Spring 1989

The dynamics of a nudibranch-hydroid predator-prey association: Cuthona nana and Hydractinia echinata

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University of New Hampshire, 1989

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THE DYNAMICS OF A NUDIBRANCH-HYDROID PREDATOR-PREY ASSOCIATION: CUTHONA NANA AND HYDRACTINIA ECHINATA

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DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

i n

Zoology

May, 1989

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1 May 1989
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ABSTRACT

THE DYNAMICS OF A NUDIBRANCH-HYDROID PREDATOR-PREY ASSOCIATION: CUTHONA NANA AND HYDRACTINIA ECHINATA

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NADINE C. FOLINO

University of New Hampshire, May, 1989

The purpose of this study was to document the biological interactions in a predator-prey relationship involving a nudibranch and hydroid, respectively. The predator is a hermaphroditic opisthobranch mollusc with direct development, Cuthona nana. Cuthona nana feeds specifically on the colonial hydroid Hydractinia echinata which occurs on hermit crab shells in a calm habitat in Gosport Harbor at the Isles of Shoals, Maine and on pilings near Gerrish Island, New Hampshire, an area of strong tidal current.

Population patterns of predator and prey were documented by collecting hermit crabs with hydroid-covered shells at Gosport Harbor and by taking photographs at Gerrish Island. Results indicate a subannual life cycle for C. nana with juveniles and egg masses present throughout the year. Preliminary observations on the occurrence of H. echinata suggest similar abundance patterns observed in populations off the coast of Maine (Yund and Parker, 1989). Hydractinia echinata colonies reproduce in the spring and are more abundant in late summer and early fall.

Growth rates for nudibranchs and hydroids were determined in the laboratory. Nudibranchs from Gerrish Island reached a maximum size of 15 mm, compared to 25 mm for animals at Gosport Harbor, perhaps suggesting an

environmental effect. Hydroids differed in growth when cultured in tanks of varying water flow. Nudibranch grazing rates for animals 3-25 mm in length were quantified for a 24 hour period. Larger nudibranchs consumed more tissue and fed on polyps, whereas smaller individuals ate less and fed on mat tissue. Grazing intensity in the field was determined by estimating the area of grazed patches on colonies on hermit crab shells. The average patch size was 5.75% of the total colony area. Spines on colonies deterred complete removal of tissue; colonies from the field had portions of polyps remaining in grazed patches.

Field and laboratory observations indicate that adult nudibranchs leave hydroid colonies to lay egg masses. A laboratory experiment using crabs with hydroid-covered shells tested these field observations. Nudibranch movement was recorded as the average number of movements per day. Adults moved on and off of colonies while juveniles did not leave the colonies on which they were orignially placed. At Gosport Harbor the crab seems to play a part in bringing food to newly hatched juvenile or adult nudibranchs on the bottom. Several crabs with hydroid colonies on their shells were caught in pit fall traps indicating the likelihood of food passing by a predator on the bottom in a 24 hour period.

The maintenance of this species-specific association can be explained by partial predation of the colonies. Spines prevent complete removal of tissue. Hydroid colonies are capable of regeneration and can withstand cropping by nudibranchs. At Gosport Harbor, hermit crab movement may be positive for both the nudibranch and hydroid. The hydroid obtains food from the sandy bottom as the crab moves about and is also moved away from predators. Nudibranchs can be dispersed by crab movement and also obtain food if a crab has a hydroid colony on its shell.

ACKNOWLEDGMENTS

I thank my thesis advisor, Larry G. Harris for his guidance and continued support and friendship throughout my graduate studies. I thank my committee members: Arthur C. Borror, Leo W. Buss, John J. Gilbert, and James T. Taylor for their helpful comments and crticisms. I am especially grateful to Leo Buss and John Gilbert for their time and suggestions. Special thanks to Leo Buss who was helpful in the development of my dissertation topic and taught me how to culture hydroids necessary for this research.

My work would not have been possible without the help of several divers:Larry Harris, Karen Verney, Liz Kintzing, Paul Martin, Steve Truchon, Mike Herman, and Paul Lavoie. Special thanks go to Captain Paul Pelliter for operating the R.V. Jere A. Chase, diving, discussing scientific ideas and being a supportive friend. I am most grateful to Walt Lambert who was always there to support me as a friend, diver and fellow graduate student. I am thankful to all the graduate students in the zoology department who encouraged me throughout the years, especially Connie Issacs, Nick Conrad, Liz McClean and Marietta Weiss.

Several friends from Durham Evangelical Church were a continued support: Dr. Wilbur Bullock, Mary Moore, Sue Spinney, Kate and Peter Andersen and others. Special thanks go to Tammy Spinney, Mary Jane Gibson and Carol Rowe; I couldn't have kept plugging without their encouragement and love. I am also very thankful to my family for their patience and support over the years. Mom and Dad, Aunt Robbie, Greg, Bob, Sandy and Robbie all continued to believe in what I was doing.

Thanks go to folks in Erie, PA at Fellowship Baptist Church and at Behrend College. They provided encouragement during the most difficult and final stages of completing the thesis while I was teaching fulltime. Special thanks go to Mike Gross, my co-worker and supportive friend at Behrend College.

This work was supported by two University of New Hampshire research grants and three summer fellowship awards, also from the University of New Hampshire.

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COMMON INTRODUCTION

Ecological processes of marine communities are determined by physical (Sousa, 1984; Connell and Keough, 1985) and biological (Connell, 1975; Dayton, 1984; Sebens, 1985) factors. In his discussion of New England subtidal communities, Sebens (1985) states that aspects of physical conditions are seasonal and that biotic communities "mirror" this seasonality; many sessile epibenthic encrusting organisms persist during the warmer months and disappear later in the colder months. Predation is also known to affect species diversity in intertidal and subtidal communities (intertidal: Connell, 1961; Dayton, 1971; Menge, 1976; Menge and Sutherland, 1976; Paine and Vadas, 1969; Underwood and Denley, 1984; subtidal: Karlson, 1978, 1981; Ayling, 1981; Sousa et al., 1981; Duggins, 1983; Keller, 1983; Sih et al., 1985; Witman, 1985; Hughes et al., 1987; Lewis et al., 1987). Many encrusting, colonial organisms in these communities, especially Cnidaria, are preyed upon by nudibranchs (Thompson and Brown, 1984).

Nudibranch predators are often specialists on a given prey type and form species-specific predator-prey associations (Harris, 1973; Todd, 1981,1983). Almost all nudibranchs in the order Aeolidacea feed upon Cnidaria and sometimes prey specifically on one species. Often in northern temperate waters aeolid nudibranchs increase in number when colonial Cnidaria increase during the spring and summer months. During the fall and winter months, the majority of hydroids die back at least partly due to nudibranch predation (review, Todd, 1983). Furthermore, fluctuations in nudibranch populations are explained in part by the prey being short-lived, as well as

being overgrazed by nudibranchs (Harris and Irons, 1982).

Unlike most colonial hydroids in New England temperate waters, colonies of the hydroid Hydractinia echinata (Fleming, 1928) live throughout the year and persist for several years (Harris et al., 1975; Karlson, 1978, 1981; Rivest, 1978; Folino, 1985). Off the coast of New Hampshire and Maine colonies of H. echinata are preyed upon by pycnogonids (Phoxichilidium femoratum) and several nudibranchs (Harris et al., 1975; Rivest, 1978; pers. observ.). One aeolid nudibranch in particular, Cuthona nana (Alder and Hancock, 1842) feeds specifically on the hydroid Hydractinia echinata. The purpose of this study is to examine ecological aspects of the predator-prey association between the nudibranch Cuthona nana (Order Nudibranchia, Suborder Aeolidacea) and the colonial hydroid Hydractinia echinata (Order Hydroidea, suborder Anthomedusae).

Hydractinia echinata is a marine, gymnoblastic hydroid (Class Hydrozoa) primarily found encrusting the shells of hermit crabs (Hyman, 1940; Schijfsma, 1939), though it also grows on floats, pilings and rocks (Sutherland, 1974; Harris et al., 1975; Karlson, 1978; Folino, 1985). Colonies consist of basal mat tissue, stolons extending out from the mat and upright polyps on both the mat and stolons. Growth occurs by peripheral extension of the basal tissue, proliferation of the number of polyps and by elongation of stolons. As the number of stolons extending out from the mat increases, they fuse to form more mat tissue. Colonies are polymorphoric, consisting of polyps specialized for feeding (gastrozooids), defense (spiralzooids and tentaculozooids) and reproduction (gonozooids) (Hyman, 1940; Burnett et al., 1967). Reproduction is both asexual and sexual with colonies being dioecious. Spawning occurs at dawn (Ballard, 1942; Bunting, 1894). Larvae selectively attach to the corners of the shell aperture at the apex (Yund et al., 1987; pers.

observ.) by discharging nematocysts (Chia and Bickell, 1978; Weiss et al., 1985). Once attached, a primary polyp initiates colony formation by asexual reproduction to cover the hermit crab shells (Schijfsma, 1939; Hyman, 1940) (Fig.1).

Previous studies reveal the existence of distinct strains or clones of Hydractinia echinata which differ in morphology and growth rates (Schijfsma, 1939; Hausenchild, 1954; Ivker, 1972; McFadden et al., 1984). When two genetically different (allogeneic) colonies come in contact, one colony will eventually overgrow the other. One or both of the colonies, depending on the morphological type, will develop hyperplastic stolons which contain nematocysts used to harm and overgrow the non-clonemate (Buss et al., 1984). If two isogeneic colonies are grown side by side, they will fuse to form a larger colony (Toth, 1967; Ivker, 1972; Buss et al., 1984; McFadden et al., 1984; Folino, 1985). Colonies of H. echinata have been classified according to growth form (matty, viney and intermediate) with viney morphs being the superior competitors (Buss et al., 1984; McFadden et al., 1984; McFadden, 1986; pers. observ.). The occurrence of competing clones on hermit crab shells is seasonal (Buss and Yund, 1988; Yund and Parker, 1989), while large colonies on pilings such as at the cribs at Gerrish Island, New Hampshire seem to be continuously interacting throughout the year (pers. observ.).

The nudibranch Cuthona nana occurs on colonies of Hydractinia echinata on hermit crab shells in Gosport Harbor at the Isles of Shoals, Maine (Harris et al., 1975; Rivest, 1978; Folino, 1985) and on pilings near Gerrish Island, New Hampshire (Harris et al., 1975; pers. observ.). Predation by C. nana involves removal of polyps, mat and stolon tissue. Smaller individuals feed on the mat and stolon tissue and portions of polyps until they are large enough to graze entire polyps (Rivest, 1978; Folino, 1985). Parts of the hydroid colonies

are capable of regeneration, allowing the colony to survive attacks by predators. Cuthona nana is a specialist on H. echinata, appears to be immune to the nematocysts, and can graze over the entire colony. Other nudibranch species are killed, presumably by nematocysts, if placed in the middle of a colony (Harris et al., 1975; pers. observ.).

Cuthona nana is hermaphroditic and has direct development (Rivest, 1978) (Fig.1). Hydractinia echinata gastrozooids pick up C. nana postlarvae that begin feeding on the colony (Rivest, 1978; pers. observ.). Currently, the only ecological information on C. nana consists of its occurrence with its prey H. echinata and its mode of development (Harris et al., 1975; Rivest, 1978). Research on its prey, Hydractinia echinata focuses on the growth and interaction among clones (Blackstone and Yund, in press; Buss et al., 1984; Buss and Yund, 1988; McFadden et al., 1984; Yund et al., 1987).

Several questions dealing with the association between Cuthona nana and Hydractinia echinata are unresolved, hence the goal of this research was to examine aspects of the life histories of Cuthona nana and Hydractinia echinata to better understand the dynamics of this nudibranch-hydroid predator-prey association. The following are specific objectives:

1)to document temporal and spatial patterns of populations of Cuthona nana and Hydractinia echinata at two sites off the coast of New England, Gerrish Island and Gosport Harbor (Chapter 1);

2)to document and compare aspects of the biology of Cuthona nana and Hydractinia echinata, such as hydroid growth rates and nudibranch growth and grazing rates from field and laboratory observations and experiments (Chapter 2);

3)to determine the role of hermit crab movement in maintaining the association between Cuthona nana and Hydractinia echinata at Gosport Harbor (Chapter 3).

CHAPTER I

POPULATION PATTERNS OF CUTHONA NANA AND HYDRACTINIA ECHINATA

INTRODUCTION

Ecologists approach the study of communities by examining various aspects of several species or specific populations of a given species (Pielou, 1974; Lomnicki, 1988). Studies of individual populations provide information about how the structures of these populations are affected by physical and biological factors. By knowing what factors regulate a population, one can understand the role of a population in the dynamics of a given community (Levinton, 1982). This chapter deals with describing general seasonal and spatial occurrences of the predator Cuthona nana and its prey Hydractinia echinata.

Few studies exist describing specific nudibranch population patterns and distributions in relationship to prey abundances (Potts, 1970; Harris , 1973; Todd, 1979; 1981). Most studies present seasonal fluctuations of populations with suggested physical or biological factors controlling these fluctuations (reviews: Harris, 1973; Todd, 1981,1983). Todd (1979) suggests that temperature and dessication control the low shore populations of the dorid nudibranch Onchidoris bilamellata off the coast of England. In this same study, Todd (1979) suggests that mid shore populations are controlled by intraspecific competition. Harris (1973, 1986) presents temperature and fish predation as factors controlling populations of the aeolid Aeolidia papillosa off the coast of New Hampshire. Both studies by Todd (1979) and Harris (1973, 1986) include

non-hydroid feeding nudibranchs and perhaps deal with prey items that are not as seasonal as hydroids. Aeolid nudibranchs are often abundant in fouling communities on colonial organisms such as hydroids (Nybakken, 1978). Often in fouling communities dominated by hydroids, nudibranchs are in close association with their prey and overgraze the colonies (Todd, 1981, 1983). The hydroids are overwhelmed by assemblages of several nudibranch species leading to a rapid elimination of colonies, and the eventual disappearance of the several nudibranchs present (Miller, 1961; Thompson, 1964; Fager, 1971; Clark, 1975; MacLeod and Valiela, 1975; Harris and Irons, 1982; Harris, 1987).

These fluctuations in nudibranch populations are classified in part by nudibranch life cycles. Thompson (1964) established two life cycle classifications for nudibranchs from observed population patterns. The first category consists of nudibranchs having a short life cycle with several generations produced in a short period of time and which grow to reach sexual maturity quickly. These animals are called subannual species (Todd, 1981). Subannual species generally feed on ephemeral types of prey such as hydroids and bryozoa. The other category consists of nudibranchs which feed on more stable prey organisms and have a yearly cycle with a discrete spawning period; these animals are called annual species (Todd, 1981). Unlike most hydroids grazed by aeolids, Hydractinia echinata is a persistent and stable food source available to Cuthona nana throughout the year. Therefore one may speculate that some other factor(s) besides food availability explain the subannual population patterns of C. nana (Rivest, 1978; Folino, 1985).

By determining the life histories of predator and prey, one can speculate how a predator and prey association is maintained. One area lacking in the literature of nudibranch ecology is the study of "single-species population" dynamics (Todd, 1981). The first step to understanding how

Cuthona nana impacts Hydractinia echinata or vice versa is to understand the seasonal dynamics of both populations.

It is with this background in nudibranch population studies that I analyzed two localized populations of Cuthona nana off the coast of New Hampshire. Rivest (1978) provided one year and Folino (1985) 1 1/2 years of information on the population ecology of C. nana, laying a foundation for this study. The focus of this chapter is to describe: 1)the population structure of Cuthona nana by documenting nudibranch densities, size frequencies and distributions from May 1986 to May 1988 at Gosport Harbor and Gerrish Island; and 2)the occurrence of Hydractinia echinata at Gerrish Island and Gosport Harbor.

METHODS

Site Descriptions and Sampling Methods

This study of Cuthona nana and Hydractinia echinata was conducted at two sites off the coast of New Hampshire and Maine: Gerrish Island and Gosport Harbor. Much of the work focuses on the association at Gosport Harbor, due to the feasibility of working in a calmer habitat and to more background work being available (Harris et al., 1975; Rivest, 1978; Folino, 1985).

