1-1-2001

Abundance and Distribution of Commensal Amphipods From Common Marine Sponges of Southeast Florida

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NSUWorks Citation

Stacie E. Crowe. 2001. *Abundance and Distribution of Commensal Amphipods From Common Marine Sponges of Southeast Florida.* Master's thesis. Nova Southeastern University. Retrieved from NSUWorks, Oceanographic Center. (306) https://nsuworks.nova.edu/occ_stuetd/306.

ABUNDANCE AND DISTRIBUTION OF COMMENSAL AMPHIPODS FROM COMMON MARINE SPONGES OF SOUTHEAST FLORIDA

BY
STACIE E. CROWE

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE

WITH SPECIALTY IN
MARINE BIOLOGY

NOVA SOUTHEASTERN UNIVERSITY
2001

MASTER OF SCIENCE
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THESIS

OF

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ABSTRACT

Marine sponges were examined from shallow waters of southeast Florida and the Florida Keys to determine species composition and distribution of commensal amphipod crustaceans from shallow reef, mangrove, and seagrass habitats. Twenty sponge species were investigated during this study, sixteen of which housed amphipods in the families Colomastigidae and/or Leucothoidae. Six species of commensal amphipods were identified. *Leucothoe spinicarpa* (Abildgaard) species "complex" was the most dominant amphipod commensal, representing 63% of the total amphipods collected. The *L. spinicarpa* "complex" contains four local morphotypes, which are diagnosed and briefly described. Common sponge hosts included *Callyspongia vaginalis, Mycale* sp., and *Myriastra kallitetilla*.

ACKNOWLEDGMENTS

I first thank my advisor, Dr. James Thomas, who provided the idea for this thesis. He has been a source of viewpoints and experiences that have helped me grow as a scientist. His expertise in amphipod systematics and biology is an inspiration in itself. I am indebted for his patience and advice throughout this research.

Special thanks go to my other committee members, Drs. Charles Messing and Martin Thiel. They were extremely helpful and generous with their time, and provided thoughtful comments and suggestions that were essential to organizing the final manuscript.

Several people helped with the various aspects of this research, but I am especially grateful to Judy Robinson for donating several hours of her time and for technical and mental assistance in times of despair. Her companionship and moral support in the field and lab have been invaluable.

Finally, I thank the members of my family. My parents have provided steady encouragement and support throughout this endeavor. Very special thanks go to my husband, David Crowe, without whose help this thesis would not have been written. His moral support, constant companionship, and sound advice are greatly appreciated.

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INTRODUCTION

Commensal relationships are common between sessile plants or animals and motile organisms. Marine environments exhibit numerous types of associations. Many marine fish (Tyler and Bohlke, 1972), crustaceans (Thomas and Cairns, 1984), and polychaete worms (Van Dover et al., 1999) are reported as commensals associated with sessile invertebrate hosts. Commensalism is an intimate association between two organisms where one party benefits, while the other is not significantly affected. Details of these associations are little studied in marine ecosystems, yet they are important in determining and evaluating evolutionary change and relationships in addition to maintaining ecosystem balance (Duffy, 1992).

Marine sponges are abundant and often serve as hosts to a variety of commensal organisms including crustaceans, polychaetes, and ophiuroids (Villamizer and Laughlin, 1991; Uriz et al., 1992; Seger and Moran, 1996). Sponges have several characteristics conducive to commensal occupation including: 1) an abundance of internal canals that supply the commensal with nutrients and particulate organic matter via feeding/respiratory currents generated by the sponge (Duffy, 1992); 2) a protective and defensible habitat conducive to development of eusocial behavior (Spanier et al., 1993), and 3) the use of internal canals as a refuge from predation.

Individual sponges can host entire communities of endocommensal species, those commensal organisms living entirely within a host. Host volume as well as size and distribution of internal channels are factors that may determine community structure and population size within any given sponge specimen. In a comparative study between the sponges *Aplysina archeri* and *Aplysina lacunosa*, Villamizer and Laughlin (1991) found a more diverse community in *A. lacunosa*, a species with a larger internal area and volume. The internal cavities of hosts may lead to eusocial behavior in the commensals as defined by cooperative brood care, reproductive division of labor, and overlap of generations (Seger and Moran, 1996).

Sponges may also provide protected breeding habitats for commensal amphipods. Many marine peracarid crustaceans (e.g., amphipods, tanaids, isopods) exhibit varying levels of extended parental care, during which parents care for their offspring for a certain period of time after hatching. Parents can provide various types of care for their juveniles including improved feeding conditions, and a protective shelter. Amphipod families known to participate in this reproductive strategy include the Caprellidae (Aoki and Kikuchi, 1991; Thiel, 1997) and Podoceridae (Mattson and Cedhagen, 1989). Thiel (1997) proposed that extended parental care within epibenthic burrow– (*Leptocheirus pinguis*) and tube–inhabiting (*Dyopedos monacanthus*) amphipods is primarily a mechanism to protect juveniles from predators. This practice may also provide shelter and nutrients to juveniles as they grow, thus decreasing their susceptibility to predators once they leave the parents. In a study along the Atlantic coast of Florida, juvenile leucothoid amphipods from the solitary ascidians *Phallusia nigra* and *Styela plicata* were presumed to remain in the host parent for long periods of time, some until sexual maturity (Thiel, 1998). Long term interactions such as these represent an adaptive foundation from which advanced social behaviors may arise within the host.

Several feeding studies show that predatory fishes are deterred from consuming sponges that contain secondary metabolites (Duffy and Paul, 1992; Chanas et al., 1996; Chanas and Pawlik, 1997; Marin et al., 1998), chemicals apparently not required for any primary metabolic processes such as cell respiration and photosynthesis (McClintock et al, 1998). They may, however, play important roles in an ecological sense. Many species of marine symbionts are highly host specific, occupying only a single host species or population (Dalby, 1996). Meroz et al. (1995) speculated that commensals directly or indirectly select their hosts in order to take advantage of toxic secondary metabolites produced by the hosts as predator deterrents, and which may also provide protection for commensals. However, Pennings et al. (1994) indicate that the ability of secondary metabolites to deter predators may depend on other factors, such as the nutritional quality of the prey organism, or the quality of the artificial diet offered in laboratory assays. Nevertheless, it is hypothesized that sponges that contain high concentrations of secondary metabolites may be better protected against predation and should host comparatively large numbers of endocommenal species.

Among the invertebrates recorded as endocommensals of sponges, amphipod crustaceans are widespread and abundant in all marine habitats worldwide. Usually free-living, they can be found in sediments, swimming near the substrate, or inhabiting a variety of domiciles including empty snail shells, crevices, tubes and burrows produced by other organisms, and coral rubble (Thomas, 1993). Like all peracarids, amphipod embryos develop in a thoracic marsupium, or brood pouch, of females, and thus lack a dispersive pelagic larval stage. As adults, most amphipods are benthic and have few opportunities or mechanisms for extensive active dispersal, increasing the probability that other events determine their distribution. Commensal amphipods that choose sessile hosts, such as sponges and ascidians have extremely limited dispersal making them excellent candidates for evolutionary and biogeographic studies. However, opportunities for passive dispersal may occur if the host attaches to a moving or floating object, as occurs frequently in the amphipod families Podoceridae, Gammaridae, Ampithoidae, and Hyalidae.

Within gammarid amphipods, Colomastigidae and Leucothoidae are often mentioned as sponge commensals (Ortiz, 1975; Biernbaum, 1981; Vader, 1983b; Costello and Myers, 1987; Barnard and Karaman, 1991; Thomas, 1993; LeCroy, 1995; Thiel, 1999). Both families are cosmopolitan in marine habitats. However, little is known concerning host preferences and specific behavior patterns for species of either family.

The Colomastigidae are found in most seas of the world with the exception of the Arctic. They have been studied most extensively in Madagascar (Ledoyer, 1979; 1982) and the eastern Gulf of Mexico (LeCroy, 1995). The family contains 41 described species in two genera, *Colomastix* and *Yulumara*. The type genus, *Colomastix*, contains 37 species worldwide, while *Yulumara* contains four species, two from Australia, and one each from Tasmania and South Africa. Colomastigids have been reported as associates with sponges (Pearse, 1932; Heard and Perlmutter, 1977), corals (Barnard, 1970; Myers, 1990; Müller, 1992), and algae (Barnard, 1970,1972; Ledoyer, 1978; 1979; 1982; Moore, 1988; Müller, 1992). Eleven species of *Colomastix* have been reported from the Gulf of Mexico (LeCroy, 1995): *C. janiceae*, *C. irciniae*, *C. halichondriae*, *C. bousfieldi*, *C. camura*, *C. cornuticauda*, *C. denticornis*, *C. falcirama*, *C. gibbosa*, and *C. tridentata*. *Colomastix halichondriae* Bousfield, 1973, has also been reported as a sponge associate from the East Coast of the United States (Biernbaum, 1981).

The Leucothoidae currently comprises 75 species in two genera, *Leucothoe* and *Paraleucothoe*. Although leucothoids are common commensals in sponges and ascidians, they may also be found in fine sand or mud (Krapp-Schickel, 1975b; Thomas and Ortiz, 1995), or in association with algae, corals, or coral rubble (Barnard, 1970; Myers, 1985c). Members of this family have been described from around the world including Africa, the Arctic Boreal, the Caribbean, and Hawaii. Extensive studies in Madagascar (Ledoyer, 1986), the Mediterranean (Ruffo and Schickel, 1967), and the tropical Indo–Pacific (Barnard, 1965) have described many new species and provided ecological information.

However, much taxonomic confusion remains at the species level. Within the genus *Leucothoe*, certain species have become a "dumping ground" for taxonomists. For example, *Leucothoe spinicarpa,* the type species of the family, was originally described by Abildgaard (1789) from the Skagerrak off Denmark. Subsequent reports of *L. spinicarpa* include both polar oceans, temperate and tropical seas, and depths ranging from intertidal to 4,000 m. In southeast Florida alone, specimens identified by various authors under the name *L. spinicarpa* probably represent several species of commensal or cryptic amphipods (Thomas, 1993).

STATEMENT OF OBJECTIVES

This study investigates the abundance, distribution, and ecology of amphipods commensal in sponges in southeast Florida and the Florida Keys — an area with abundant and diverse sponge communities. To date, few published records concerning commensal amphipod ecology or behavior exist. Early studies from the Dry Tortugas (Pearse, 1932) reported *Leucothoe spinicarpa* and *Colomastix pusilla* Grube within the loggerhead sponge, *Spheciospongia vesparium*. In 1977, Heard and Perlmutter described *Colomastix janiceae* (formerly *C. pusilla*) as a sponge commensal from the Florida Keys. Thomas (1979) reported *Anamixis pottsi* (Shoemaker, 1933) as a commensal with the tunicate *Ecteinascidia turbinata* Herdman, 1880, and *L. spinicarpa*, *Anamixis cavitura* (Thomas, 1997), and *C. janiceae* as sponge associates from Big Pine Key, FL.

This study was undertaken to: 1) document commensal amphipod species and their sponge hosts, with emphasis on patterns of distribution and host/commensal relationships; 2) investigate ecological relationships such as sex ratio, population structure, and within–host distributions, and 3) clarify the taxonomy of local commensal amphipods, especially leucothoids.

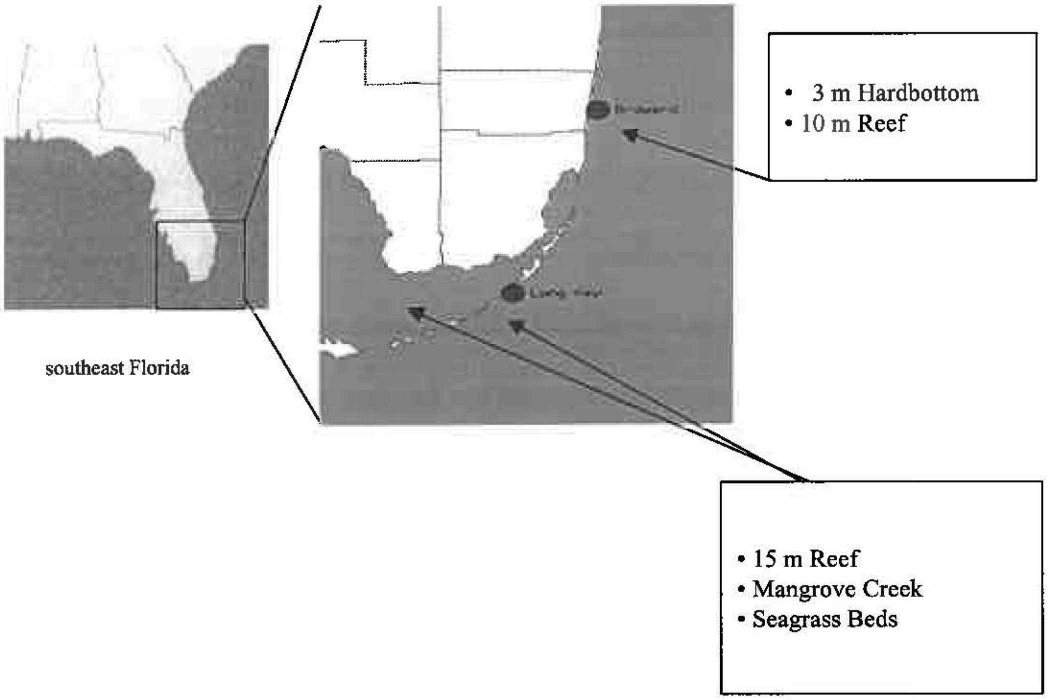
The results obtained from this study constitute the first record of commensal amphipod abundance and ecology off the southeastern coast of Florida.

MATERIALS AND METHODS

Sponges were collected between May and September 1999 in southeast Florida and the Florida Keys. Five different habitat types were sampled during this study in Broward and Monroe counties (Fig.1). Broward County stations included reef (N 26°09.163', W 26°05.341') and hardbottom (N 26°09.774', W 80°05.435') habitats. Stations in Monroe County included seagrass beds (N 24°50.543', W 80°49.633'), a patch reef (N 24°50.175', W 80°43.740'), and a mangrove creek (N 24°49.567', W 80°48.865'). An initial survey was conducted at each site to determine relative species abundance of sponges. Species consistently sighted at least twice per 3 m^2 –area were considered abundant and ten replicates were collected of each. Each sponge collected was covered by a plastic bag, cut at its base with a knife, and immediately sealed inside the bag to minimize loss of commensals. Sponge volume was measured by water displacement after draining the canals (error ± 5%). Internal canal size of a sponge species was determined by randomly measuring the diameter of ten of the largest canals in each individual sponge and calculating an average. Initial removal of fauna was accomplished by placing sponges in a 4% seawater formalin solution that forced commensals from the canals. The remaining water was passed through a 0.5 mm mesh sieve to insure capture of animals larger than 1 mm. Sponges were subsequently dissected to locate remaining commensals. All amphipods were preserved in a buffered 4% seawater formalin solution for 24 h, then transferred to 70% ethanol. Non-amphipod taxa found within each sponge were not scored. Amphipods were identified to species and measured from rostrum to telson using a compound microscope with a camera lucida attachment. Specimens were prepared for SEM by dehydrating through an acetone series and drying with HMDS. After palladium coating, samples were examined with a ISI–DS–130 dual state SEM. The following classification scheme was used to record sexual development: 1) adult males exhibited visible penes; 2) adult females bore oostegites; 3) ovigerous females exhibited a brood in the marsupium; and 4) juveniles showed no characteristics of sexual maturity [i.e., no penes or oostegite buds, and reduced first gnathopod (colomastigids)]. Host sponges were identified using photographs, spicule preparations, and by Kate Smith, an expert in sponge taxonomy at Smithsonian Institution, Washington, DC.

