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Ecology, Population Dynamics, and Sexual Characteristics of Commensal Leucothoid Amphipods with the Sponge Cliona varians in the Florida Keys (Crustacea: Amphipoda)

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Nova Southeastern University Oceanographic Center

Ecology, population dynamics, and sexual characteristics of commensal leucothoid amphipods associated with the sponge *Cliona varians* in the Florida Keys (Crustacea: Amphipoda).

By

Stephanie Lynn Andringa

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ABSTRACT

Recent observations have identified a new species of leucothoid amphipod, *Leucothoe* “sp. F,” associated with the sponge *Cliona varians.* This project examined the relationship between this amphipod and its sponge host at three sites in the Florida Keys with differing hydrodynamic regimes. Ninety-eight sponge samples with a total of 2,030 amphipods were collected between December 2011 and September 2012. *Leucothoe* “sp. F” is currently a common species in the Florida Keys strongly associated with *C. varians*; its distribution strongly coincides with open tidal currents from the Gulf of Mexico. Seasonality, depth, and tidal regimes not only influence population dynamics and sexual characteristics of *Leucothoe* “sp. F,” but also the abundance and volume of its host.

Keywords: *Leucothoe* “sp. F,” *Leucothoe* “sp. B,” Gulf of Mexico, seasonality, depth, tidal regimes, sexual characteristics

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

STATEMENT OF OBJECTIVES

Examine:

1.) The relationship between species of leucothoid amphipods and *Cliona varians* in the Florida Keys.

2.) The effects, if any, that various tidal regimes influence *Cliona varians* and its commensal leucothoid amphipods.

3.) Ecology, population dynamics, and sexual characteristics of *Leucothoe* "sp. F" populations in *Cliona varians*.

The null and alternative hypotheses are as follows:

- **H_{o1}**: A relationship, either commensal, mutualistic, or parasitic, exists between *Cliona varians* and *Leucothoe* species in the Florida Keys.
- **H_{a1}**: No relationship, either commensal, mutualistic, or parasitic, exists between *Cliona varians* and *Leucothoe* species in the Florida Keys.

INTRODUCTION

Commensal/host associations

Associations between mobile cryptic and sessile invertebrates are key features of marine environments (Biernbaum, 1981; Levinton, 1982). Some of these associations are parasitic, arising out of one organism's need to survive off another, while other associations are mutualistic, arising from a pair of organisms benefiting from one another. However, the relationship between a host and its associate is not always known or fully understood (Duffy, 1992; Poore et al., 2000). Lincoln et al. (1982) used the term "commensalism" to describe the association between two organisms that do not have a parasitic or mutualistic relationship, but which have a relationship in which one organism benefits from the other, while the other remains unaffected.

Commensal relationships are influenced by predation, habitat, or access to food (Thiel, 1999; Duffy, 1992; Henkel and Pawlik, 2005; Thomas and Klebba, 2007). Pressures from predation, limited food, or lack of habitat can force cryptic organisms to adopt host-specialization (Roughgarden, 1975; Thiel, 1999; Poore et al., 2000). Duffy (1996a) found that synalpheid shrimp species tend to be host specific, while other organisms such as the gammaridean amphipod *Colomastix janiceae* are not (LeCroy, 1995). The degree of host specialization among different organisms could result in intraspecific competition among associates, leading to a more advanced social hierarchy (Duffy, 1996b). For host-specialization to occur, Roughgarden (1975) proposed three factors: the host should be easily accessible and easily located; the associate and host should live compatibly; and the associate should benefit from the host.

Although sessile invertebrates are taxonomically diverse, sponges are the most common hosts of commensals (Biernbaum, 1981; Duffy, 1992). Ardnt (1933) reported roughly three hundred crustacean species associated with sponges, 53 of which were amphipods. Sponges vary in size, shape, cavity morphology, and filtration activity, which make them accessible to an array of organisms (Thiel, 1999; Henkel and Pawlik, 2005; Thomas and Klebba, 2007). One of the key features determining a sponge's efficacy as a host is its internal canal structure and generation of feeding currents (Duffy, 1992; Henkel and Pawlik, 2005). Henkel and Pawlik (2005) found that the dimensions of the osculum and internal canal space greatly affected the access of predators to associates as well as the size of commensals. As a result, sponges not only provide habitat, but also protection against predators, and a rich food source (Eggleston et al, 1990; Henkle and Pawlik, 2005).

Sponges generate feeding currents via choanocytes in the body wall, which provide a steady stream of particulate food material to leucothoids in the sponge interior (Fedra et al., 1976 Hendler, 1984; Thomas, 1997). Limits on suitable host habitats for amphipods may induce competition amongst associates (Duffy, 1996b). Since amphipods lack a larval phase, adults are able to directly distribute juveniles within a host (Thiel, 1995; Poore and Steinberg, 1999). By doing so, adults express extended parental care, which allows juveniles to avoid predation during this vulnerable stage in their lives, while having access to a steady food supply (Thiel, 1999).

Firth (1976) speculated that amphipod associates locate their hosts through chemosensory or tactile methods. Once a potential sponge host is located, leucothoids may inspect the internal canal system and oscular diameters before settlement. This is believed to be a primary factor of host selection (Shuster, 1992; Thiel, 1999; Henkle and Pawlik, 2005; Thomas and Klebba, 2007). Shuster (1992) found that, for male *Paracereis sculpta* isopods, the size of the osculum played a major role in whether or not the sponge was chosen as a host.

Pearse (1950) found a direct correlation between the size of a sponge and the number of associates within. Sponge size positively correlated with both size of individual associates and their abundance. Crowe (2001) found similar results, but determined that the size of the sponge had less influence over amphipod abundance and more over the size of an individual amphipod. Dalby (1996) concluded that larger sponge hosts may be favored by amphipods, because they are easier to locate, can provide more food, and have more room for colonization over long time periods. It should be noted, however, that large size does not necessarily correlate with the internal cavity volume available for occupation by amphipod commensals.

Amphipoda

Amphipods make up ~16% of all extant marine crustacean species globally and are found in marine habitats worldwide, from the poles to the tropics (Calman, 1904; Bousfield, 1973; Thomas, 1993a). Their size range (1 mm-28 cm) and geographical diversity allow them to occupy a variety of niches. They are mostly free-living, either epibenthic or planktonic, but also burrow, dwell in tubes, or live interstitially, parasitically, mutualistically, or commensally with a variety of organisms (Bousfield, 1973).

Amphipods belong to the superorder Peracarida, which is composed of eight orders: Amphipoda, Mysidacea, Tanaidacea, Isopoda, Cumacea, Spelaeogriphacea, Mictacea, and Thermosbaenacea (Calman, 1904; Bousfield, 1973). Peracarids are unique in having at least one thoracic segment fused to the head, and a ventral brood pouch (Calman, 1909; Bousfield, 1973). Peracarids lack a dispersive larval stage; their young emerge as fully formed juveniles (Calman, 1909; Bousfield, 1973; Johnson et al., 2001; Spears et al., 2005). Male amphipods directly mate with females by injecting sperm into the female's brood pouch before ovulation (Bousfield, 1973; Thiel and Duffy, 2007). The oocytes are fertilized and incubated in that pouch for a varied amount of time depending mostly on temperature (Bousfield, 1973). Thiel and Duffy (2007) suggested that the combination of direct development and the emergence of young in the same host of their mother may lead to "closely related kin groups" or extended parental care.

Amphipoda includes four suborders within the order: Corophiidea, Ingolfiellidea, Hyperiidea, and Gammaroidea. The latter, with approximately 6,200 species, is the richest major peracarid taxon (Myers and Lowry, 2003). Gammaroids are important food resources for many fish and make up a considerable amount of marine benthic community biomass (Thomas, 1993b). This suborder includes several families dominated by cryptic and commensal species, e.g., Colomastigidae, Anamixidae, Pagetenidae, and Leucothoidae *sensu stricto* (Thomas, 1993a).

Leucothoidae currently consists of five genera and 176 species (White, 2011; White and Reimer, 2012). Members of this family are common commensals of sponges, ascidians, and bivalve mollusks (Biernbaum 1981; Cotello & Myers, 1987; Thomas 1993a; Thomas, 1979; Thiel 1999; Poore et al. 2000; Thomas & Klebba 2007; and White and Thomas 2009). The close association with sponges and ascidians could be a result of the relative longevity of many host species. Such organisms create the stability needed for associates to carry out extended parental care, access food resources, and avoid predation (Thiel, 1999; Thiel, 2000; Thiel, 2003; Thomas and Klebba, 2007).

Symbiont: *Leucothoe* "sp. F"

This study focused on *Leucothoe* "sp. F" (LeCroy, 2011), which was first observed by J.D. Thomas in 1997 (Thomas, J.D., personal observation) from ascidian hosts off Panama City, Florida. Its association with the sponge *Cliona varians* (Duchassaing and Micheloti, 1864) is an interesting and recent development possibly related to environmental mechanisms (Thomas, J.D. and Andringa, S.L., personal observation). Little is known about the ecology, population dynamics, or behavior of *Leucothoe* "sp. F." LeCroy (2011) reported it in association with the sponge *Spheciospongia vesparium* in the Florida Keys. Prior to the current study, the species had never been documented from *C. varians* (Thomas, J.D., personal communication). In fact there are no records indicating any amphipod commensals for *C. varians* despite extensive research and ongoing sampling since the 1970's (Thomas, J.D., personal communication), except one from Crowe (2001), whom found *Leucothoe spinicarpa* "complex" morphotype 1 in *C. varians* on Old Dan Bank off Long Key, FL, but it has not been observed since that study. Klebba (2005) found no commensal associates in *C. varians* in Belize. The current study provides documentation of widespread occurrences and high numbers of *Leucothoe* "sp. F" in *C. varians* in the Florida Keys.

Although the complete geographical distribution of this species is unknown, it has been reported from Molasses Key (LeCroy, 2011; Thomas and Andringa, personal observations), Bahia Honda Key, Spanish Harbor Key (LeCroy, 2011), Layton Key, Big

Pine Key (Thomas, J.D. and Andringa, S.L., personal observations), and Panama City, Florida (Thomas, J.D., personal observation, 1999).

Host: *Cliona varians*

Cliona varians (Demospongiae, Hadromerida, Clionaidae (Hill et al., 2013)) was originally described as *Thalysias varians* Duchassaing and Michelotti, 1864, subsequently treated as *Anthosigmella varians* and more recently *Cliona varians* (Rützler and Hooper, 2000). It was transferred from Spirastrellidae into the family Clionaidae d'Orbigny (1851) due to its calcium carbonate excavating capabilities (de Laubenfels, 1936; Lopez-Victoria et al., 2004; Hill et al., 2011).

Common characteristics of *C. varians* include: green, brown, or tan coloration (Sara and Liaci, 1964; Schonberg, 2000); zooxanthellae associates (Sara and Liaci, 1964; Rützler, 1990; Hill, 1996; Schonber, 2000; Weisz et., 2010; Hill et al., 2011; Hill and Hill 2012); skeleton of spirasters and tylostyles (Rosell and Uriz, 1997; Schonberg, 2000; Hill and Hill, 2002), and bioeroding characteristics (Vicente, 1978; Schonberg, 2000; Rützler, 2002; Lopez-Victoria et al., 2003; Schonberg et al., 2005). The spirasters of *C. varians* are primarily C-shaped, but occasionally S-shaped (Fig. 1 B-E). The tylostyles are long rods that taper to a point at one end and are bulbous at the other (Fig. 1 A). Their mean length ranges between 200 and 400 µm (Rosell and Uriz, 1997; Schonberg, 2000; Hill and Hill, 2002).

Three infrasubspecific morphological forms of *C. varians* have been reported: *incrustans*, *rigida*, and *varians* (Wiedenmayer, 1977; Hill, 1999). Both the *rigida* and *varians* forms were found and analyzed during this study. Form *incrustans* is an encrusting morph found at depths of 0.5-16 m in areas of strong currents and high wave energy along fore- and back-reefs and other hard bottoms (Wiedenmayer, 1977; Vincent, 1978; Hill and Hill, 2002; Hill, 2009). Form *varians* is an irregular lobate branching form found in shallow, calm lagoonal areas to 3 m in depth. Branches of this form have been reported to reach over 40 cm tall (Hill and Hill, 2002). Form *rigida* has branching similar to form *varians* but differs by having a more dense and rigid skeletal structure. It is found at depths of 1.3-7.5 m in low wave-energy environments or turbid bay areas (Wiedenmayer, 1977; Vincent, 1978; Hill, 1999). Forms *rigida* and *varians* also differ in spicule concentration, substylostyle length/width ratio, and anthosigma shape (Table 1) (Hill and Hill, 2002).

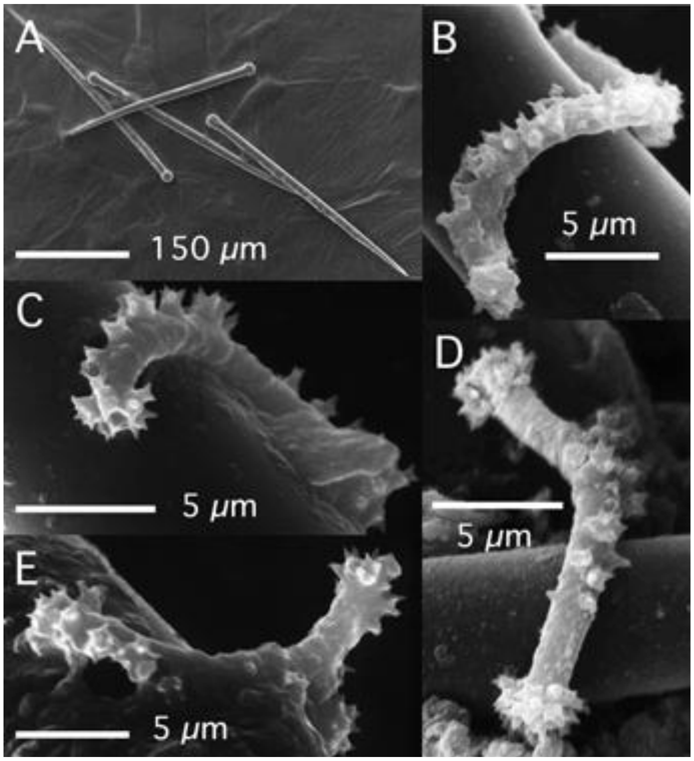

Fig. 1. *Cliona* varians: A. Tylostyles. B-E. Spirasters. B. S-shaped anthosigma. C-E. C-shaped anthosigma (Schonberg, 2000).

