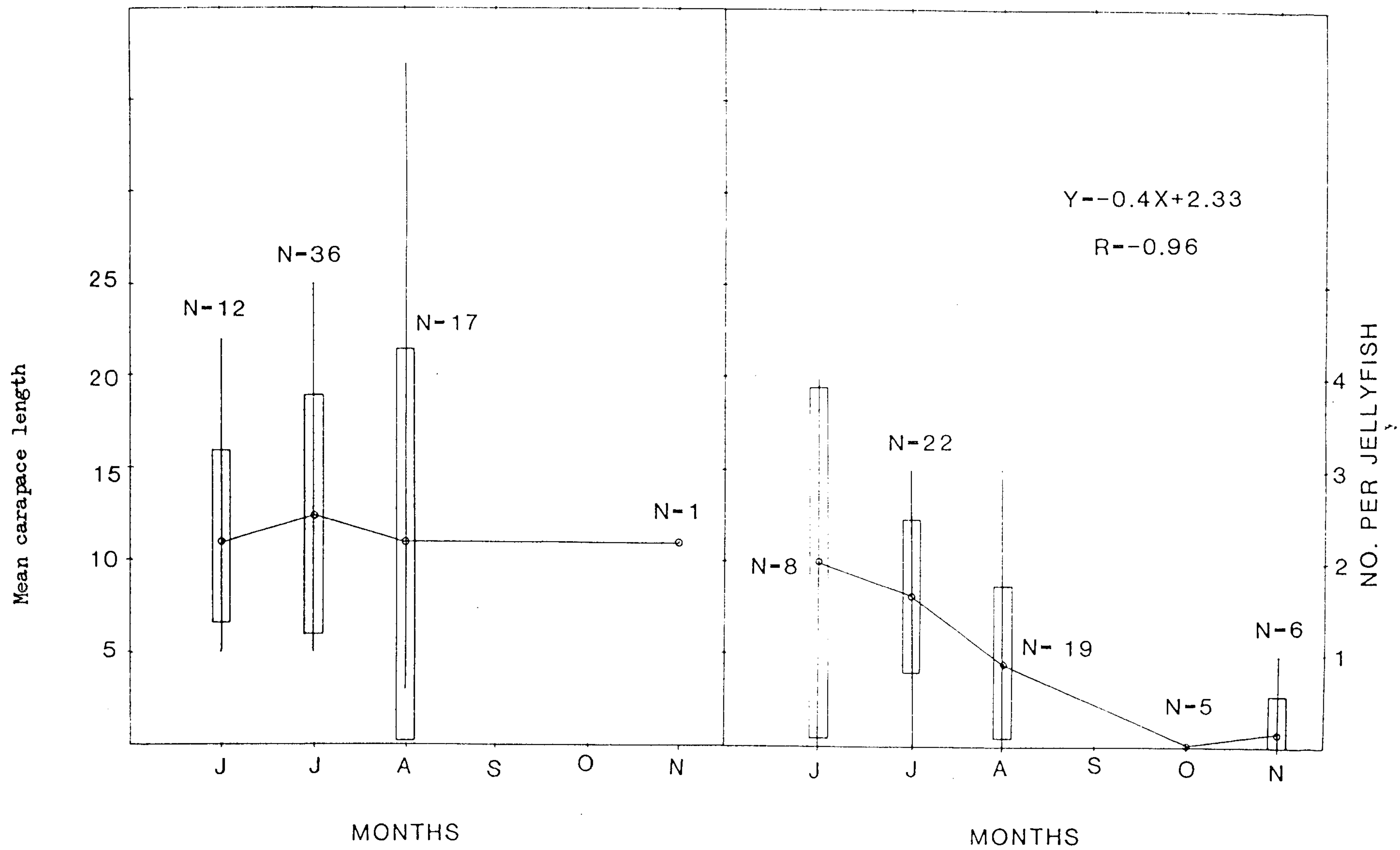

Figure 8. Mean monthly carapace length and mean number of crabs per medusa for <u>Libinia dubia</u> symbionts of <u>Stomolophus</u>.

exterior apex of the bell (See Figure 9 for the usual locations of symbiotic crabs and fish in relation to the medusa).

The planehead filefish Monacanthus hispidus was also collected with Stomolophus throughout the time period. The size, mean number per medusa and percent frequency all decline from a peak in June (Figure 10). The June population associating with Stomolophus was not significantly different from the population associating with sargassum weed at 80% confidence interval. In my previous unpublished study, (Rountree, 1982 Bio. 457 paper), I found that M. hispidus progressed from a mean standard length of 17.5 mm when pelagic (associating with Stomolophus or sargassum), to 32.9 mm when they moved into a midwater and benthic habitat among cover in protected waters such as estuaries. The largest specimens, with a mean standard length of 66.7 mm were found in the Atlantic Intracoastal Waterway around floating docks and Piers (Figure 11). The filefish were observed to swim behind the jellyfish in close association with the oral arm mass. Often they were seen to hold on to the oral arm mass with its mouth in a manner similar to that observed when resting with sargassum. Its color and small size made it very difficult to detect underwater even when observed from only a few inches away! When frightened it did not hesitate to enter the subumbreller cavity or cram itself into the anastomosis of the oral arm mass, and wedge itself in place by erecting its large dorsal spine. If several individuals where together, some of them would opt to abandon their host and swim off, this choice became predominate in the colder months.

Specimens of Caranx hippos were collected with Stomolophus and with sargassum only during June. Their was no significant difference between populations associating with sargassum and Stomolophus (Table 4). The mean length of C. hippos associating with Stomolophus was 33 mm, the mean number per jellyfish was

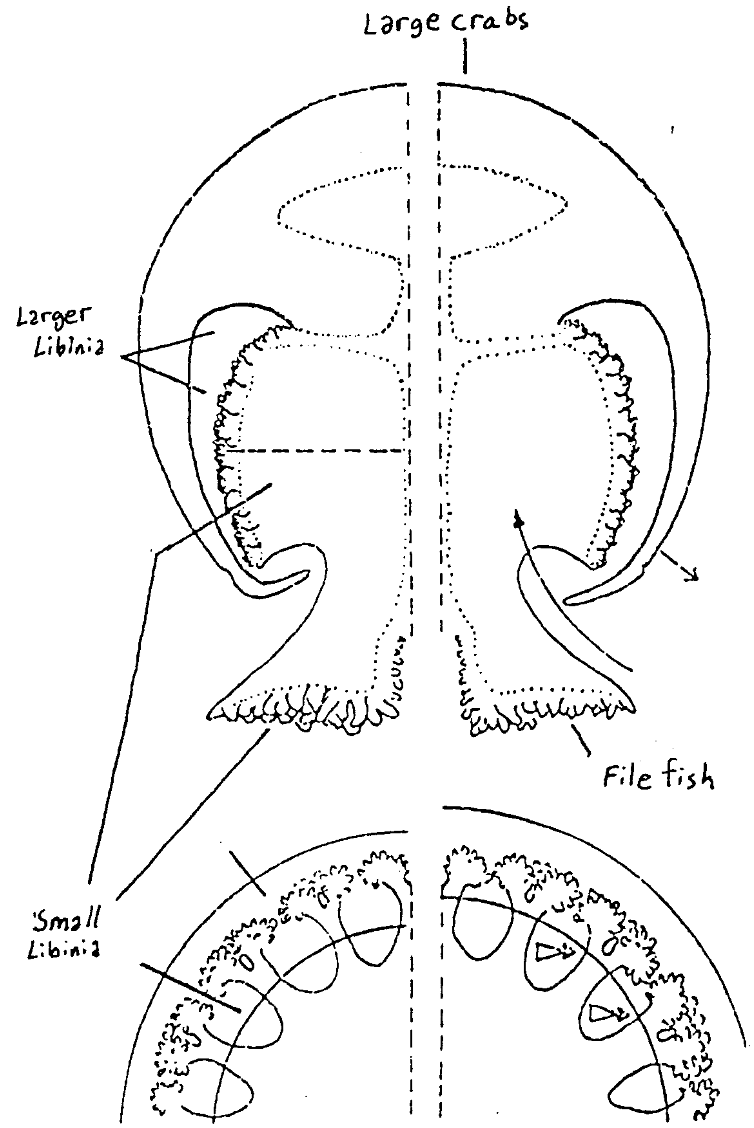

Figure 9. Locations where Libinia dubia and Monacanthus are most likely to be found with Stomolophus.