Density of amphipods per 10ml of sponge is reported followed by ± 1 standard error. Amphipod densities were calculated for each sponge species at each sampling location. A student's t-test was used to determine if average density of amphipods per 10ml of sponge volume differed between two sites. Similarly, an ANOVA was used to determine differences between densities of amphipods per 10ml of sponge volume from host species collected at three sites. The non–parametric Spearman Rank test was used to determine relationships between sponge volume and total number of amphipod inhabitants.

Figure 1. Study areas in southeast Florida and the Florida Keys.



RESULTS

Sponges

Twenty sponge species were collected from the sampling locations in southeast Florida and the Florida Keys (Broward and Monroe counties), sixteen of which contained colomastigid and/or leucothoid amphipods (Table 1). Sponges representing various growth forms were collected and examined (Table 2): massive (*Amphimedon* sp., *Anthosigmella varians,* unidentified brown sponge, *I. felix, Myriastra kallitetilla, Spheciospongia vesparium* and *Tedania ignis),* branching (*Agelas sceptrum, Aplysina fistularis, A. fulva, Amphimedon compressa, I. birotulata,* and *Niphates erecta*), encrusting (*Holopsamma helwigi, Niphates amorpha*), tubular (*Callyspongia vaginalis, Haliclona sp., Mycale* sp., *Niphates digitalis*), and vase (*Ircinia campana*). Sponges collected at the mangrove creek (unidentified brown sponge, *Haliclona* sp., *Mycale* sp., *T. ignis*) encrusted on the roots of red mangroves (*Rhizophora mangle* L.). Commensals were not found in four sponge species, *Aplysina fistularis*, *A. fulva*, *Agelas sceptrum*, and *Iotrochota birotulata.*

The average volume of sponge species from the five sites varied considerably (Fig. 2). The Broward hardbottom area had the most abundant sponge population: 120 individuals belonging to 12 species were collected. Average volumes (±1 SE) ranged from 18.1±2.46 ml (*Aplysina fistularis*) to 109±24.9 ml (*Ircinia campana*) in this area, with most (7 of 9) species averaging <40ml. Data was not reported for sponges in this area that did not house amphipods: *Agelas sceptrum, Aplysina fistularis,* and *Iotrochota birotulata.* The mangrove creek in the Florida Keys had the lowest sponge abundance with only four species and 36 individual sponges collected. Average volumes in the

Sponge Species	% Leucothoidae	% Colomastigidae
Agelas sceptrum	0	0
Amphimedon compressa	0.4	3.9
Amphimedon sp.	10.0	8.8
Anthosigmella varians	3.0	0
Aplysina fistularis	0	0
Aplysina fulva	0	0
Brown sponge	0.4	12.4
Callyspongia vaginalis	44.0	0
Haliclona sp.	1.5	0.3
Holopsamma helwigi	0.2	0.4
Iotrochota birotulata	0	0
Ircinia campana	1.8	0.8
Ircinia felix	6.8	1.5
Mycale sp.	0.4	36.5
Myriastra kallitetilla	2.3	26.0
Niphates amorpha	1.7	1.7
Niphates digitalis	12.0	2.5
Niphates erecta	6.8	0.2
Spheciospongia vesparium	3.1	0
Tedania ignis	5.6	5.0

Table 1. Percent of total leucothoid (n=1,213) and colomastigid (n=717) amphipods collected in each sponge species.

Table 2. Characteristics of sponge hosts.

Sponge Host	**Average Interior Canal Size (mm)**	**Description** (Wiedenmayer, 1977)
Amphimedon compressa	2.71±0.16	Thin, incrusting or ramose. Numerous scattered oscules (1-3mm) do not penetrate into the sponge interior. Consistency is tough and spongy.
Amphimedon sp.	4.68±0.22	Amorphous lobes that stem from an encrusting mass at the base of the sponge. Large (4-6mm), scattered oscules lead to deep meandering canals. Interior is firm and easy to tear.
Anthosigmella varians	6.23±0.19	Massive amorphous, irregularly lobate with "antlers" that have apical oscules. Firm, rubbery consistency with many interior canals and cavities.
Brown Sponge	5.00±0.58	Amorphous, encrusting with very small, inconspicuous oscules. Interior is very rubbery, laden with small cavities.
Callyspongia vaginalis	2.06±0.07	Clusters of cylindrical tubes. Surface contains numerous small oscules (0.5-2mm).
Haliclona sp.	1.84±0.12	Series of branching tubes with apical oscules. Very soft, compressible and easily torn.
Holopsamma helwigi	N/A	Encrusting with small "volcanic" oscules. Interior is very soft, easily torn with small cavities.
Ircinia campana	1.74±0.15	Vase sponge with numerous scattered oscules 0.5-4.0mm in diameter. Very spongy, tough, and hard to tear. Interior contains small cavities.
Ircinia felix	4.35±0.29	Massive, lobate, often branching. Very spongy, tough, and hard to tear. Finely conulose exterior with scattered oscules 1-5mm in diameter.
Mycale sp.	2.00±0.18	Branching tubes with apical oscules. Exterior is slightly convoluted. Very soft, easily torn.
Myriastra kallitetilla	7.35±0.37	Massive, subspherical, sometimes amorphous, with compound convolutions on the surface. Interior is firm,yet resilient and easy to tear. Many interior canals and some flattened cavities throughout the sponge.
Niphates amorpha	NA	Small, encrusting, with small (1-5mm) scattered openings. Interior is soft with small meandering canals.
Niphates digitalis	NA	Fuzzy tubes or vases with numerous tiny (0.5-2.0mm) oscules on the exterior.
Niphates erecta	3.01±0.09	Thin, fuzzy branches with scattered oscules. Interior is resilient with small meandering canals.
Spheciospongia vesparium	8.88±0.91	Massive, subspherical with flattened top. Hard, leathery exterior with dark brown central depression containing numerous excurrent openings. Interior has numerous canals and cavities.
Tedania ignis	3.70±0.24	Massive, subspherical to lobate, sometimes encrusting on mangrove roots. Surface is sometimes convoluted with medium-sized (2-7mm) excurrent openings. Interior is compressible and easily torn.

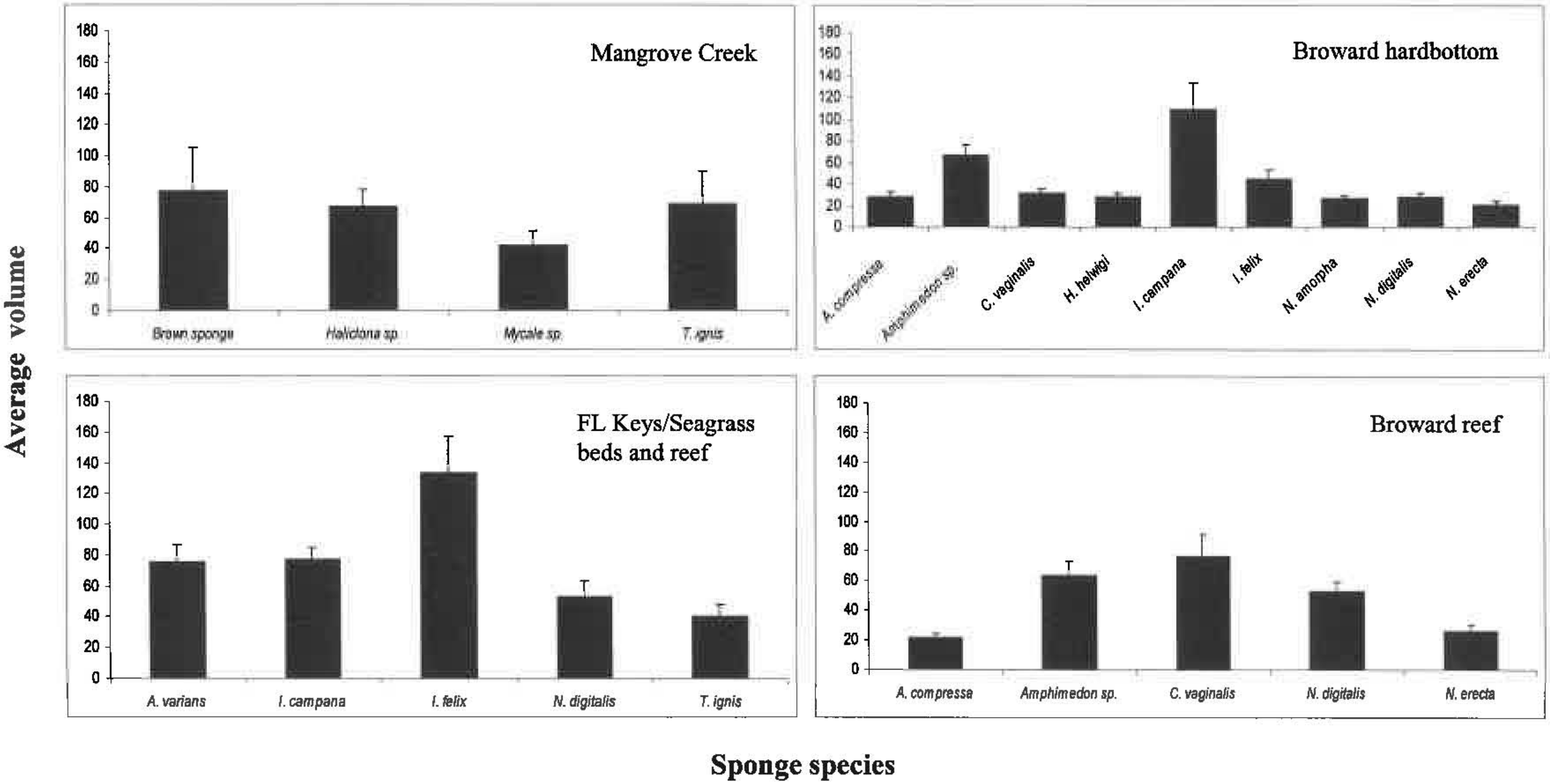


Figure 2. Average volume (Mean ± SE) of each sponge species from the sampling locations. No data is reported for *Myriastra kallitetilla* or *Spheciospongia vesparium*.

mangrove creek ranged from 42.3±9.26 ml (*Mycale* sp.) to 77.6±27.8 ml (unidentified brown sponge). Five and eight sponge species respectively were collected at the Broward reef and Florida Keys seagrass beds/reef sites. Average volumes ranged from 26.5±4.21 ml (*Niphates erecta*) to 77.1±14.4 ml (*Callyspongia vaginalis*) at the Broward reef. Sponge species at the Florida Keys sites ranged from 40.7±7.42 ml (*Tedania ignis*) to 134.1±23.5 ml (*I. felix*), with four of the five species averaging <80ml. Data was not reported for *Aplysina fulva* in the Florida Keys as it did not house amphipods. *Myriastra kallitetilla* and *Spheciospongia vesparium* were processed in the field due to their extremely large size and therefore, no volume data was collected.

When pooling all individuals of each host sponge species, *Callyspongia vaginalis* and *Ircinia felix* showed a significant correlation between host size (expressed as volume) and number of individuals (Spearman Rank Correlation, $p < 0.05$; Fig. 3). By contrast, no significant correlation was found between host size and total number of amphipods in 12 of the sponge species (*Amphimedon compressa*, *Amphimedon* sp., *Anthosigmella varians*, unidentified brown sponge, *Haliclona* sp., *Holopsamma helwigi, Ircinia campana*, *Mycale* sp., *Niphates amorpha, N. digitalis, N. erecta*, and *Tedania ignis*). *Myriastra kallitetilla* and *Spheciospongia vesparium* were omitted as well as non–host sponges.

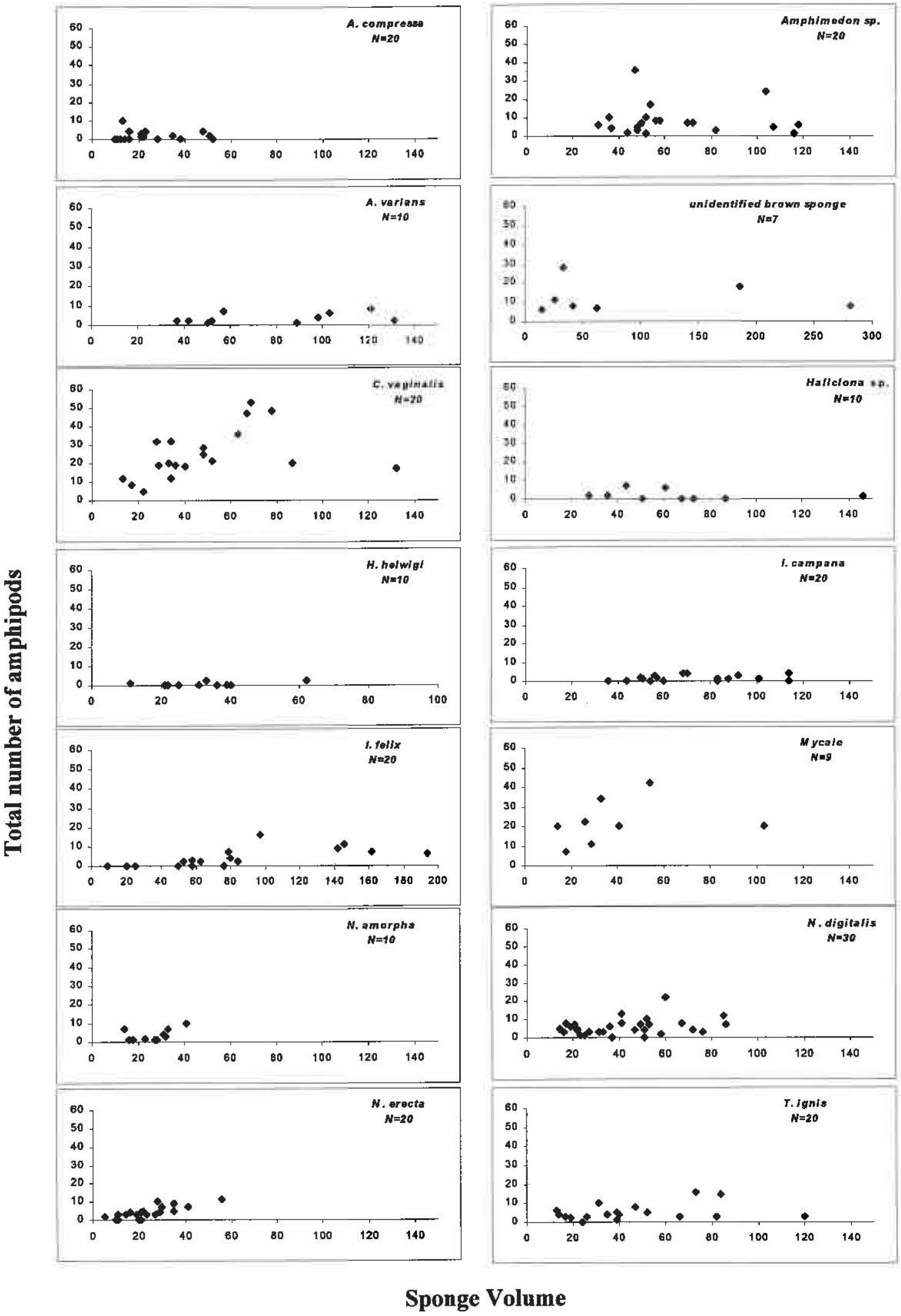


Figure 3. Relationship between volume and total number of amphipods for individual host sponges of each species.

In Table 2, average interior canal size is reported for 12 of the sponge host species: *A. compressa*, *Amphimedon* sp., *Anthosigmella varians*, unidentified brown sponge, *Callyspongia vaginalis*, *Haliclona* sp., *Holopsamma helwigi*, *Ircinia campana*, *I. felix*, *Mycale* sp., *Myriastra kallitetilla*, *Niphates erecta*, and *Tedania ignis*. Overall, average interior canal sizes varied from 1.74 mm (*I. campana*) to 7.35 mm (*M. kallitetilla*). Sponges with massive growth forms (*Amphimedon* sp., *A. varians*, unidentified brown sponge, *I. felix*, *M. kallitetilla*, and *T. ignis*) had substantially larger average canal sizes (>3.7mm) in comparison to branching, tube, or encrusting forms. All tube sponges, *C. vaginalis*, *Haliclona* sp., and *Mycale* sp., had average canal sizes of <2.06mm, as did the only vase sponge, *I. campana*(1.74 mm).