Gerrish Island

One of the two known locations of Cuthona nana and Hydractinia echinata is at a series of old cribs near Gerrish Island, New Hampshire (43° 04' N; 70° 42' W) (Fig. 2). The habitat is one of strong tidal currents with colonies of Hydractinia echinata growing on non-mobile substrata such as snail and mussel shells, rocks and the wooden beams of the cribs. Both the hydroid H. echinata and the nudibranch C. nana were collected from the second crib from Wood Island. The first crib from Gerrish Island also has colonies of H. echinata with C. nana, while the remaining cribs northeast of the second crib lack colonies and nudibranchs. This may be due to the current being the strongest at the first and second cribs closest to Wood Island. Information on the ecology of C. nana and H. echinata was collected sporadically at this site from November 1986 through May 1988. Observations and collections were made using SCUBA in 3 to 7 m of water. The crib is 5.0 by 4.5 meters in size with square beams 0.3 meters on each side and 5.0 meters long (Fig.2). Colonies grow on the lower 3-4 beams. To sketch their shape, the colonies were measured by using a tape measure. Colony surface area was roughly estimated

from the sketches. Nudibranchs were aggregated on colonies covering the two corners of the crib facing the Gulf of Maine and on rocks covered with colonies adjacent to the corners. Nudibranchs were suctioned off the colonies using a squirt bottle to prevent loosing them in the strong current. By using this method, sampling was biased towards collecting larger animals. Observations on egg laying behavior and size frequencies of nudibranchs were recorded by using a Nikonos IV with either a 3:1 or 2:1 framer or a magnifying glass and ruler underwater. Nudibranch densities per area of prey at Gerrish Island were not quantified due to the difficulty of sampling in an area of such strong current. The months sampled were: November, 1986, March, 1987, September through December 1987 and January through May 1988. Length frequency histograms were constructed for nudibranchs measured for each sample month.

Gosport Harbor

Gosport Harbor is located in Haley Cove at the Isles of Shoals, Maine approximately 6 miles from the coast of New Hampshire (42° 59' N; 70° 36' W) (Fig. 3). Hydractinia echinata encrusts the shells of the hermit crab Pagurus acadianus, and less frequently, the shells of P. arcuatus. Large populations of hermit crabs occur at a depth of 5-10 m providing a mobile prey for Cuthona nana instead of a stationary prey as exists on the crib at Gerrish Island. Portions of the bottom of Gosport Harbor are covered with cobble and dead mussel shells; the majority of crabs are found on the sandy portions. Two types of sampling were conducted: 1) grab samples of 37 to 160 crabs which entailed collecting any hermit crab within reach and 2) random collections of 21 to 90 crabs within reach, with shells covered approximately 100% with H. echinata. This latter type of collection insured obtaining nudibranchs to determine the seasonal abundances and size frequencies for C. nana. The two

types of sampling will be referred to as grab and covered samples.

The covered shells were placed in individual containers to insure that nudibranchs remained on their original colonies. The containers were either plastic vials or mesh containers (mesh size approximately 164 um) called Toby Tea-boys (ordered from Daniel Peilin Company, Silver Spring , Maryland). Although efforts were made to collect all sizes of shells with H. echinata, larger shells are more visible making the samples biased towards larger shells. Shell sizes were summarized by arbitrarily creating six size categories for the 3 years of sampling. Colonies were examined for nudibranchs using a dissecting microscope under 12X magnification. The number, size and location of nudibranchs, and size of grazed patches were recorded for 23 months sampled from May 1986 to May 1988. Patches consisted of cropped polyps, with nudibranch mucous often present. Length frequency histograms were constructed to examine nudibranch age-class structures by month and were compared for yearly differences using Kolmogrov-Smirnov tests (Sokal and Rohlf, 1981). Histograms for non-reproductive and reproductive individuals for each month were also constructed. In May 1988, ten m^2 quadrats were taken randomly at Gosport Harbor to sample for nudibranchs off of hydroid colonies on hermit crab shells. To describe aspects of hermit crab populations the following parameters were recorded for each hydroid-covered hermit crab: crab species within the shell, shell length X width (measured in mm with a caliper), and shell type.

Grab samples were collected at irregular intervals beginning in June 1985 through December 1987 by putting several hermit crabs into plastic bags or in individual containers for analysis at the laboratory. Included in the grab samples for four months in 1988 were crabs caught in a pitfall experiment described in chapter 3.

The following characteristics of H. echinata were recorded for both grab and covered shells when applicable: the percentage of shells with H. echinata; the percentage of small and large colonies (percentages of small and large colonies of Hydractinia echinata were summarized according to criteria of Yund and Parker (in press):estimates of 20% and 80% cover, respectively); sex of the colony; whether two or more colonies were present, and the location of juvenile colonies. Additional observations of shell epifauna other than H. echinata colonies included the presence of Crepidula plana, the barnacle Semibalanus balanoides, the coralline alga of the genus Clathromorphum, and the serpulid Spirorbis. The information from the grab samples is preliminary data summarized after the fact with no prior sampling procedures designed. Therefore, this information is represented in the Appendix.

Prey abundances at Gosport Harbor were determined by estimating crab densities and recording the percentage of shells with and without colonies. Densities of hermit crabs at Gosport Harbor were determined by cofferdam sampling and band transects. A cofferdam is simply a metal cylinder (.153 m^2) placed on the ocean bottom which prevents hermit crabs from escaping before being counted. Cofferdam samples were taken in May and October 1987 and February through May 1988. Shells were turned over to make sure withdrawn crabs were not overlooked; the same was done for the band transect samples.

Band transects were also used to determine the densities of hermit crabs at Gosport Harbor and were taken from February through May 1988. A 10 meter transect line was randomly placed on the bottom of Gosport Harbor and all hermit crabs within a 1 meter band on one side of the line were counted providing the number of crabs in an area of 10 m^2. Four to five replicate transects were taken for each month. Shells covered with H. echinata but

without a crab, as well as adult C. nana on the sand, were also recorded when observed. Mean numbers of crabs per 10 m^2 were calculated and compared by ANOVA after the original values were log transformed because of heterogenity of variances among sampling dates (Harley's Fmax test, Ott, 1984). Differences among means were determined using the Scheffee test (Zar, 1984).

Crab densities were converted to numbers per m^2 to compare similar months for both sampling techniques. The cofferdam estimates gave greater numbers of crabs per m^2 (Feb. 1988: $30/m^2$) than the band transect estimates (Feb. 1988: $10/m^2$). This may be explained by the patchiness of hermit crabs in the area sampled.

RESULTS

Prey Characteristics

Gerrish Island

Water temperature for each sample month was taken and ranged from 2.5°C in February 1987 to 16°C in July 1987 (Fig. 4 A). Much of the data collected at Gerrish Island are qualititative, but they provide pertinent ecological information on the association between Cuthona nana and Hydractinia echinata. Colonies of H. echinata at Gerrish Island averaged 821.57 cm^2 (N=11, STD=548.59) and often were interacting intraspecifically. Interacting zones were observed throughout the entire sampling period from November 1986 to May 1988. General observations suggest that colonies were grazed more in the fall months by nudibranchs, pycnogonids and sometimes urchins. The colony edges were grazed by nudibranch species other than C. nana, leaving the chitinous base and spines attached to the piling. From photographs during the colder months, the number of predators seemed to decrease and the colonies regenerated by growing back over the chitinous bases (pers. observ.).

Gosport Harbor

Crab Densities. Water temperatures were recorded for each month; temperatures peaked in the summer months between 14.5 and 15.5°C and were as low as 2°C in February and March 1987 (Fig. 4 B). Crab densitites were determined using a cofferdam and band transects. All possible comparisons for mean densities of crabs in the cofferdam samples varied among the months sampled with a significant decrease in crabs from May 1987 to October 1987 ($p<.05$) (Fig. 5 A). The mean densities also varied for samples in 1988 with a

greater number of crabs in May compared to March and April ($p<.05$).

Although the band transect area sampled is greater than that of the cofferdam area, a similar pattern in crab densities is seen. Significant differences exist among the band transect mean number of crabs ($F=7.783;3,15;p<.002$) with May densitites being greater than densities of February and March (Fig. 5 B). April densities are significantly greater than March densities but not significantly lower than those of May. Therefore, there is a general increase in the number of crabs per 10 m^2 from February to May 1988. As mentioned, these results parallel the densities obtained from the cofferdam samples except for the increase in cofferdam densitites for February 1988 suggesting that both techniques provide similar estimates in crab densities.

Shells with H. echinata but without crabs were also recorded in the band transects and cofferdam samples (Appendix, Table 1). Overall, few of these shells were present during both types of sampling. The highest mean number of shells from cofferdam samples in March 1988 was $0.20 \pm .408$ shells/$.153m^2$(STD,N=25) while band transects in May 1988 had 4.0 ± 2.72 shells/$.153\ m^2$ (STD,N=5).

Percentage of Shells with Hydractinia echinata. Estimates of prey availability are provided from the grab samples of hermit crabs from August through December 1985 and November 1987 through May 1988. A declining trend in the percentage of shells with H. echinata is seen from August to December 1985 (Fig. 6). Lower percentages of shells with H. echinata exist in the colder months. Hydractinia echinata seems to be more abundant in the summer and fall, though these data are insufficient to speculate on seasonal trends. Nevertheless, the percentage of shells with colonies was no lower than 20%, which occurred in March 1988.

Percentage of Shells with Small and Large Colonies. The grab-sampled shells were used to summarize the occurrences of small (<20% coverage) and large (≥80% coverage) colonies. In all months there was a greater percentage of shells with smaller than larger colonies (Fig. 7). There is a decline in the number of larger colonies in 1985 from July to December. The diving time required to find H. echinata-covered shells was greater in the winter months than in the summer throughout the sampling from May 1986 to May 1988 suggesting fewer colonies present, although that could be due to lower crab densities.

Reproductive Colonies and Sex Ratios The percentages of Hydractinia echinata colonies with reproductive structures are presented for the grab samples only. In 1985, the highest percentage of reproductive colonies occurred in July with 66% of the colonies having reproductive structures. The remaining months changed little in percentage (Fig. 8). Thirty-one percent of the colonies were reproductive in November 1987, with fewer having gonozooids in February 1988 (15.5%), and more with gonozooids in May 1988 (41%). The majority of colonies observed on the covered shells were reproductive (approximately >90%) with a few exceptions. December 1986 and January 1988 had 77% of the colonies reproductive and October and November 1987 had approximately 85% reproductive colonies.

Chi-square tests were used to test for differences in sex ratios for colonies of Hydractinia echinata for the grab samples (1985, 1987, 1988) and for the shells completely covered with H. echinata (1986, 1987, 1988). Sexes of colonies did not vary for 1985 and 1988 for the grab samples but did vary for 1987 (X^2=5.26, df1, p<.002, N=23) with more female colonies being present. The sexes for the colonies collected for 1985 and 1988 showed a 1:1 ratio. The same pattern exists for the H. echinata-covered shells. Sex ratios of 1:1 exist for the

1986 and 1988 data while a higher number of female than male colonies were present for 1987 (X^2=7.22, df1, p<.007, N=718).

Interacting Colonies. As previously mentioned, when 1 or more colonies of Hydractinia echinata come in contact, interference competition occurs through the use of hyperplastic stolons. Since these interactions are seen more often on shells with smaller colonies, interactions are more common on shells that are not completely covered with H. echinata. Therefore, information from the grab samples was used to determine the percentages of interactions. Of the grab sample shells (collected from June 1985 to May 1988), no more than 11% (July 1985) of the shells had colonies interacting (Fig. 9). The data are insufficient on a monthly basis to speculate about the seasonal occurrences of interactions.

Species of Crabs. The majority of the grab sample shells were inhabited by Pagurus acadianus and of these, 10 to 63% had colonies of H. echinata (Fig. 10 A,B). The percentages of shells with P. arcuatus were no greater than 10% for all months sampled; the highest percentage observed was in November 1987 with 10% (Fig 10 C). Of the shells with P. arcuatus, only a small percentage had colonies of H. echinata. In March and May 1988, none of the P. arcuatus shells had H. echinata colonies (Fig. 10 D). In the covered shell samples, 18 of the 23 months sampled did not have P. arcuatus inhabiting the shells. Of the 5 months with P. arcuatus inhabiting shells covered with H. echinata, the highest percentage of shells with P. arcuatus was 3.5%.

Shell Types and Sizes. Shells were classified into two groups: 1)Littorina littorea shells and 2) 'other' including Nucella (Thais), Buccinum and Colus spp. The majority of the shells inhabited by hermit crabs in the grab samples were Littorina littorea shells (N=2240) (Fig. 11 A). Similar results are seen with the H. echinata-covered shells for 1986, 87, 88 (N=1375) (Fig. 11 B); 97% of the

shells were L. littorea and the remaining 3% consisted of the 'other' types. At least 95% of the shells collected for both sets of data were Littorina littorea.

The sizes of the shells inhabited by hermit crabs included only the H. echinata-covered shells which had nudibranchs on the colonies (Fig 12). Each histogram for the 3 years is normally distributed, with the greatest number of shells in the 401-600 m^2 size class, and do not differ in distributions from year to year (all comparisons, Kolmogrov-Smirnov, $p<.20$). The greatest percentage of shells for each year, approximaltey 89%, fell into the 201-800 m^2 range.

Shell Epifauna. Epifauna other than Hyractinia echinata on the shells were recorded for both grab-sampled and H. echinata-covered shells. The following four organisms were recorded: the prosobranch Crepidula plana (inside the lip of the shell), the barnacle Semibalanus balanoides, the smooth encrusting coralline alga Clathromorphum sp. and the serpulid Spirorbis.

The percentages of shells with Crepidula plana were never higher than 16% (December 1985) for the 10 months of random samples (Appendix, Table 2). The percentage of covered shells with C. plana varied throughout the 23 month period from May 1986 to May 1988, and was no greater than 6.85% (February 1987). Semibalanus balanoides did not occur on the shells in the grab samples or the H. echinata-covered samples for most of the months. The grab samples had the greatest percentages in May 1988 with approximately 13% of the shells having barnacles. Several newly settled S. balanoides were seen in this month. The percentages of hydroid-covered shells with S. balanoides were highest in both May and July 1986 and May 1988 (Appendix, Table 2). The barnacles observed were either overgrown by H. echinata or occurred in small bare areas on shells that had approximatley 80-90% hydroid coverage.

The grab sample percentages of shells with coralline algae were

calculated by only counting the shells with coralline algae and H. echinata. Percentages of shells with coralline algae and H. echinata in the grab samples were highest in December 1985, 1987, and January and February 1988 while those for hydroid-covered shells were no greater than 6.52% (May 1986) (Appendix, Table 2).

Another epifaunal species observed on the hermit crab shells from Gosport Harbor was the serpulid, Spirorbis sp. Only shells from two months in 1988 were thoroughly examined for Spirorbis: March and May 1988. The percentage of shells with Spirorbis was greater in March (21.9%, N=99) than that of May (16.7%, N=98). Among those shells with Spirorbis, only one shell for each month also had a colony of H. echinata present; all other shells with Spirorbis did not have H. echinata colonies.

Predator Population Patterns

Gerrish Island

The monthly size frequencies for animals from Gerrish Island indicate some seasonal trends for the population. Size frequency histograms for November 1986, March, 1987 September through December 1987, and January through March and May 1988 are presented in the Appendix. Two major points can be made from these monthly size frequency histograms of C. nana. First, by analyzing the monthly histograms for each year sampled, one can see that reproduction occurs throughout each year. Adult nudibranchs are present in November of 1987 with juveniles present in December 1987 through March 1988 (Appendix, Fig. 1). In May of 1988, larger animals are present; this most likely represents growth of smaller animals present in prior months. Secondly, an interesting factor to note is that the maximum size of Cuthona nana at this site is 15mm (September 1987), while individuals at Gosport Harbor

reach 22-23 mm in length (Appendix, Fig. 4, April, 1988).

Gosport Harbor

Monthly size class histograms for C. nana are presented in the Appendix as percent frequencies with sizes ranging from <1 to 23 mm in length. In May 1986 both small and large animals are present while in July, August and September smaller, non-reproductive individuals are more abundant. Larger animals were present in October and December 1986 (Appendix, Fig. 2). Similarly, larger adult C. nana were present in the earlier months of 1987 (February, March and April), with smaller individuals occurring in May (Appendix, Fig. 3). The majority of these smaller individuals present in May (approximately 38%) were 2mm in size. June 1987 samples had more adults present, while July and August showed another increase in the number of smaller nudibranchs. Larger animals were present in September and October 1987, suggesting growth of juveniles present in July and August. Size frequencies for January through May 1988 are similar to those seen in corresponding months of 1987 (Appendix, Fig. 3).