Table 1. *Cliona varians* morphology according to spicule concentration (Hill and Hill, 2002)

Character	forma *rigida*	forma *varians*
Spicule concentration (mg cm^{-3})	168	112
Subtylostyle length (µm)	375	375
Subtylostyle width (µm)	8	12
Anthosigma shape	Single bend	two or more bends

Sponge defenses against predators include secondary metabolites, spicules and fibrous tissues (Randall and Hartman, 1968; Hay and Steinberg, 1992; Pawlik et al, 1995). Although *C. varians* is not chemically defended (Pawlik et al., 1995; Hill and Hill, 2002), its dense skeletal composition may deter potential predators (Hill, 1999; Hill and Hill, 2002). Form *rigida* is believed to avoid predation by producing higher concentrations of spicules, leading to a thicker, more resistant cortex. Form *varians* is thought to avoid predation by occupying periodically stressed or restricted habitats with low predation rates and occurrences, such as shallow lagoons (Pawlik, 1998; Hill and Hill, 2002). Based on transplantation and simulated predation experiments, Hill and Hill (2002) found that, when form *rigida* lacked predators, such as spongivorous fish, i.e., angelfish (Randall and Hartmann, 1968; Wulff, 1994; Hill, 1998), the usually high spicule concentration diminished; by contrast, form *varians* produced more spicules when exposed to habitats with increased predators. Their study demonstrates that spicule concentration along with habitat location could be a significant deterrent against predation on *C. varians*.

Habitat distribution among various morphologies of *C. varians* may not be a primary response to predation but a result of biotic and abiotic factors that affect their ability as bioeroders (Hill, 1996). In the Florida Keys, sponges are integral components of the structure of lagoonal and shallow water hard-bottom habitats (Chiappone and Sullivan, 1994; Field and Butler, 1994), where they contribute up to 30% of the sediments (Fütterer, 1974; Rützler, 1975; Schonberg, 2002). Bioeroding sponges are the most destructive and competitive of sponge species. Their ability to burrow into limestone substrates makes them a key threat to coral reef communities (Rosell and Uriz, 1992). *Cliona varians* can penetrate these substrates via chemical etching; it then infills the resulting cavities with its tissue and removes eroded sediment through its canal system (Rützler, 1975; Rützler, 2002; Zundelevich et al., 2007). Hill et al. (2011) found that *C. varians* harbor a zoozanthella clade that dates to the late Eocene (Pochon et al., 2006) and may have therefore evolved a tolerance to external stressors such as bleaching (Vincente, 1990; Hill and Wilcox, 1998; Schonberg et al., 2008) in the Florida Keys. Rosell and Uriz (1992) and Hill (1996) determined that the presence of zooxanthellae in *C. varians* improves its longevity, growth, and level of bioerosion.

Ecology of the Florida Keys

The Florida Keys is an archipelago of approximately 1,700 islands that extends south and west from southeastern Florida, bordered by the Gulf of Mexico and Florida Bay to the northwest and the Straits of Florida to the east and south. Hawk Channel parallels the Keys on the seaward side between the islands and the Florida Keys Reef tract. Salinity and temperature at inshore communities around the Keys are more influenced by rainfall, groundwater runoff, and atmospheric temperatures (Lidz et al., 1997). Water flow from Hawk Channel and through tidal channels from the Gulf of Mexico and Florida Bay are key components to circulation and nutrient transport into the Lower and Middle Keys (Pitts, 1997; Pitts, 2000; Smith, 1998) and may dramatically affect the abundance and distribution of marine organisms found there. The tropical waters surrounding the keys have been protected since 1990 under NOAA's National Marine Sanctuary program as the 2,900-km^2 Florida Keys National Marine Sanctuary.

The Florida Keys Reef Tract and sponge habitats have experienced a number of external stressors such as bleaching, algal blooms, hurricanes, and temperature extremes. In January 2010, the coral reefs and sponges were affronted by the first severe cold event since 1981 (Walker et al., 1982), which lasted for 12 days (Colella et al., 2012). Colella et al. (2012) surveyed the Upper, Middle, and Lower Keys from summer 2009 through Winter 2010 and reported the following major declines: scleractinian and sponge cover by ~39%, gorgonian cover by ~48%, macroalga1 cover by ~91%, the coral *Orbicella annularis* by ~86%, and >50% of all *Porites astreoides* and *Montastraea cavernosa* were partially or completely killed.

Between 1991 and 1995, two major plankton blooms in the Florida Keys drastically affected sponge populations (Butler et al., 1995; Stevely and Sweat, 1995). Stevely et al. (2011) reported that *C. varians* rapidly declined in 1993 but gradually recovered from 1994-2006 to levels found prior to the 1991 bloom event. However, as an example of its resistance to physical disturbances, *C. varians* was not significantly impacted by Hurricane Wilma (wind speed ~105 knots) in the Florida Keys in 2005

(Stevely et al., 2011). These results illustrate the hardiness and resilience of *C. varians*, which suggest that this species might occupy space dominated by less resilient sponges following disturbances. Thus, stressors such as the plankton bloom in 1991 and the cold snap of 2010, which caused severe die offs of corals and other sponges, may have allowed *C. varians* to increase in abundance, colonize empty limestone substrates, and therefore create more host opportunities for amphipod commensals.

To date, little information regarding population estimates exists about historical or recent *C. varians* levels. There are no reports of *Leucothoe* “sp. F” as a commensal in *C. varians*. This study discusses the ecology, population dynamics, and sexual characteristics of *Leucothoe* “sp. F” in the Florida Keys and its commensal and population structure within the sponge host *C. varians*.

MATERIALS AND METHODS

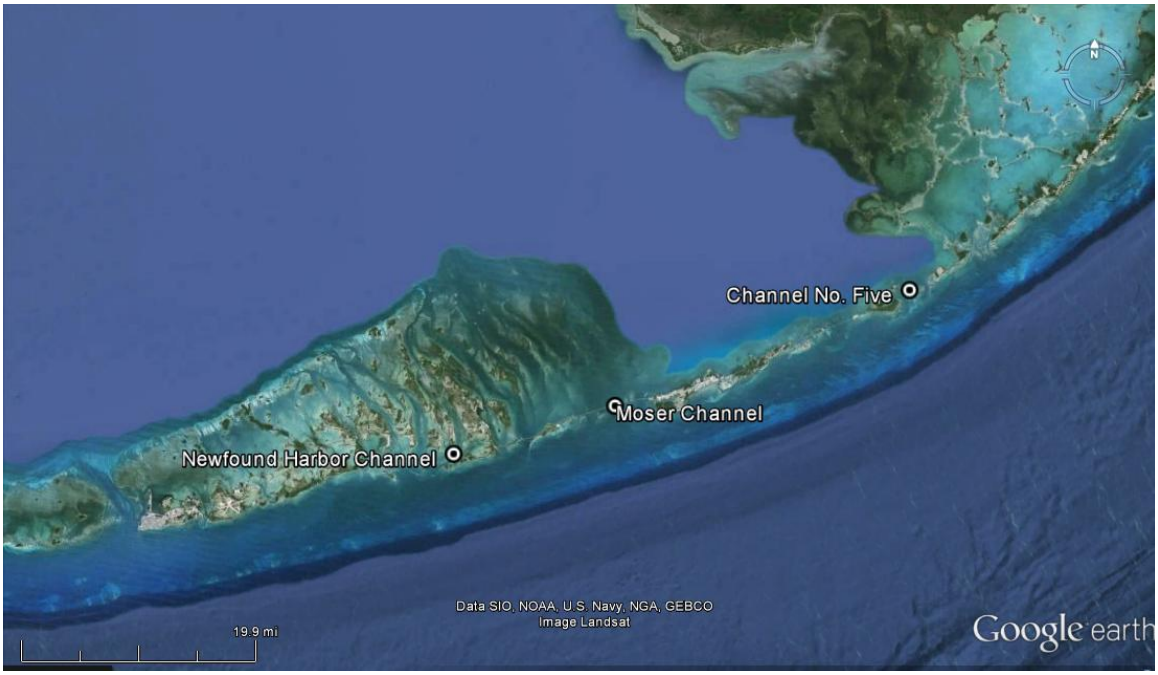

Fig. 2. Google Earth image of the three sites in the Florida Keys from December 2011 to September 2012.

Amphipods were collected *in situ* from *C. varians* at three locations in the Florida Keys: Channel No. 5 (between Lower Matecumbe Key and Long Key), Moser Channel at Molasses Key off the 7 Mile Bridge, and Newfound Harbor Channel (NHC), Big Pine Key, during all four seasons from December 2011 to September 2012 (Figure 2 and Table 2). Two sites were sampled at Moser Channel and at NHC, one in shallow (≤1 m) and one in deeper (~2 m) water. At NHC, samples were taken from Bird Island (shallow) and Munson Island (deep). Channel No. 5 site was never measured shallower than 2 m, and therefore only had a deep-water site. It was only sampled twice due to limited funding. Entries of zero samples in table 3 below were due to inclement weather.

Specimens were collected via snorkeling in shallow-water habitats approximately ≤2 m in depth. Sponges were covered by zip-lock bags, cut free at the base, and immediately sealed to avoid any loss of associates following Thomas and Klebba (2006). At the surface sponges were dissected to remove amphipods, which were placed in vials of 2% buffered formalin solution in seawater. Sponges were then measured (length, with, and height in cm) (Fig. 3) and photographed. Sponge volume was calculated by placing dissected sponge pieces into a 500- or 1,000-ml graduated cylinder and measuring the displacement. Subsamples of sponges were placed in a 2% buffered formalin seawater mixture for further lab analysis.

Fig.3. Molasses Key (Shallow): *C. varians.*

In the lab, subsamples of sponges were dissociated in bleach to remove tissue and expose spicules for proper identification (Table 1). Amphipods were rinsed in water and preserved in 70% EtOH. Amphipods were sorted under a WILD® M5A dissecting microscope according to genus and species. *Leucothoe* “sp. F” was distinguished from other amphipods by LeCroy (2011); see diagnosis in Table A1. Table A2 lists amphipod species found during this study.

Individuals of *Leucothoe* “sp. F” were separated by sex and measured for body length by pencil drawings using a WILD® 256576 camera lucida at a fixed magnification (10 x). Body length was measured along the dorsal curvature starting at the anterior end of the ocular lobe and extending to the posterior end of the telson. Individuals with penial processes were identified as male and those without as females. Females were separated as ovigerous or non-ovigerous based on the presence or absence of oocytes or brood lamellae.

Table 2. Station Data 2011-2012

Site/station	Date	Latitude	Longitude	Depth (m)	Description
Upper Keys					
Channel No. 5	4/12/2012	24.823720°	80.765323°	2	Patch reef; open tidal flow channel connected to Gulf of Mexico; *C. varians*: dense/rigid structure; heavy area coverage.
	9/13/2012	24.823880°	80.764740°	2	
Lower Keys					
Moser Channel					
Molasses Key (SH)	12/17/2011	24.684246°	81.190402°	< 1	Patch reef/seagrass beds; open tidal flow channel connected to Gulf of Mexico; *C. varians*: dense/rigid structure; heavy area coverage.
	4/12/2012	24.684246°	81.190402°	< 1	
	6/18/2012	24.684246°	81.190402°	< 1	
	9/15/2012	24.684246°	81.190402°	< 1	
Molasses Key (DP)	4/12/2012	24.682904°	81.189477°	2	Patch reef; open tidal flow channel connected to Gulf of Mexico; *C. varians*: dense/rigid structure; heavy area coverage.
	6/18/2012	24.682904°	81.189477°	2	
	9/15/2012	24.682904°	81.189477°	2	
Newfound Harbor Channel					
Bird Island (SH)	12/18/2011	24.637160°	81.392340°	<1	Seagrass beds/loose coral rubble; embayment with restricted tidal flow from Gulf of Mexico; *C. varians*: soft/less dense structure; low area coverage.
	4/14/2012	24.635991°	81.392030°	<1	
	6/17/2012	24.636114°	81.392751°	<1	
	9/15/2012	24.636114°	81.392751°	<1	
Munson Island (DP)	12/18/2011	24.617757°	81.399556°	2	Patch reef/seagrass beds; embayment with restricted tidal flow from Gulf of Mexico; *C. varians*: dense/rigid structure; moderate area coverage.
	4/14/2012	24.616543°	81.401346°	2	
	9/15/2012	24.616407°	81.396175°	2	
					*Lat/Long: dropped anchor.
					*SH-shallow water sites (≤ 1m); DP-deep water sites (~2m)

RESULTS

Ninety-eight samples of *C. varians* were collected (Table 3). Limited habitat availability and few sponges were found at NHC sites; fewer at Bird Island than Munson Island. At Bird Island, the shallow NHC site, sponges were scattered, either detached along the silt/sediment bottom on unanchored fragments of coral, or attached to small corals. None were found attached to limestone hard bottoms. At Munson Island, the deep NHC site, sponges varied in size and were found attached to anchored corals or limestone substrate. Sponges at this site also had a firmer, dense texture, compared to those at Bird Island, which was similar to those found at Channel No. 5 and Moser Channel.

Table 3. Number of *C. varians* taken at each location during each season.