A majority (12 of 20) of the sponge species collected in this study were previously reported to contain secondary metabolites, chemicals apparently not required for any primary metabolic processes such as cell respiration and photosynthesis (McClintock et al, 1998) (Table 3). Three sponge species (*A. sceptrum*, *A. fistularis*, *T. ignis*) which produce secondary metabolites were found to be palatable to predatory fish in laboratory and/or field experiments, as opposed to six sponge species producing secondary metabolites which were deterrent to predatory fish (Table 5). Eight sponge species either did not contain secondary metabolites (*C. vaginalis*, *N. erecta*) or the information was unavailable (*A. varians*, unidentified brown sponge, *H. helwigi*, *I. birotulata*, *M. kallitetilla*, *S. vesparium*).

Table 3. Secondary metabolite data from sponge hosts examined in this study.

Sponge Species	**Total number of amphipods**	**Secondary Metabolites**	**Results of Laboratory and/or field experiments**	**Reference**
Agelas sceptrum	0	brominated pyrrol compounds	palatable to angelfishes	Randall and Hartman, 1968; Pawlik et al., 1995; Chanas et al., 1996
Aplysina fistularis	0	aerothionin, bromotyrosine derivatives	palatable to trunkfishes in field observation (Wulff, 1994) ; deterrent in laboratory assays to *Thalassoma bifasciatum*	Wulff, 1994; Pawlik, 1993;Pawlik et al., 1995
Aplysina fulva	0	bromotyrosine derivatives	deterrent in laboratory assays to *Thalassoma bifasciatum*	Pawlik et al., 1995
Amphimedon compressa	33	polymeric pyridinium alkaloid - amphitoxin	deterrent in laboratory assays to *Thalassoma bifasciatum*	Pawlik et al., 1995; Albrizio et al., 1995
Amphimedon sp.	185	icosadienoic acids	NA	Sarma et al., 1993
Anthosigmella varians	34	NA	palatable	Pawlik et al., 1995
Brown sponge	94	NA	NA	
Callyspongia vaginalis	529	no chemical defense	palatable	Pawlik et al., 1995
Haliclona sp.	21	alkaloids	NA	Pawlik et al., 1995
Holopsamma helwigi	5	NA	palatable	Pawlik et al., 1995
Iotrochota birotulata	0	NA	palatable	Pawlik et al., 1995; Pawlik, 1997
Ircinia campana	28	furanosesterterpene tetronic acids	deterrent in laboratory assays to *Thalassoma bifasciatum*	McFall, 1999; Pawlik et al., 1995
Ircinia felix	94	furanosesterterpene tetronic acids	deterrent in laboratory assays to *Thalassoma bifasciatum*	McFall, 1999; Pawlik et al., 1995
Mycale sp.	268	Nitrogenous macrocyclic alkaloids	generally thought to be deterrent (See Meroz & Ilan, 1995)	Sarma et al., 1993; McClintock, 1987;
Myriastra kallitetilla	215	NA	not deterrent	Pawlik et al., 1995
Niphates amorpha	33	Niphatynes, niphatesines	NA	Sarma et al., 1993
Niphates digitalis	164	Niphatynes, niphatesines	deterrent in laboratory assays to *Thalassoma bifasciatum;* variably deterrent to *P. punticeps* in lab assays	Pawlik et al., 1995; Waddell and Pawlik, 2000; Sarma et al., 1993
Niphates erecta	84	no chemical defense	palatable	Pawlik et al., 1995; Pawlik, 1997
Spheciospongia vesparium	38	NA	palatable	Pawlik et al., 1995
Tedania ignis	94	diketopiperazines	palatable in field experiments to parrotfish and angelfish	Pawlik, 1997; Dunlap and Pawlik, 1996; Sarma et al., 1993

Leucothoidae

Due to current taxonomic constraints, all leucothoid specimens in this study are referred to as a single species "complex". Imprecise descriptions make identification of any leucothoid to species difficult. The *Leucothoe* "complex" exists largely because of random "dumping" of species where authors provided inadequate descriptions, or were unsure of the material they examined. While the scope of this paper is not taxonomic in nature, the persistent taxonomic constraints related to suspect *Leucothoe spinicarpa* identifications must be addressed before any further detailed ecological and behavioral studies are initiated.

Abildgaard (1789) originally described *Leucothoe spinicarpa* from the Skagerrak Sea off Denmark. Since that time, several authors have labeled amphipods as *L. spinicarpa,* which do not show consistency with the type description. For example, one of the more common morphotypes in this study (Morphotype 4) is characterized by multiple long setae on the anterior edge of article 2 of gnathopod 2, a feature not found in the original type description of *L. spinicarpa*. Four distinct morphotypes are recognized in this study and are briefly diagnosed, described, and illustrated. Also, two distinct color morphs are reported, a completely white morph (displayed by the majority of *L. spinicarpa*) and one occurrence of a deep purple morph found in *Spheciospongia vesparium*.

There have probably been a significant number of commensal or cryptic amphipods identified by various authors under the name *L. spinicarpa* in the southeast Florida region (Thomas, 1993). There is no sure way to solve this taxonomic ambiguity without a complete revision of the family. However, by at least distinguishing recognizable morphotypes in a *Leucothoe spinicarpa* "complex", this study will not add to the current problematic situation.

The four local morphotypes are as follows:

***Leucothoe spinicarpa* "complex" morphotype 1** (Fig. 4)

Diagnosis: A series of long, complex setae present on the posterior margin of article 2 of gnathopod 1 in females.

Description of female: Gnathopod 1 with long, complex setae on posterodistal margin of article 2; 7 subequal anterodistal spines on palm; palmar margin lined with small appressed serrations; carpus with fine medial dentitions. Gnathopod 2 with multiple (3–11) long setae on proximal margin of basis; mediofacial setae reaching 72% of the length of anterior margin of propodus; propodus elongate; palm with series of truncate processes at base of dactyl; carpus approximately 0.33 length of propodus, scalloped distally.

Description of male: Similar to female except lacking complex setae on basis of gnathopod 1; gnathopod 2 with 4–6 short spines on basis and mediofacial setae reaching 55% along anterior margin of propodus (versus 72% in female).

Color: Bright white.

Adult size: Sexually mature at approximately 5 mm.

Distribution: Found in all samples of the sponge *Anthosigmella varians* collected from Old Dan Bank in Long Key, Florida, and one sample of *Amphimedon* sp. in Broward County, Florida (Table 4).

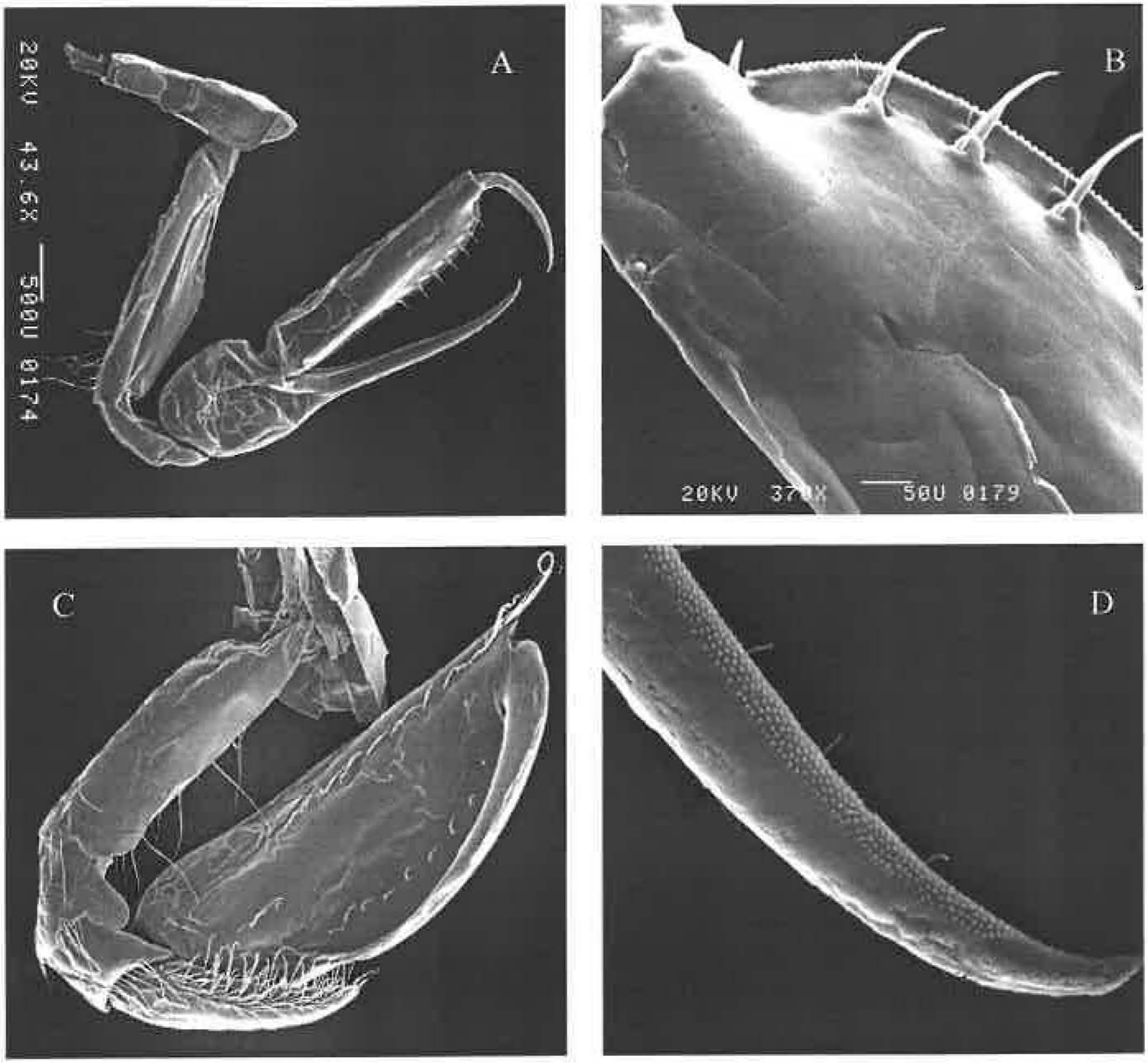


Figure 4. *Leucothoe spinicarpa* morphotype 1. **A.** Female gnathopod 1; **B**. Female gnathopod 1 propodus; **C**. Female gnathopod 2; **D**. Female gnathopod 1 carpus.

Host Sponge	Habitat	Morphotype 1	Morphotype 2	Morphotype 3	Morphotype
Amphimedon compressa	[1]HB (n=10)	-	-	-	4
	[2]BR (n=10)	-	-	-	1
Amphimedon sp.	HB (n=10)	1	-	-	69
	BR (n=10)	-	-	-	52
Anthosigmella varians	[3]SB (n=10)	34	-	-	-
Brown Sponge	[4]MC (n=7)	-	-	-	5
Callyspongia vaginalis	HB (n=10)	-	-	~12	~198
	BR (n=10)	-	-	-	319
Haliclona sp.	MC (n=10)	-	-	-	19
Holopsamma helwigi	HB (n=10)	-	-	-	2
Ircinia campana	HB (n=10)	-	-	-	9
	SB (n=10)	-	-	-	13
Ircinia felix	HB (n=10)	-	-	-	6
	SB (n=8)	-	-	-	77
Mycale sp.	MC (n=9)	-	-	-	6
Myriastra kallitetilla	SB (n=10)	-	-	-	29
Niphates amorpha	HB (n=10)	-	-	-	21
Niphates digitalis	HB (n=10)	-	-	-	35
	BR (n=10)	-	-	-	63
	[5]PR (n=10)	-	-	-	48
Niphates erecta	BR (n=10)	-	-	-	52
	HB (n=10)	-	-	-	31
Spheciospongia vesparium	SB (n=10)	-	38	-	-
Tedania ignis	SB (n=10)	-	-	-	46
	MC (n=10)	-	-	-	23

Table 4. Abundance and distribution of *Leucothoe spinicarpa* "complex" morphotypes within sponge hosts. ([1]Hardbottom Area, [2] Broward Reef, [3] Seagrass Beds, [4] Mangrove Creek, [5] Patch Reef)

Leucothoe spinicarpa "complex" morphotype 2 (Fig. 5)

Diagnosis: A series of serrations present on the posterodistal margin of coxa 1 of gnathopod 1, and 2 rows of mediofacial setae on the propodus of gnathopod 2 in both male and female.

Description: Gnathopod 1 with 7–9 spines on palm, 5–7 short setae on basis. Gnathopod 2 propodus width to height ratio 2.5:1 (2:1 in the other leucothoid morphotypes collected in this study), palm moderately scalloped with 2 rows of mediofacial setae — anterior row reaching approximately 70% across margin of propodus; shorter posterior row reaching end of anterior row distally; carpus reaching approximately 40% across propodus.

Color: Deep purple or white.

Adult Size: Males appeared to reach sexual maturity at approximately 5 mm, with a maximum of 11 mm. Females appeared to be sexually mature at approximately 3 mm, and reached a maximum size of approximately 9 mm.

Distribution: Found only in *Spheciospongia vesparium* collected from Big Pine Key, Florida (Table 4).

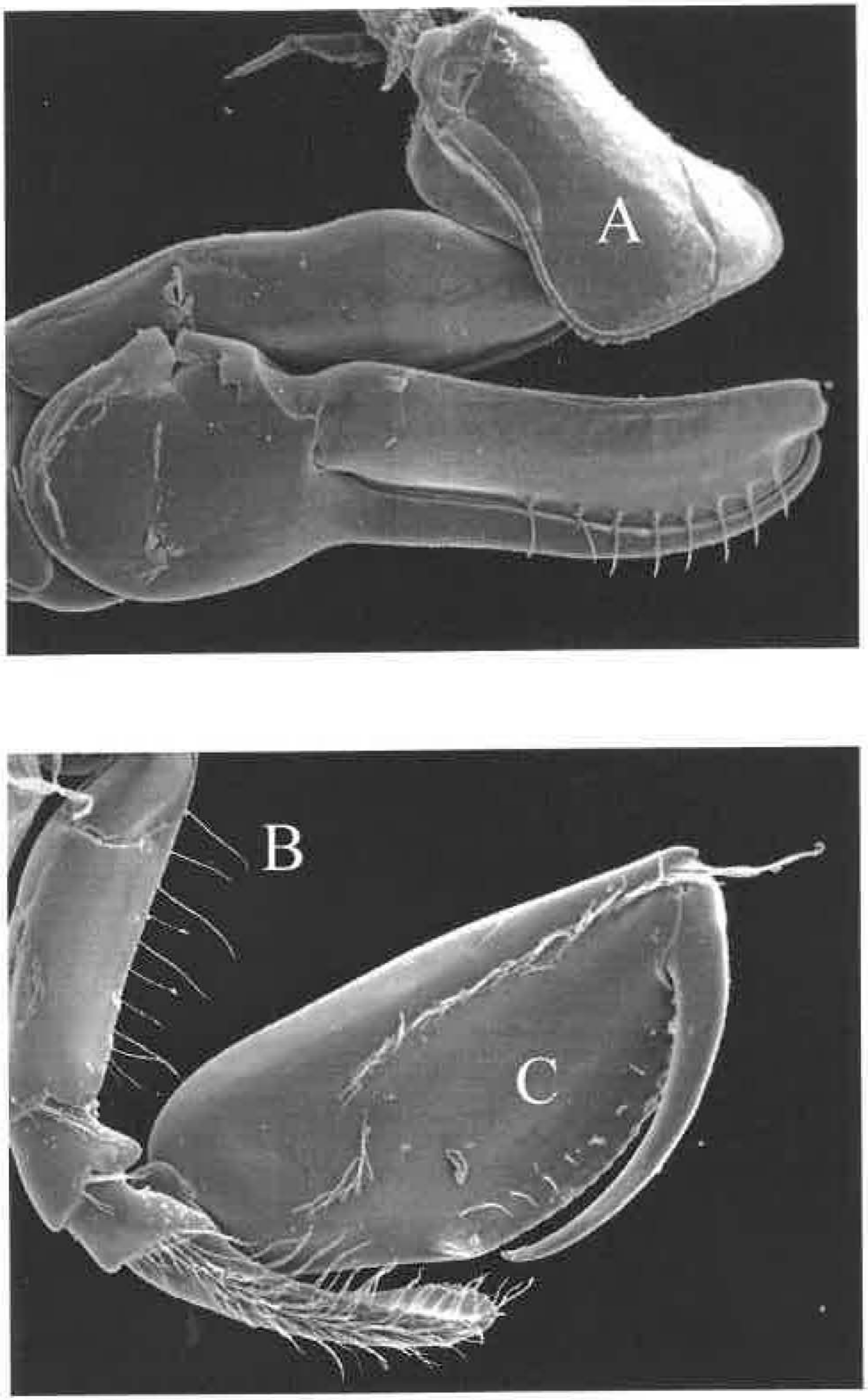


Figure 5. *Leucothoe spinicarpa* morphotype 2, upper photo = male gnathopod 1, lower photo = male gnathopod 2. A= coxa 1, B= gnathopod 2 basis, C= gnathopod 2 propodus.