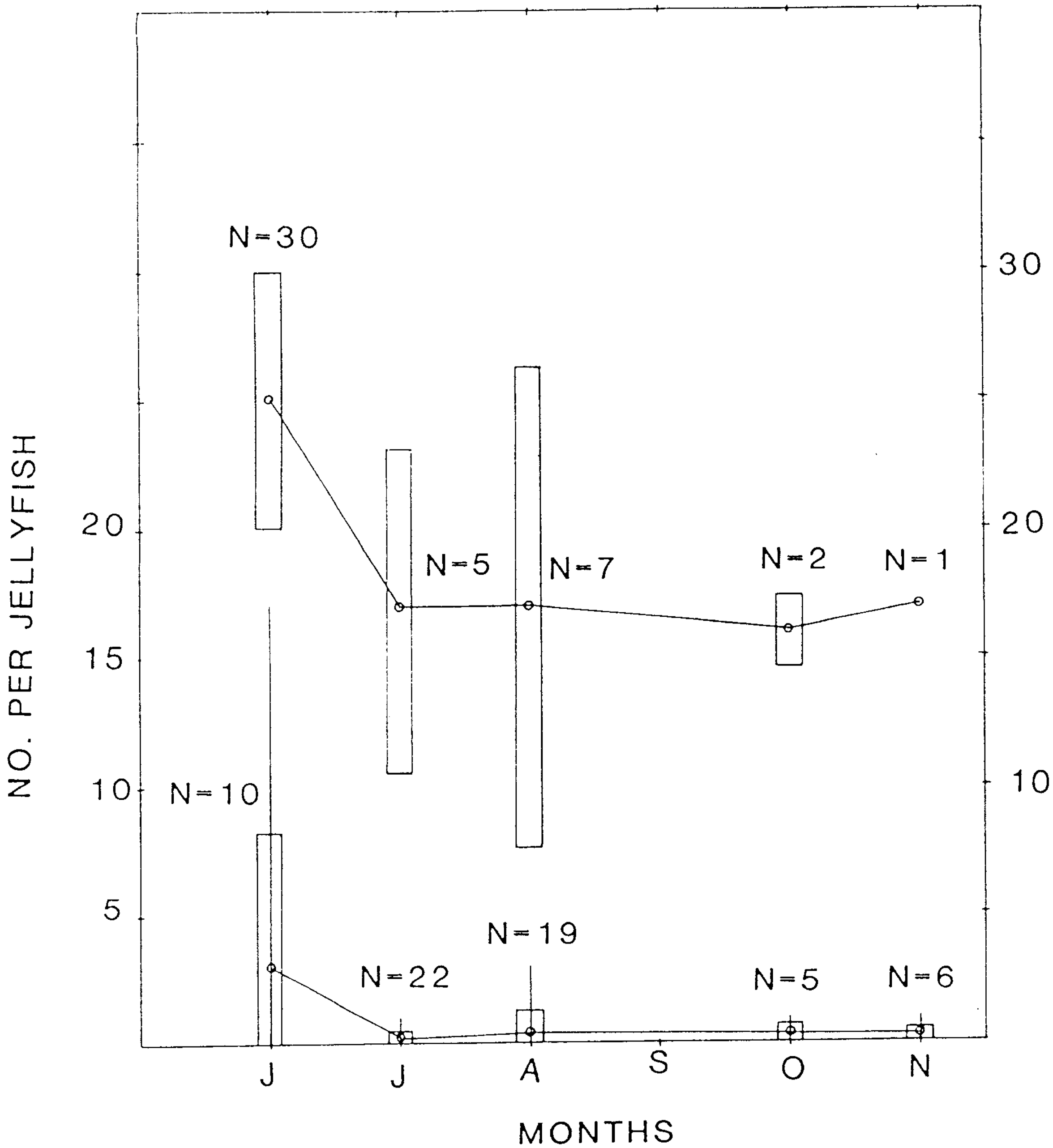

Figure 10. Mean standard length and number per medusa by month of <u>Monoacanthus hispidus</u> occurring with <u>Stomolophus</u>.

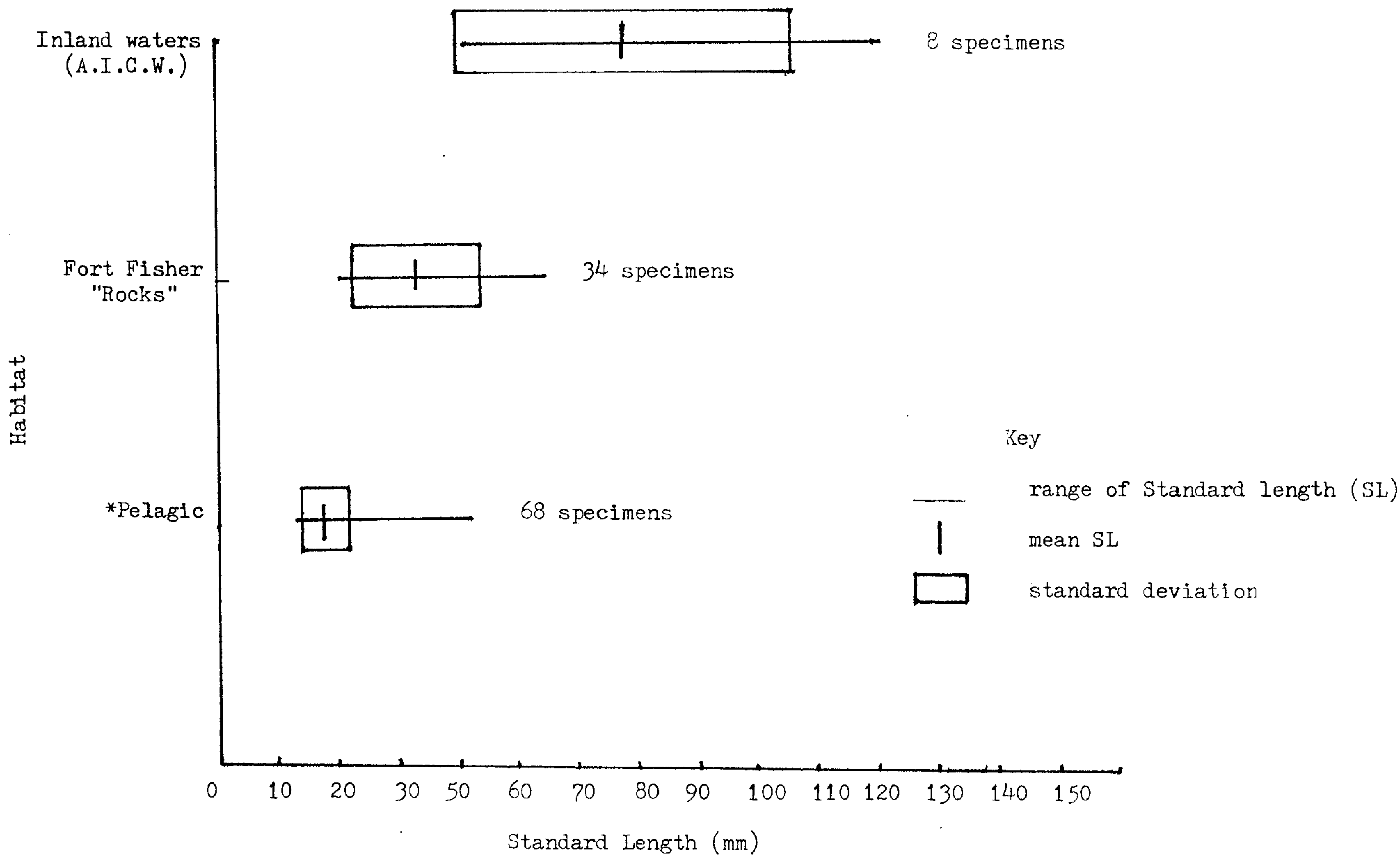

Figure 11. Size range of Monacanthus hispidus as a function of habitat.
All populations are highly significant
*Associating with Stomolophus meleagris or Sargassum

1.36 and the association occurred in twenty seven percent of the jellyfish.

One specimen of Caranx bartholomaei was collected with Stomolophus in July. One specimen of Alutera schoepfi was collected with Stomolophus in July, although one escaped from the same jellyfish and another was seen earlier that same day.

The butterfish Peprilus triacanthus was collected with Stomolophus only in June. No specimens occurred with Sargassum. The mean standard length was 19.5 mm, mean number per jellyfish was 2.8 while sixty four percent of the jellyfish harbored a symbiotic butterfish. The assocation stopped very suddenly near the end of June (within a two week period), after which time no additional specimens were recorded. Peprilus associates usually followed the jellyfish from behind but sometimes moved ahead of the host. When frightened they usually attempted to enter the subumbrellar cavity of the medusa.