The monthly size class histograms mentioned above are summarized by grouping individuals collected for each month into two size classes: 1) non-reproductive individuals, <1-9 mm, and 2) reproductive individuals, >10 mm. All three years had more non-reproductive than reproductive individuals present each month (Fig. 13). During the warmer months from May through August for 1986 and 1987 and May 1988, I observed several adults crawling on the bottom. Five to six adults greater than 15mm were observed mating and laying eggs on the bottom on rocks in May of 1986 and 1987. A mean number of 2 adults per $10m^2$ on the bottom was observed in May 1988. The presence of non-reproductive C. nana throughout the year suggests continual reproduction, and not just one pulse of reproduction as is true for other

nudibranchs (Todd, 1981). Reproductive adults were present in all months for 1986 except July and November, and were absent in August, November and December 1987 (Fig. 13). All five months sampled in 1988 had adults present. The percentage of adults in the summer months varied for 1986 and 1987 and decreased in late summer and early fall, followed by an increase in October for both years. The variability during the warmer months may be due to an increase in adult mobility on and off of colonies on crabs, as well as adults dying after maximum size and reproductive output are reached.

Gosport Harbor Nudibranch Densities. Monthly collections of crabs with shells covered with H. echinata provided seasonal estimates of the population of C. nana at Gosport Harbor. The percentage of hydroid-covered shells with C. nana fluctuated over the 21 month sampling period. The greater percentages for 1986 were seen in July and August with 55% and 56%, respectively, while 1987 and 1988 showed the greatest percentage of colonies with nudibranchs in April and May (Fig.14). Percentages declined in the fall months in 1986 and 1987 and began to increase in December and November, respectively. An asynchronous relationship seems to exist between the percentage of shells with nudibranchs and temperature for 1987; this pattern is not as clear for 1986 and 1988 since data are only available for portions of each year. These results suggest that temperature is not the only factor controlling the increase in nudibranch numbers. The increases in the spring months suggest the onset of reproduction in juveniles hatched in the winter months which have reached sexual maturity .

The mean number of nudibranchs per colony collected from May 1986 to May 1988 was fairly constant over the 23 month sampling period (Fig.15). There is a slight increase in the late winter months of 1986 into the spring months of 1987. The greatest mean number occurred in May 1987 and most of

those individuals were < 4mm in length (Appendix, Fig. 3).

Seasonal fluctuations occur in the mean sizes of C. nana over the 3 year sampling period (Fig.16). The general trend is an increase in mean size from July to October for both 1986 and 1987. There is a drop in the average length of C. nana during the winter months of 1986; this same pattern is not seen in 1987 with mean sizes fluctuating more. Field observations suggest that animals are generally larger in the fall and winter months but the variations in mean size prevent stating a clear relationship.

Gosport Harbor Nudibranch Distributions. The number of C. nana on covered shells was used to determine the distribution of nudibranchs by month. The frequency distributions for each month were tested against a Poisson distribution to test the hypothesis that nudibranchs are randomly distributed on colonies on hermit crab shells. To determine the degree of aggregation, the coefficients of dispersion (mean/variance ratios) were calculated. Nudibranchs were strongly aggregated for all months sampled from May 1986 to May 1988; tests could not be performed for October, November and December 1986 and 1987 due to too small of a range of frequencies (Table 1). The chi-square values for the months tested were all highly significant, indicating a non-random distribution of nudibranchs on colonies of H. echinata. Coefficients of dispersion greater than one indicate a clumping or aggregation of nudibranchs on colonies. All coefficients were greater than one confirming an aggregated distribution. A large portion of colonies had no nudibranchs and the range of distribution varied by month (Table 2). May 1987 and April 1988 show a greater range of frequencies, with some colonies having as many as 11-19 nudibranchs on one colony. The ranges of frequencies in the winter months (Oct. through Jan.) were smaller, indicating that fewer animals are present during the colder months.

To determine if colony size affected the number of nudibranchs present on a colony, correlation coefficients were calculated to see whether a relationship existed between nudibranch number and colony size for each sampling month. Since some months had a small number of samples with nudibranchs, months were pooled for each year, providing correlations for shell size and nudibranch number for 1986,87 and 88. Hermit crab shell size was estimated by using the product of shell length by shell width. Shell size was determined for the hydroid-covered shells collected monthly from May 1986-May 1988. There were no significant correlations between nudibranch number and shell (colony) size for all three years (1986: N=84,r=-.080; 1987: N=241,r=.068; 1988:N=128,r=.015). Correlation coefficients were also determined for shell size and the number of nudibranchs <5 mm based on the assumption that larger colonies would pick up more juvenile nudibranchs on the ocean bottom. Again, no significant correlations were obtained for all three years (1986:N=60,r=-.098; 1987:N=160,r=.086; 1988:N=84,r=-.010). This unexpected result may be explained by some aspect of crab behavior.

To see if differences existed in aggregation relative to the reproductive state of the nudibranchs, each nudibranch collected on H. echinata-covered shells was scored according to how many other nudibranchs or neighbors were present on the same colony. Individuals were scored as being alone, paired or with 3 or more nudibranchs. The nudibranchs were divided into non-reproductive (1-9mm) or reproductive (<10mm) groups. Chi-square analyses indicate no significant pattern for reproductive adults being alone, paired or with 3 or more individuals (P<.111,df2, N=95). Of all the reproductive animals on shells with colonies, approximately equal numbers were found alone, paired or with 3 or more nudibranchs; the 3 or more category had the lowest percentage. On the other hand, juvenile or non-reproductive

nudibranchs show a significant pattern of aggregation (P<.0001,df2, N=768) (Fig.17). For the non-reproductive animals, the paired category had the lowest percentage (29%) followed by the alone category (22%). Forty-nine percent of the animals were aggregated with 3 or more on a colony, while the remaining 51% were either alone or paired. Significant differences exist in the three categories for both the reproductive and non-reproductive individuals, suggesting behavioral differences between juvenile and adult nudibranchs (G test, $p<0.001$).

DISCUSSION

Prey Availability

Colonies of Hydractinia echinata at Gerrish Island are larger and non-mobile compared to those on hermit crabs at Gosport Harbor. Gerrish Island colonies averaged 821.57 cm ^{2} (N=11) in area, while the average surface area of crab shells collected was 8.1386 cm^2 (N=22) (ch. 2). Perhaps the Gerrish Island colonies provide a more reliable food source for the Cuthona nana population, since they are larger and are stationary. At Gerrish Island, the availability of prey for C. nana is affected by the degree of predation from predators such as other nudibranch species, pycnogonids and urchins. However, colonies were never depleted completely during the years of observation, suggesting that prey abundance is not the major factor controlling the growth of the C. nana population at Gerrish Island.

The colonies at Gerrish Island are in the same locations on the cribs as observed by Harris in 1972, suggesting long-lived colonies with minimal temporal and spatial variation (Harris, pers. comm). Colonies observed off the coast of North Carolina were also long-lived (2 1/2 years) and persistent even when exposed to urchin predation (Sutherland and Karlson, 1977; Karlson, 1978). In both studies, Hydractinia echinata was resistant to mortality because of its ability to regenerate if partially grazed, as is true for other clonal organisms (Jackson, 1979,1985). Thus the colonies at Gerrish Island are persistent and are a stable food source for C. nana. One would assume the same to be true for colonies of H. echinata on hermit crab shells. As a competitor, H. echinata is persistent in maintaining shell substrata on shells in Delaware

(Karlson and Shenk, 1983) and in Gosport Harbor (pers. observ). Colonies in this study were observed overgrowing most epifauna such as coralline algae, barnacles and polychaetes sharing the same shell (pers. observ). The only competitive contenders for shell space were other colonies of H. echinata (Fig. 9; Yund and Parker, 1989). Therefore, availability of prey for the Cuthona nana population at Gosport Harbor is more likely affected by changes in hermit crab densities due to crab migration. Although H. echinata may be persistent on the shells, colonies may not be overly abundant for C. nana in the colder months if the crabs migrate to deeper waters. Crab densities seem to be lower in the colder months (Figure 5,A,B) and increase in the spring when water temperatures begin to increase. Studies with Pagurus longicarpus off the coast of Maryland document crabs migrating to deeper water in the autumn and winter when temperatures fall to 10°C (Rebach, 1974, 1981). Presumably the crabs go to deeper water in the winter, where the environment is more stable and perturbation from winter conditions is less severe (Rebach, 1974). The changes in Pagurus spp. densities roughly estimated in this study somewhat parallel those documented for Pagurus longicarpus, with fewer crabs present in shallow water during the winter (Fig. 5A,B). Future studies at Gosport Harbor should include sampling at deeper depths, especially during the winter months. Some C. nana may be carried on H. echinata colonies to deeper water with the migrating crabs. They would be carried to shallow, warmer water in the spring and begin to grow and eventually reproduce. The continuous reproductive pattern and presence of C. nana at Gosport Harbor could also be explained by the presence of some crabs with colonies in the winter. Though fewer in number than in the summer, these colonies could sustain a portion of nudibranchs to maintain the population through the winter. More thorough estimates of crab densities,

combined with the percentage of crabs with colonies, are needed to infer the effects of prey on the population dynamics of Cuthona nana.

The observations of Hydractinia echinata recruitment (smaller colonies) and the percentage of reproductive colonies agree with results of Yund and Parker (1989). Yund and Parker (in press) observed a greater percentage of reproductive colonies in the warmer months and an increase in recruitment in the late summer and early fall. Preliminary data (Fig. 7) suggest that the population of H. echinata in Gosport Harbor follows the same pattern of recruitment as reported for the Maine population observed by Yund and Parker (in press). Although my data are similar to those obtained in Maine, more consistent sampling on a monthly basis is needed to draw more definite conclusions

Patterns of Cuthona nana

The population pattern of Cuthona nana at Gosport Harbor indicates a subannual life cycle (Miller, 1962; Thompson, 1964; Harris, 1973, 1975; Todd, 1981, 1983). A subannual species of nudibranch is described as undergoing several generations in a year, being small and cryptic and preying upon ephemeral hydroids (Todd, 1981, 1983). Previous work by Rivest (1978) and Folino (1985) demonstrate similar patterns of seasonal size frequency and reproductive periods. Reproduction is greater during the late spring and summer months with an increase in the percentage of shells with Cuthona nana (Fig. 14). These results are similar to Rivest's (1978) and Folino's (1985), but provide more information on the abundances in the summer months, a part of the year when information had not been previously obtained. The presence of juveniles throughout the months of collection suggests several generations per year (Fig. 13). Larger Cuthona nana are present in the summer and fall suggesting that January and February juveniles reach

adulthood in April and May, and produce juveniles which reach adulthood in September and October (Fig. 16). This pattern is especially evident in the monthly length histograms for 1987 (Appendix, Fig. 13). Cohorts overlap because of egg-laying throughout the year, and because of differential growth rates of cohorts due to temperature. Both Rivest (1978) and I (this study, Chapter 2) observed 11-14 weeks, or approximately 3 months, as the time from egg to egg at 12°C. Temperatures in June/July to October range from 10-15°C; therefore juveniles present in May could reach adult size in August or September and reproduce in the colder months. Therefore, by analyzing Rivest's (1978) work on growth rates and information on seasonal patterns presented here, I predict 3-4 generations for C. nana per year.

The majority of nudibranchs with several generations per year feed on seasonally variable prey items (Miller, 1962; Clark, 1975; Harris, 1973; Todd, 1981,1983). Furthermore, these nudibranchs are often closely associated with their prey items and undergo population fluctuations relative to prey abundance (see review Todd, 1981,1983). However, there are nudibranchs with subannual life cycles which feed on specific prey items which are more stable than the ephemeral hydroids common to most subannual species. For example, Phestilla spp. produce several generations per year and feed on slow-growing hermatypic corals in the genus Porites (Harris, 1975). Cuthona nana, like Phestilla, is different from most subannual species in that its prey, H. echinata, is persistent at both Gerrish Island and Gosport Harbor.

Gosport Nudibranch Distributions

Cuthona nana is distributed non-randomly on colonies of H. echinata and show patterns of aggregation depending on reproductive state. Several studies of nudibranch populations quantify abundances of nudibranch species, but do not determine these abundances relative to the abundances of

prey (Miller, 1962; Clark, 1975; Todd, 1981,1983). More often than not, the distributional patterns of organisms are non-random as is true for Cuthona nana. Todd (1978a) observed seasonal changes in patchiness for the dorid Onchidoris muricata; patchiness or aggregation increased during the spawning season. Todd (1978b) further demonstrates a change in behavior prior to and during the reproductive period, and proposes that mucous trails are involved in the process of aggregation as presented in other studies (Lowe and Turner, 1976; Todd, 1979; Gerhart, 1986; see review: Hadfield and Switzer-Dunlap, 1984). A similar phenomenon of aggregation or clumping occurs with Cuthona nana on crab shells covered with H. echinata. Rivest (1978) documented a non-random distribution, as I have observed in this study. There are two ecological explanations for this pattern, based on the biology of Cuthona nana as well as the role of the hermit crab. First, Rivest (1978) demonstrated that postlarvae of C. nana are picked up by the gastrozooids of H. echinata which sweep along the ocean bottom. This partially explains the significant occurrence of juvenile C. nana on colonies with three or more individuals (Fig. 17). When juveniles hatch from an egg mass in the field, they probably move some but remain somewhat concentrated in the area around the egg mass. When a hermit crab shell covered with H. echinata passes by with trailing gastrozooids, several juveniles are picked up. The second explanation for aggregation in C. nana is the behavior of adults. Adults leave colonies to mate and lay eggs (Harris et al, 1975; Rivest, 1978; pers. observ) and perhaps follow mucous trails to find mates, as seen with other molluscs. This explains why the majority of Cuthona nana greater than or equal to 10mm are found alone or paired on colonies (Fig. 17), or mating on rocks and mussel shells (pers. observ.). They return to colonies either to feed for continued growth, and/or to reproduce by mating on colonies.

In summary, Gerrish Island and Gosport Harbor differ in availability and mobility of Hydractinia echinata. Gerrish Island colonies are larger, stationary and persistent throughout the year, while colonies on hermit crab shells at Gosport Harbor are mobile and may fluctuate in abundance due to migration of the hermit crabs. However, since H. echinata is a persistent hydroid (unlike most ephemeral hydroids grazed by other aeolids), it represents a stable food source. Cuthona nana at both sites produce several generations per year (approximatley 3-4) and can therefore be classified as having a subannual life cycle versus an annual cycle where there is no generation overlap.

CHAPTER II

GROWTH OF HYDRACTINIA ECHINATA; DEVELOPMENT, GROWTH AND FEEDING IN CUTHONA NANA

INTRODUCTION

Aspects of growth, development and feeding for associated predator and prey are important in documenting the life histories of each organism. This chapter deals with growth rates of Hydactinia echinata strains under varying current regimes and the initiation of growth for a specific type of polyp, the tentaculozooid. Aspects of development, growth and feeding for Cuthona nana are presented.

Growth Rates of Hydractinia echinata

Several studies describe hydroid growth form and rates (Crowell, 1957; Fulton, 1962; Braverman, 1963a,b, 1971; Braverman and Schrandt, 1966; Stebbing, 1979, 1981a,b,c). Factors regulating metamorphosis and pattern formation in Hydractinia echinata have been documented (Muller and Plickert, 1982; Berking 1984,86; Kemmner, 1986) and the growth dynamics for strains of H. echinata have been measured (McFadden et al., 1984; Buss et al., 1984; Folino, 1985; McFadden, 1986). However, none of the above studies have considered the environmental effect of water flow intensity (current speed) on growth parameters. Palumbi (1984) observed differences in growth under varying degrees of wave action in a sponge species. Since H. echinata grows asexually as do sponges, perhaps this phenomenon of varying growth due to

differences in current exists for H. echinata at Gerrish Island and Gosport Harbor. Preliminary laboratory observations suggested that colonies grew differently in varying water movement conditions, prompting experiments to test for variation in growth for strains of H. echinata from each site.

Tentaculozooids in Hydactinia echinata

Marine ectoprocts develop defenses in response to predators to deter predation. Harvell (1986) found that the spines of the ectoproct Membranipora membranacea affect the feeding rates of three nudibranch species. As previously mentioned, tentaculozooids and spiralzooids are grouped as dactylazooids and are believed to function as defensive polyps in H. echinata (Hyman, 1940). The occurrence of tentaculozooids on colonies is poorly documented. Previous observations suggest the occurrence of these polyps to be rare, though they became evident in more recent collections from Gosport Harbor (pers. observ). The presence of tentaculozooids in relationship to the presence of predators and competitors was monitored in both field-collected and laboratory-cultured colonies. H. echinata colonies found with and without tentaculozooids were established in the laboratory and subjected to predation to see whether tentaculozooids would develop.