Season	Channel No. 5 (Deep ~ 2 m)	Moser Channel (Shallow ≤ 1 m)	Moser Channel (Deep ~2 m)	NHC (Shallow ≤ 1 m)	NHC (Deep ~2 m)
Winter 2011	0	13	0	5	5
Spring 2012	10	5	5	5	5
Summer 2012	0	6	4	5	0
Fall 2012	10	5	5	5	5

By contrast, *C. varians* appeared to be qualitatively more abundant at both Channel No. 5 and Moser Channel than at the NHC sites, and occurred in an array of sizes and with a firm, dense texture. Sponges were always found attached to anchored corals or limestone substrate. Channel No. 5 is open, directly connected with the Gulf of Mexico's hydrodynamic regimes, and has high tidal flows; Moser Channel is also strongly connected to the Gulf of Mexico's hydrodynamic regimes, with high tidal flow, but with a slight island barrier; whereas tidal flow from the Gulf of Mexico at the NHC sites is restricted due to shallow waters and multiple islands and shoals (Figure 2; Table 2). Mean volumes of *C. varians* were also greater at open vs. restricted tidal flow sites (p=0.0010*; Steel-Dwass Nonparametric Comparison) (Figure 4) but did not significantly differ with depth (p=0.6956; Steel-Dwass Nonparametric Comparison) except when measured by site: significant values were found for sponges having a greater volume at Channel No. 5 compared to Moser Channel deep (p= <0.0001*; Steel-Dwass Nonparametric Comparison), Channel No. 5 compared to NHC deep (p= <0.0079*; Steel-Dwass Nonparametric Comparison) and Moser Channel shallow compared to NHC shallow (p= <0.0190*; Steel-Dwass Nonparametric Comparison). Sponge volumes ranged from 20-800 ml at both shallow and deep Moser and NHC sites; Channel No. 5 was only sampled at deep sites.

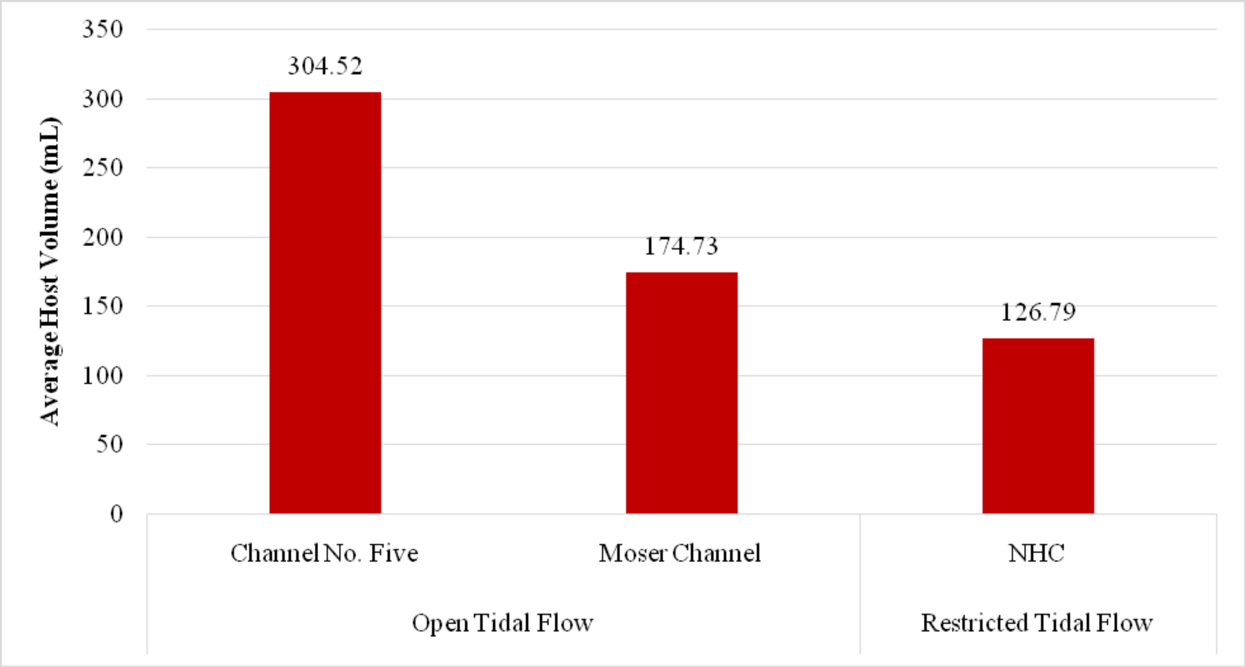

Fig 4: Mean volume of *C. varians* related to open vs. restricted tidal flow from the Gulf of Mexico.

Nine different amphipod species were found in the 98 sponge samples (Figure 5), five of which were ectocommensal (living on the host exterior) and four endocommensal (living within the host) (Table 4). Ectocommensals will not be discussed further. Endocommensals dominated, with *Leucothoe* “sp. F” the most abundant, present in all 98 samples and comprising 87% of the total population. Although *Leucothoe* “sp. B” (LeCroy, 2011), described in Table A3, occurred most frequently with *Leucothoe* “sp. F,” it only occurred in 34 samples and accounted for only 11% of the total endocommensals, not enough to be considered a significant co-inhabitant. The remaining two endocommensals comprised less than 2% of the total abundance and appeared in ≤13 of the total 98 sponges and were therefore not considered further in this study.

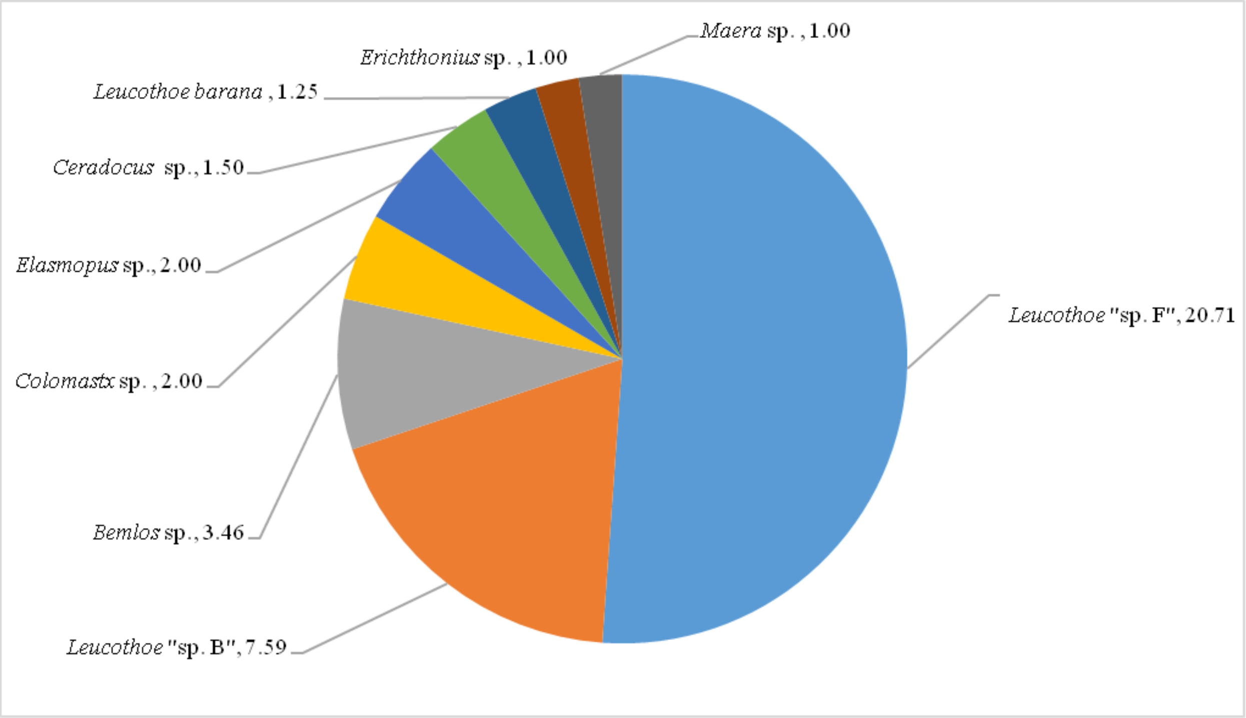

Fig 5: Overall average amphipod species abundances expressed as percentages of all specimens for all locations sampled 2011-2012.

At shallow-water sites, *Leucothoe* “sp. F” contributed 29% of the total population (7% found at NHC and 22% at Moser Channel), and *Leucothoe* “sp. B” made up 9% of the total population (2% at NHC and 7% at Moser Channel). At deep-water sites *Leucothoe* “sp. F” contributed 60% of the total population (32% at Channel No. 5; 16% at Moser Channel, and 11% and NHC). However, *Leucothoe* “sp. B” only made up approximately 2% (1% at Channel No. 5 and Moser Channel, and <1% at NHC) (Table 5).

Table 4. Total and average abundance of ecto- and endocommensal species found within *C. varians*.

	Total number of amphipods(N)	**Total number of *C. varians* samples (N)**	**Average Abundance**
Endocommensals			
Leucothoe "sp. F"	2030	98	20.71
Leucothoe "sp. B"	258	34	7.59
Leucothoe barana	10	8	1.25
Colomastix sp.	26	13	2
Total	2,324	98	23.71
Ectocommensals			
Bemlos sp.	45	13	3.46
Elasmopus sp.	2	1	2
Ceradocus sp.	3	2	1.5
Maera sp.	1	1	1
Erichthonius sp.	1	1	1
Total	53	13	4.08

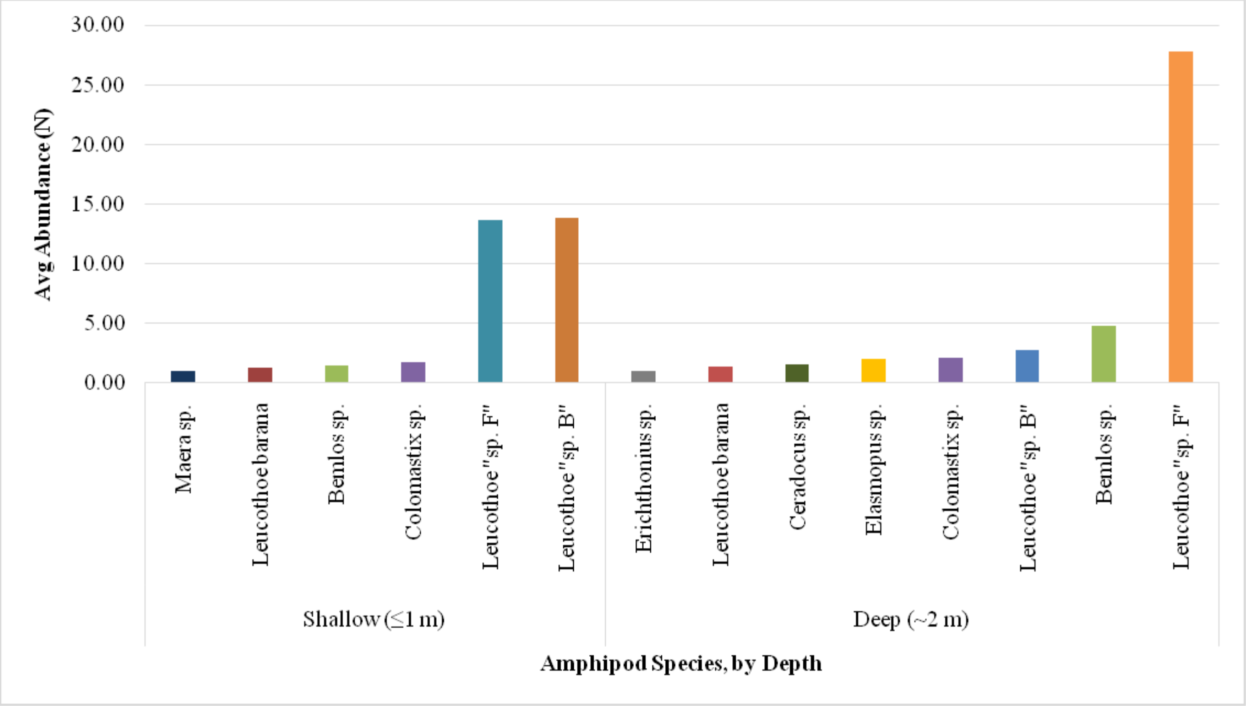

Fig. 6: Average abundance of all amphipod species by shallow vs. deep water sampling locations.

Table 5. Total and average abundance of *Leucothoe* "sp. F" and "sp. B" found within *C. varians* by depth at each site.

	***Leucothoe* "sp. F"**		
Site	**Total number of amphipods (N)**	**Total number of *C. varians* samples (N)**	**Average Abundance**
SHALLOW	668	49	13.6
Bird Island (NHC)	171	20	8.55
Moser Channel	497	29	17.14
DEEP	1,362	49	27.8
Channel No. 5	739	20	36.95
Moser Channel	366	14	26.14
Munson Island (NHC)	257	15	17.13
	***Leucothoe* "sp. B"**		
Site	**Total number of amphipods (N)**	**Total numbers of *C. varians* samples (N)**	**Average Abundance**
SHALLOW	207	15	13.8
Bird Island (NHC)	44	1	44
Moser Channel	163	14	11.64
DEEP	51	19	2.68
Channel No. 5	26	9	2.89
Moser Channel	24	9	2.67
Munson Island (NHC)	1	1	1

Total numbers of amphipods were generally greater at deeper sites, at more open sites with less restricted tidal flow, and with greater host volume. An exception was Moser Channel, where total abundance was greatest at the shallow site, which could be due to skewed collections of *C. varians* mentioned in Table 3.

Leucothoe “sp. F” was originally unknown as a commensal of *C. varians* in the Florida Keys, but in this study constituted the largest population and greatest percentage of amphipods encountered. It is therefore the focus of this study. Average abundances of *Leucothoe* “sp. F” were greater at deeper sites, at more open sites with less restricted tidal flow (Figure 7), and with greater host volume (except for two outliers; Figure 8). Their numbers decreased from spring to winter (Figure 9). Males accounted for 44% (N=889) of all *Leucothoe* “sp. F” collected, and female 56% (N=1,141). Females were more abundant than males at all locations and also decreased in total abundance from spring to winter (Figure 10).