Leucothoe spinicarpa **"complex" morphotype 3"** (Fig. 6; 7A,B)

Diagnosis: A series of nipple-like projections present on the posterior margin of the palm of gnathopod 1. Gnathopod 2 bearing a series of truncate processes on the posterodistal margin of the palm, and a strongly serrate medial carpal lobe.

Description: Gnathopod 1 with 3–5 spines on palm; nipple–like serrations spaced along entire distal palmar margin. Gnathopod 2 elongate with 6–14 long setae along anterior margin of basis; carpus strongly serrate and reaching approximately 40% across propodus; mediofacial setae reaching approximately 51% along anterior margin of propodus.

Color: Translucent.

Adult size: Sexually mature males and females at approximately 2 mm; maximum size approximately 4 mm.

Distribution: Twelve specimens were found only in *Callyspongia vaginalis* from Broward County, Florida (Table 4).

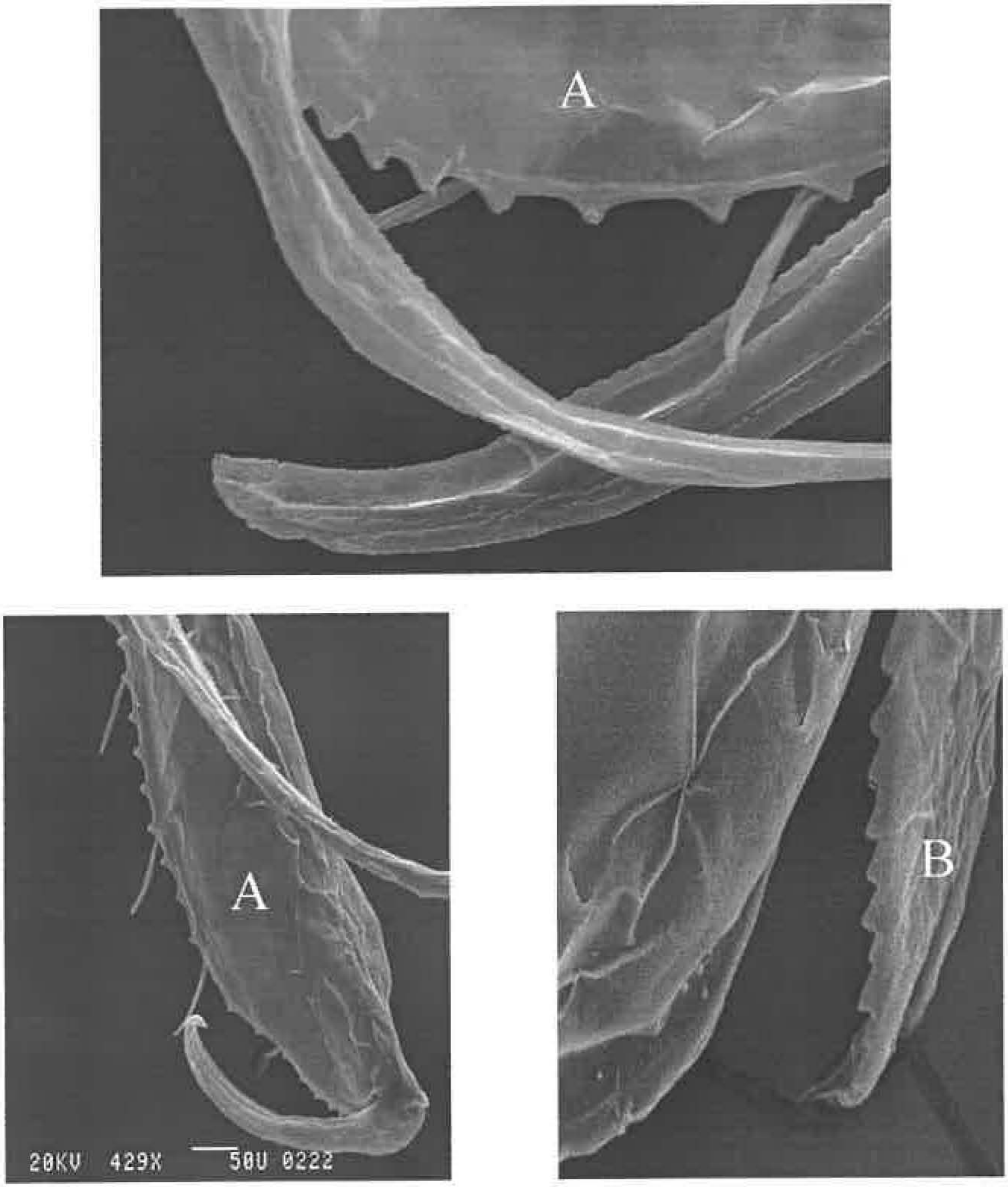


Figure 6. *Leucothoe spinicarpa* morphotype 3, upper photo = female gnathopod 1 palm, lower left photo = female gnathopod 1, lower right photo = female gnathopod 2 carpus. A= gnathopod 1 serrations, B= serrate carpal lobe.

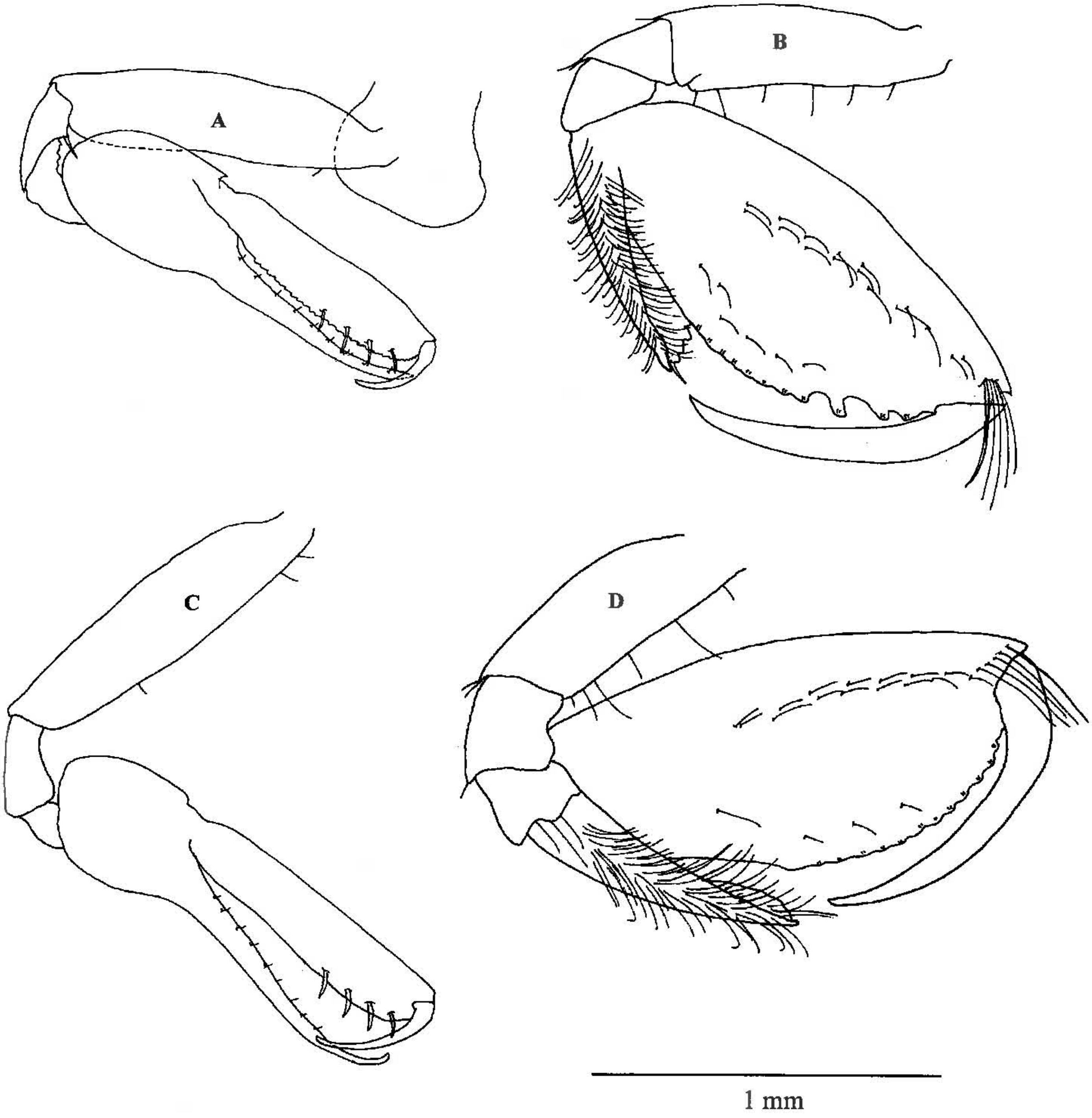


Figure 7. **A**, Morphotype 3, Male, gnathopod 1; **B**, Morphotype 3, Male, gnathopod 2; **C**, Morphotype 4, Male, gnathopod 1; **D**, Morphotype 4, Male, gnathopod 2.

Leucothoe spinicarpa **"complex" morphotype 4** (Fig. 7C,D)

Diagnosis: Anterior margin of the basis of gnathopod 2 furnished with extremely long setae alternating with shorter setae, and weak scalloping the entire length of the palm.

Description: Gnathopod 1 with 4–8 spines on palm, 5–7 short setae on basis. Gnathopod 2 propodus stout; palm with minor scalloping; 1 row of mediofacial setae projecting approximately 65% across anterior margin; carpus reaching approximately 40% across propodus.

Color: Translucent to pale white.

Adult size: Apparently sexually mature at approximately 2 mm; maximum size approximately 6 mm.

Distribution: Found in several sponge species including *Amphimedon compressa, Amphimedon* sp., *Niphates amorpha, N. digitalis, N. erecta, Ircinia campana,* and *I. felix* in all habitats sampled (Table 4).

Amphipod species and abundance

A total of 1,930 amphipods of five known species and one species "complex" consisting of four morphotypes were collected from 244 sponges sampled (Table 1,4,5). Specimens identified as the *Leucothoe spinicarpa* (Abildgaard) "complex" were the most abundant commensal amphipods, comprising 63% (n=1,213) of the total (Table 4), and present in all sponge species that contained amphipods. *Callyspongia vaginalis* and *Niphates digitalis* were the most common hosts of leucothoid individuals (Table 4). *Leucothoe spinicarpa* morphotype 4 was the most abundant, accounting for 93% (n=1128) of the total. The maximum number of leucothoids found in any single sponge was 53 in *C. vaginalis* from the shallow reef area in Broward County. Overall, 73% of the individual host sponges harbored leucothoid commensals (Fig. 8).

The average number of leucothoids per 10 ml of sponge varied from 0.06±0.01 (*Holopsamma. helwigi*) to 5.57±0.57 in *Callyspongia vaginalis* (Fig. 9A). A majority (10 of 14) of the sponges had amphipod densities of <1 per 10 ml. Leucothoid densities of four sponge species (*Amphimedon* sp., *C. vaginalis*, *Niphates digitalis*, and *N. erecta*) were above 1.0 per 10 ml. No significant differences existed between average number of leucothoids per 10 ml of sponge species sampled at any two locations (t-test, $p>0.05$). *Niphates digitalis* was the only sponge species sampled at three locations (Broward hardbottom, Broward reef, Monroe patch reef), and average number of leucothoids per 10 ml volume did not differ significantly among them (ANOVA $p<0.05$).

Host Sponge	Habitat	*Colomastix bousfieldi*	*Colomastix falcirama*	*Colomastix halichondriae*	*Colomastix irciniae*	*Colomastix janiceae*
Amphimedon compressa	[1]HB (n=10)	-	-	-	-	1
	[2]BR (n=10)	-	-	-	-	27
Amphimedon sp.	HB (n=10)	-	-	28	-	-
	BR (n=10)	-	-	35	-	-
Anthosigmella varians	[3]SB (n=10)	-	-	-	-	-
Brown Sponge	[4]MC (n=7)	-	89	-	-	-
Callyspongia vaginalis	HB (n=10)	-	-	-	-	-
	BR (n=10)	-	-	-	-	-
Haliclona sp.	MC (n=10)	-	2	-	-	-
Holopsamma helwigi	HB (n=10)	-	-	-	-	3
Ircinia campana	HB (n=10)	-	-	-	2	-
	SB (n=10)	-	-	-	4	-
Ircinia felix	HB (n=10)	-	-	-	-	-
	SB (n=8)	-	-	-	11	-
Mycale sp.	MC (n=9)	-	262	-	-	-
Myriastra kallitetilla	SB (n=10)	-	-	-	-	186
Niphates amorpha	HB (n=10)	12	-	-	-	-
Niphates digitalis	HB (n=10)	-	-	-	-	8
	BR (n=10)	-	3	-	-	-
	[5]PR (n=10)	-	7	-	-	-
Niphates erecta	BR (n=10)	-	-	1	-	-
	HB (n=10)	-	-	-	-	-
Spheciospongia vesparium	SB (n=10)	-	-	-	-	-
Tedania ignis	SB (n=10)	-	-	-	-	25
	MC (n=10)	-	11	-	-	-

Table 5. Abundance and distribution of *Colomastix* species within sponge hosts. ([1]Hardbottom Area, [2] Broward Reef, [3]Seagrass Beds, [4] Mangrove Creek, [5] Patch Reef).