Teeth, Development, Growth and Feeding in Cuthona nana

Teeth and Development

Anatomical, behavioral and developmental features are the basis for differentiating species. Distinctions among morphological features are used in phylogeny and taxonomy of opisthobranchs such as nudibranchs (Ghiselin, 1965; McFarland, 1966; Brown, 1980; Gosliner, 1981; Thompson and Brown, 1984; Gosliner and Millen, 1984). Some standard morphological features used in nudibranch taxonomy include radular teeth, reproductive systems and the type of veliger development. Preliminary observations of radular teeth and

the mode of development for Cuthona nana at Gerrish Island and Gosport Harbor reveal potential population differences which suggested the existence of a new or sibling species. In this study, anatomical (radular teeth) and developmental characteristics were used to compare the two populations of Cuthona nana at Gerrish Island and Gosport Harbor.

Previous observations (Harris et al., 1975; Rivest, 1978) of different developmental types for Cuthona nana suggested the possibility of poecilogony or two modes of development in the same species. Hoagland and Robertson (1988) reviewed the subject for marine invertebrates. Poecilogony is documented for a few molluscs such as the prosobranch Crepidula dilata (Gallarado, 1977), a cephalaspid (Franz, 1970) and the nudibranch Tenellia pallida (Eyster, 1979) The latter two examples by Franz (1970) and Eyster (1979) illustrate different developmental modes for animals from the same location. If poecilogony had existed for C. nana off the coast of New Hampshire, it may have been related to site differences based on previous observations (Harris et al., 1975; Rivest, 1978). The two sites, Gerrish Island and Gosport Harbor, differ in current speed and prey mobility.

Feeding and Growth Rates for Cuthona nana.

Aspects of nudibranch feeding, such as prey preferences and feeding-related anatomy, have been documented for several types of nudibranchs while most feeding rates have been determined for bryozoan-grazers (review: Todd, 1981; Harvell, 1986). Fewer studies have determined nudibranch growth rates (Harris, 1975; Christensen, 1977; Hall and Todd, 1986). Christensen (1977) describes the feeding and growth rates of the nudibranch Precuthona peachi (now synonomized with C. nana; Todd, 1981; Thompson and Brown, 1984), at 6to 8°C. Rivest (1978) documented postlarval growth for C. nana at 12 °C from metamorphosis to 12mm in length,but did not present weekly/biweekly

increments of growth. In this study, I measured growth rates of Cuthona nana from Gerrish Island and Gosport Harbor, and feeding rates for nudibranchs from Gosport Harbor.

METHODS

Hydractinia echinata Experiments

Both field and laboratory experiments were done to see whether clones of Hydractinia echinata from Gerrish Island and Gosport Harbor grew differently under varying current regimes. Colonies were cultured on plexiglas panels for the field experiments and on glass microscope slides for the laboratory experiments.

Field Experiments

Thirty-six colonies of Hydractinia echinata were established in the laboratory on plexiglas panels (9.0 X 9.0 cm), using tissue with 10 polyps as starter pieces. Eighteen of the 36 panels had colonies collected from Gerrish Island and the remaining 18 were from Gosport Harbor. Colonies were grown for 3 weeks prior to being placed in the field. At each site 9 colonies from Gerrish Island and 9 colonies from Gosport Harbor were suspended on ropes approximately 1 meter above the bottom. Initial photographs were taken of each panel to monitor potential changes in growth. After 10 days, the colonies at Gerrish Island had been dislodged due to high currents. Therefore, the panels were removed, but those at Gosport Harbor were doing well and were left in and photographed every 2 weeks for a month. A similar set of 36 panels to that mentioned above was established in the laboratory for a second attempt. Month-old colonies from both sites were suspended at each site, but this time lines were suspended perpendicular to the crib at Gerrish Island. Again, colonies at Gerrish Island did not survive, while those at Gosport Harbor did and were photographed monthly for the next 2 months. The growth of colonies at Gosport Harbor was recorded in terms of survival and was not

quantified over time.

Laboratory Experiments

It is necessary to mention that laboratory experiments with both Hydractinia echinata and Cuthona nana were conducted in a closed seawater system. Several attempts and modifications in techniques were needed to get successful results. To determine effects of current on hydroid growth, colonies of H. echinata were grown in the laboratory in two aquaria: one with calm flow similar to that at Gosport Harbor, and the other with 2 water pumps (called universal powerheads, Mail Order Pet Shop, Deer Park, N.Y.), creating a high turbulence habitat similar to that of Gerrish Island. I conducted two trials. The first trial used a viney morph from each site while the second trial included a matty morph from Gosport Harbor and a viney morph from Gerrish Island. A matty morph from Gerrish Island was not used because all of the colonies collected from that site were viney. Colonies were grafted to glass microscope slides using pieces of colony with 5 polyps and kept in microscope slide trays which had the bottoms melted out to enhance water circulation . Twenty-four slides of each colony were established; 12 of each colony were placed in the calm tank and 12 in the high current tank. Tracings were made weekly for 5 weeks using a camera lucida attached to a WILD microscope at 60X and 120X magnification. The following parameters were recorded to quantify growth: 1)mat area 2)stolon area 3)the number of polyps per mat area and 4)the number of polyps per stolon area. Areas (mm^2) of mat and stolon were quantified using an Apple II graphics tablet. Mean values for mat and stolon area (mm^2) and for the number of polyps/mat area and polyps/stolon area were plotted over time. Mann-Whitney U-tests were used to compare the treatment and control means at the end of the experimental period (Zar, 1984).

Tentaculozooid Experiments

The occurrence of tentaculozooids in colonies of Hydractinia echinata was observed in 3 instances: 1)field observations from colonies at both sites; 2) on the panels with colonies used for nudibranch recruitment experiments, and 3) around the holes drilled in hermit crab shells for the recruitment experiment. An experiment was done to see whether grazing by Cuthona nana would trigger the development of tentaculozooids. Three colonies on hermit crab shells from Gosport Harbor with tentaculozooids were selected and cultured onto slides. Eight slides were established for each of the three colonies. For each colony, four of the eight slides consisted of a colony which had tentaculozooids present while the remaining four slides had a colony without tentaculozooids. This was done to see whether there was something unique about a part of a colony which actually had tentaculozooids present. After 2 1/2 weeks of growth, 2 of the 3 colonies were grazed, with the third set serving as the control. The 14 colonies (2 slides did not grow well) were grazed for a 24 hour period and were checked for the development of tentaculozooids 1 day, 1 week and 2 weeks after grazing. Tracings of colonies before and after grazing provided information on grazing rates.

Cuthona nana

Radulae SEM

The radulae from four adult Cuthona nana from Gerrish Island and four adults from Gosport Harbor were prepared for observation using a scanning electron microscope to see whether the teeth arrangement varied from that of animals from Gosport Harbor. The radulae and jaw were isolated and stored in 90% ethanol, and were then soaked in 50% bleach for 2-5 minutes until the tissue of the buccal mass was dissolved. During this time, specimens were checked frequently to prevent complete dissolution. The parts were then sonicated in freshwater for 1-2 minutes, treated in HMDS

(hexamethyldisilazane) for 5-10 minutes to critical point dry, and mounted on aluminum stubs and coated with a 300 Ao coating of gold paladium. They were viewed using an AMR 1000 scanning electron microscope. Cleaning and mounting of the jaws were unsuccessful. Therefore only radular photographs are available for animals from each site.

Nudibranch Development

The development of Cuthona nana at Gosport Harbor and Gerrish Island was compared. Techniques for culturing veligers were similar to those used by Hadfield and Scheuer (1985). Seawater was filtered using a 0.22 um pore size and then treated with the antibiotics, penicillin G (0.228g/liter) and streptomyocin sulfate (0.190g/liter). After several unsuccessful attempts, the dosage of each antibiotic was tripled and the chamber was modified from a drip method to placing an airstone directly into the hatching chamber. Hatching was sucessful for 5 egg masses from each site. Two of the five Gosport Harbor egg masses were laid in the field while the other 3 were laid in the running seawater tables in Spaulding Life Sciences Building. The water in each chamber was changed daily. Egg size and time of hatching were recorded for each egg mass. Juveniles from Gerrish Island egg masses did not survive for more than 1-2 weeks, while Gosport Harbor juveniles survived to adulthood and were used to determine growth rates of C. nana.

Nudibranch Recruitment

Since it was suspected that the Gerrish Island population of Cuthona nana may differ in development from the Gosport Harbor population, a recruitment experiment similar to that of Rivest (1978) was used to test for planktonic veligers at both sites. My first run entailed culturing colonies from both sites on plexiglas panels (9.0 X 9.0 cm) until at least 50-75% of the panels were covered (4 months of growth). Forty panels were established with

20 colonies from Gosport Harbor and 20 colonies from Gerrish Island. Colonies from each site were placed at each site to see whether there was a difference in settlement relative to the original location of the colonies. At Gosport Harbor, 20 panels (10 with Gerrish Island colonies and 10 with Gosport Harbor colonies) were suspended approximately 2/3 m off the bottom, and an identical set of 20 panels was suspended approximately 1 m off the bottom at Gerrish Island. The panels were put in the field for 2 weeks, and then bagged in mesh bags and brought into the laboratory to check for veligers. Portions of colonies were dislodged from the panels when retrieved, so shells covered with H. echinata from Gosport Harbor were used for the remainder of the experiment. Holes were drilled in the lips of the shells with a 3mm bit and suspended on lines using plastic-coated wire. Eight to twelve shells were suspended at each site for 2 weeks before being replaced with another set of shells. The experiment ran for a total of 54 days from mid-July to the end of Septemeber 1987. I chose this time of year for the experiments since summer is the peak reproductive season for Cuthona nana (Rivest, 1978; Folino,1985).

Nudibranch Growth Rates

Growth rates of Cuthona nana from Gerrish Island and Gosport Harbor were quantifed by measuring body length. Fourteen animals from Gerrish Island were kept in plastic containers with mesh sides at 12°C. Two containers were held in a larger container and these larger containers were placed on a wooden stairstep frame to create a cascade effect so that animals would be exposed to high levels of current (Appendix, Fig. 5). Nudibranchs were fed colonies from Gerrish Island.

Growth measurements for Gosport Harbor animals were taken for two groups:1) animals collected from the field and 2) those reared from an egg mass hatched in the laboratory. Animals were also kept in containers similar

to those described above, and were held in calm water with sufficient flow to maintain aeration. They were fed Gosport Harbor hydroid colonies. Growth rates for 11 animals from the field and 17 animals from one egg mass were determined. Some died before reaching maximum sizes therefore those which grew for 5 weeks or longer were included in the analyses. Animals were placed in 5cm plastic petri dishes and were allowed to relax and extend themselves for crawling before a measurement was taken. Measurements of animals from each site were taken weekly for up to 11 weeks. Nudibranch growth rates were plotted as changes in body length over time or by using linear and nonlinear regression techniques when the data met the assumptions of normality and homogeneity of variances. The proportion of the length at time 1 minus the length at time 2, divided by the length at time 2 was arcsin-transformed for regression analysis (Sokal and Rohlf, 1981).

Nudibranch Feeding Rates

Feeding rates of Cuthona nana were determined using nudibranchs from Gosport Harbor on cultured colonies of Hydractinia echinata. Thirty-five colonies were grazed for 24 hours by nudibranchs ranging in size from 3-25 mm with 8 colonies serving as controls. Four parameters were measured before and after predation: 1)mat area 2)stolon area 3) the number of polyps per mat area, and 4) the number of polyps per stolon area. Differences in these parameters before and after grazing were determined and plotted with animal size to determine grazing rates. The amount of colony portions eaten was converted to mg of wet weight tissue consumed by using constants determined for polyps and mat tissue. Forty polyps, 20 from each of 2 strains,were removed and weighed to determine an average polyp wet weight. The polyp weights for the two strains were not significantly different, therefore the 40 wet weights were combined to calculate a constant for

determining the total wet weight in polyps eaten by each nudibranch. Similarly, a constant for mat tissue (mg) was obtained using 18 pieces of tissue and was used to determine the amount of mat tissue consumed by each nudibranch. It was difficult to determine changes in stolon tissue due to grazing therefore wet weights are calculated only for changes in mat tissue, mat polyp number and stolon polyp number. These 3 parameters were added to obtain the total amount of tissue eaten in mg. In quantifying nudibranch feeding rates, Spearman correlations were used to determine the relationship between animal size and amount of tissue consumed (Zar, 1984).

Grazed patches on Hydractinia echinata colonies covering hermit crab shells were measured and recorded throughout the 23 month sampling period. Patches were identified as areas with cropped polyps and sometimes nudibranch mucus present. Length and width, of the grazed patches were used to calculate the area grazed; length was multiplied by width equating the patch area to the area of a rectangle. The area of a given Littorina littorea shell was estimated by a technique used by Shenk and Karlson(1986). Twenty-two L. littorea shells of varing sizes were covered with aluminum foil as carefully as possible. The foil was removed, flattened and the area was determined by tracing the foil pieces on an Apple II graphics tablet. A linear regression was constructed for shell size (length X width) and foil area ($y=127 + 1.194X$ $R^2 = 0.94$). From the regression equation, the total area of colonies completely covering hermit crab shells with grazed patches was determined by using shell length X width measurements. Then, knowing the area of the shell and the area of the grazed patch, the percentage of colony grazed in terms of area (mm^2) was determined. This technique seemed more accurate in estimating shell surface area than using length X width alone as was done in summarizing shell types in chapter 1.

RESULTS

Hydractinia echinata Experiments

Attempts were made to transplant Hydractinia echinata from each site to opposing sites to see if colonies grew differently under varying current regimes. As mentioned in the methods section, the two field attempts failed. However, the colonies that survived at Gosport Harbor (approximatley 90% survived) grew for several months until overgrown by the tunicate Botrylloides sp. Laboratory experiments were conducted as an alternative. In trial one, the viney morph from Gerrish Island differed in mat and stolon area with mean mat and stolon areas greater for the control colonies grown in the high current tanks (mat area: $U=61$, $p<0.01$; stolon area: $U=62$, $p<0.01$) than those maintained in calm conditions (Fig. 18). There were no differences in the number of polyps/mat and polyps/stolon between treatment and control colonies for this morph ($U=23.5$, $p<0.20$). The viney colony of Gosport Harbor differed only in stolon area after 36 days of growth under high current velocities when compared to control colonies($u=91$, $N=9,11$, $p<0.001$)(Fig. 19).

The data from trial 2 showed few differences in growth for the viney morph from Gerrish Island. There were no differences in mat area, stolon area and the number of polyps/mat area after 46 days of growth (Fig. 20). However, this morph did vary in the number of polyps/stolon ($U=124$, $p<0.0001$). The matty morph from Gosport Harbor did not differ in mat area, but did vary in the number of polyps/mat area. This morph did not produce stolons during the entire experimental period of 46 days. Colonies grown in

the higher current tanks produced a greater number of polyps/mat area than did the control colonies in the calm water tank ($U=76$, $p<0.02$)(Fig. 21).

Hydractinia echinata Tentaculozooids

The occurrence of tentaculozooids was recorded for the hydroid-covered shells and the grab-sampled shells with Hydractinia echinata (Fig. 22). The percentage of shells with tentaculozooids in the covered shells is greater in the spring and early summer months (Fig. 22 A). There was a slight increase in percent in February followed by a drop in March for 1987 and 1988. The grab-sampled shells were not collected in consecutive months although a greater number of shells with tentaculozooids occurred in the summer (1985) and declined in the fall (1985) (Fig. 22 B). The grab samples for the spring months showed an increase in the percentage of tentaculozooids similar to observations for the covered shells.

To see if the presence of tentaculozooids was associated with an indication of predation (the presence of C. nana or a grazed patch), G-test analyses were done by month and also for all months combined for the Hydractinia echinata-covered shells. Duplicated months were combined for the monthly G-tests. No association existed between the presence of tentaculozooids and evidence of predation (G-test, p values < 0.10 to 0.97 for individual months and $p < 0.99$ for all the months combined).

Experiments were conducted to see whether predation by Cuthona nana would induce the production of tentaculozooids in laboratory-cultured colonies of Hydractinia echinata. Of the twenty-one colonies established with and without tentaculozooids present, none developed tentaculozooids. The colonies with tentaculozooids lost those present. They were reabsorbed or became gastrozooids.