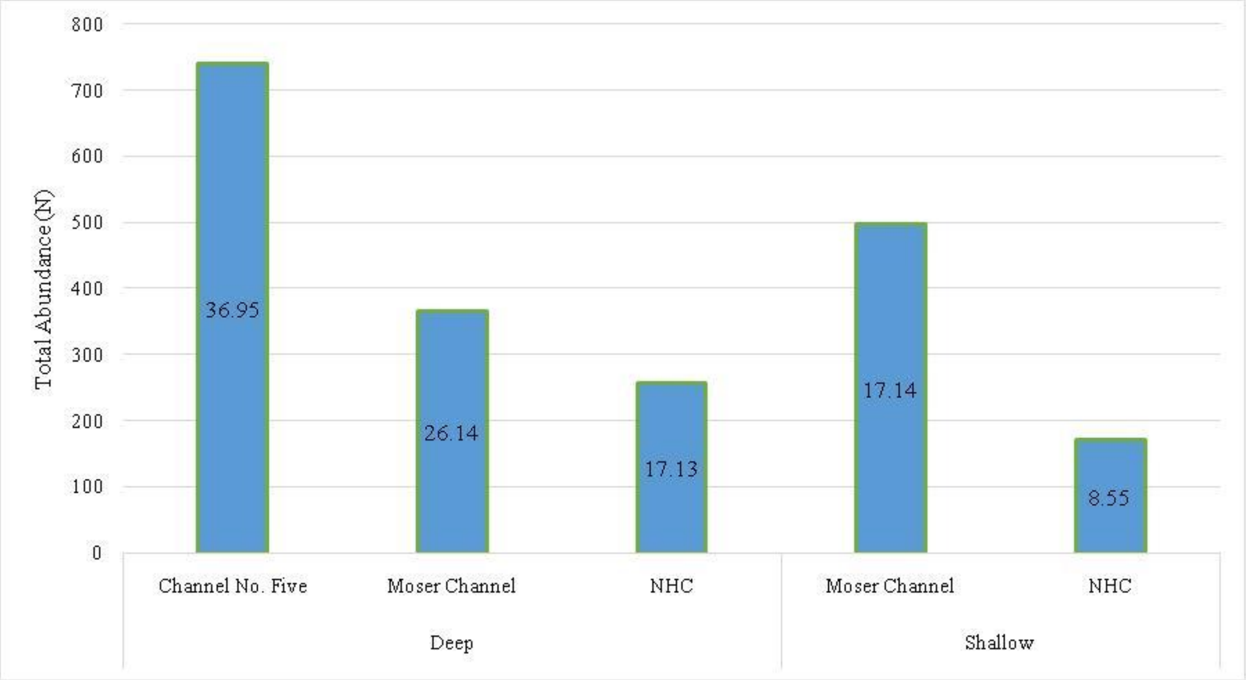

Fig. 7: Total abundance (average abundance in center of bars) of *Leucothoe* “sp. F” by location and depth of sampling site.

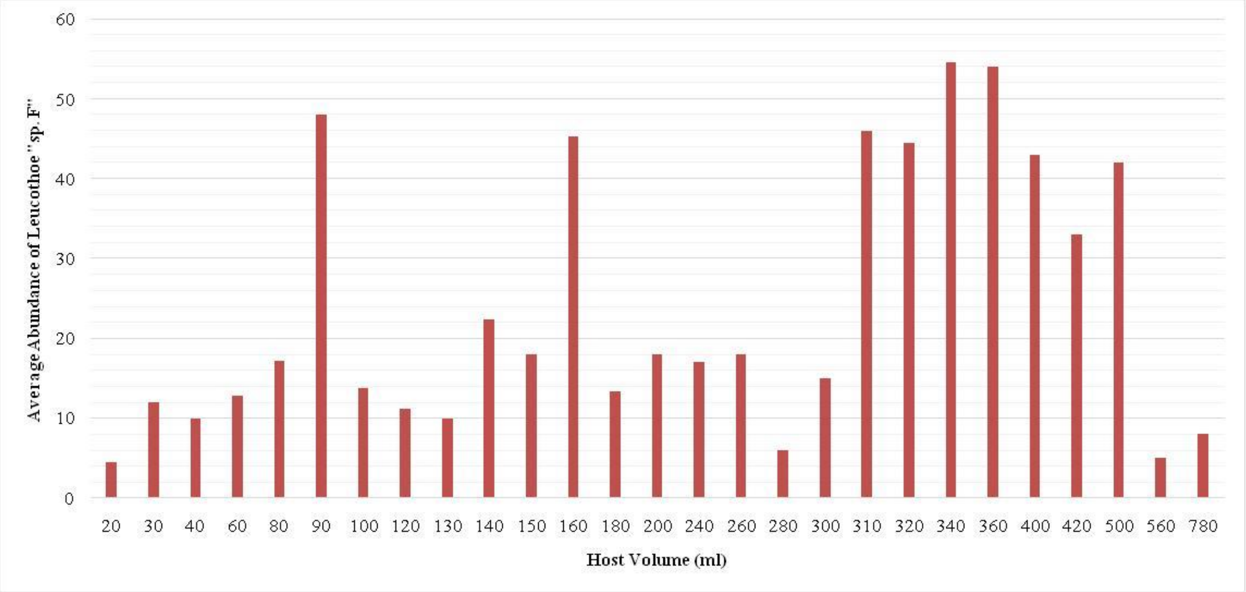

Fig. 8: Average abundance of *Leucothoe* “sp. F” relative to *C. varians* volume (ml).

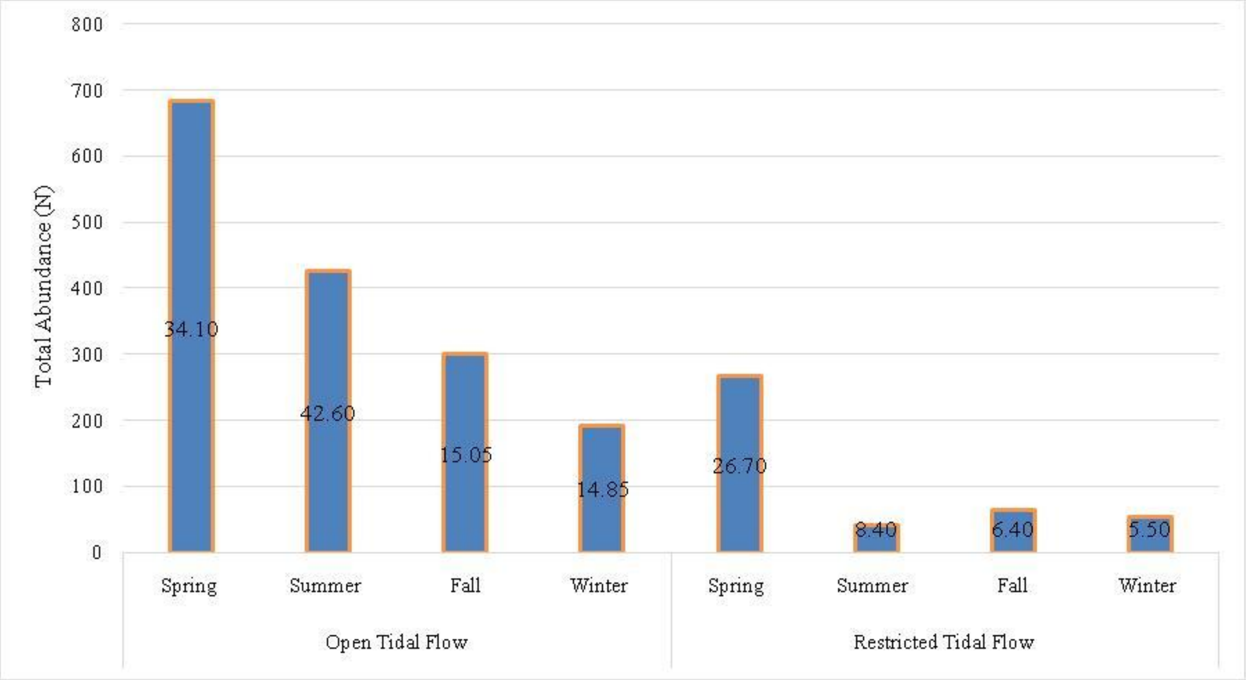

Fig.9: Total abundances (average abundance in center of bars) of *Leucothoe* ‘sp F’ by season and tidal variations of sampling site, as influenced by the Gulf of Mexico.

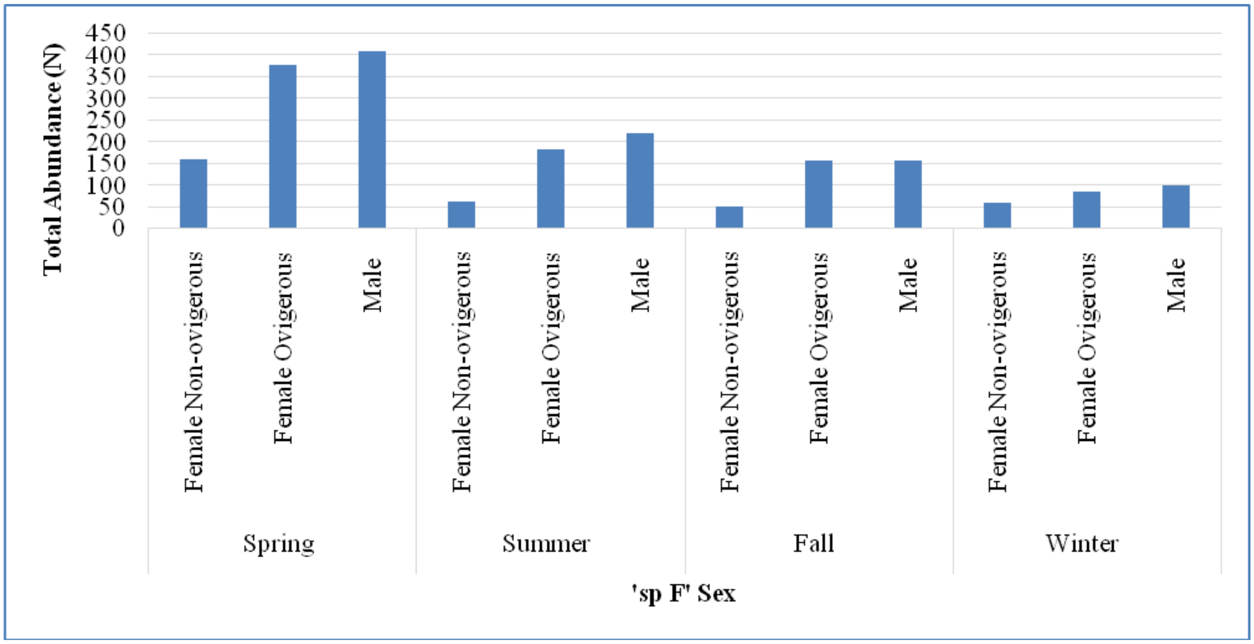

Fig. 10: Total abundance of *Leucothoe* "sp. F" sexes by sampling seasons, 2011-2012.

Males and females were separated according to secondary sexual characteristics (Table 6) and grouped into juvenile, intermediate, or adult subgroups (Table 7) according to length in mm. Figure 11 illustrates female gnathopod 1 and male gnathopod 2, with key diagnostic characteristics. ANOVA analysis showed significance between mean body length and sex (p=0.0001*, ANOVA Steel-Dwass Non-parametric comparison) (Figure A1). Adult, sexually mature females ranged in size from 5.6 to 12.5 mm and males from 6.1 to 12.5 mm; intermediate, sexually mature or immature females from 5.0 to 7.5 mm and males from 5.6 to 10 mm, and juvenile, sexually immature females from 2.0 to 6.5 mm and males from 2.6 to 8.0 mm. Specimens <2 mm in length were found in the brood pouch (Figures 12-15).

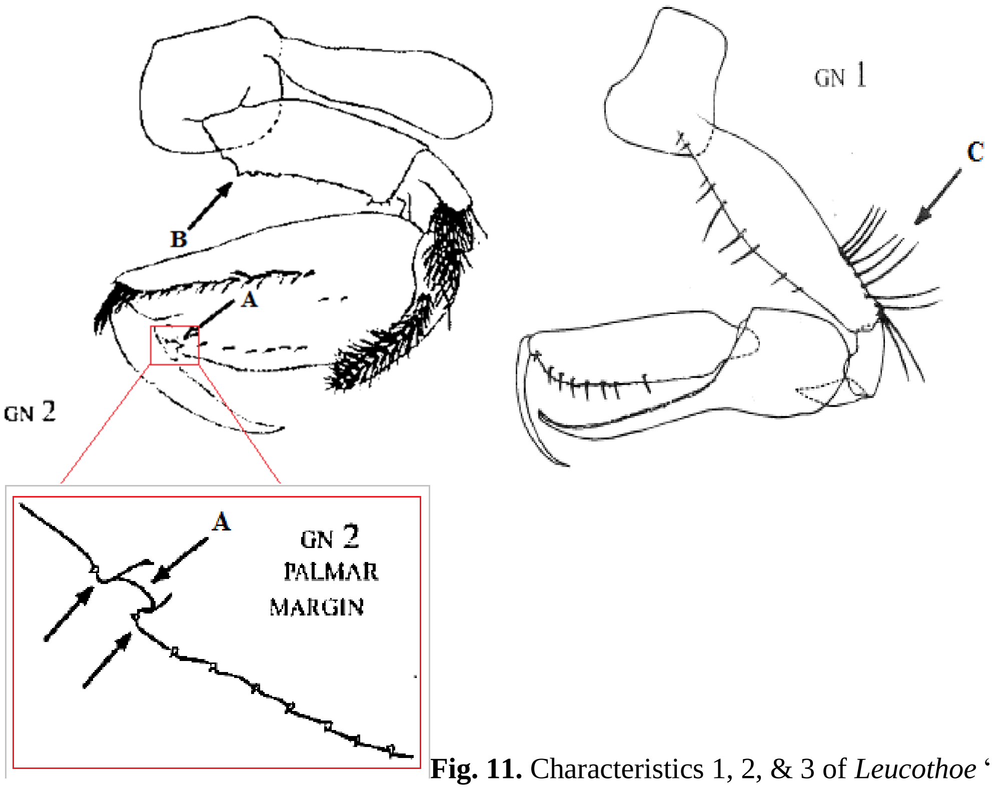

Fig. 11. Characteristics 1, 2, & 3 of *Leucothoe* “sp. F”. Male gnathopod 2 (GN 2, upper left): (A) characteristic 1 (inset, lower left): propodus with 2 large distal palmar processes separated by a broad, U-shaped gap; (B) characteristic 2: anterior margin of the basis on gnathopod 2 lined with sharp tubercles proximally. Female gnathopod 1(GN 1, upper right): (C) characteristic 3: posterior margin of basis on gnathopod 1 with distal cluster of long setae. Drawings from LeCroy (2011).