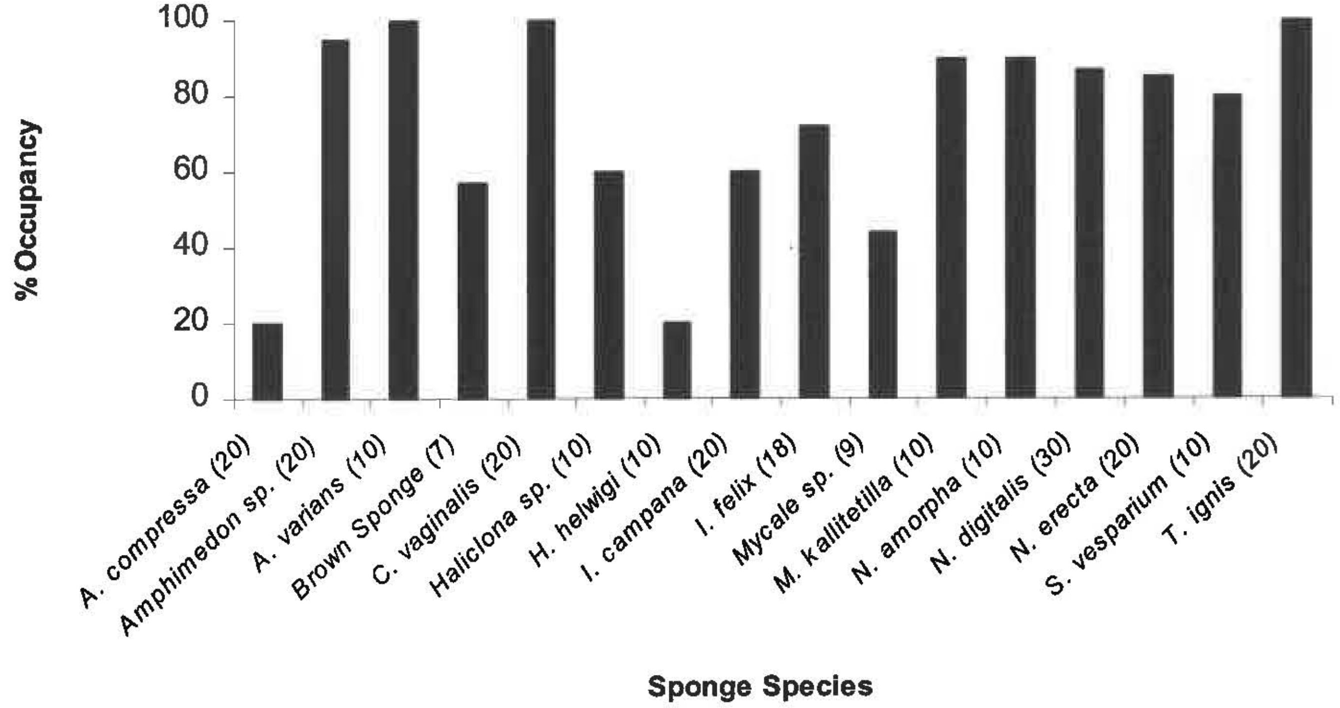


Figure 8. Percent of individual sponges with *Leucothoe spinicarpa* "complex" amphipods; (n)= number of individual sponges examined.

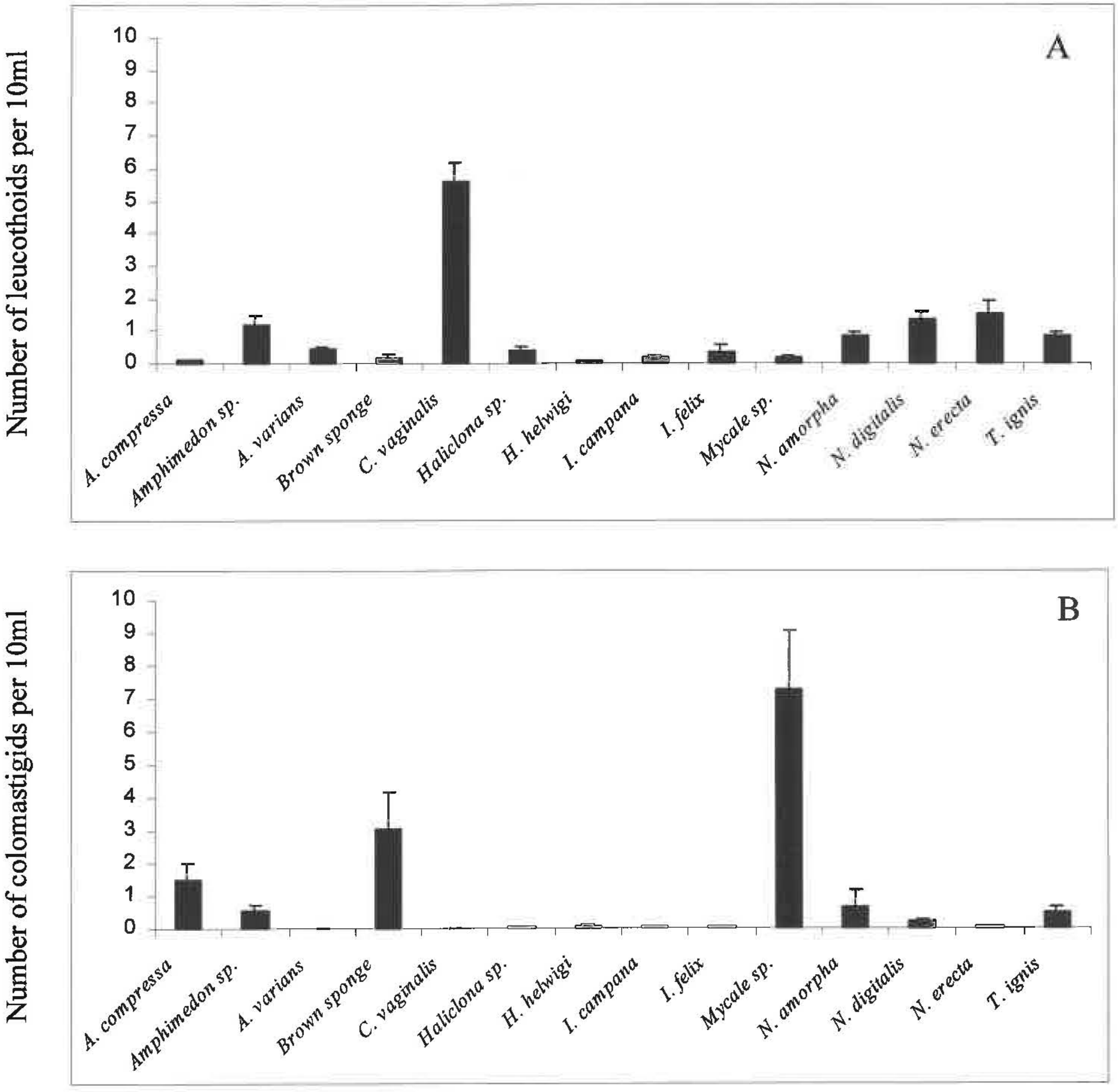


Figure 9. Average number (± 1 SE) of leucothoid (A) and colomastigid (B) amphipods inhabiting each sponge species.

By contrast with *Leucothoe*, all species of Colomastigidae were distinguishable. A total of 717 colomastigids belonging to five species were collected: *Colomastix bousfieldi* LeCroy, *C. falcirama* LeCroy, *C. halichondriae* Bousfield, *C. irciniae* LeCroy, and *C. janiceae* Heard and Perlmutter (Table 5). *Colomastix* amphipods inhabited 41% of all sponges sampled (Fig. 10). They were commonly found in *Myriastra kallitetilla* and *Mycale* sp. (Table 5), and were never found in three sponge species, *Anthosigmella varians*, *C. vaginalis*, and *Spheciospongia vesparium*. *Colomastix falcirama* was the most abundant species, comprising 52% (n=375) of the population. Almost all (97%) were collected from the mangrove creek in Monroe County. *Colomastix falcirama* also accounted for the greatest number of *Colomastix* individuals found in any single sponge: 76 in *Mycale* sp.

The average number of colomastigids per 10ml of sponge ranged from 0.04±0.02 (*Ircinia campana*) to 7.27±1.76 in *Mycale* sp. from the mangrove creek (Fig. 9B). A majority of the sponge species had densities of <1 amphipod per 10 ml. Colomastigid densities were above 1.0 per 10 ml in three sponge species (*Amphimedon compressa*, unidentified brown sponge, and *Mycale* sp.). No significant differences existed between the average number of colomastigids in 10ml of any given sponge species between any two locations (t-test, $p>0.05$). *Niphates digitalis* was the only sponge species sampled at three locations (Broward hardbottom, Broward reef, Monroe patch reef), and average number of colomastigids per 10 ml volume did not differ significantly among them (ANOVA $p<0.05$).

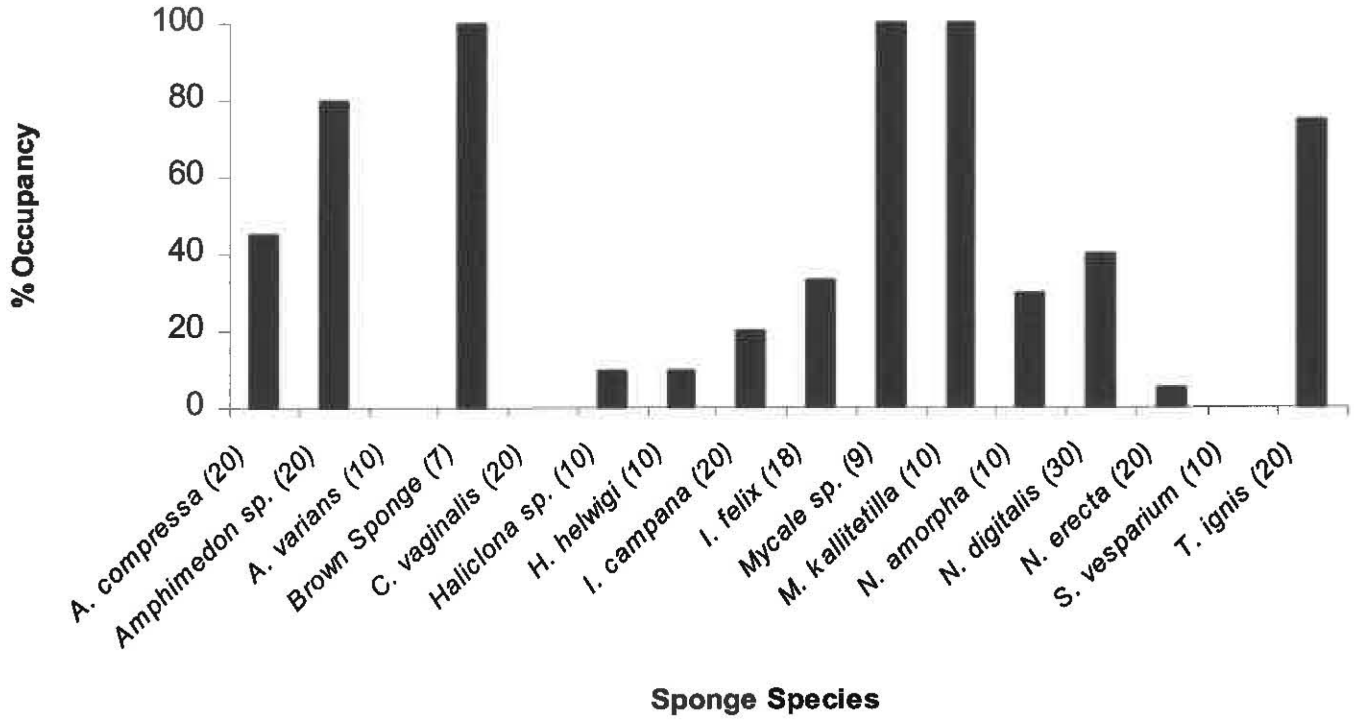


Figure 10. Percent of individual sponges with *Colomastix* amphipods; (n)= number of individual sponges examined.

Amphipod population structure

Leucothoid and colomastigid amphipods collected in this study range from juveniles to mature adults. Adult females, distinguished by the presence of oostegites, dominated populations within both families, accounting for 42% (n=509) of leucothoids and 54% (n=387) of colomastigids (Fig. 11). Ovigerous females comprised only 5% and 14% of female populations, respectively. The percentage of adult males, distinguished by visible penes, was similar for both families: 36% (n=437) and 33% (n=237) of leucothoids and colomastigids, respectively. There was a higher percentage of juvenile leucothoids (22%) as opposed to colomastigids (13%) (Fig.11). Within leucothoids, juveniles were rarely found without the presence of an adult. Similarly, juvenile colomastigids were found without an adult in only five of 12 specimens of *N. digitalis* and six other scattered occurrences. In *M. kallitetilla*, juveniles were often nestled with adult females in a cavity, while in *Mycale* sp. only 11 juveniles were found in a total of 262 colomastigids, eight of which were nestled in a single specimen with a group of females.

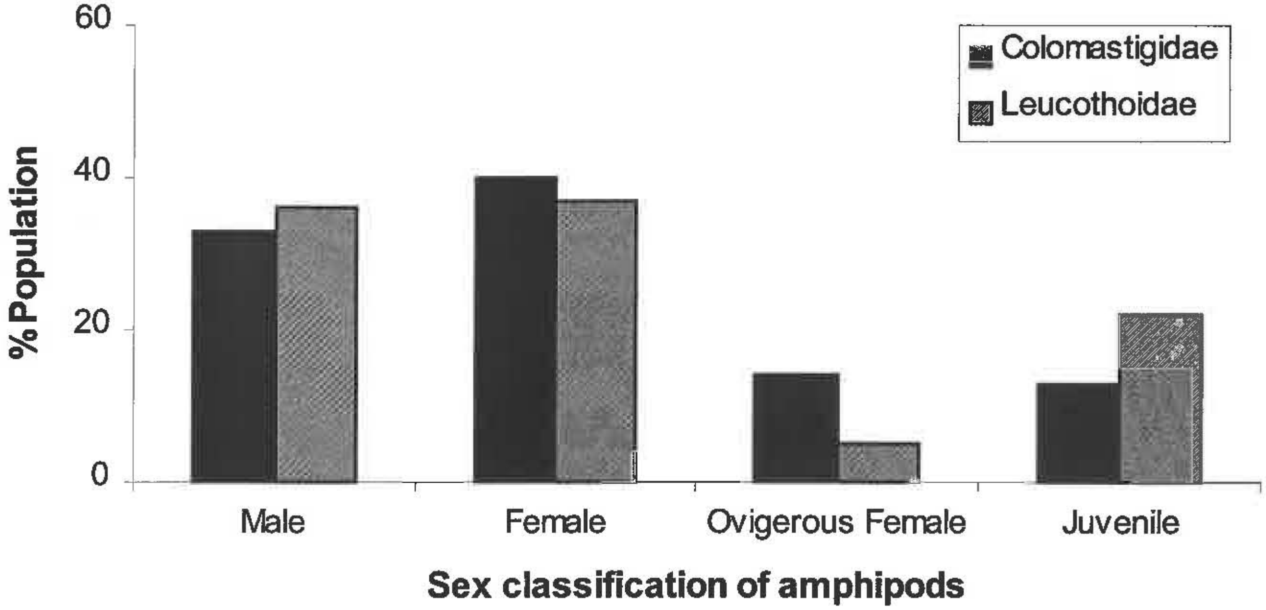
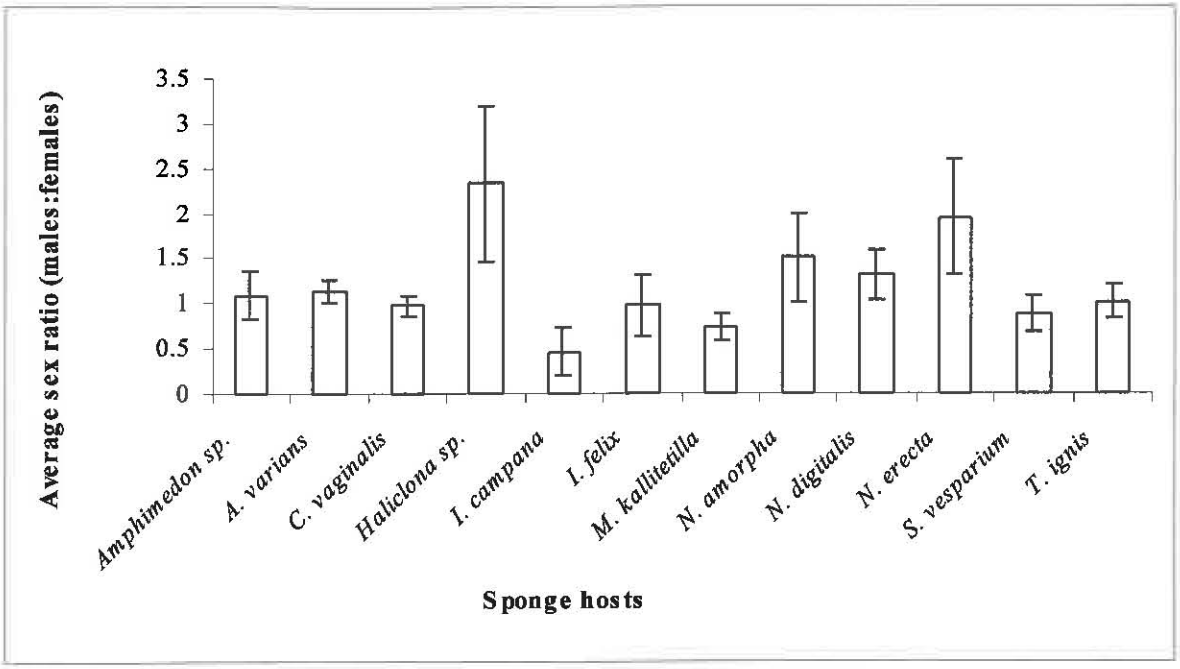


Figure 11. Overall population represented by growth stages of leucothoid and colomastigid amphipods.