The first specimens of the Atlantic bumper, Choloroscombrus chrysurus, were taken in June on only one occasion. Most of the bumpers appeared in a sudden wave in July, which corresponded with the disappearence of Peprilus triacanthus. The bumper was the only fish symbiont of Stomolophus which exhibited an increase in the mean number of fish per jellyfish after June (Figure 12). The number of fish peaked at 3.74 per medusa in August and then declined to zero in the fall. Chloroscombrus showed a decrease in its mean standard length from 17.5 mm in June to 13 mm in August (Figure 12). The smallest specimens (7 mm) were captured with a single sea nettle in August. In this specimen forty three bumpers averaging 10.55 mm in standard length were taken with two specimens, 50 and 55 mm S.L., of Peprilus alepidotus (many more bumpers captured with the sea nettle were destroyed before they could be separated from it in the lab). No specimens occurred symbiotically with Stomolophus in October or November, however, they did

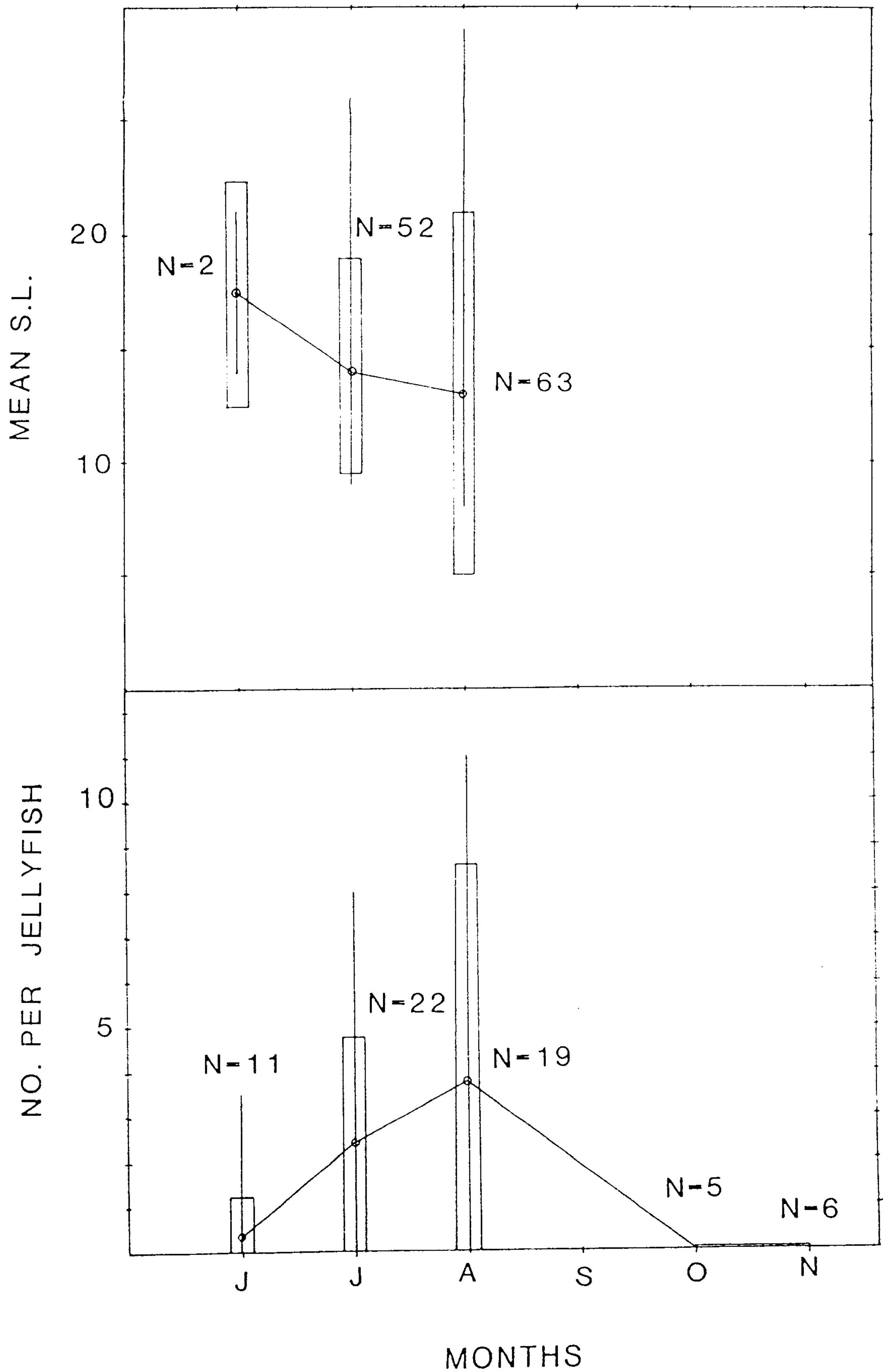

Figure 12. Mean standard length and number per medusa of <u>Chloroscombrus chrysurus</u> with <u>Stomolophus</u> by month.

occur concurrently in association with the moon jelly Aurelia aurita (see Table 1). Underwater observations confirmed that the bumbers associated with Aurelia exclusively, although both Aurelia and Stomolophus were present together in large numbers. It was also noted that all the bumpers were significantly larger than specimens from the summer.

Bumpers were observed to make use of both Stomolophus and Aurelia for protection in the following manner. When a diver approached in an aggressive manner the fish would attempt to keep the body of the medusa between themselves and the attacker. If left undisturbed they followed the jellyfish in a tight formation. The associates with Stomolophus refused to leave their host even if it were vigorously attacked. They would dash around and around the surface of the medusa (without touching) it in a frantic manner. Even if the medusa was roughly seized and shaken they would remain as close as possible. The fish even attempted to stay with the jellyfish when it was removed from the water, some to the point of entering the bell cavity of the medusa. Those individuals which were left behind would display a confused, disoriented behavior, forming a tight school which darted back and forth. If the jellyfish was returned to the water they usually rejoined it. On one occasion a bumper was seen swimming between two of the scapulets, orienting to the jellyfish substrate so as to swim upside down.

The number of symbionts per jellyfish decreased from a high in June into November (Figure 13), producing a negative linear regression line of $Y= -1.55x + 8.9$ with a correlation coefficient of -0.95. The number of fish symbionts per jellyfish reflected a similar trend with a linear regression line of $Y = -1.38x + 7.2$ and a linear coefficent of -0.89 (Figure 14). The percentage of jellyfish with associates by species and month are shown in Figure 15, only Chloroscombrus showed an increased abundance after June. Generally, the percent frequency of Libinia dubia