Cuthona nana

Radulae SEM

The radulae of Cuthona nana from Gerrish Island and Gosport Harbor are similar in tooth arrangement. The radulae are uniserate with 13-19 teeth for animals ranging 11-16 mm in length (Appendix, Fig. 6 A,B). The central cusp is larger in length and width than the six to nine laterals on each side. There are no major differences in the radulae for animals from the two sites, though examinations of teeth arrangement for a greater size range of animals would be necessary to make more definite conclusions.

Nudibranch Development

Five eggs masses from each site, Gerrish Island and Gosport Harbor, were reared in the laboratory to examine potential differences in development between the two populations. All ten egg masses developed directly with juveniles crawling on the bottom of the dishes. Swimming was not observed. Hatching occurred in 20-23 days for egg masses laid in the laboratory with metamorphosis occurring in 1-2 days. These results are similar to those presented by Rivest(1978) for animals from Gosport Harbor. Measurements of egg and shell size were taken for veligers from various egg masses. There were no significant differences in egg and shell size ($p<.197$, N=16; $p<.440$, N=49,50 respectively), with eggs averaging 160 um and shells 234 um (Fig. 23). The egg capsules for Gerrish Island nudibranchs, averaging 259 um (SE=3.98, N=49) in length, were significantly larger ($p<.015$) than those of Gosport Harbor which averaged 245um (SE=3.99, N=56) (Fig. 23).

The diameters of egg masses laid in the laboratory by animals from each site were not significantly different ($U=203.0$, $p<.48$) (Fig. 24 A). Similarly, the mean number of eggs per mass did not differ between animals from each site ($U=42$, $p<.47$) (Fig. 24 B). Egg mass diameters measured in the field at Gerrish

Island did not differ significantly in size when compared to those laid in the laboratory (U=953.5, p<.50; N=34 (lab), 57 (field)). Bar graphs for the mean egg mass diameter and number of eggs per mass visually suggest differences, but the standard deviation bars indicate large variation in each data set (Fig. 24 A,B). Spearman correlations were used to see whether relationships existed between nudibranch size and the diameter of the egg mass. No significant relationships existed for animals from either site (Gerrish Island: r_S= .236, p<.18, N=34; Gosport Harbor: r_S= .177, p<.17, N=62).

Nudibranch Recruitment

Panels with colonies of Hydractinia echinata were placed at each site to see whether planktonic Cuthona nana were present. Of all the panels and shells covered with H. echinata placed in the field, no newly hatched or metamorphosed C. nana were observed during the experimental time from July to September 1987. These results somewhat support the observations of direct development observed in the laboratory, although a full-year recruitment experiment is necessary to make a definite statement about the existence of planktonic veligers in the field.

Nudibranch Growth Rates

Gerrish Island. Fourteen nudibranchs from Gerrish Island were grown in the laboratory under high current to determine growth rates. Individuals were divided into 2 size groups: 1) 4-7mm(N=9) and 2) 8-10mm(N=5). The average body length (mm) and percent increase per day describe growth rates and are calculated for a 42 day period. The average increase in length per day for the smaller size class was greater overall for the first 29 days compared to the larger class (Table 3). Both size groups showed minimal growth or decreased in size for the remaining 13 days. A similar pattern exists for the average percent increase per day. The smaller individuals increased more

after 14 days with a 3.83% increase in body length followed by a 1.61% increase after 21 days. The larger individuals did not exceed a 2.35% increase in body length. The average maximum size and days survived for Gerrish Island animals in the laboratory was 10.6mm ± 2.03 SD and 36.9 days ± 8.30 SD respectively. The maximum sizes for small and larger animals did not differ (U=18.0; p<.50), therefore all 14 animals were used to calculate the mean size obtained.

Gosport Harbor. Growth rates for Gosport Harbor Cuthona nana consisted of measurements for three groups: 1) field-collected animals of varying initial sizes, 2) 4 animals with initial sizes of 3mm and 3) newly hatched veligers from an egg mass laid in the laboratory. Growth for field-collected animals is grouped similarly to that of Gerrish Island animals; small animals include individuals 1-5m in body length (N=4) and the larger group includes those 10-12 mm (N=3). There were fewer measurements of the larger group for the study period because some individuals died sooner than those in the small size class. A trend in the average growth per day in mm is similar to that seen with the Gerrish Island animals; smaller animals grew more per day than larger animals and decreased in growth at 49 days (Table 4). The same trend of greater growth in the smaller group is seen for the average percent increase in body length, with 5-6% increases during the first two weeks of the study period (Table 4). The average maximum size obtained in the laboratory for both groups of animals combined was 19.2 mm ± 1.72 SD, with an average survival in the lab of 42.3 days ± 20.9 SD. The average number of days survived in the lab for Gerrish Island animals did not differ from that of Gosport Harbor animals (U=53.0; p<.50), though differences existed for maximum sizes obtained. Gosport Harbor animals reached a significantly larger maximum size in the laboratory compared to Gerrish Island individuals (p<.0001; t-test) suggesting

differences in size obtained for C. nana in the laboratory from the two locations.

The second set of growth data for field-collected Gosport Harbor Cuthona nana consisted of 4 individuals with an initial size of 3mm. Body length was measured weekly for 6 weeks (42 days), and all 4 growth sequences were combined since initial sizes were equal. The lengths were log transformed and plotted against time. A curvilinear, quadratic equation best describes the growth (r^2 = .97, F=159.1, p<.0001, df=2,18) (Fig. 25 A). Animals increase at a given rate and begin to level off in growth after approximately 35 days. The size at which this leveling off occurs is approximately 20mm, very close to the maximum size of 19.2mm for the first set of growth data for Gosport Harbor animals previously discussed. It is at this size that animals have produced several egg masses (most begin reproducing at 9-11mm) and begin decreasing slightly in length prior to death. The percent change in growth for these same animals decreases and is linear with time (r^2=.79, F=32.27, p<.0001, df=1,19) (Fig. 25 B). For example, the average percentage increase in growth per day was approximately 7% after 7 days in the laboratory and decreased to 0.60% by day 42 of the study period. One would expect this pattern of growth as animals approach their maximum size and begin reproducing.

The nudibranchs from the Gosport Harbor egg mass hatched in the laboratory showed a similar growth rate pattern compared to the 3mm Gosport Harbor animals previously mentioned. The hatched veligers reached a mean size of 1.06mm in 56 days and increased in size, averaging 18.6mm after 122 days (Fig. 26 A). The growth curve begins to level off near 19-20mm, the same size where leveling off occurred for the growth of field collected Gosport Harbor animals with initial sizes of 3mm. The percent change in body length (mm) per day averaged 5% initially, dropped to 4.5% and then increased to 6%

for the next 2 weeks of growth (Fig. 26 B). The percent change in body length begins to decline after 86 days or when the animals are 9-10 mm in length and begin reproducing. The percent change in body length continues to decline to less than 1% by 122 days (approximately 4 months) after hatching.

Nudibranch Feeding Rates

Laboratory Experiments. Grazing rates were determined for 35 Cuthona nana ranging in size from 3-25mm from Gosport Harbor. Mat and stolon area and the number of polyps per mat and stolon area were obtained for colonies of varying sizes before and after grazing. A positive correlation exists for nudibranch length and the total amount of hydroid tissue eaten in a 24 hour period (r_S=0.340, N=35, $p<0.04$); larger nudibranchs consume more colony tissue whether it be mat or polyp tissue (Fig.27). In the laboratory, Rivest (1978) and I have observed smaller C. nana feeding on mat tissue, while larger animals bit off polyps, though each size group does not feed on these portions exclusively. If one considers just the mg of mat polyps versus nudibranch size, a positive relationship exists (r_S=0.733, N=35, $p<0.0001$), indicating that as animals become larger, they do eat more polyps. Stolon polyps were not considered since the majority of polyps grazed were on mat tissue. If nudibranch size is divided into two groups, one might expect a positive relationship between the amount of polyp tissue consumed and animal size. The grazing data were divided into polyp and mat tissue wet weights and analyzed according to small (<1-8mm) and large (9-25mm) individuals to see if feeding differences according to size were evident. No positive correlations existed for small or large animals for mg of polyp tissue and animal size (small:r_S=0,115, N=15, $p<0.683$; large:r_S=0.282, N=20, $p<0.228$) (Fig. 28 A,B). However, positive results exist for mat tissue eaten by small and large animals. Smaller animals show a significant positive relationship between animal size and the amount of mat tissue consumed

(r_S=0.65, N=15, p<0.009) (Fig. 29 A), while larger animals exhibit a significantly negative relationship between animal size and mg of mat tissue (r_S=-0.521, N=20, p<0.019) (Fig. 29 B). Smaller animals feed on mat tissue until they are large enough to bite off entire polyps, while larger nudibranchs feed on polyps more than do the juveniles. The mean changes in mat polyps, mat area and stolon polyps for the nine control colonies were: 16.22 $\pm$ 38.04 SD, 9.76 $\pm$ 18.84 SD, and -0.444 $\pm$ 0.726 SD, respectively. As indicated by the standard deviations, there was much variation among the nine colonies (Table 5).

Field Grazing. The average grazed patch size on hydroid-covered colonies in the field was 37.0mm^2 ($\pm$ 31.4mm^2, N=80), or an average 5.75% (SD = 5.225, N = 80) of the total colony area. The percentages varied greatly by month (Fig. 30), but of the 80 colonies sampled, 85% were grazed less than 10% of the total colony area, indicating a minimal amount of damage. The percentage of hydroid-covered shells with grazed patches was greatest during the months of high nudibranch densities (Fig. 31).

DISCUSSION

Hydroid Growth

Previous work has shown phenotypic changes in growth forms in scleractinians (Foster, 1979), gorgonians (Leversee, 1976; Velimirov, 1976) sponges (Palumbi, 1984) and hydroids (Hughes, 1986). Strains of Hydractinia echinata seem to vary in growth in some instances under different current regimes in the laboratory. One of the strains from Gosport Harbor produced more stolons under higher water flow, which could increase its competitive ability since colonies with greater stolon production are superior competitors (Buss et al., 1984). At least in the first trial, the Gerrish Island clone produced more mat and stolon area in higher than lower water flow (Fig. 18). Since the Gerrish Island colonies occur naturally in an area of greater water flow and show diminished growth in the laboratory under low flow, one might speculate that clones of Hydractinia echinata from Gerrish Island are adapted to areas of greater flow. The only places where colonies have been observed on nonmobile substrata are in areas of high current such as Fort Stark in Newcastle, N.H. and at Gerrish Island. Populations of hermit crabs in calm habitats have colonies on their shells at locations such as Gosport Harbor, and under the Portsmouth Fishing Pier and the Coast Guard Pier, both in N.H. Buss and Yund (pers. comm.) have proposed the existence of sibling species with the classification of H. echinata, although the information is not yet published. Perhaps the colonies of H. echinata at Gosport Harbor and Gerrish Island are sibling species. This may explain potential differences in growth, although C. nana shows no preference among colonies from the two sites when feeding. Whether the colonies at Gerrish Island are genetically

different from those at Gosport Harbor has yet to be determined.

Tentaculozooids in Hydractinia echinata

The development of tentaculozooids was not induced in colonies grazed by Cuthona nana, but field data suggest that they may play a defensive role in competition. Stokes (1974 a,b) observed tentaculozooids at the growing edges of colonies surrounding other organisms which settled on the hermit crab shells. My observations in both the grab sampled and hydroid-covered shells indicate a similar phenomenon, with the majority of tentaculozooids located at the growing edges of the colony. Settlement of organisms such as barnacles and algae on hermit crab shells occurs in the spring and early summer (Osman, 1977; Harris and Irons, 1982; Lambert, 1985; pers. observ.). This corresponds to the time of greatest occurrence of tentaculozooids in colonies in this study (Fig. 22). Furthermore, the panels with Hydractinia echinata used for Cuthona nana recuitment support the hypothesis of tentaculozooids being involved in competition. Of the 17 colonies with tentaculozooids, 13 developed tentaculozooids in 2 weeks around the stolons of Tubularia colonies which settled onto the panels.

Tentaculozooids also developed around the holes drilled to hang shells with colonies for the recruitment experiments and seem to be the precursor polyp type for spiralzooids occurring around the aperture of the hermit crab shell (Schijfsma, 1939; Podocoryne: Braverman, 1960). Burnett et al. (1967) also observed tentaculozooids transform into gastrozooids. I observed this in the pieces of colony with tentaculozooids used to start colonies to see whether grazing induces the development of tentaculozooids. The tentaculozooids were either resorbed or became gastrozooids. Polymorphism in Hydractinia echinata is flexible and may allow quick transformations from one polyp type

to another to enhance the feeding or defending of a colony.

Nudibranch Development, Growth and Feeding

Nudibranch Development

The question still present concerning the classification of Cuthona nana is the possible difference in development type. As previously mentioned, Harris et al. (1975) observed planktonic development for C. nana collected from the Gerrish Island population. It was a few years later when Rivest (1978) documented direct development for the population at Gosport Harbor. This possible phenomenon of two modes of development, poecilogony, is recently summarized and critiqued for invertebrates by Hoagland and Robertson (1988). These authors agree that the pattern of development is an important component in invertebrate systematics, but feel that documentations of poecilogony are poorly illustrated. Further documentation of development is still necessary for the two populations of Cuthona nana of this study. Although I observed direct development for both Cuthona nana populations, previous observations of both types of development may be explained by the timing of egg mass breakdown. This explanation was proposed by Harris et al. (1980) in their work with the nudibranch Tenellia fuscata. The purpose of their study was to see whether temperature and/or salinity would affect development type as suggested by Rasmussen (1944). Their results suggest that salinity and temperature affect the developmental rate of Tenellia fuscata, and they propose that the timing of egg mass breakdown may be a possible factor in two types of development observed in other nudibranchs. Harris (1973,1975) discusses factors involved in egg mass break down, such as bacterial action and water motion. Perhaps the current at Gerrish Island may break down Cuthona nana egg masses prematurely, releasing veligers capable of swimming. Observations of Cuthona nana

development (Harris et al., 1975; Rivest, 1978; per. observ.) indicate a velum present at 7-9 days, the hatching time of planktonic veligers observed by Harris in 1971. Conceivably, animals could swim if the egg mass broke down "prematurely" releasing a lecithotrophic veliger. Perhaps it is advantageous to have the ability to swim at a site where current is strong such as at Gerrish Island. The possibility of poecilogony still exists for Cuthona nana, although my results suggest that it does not occur. More thorough experiments are necessary under more favorable laboratory conditions. Egg masses from various populations, or at least from Gerrish Island and Gosport Harbor, should be reared under various environmental conditions such as salinity, temperature and current. Future work should involve anatomical, developmental and especially electrophoretic studies to clarify the confusion of species among populations with different modes of development (Hoagland and Robertson 1988). Electrophoretic analyses would reveal whether these two populations of C. nana differ genetically or phenotypically.

Differences in development for Cuthona nana populations around the world are discussed by Brown (1980) and Thompson and Brown (1984). The European population observed by Christensen (1977) feeds on H. echinata, deposits egg masses on the hydroid colonies, and releases planktonic larvae in three weeks. The observations of Rivest (1978) and I are different from those of the above authors in that Cuthona nana at Gosport Harbor leave the colonies to lay eggs and egg masses release nonplanktonic juveniles, while nudibranchs at Gerrish Island do not leave the colonies (ch. 1). Once off a colony in Gosport Harbor, finding food seems not to be a problem since the colonies on the shells are mobile (see ch. 3). Individuals at Gerrish Island lay egg masses on grazed portions around the edges on the chitinous base of H. echinata or on the interacting zones of colonies where gastrozooids are

lacking (Harris at al., 1975; pers. observ). I observed the same behavior in the laboratory. Brown (1980) suggests that differences in spawning behavior may be related to the two types of development for the European and American Cuthona nana. It is proposed that boreal and arctic nudibranchs generally exhibit direct or lecithotrophic development (Calow, 1983). The lack of a pelagic larva leads to locally adapted populations (Gallardo and Peron, 1982). Perhaps C. nana at Gosport Harbor exhibit direct development because of the selective pressure of a mobile prey source.