Sponges containing amphipod commensals were examined for male–female pairs. Twelve sponge species contained male–female pairs of leucothoids: *Amphimedon* sp., *Anthosigmella varians, Callyspongia vaginalis, Haliclona* sp., *Ircinia campana, I. felix, Myriastra kallitetilla, Niphates amorpha, N. digitalis, N. erecta, Spheciospongia vesparium*, and *Tedania ignis.* The majority of individual sponge hosts (106 of 169) contained male–female pairs of leucothoids. Individual sponges with zero pairs of adults were excluded from the ratio calculation so averages were not skewed. The ratio of adult males to adult females range from 0.46±0.26 (*Ircinia campana*) to 2.33±0.88 (*Haliclona* sp.) (Fig. 12A). *Niphates amorpha* contained male-female pairs in only two of six sponges, while *Haliclona* sp. and *M. kallitetilla* contained pairs in three of six and three of 10, respectively. The ratio within the leucothoids was split equally, with six of the 12 sponge hosts showing male bias, and six also showing female bias (Fig. 11A). Sponges that did not host male–female pairs (*A. compressa*, unidentified brown sponge, *Holopsamma helwigi*, and *Mycale* sp.) frequently contained only individual adults. No adult leucothoids were found in the samples of *Holopsamma helwigi.*

A



B

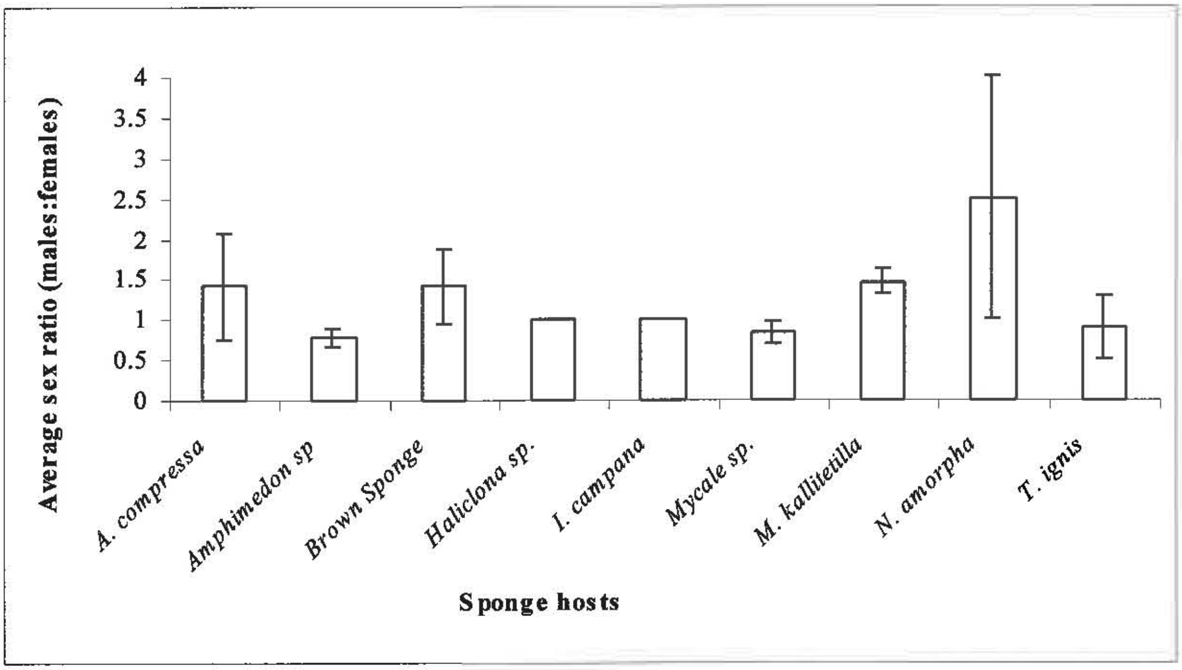


Figure 12. Average ratio (±1 SE) of adult male: adult female leucothoid (A) and colomastigid (B) amphipods from sponge host species with individual sponges harboring adult amphipods.

Individual hosts of nine sponge species contained male–female pairs of colomastigids: *A. compressa*, *Amphimedon* sp., unidentified brown sponge, *Haliclona* sp., *I. campana*, *Mycale* sp., *M. kallitetilla*, *N. amorpha*, and *T. ignis* (Fig. 12B). Of 91 individual hosts representing the eight sponge species, 39 contained adult pairs. Sex ratios ranged from 0.78±0.11 (*Amphimedon* sp.) to 2.50±1.5 (*Niphates amorpha*). Males dominated in six of the nine sponge species, while females dominated in the other three: *Amphimedon* sp., *Mycale* sp., and *Tedania ignis* (Fig. 12B). *Haliclona* sp. and *I. campana* contained only one male–female pair in one and four sponges, respectively, while *N. amorpha* contained two pairs in three samples. No adult colomastigids were found in samples of *Anthosigmella varians, Callyspongia vaginalis,* and *Spheciospongia vesparium*, while *Niphates erecta* housed only a single adult male.

Body lengths (rostrum to telson) of all amphipods ranged from <1.0 mm to 10.0 mm. Colomastigids were relatively smaller than leucothoids, with an average size of 2.78 mm, while the average leucothoid was 4.72 mm. The majority of juveniles representing both genera were <3mm (Fig. 13A,B). Specimens from both families span the same size range, but there were fewer colomastigids <5mm, than leucothoids. In particular, most female colomastigids were 3–4 mm but no more than 5 mm, while most female leucothoids were also 3–4 mm, but reached 9 mm.

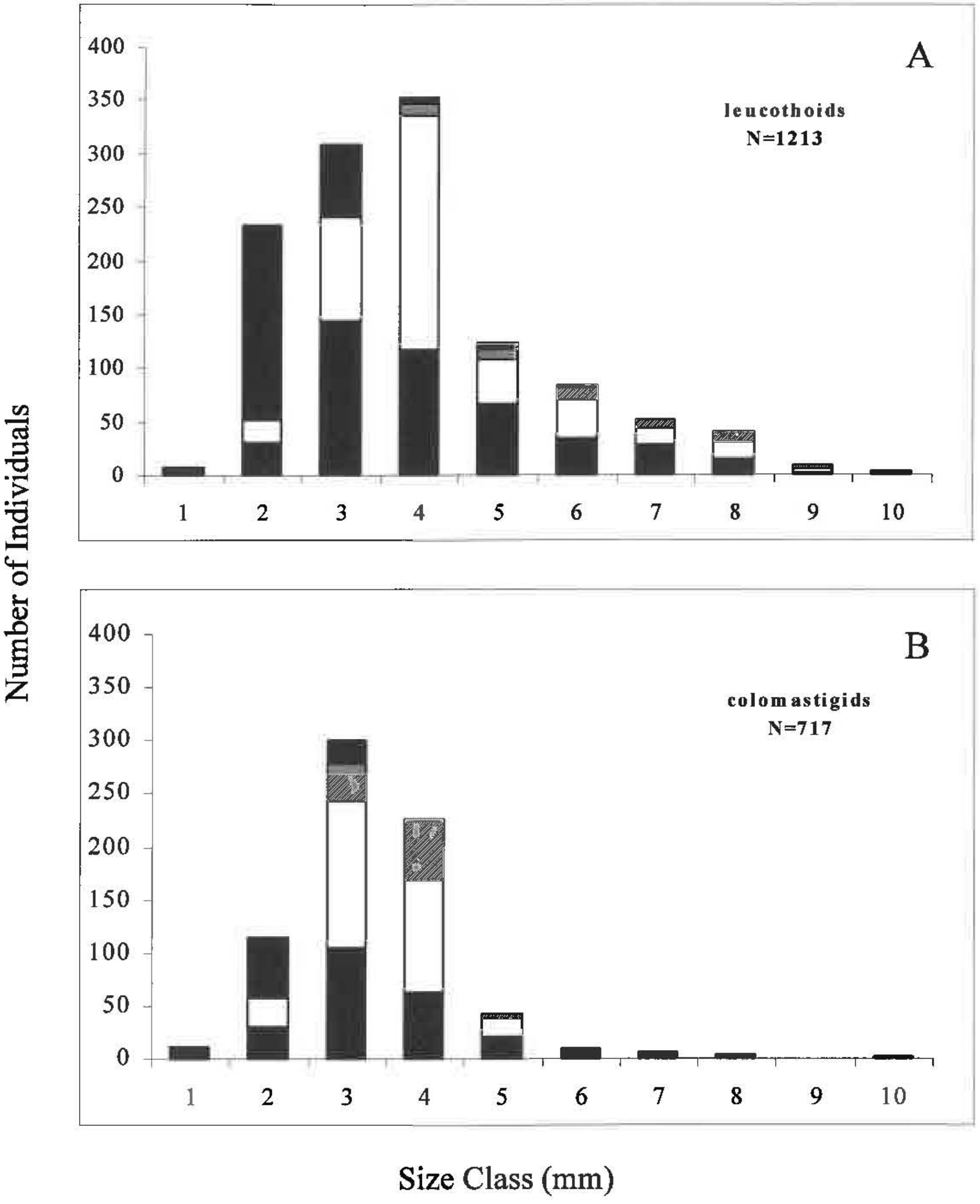


Figure 13. Number of individual leucothoids (A) and colomastigids (B) collected in 1 mm size classes.

▮ Male ☐ Female ▨ Female with Brood

▮ Juvenile

Figure 14 shows the population structure of leucothoid and colomastigid amphipods for each sponge species by the percentage of amphipods in each 1.0–mm size class. The wide range of amphipod size classes in sponges reflects the widespread presence of both adults and juveniles in individual sponge hosts. In certain sponge hosts (*Amphimedon compressa, Callyspongia vaginalis, Niphates digitalis)*, leucothoids appeared to reach a maximum growth size of approximately 4–5 mm. In other instances (*Anthosigmella varians,* unidentified brown sponge, *Mycale* sp.), only larger leucothoids (>5mm) appeared to colonize the host species. Colomastigid amphipods larger than 5.0 mm were found in only two host species, *Myriastra kallitetilla* and *Mycale* sp. There was substantial lack of overlap between the two families in the unidentified brown sponge and *Mycale* sp.

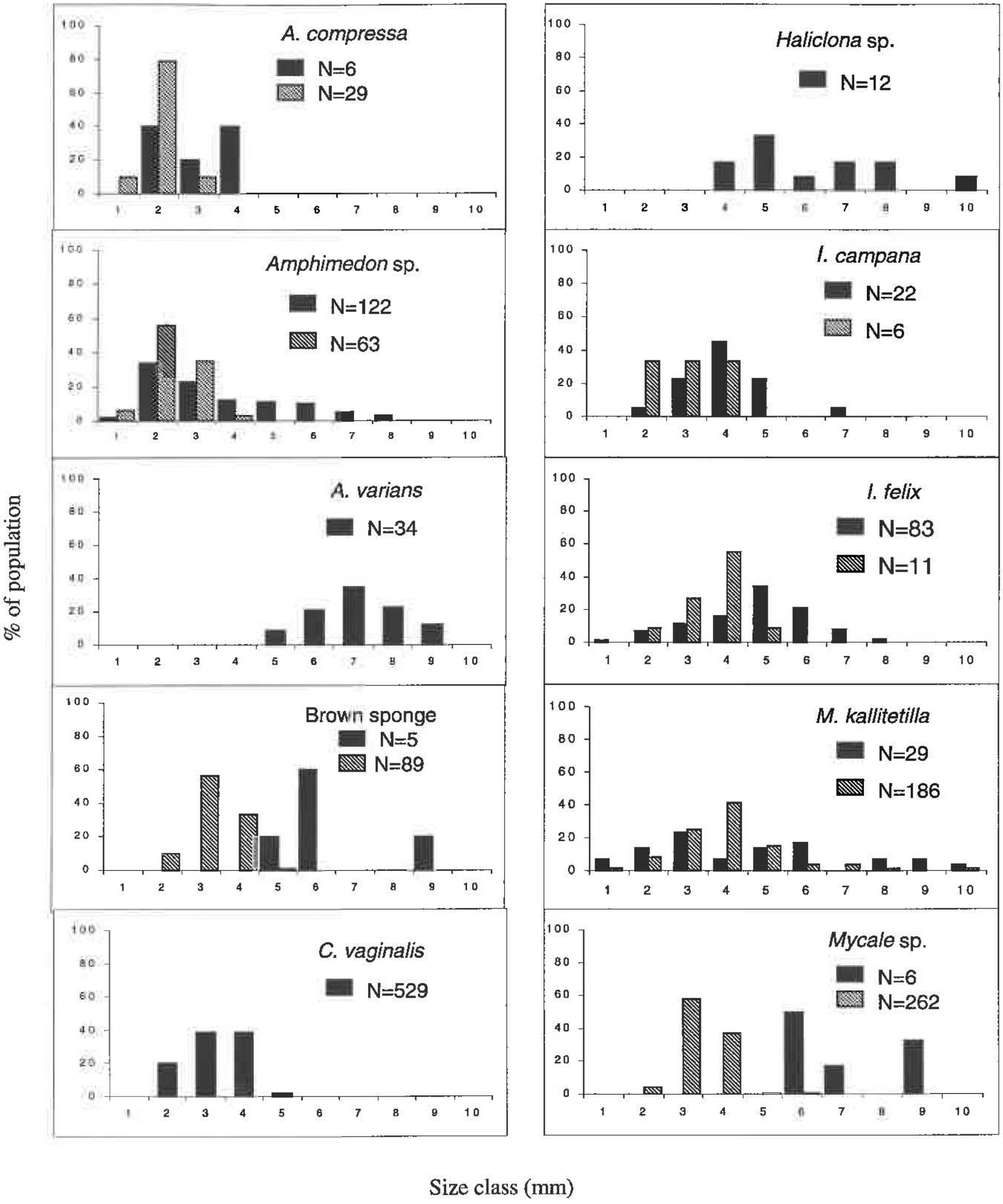


Figure 14. Size classes of leucothoid (■) and colomastigid (▨) amphipods for each sponge species shown by the percentage of amphipods per 1.0 mm size class. N= total number of individuals.