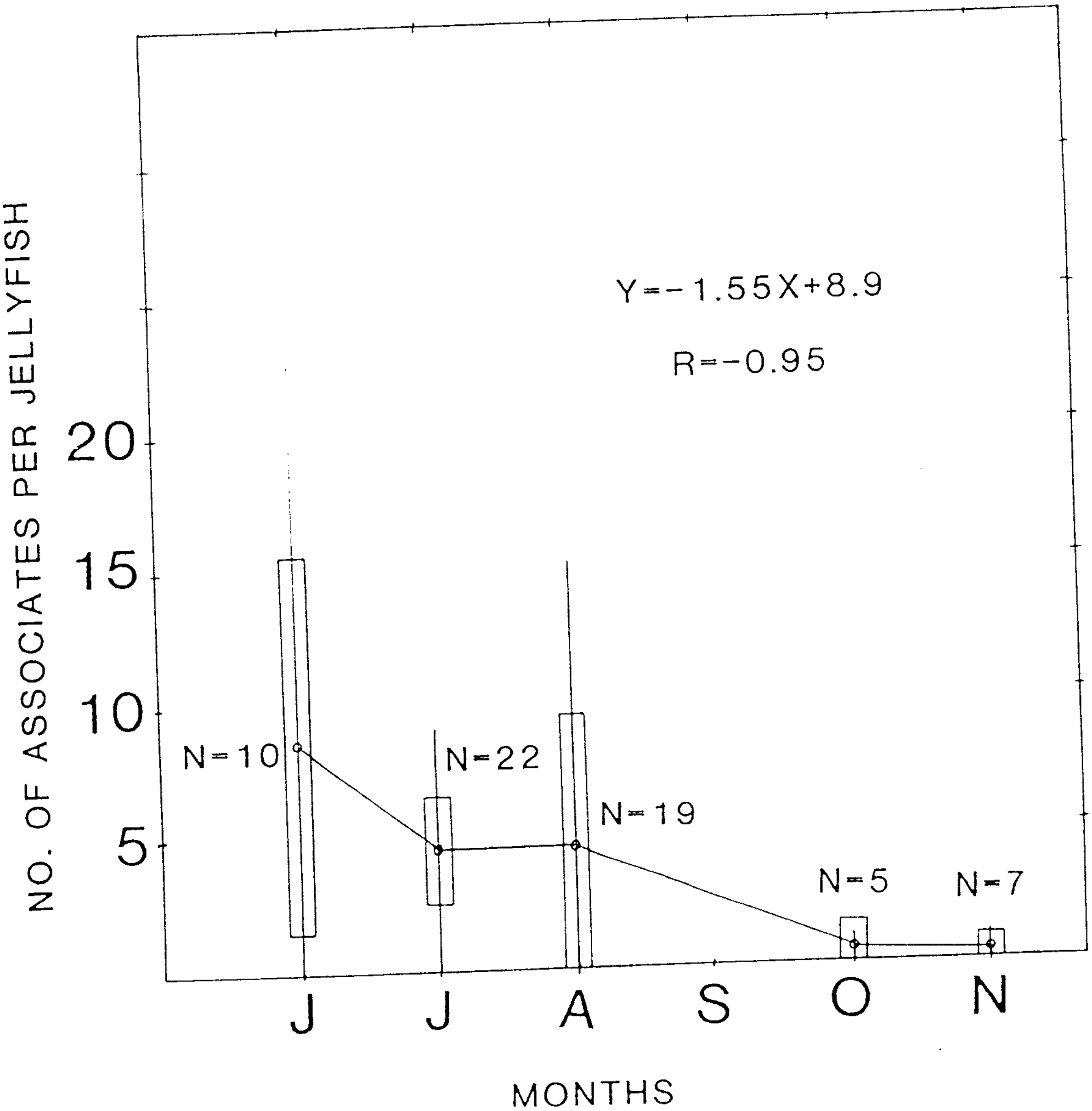

Figure 13. Mean number of symbionts occurring with <u>Stomolophus</u> by month.

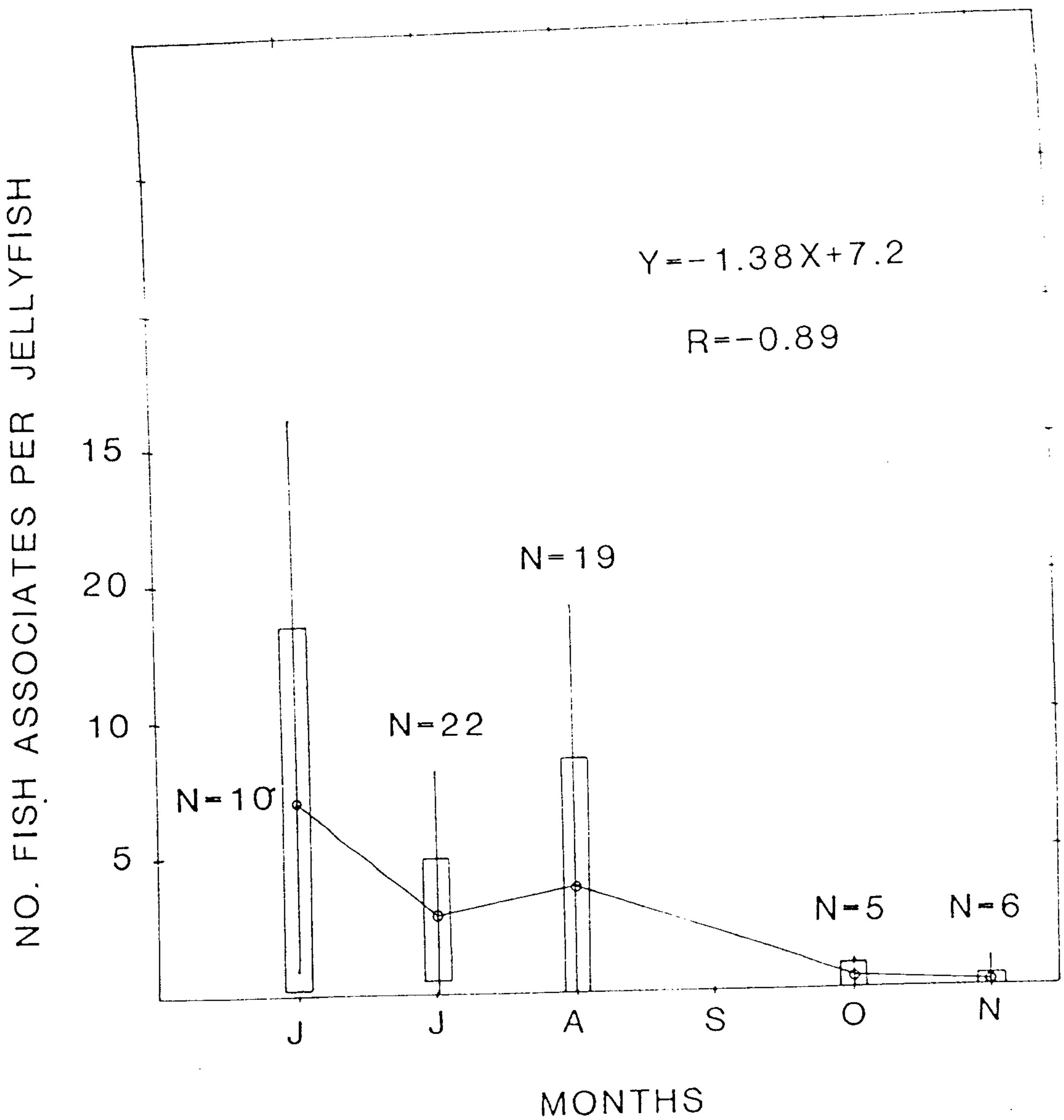

Figure 14. Mean number of fish occurring with <u>Stomolophus</u> by month.