Table 6. Sexual Characteristics of *Leucothoe* “sp. F”

Leucothoe “sp. F” sex	Characteristic 1	Characteristic 2	Characteristic 3
Female	Not present	Not present	Posterior margin of basis on gnathopod 1 with distal cluster of long setae.
Male	Propodus with 2 large distal palmar processes separated by broad, U-shaped gap.	Anterior margin of basis on gnathopod 2 lined with sharp tubercles proximally.	Not present

Table 7. Description of *Leucothoe* "sp. F" life stage according to sexual characteristics and body length (Figures 12-15).

Sex	**Body Length (mm)**	**Description**	
Female		Oocytes	Sexual Characteristic (Table 6)
Juvenile	2.0-6.8	Absent	Characteristic 3 absent.
Intermediate	5-7.6	Absent	Characteristic 3 has few distal short setae.
Adult	4.9-12.5	Present	Characteristic 3 present.
Male			
Juvenile	2.6-7.7	Absent	Characteristics 1 & 2 absent.
Intermediate	5.3-9.3	Absent	Characteristic 1 present; characteristic 2 absent.
			-OR-
			Characteristic 1 absent; characteristic 2 present.
Adult	6.5-12.5	Absent	Characteristics 1 & 2 present.

Adults always comprised the majority of the total population in each sampling season. Of the total number of females, 80% were classified as adults, 5% as intermediates, and 15% as juveniles (Figure 12; Table 8); 71% were ovigerous and 29% non-ovigerous. Ninety-nine percent of ovigerous females exhibited characteristic 3 (Table 6), and 1% had characteristic 3 described in Table 7 as female intermediate (Figure 13). This ovigerous intermediate stage could represent females that have just become sexually mature. Among non-ovigerous females 34% were classified as adult, 16% as intermediate, and 50% as juveniles (Figure 14; Table 8). Of the total number of males, 59% were classified as adults, 11% as intermediates, and 30% as juveniles (Figure 15; Table 8).

Table 8. Total abundance (N) *Leucothoe* "sp. F" by sex and life history stage.

Life Stage	**Male**	**Female**	**Ovigerous**	**Non-ovigerous**
Adult	521	908	795	113
Intermediate	103	65	11	54
Juvenile	265	168	0	168
Total	889	1,141	806	335

Juvenile males emerge from the brood pouch in spring at a smaller length than during the other seasons (2.6:3.1 mm) (Figure A2), but females emerge from the brood pouch at a smaller length during fall (2.0 mm) (Figure A3). Females emerge at their greatest length during winter (4.6 mm) and emerge as smaller in spring, summer, and fall. Durations of juvenile and or intermediate stages do not appear to correlate with season. However, in spring adult females vary in length by 8 mm and only 4 mm in all other seasons. Males do not vary significantly in length according to life stages.

Total amphipod abundance varied with collection depth, but length at any given life history stage did not. Of the total adult female population, 66% were found at deep versus 34% at shallow sites (Figure A4); 80% of intermediates at deep versus 20% at shallow sites, and 73% of juveniles at deep versus 27 % at shallow sites. Males were also more abundant overall at deep sites: 65% of the total adult male population was found at deep versus 35% at shallow sites; 72% of intermediates at deep versus 28% at shallow sites, and 65% of juveniles at deep versus 35% at shallow sites (Table A4; Figure A5).

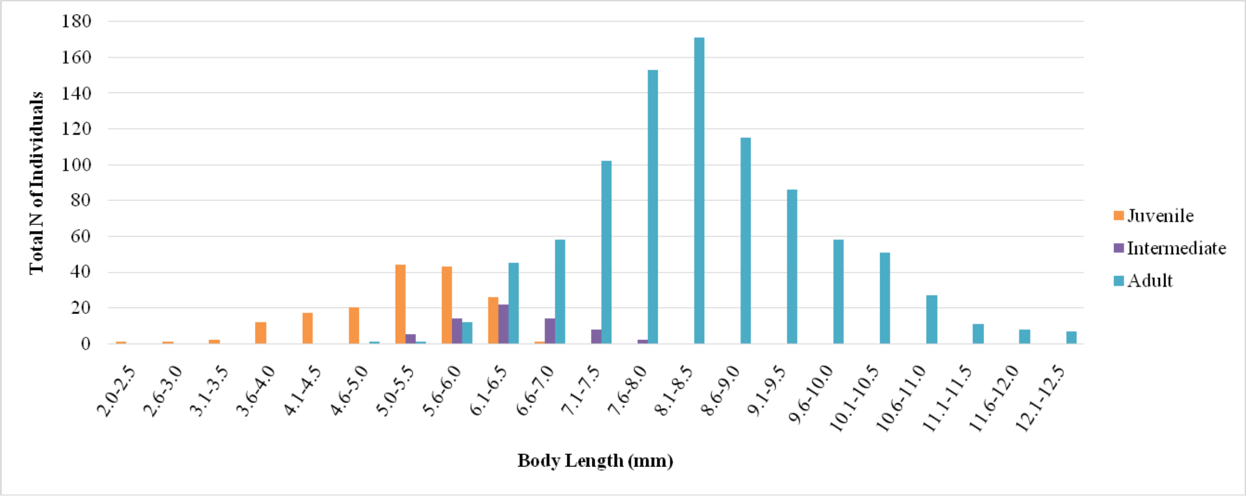

Fig. 12. Non-ovigerous and ovigerous female body length (mm) distribution relative to *Leucothoe* “sp. F” characteristic 3.

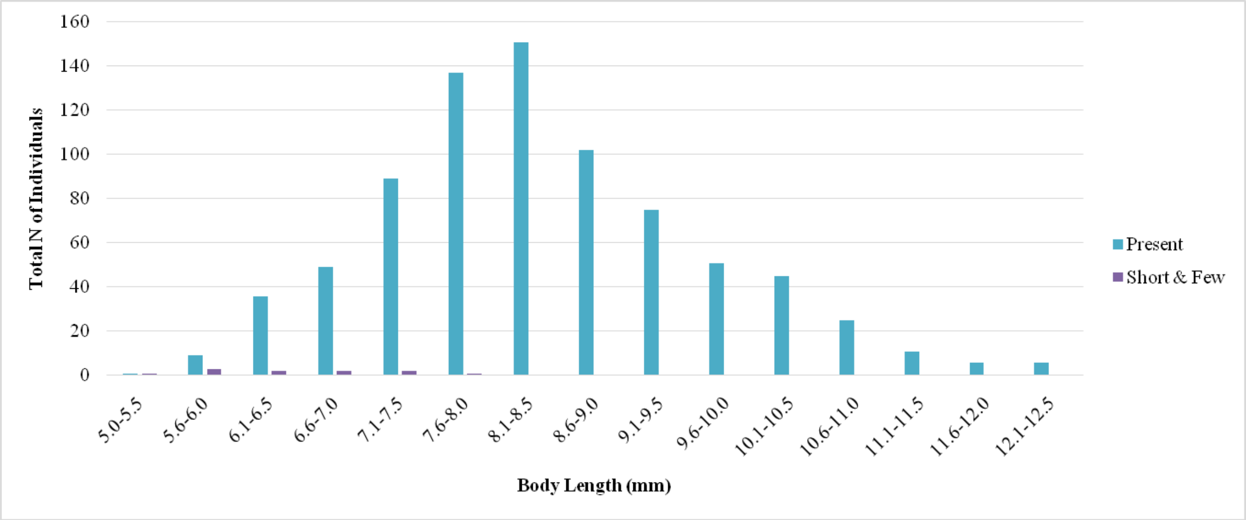

Fig. 13. Ovigerous female body length (mm) distribution relative to *Leucothoe* “sp. F” characteristic 3.

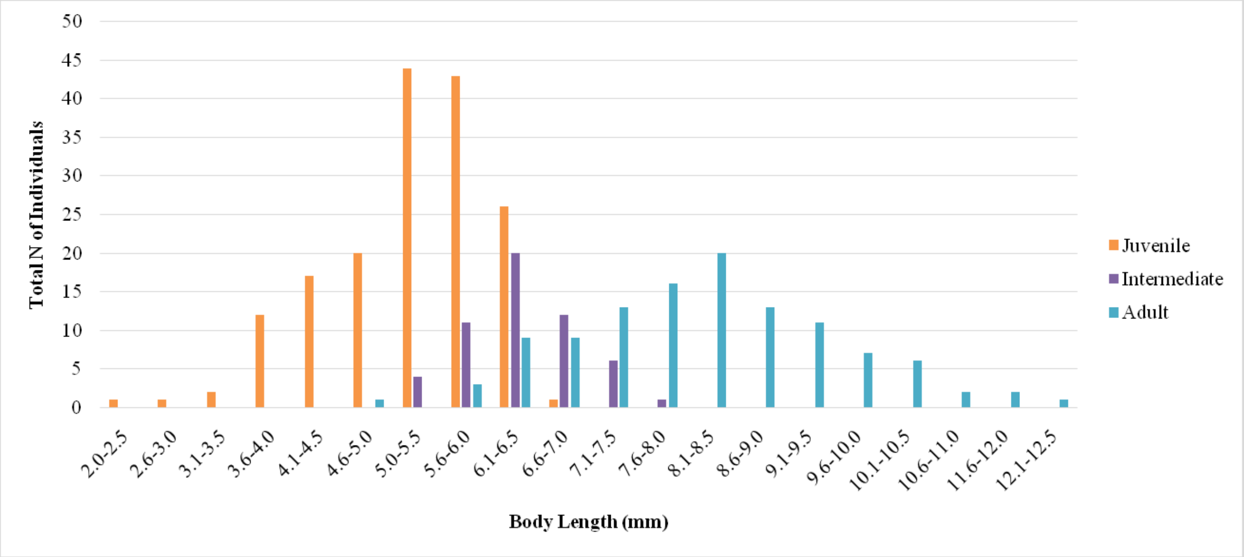

Fig. 14. Non-ovigerous female body length (mm) distribution relative to *Leucothoe* "sp. F" characteristic 3.

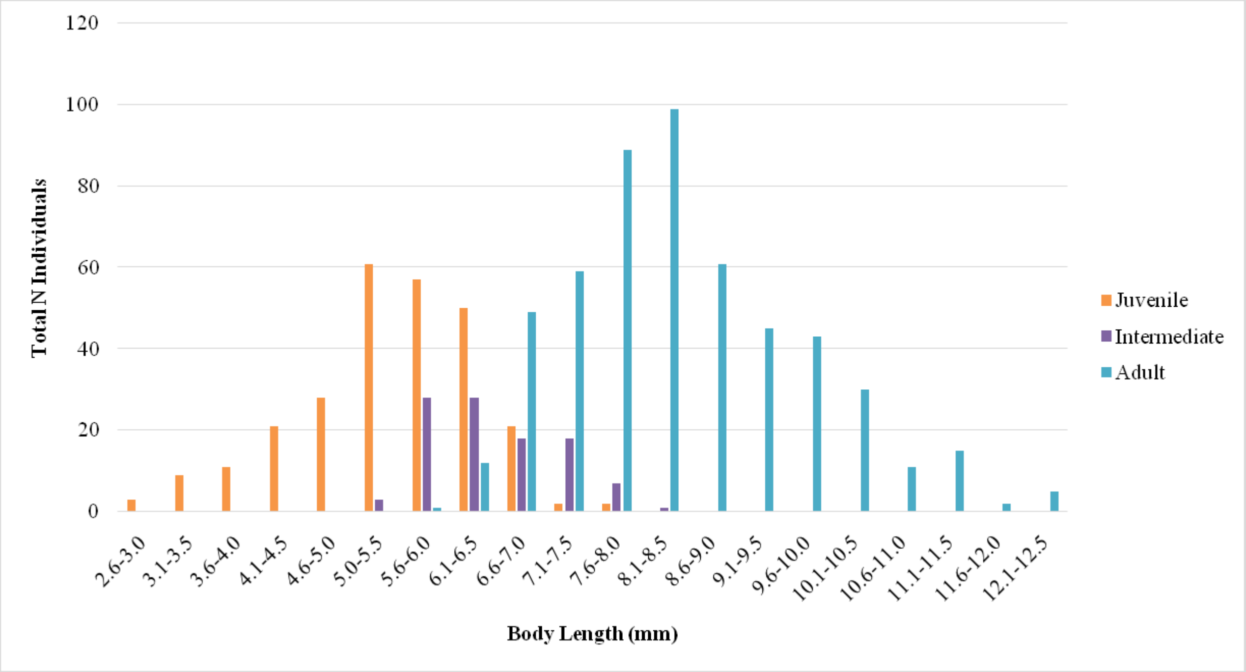

Fig. 15. Male body length (mm) distribution relative to *Leucothoe* "sp. F" characteristics 1 and 2.

DISCUSSION

Abundance and internal volume (ml) of *C. varians* differed among the three locations sampled. Habitat/sponge abundance was a limiting factor at NHC sites, and more so at shallow than the deep sites. Sponges at these sites had a lower average volume (126.79 ml) than at the other two sites (Channel No. 5 and Moser Channel), where *C. varians* was plentiful and had a higher average volume (304.53 ml). At least two factors could contribute to these differences: 1) *C. varians* requires a solid substrate for at least initial settlement (Rützler, 1975, 2002; Zundelevich et al., 2007), and 2) internal volume and abundance may be affected by tidal flow. At Bird Island, NHC, sponges attached to small anchored coral or were found rolling along the silty sediment bottom attached to unanchored fragments of coral. Conditions at this site were not ideal for sponges to settle and grow, due to the lack of extended limestone substrate. At Munson Island, NHC; Channel No. 5, and Moser Channel, sponges were always found anchored to corals or limestone substrates, which reflects a more stable environment for this host species.

The NHC sites were sheltered from strong tidal flow from the Gulf of Mexico, and Bird Island was additionally sheltered from currents from the Straits of Florida. Weaker flow may have reduced nutrient delivery or forced *C. varians* to direct greater energy resources toward generating its filtration current, thus limiting recruitment and survival, although other factors may have contributed as well. By contrast, both the Channel No. 5 and Moser Channel sites, which supported more numerous *C. varians* with on average larger volumes, were both subject to strong tidal flow from the Gulf of Mexico as well as to influences from the Atlantic Ocean. Average sponge volume also differed at deep (198.82 ml) versus shallow (181.39 ml) sites, but not significantly. It could be that sponge volume is affected more by tidal regimes and substrate than depth.