Nudibranch Growth

The lack of growth rate information for aeolids is mentioned by Harris (1973) and is an area of needed work as suggested by Todd (1981) in his review of nudibranch ecology. As Todd (1981) indicates, most growth and life cycle information is for animals collected and measured in the field (Miller, 1962; Clark, 1975; Todd, 1979; Nybakken, 1978) with few studies involving individuals reared in the laboratory (Carefoot, 1967; Holleman, 1972; Harris, 1975; Eyster, 1981; Eyster and Stancyk, 1981; Smith and Sebens, 1983; Hall and Todd, 1986). Only two of these studies deal with aeolid growth (Harris, 1975; Hall and Todd, 1986). Rivest (1978) summarizes growth of Cuthona nana in terms of length relative to time, but does not present specific growth rates. He also mentions a great amount of variation in growth for individuals from the same egg mass; this is demonstrated by my results for the 17 individuals reared in the laboratory at 12°C. I also observed animals maturing and laying egg masses after approximately 86 days or 12 weeks (Fig. 25 A), approximately the same as Rivest's (1978) observations of 11 weeks from egg mass to the laying of the first egg mass at 11-13°C. It took approximately 8 weeks for juveniles from metamorphosis to reach 1-2mm in length, while Rivest's (1978) animals took 6 weeks; perhaps this slight difference is due to variation in temperature. I did

not measure weekly increments of growth during the 8 week period to the 1-2 mm size but Rivest (1978) did provide such information. If one calculates the percent change in body length per day from Rivest's (1978) information for growth in the first 5 weeks after metamorphosis, one gets about a 5% change in growth from the second to third week. The percentage then drops between the third and fifth week (growth to 1mm) to approximately 3% change in body length per day. This change is followed by an increase in the percentage to 5% again from the fifth to the seventh week (from 1 to 4 mm) for Rivest's (1978) work, which is similar to the results I obtained for animals of similar sizes (Fig. 26 B). In this study, the percent change in body length begins to decrease slightly after 86 days of growth or at 9mm, the size of sexual maturity and the onset of egg mass laying (Fig. 26 B). The data for the field-collected animals from Gosport Harbor with initial sizes of 3mm showed a decrease in growth after 35 days which corresponds to a maximum size of 20mm (Fig. 26 A). This drop in growth is observed in other aeolid studies (Harris, 1975; Hall and Todd, 1986) and is explained by senescence.

There were obvious differences in growth and survival of Cuthona nana from Gerrish Island and Gosport Harbor; Gerrish Island animals did not grow beyond 10 mm or survive well in the lab. Other marine invertebrates such as Asterias vulgaris, Strongylocentrotus droebachiensis and Metridium senile from high current areas off the coast of New Hampshire do not do well in the laboratory (Harris, pers. comm.). Maybe the Gerrish Island population is more sensitive to water movement or oxygen concentration compared to the Gosport Harbor population. Gerrish Island animals were also smaller in maximum size compared to Gosport Harbor animals; these sizes parallel those observed in the field (ch. 1). Perhaps Gerrish Island animals are smaller to minimize the possibility of being dislodged from the colonies of H. echinata on the cribs.

Feeding Rates of Cuthona nana.

The results for the total amount of Hydractinia echinata tissue consumed by Cuthona nana are as expected; a positive relationship between size and amount eaten exists (Fig. 27). More interesting is the positive relationship for small C. nana and the negative relationship for large C. nana with consumption of hydroid mat tissue (Fig. 29 A,B). Juvenile Cuthona nana are picked up by gastrozooids of a H. echinata colony and have been seen on the manubrium of gastrozooids (Rivest, 1978; pers. observ). Entire polyps are too large for consumption, so parts of polyps or mat tissue are grazed. Christensen (1977) observed Precuthona peachi (= Cuthona nana) smaller than 2mm feeding on the basal mat or biting off pieces of polyps. The larger nudibranchs in this study ate 200-500 polyps in a 24 hour period. These results are comparable to those obtained by Christensen (1977). Christensen (1977) also observed larger nudibranchs interrupting their feeding by spawning (and copulating) as I did. This behavior increased the variability of the amount of colony eaten relative to size for sexually mature animals (Fig. 27).

For colonies completely covering hermit crab shells, the mean proportion of colony grazed was less than 10 %, indicating minimal damage to the colony as a whole (Fig. 30). The percentage of shells with grazed patches paralleled the percentage of colonies with Cuthona nana (Fig. 31). Obviously,the extent of damage to a colony depends upon the colony size and a size refuge probably exists for H. echinata relative to predation. The greater the amount of tissue for a colonial animal, the greater the probability of colony survival if damaged by a predator (Jackson, 1979). Often, Cuthona nana begin grazing colonies on the underside of shells. The underside is where colonies settle and are initially smaller. Cuthona nana could wipe out entire colonies, however even these smaller colonies have chitinous spines which

prevent complete removal of polyp tissue. Several of the grazed patches consisted of half polyps left below the height of the spines. Assuming that some gastrozooids remain for feeding, colonies of Hydractinia echinata can regenerate. So, it seems that spines can minimize the degree of damage from predation, though experiments comparing grazing rates on colonies with and without spines are needed.

Predators are not effective in destroying colonies because regeneration rates (in larger colonies) can equal or exceed grazing rates. Previous results with a semi-stoloniferous strain of Hydractinia echinata showed that regeneration rates of polyps on mat tissue were greater than polyp production rates on ungrazed colonies (Folino 1985). This phenomenon was also observed by Braverman (1963b) with the hydroid Podycoryne. Clonal animals tend to have a greater ability to regenerate when preyed upon compared to solitary invertebrates, especially those with sheet growth forms (Jackson, 1977,1979,1985; see review: Hughes and Cancino, 1985). Sheet growth forms have greater interzooid connections to pass food to damaged areas compared to some of the viney hydroids which grow using runners. Hydractinia echinata's ability to regenerate may be one of several factors contributing to the persistence of colonies for greater than a year, compared to more ephemeral hydroids.

Large colonies of Hydractinia echinata are not consumed by Cuthona nana and more grazed patches are observed in months with higher number of nudibranchs (Rivest, 1978; this study). Spines have been proposed to minimize predator damage but the egg-laying behavior of Cuthona nana could be important since nudibranchs leave colonies to lay egg masses (Harris et al. 1975; Rivert, 1978; this study). This behavior is addressed more thoroughly in chapter 3, but may prevent total grazing of colonies. A third possibility,

besides the presence of spines and nudibranch egg-laying behavior, is the inducible defense hypothesis proposed by Harvell (1984). Harvell observed intraclonal differences in palatability in bryozoa colonies for dorid nudibranchs. Studies with the gastropod Cyphoma gibbosum suggest short residence feeding times on gorgonians, perhaps due to a morphological or chemical change in the gorgonians after predation (Gerhart, 1986; Harvell and Suchaneck, 1987). Maybe a substance is produced in Hydractinia echinata which makes colonies less palatable once grazed. Laboratory observations seem to indicate that once grazed, colonies are grazed again, but this may be due to the grazed colonies being the only available food for Cuthona nana. Furthermore, juvenile Cuthona nana remain on colonies for up to eight weeks until sexual maturity is reached, suggesting the lack of a noxious substance being produced. Detailed experiments examining residence time on colonies grazed versus those not previously grazed would address this hypothesis in Hydractinia echinata.

CHAPTER III

THE ROLE OF HERMIT CRABS IN THE ASSOCIATION OF CUTHONA NANA AND HYDRACTINIA ECHINATA

INTRODUCTION

The relationship between H. echinata and hermit crabs is considered mutualistic. Hydractinia echinata protects the crabs from predators (Grant and Ulmer, 1974; Brooks and Mariscal, 1985b), other organisms settling on the shells (Conover, 1979) and may reduce competition for shells among crabs (Karlson and Cariolou, 1982; Mercando and Lytle, 1980; Wright, 1973). All of these factors are proposed to enhance the crab's survival. Other papers present the benefits of hermit crabs inhabiting shells with Hydractinia echinata, and show selection preferences for colony-covered shells by the crabs when offered shells with and without H. echinata (Jensen, 1970, 1975; Grant and Pontier, 1973; Wright, 1973; Conover, 1976; Mercando and Lytle, 1980; Brooks and Mariscal, 1985a). Crab movement provides food for H. echinata (Christensen, 1967) and keeps the hydroid from being buried in the sediment (Conover, 1979). Movement patterns of hermit crabs have also been studied (Hazlett, 1981; Rebach, 1974, 81; Asakura and Kikuchi, 1984), but to my knowledge, no studies deal with how hermit crab movement affects the accessibility of predators to epifaunal prey organisms on the shells.

Cuthona nana has direct development and eggs are laid off the hydroid colonies on hermit crab shells (Rivest, 1978, chapter 2). This requires juvenile nudibranchs and egg laying adults to find moving colonies of Hydractinia

echinata. It is therefore the movement of the hermit crab that is important in bringing the prey, Hydractinia echinata, to the slow-moving predator, Cuthona nana. Knowing the probability of a hermit crab passing a given position on the ocean bottom would provide information on the chances of C. nana encountering food. Postlarval C. nana are picked up by the gastrozooids of the hydroid colony passing by (Rivest, 1978). Adults leave colonies to mate and lay egg masses and are faced with returning to a colony for food. Thus, the movement of hermit crabs may play different roles for immature and mature Cuthona nana. Preliminary field observations indicate that larger, sexually mature C. nana leave colonies of H. echinata more than do juveniles (Rivest, 1978; pers. observ). The purpose of this study is to measure the dynamics of nudibranch and hermit crab movement. This chapter includes two experiments: one experiment dealt with differences in juvenile and adult Cuthona nana movement onto and off of H. echinata colonies in the laboratory. The other experiment looked at the movement of hermit crabs in the field to estimate prey accessibility for C. nana.

METHODS

Nudibranch Movement

The first portion of this study dealt with differences in movement between immature and juvenile Cuthona nana onto and off of colonies of Hydractinia echinata covering hermit crab shells. In the laboratory, hermit crabs were kept in trays (76cm x 64cm x 9cm) with sand from Gosport Harbor. Crab shells were labeled with beetags (from Chr. Graze KG, West Germany) to monitor the presence or absence of nudibranchs. Tagging the shells provided an indirect way of recording nudibranch movement onto or off of a given colony since nudibranchs are difficult to tag. Each tray contained 10 tagged crab shells with H. echinata and 4 nudibranchs. The densities of both animals were determined from the highest densities recorded from the cofferdam samples (May 1987) presented in chapter 2. Two trials with two replicate trays were run using adult nudibranchs 12-20 mm in length. Each trial lasted 12 days and crab shells were checked 2 times a day for the presence or absence of nudibranchs. Nudibranch movement was measured by calculating the mean number of moves on or off of a colony per day. A similar experiment was conducted using juveniles 2-4 mm in length. One trial was run with four trays as replicates; the trial lasted 21 days.

Hermit Crab Movement

It seems that hermit crab movement is important in bringing the prey, Hydractinia echinata, to the slow moving predator, Cuthona nana. Thus, knowing the probability of a hermit crab passing a given position on the ocean bottom is valuable. Hermit crab movement was estimated by setting out pitfall traps (Uetz and Unzicker, 1976) on the bottom of Gosport Harbor to catch

crabs passing a given point in a 24 hour period. The traps were plastic containers approximately 11 cm in diameter and 15 cm deep. Two imaginary grids measuring 5x5 meters were used to randomly position the 20 pitfall traps. Holes were dug in the sand using an airlift; containers were placed in the holes and sand was leveled flush with the lips of the containers. Each container was marked with a numbered flag to insure that the containers could be found although a few traps were filled in and were not located during 2 of the 4 trials. During a given trial, the traps were left uncovered for 24 hours from mid-morning to mid-morning. The following day each trap was emptied and covered until the next run. Runs were done monthly from Jaunary through May 1988; April was excluded.due to rough seas. The number of crabs caught in each trap and the presence or absence of H. echinata colonies on the shells of each crab were recorded. Other characteristics were recorded for each crab such as: 1) crab species, 2) shell type, 3) the sex and estimated % cover of hydroid colonies, 4) the presence of tentaculozooids, 5) the presence of interacting colonies of H. echinata, and 6) the presence of C. nana. These results provided general information on hermit crab epifauna discussed in the previous two chapters. The percentage of shells with H. echinata estimated colonies passing a given area with prey potentially available for C. nana.

RESULTS

Nudibranch Movement

The results of nudibranch movement on and off of H. echinata colonies showed that juvenile nudibranchs (2-4mm) did not leave shells covered with Hydractinia echinata (Fig. 32). No juvenile nudibranchs left the colonies they were initially placed on in any of the four trays during the 21 day trial. In contrast, adult nudibranchs (12-20mm) in both trials, each lasting 12 days, showed movement. The adults moved on and off of colonies, often averaging 1 to 2 moves per day. Activity was obviously much greater for adults when compared juveniles. Often during the adult trials, I observed animals mating and laying egg masses on rocks and the sides of the seawater tables. No egg masses were laid on colonies of H. echinata on the hermit crab shells during the experiment, which is what was seen in field observations (ch. 2).

Hermit Crab Movement

The results of this experiment indicate a great amount of hermit crab activity over a 24 hour period. In a 24 hour period, the mean number of crabs caught per trap ranged from 15-26 (Table 6). The mean number of crabs caught with H. echinata on the shells ranged between 3-8 (Fig. 33). An average of 6 crabs with a colony passing a given point in a 24 hour period suggests a high probability of prey encounter for a nudibranch on the bottom of Gosport Harbor. The data also show an increase in the number of shells with Hydractinia echinata from March to May.

DISCUSSION

The results of the nudibranch movement experiment indicate behavorial differences in juvenile and adult Cuthona nana. Juveniles appear to remain on a colony of Hydractinia echinata for as long as food is available or until sexually mature. Most other hydroid-feeding aeolids have planktonic larvae which settle on sessile colonies (Todd, 1981, 1983). Other nudibranchs, like dorids, also feed on stationary prey, such as barnacles, and settle near the prey. In both examples presented, encounters for mating are enhanced if several individuals are attracted to settle near the same prey item (Potts, 1970; Todd, 1978a,1979). Potts' (1970) work with Onchidoris fusca suggests that the nudibranchs probably remain on the same rock they initially settled on since ample food and mates are present. Field experiments by Todd (1978a, 1979) on Onchidoris muricata and O. bilamellata show an increase in aggregation during the breeding season. This distribution during the reproductive season suggests decreased crawling to stay within the area of food and sexually mature individuals. Todd (1979) proposed the use of mucous trails by these animals to find either new food or mates. Other examples besides Todd's (1979) exist for opisthobranchs documenting the role of mucous trails in finding either food and/or mates (Lowe and Turner, 1976; Hadfield and Switzer-Dunlap, 1984; Gerhart, 1986). Nudibranchs use their rhinophores as chemoreceptors to detect prey items and/or mates (Harris, 1973; Hadfield and Switzer-Dunlap, 1984). Once off a colony, mucous trails may be important for C. nana in finding mates.

Compared to the observations of Potts (1970) and Todd (1978a, 1979), the opposite behavior seems to exist for Cuthona nana. Movement of adult C. nana

off of colonies increases the chances of encountering both prey and mates. Sexually mature individuals increase activity to find food, mates and/or a place to lay eggs masses.

Cuthona nana at Gosport Harbor lay egg masses completely off colonies of H. echinata onto rocks, Chondrus and mussel shells (Rivest, 1978; pers. observ.). A similar behavior was observed with Phestilla melanobranchia (Harris, 1975). P. melanobranchia laid egg masses in areas where coral tissue had been cleared away by grazing. Adult C. nana are more common crawling on the bottom of Gosport Harbor during the reproductive months of April through September as observed by Rivest (1978) and I. The results of the laboratory nudibranch movement experiment support these field observations of adult activity (Fig. 32). If hermit crab shells are small in area compared to adult C. nana, areas of hydroid colony void of gastrozooids may be too small for depositing egg masses where hatching juveniles would not be consumed by polyps. As previously mentioned, hydroid-feeding aeolids often settle on a colony, undergo metamorphosis and begin feeding within the colony (Todd, 1981,1983). Therefore, once an individual is within a colony, ample food is most likely available for growth through sexual reproduction. Egg masses are normally laid within the colonies; veligers are planktonic providing a means of dispersal to locate new food sources. In contrast, Cuthona nana at Gosport Harbor lacks a planktonic veliger and deals with a mobile prey. Up to several hundred eggs are deposited in an egg mass (ch. 2); thus, numerous juveniles are present in a given area at hatching. If an egg mass were laid on a colony, the young nudibranchs would be concentrated in number on the colony and would quickly consume the prey. Recall that juvenile C. nana are presumably picked up by gastrozooids sweeping along the bottom as a crab passes by. This

movement of hermit crabs may help to distribute juvenile nudibranchs so that the immediate food source is not depleted quickly.