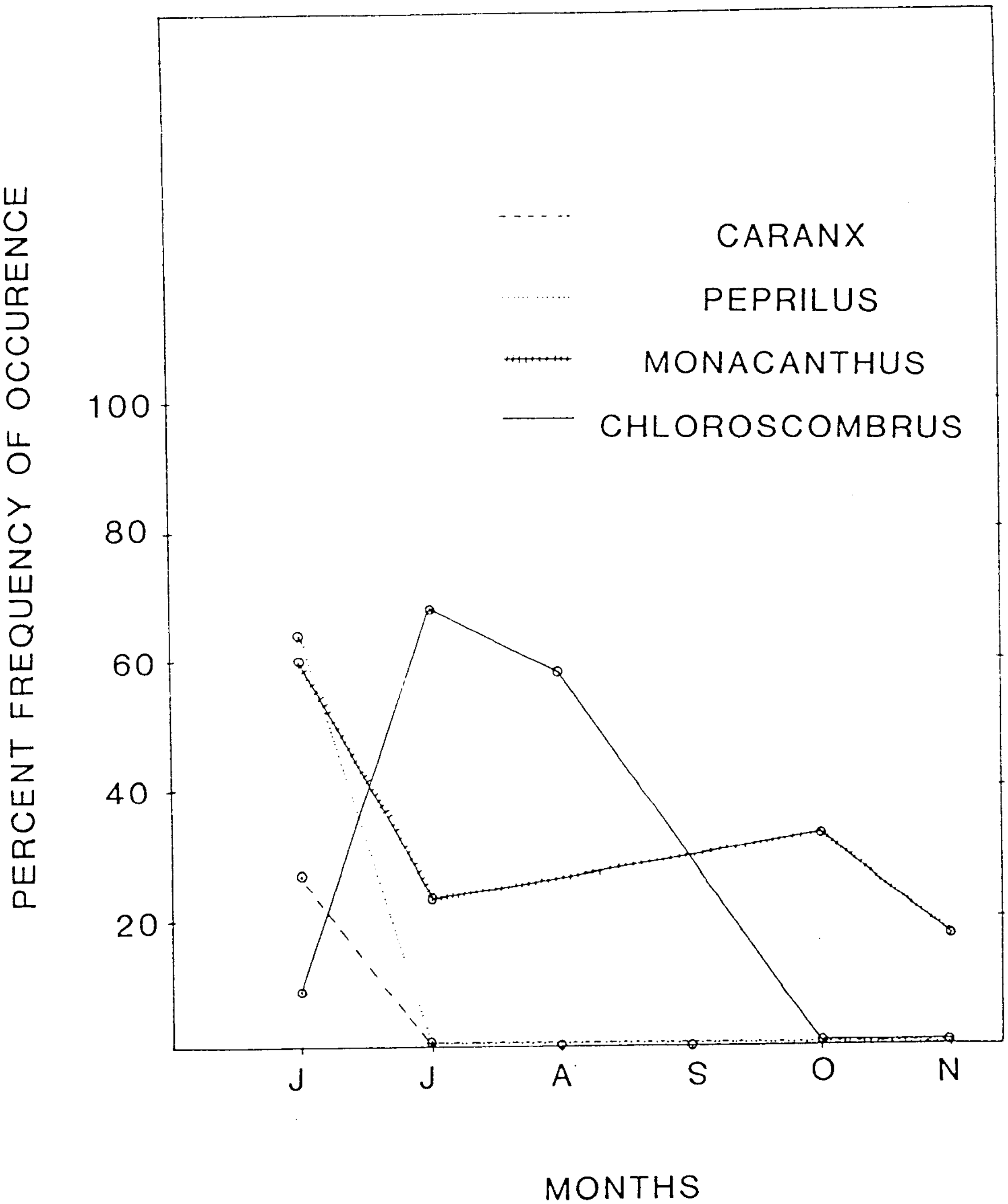

Figure 15. Percent of Stomolophus harboring symbionts by month and species.

peaked in July and then declined, the percent frequency of fish with Stomolophus declined from a peak of 100 percent in June, and the percent frequency of symbionts declined from a peak of 100 percent in June and July (Figure 16).

Discussion

The seasonality exhibited by the schyphozoans during this study is clearly evident from Table 3. The appearance of Chrysaora in July-August in the beach waters agrees with the literature (Kraeuter and Setzler, 1975; Schwartz and Chestnut, 1974). The fall apperence of Aurelia is also consistant with the literature (Schwartz and Chestnut, 1974), while the occurrence of Stomolophus from May to December in the study is similar to that recorded by Brooks (1882) and Kraeuter and Setzler (1975). The literature suggests that each of these species of jellyfish exhibit some sort of seasonal movement into or out of estuarine waters. This pattern is best established for Chrysaora which moves from brackish waters as young, into more saline waters as it grows, usually reaching the ocean in the mid-summer. Aurelia has not been shown to move in such a way, but from my interpretation of the literature, it appears that Aurelia moves from low salinity waters in the summer to higher salinity waters in the fall and winter.

The seasonal movements of Stomolophus as seen in my study and from the literature, particularly from Kraeuter and Setzler's study (1975), appears to be as follows (See Figure 17). Small populations of large adults appear offshore in the spring and move inshore by early summer. The origin of these populations of adults has not been determined, but it seems likely that they are survivors from the previous season (Kraeuter and Setzler, 1975). It is also possible that they are early spawned medusae from more southern waters which are carried north by prevailing

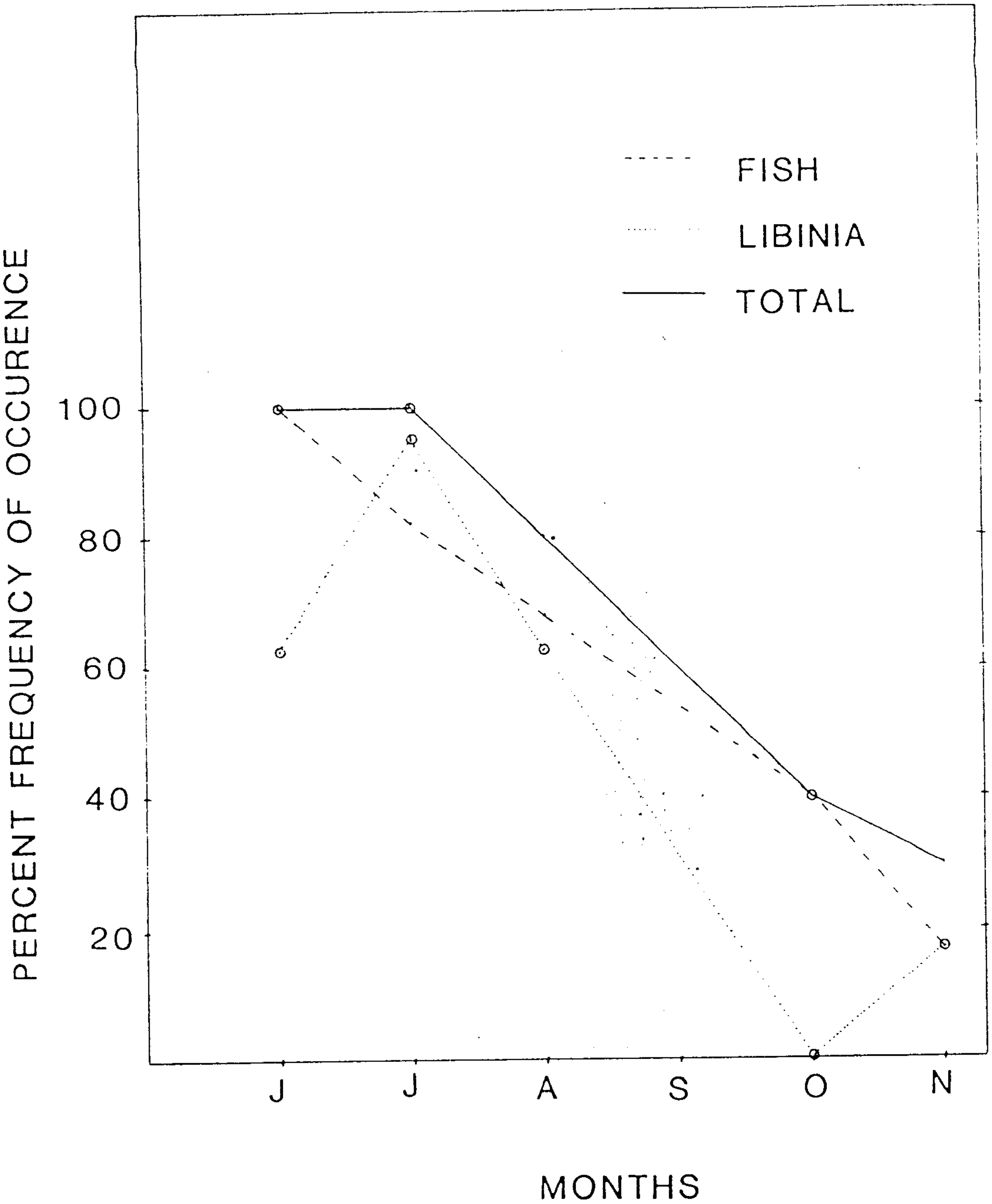

Figure 16. Percent of Stomolophus harboring symbionts by month.