With respect to physical consistency, sponges at NHC, especially at Bird Island, were softer, less dense, and easily torn relative to those gathered at Munson Island, Moser Channel, and Channel No. 5, which were firm, dense, and hard to pull apart and required opening with a knife. Specimens at Bird Island appeared to be *C. varians* form *varians*, whereas those at the other three sites were likely *C. varians* form *rigida*, perhaps as responses to different environments, as described in Hill (1999) and Hill and Hill (2002). Their studies showed that sponges produced differing morphologies based on predation stressors. Sponges subjected to high levels of predation produced more spicules and a denser cortex versus those exposed to limited predation.

Tidal regime does not seem to be a major contributor to sponge morphology. Munson Island, with its restricted tidal flow, and Channel No. 5 and Moser Channel, with strong flow, all supported sponges with similar consistencies. By contrast, a strong relationship appears to exist between sponge consistency and the availability of limestone/coral substrates. The Channel No. 5, Moser Channel, and Munson Island sites, which supported similar sponge consistencies, all had established patch reefs with limestone and coral substrates, whereas Bird Island, with less solid substrate and more sediment, supported the less dense *C. varians* form *varians*.

C. varians examined in this study had multiple central oscules with interior subdivisions, both of which varied in number and size. These features were not measured but could affect endocommensal abundance. Endocommensals were most often associated with the larger central osculum, but were also found moving throughout smaller internal canals. They were less abundant or absent in the denser tissues, chimneys, or base of the sponge.

Tidal regime, depth, and hosts volume also seemed to affect amphipod abundance. *Leucothoe* “sp. B” appears to prefer areas of strong tidal flow; it was found in 32 sponge samples between Moser Channel and 9 at Channel No. 5 and was more abundant at shallow-water sites. By contrast only two samples at NHC hosted this species. It may be more easily transported via tidal currents at unrestricted flow sites, or perhaps it prefers larger sponges with larger central canals. This species does not appear to be a constant cohabitant with *Leucothoe* “sp. F,” as it only appeared in 34 of the 98 sponges sampled (Table 4).

Leucothoe “sp. F” occurred at greater abundances in deep versus shallow water sites (1,362: 668) and also preferred strong flow versus restricted tidal locations (1,602: 428). This could possibly be explained by: 1) access to the Gulf of Mexico; 2) host availability; 3) high current regimes, or 4) more sponges were sampled at open flow sites (Table 3). If *Leucothoe* “sp. F” abundance correlates with the influence of the Gulf of Mexico, this could mean that this species is being introduced or transported via strong currents from the Gulf of Mexico through channels such as Channel No. 5 and Moser Channel and then spreading to restricted sites via Hawk Channel. This study found *Leucothoe* “sp. F” more abundant at open tidal locations and at greater depths, suggesting a correlation with host availability. Since abundance correlates with strong currents, this could mean that locations with this variable are subject to higher nutrient levels, supplying *C. varians* and its endocommensal amphipods with a greater food supply. However, these factors are all occurring at Channel No. 5 and Moser Channel sites, so it is hard to determine without further studies which most directly influences species or host abundance. Both abundance and size of host and amphipod are limited at NHC, which indicates that these physical environmental conditions could be key factors in host and amphipod development.

Numbers of *Leucothoe* "sp. F" were greatest during spring and decreased thereafter, perhaps reflecting seasonal variations in nutrient availability or temperature. If nutrient levels are highest during spring, they may increase potential food supplies and thus influence reproduction and growth. Bousfield (1973) found that temperature influences amphipod egg development and therefore could contribute to juveniles emerging more frequently, adding to the population. If this is an accurate representation of amphipod abundance correlating with season, then it is plausible that as nutrient levels decrease and temperatures fluctuate, heating during summer and then cooling off into fall, so too would the abundance of amphipods.

In this study, the average abundance of *Leucothoe* "sp. F" correlated not only with tidal regimes, depth, and season, but also with host volume. In hosts with volumes >300 ml, amphipod average abundances were ≥30, while in hosts with volumes ≤300 ml, most amphipod average abundances were rarely ≥20. Sponge and amphipod abundances increased with depth and open tidal flow sites, suggesting that amphipod abundance is not only influenced by tidal regimes, season, and depth, but also by sponge availability. Amphipod abundance also increased with sponge volume suggesting that a large host sponge with a larger volume is capable of providing more potential food and space for larger population of amphipods at all life stages.

Lengths of *Leucothoe* “sp. F” did not correlate with season, location, depth, tidal regimes, or host volume like the amphipods mentioned by Pearse (1950), Thiel (2000), Crowe (2001), and Henkel and Pawlik (2005). Thus, amphipod length appears to be species specific rather than influenced by environmental factors. Length does coincide with sexual maturity.

Female *Leucothoe* “sp. F” (N=1,141) were more abundant than males (N=889). Such skewed sex ratios have been documented for other amphipods, and could be associated with food availability or gender-related longevity (Moore, 1981 and Wenner, 1972). Abundances of different life history stages decreased as follows: adult females, adult males, juvenile males and females, and intermediate males and females. Thus, reproductive individuals make up the majority of the population followed by juveniles. Also, juveniles emerging from the brood pouch were smaller in the spring and fall and largest during winter. Each life history stage decreased in abundance at the same frequencies by season (spring to winter), which could result from decreasing nutrient availability (Table A5). The same was true for depth and tidal regime areas, corresponding with population abundance measurements.

Breeding appears to be continuous throughout the year; every life history stage was found at every depth, season, and location, and ovigerous females and juveniles were found at various sizes. Results from this study further support previous suggestions that amphipods spend their entire life cycle inside the host (Thiel, 1999).

It is not known how host specific *Leucothoe* “sp. F” may be. Thomas (1997) found it in an ascidian off Panama City, FL, and LeCroy (2011) reported it in *Spheciospongia vesparium* in the Florida Keys, but it has not been found in any other sponge so far. *Cliona varians* may be favorable as a host due to its availability and relatively limited numbers of other endocommensals. The increase in sponge availability could be a result of extreme environmental factors such as the plankton blooms in 1991-1995 and the cold front of January 2010. Such factors could have allowed *C. varians* to increase in abundance by colonizing empty limestone substrates and therefore providing more host opportunities for endocommensal amphipods. The lack of reported *C. varians* associates could have allowed *Leucothoe* “sp. F” to fill an empty niche and thus there was little competition from existing commensals allowing for *Leucothoe* “sp. F” to thrive.

CONCLUSION

The data analyzed in this study document a commensal relationship between the sponge *C. varians* and amphipod *Leucothoe* “sp. F.” Host abundance was found to correlate with depth, limestone/coral coverage, and tidal regimes, while host volume correlated strongly with tidal regimes. Amphipod abundances correlated with season, depth, tidal regimes, and host volume. Amphipod length did not correlate with the previous factors, but did correlate with the onset of sexual characteristics. The various lengths of ovigerous females throughout the seasons suggest continuous breeding. Although other species of endo- and ectocommensal amphipods were observed with *C. varians*, none besides *Leucothoe* “sp. F” occurred regularly or as abundantly. This study demonstrates that *Leucothoe* “sp. F” is now a common species in the Florida Keys strongly associated with the sponge *C. varians*. The lack of local reports of this species prior to recent years suggests the possibility that it was introduced via tidal transport from the Gulf of Mexico, where it was previously observed by Thomas (1997).

Further sampling and detailed studies are needed to determine the full distribution of *Leucothoe* “sp. F,” the parameters of its associations with host sponges, and its ecology, physiology and nice requirements, e.g., in relation to temperature, salinity, nutrient levels, hydrodynamics, and other endocommensals. A formal taxonomic description and naming is also needed, as well as its phylogenetic status relative to other species in the genus. Lastly, it would be valuable to study its sexual characteristics to better understand their functions relative to those of other amphipod species.

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APPENDIX

Table 1. Diagnostic characteristics of *Leucothoe* "sp. F" (LeCroy 2011).

Structure	Diagnostic characters
1. Ocular lobe:	“Angled, midventral keel; anterior margin concave, without small central bump**;** anteroventral angle subquadrate, extending forward subequally with anterodorsal angle.”
2. Mandible:	“Incisor process strongly dentate; spines in raker row long; left lacinia mobilis unreduced, fan-shaped; apical margin dentate or serrate; palp article 2 with 12-14 long marginal setae; article 3 stout, not tapering distally, approximately one third length of article 2, with 2 apical setae; shortest apical setae at least one-half length of longest.”
3. Coxae:	“1-4, ventral margins entire; coxa 1 without long, anteroventral submarginal seta on medial surface; anterovenral angle produced; coxa 2 subquadrate; coxa 4 excavate posteriorly, ventral margin strongly convex, anteroventral angle rounded, entire."
4. Gnathopod 1:	“Basis, posterior margin without proximal or central row of short setae that of female, posterior margin with distal cluster of long setae; carpal lobe slender, without long seta on distomedial surface, posterior margin not lined with long setae; propodus, posterior margin minutely serrate, dactyl long, tip extending well past tip of carpal lobe.”
5. Gnathopod 2:	“Basis, anterior margin of male lined with sharp tubercles serrations proximally, sparsely lined with short setae only, expanded distally, forming small lobe, that of female sparsely lined with long and short setae, with separate cluster of long, close-set setae distally; carpal lobe not broadly expanded, subtruncate distally, distal margin weakly serrate or crenulate, lateral margin entire; propodus without long, blade-like anterodistal process overhanging insertion of dactyl, primary mediofacial setal row diverging slightly from anterior margin, secondary mediofacial setal row present, well-developed; palm convex, oblique, that of male longer than hind margin, with 2 large distal processes separated by a broad u-shaped gap, that of female continuous with hind margin, crenulate, with 0-1 very small, subacute process distally; dactyl slender, strongly curved, without apical nail, posterior margin entire, without fine setules.”
6. Peraeopod 7:	"Basis narrowing distally, posterior margin strongly convex."
7. Epimeron 1:	“With cluster of setae on anteroventral margin.”
8. Epimeron 3:	"Posteroventral angle subquadrate."
9. Uropod 3:	“Peduncle slightly longer than inner ramus; inner ramus slightly longer than outer."

Table 2. Amphipod abundance by species, sample, season, location, depth, and host volume.

Middle Keys

Channel No. Five

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S12APR12-01	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	83	160
S12APR12-02	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	5	100
S12APR12-02	Spring 2012	Channel No. Five	~2	*Colomastix* sp.	1	100
S12APR12-02	Spring 2012	Channel No. Five	~2	*Bemlos* sp.	1	100
S12APR12-03	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	87	340
S12APR12-03	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	5	340
S12APR12-03	Spring 2012	Channel No. Five	~2	*Colomastix* sp.	2	340
S12APR12-04	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	48	90
S12APR12-05	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	12	30
S12APR12-06	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	18	150
S12APR12-07	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	207	770
S12APR12-07	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	5	770
S12APR12-07	Spring 2012	Channel No. Five	~2	*Leucothoe barana*	1	770
S12APR12-07	Spring 2012	Channel No. Five	~2	*Colomastix* sp.	1	770
S12APR12-08	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	22	340
S12APR12-08	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	2	340
S12APR12-08	Spring 2012	Channel No. Five	~2	*Colomastix* sp.	3	340
S12APR12-09	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	19	320
S12APR12-09	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	1	320
S12APR12-09	Spring 2012	Channel No. Five	~2	*Colomastix* sp.	3	320
S12APR12-10	Spring 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	5	20

Table 2. Continued.

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S12APR12-10	Spring 2012	Channel No. Five	~2	*Colomastix* sp.	1	20
S13SEP12-01	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	33	420
S13SEP12-01	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	7	420
S13SEP12-01	Fall 2012	Channel No. Five	~2	*Colomastix* sp.	2	420
S13SEP12-02	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	42	500
S13SEP12-02	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	2	500
S13SEP12-02	Fall 2012	Channel No. Five	~2	*Colomastix* sp.	1	500
S13SEP12-02	Fall 2012	Channel No. Five	~2	*Bemlos* sp.	1	500
S13SEP12-03	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	16	200
S13SEP12-03	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	2	200
S13SEP12-04	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	13	100
S13SEP12-05	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	20	100
S13SEP12-06	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	14	200
S13SEP12-06	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	1	200
S13SEP12-06	Fall 2012	Channel No. Five	~2	*Colomastix* sp.	1	200
S13SEP12-07	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	17	140
S13SEP12-08	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	14	80
S13SEP12-09	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	10	180
S13SEP12-10	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. F”	54	360
S13SEP12-10	Fall 2012	Channel No. Five	~2	*Leucothoe* “sp. B”	1	360
S13SEP12-10	Fall 2012	Channel No. Five	~2	*Colomastix* sp.	6	360
Lower Keys						

Table 2. Continued.