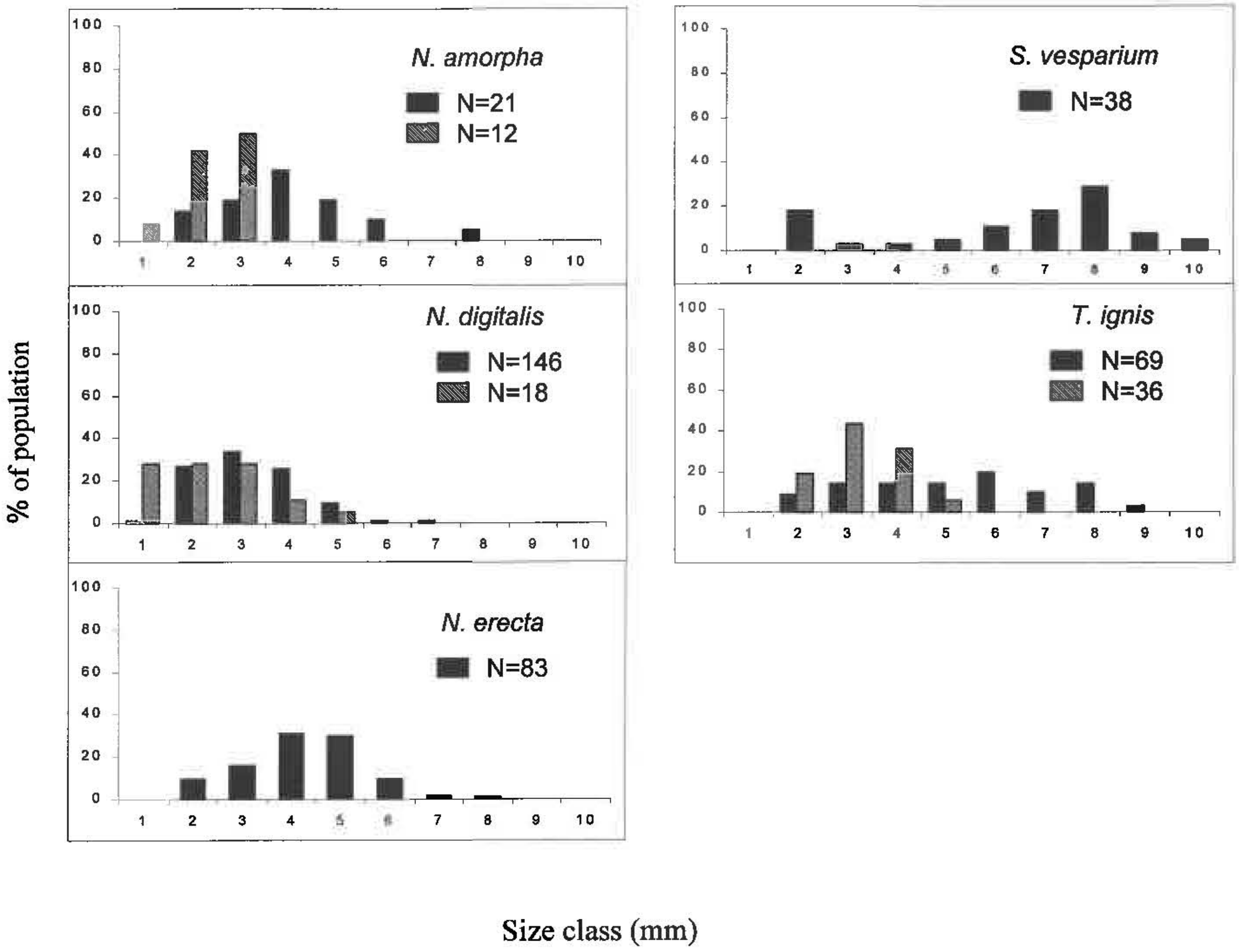


Figure 14 continued. Size classes of leucothoid (■) and colomastigid (▨) amphipods for each sponge species shown by the percentage of amphipods per 1.0 mm size class. N= total number of individuals.

DISCUSSION

Marine sponges examined harbored five species and 4 morphotypes of colomastigid and leucothoid amphipods, respectively (Table 4,5). Of 20 sponge species examined, 16 housed colomastigid and leucothoid amphipods, indicating they are quite common in the study areas (Table 1). Sponges in the genera *Aplysina*, *Agelas*, and *Iotrochota* did not harbor commensal amphipods, although species in the former two do so elsewhere (LeCroy, 1995; Villamizer and Laughlin, 1991). Species of *Agelas* have also been documented to host commensal shrimp (Duffy, 1992). All *Aplysina* examined were quite small (average volume = 18ml), and larger sponges in this genus may house amphipod commensals.

Sponges as hosts

Factors affecting the occupation of host sponges by commensal amphipods are virtually unknown. Host characteristics such as size, internal volume, diameter of canals, presence or absence of secondary metabolites that may deter predators and structural complexity are all potential factors that could affect the occupation of host species by symbiotic associates. Other parameters may include host growth form, distribution, and densities, as well as water temperature, salinity, and depth.

Several studies have investigated sponge size and volume in relation to abundance of associated fauna (Westinga and Hoetjes, 1981; Costello and Myers, 1987). LeCroy (1995) found a significant difference in volume between host sponges that housed *Colomastix* and those that did not, but did not find a correlation between host size and number of species or individual amphipods. In a similar study, Thiel (1999) found no significant relationship between host size (ascidians) and number of individual *Leucothoe spinicarpa* "complex" amphipods. Costello and Myers (1987) reported amphipod abundance increased significantly with increasing sponge size, while Westinga and Hoejtes (1981) concluded that the number of taxa increased logarithmically with sponge volume. However, estimates of potential canal volume have proved problematic, incorporating two measures: volume displacement (LeCroy, 1995), and dry weight (Biernbaum, 1981). These methods give a measure of sponge tissue; not the internal spaces where the commensals are commonly located. Therefore, while volume displacement gives a rough estimate of sponge size in relation to other specimens of the same species, it does not provide an accurate correlation when compared to abundance of fauna. A more appropriate measure of volume is to somehow assess the amount of available space for inhabitants by documenting channel (canal) diameter. Duffy (1992) found that the commensal snapping shrimp, *Synalpheus,* occurred more commonly in hosts, such as *Spheciospongia vesparium,* that exhibited a diversity of canal widths. Villamizer and Laughlin (1991) also suggested that sponges offering a system of channels and meanders that could provide a complex domicile may support a greater number of individuals and diversity of taxa.

In this study, volume data was recorded to give an indication of the strong variation of size among hosts. Overall, host sponges varied between 18.1±2.46 ml (*Aplysina fistularis*) and 134.1±23.5 ml (*Ircinia felix*) (Fig. 2). Additionally, volume was considered in relation to the total number of amphipods per sponge species. Only two sponge species, *Callyspongia vaginalis* and *Ircinia felix* showed a positive correlation between host size (expressed as volume) and total number of amphipods, while no correlation was found in the other 12 of 14 sponge species for which volume data was available (Fig. 3).

Host sponges differed in overall size (expressed as average total volume) (Fig. 2) and morphology (Table 2). However, while more difficult to access, structural complexity of sponges may be a more accurate indicator of host suitability than gross volume. Frith (1976) found that larger branched or fistulose sponges hosted more individuals and species of associates than flatter, or unbranched colonies. In the present study, it would appear that canal size might have a greater affect on the size of individual amphipods than the overall number of amphipods in a host. For example, the host sponge *Anthosigmella varians* had an average canal size of 6.23 mm (Table 2), and leucothoids from that host ranged in size from 5.2 mm to 9.1 mm (Fig. 14). Alternatively, *Callyspongia vaginalis,* which has an average interior canal size of only 2.06 mm, housed leucothoids that ranged from 1.4 mm to 4.8 mm.

It is possible that the internal architecture of a sponge may limit the maximum growth size of commensals. Although it would be difficult for a large (>5mm) adult amphipod to find suitable habitat in sponges with small interior canals, the smaller canals may provide a suitable habitat for juveniles and subadults. Thiel (1999) hypothesized that micro-habitats, such as the zooids of the stoloniferous ascidian *Clavelina oblonga,* which prove unsuitable for adult leucothoid amphipods, may in fact be safe alternatives in which juveniles and subadults may avoid intraspecific aggression, and therefore ensure reproductive success. The sponges, *Callyspongia vaginalis* and *Niphates digitalis* were occupied by leucothoid amphipods with average sizes of 3.16 mm and 3.14 mm respectively. One and three percent of these respective populations were represented by ovigerous females as compared to hosts with larger canals such as *Myriastria kallitetilla* (average size = 4.61 mm) and *Spheciospongia vesparium* (average size = 6.25 mm) that contained 17% and 10% ovigerous females, respectively. The lack of ovigerous females in sponges with smaller (1–4 mm) canal systems indicates that females and juveniles may seek shelter in certain hosts until they reach reproductive maturity and search for a suitable host in which to reproduce. Host sponges such as *C. vaginalis* and *N. digitalis* present a unique habitat in that the amphipods are living in small, shallow canals, yet appear to be safe from predators within deep tubes. Another, and possibly more important, factor in host preference may be the overall internal structural morphology of the sponge. One common factor among the sponges with the highest number of inhabitants, such as *C. vaginalis*, *Mycale* sp., *Myriastra kallitetilla*, is the presence of numerous meandering canals, cavities, or easily accessible oscules (Table 2).

Host sponges may also influence commensal populations through the presence of compounds, such as secondary metabolites that serve as predator deterrents. Feeding studies have indicated that certain sponge tissues yield deterrent extracts to the Caribbean wrasse, *Thalassoma bifasciatum* (Pawlik et al, 1995). Many sponges that contained significant numbers of amphipods, including *Callyspongia vaginalis* and *Niphates erecta*, did not contain secondary metabolites and constituted the largest component of spongivore fish (fish that feed predominantly on sponges) diets in the field (Pawlik et al., 1995; Pawlik, 1997) (Table 3). The large amount of amphipods found in those sponges may indicate that amphipods themselves do not "like" secondary metabolites. However, the host sponge *Mycale* sp., which contains Nitrogenous macrocyclic alkaloids that are generally thought to be predator deterrents, also contained several amphipods. It is possible that chemical compounds do not affect the commensals because they are not actually eating the sponge tissue, and therefore the presence or absence of these compounds do not contribute to host selection.

Taxonomy

The Colomastigidae, which has been recently monographed (Atlantic and Gulf of Mexico species) (LeCroy, 1995), allowed for easy species identifications. In contrast, the Leucothoidae, which is in dire need of revision, were problematic. Previous studies have attempted to document abundance of leucothoid amphipods (Thiel, 1999; Ortiz, 1975), but apparently distinct taxa have been placed together in *L. spinicarpa*. Thiel (2000) reported two members of the *L. spinicarpa* complex from ascidians and sponges and labeled them *L. "ascidicola"* and *L. "spongicola"* (his quotes) respectively. Without precise taxonomic descriptions and a comprehensive revision of the family, studies incorporating leucothoids will continue to be taxonomically limited, and ambiguities will remain. In an effort to address the need for taxonomic clarification, this study identified and diagnosed four distinct morphotypes of the *Leucothoe spinicarpa* "complex".

Abundance and distribution of the genera Leucothoe and Colomastix

Members of the *Leucothoe spinicarpa* "complex" discussed in this study do not appear to be host specific. They inhabit all sponge species that harbored amphipods in this study, and 73% of individual hosts (n=244), suggesting that the availability of a host may be an important factor in determining distribution and occurrence. Morphotypes 1, 2, and 3 showed some degree of host specificity with the sponges *Anthosigmella varians*, *Spheciospongia vesparium*, and *Callyspongia vaginalis*, respectively (Table 4).

Morphotypes 1 and 2 were large and are probably restricted to sponges with larger canal systems. Morphotype 3 was found inhabiting some of the same sponge hosts as Morphotype 4 and closer examination of the 529 leucothoids collected from *C. vaginalis* may reveal additional specimens. In terms of number of individuals, the most common hosts of this complex were *C. vaginalis*, *Niphates digitalis*, and *Amphimedon* sp. Two hosts, *C. vaginalis* and *N. digitalis* are tubular sponges. Ortiz (1975) noted that amphipods attributed to *L. spinicarpa* in Cuba appeared to show preference for tubular sponges such as *Cribrochalina* sp. and *Callyspongia* sp. Other commensals (e.g., polychaetes, decapods) were noticeably absent from the tubular sponge hosts, possibly because the channel diameters and ostia in these hosts were too small for them to enter. Individual *C. vaginalis* and *N. digitalis* sponges parasitized by the zooanthid *Parazoanthus parasiticus*, did not house commensal amphipods, possibly because the zooanthid occupying the ostia leading into the canal system prevented amphipods from entering the sponge. *Mycale* sp., *Holopsamma helwigi*, and *Amphimedon compressa* harbored the fewest numbers of leucothoids. Ortiz (1975) did not report commensals from any samples of *H. helwigi* in Cuba.

Colomastigids occupied 41% of individual host sponges (Fig. 10). *Colomastix janiceae* and *C. falcirama* showed a very generalized distribution among hosts and sampling locations (Table 5). *Colomastix janiceae* occurred in sponges at all sampling locations, with the exception of the mangrove creek station. In a Gulf of Mexico study, (LeCroy, 1995) it was the commonest *Colomastix* encountered, and was proportionally more abundant in *Geodia* sp. than in any other host taxa. *Geodia* tends to have large internal canals and cavities, as does the most common host of *C. janiceae* in this study, *Myriastra kallitetilla*, which may indicate that sponges with this particular characteristic may provide more living space than sponges with smaller or fewer canals and/or cavities. Another previously recorded host of *C. janiceae*, *Spheciospongia vesparium* (Heard and Perlmutter, 1977; Thomas, 1979; Westinga and Hoetjes, 1981), also has large internal canals and cavities. It is possible that *C. janiceae*, a larger species [maximum of 9.4mm (Heard and Perlmutter, 1977; LeCroy, 1995), maximum of 9.5mm present study] prefers or requires hosts with relatively large interior canals or cavities.

Colomastix falcirama dominated the colomastigid population at the Mangrove Creek and was the most common *Colomastix* species encountered in this study. LeCroy (1995) documented a variety of hosts including *Agelas dispar*, *Callyspongia vaginalis*, *Ircinia strobilina*, and *Aplysina* sp. In addition, she reported findings from the Grenadines, British West Indies (1956 Smithsonian–Bredin Caribbean Expedition, unpublished station notes) where specimens of *C. falcirama* were collected from a submerged wreck near a mangrove creek, and theorized that the amphipods probably occupied sponges growing on the wreck. This species may thus be characteristic of mangrove environments.

By contrast, *C. irciniae* preferred hosts of the genus *Ircinia*, but did not prefer one species to another. These data are consistent with patterns of *C. irciniae* reported from the Gulf of Mexico (LeCroy, 1995).

Colomastix bousfieldi, previously recorded as a sponge commensal (LeCroy, 1995, Thiel, 2000), was only collected at a single location, the Broward hardbottom area, in the host sponge, *Niphates amorpha*. Three of the ten samples of *N. amorpha* at this site contained *C. bousfieldi*.

Colomastix halichondriae, previously recorded as an associate of the sponges *Haliclona loosanoffi*, *Halichondria bowerbanki*, *Lissodendoryx isodictyalis* and *Microciona prolifera* (Bousfield, 1973; Biernbaum, 1981) and *Agelas dispar*, *Callyspongia vaginalis* and *Geodia gibberosa* (LeCroy, 1995), were primarily found in *Amphimedon* sp. at both the Broward hardbottom area and the Broward reef. Only one specimen, a subadult male, was found in another host, *N. erecta*, at the Broward Reef. Past records indicate this species is not host specific, although it appears to prefer *Amphimedon* sp. to other hosts in the study area.