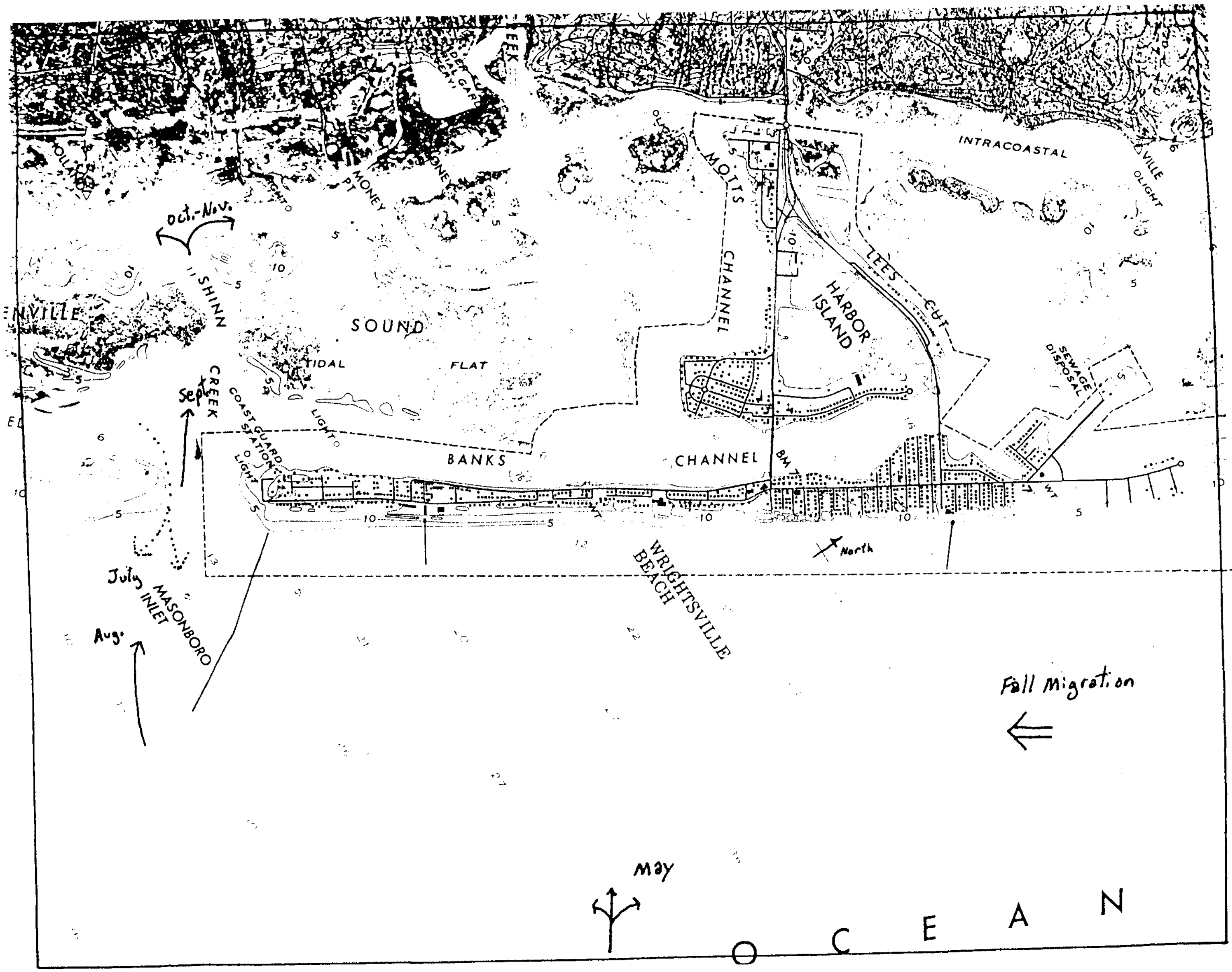

Figure 17. Hypothetical seasonal movement of <u>Stomolophus</u> based on evidence presented in this study and from the literature (Kraeuter and Setzler, 1975). Solid line indicates large adult medusae and dottled indicates small young medusae.

spring ocean currents. The increase in the population size through the summer (Figure 4), with the subsequent decline in the mean weight of the jellyfish observed in this study, was probably due to the recruitment from the estuarine population of young individuals which are suggested to move out from the protected waters by Kraeuter and Seltzer (1975). Kraeuter and Setzler (1975), found the young medusae move out from estuarine waters into more saline waters as they grow, in a manner similar to that exhibited by Chrysaora. The older generation continues to move into less saline and more protected waters as observed in my study, possibly being triggered to move into these waters by temperature conditions as suggested by Copeland (1965). Two concurrent events are therefore hypothesized: 1) first generation populations move from offshore in the spring to inshore waters in the summer and finally into brackish waters in the fall; 2) second generation populations move out from estuarine waters beginning in the mid-summer and continuing through the fall.

The masses of dead individuals reported during my study in October inside the protected waterways behind Wrightsville Beach, may result from the death of the older generation, but may also be the result of storm activity. The fate of the younger generation is unknown but two prominant possibilities exist. As already mentioned, Kraeuter and Setzler (1975), suggested a possible southern migration of individuals in the fall. This could explain the apparent influx and extreme abundance of Stomolophus observed in my study during November. The population density of the time period was not significantly different from that of the preceding time period. General observations indicated that the population had begun to decline before this time, and that this "swarm" of jellyfish appeared suddenly and disappeared equally fast. This may support the idea of a southern migration of Stomolophus populations from more northern waters in the fall. A possible mechanism for this migration may be found in the nearshore current patterns which are in a predominantly southern direction during the late fall from the North Carolina coast to northern Florida (Bumpus, 1973).

The only stage other than the medusa of Stomolophus which has been reported in nature is that of the ephyrae (Phillips, 1971) in the Gulf of Mexico. It is significant that the youngest medusae are collected from estuarine and protected waters (Kraeuter and Setzler, 1975) and that the smallest specimen, measuring three millimeters in diameter, was collected by Mayer (1910) from Charleston Harbor. This suggests that the young medusa are spending their early life in estuarine waters, and are produced by overwintering stages. These stages could then produce ephyrae in the spring and throughout the season, which is suggested by the continual recruitment of young individuals into the population. However, the presence of sexually mature individuals in March and July (Calder, 1982) seems to support the idea that planulae are produced throughout the season. But yet, in my study, no individuals of Stomolophus ventured beyond the mouth of Masonboro Inlet until the fall. This raises the question: Why do adult medusae actively move into estuarine waters with the onset of cold weather? The most plausible answer is that they move into these areas to release planulae, which would overwinter in the estuaries. Yet the adults appear to be mature throughout the season, and no overwintering stage has ever been found in these areas. More attention needs to be given to the seasonal movements of Stomolophus and its reproduction if this question is to be resolved.

The diving behavior of Stomolophus observed in this study, has been reported once before (Brooks, 1882), and is extremely fascinating. It seems that the jellyfish is responding to vibrations in the water, the stronger the vibrations the more likely the response is to be initiated (larger boats induce the response more often). It may be hypothesized that this behavior developed in response to rough surface conditions during storms, at which time it is safer for the jellyfish in deeper water.

The mechanics of the response are also of interest, as the jellyfish appears to pivot from the normal horizontal swimming position to a position with the bell directed downward. The mechanics of this phenomenon are unknown, but the medusa seems to make use of its marginal flaps (which are formed by the division of the bell margin by the eight rhopalia) in the manaeuver.

The ecological impact of jellyfish on the marine ecosystem has largely been ignored, with Phillips et al. (1969), Miller and Williams (1972) and Phillips (1971) making the most significant contributions. From these few studies it is apparent that jellyfish have a tremendous impact on zooplankton population, and thus are very important to the ecosystem. The method by which the energy captured by jellyfish populations gets back into the ecosystem and the position of jellyfish in food webs, has not been studied with the exception of Phillips et al. (1969). To illustrate the widespread importance of coelenterates as food for other organisms, and thereby provide an indication of their importance, the literature has been reviewed for records of organisms feeding on medusae and compiled in Table 5. From the wide varitey of organisms which are seen to use medusae as food in Table 5, it seems that the widespread assumption that jellyfish are of little importance as food for other organisms due to their low nutritional value (Mansueti, 1963; corrington, 1927), an idea which is based on studies indicating a high water content for medusae (Hyman, 1943; Lowndes, 1942; 1943), seems to be falsely grounded.

The associations between fishes and jellyfish are widely varied in nature, ranging from a simple opportunistic relationship (Mortensen, 1917; Mansueti, 1963; Haedrich, 1967 and Horn, 1970) to commensalism (Mansueti, 1963; Haedrich, 1967 and Horn, 1970) and parasitism (Scheuring, 1915; Mansueti, 1963; Haedrich, 1967). Opportunistic species are those that take advantage of any relatively passive cover near the surface like debris and sargassum. Caution shoud be exercised when appling any symbiotic term to an association without adequate data due to the lack of