Moser Channel

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S13APR12-01	Spring 2012	Molasses	≤1	*Leucothoe* “sp. F”	8	180
S13APR12-04	Spring 2012	Molasses	≤1	*Leucothoe* “sp. F”	19	240
S13APR12-04	Spring 2012	Molasses	≤1	*Leucothoe* “sp. B”	4	240
S13APR12-06	Spring 2012	Molasses	≤1	*Leucothoe* “sp. F”	12	280
S13APR12-06	Spring 2012	Molasses	≤1	*Leucothoe* “sp. B”	12	280
S13APR12-07	Spring 2012	Molasses	≤1	*Leucothoe* “sp. F”	8	780
S13APR12-07	Spring 2012	Molasses	≤1	*Leucothoe* “sp. B”	11	780
S13APR12-09	Spring 2012	Molasses	≤1	*Leucothoe* “sp. F”	9	100
S13APR12-09	Spring 2012	Molasses	≤1	*Leucothoe* “sp. B”	8	100
S13APR12-02	Spring 2012	Molasses	~2	*Leucothoe* “sp. F”	10	80
S13APR12-03	Spring 2012	Molasses	~2	*Leucothoe* “sp. F”	30	80
S13APR12-03	Spring 2012	Molasses	~2	*Leucothoe* “sp. B”	2	80
S13APR12-05	Spring 2012	Molasses	~2	*Leucothoe* “sp. F”	49	100
S13APR12-05	Spring 2012	Molasses	~2	*Leucothoe* “sp. B”	2	100
S13APR12-08	Spring 2012	Molasses	~2	*Leucothoe* “sp. F”	15	40
S13APR12-08	Spring 2012	Molasses	~2	*Leucothoe* “sp. B”	1	40
S13APR12-10	Spring 2012	Molasses	~2	*Leucothoe* “sp. F”	16	80
S13APR12-10	Spring 2012	Molasses	~2	*Leucothoe* “sp. B”	2	80
S18JUNE12-01	Summer 2012	Molasses	≤1	*Leucothoe* “sp. F”	26	80
S18JUNE12-02	Summer 2012	Molasses	≤1	*Leucothoe* “sp. F”	28	140
S18JUNE12-03	Summer 2012	Molasses	≤1	*Leucothoe* “sp. F”	43	400
S18JUNE12-03	Summer 2012	Molasses	≤1	*Leucothoe* “sp. B”	16	400

Table 2. Continued.

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S18JUNE12-04	Summer 2012	Molasses	≤1	*Leucothoe* “sp. F”	46	310
S18JUNE12-04	Summer 2012	Molasses	≤1	*Leucothoe* “sp. B”	2	310
S18JUNE12-05	Summer 2012	Molasses	≤1	*Leucothoe* “sp. F”	70	320
S18JUNE12-05	Summer 2012	Molasses	≤1	*Leucothoe* “sp. B”	6	320
S18JUNE12-05	Summer 2012	Molasses	≤1	*Maera* sp.	1	320
S18JUNE12-06	Summer 2012	Molasses	≤1	*Leucothoe* “sp. F”	24	180
S18JUNE12-06	Summer 2012	Molasses	≤1	*Leucothoe* “sp. B”	15	180
S18JUNE12-07	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. F”	33	80
S18JUNE12-07	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. B”	4	80
S18JUNE12-07	Summer 2012	Molasses	~ 2	*Elasmopus* sp.	2	80
S18JUNE12-08	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. F”	42	60
S18JUNE12-08	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. B”	2	60
S18JUNE12-09	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. F”	53	120
S18JUNE12-09	Summer 2012	Molasses	~ 2	*Ceradocus* sp.	1	120
S18JUNE12-10	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. F”	61	160
S18JUNE12-10	Summer 2012	Molasses	~ 2	*Leucothoe* “sp. B”	6	160
S18JUNE12-10	Summer 2012	Molasses	~ 2	*Bemlos* sp.	2	160
S15SEP12-01	Fall 2012	Molasses	≤1	*Leucothoe* “sp. F”	1	60
S15SEP12-01	Fall 2012	Molasses	≤1	*Leucothoe* “sp. B”	39	60
S15SEP12-01	Fall 2012	Molasses	≤1	*Leucothoe barana*	1	60
S15SEP12-02	Fall 2012	Molasses	≤1	*Leucothoe* “sp. F”	2	120
S15SEP12-02	Fall 2012	Molasses	≤1	*Leucothoe* “sp. B”	3	120

Table 2. Continued.

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S15SEP12-03	Fall 2012	Molasses	≤1	*Leucothoe* “sp. F”	5	560
S15SEP12-03	Fall 2012	Molasses	≤1	*Leucothoe* “sp. B”	42	560
S15SEP12-04	Fall 2012	Molasses	≤1	*Leucothoe* “sp. F”	2	100
S15SEP12-04	Fall 2012	Molasses	≤1	*Leucothoe barana*	1	100
S15SEP12-05	Fall 2012	Molasses	≤1	*Leucothoe* “sp. F”	1	120
S15SEP12-06	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. F”	6	100
S15SEP12-06	Fall 2012	Molasses	~ 2	*Bemlos* sp.	2	100
S15SEP12-07	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. F”	22	120
S15SEP12-08	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. F”	10	130
S15SEP12-08	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. B”	1	130
S15SEP12-09	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. F”	5	60
S15SEP12-10	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. F”	14	140
S15SEP12-10	Fall 2012	Molasses	~ 2	*Leucothoe* “sp. B”	4	140
S17DEC11-01	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	15	60
S17DEC11-02	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	3	40
S17DEC11-03	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	7	40
S17DEC11-04	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	24	200
S17DEC11-05	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	26	140
S17DEC11-05	Winter 2011	Molasses	≤1	*Leucothoe* “sp. B”	2	140
S17DEC11-06	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	16	40
S17DEC11-07	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	8	240
S17DEC11-08	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	18	140
S17DEC11-09	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	15	120
S17DEC11-10	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	19	180

Table 2. Continued

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S17DEC11-10	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	19	180
S17DEC11-10	Winter 2011	Molasses	≤1	*Leucothoe* “sp. B”	2	180
S17DEC11-11 (16)	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	33	240
S17DEC11-11 (16)	Winter 2011	Molasses	≤1	*Leucothoe* “sp. B”	1	240
S17DEC11-12 (20)	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	4	100
S17DEC11-13 (17)	Winter 2011	Molasses	≤1	*Leucothoe* “sp. F”	5	40

Newfound Harbor Channel

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S14APR12-01	Spring 2012	Bird Island	≤1	*Leucothoe* “sp. F”	24	160
S14APR12-03	Spring 2012	Bird Island	≤1	*Leucothoe* “sp. F”	17	60
S14APR12-03	Spring 2012	Bird Island	≤1	*Leucothoe barana*	1	60
S14APR12-03	Spring 2012	Bird Island	≤1	*Bemlos* sp.	1	60
S14APR12-05	Spring 2012	Bird Island	≤1	*Leucothoe* “sp. F”	16	80
S14APR12-08	Spring 2012	Bird Island	≤1	*Leucothoe* “sp. F”	23	40
S14APR12-08	Spring 2012	Bird Island	≤1	*Bemlos* sp.	2	40
S14APR12-09	Spring 2012	Bird Island	≤1	*Leucothoe* “sp. F”	21	140
S14APR12-09	Spring 2012	Bird Island	≤1	*Leucothoe barana*	1	140
S14APR12-09	Spring 2012	Bird Island	≤1	*Bemlos* sp.	1	140
S14APR12-02	Spring 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	30	260
S14APR12-04	Spring 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	25	100
S14APR12-04	Spring 2012	Munson Island	~ 2	*Ceradocus* sp.	2	100
S14APR12-04	Spring 2012	Munson Island	~ 2	*Bemlos* sp.	23	100
S14APR12-06	Spring 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	64	140
S14APR12-07	Spring 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	29	140

Table 2. Continued.

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S14APR12-07	Spring 2012	Munson Island	~ 2	*Bemlos* sp.	3	140
S14APR12-10	Spring 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	18	60
S14APR12-10	Spring 2012	Munson Island	~ 2	*Bemlos* sp.	4	60
S14APR12-10	Spring 2012	Munson Island	~ 2	*Erichthonius* sp.	1	60
S17JUNE12-01	Summer 2012	Bird Island	≤1	*Leucothoe* “sp. F”	13	160
S17JUNE12-02	Summer 2012	Bird Island	≤1	*Leucothoe* “sp. F”	3	60
S17JUNE12-03	Summer 2012	Bird Island	≤1	*Leucothoe* “sp. F”	15	300
S17JUNE12-04	Summer 2012	Bird Island	≤1	*Leucothoe* “sp. F”	5	80
S17JUNE12-10	Summer 2012	Bird Island	≤1	*Leucothoe* “sp. F”	6	120
S15SEP12-01	Fall 2012	Bird Island	≤1	*Leucothoe* “sp. F”	1	100
S15SEP12-02	Fall 2012	Bird Island	≤1	*Leucothoe* “sp. F”	1	120
S15SEP12-03	Fall 2012	Bird Island	≤1	*Leucothoe* “sp. F”	4	280
S15SEP12-03	Fall 2012	Bird Island	≤1	*Colomastix* sp.	2	280
S15SEP12-04	Fall 2012	Bird Island	≤1	*Leucothoe* “sp. F”	6	180
S15SEP12-04	Fall 2012	Bird Island	≤1	*Colomastix* sp.	2	180
S15SEP12-04	Fall 2012	Bird Island	≤1	*Bemlos* sp.	2	180
S15SEP12-05	Fall 2012	Bird Island	≤1	*Leucothoe* “sp. F”	1	120
S15SEP12-05	Fall 2012	Bird Island	≤1	*Colomastix* sp.	1	120
S15SEP12-05	Fall 2012	Bird Island	≤1	*Bemlos* sp.	1	120
S15SEP12-01	Fall 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	18	100
S15SEP12-01	Fall 2012	Munson Island	~ 2	*Bemlos* sp.	2	100
S15SEP12-02	Fall 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	6	260
S15SEP12-02	Fall 2012	Munson Island	~ 2	*Leucothoe barana*	1	260
S15SEP12-03	Fall 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	14	40

Table 2. Continued.

Sample	Season	Location	Depth (m)	Amphipoda spp.	Abundance (N)	Host Volume (ml)
S15SEP12-04	Fall 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	13	80
S15SEP12-04	Fall 2012	Munson Island	~ 2	*Leucothoe barana*	2	80
S15SEP12-05	Fall 2012	Munson Island	~ 2	*Leucothoe* “sp. F”	0	120
S18DEC11-01	Winter 2011	Bird Island	≤1	*Leucothoe* “sp. F”	2	280
S18DEC11-01	Winter 2011	Bird Island	≤1	*Leucothoe barana*	2	280
S18DEC11-04	Winter 2011	Bird Island	≤1	*Leucothoe* “sp. F”	3	40
S18DEC11-04	Winter 2011	Bird Island	≤1	*Leucothoe* “sp. B”	44	40
S18DEC11-06	Winter 2011	Bird Island	≤1	*Leucothoe* “sp. F”	4	20
S18DEC11-07	Winter 2011	Bird Island	≤1	*Leucothoe* “sp. F”	4	40
S18DEC11-10	Winter 2011	Bird Island	≤1	*Leucothoe* “sp. F”	2	60
S18DEC11-02	Winter 2011	Munson Island	~ 2	*Leucothoe* “sp. F”	2	140
S18DEC11-02	Winter 2011	Munson Island	~ 2	*Leucothoe* “sp. B”	1	140
S18DEC11-03	Winter 2011	Munson Island	~ 2	*Leucothoe* “sp. F”	5	80
S18DEC11-05	Winter 2011	Munson Island	~ 2	*Leucothoe* “sp. F”	4	140
S18DEC11-08	Winter 2011	Munson Island	~ 2	*Leucothoe* “sp. F”	8	240
S18DEC11-09	Winter 2011	Munson Island	~ 2	*Leucothoe* “sp. F”	21	80

Table 3. Diagnostic Characteristics of *Leucothoe* "sp. B" (LeCroy, 2011)

Structure	Diagnostic characters
1. Ocular lobe:	“Rounded, midventral keel; anterior margin sinuous, with small central bulb; anteroventral angle angled, extending forward subequally with anterodorsal angle."
2. Mandible:	“Incisor process strongly dentate; spines in raker row long; left lacinia mobilis unreduced, fan-shaped; apical margin dentate or serrate; palp article 2 with 10-15 long marginal setae; article 3 slender, not tapering distally, approximately one-half length of article 2, with 2 apical setae; shortest apical setae at least one-half length of longest.”
3. Coxae:	“1-4, ventral margins entire; coxa 1 without long, anteroventral submarginal seta on medial surface; anteroventral angle produced; coxa 2 subquadrate; coxa 4 excavate posteriorly, ventral margin strongly convex, anteroventral angle rounded, entire."
4. Gnathopod 1:	“Basis, posterior margin without proximal or central row of short setae, that of female without distal cluster of long setae; carpal lobe slender, without long seta on distomedial surface, posterior margin not lined with long setae; propodus, posterior margin minutely serrate, dactyl long, tip extending well past tip of carpal lobe.”
5. Gnathopod 2:	“Basis, anterior margin with separate cluster of 2-4 close-set setae distally; that of male entire, not lined with sharp tubercles proximally, sparsely lined with moderately long and short setae, not expanded distally; that of female sparsely lined with long and short setae; carpal lobe broadly expanded, rounded distally, distal and lateral margins crenulate; propodus without long, blade-like anterodistal process overhanging insertion of dactyl, primary mediofacial setal row diverging slightly from anterior margin, secondary mediofacial setal row present, well-developed; palm convex, oblique, that of male longer than hind margin, with 2-7 small processes in distal half, processes separated by moderately broad u-shaped gaps, that of female continuous with hind margin entire, weakly crenulate distally; dactyl slender, strongly curved, without apical nail, posterior margin entire, without fine setules."
6. Peraeopod 7:	"Basis narrowing distally, posterior margin strongly convex."
7. Epimeron 1:	“With cluster of setae on anteroventral margin."
8. Epimeron 3:	"Posteroventral angle subquadrate."
9. Uropod 3:	“Peduncle slightly longer than inner ramus, inner ramus slightly longer than outer."

Table 4. Total abundance of *Leucothoe* "sp. F" male and female relative to depth and location.

	Female Total Abundance (N)			Male Total Abundance (N)		
Depth (mm)	**Adult**	**Intermediate**	**Juvenile**	**Adult**	**Intermediate**	**Juvenile**
Shallow ≤ 1	307	13	45	182	29	92
Deep ~ 2	601	52	123	339	74	173
Location						
Channel No. 5	306	39	82	177	33	103
Moser Channel	404	17	55	238	50	98
Newfound Harbor Channel	198	9	31	106	20	64
Total Abundance (N)	908	65	168	521	103	265

Table. 5: Frequencies of *Leucothoe* "sp. F" characteristics 1-3 by female and male life history stages relative to season, depth, and location.