The sponges *Mycale* sp., *Myriastra kallitetilla*, and unidentified brown sponge contained the greatest number of individual colomastigids, while harboring far fewer leucothoids. In *M. kallitetilla* and one single *Mycale* sp., groups of up to six colomastigid females and juveniles were found nestled together within a cavity, and may indicate extended parental care within this genus. According to Barnard and Karaman (1991) the cylindrical body shape of colomastigids suggests that colomastigids may be tunnellers, in which case soft-bodied sponges such as *Mycale* sp. and unidentified brown sponge would be ideal hosts in which to seek shelter. Colomastigids were not found in *Anthosigmella varians, Callyspongia vaginalis,* and *Spheciospongia vesparium.* Westinga and Hoetjes (1981) did not record *Colomastix* from a study of *S. vesparium* at Curaçao and Bonaire, although Heard and Perlmutter (1977) and Thomas (1979) reported *C. janiceae* from *S. vesparium* in the lower Florida Keys.

CONCLUSIONS

The information compiled in this study demonstrates that commensal amphipods of the families Colomastigidae and Leucothoidae are abundant members of the ecological community within sponge hosts. However, before the dynamics of this unique community structure can be explored, there must be clarification of the taxonomic discrepancies within the Leucothoidae. Commensalism itself bonds tightly with genetic adaptations such as mutation, inbreeding, etc. Commensal organisms such as the snapping shrimp, *Synalpheus,* and *Leucothoe spinicarpa* have demonstrated advanced social behaviors within hosts including eusociality (Duffy, 1996; 2000) and parental care (Thiel, 1999), respectively. Further studies on advanced social behaviors require precise taxonomic identifications of the commensal amphipods.

Traditionally, scientists have focused on the morphology and behavior of organisms in recognizing species. The study of biodiversity and interrelationships between organisms depends upon the accurate identification of the species being studied. Cryptic species, such as commensal amphipods, which resemble one another so closely as to sometimes be indistinguishable, are often incorrectly identified. New sources of data such as chromosomes and DNA are utilized as powerful tools for documenting the genetic basis of organisms. An understanding of genetic variation among species, as well as morphological and behavioral information will provide more accurate species level identifications. Studies using molecular systematics will help resolve questions about the nature, history, and evolution of biological diversity.

There are several factors that could influence the selection of a host among commensal amphipods. It appears from this study that structural morphology of the host may be of great importance. In order to justify this, it would be beneficial to develop a means of measuring internal canals and cavities that are suitable as living space for the commensals. This would also allow for a more accurate correlation between host volume and abundance of fauna. Other important factors include sponge location and chemical ecology of the host. Once again, further studies would be required to assess the importance of these factors.

This study serves as a stepping stone for research involving commensal amphipods and their sponge hosts. The identification of colomastigid and leucothoid commensal amphipods as a component of the benthic community in a variety of southeast Florida habitats opens the door for further research including basic aspects of amphipod biology and ecology, such as systematics, social behavior, growth, dispersal and reproduction.

LITERATURE CITED

Abildgaard, P.C. 1789.—*In*: Muller, O.F. Zoologica Danica seu Animalium Daniae et Norvegiae...Havniae 3:1–71.

Albrizio, S., P. Ciminiello, E. Fattorusso, S. Magno, and J.R. Pawlik. 1995. Amphitoxin, a new high molecular weight antifeedant pyridinium salt from the Caribbean sponge *Amphimedon compressa*.—Journal of Natural Products 58(5): 647–657.

Aoki, M. and T. Kikuchi. 1991. Two types of maternal care for juveniles observed in *Caprella monoceros* Mayer, 1890 and *Caprella decipiens* Mayer, 1890 (Amphipoda: Caprellidae).—Hydrobiologia 223: 229–237.

Barnard, J.L. 1965. Marine amphipods of atolls in Micronesia.—Proceedings of the United States National Museum, 117: 459–522, 35 figures.

———. 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands.—Smithsonian Contributions to Zoology 34:1–286.

———. 1972. Gammaridean Amphipoda of Australia, Part1.—Smithsonian Contributions to Zoology 103: 1–333.

———, and G. S. Karaman. 1991. The Families and Genera of Marine Gammaridian Amphipoda (Except Marine Gammaroids).—Records of the Australian Museum Supplement 13.

Bergquist, P.R. 1978. Sponges.—University of California Press. Los Angeles, California.

Biernbaum, C.K. 1981. Seasonal changes in the amphipod fauna of *Microciona prolifera* (Ellis and Solander) (Porifera: Demospongiae) and associated sponges in a shallow salt–marsh creek.—Estuaries 4(2): 85–96.

Bousfield, E.L. 1973. Shallow-water Gammaridean Amphipoda of New England.—Cornell University Press, Ithaca, New York. Pp. 313.

Chanas, B., J.R. Pawlik, T. Lindel, and W. Fenical. 1996. Chemical defense of the Caribbean sponge *Agelas clathrodes*.—Journal of Experimental Marine Biology and Ecology 208: 185–196.

———, and J.R. Pawlik. 1997. Variability in the chemical defense of the Caribbean reef sponge *Xestospongia muta*.—Proceedings of the 8th International Coral Reef Symposium 2: 1363–1368.

Costello, M.J. and A. A. Myers. 1987. Amphipod fauna of the sponges *Halichondria panicea* and *Hymeniacidon perleve* in Lough Hyne, Ireland.—Marine Ecology Progress Series 41: 115–121.

Dalby, J.E. 1996. Nemertean, copepod, and amphipod symbionts of the dimorphic ascidian *Pyura stolonifera* near Melbourne, Australia: specificities to host morphs, and factors affecting prevalences.—Marine Biology 126: 231–243.

Duffy, J. E. 1992. Host use patterns and demography in a guild of tropical sponge-dwelling shrimps.—Marine Ecology 90: 127–138.

———, and V.J. Paul. 1992. Prey nutritional quality and the effectiveness of chemical defenses against tropical reef fishes.—Oecologia 90: 333–339.

———, and K.S. Macdonald. 1999. Colony structure of the social snapping shrimp *Synalpheus filidigitus* in Belize.—Journal of Crustacean Biology 19: 283–292.

———, C.L. Morrison and R. Rios. 2000. Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*).—Evolution 54: 503–516.

Dunlap, M. and J.R. Pawlik. 1996. Video-monitored predation by Caribbean reef fishes on an array of reef and mangrove sponges.—Marine Biology 126: 117–123.

Frith, D.W. 1976. Animals associated with sponges at North Hayling, Hampshire.—Zoological Journal of the Linnean Society 58: 353–362.

Heard, R.W. and D.G. Perlmutter. 1977. Description of *Colomastix janiceae* n. sp., a commensal amphipod (Gammaridea: Colomastigidae) from the Florida Keys, U.S.A.—Proceedings of the Biological Society of Washington 90(1): 30–42.

Krapp-Schickel, G. 1975b. Revision of Mediterranean *Leucothoe* species (Crustacea, Amphipoda).—Bollettino del Museo Civico di Storia Naturale, Verona, 2: 91–118, figures 1–15.

LeCroy, S.E. 1995. Memoirs of the Hourglass Cruises: Amphipod Crustacea III Family Colomastigidae.—Florida Department of Environmental Protection: v.IX, part II.

Ledoyer, M. 1978. Amphipodes gammariens (Crustacea) des biotopes cavitaires organogenes recifaux de I'ile Maurice (Ocean Indien).—Bull. Mauritius Inst. 8(3): 197–332.

———. 1979. Les gammaraiens de la pente externe du grand recif de Tulear (Madagascar), (Crustacea: Amphipoda).—Memorie del Museo Civico di Storia Natuale di Verona 2: Pp. 149.

———. 1982. Faune de Madagascar, 59(1), Crustaces amphipodes gammariens, familles des Acanthonotozomatidae a' Gammaridae.—Centre National de la Recherche Scientifique: 598 pages, 226 figures.

———. 1986. Faune de Madagascar, 59(2), Crustaces amphipodes gammariens, familles des Haustoriidae a' Vitzazianidae.—Orstom, Paris (France) Pp. 1112.

Marin, A., M.D. López, M.A. Esteban, J. Meseguer, J. Muñoz, and A. Fontana. 1998. Anatomical and ultrastructural studies of chemical denence in the sponge *Dysidea fragilis*.—Marine Biology 131: 639–645.

Mattson, S and T. Cedhagen. 1989. Aspects of the behaviour and ecology of *Dyopedos monocanthus* (Metzgar) and *D. porrectus* Bate, with comparative notes on *Dulichia tuberculata* Boeck (Crustacea: Amphipoda: Podoceridae).—Journal of Experimental Marine Biology and Ecology 127: 253–272.

McClintock, J.B. 1987. Investigation of the relationship between invertebrate predation and biochemical composition, energy content, spicule armament and toxicity of benthic sponges at McMurdo Sound, Antarctica.—Marine Biology 94:479–487.

———, and B.J. Baker. 1998. Chemical Ecology in Antarctic Seas.—American Scientist 86: 254-263.

McFall, G. 1999. Chemical defense in the Caribbean reef sponges of the genus *Ircinia*.—Twenty-eighth Benthic Ecology Meeting. Baton Rouge, LA. Pp. 67.

Meroz, E. and M. Ilan. 1995. Life history characteristics of a coral reef sponge.—Marine Biology 124: 443–451.

Moore, P.G. 1988. New and little–known marine Amphipoda (Crustacea) from Tasmania and Western Australia.—Journal of Natural History 22:149–174.

Müeller, H.G. 1992. Colomastigidae from coral reefs in the Society Islands. Descriptions of two new species (Crustacea, Amphipoda, Gammaridea).—Cah. Biol. Mar. 33: 425–432.

Myers, A.A. 1985. Shallow–water, coral reef, and mangrove Amphipoda (Gammaridea) of Fiji.—Records of the Australian Museum Supplement 5: 1–143.

———. 1990. Amphipoda from the South Pacific: the Cook Islands.—Records of the Australian Museum 42: 149–157.

Ortiz, L.M. 1975. Algunos datos ecológicos de *Leucothoe spinicarpa* Abildgaard (Amphipoda, Gammaridea) en aguas Cubanas.—Ciencias, Serias 8, Investigaciones Marinas 16: 1–12.

Pawlik, J.R. 1993. Marine invertebrate chemical defenses.—Chemical Review 93: 1911–1922.

———. 1997. Fish predation on Caribbean reef sponges: An emerging perspective of chemical defenses.—Proceedings of the Eighth International Coral Reef Symposium 2:1255–1258.

———, B. Chanas, R.J. Toonen, and W. Fenical. 1995. Defenses of Caribbean sponges against predatory reef fish: I. Chemical deterrency.—Marine Biology Progress Series 127: 183–194.

Pearse, A.S. 1932. Inhabitants of certain sponges at Tortugas. —*In* Papers from the Tortugas Laboratory. 7. Carnegie Inst. Wash. Pub. 435: 119–123.

Pennings, S.C., S.R. Pablo, V.J. Paul, and J.E. Duffy. 1994. Effects of sponge secondary metabolites in different diets on feeding by three groups of consumers. —Journal Experimental Marine Biology and Ecology 180: 137–149.

Randall, J.E. and W. D. Hartman. 1968. Sponge feeding fishes of the West Indies.—Marine Biology 1: 21–225.

Ruffo, S. and G. Schickel. 1967. Nota su tre interessanti specie di Crostacei Anfipodi Mediterranei.—Memorie del Museo Civico di Storia Naturale (Verona) 15: 85–95.

Sarma, A.S., T. Daum and W. E. G. Müller. 1993. Secondary Metabolites from Marine Sponges.—Ullstein Mosby, Berlin Pp. 168.

Seger, J. and N. A. Moran. 1996. Snapping Social Swimmers.—Nature 381: 473–474.

Shoemaker, C.R. 1933. Two new genera and six new species of Amphipoda from the Tortugas.—Papers of the Tortugas Lab, Carnegie Institute of Washington 28:245–256.

Spanier, E., J.S. Cobb, and M. James. 1993. Why are there no reports of eusocial marine crustaceans?—OIKOS 67: 573–576.

Thiel, M. 1997. Reproductive biology of a filter-feeding amphipod, *Leptocheirus pinguis*, with extended parental care.—Marine Biology 130: 249-258.

———. 1998. Reproductive biology of a deposit-feeding amphipod, *Casco bigelowi*, with extended parental care.—Marine Biology 132: 107–116.

———. 1999. Host-use and population demographics of the ascidian-dwelling amphipod *Leucothoe spinicarpa* indication for extended parental care and advanced social behaviour.—Journal of Natural History 33(2): 193–206.

———. 2000. Population and reproductive biology of two sibling amphipod species from ascidians and sponges.—Marine Biology 137: 661–674.

Thomas, J. D. 1979. Occurrence of the amphipod *Leucothoides pottsi* Shoemaker in the tunicate *Ecteinascidia turbinata* Herdman from Big Pine Key, Florida, U.S.A.—Crustaceana 37(1): 107–109.

———. 1993. Biological monitoring and tropical biodiversity in marine environments: A critique with recommendations, and comments on the use of amphipods as bioindicators.—Journal of Natural History 27: 795–806.

———. 1993. Identification manual for marine amphipoda (Gammaridea): I. Common coral reef and rocky bottom amphipods of South Florida.—Department of Environmental Protection. Tallahassee, Florida Pp.1–83.

———. 1997. Systematics, Ecology and Phylogeny of the Anamixidae (Crustacea: Amphipoda).—Records of the Australian Museum 49: 35–98.

———, and K.D. Cairns. 1984. Discovery of a majid host for the commensal amphipod *Stenothoe symbiotica* Shoemaker, 1956.—Bulletin of Marine Science 34(3): 484–485.

———, and M. Ortiz. 1995. *Leucothoe laurensi*, a new species of leucothoid amphipod from Cuban waters (Crustacea: Amphipoda: Leucothoidae).—Proceedings of the Biological Society of Washington 108: 613–616.

Tyler, J.C. and J. E. Bohlke. 1972. Records of sponge-dwelling fishes, primarily of the Caribbean.—Bulletin of Marine Science 22: 601–642.

Uriz, M., D. Rosell, and M. Maldonado. 1992. Parasitism, commensalism or mutualism? The case of Scyphozoa (Coronatae) and horny sponges.—Marine Ecology Progress Series 81: 247–255.

Vader, W. 1983b. Associations between amphipods (Crustacea: Amphipoda) and sea anemones (Anthozoa, Actiniaria).—Memoirs of the Australian Museum 18: 141–153.

Van Dover, C.L., J. Trask, J. Gross, and A. Knowlton. 1999. Reproductive biology of free-living and commensal polynoid polychaetes at the Lucky Strike hydrothermal vent field (Mid-Atlantic Ridge).—Marine Ecology Progress Series 181: 201–214.

Villamizer, E. and R. A. Laughlin. 1991. Fauna associated with the sponges *Aplysina archeri* and *Aplysina lacunosa* in a coral reef of the Archipielago de Los Roques, National Park, Venezuela.—*In:* Reitner, J and H. Keupp eds. Fossil and Recent Sponges. Springer–Verlag, Berlin Pp.522–542.

Waddell, B., and J.R. Pawlik. 2000. Defenses of Caribbean sponges against invertebrate predators I. Assays with hermit crabs.—Marine Ecology Progress Series 195: 125–132.

Westinga, E. and P. Hoetjes. 1981. The intrasponge fauna of *Spheciospongia vesparium* (Porifera, Demospongiae) at Curaçao and Bonaire.—Marine Biology (Berl.) 62: 139–150.

Wiedenmayer, F. 1977. Shallow–water Sponges of the Western Bahamas.—Experimental Supplement. (Basel) 28. Birkhaüser Verlag, Basel and Stutthart. Pp. 287.

Wulff, J.L. 1994. Sponge feeding by Caribbean angelfishes, trunkfishes, and filefishes.— *In:* van Soest, R.W.M., T.M.G. van Kempen, and J.C. Brackman eds. Sponges in time and space. Balkema, Rotterdam, Pp. 265–271.