Table 5

Organisms using jellyfish as food

Crustaceans		
Jasus lallandes	hydromedusae	Thomas (1963)
Emerita pacifica	Physalia	Bonnet (1946)
Callinectes	Cyanea capillata	Farr (1978)
"	Stomolophus meleagris	Farr (1978); Phillips et al. (1969)
Menippe mercenaria	Stomolophus meleagris	Powell and Gunter (1968: 296); Phillips et al. (1969)
Pagurus pollicaris	Scyphomedusae	Phillips et al. (1969)
Pagurus floridanus	Scyphomedusae	Phillips et al. (1969)
Ocypode quadrata	Physalia physalia	Phillips et al. (1969)
Libinia dubia	Scyphomedusae	Phillips et al. (1969)
"	Aurelia aurita	Jachowski (1963)
Fish		
Squalus acanthias	Ctenophores	Hargitt (1905: 25)
Haddock	Jellyfish	Wiborg (1960: 12-14)
Chaetodipterus faber	Stomolophus meleagris*	Millus (1982)
Mackerel	Jellyfish	Baird (1889: 79-80)
Caesio fusiliers	Ctenophore	Zann (1980: 208)
Pampus argenteus	Jellyfish	Masuda et al. (1975: 247)
Peprilus paru	Chrysaora quinquecirrha	Cargo (1962)
"	Mnemiopsis leidyi	Dunningham and Mansueti (1955)
Psenes cyanophrys	Physalia	Masuda et al. (1975: 246)
Peprilus triacanthus	Mnemiopsis leidyi	Oviatt and Kremer (1977)
Schedophilus pemarco	Jellyfish	Haedrich and Cervigon (1969)
Filefish	Rhopilema esculenta*	Hickson (1906: 312)
"	Rhopilema verrucosa*	Hickson (1906: 312)
Alutera schoepfi	Ctenophore	Hargitt (1905: 25)
"	Jellyfish	Hargitt (1905: 25)
Mola mola	Jellyfish	Hargitt (1905: 25)
"	Ctenophore	Hargitt (1905: 25)
"	Jellyfish	Sumner et al. (1913: 763)
Other		
Sea turtles	Chrysaora	Schwartz and Chestnut (1974)
Man	Lobonema smithi	Omori (1981)
"	Lobonemoides gracilis	Omori (1981)
"	Rhopilema esculentum	Omori (1978); Omori (1981); Hickson (1906: 312-313)
"	Rhopilema hispidum	Omori (1981); Hickson (1906: 312-313)
"	Rhopilema verrucosa	Hickson (1906: 312-313)
"	Stomolophus meleagris	Omori (1981)
"	Stomolophus nomurai	Omori (1978)

*Used as fishing bait

clear cut boundaries between the types of behavior. For this reason the terms used herein, should be taken in the broadest sense.

The reasons for the association of fishes with jellyfish are controversial. One possible reason is that the jellyfish serves as a food source for the associated fish (Scheuring, 1915; Mansueti, 1963; Haedrich, 1967; Horn, 1970). Another possible factor is that the jellyfish offers protection to the associated fish (Dahl, 1961; Mansueti, 1963; Haedrich, 1967; Horn, 1970; Van Hyning and Cooney, 1974). Mansueti (1963) holds that the associations are largely fortuitous and that the fish may have a selective advantage over non-symbionts in that they are assured a continous food supply, protection and possibly gradual immunity to jellyfish toxin. No single factor can totally explain all the associations, and it is likely that they result from a combination of factors. The nature of the associations between the known fish symbionts of Stomolophus (Table 6) will be described in more detail individually.

Libinia dubia - spider crab

It is clear that the average size of symbiotic specimens of Libinia dubia, changes very little over the summer (Figure 8). Only juvenile crabs under forty millimeters in carapace length are found associated with Stomolophus. The size range, however, increased throughout the summer. The increase in the size range is due to a constant recruitment of young crabs into the population and to the growth of the older crabs. This indicates that the crabs drop out of the association befgore reaching 40 mm in carapace length, since one would expect the average size of the crab to increase through the season in a nonassociation population. The decline in the number of crabs per medusa from a high in June to lows in the fall is certainly a function of the increasing jellyfish population, so that even if the crab population were to remain constant through time, the average number of crabs

Table 6

Known Fish Associates
of
Stomolophus meleagris

North Carolina

Aluterus schoepfi (New record)
Caranx bartholomaei (New record)
Caranx hippos (New record)
Chloroscombrus chrysurus (New record)
Monacanthus hispidus (New record)
Nomeus gronovii (Smith, 1907; Jenkins, 1887)
Peprilus triacanthus (Smith, 1907)

World Wide

Aluterus schoepfi (Hargitt, 1905; Cargo and Schultz, 1966)
Caranx bartholomaei (New record)
Caranx fusus (Gunter, 1935; McKenny et al., 1958)
Caranx hippos (Gunter, 1938)
Chloroscombrus chrysurus (Baughmann, 1950; Phillips et al., 1969)
Hemicaranx amblyrhynchus (Hildebrand, 1954)
Peprilus burti (Horn, 1970; Phillips et al., 1969)
Peprilus triacanthus (Hildebrand, 1954; Hoese et al., 1964)

per mudusa would decline. The monthly percent frequency of Libinia with Stomolophus showns a peak in July of 95 % occurrence. Since the jellyfish population has increased in July over what in was in June, the population of Libinia must have correspondingly increased. It can therefore be concluded that the population of juvenile Libinia peaked around July. The subsequent drop in the number per medusa and in the percent frequency, was probably due to a decline in the recruitment of new juveniles with the onset of colder temperatures and to the large increase in the jellyfish population after July (Figure 4).

An examination of the locations where the crabs were found on the jellyfish revealed that most of the smaller crabs were found between the scapulets. This suggests that they were most likely feeding on zooplankton captured by the medusae since this is the site of capture of the zooplankton (Larson, 1978). This was supported by the fact that crabs given the choice of feeding on medusae tissue or other food items such as shrimp, invariably chose the latter in my observation, although they readily fed on the medusae tissue if nothing else was available. Larger crabs were positioned as shown in Figure 9. From this position they can easily reach out and get food from the scapulets. This position is also likely to be favored because it is the most stable part of the constantly contracting umbrella. The larger crabs occasionally found on the exterior of the bell were probably those individuals which will soon abandon the jellyfish host. The predation of the crab on the jellyfish probally does not seriously impair it since its regenerative powers are remarkable. I have observed many specimens with scars from very large wounds which probably resulted from an encounter with the propellar of a boat.

Monacanthus hispidus - planehead filefish

The planehead filefish, *Monacanthus hispidus*, is an opportunistic associate of *Stomolophus*. The mean number per medusa, mean standard length and peak percent frequency corresponded to their concurrent occurrence in sargassum in the study area (Table 4). The populations of *M. hispidus* associating with sargassum and *Stomolophus* were identical. After June, when the sargassum has dissappeared these parameters remain relatively constant and probably reflect the continuous recruitment of young fish into the population which is consistant with the literature on the occurrence of juvenile filefish (Martin and Drewry, 1978; Berry and Vogele, 1961; Fahay, 1975). The association of *Monacanthus* with sargassum is well documented (Weis, 1968; Fine, 1970; Dooley, 1972), but the association with *Stomolophus* is poorly known. One specimen was collected with *Stomolophus* by Phillips et al. (1969), in the Mississippi Sound and Phillips (1971), later indicates that it is a common associate with *Chrysaora*, *Stomolophus* and *Cyanea*. Juveniles are pelagic and associate with *Stomolophus*, sargassum and floating debris. Small juveniles appear to begin dropping out of the associations at around 30 mm S.L. (Figure 11). A similar trend occurs with haddock and *Cyanea* in which juveniles associate with jellyfish during their pelagic life and begin to move to a benthic habitat at a length of about 100 mm (Colton and Temple, 1961).

Although this association is here described as an opportunistic one, its importance to the fish should not be discounted. Since the abundance of *Stomolophus* in the study area was much greater than the abundance of sargassum, and occurred for a prolonged season, the population of filefish associating with jellyfish was large at times.

Observations of the symbiotic behavior of Monacanthus suggests several advantages for the fish: 1) the fish feeds on the medusa (Phillips, 1971) and on the zooplankton captured by it; 2) the medusa provides considerable protection for the filefish, especially for those individuals which wedge themselves amoung the oral arm mass; 3) the coloration of the fish also contributes to the protective value of the association since the filefish is very difficult to see when it swims in close proximity to the oral arm mass; and 4) the filefish can hitch a free ride with the medusae. To explain the latter, the filefish were always observed to swim behind the oral arm mass. In this position it need expend very little effort in swimming as it gets pulled along with the medusae by its swimming and feeding action. Filefish were also observed to hold on to the oral arm mass with its mouth in a manner similar to that observed with filefish resting with sargassum, so that it need not swim at all.

Alutera schoepfi - orange filefish

This species has been described as a predator of jellyfish, rather than as a symbiont based on a report by Cargo and Schultz (1966) in which it was described as feeding on Chrysaora. A little known earliar report of this behavior was given by Hargitt (1905) in which Alutera was said to feed on jellyfish and ctenophores. In this study I collected one specimen with a jellyfish from which another escaped. That same day another specimen was observed but not collected. Also of interest was the occurrence of mucous strands trailing behind the medusa behind which Alutera was following, possibly indicating that the jellyfish was being irritated by the fish. I did not, however, observe the fish feeding on the jellyfish. This response on the part of the jellyfish, toward an irritant may explain the conflict between the observations of mucous strands by Phillips et al. (1969) and Larson's (1978) findings that it is a response to handling and not a food capture mechanism.

Caranx fusus - blue runner

Little is known of the association of the blue runner with jellyfish other than it occurs occasionally with Stomolophus (Gunter, 1935; McKenney et al. 1958).