This phenomenon of juveniles being picked up by the prey is somewhat similar to a host-parasite relationship, such as seen with intermediate stages of parasitic trematodes, flukes or hookworm larvae (Cheng, 1970). Cuthona nana (or "parasite") may wait for the prey (or "host") to pass by on a hermit crab shell. Cuthona nana (and other nudibranchs; Harris, 1973) is perhaps also similar to a parasite by being a specialist on H. echinata. Again, similar to parasites, (Price, 1980), C. nana is not a fast-moving predator, "chasing" colonies of H. echinata moving about on hermit crab shells. It seems probable that crabs sit stationary long enough for adult C. nana to crawl onto a colony on the shell. Hermit crabs are known to remain stationary and filter feed (Gerlach et al; 1976; pers observ: field and lab). Less active juvenile nudibranchs can survive for 6 weeks at 12°C or 10 weeks at 4°C without food (Rivest, 1978). This leaves plenty of time for a hermit crab to pass by with prey. The results of the pitfall experiment indicate that crabs with colonies of H. echinata are fairly active in a twenty four-hour period, providing sufficient encounters with prey for both juvenile and adult C. nana. Thus, the movement and egg-laying behavior of C. nana adults seems to be advantageous, at least at Gosport Harbor, for encountering a mobile prey and for finding mates to then lay egg masses where juvenile survival will be enhanced.

SUMMARY

Numerous studies demonstrate the importance of predation in influencing the structure of terrestrial, freshwater and marine communities. A great deal of the terrestrial literature pertains to insects and their plant prey (see review: Futuyma, 1983) while several aquatic predator-prey examples deal with various marine and freshwater organisms (review: Kerfoot and Sih, 1987). It is important to examine the dynamics of specific predator-prey interactions so one can predict what role such interactions play in forming the structure of a given community (Hassell, 1978). Furthermore, information about specific predator-prey associations provides insight for understanding the mechanisms involved in maintaining these associations. Characteristics such as behavior, population patterns, growth and development for both predator and prey allow one to speculate about possible selective pressures in the establishment of specific associations (Price, 1980). Presumably selective pressures between predator and prey may act in the coevolution of a specific association (Vermeij, 1983). However it is often hard to document such pressures that predator and prey have on one another in a coevolving relationship (Futuyma and Slatkin, 1983). One hypothesis of coevolution states that both predator and prey adapt 'to stay even with one another' (Roughgarden, 1983) by reciprocal counteradaptations. This phenomenon of reciprocal adaptation is especially exemplified in organisms which occur intimately, such as those in parasite-host relationships (Price, 1980).

Several species of the nudibranch genus Doto such as Doto pinnatifida and Doto tuberculata are specialists on their hydroid prey (Todd, 1981). This

specificity with the prey is similar to that of parasites in symbiotic relationships with hosts (Rees, 1967; Harris, 1973). Swennen (1959) proposed that some nudibranchs be considered ectoparasites. Rees (1967) later suggested that nudibranchs which feed on one hydroid type are obligate predators and are therefore similar to parasites. Cheng (1970) defines parasitism as an "intimate and obligatory relationship between two heterospecific organisms". Since C. nana is an obligate specialist on H. echinata, one can classify this association as symbiotic and as being similar to a parasite-host association. Cuthona nana feeds exclusively on H. echinata and is adapted to its prey by being immune to the nematocysts of H. echinata. This immunity allows for movement and feeding throughout colonies. Other nudibranchs such as Dendronotus frondosus and Coryphella verrucosa must feed around the periphery of H. echinata colonies, otherwise they are killed by nematocysts (Harris et al., 1975; pers. observ.).

Parasitism is further explained as one organism benefiting at the expense of another without the host (prey) being completely consumed or killed by the parasite (predator) (Ahmadjiam and Parcer, 1986; Smith and Douglas, 1987). A nudibranch considered an obligate parasite on its prey rarely destroys its colonial prey (Rees, 1967; Harris, 1973). The only previously documented association which parallels Cuthona nana's association in terms of partial predation is the nudibranch Dendronotus iris and its specific anthozoan prey, Cerianthus sp. (Wobber, 1970). Dendronotus iris crops and does not destroy its long-lived prey (Wobber, 1970). Wobber (1970) suggests that D. iris and its prey evolved forming an intimate association similar to that of a parasite and host. Again, C. nana fits this classification in that it generally does not consume or kill its prey. The host is only partially consumed and can survive attacks by regenerating (both sites), being large

(Gerrish Island) and being mobile on the shells of hermit crabs (Gosport Harbor).

Importantly, one must understand the life histories of the organisms in a predator-prey (parasite-host) association to discover how these relationships are maintained (Feder and Lauder, 1986). By documenting the life histories of each organism involved, one can suggest possible evolutionary adaptations. Aspects of an animal's life cycle such as seasonal abundances, mode of reproduction, and growth and feeding biology are important in proposing evolutionary adaptations. I have documented aspects of the life histories of the predator Cuthona nana and its prey Hydractinia echinata to better understand potential mechanisms of adaptation between each organism in this species-specific association. I propose that unilateral (and not reciprocal) coevolution may be responsible for some aspects of the life histories of C. nana and H. echinata. Unilateral coevolution is the 'evolution of one of the members of an association without a specific counteradaptation by the other' (Vermeij, 1983). Predation by C. nana is probably not the most important selective force for the life history features in H. echinata. I believe predation by other organisms, competition and/or benefits from the mutalistic association of growing on hermit crab shells are important factors affecting the life history of H. echinata. On the other hand, prey availability may be the more important selective force for life history features in C. nana.

My work emphasizes the life history of the predator C. nana. I also summarize aspects of the prey's biology using results from this work and information in the literature. To summarize chapters one through three, I will first address aspects of the prey by discussing features such as regeneration and growth, the presence of spines and mobility due to growth on hermit crab shells (Gosport Harbor), which enhance survival relative to

predation. Again these features may not be direct reciprocal adaptations to predation by C. nana, but do enhance the survival of H. echinata when grazed by C. nana. I will then address the life history of the predator and discuss aspects of coevolution to its prey such as abundance, developmental biology and egg-laying behavior. Similarities to parasite-host associations will be presented where applicable.

Hydractinia echinata: The Prey

Being a colonial organism is one aspect of Hydractinia echinata which deters or minimizes complete removal of colonies in a population by predation. Partial predation has received increased attention in recent years in both plants and animals (see reviews: Jackson, 1985; Coates and Jackson, 1985; Harper, 1985; Harvel and Suchanek, 1987). Since Hydractinia echinata is a colonial (and clonal) hydroid, it possesses the ability to regenerate when damaged by predation (Christensen, 1967; Sutherland and Karlson, 1977; Karlson, 1978; Buss et al., 1984; Folino, 1985; McFadden et al., 1986). The collecting data show that a large percentage of a colony remains after predation for regeneration, whether it is a large colony at Gerrish Island or a smaller colony which completely covers a hermit crab shell at Gosport Harbor. The average grazed patch on H. echinata colonies covering hermit crab shells at Gosport Harbor was 37.0 mm^2 (SD=31.4 mm^2, N=80), or an average of 5.57% (SD=5.23, N=80) of the colony (ch.2, Fig. 30). Previous colony measurements of the number of polyps per given area of mat tissue indicate approximately 110.3 (SD=49.2, N=23) polyps on an average mat area of 34. 8 mm^2 (SD=9.55, N=23) (Folino, 1985). These are only estimates since colonies of H. echinata vary in morphology (Buss et al., 1984; McFadden et al., 1984; Folino, 1985), but are useful to make predictions about smaller colonies being completely consumed by C. nana. In addition, a shell completely covered with H. echinata is

estimated to have an average surface area of 813.86 mm^2 (SD=342.96, N=22) (Ch. 2). If 5.57% of a colony consists of approximately 110 polyps (from the above estimates), then a large C. nana would graze approximately 23% of a colony completely covering a shell based on grazing rates obtained in chapter 2. This is less than one-fourth of a colony and leaves a substantial portion for continual growth, assuming that the adult leaves the colony to find a mate or lay egg masses.

Estimates of grazing consider only one large nudibranch on a colony; obviously 2 or more animals would do more damage. Even so, grazing by the predator does not seem to remove prey to the degree of affecting its food supply. If colonies do not cover the shells 100%, then the possibility of being completely consumed exists. Jackson (1985) points out that several colonial marine organisms can withstand predation depending upon their size and are therefore protected against death by a given size refuge. The same appears to hold true for H. echinata. As mentioned in chapter 2, larger C. nana consumed approximately 200-500 polyps in 24 hours suggesting a size refuge for colonies larger than 200 polyps. This is especially evident for the larger colonies at Gerrish Island that are exposed to predation by several nudibrnachs at a given time.

Other deterrents to predation in some colonial marine organisms are structural features such as spines. Spines were induced in response to nudibranch predation in bryozoa and dampen feeding rates (Harvell, 1984). Complete consumption of a H. echinata colony seems to be deterred by the presence of chitinous spines, which prevent complete removal of polyps by large individuals of C. nana (ch. 2). Most if not all colonies observed in the field had spines, which protect polyps from being cropped to the colony base. The remaining polyp "stubs" would allow much quicker regeneration than if

entire polyps and basal tissue were removed. Spine development was not induced in H. echinata in the laboratory when grazed by C. nana (ch. 2), which suggests that spine development may not be an antipredatory mechanism which evolved specifically to deter predation by C. nana. It is possible that spines developed in response to physical abrasion. Spines may protect colonies from being crushed when hermit crabs roll or bury themselves into the sand (Rebach, 1981, pers. observ.), although colonies growing on rocks and pilings also have spines. Whatever the selective pressures for spine development may be, spines do prevent complete removal of polyps and allow for colony regeneration.

Growth and regeneration rates have been estimated for various strains of H. echinata. McFadden et al. (1984) grew colonies of H. echinata at room temperature (approximately 20°C) and estimated colonies to have 500-600 polyps after 50 days. Folino (1985) grew H. echinata at 12°C; the colonies had an average of 235 polyps (SD=93.59, N=8) after 50 days. One can see that estimated growth rates during the early ontogeny of colonies cannot directly compensate for polyp removal by large C. nana on small colonies on hermit crab shells in Gosport Harbor. However, growth rates increase with colony size (pers. observ.), suggesting that larger colonies may be able to produce polyps at a rate closer to that of polyp removal by predators. Therefore, the larger colonies at Gerrish Island may withstand predation better than smaller colonies on hermit crab shells at Gosport Harbor due to their large size. Regeneration rates of H. echinata are greater than early ontogenetic growth rates, presumably due to the presence of several polyps to continue feeding and supplying resources to grow back lost polyps (Folino, 1985). Conceivably, a colony can further withstand predation by means of its ability to regenerate eaten polyps quickly.

The mobility of the hermit crab may limit the degree of predation on Hydractinia echinata at Gosport Harbor. A colony may be partially grazed by C. nana, but may be kept from further predation by other C. nana because of the movement of the crab (Rivest, 1978; this study, ch. 3). (This adaptation is coupled with the behavior of the predator which will be addressed shortly). Therefore, crab movement may help to maintain genetic variability in the population of H. echinata in Gosport Harbor by preventing the complete removal of specific genotypes. Thus, H. echinata's mutualistic association with hermit crabs is a means of minimizing damage due to predation by C. nana.

Cuthona nana: The Predator

It is to the predator's (parasite's) advantage to limit prey (host) damage for the sake of its own survival. This phenomenon is believed to be selected for in host-parasite relationships and is referred to as the prudent parasite model (Holmes, 1983). In terms of survival, this allows for longer life for the host (or prey) and maintains host (or prey) availability for the predator or parasite. The incidence of predators on colonies at Gosport Harbor is also important in discussing the degree of damage to the prey. The percentages of shells with one or more nudibranchs were below 50% except in early spring and summer when percentages were no more than 60% (ch. 1, Fig. 14). Thus, even when predation is heavy in the early spring and summer, nudibranchs only infest half of all of the colonies in the population. This suggests a similarity to a host-parasite association. The fact that C. nana does not swarm its prey may be an evolutionary adaptation which maintains C. nana's association with H. echinata.

Often fluctuations in predator abundances are correlated with prey abundances in species-specific associations (Todd, 1981, 1983). My results support the classification of Cuthona nana as having a subannual life cycle

since several generations are produced per year (ch. 1). In other hydroid-feeding nudibranch life cycles prey abundances decline, followed by a decline in predator numbers (Clark, 1975; Todd, 1981,83). However, H. echinata is a long-lived hydroid so prey abundance is probably not the major factor causing the decline in the population of C. nana in the fall

The longevity of H. echinata colonies provides a stable food source for C. nana. In contrast to small colonies on crab shells at Gosport Harbor, colonies at Gerrish Island are large and stationary (Ch. 1). These colonies are persistent and have existed on the cribs at least since 1970 (Harris, 1975). I have also observed colonies of similar size growing on floats at the Portsmouth Fishing Pier, Portsmouth, New Hampshire. These colonies are at least 5 years old and are in the same locations as first observed in 1983, suggesting that they are the original colonies. Since the colonies at Gerrish Island are long-lived, they provide a stable source of food for the present population of C. nana. Cuthona nana have been observed on colonies at Gerrish Island throughout the year (ch. 1), again indicating that the predators do not disappear due to overwhelming the prey. Although food seems unlimited, these organisms do not grow as large as the C. nana at Gosport Harbor (Ch.2). This, as mentioned earlier, may be due to living in an area of high current; larger animals may be dislodged more easily. Furthermore, if food is readily available to C. nana at this site, then why do not more of the hatching juveniles from egg masses swarm the colonies? Food is probably not the primary factor regulating the Gerrish Island population. Perhaps the egg masses break open before complete metamorphosis, with most juveniles being removed from the area by the strong current. This may also explain the observations of indirect development seen in the 1970's.

Unlike Cuthona nana, most subannual species of aeolids prey upon

seasonally transitory food sources (Todd, 1981). These nudibranch populations show large fluctuations in abundances and are therefore in an unstable relationship with their prey. By analyzing the monthly size classes (ch.1), growth rates (Rivest, 1978; this study, ch. 2) and seasonal changes in temperature, I predict C. nana to have 3-4 generations per year. Throughout these generations,the mean number of C. nana per hydroid-covered shell remained fairly constant (Fig. 15,ch. 1), suggesting a stable relationship between C. nana and its prey. Even with the possibility of crabs migrating to deeper water and thus removing food from the habitat where egg masses are hatching, juveniles can survive for approximatley 10 weeks at 4°C without food (Rivest, 1978), the average temperature during the winter months when crabs seem less abundant in Gosport Harbor. However, there are still crabs present with colonies available as prey in the winter although crabs are more inactive and less mobile (Rebach, 1974; pers. observ.). . So, the population of C. nana at Gosport Harbor survives throughout the year due to slower growth rates in the winter, and the ability of juveniles to survive without food for an extended period.

Predator behavior may play an important role in distributing the impact of grazing on the smaller colonies at Gosport Harbor and thus maintaining prey availability. Adult C. nana repeatedly leave the hydroid colonies in the field and laboratory to lay egg masses (Rivest, 1978; pers. observ.). The results of the nudibranch movement experiment indicate that adults leave colonies 1-2 times per day, most likely to find a mate or lay egg masses (ch. 3). This frequent leaving of colonies by the predator would decrease the degree of grazing on an individual colony. If an adult C. nana remained on a colony covering a crab shell for several days, then perhaps the colony could be compeletely cropped, but this residence time seems unlikely

(ch. 3).

Juvenile C. nana stay- on hydroid colonies much longer (several weeks, chapter 3), but eat less than adults (ch. 3). This behavior is similar to that of plant bugs (Miridae) (Price, 1980). Adult plant bugs are large ectoparasites and are mobile, whereas the immature stages spend most if not all of their time on a single host. Juvenile C. nana show a similar behavior and do not switch colonies in the laboratory, while adults switch 2 times a day on average (ch. 3). Thus differences exist between adult and juvenile residence time, which may affect the degree of grazing on the prey.