		Female				**Male**	
Season	**Juvenile**	**Intermediate**	**Adult**	**Season**	**Juvenile**	**Intermediate**	**Adult**
Spring	0.17	0.07	0.77	Spring	0.31	0.1	0.6
Summer	0.17	0.05	0.78	Summer	0.3	0.14	0.56
Fall	0.13	0.09	0.79	Fall	0.35	0.15	0.5
Winter	0.06	0	0.94	Winter	0.17	0.08	0.75
Depth	**Juvenile**	**Intermediate**	**Adult**	**Depth**	**Juvenile**	**Intermediate**	**Adult**
Deep (~2 m)	0.16	0.07	0.77	Deep	0.3	0.13	0.58
Shallow (≤1 m)	0.12	0.04	0.84	Shallow	0.3	0.1	0.6
Location	**Juvenile**	**Intermediate**	**Adult**	**Location**	**Juvenile**	**Intermediate**	**Adult**
Moser Channel	0.12	0.04	0.85	Moser Channel	0.25	0.13	0.62
Channel No. 5	0.19	0.09	0.72	Channel No. 5	0.33	0.11	0.57
Newfound Harbor Channel	0.13	0.04	0.83	Newfound Harbor Channel	0.34	0.11	0.56

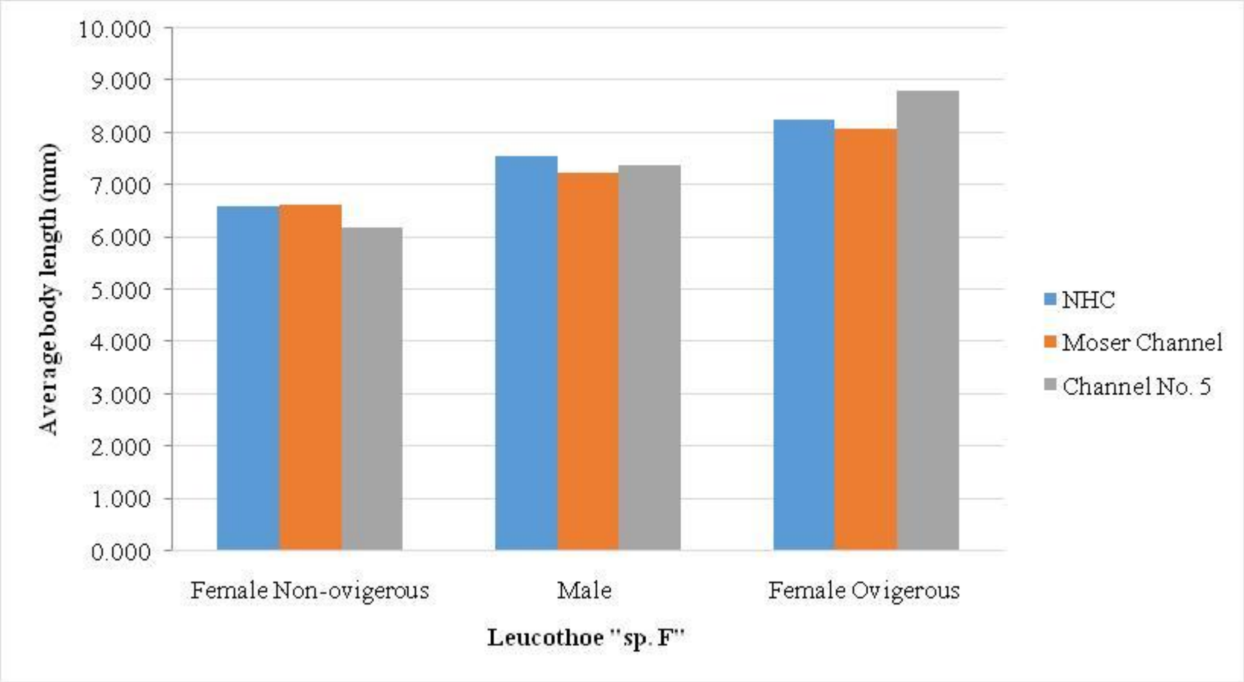

Fig. 1: Average body length (mm) of *Leucothoe* "sp. F" by sex, reported for each sampling location.

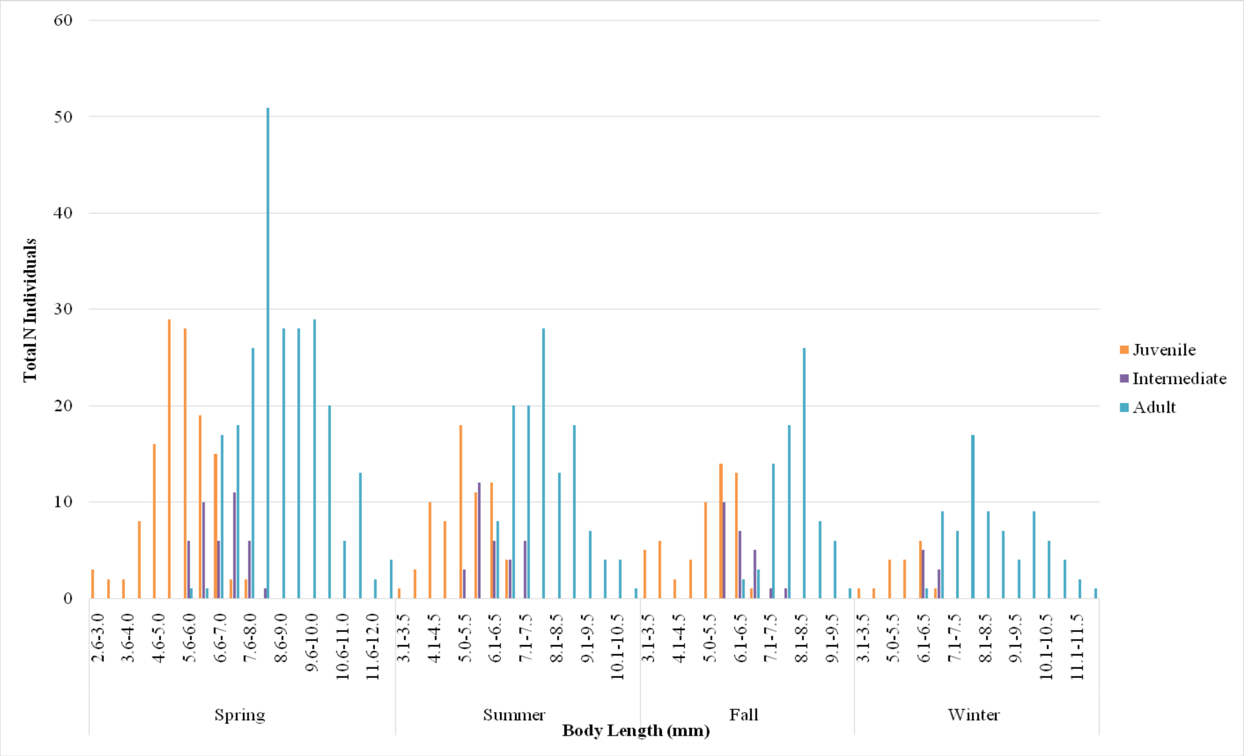

Fig. 2: Male body length (mm) distribution by season relative to *Leucothoe* "sp. F" developmental stages: juvenile, intermediate, and adult.

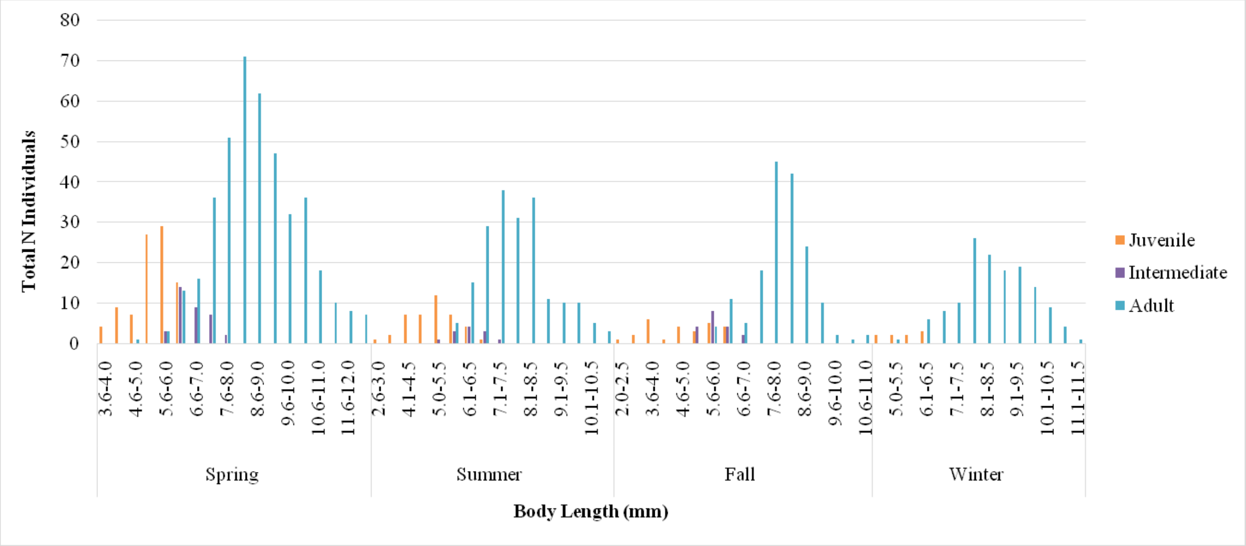

Fig. 3. Non-ovigerous and ovigerous female body length (mm) distribution by season relative to *Leucothoe* “sp. F” characteristic 3.

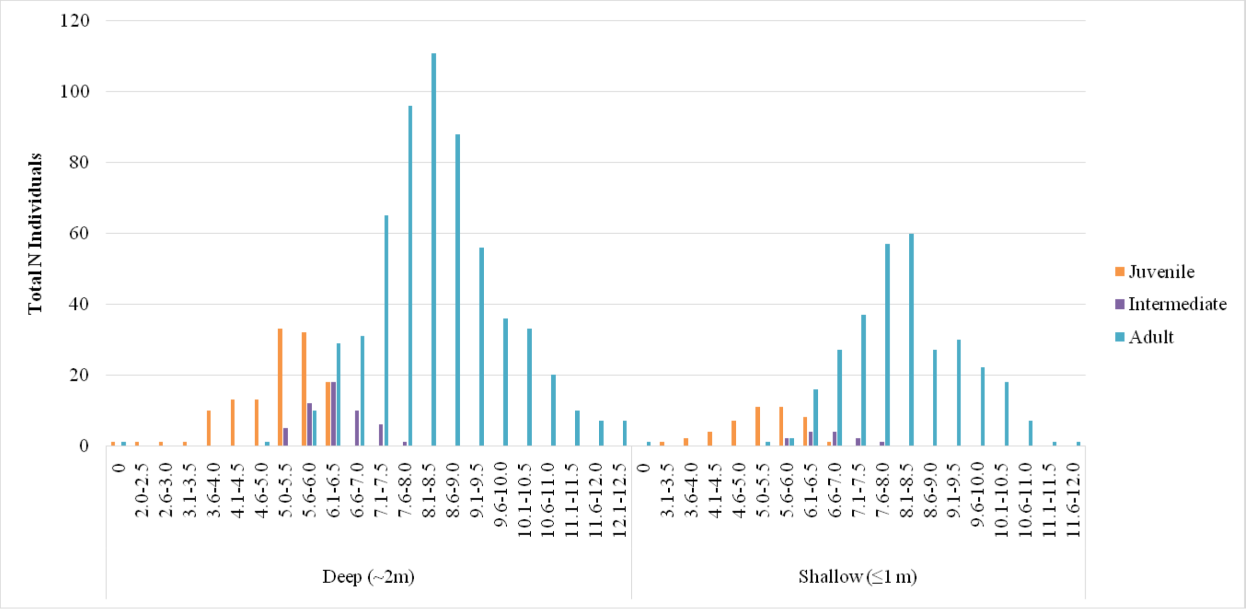

Fig.4: Non-ovigerous and ovigerous female body length (mm) distribution by depth relative to *Leucothoe* “sp. F” characteristic 3.

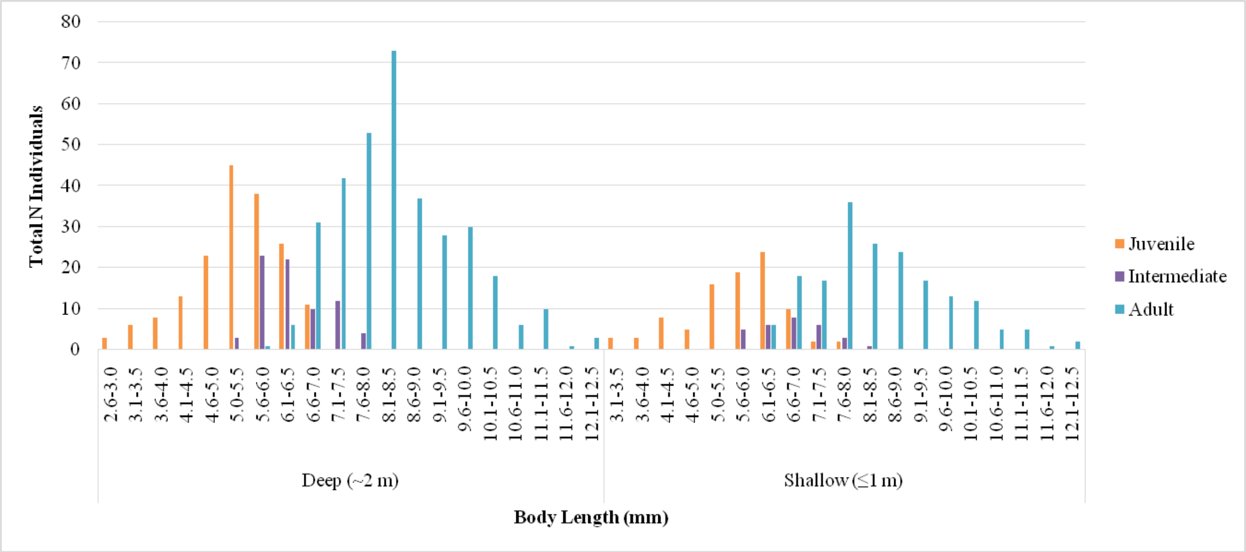

Fig.5. Male body length (mm) distribution by depth relative to *Leucothoe* “sp. F” developmental stages: juvenile, intermediate, and adult