Caranx hippos - crevalle jack

This species has only been reported as an associate of Stomolophus (Gunter, 1938). Caranx hippos is here considered to have an opportunistic relationship with Stomolophus since it occurs concurrently with sargassum in the study area and the two populations were identical. Very little more can be said regarding this association because of the lack of data. I did not observe the behavior of this species in the field. The status of the associations of carangids in general are very poorly understood, though jellyfish symbiosis with the jacks are the most widespread, with twenty-three species of fish known to associate with twenty species of jellyfish (Mansueti, 1963). The overall pelagic nature of the family is probably the main reason for the many associations.

Caranx bartholomaei - yellow jack

Again little is known of this association, it has been recorded only twice in the literature (Berry, 1959; and Fowler, 1945) and I collected one specimen in July. The occurrence was not related to sargassum. The status of this association remains undetermined.

Hemicaranx amblyrhynchus - bluntnose jack

Very little is known of the association reported by Hildebrand (1954).

Oligoplites saurus - leather jacket

Copeland (1965), indicated that it associates with Stomolophus citing Hildebrand (1954) and Mansueti (1963), but neither author mentions this fish. Further, there seems to be no record of this association in the liturature so I assume the record to be false. However, it is not an unlikely association since the fish does associate with floating debris and leaves in a mimic behavior (Breder, 1942).

Nomeus gronovii - man-of-war fish

This species is most often associated with Physalia sp. and is reported as commonly associated with Stomolophus from Beaufort, North Carolina (Smith, 1907).

Peprilus burti - harvestfish

The harvestfish is recorded by Horn (1970) as associating with Stomolophus in the Gulf of Mexico. Very little is known of this association primarily due to its frequent confusion with P. triacanthus (Horn, 1970).

Peprilus triacanthus

The association of Peprilus triacanthus with jellyfish was reviewed by Mansueti (1963) who indicated it to be an ectoparasite. It has been found to drop out of the association by about 30mm Horn (1970). Mansueti proposed that it behaved much like P. paru (=alepidotus), which begins as a commensal with

Chrysaora quinquecirrha the "Sea Nettle" while very young in June. It gradually becomes an ectoparasite as it grows and finally a predator in the fall. He supports this with gut analysis and observations which indicated the fish feeds heavily on the tentacles and to a lesser extent on other parts of the jellyfish (Mansueti, 1963). Another study indicated that the butterfish feeds on the jellyfish only infrequently (Buhler, 1930).

Mansueti (1963) also noted an average of two fish per jellyfish, decreasing from several smaller fish to a few larger fish with time. In my study, I found an average of 2.8 fish per jellyfish, but as I indicated under the discussion of the association of Libinia and Monacanthus, the number of fish per jellyfish was found to most strongly reflect the population changes of the host and consort. Observations of larger and fewer fish with time are expected if the fish are growing and the jellyfish population is increasing. This concept is important, and has not been recognized in other studies.

Accounts of the association of P. tricanthus with Stomolophus are less frequent, recorded in the literature three times (Smith, 1907; Hildebrand, 1954; Hoese et al. 1964). The seasonality of the association of Peprilus with Stomolophus is not clear. In this study, Peprilus were taken only during June, but none were taken with sargassum. I was quite surprized by the early disappearance of P. triacanthus after June, as I had taken one specimen in November of 1981 and had seen others that fall. What this disappearance means is uncertain and more data is needed.

Peprilus exhibits a strong behavioral attraction to Stomolophus, often refusing to leave it even when threatened. I once captured one inside the bell of a specimen of Stomolophus which I had snagged while fishing from a ocean pier. The fish remained with the jellyfish even after being dragged at least ten yards through the water and hauled twenty feet through the air. On other occasions, however, the fish scatter from the jellyfish when threatened, this may indicate that they associate with Stomolophus for other reasons than just for protection. One possible explanation for this scattering could be that only a few fish can fit safely inside the bell cavity of the jellyfish and enjoy the greatest protection. This may also explain why only one or two fish are uslly found within the bell cavity when captured, the rest of the fish either escape or are captured in the net. Mansueti (1963), found the number of individuals associating with a jellyfish to decrease with size, this may reflect a sampling bias caused by the loss of associates due to the use of a small net. From my observations, most of the fish do not enter the bell when threatened but remain in very close association with the jellyfish. The first fishes to get in the cavity may prevent others from entering, and the strong reluctance to leave the bell cavity may be a result of competition for that space.

Chloroscombrus chrysurus- Atlantic bumper

Very little is known of the biology or seasonality of Chloroscombrus chrysurus, neither the larval or juvenile forms have been described (Johnson, 1978). Johnson (1978) has compiled information on the species, and it is usually considered a shallow water form (Klima, 1971). Records of symbiosis between bumpers and jellyfishes are compiled in Table 7.

From the mean number of fish per jellyfish and mean monthly standard length (Figure 12), it is clear that the youngest and most abundant populations of bumper fish occurred during July and August, suggesting a peak spawning period at this time. It should be emphasized that the increased number of jellyfish in the population, during the late summer, requires the population of bumper fish to increase substantially in order to reflect the increased numbers per jellyfish.

Table 7

Records of *Chloroscombrus chrysurus* Associating with jellyfishes

Jellyfish	Source
Aurelia aurita	Zann (1980: 214); McKenny (1965: 104); Longely and Hildebrand (1941: 76); Franks (1970: 55-56)
Chiropsalmus quadrumanus?	Beebe (1928: 29-30); Beebe and Tee-Van (1928: 11)
Chrysaora quinquecirrha	Agassiz (1865: 49);* Agassiz and Mayer (1898: 6);* Phillips et al. (1969); Phillips (1971); Smith (1907: 211); Matthews and Showmaker (1952: 270)
Stomolophus meleagris	Gunter (1935: 40); Baughman (1950: 246); Phillips et al. (1969); Phillips (1971)
Mastigas scintila	Moreira (1961: 16-18)+
Tamoya haplonema	Beebe (1928: 84-85)
Unidentified	Fowler (1945: 193); Reid (1954: 33); Hastings (1972: 213-214)

*Described as a "Clupeoid" fish, I include the records here because they are most likely Atlantic bumpers.

+From Mansueti (1963)

The occurrence of the smallest specimens of Chloroscombrus in large numbers with the low population of Chrysaora in July, may indicate that the fish are moving with the jellyfish as they "outflow" from the estuaries. It is interesting that the peak in the mean number of fish per Stomolophus meleagris occurs at the time when the jellyfish are just about ready to begin entering the inlets and backwaters, and that the association with Stomolophus ends when they move into these areas in large numbers in the fall. At this time the bumpers preferentially associate with Aurelia. If Aurelia does exhibit a movement to higher salinity water as speculated earliar, this may explain the preferential behavior. A pattern of movement of juvenile bumpers out of estuarine waters in the midsummer is then seen. Again, it is the pattern of the movement of the jellyfish and of the fish which dictates not only the size and numbers of fish per jellyfish, but also which jellyfish make a suitable host.

The symbiotic association of the bumper fish with jellyfish, appears to be the strongest of those examined. Beebe (1928) remarks that he thought the newly hatched young of Chloroscombrus seeks out the first jellyfish it could find and immediately takes up residence. However, they begin to quit the association by about 40 mm (Phillips et al. 1969). My observation made of the individual swimming between the scapulets seems to support the idea that these fish feed on zooplankton captured by the medusae.

The general trends of decreasing symbionts per medusae (Figure 13 & 14) and decreasing percentage of occurrence (Figure 15 & 16) observed in this study, are a reflection of the increasing population of jellyfish and the decreasing population of young consorts. Any correlations of size and number of fish to the weight of the host, must take into account the trends of growth of the fish and the jellyfish.

Conclusion

The symbiosis of fishes with Stomolophus appears to be largely a function of the population dynamics of each. The size of the fish associates of Stomolophus are a function of the season and the growth of the fish and host, as opposed to a "carrying capacity" of the host. The percentage of jellyfish which have symbiotically associated fish or crabs is a function of the size of the jellyfish population and of the fish population. If the jellyfish population remains constant and the total population of the symbiont increases, the frequency of the association and the number of associates per medusae will correspondingly increase. On the other hand, if the host population increases, and the symbiont population decreases, the percent frequency and number of symbionts per medusae can be expected to decrease. The size of the symbionts are a function of their growth and not of the size of the host jellyfish. The associations are therefore considered nonspecific with respect to the host jellyfish, but are determined by which jellyfish are available to it within the context of its own movement patterns.

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