Differences in the two populations of C. nana exist in the location of egg mass deposition. Cuthona nana at Gosport Harbor lay egg masses completely off the colonies of H. echinata covering hermit crab shells, while Gerrish Island C. nana lay masses on the interacting zones or on the chitinous bases of colonies void of hydroid tissue (ch. 2). It does not seem that C. nana at Gosport Harbor jeopardizes the juveniles' probability of finding food, since hermit crab movement will bring prey to juveniles on the bottom (Rivest, 1978; this study, ch. 3). If an egg mass was laid on a small colony, the immediate food source could be quickly wiped out. This behavior in C. nana seems to support the prudent parasite model since, again, preservation of the prey is important to the predator's survival (Holmes, 1983).

Direct development in the C. nana population at Gosport Harbor may be an adaptation to a mobile prey (ch. 2). Most prey of aeolid nudibranchs are stationary (Todd, 1981). Todd (1983) emphasizes the close relationship between the reproductive and trophic ecology among nudibranchs and summarizes larval types in this group of opisthobranchs. Most nudibranch species have pelagic, planktonic larvae while C. nana has nonplanktonic, lecithotrophic larvae. With yolk present at metamorphosis, juveniles can survive for up to 6

weeks without food at 12°C (Rivest, 1978). This is ample time for a crab to bring by food (ch. 3, Fig. 33). Furthermore, Rivest (1978) and I have observed that contact with the prey is not necessary for metamorphosis, another feature of direct development favoring the survival of juveniles until their encounter with prey passing by on a hermit crab shell.

Since juvenile C. nana at Gosport Harbor may not disperse as extensively as they might if the larvae were planktonic, we may be seeing a genetically isolated population with local adaptations of development in relationship to prey mobility (Gallardo and Peron, 1982). Since there are suggested discrepancies in the development of C. nana at Gosport Harbor and Gerrish Island, perhaps the population at Gosport Harbor has/is adapting locally to the mobility of the prey by means of development to insure limited dispersal from a habitat where food is stable. The observations of planktonic development in C. nana at Gerrish Island (Harris et al., 1975) support this possibility of a local adaptation in development for C. nana, although a more extensive examination of development type for each location is needed.

Harris (1971, 1973) discusses nudibranch associations as symbioses and stresses that these associations can be used as models in understanding the biological mechanisms involved in predator-prey adaptations. Harris (1973) further suggests using these associations in speculating about the evolution of species-specific predator-prey relationships. I have discussed life history features of C. nana and H. echinata and have speculated on possible evolutionary adaptations. As mentioned, the association between C. nana and H. echinata is most likely unilateral and not reciprocal coevolution. Aspects of H. echinata which function in maintaining this association are probably adaptations not directly caused by C. nana predation. Being colonial, having the capability to regenerate, having spines and being mobile (Gosport Harbor)

may be results of: 1) predation from several predators, 2)competition or 3) aspects involved in the mutualistic association with hermit crabs. Cuthona nana is an obligate predator and is at the mercy of H. echinata in terms of survival. Thus adaptations in growth, mode of development and behavior are most likely a result of C. nana's response to aspects of its prey's life history.

This association between Cuthona nana and Hydractinia echinata can serve as a model for studying similar associations involving colonial (and clonal) prey whether plant or animal. For example, some insects are similar predators to C. nana in that they feed on portions of plants which can regenerate (Silander, 1985). Several marine organisms, particularly other nudibranchs feed on colonial hydroids and bryozoa (Todd, 1981, 1983). Life history traits similar to those of C. nana may exist in other nudibranchs which feed on colonial organisms. The similarites of C. nana to a parasite, in terms of not killing the prey and waiting for prey or host to come by, may shed light on possible mechanisms for other nudibranchs in species-specific associations with their prey. It may also help explain how and why associations have evolved or are evolving among various populations of C. nana.

A unique feature about the association of C. nana and H. echinata at Gosport Harbor is that these two organisms are involved in a 'symbiotic web' (Rees,1967). Rees (1967) suggests, and I agree, that several interactions are occurring in the web on a hermit crab shell. Hydractinia echinata and the crab live mutualistically, while small worms live within the crab shell and feed on loose food particles when the crab feeds. Parasites are housed in the branchial chambers of the crab, while H. echinata polyps feed on the eggs of the pagurid crab. Competitors of H. echinata also exist on the shell (Karlson and Shenk, 1983). Predators such as C. nana may enhance the survival of the hermit crab eggs by cropping polyps on the undersides of the shell where

eggs are most often caught (Rees, 1967; pers. observ.) and may affect competitive outcomes involving H. echinata (Folino, 1985). The majority of C. nana occur on colony portions on the undersides of shells since juveniles are picked up by the hydroid's gastrozooids.

Cuthona nana and Hydractinia echinata coexist as predator and prey by adaptive features present in each as summarized in Figure 34. Hydractinia has spines wich allow only portions of colonies to be consumed. Colonies are capable of regenerating, which prevents complete comsumption of an entire colony. The reproductive biology of C. nana also leads to partial predation in that adults crawl off of colonies. Crab mobility is beneficial to the hydroid colony by moving the colony from the area of predators and by bringing the colony into contact with food on the ocean bottom. Crab mobility can be important for C. nana in helping to disperse nudibranchs amongst colonies and minimize intraspecific competition for food.

Thus,the association between C. nana and H. echinata can shed insight on other species-specific relationships in various systems and can perhaps bring to light some of the possible evolutionary mechanisms involved in maintaining intimate associations between predator and prey or parasite and host. Interactions are often interrelated as suggested by Rees (1967) and others. By understanding the mechanisms and selective pressures in specific associations, steps can be taken to understand and appreciate the complexity of how these associations interact to form a given community.

In summary, the major points of this study are:

1. Unilateral and not reciprocal coevolution may exist in the establishment of the species-specific association of Cuthona nana and Hydractinia echinata.

2. Hydractinia echinata is a persistent prey with the ability to

regenerate and withstand partial predation by Cuthona nana at Gerrish Island and Gosport Harbor (chs. 1,2).

3. The presence of spines on colonies of H. echinata deters the elimination of colonies by C. nana and therefore acts as an antipredatory mechanism, but may not have evolved solely to deter predation by C. nana (ch. 2).

4. At Gosport Harbor, mobility of colonies due to growth on hermit crabs and the behavior of C. nana leaving colonies may enhance the survival of H. echinata by dampening the degree of colony damage by C. nana.

5. Direct development in C. nana at Gosport Harbor may be an adaptation to a mobile food source of H. echinata colonies on the shells of the hermit crabs Pagurus acadianus and P. arcuatus.

6. The species-specificity between Cuthona nana and its prey Hydractinia echinata is similar to symbiotic parasite-host relationships. This association may be used as a model to speculate about evolutionary adaptations and how these adaptations are maintained in different habitats where prey specificity exists.

7. The association of Cuthona nana with Hydractinia echinata on hermit crabs at Gosport Harbor suggests that there are other organisms involved with species-specific associations which need to be considered to understand the complexity of interactions in given communities.

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TABLES

Table 1. The actual frequency distributions of the number of Cuthona nana per hermit crab shells covered with Hydractinia echinata from May 1986 to May 1988. The majority of shells collected had no nudibranchs while those with 1-19 nudibranchs varied over time.

	1986							1987											1988				
# of C. nana	MY	JY	AG	ST	OT	NV	DC	FB	MR	AR	MY	JE	JY	AG	ST	OT	NV	DC	JN	FB	MR	AR	MY
0	18	17	20	69	62	32	54	61	40	27	36	39	56	49	73	70	33	14	39	37	33	25	30
1	5	15	12	9	3	1	4	7	7	18	15	14	18	8	19	9	9	5	11	15	15	19	21
2	3	4	8	5	3		3	4	1	12	14	4	5	6	5	3	2	1	5	3	2	10	7
3	2	0	4	1				1	3	4	7	4	4	1	0	1		1	1	1	3	0	3
4		2	1						0	0	3	1	0	0	1					2	3	0	0
5									0	0	4	1	1	0						0		1	1
6									0	1	0		1	0						0		0	0
7									0	1	1		1	0						1		0	0
8									0		4		1									0	0
9									1		1											0	1
10											1											1	
11											1											1	
12											0												
13											0												
14											1												
15											0												
16											1												
17											0												
18											0												
19											1												
TOTAL	28	38	45	84	68	33	61	73	52	63	90	63	86	65	98	83	44	21	56	59	56	57	63

Table 2. The coefficients of dispersions (variance/mean ratios) and significance of chi-square tests of the fit of the number of hydroid-covered shells with 0-19 Cuthona nana to poisson distributions from May 1986 to May 1988. The numbers in parentheses following the significance values are the degrees of freedom.

1986	variance/mean ratio	X^2 (df)
MAY	1.94	.001 (1)
JUL	6.48	.001(1)
AUG	4.90	.001(2)
SEP	4.19	.001(1)
OCT	.333	------
NOV	1.0	------
DEC	.356	------
1987		
FEB	3.04	.001(1)
MAR	5.83	.001(1)
APR	9.87	.001(2)
MAY	9.30	.001(4)
JUN	3.81	.001(1)
JUL	5.08	.001(2)
AUG	12.93	.001(1)
SEP	9.81	.001(1)
OCT	3.33	------
NOV	4.70	------
DEC	1.73	------
1988		
JAN	4.77	.001(1)
FEB	5.64	.001(1)
MAR	4.56	.001(1)
APR	10.99	.001(1)
MAY	9.33	.001(2)

Table 3. Gerrish Island growth rate data for 14 individuals collected from the field. Animals were divided into 2 groups based on initial size: 1) individual 4-7mm(N=9) and 8-10(N=5). Portion A represents the average growth of body length(mm) per day and portion B represents the average percentage in growth per day.

A. The average growth of body length (mm) per day.

	4-7 mm			8-10 mm		
DAYS	X	STD	N	X	STD	N
7	.016	.048	9	0	0	5
14	.341	.128	9	.086	.128	5
21	.159	.128	9	.257	.119	5
29	.018	.172	7	-.029	.120	5
35	-.057	.128	5	0	.248	3
42	-.095	165	3	-.072	.303	2

B. The average percent increase in body length (mm) per day.

	4-7 mm			8-10 mm		
DAYS	X	STD	N	X	STD	N
7	.199	.060	9	0	0	5
14	3.83	1.24	9	.858	1.28	5
21	1.61	1.25	9	2.35	1.10	5
29	.013	1.76	7	-.286	1.06	5
35	-.520	1.16	5	.037	2.22	3
42	-.867	1.50	3	-.835	2.86	2

Average Maximum Size: 10.6mm (±2.03)
Average Number of Days Survived:36.9 days (±8.30)
Maximum Size Observed: 12 mm

Table 4. Gosport Harbor growth data for 7 individuals collected from the field. Animals were divided into groups of small (1-5mm, N=4) and large (10-12mm, N=3) based on inital size.

A. The average growth in body length (mm) per day.

	1-5mm			10-12mm		
DAYS	X	STD	N	X	STD	N
7	.468	.243	4	.500	.071	3
14	.652	.301	4	.476	.436	3
21	.337	.413	4	.286	.000	2
28	.307	.448	4			
35	.286	.286	4			
42	.143	0	2			
49	-.072	.101	2			
56	-.732	.025	2			

B. The average percent change in body length (mm) per day.

	1-5mm			10-12mm		
DAYS	X	STD	N	X	STD	N
7	6.81	1.38	4	3.36	.626	3
14	5.67	1.21	4	2.49	2.23	3
21	3.60	2.76	4	1.37	.092	3
28	2.10	1.33	4			
35	.757	.798	3			
42	-.135	1.25	2			
49	-1.96	2.79	2			

Average Maximum Size: 19.2 (± 1.72)
Average Number of Days Survived: 42.3 (± 20.9)
Maximum Size Observed: 23 mm

Table 5. Nine control colonies used in determining grazing rates for Cuthona nana. Stolon area is not respresented since it changes as the mat area increases.

Colony	Change in mat polyp #	Change in mat area mm^2	Change in stolon polyp #
1	-28.0	11.57	-1
2	0 11	-3.11	-2
3	0 35	3.41	0
4	102	-0.17	0
5	0 29	58.44	0
6	0 12	3.84	0
7	0	0.42	0
8	5.00	9.95	0
9	-20.0	3.48	-1

Table 6. The mean number of crabs caught per pitfall trap. Also listed are the standard deviations of the means, total number of crabs caught in all traps sampled and the total number of traps for each month.

	X	STD	N	# of Traps
January	15.4	10.20	308	20
February	21.3	11.02	383	18
March	15.0	11.0	255	17
April	26.65	13.91	533	20

FIGURES

Fig. 1. Life cycle diagrams for the nudibranch Cuthona nana and the hydroid Hydractinia echinata. The drawing of the H. echinata life cycle is modified from McFadden et al. (1984).

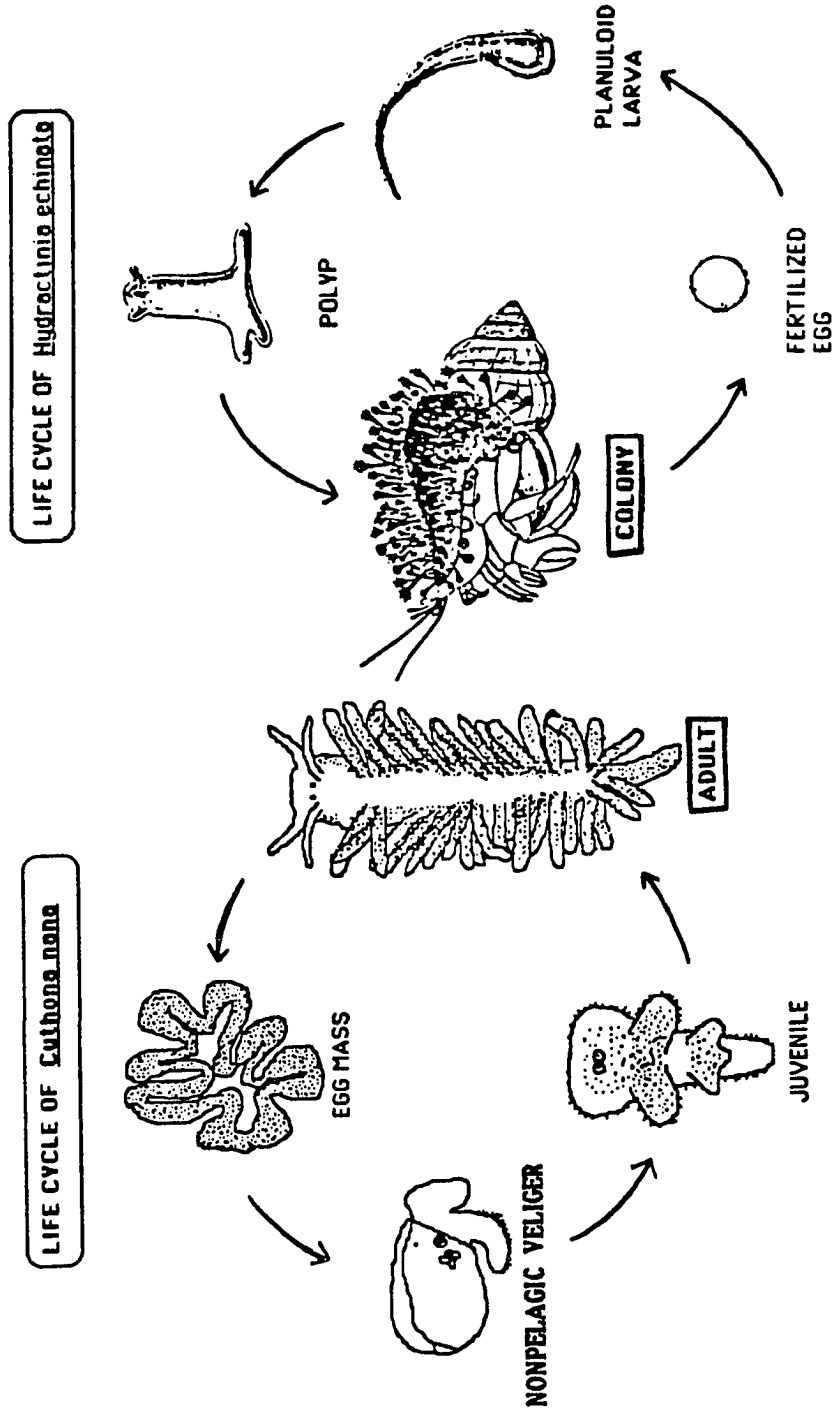


Fig. 2. A map showing the Gerrish Island collecting site, one of the two locations with Hydractinia echinata and Cuthona nana. The cribs are exposed to strong currents in the tidal channel. Collection of data was conducted at the second crib in from Wood Island.

Figure 2

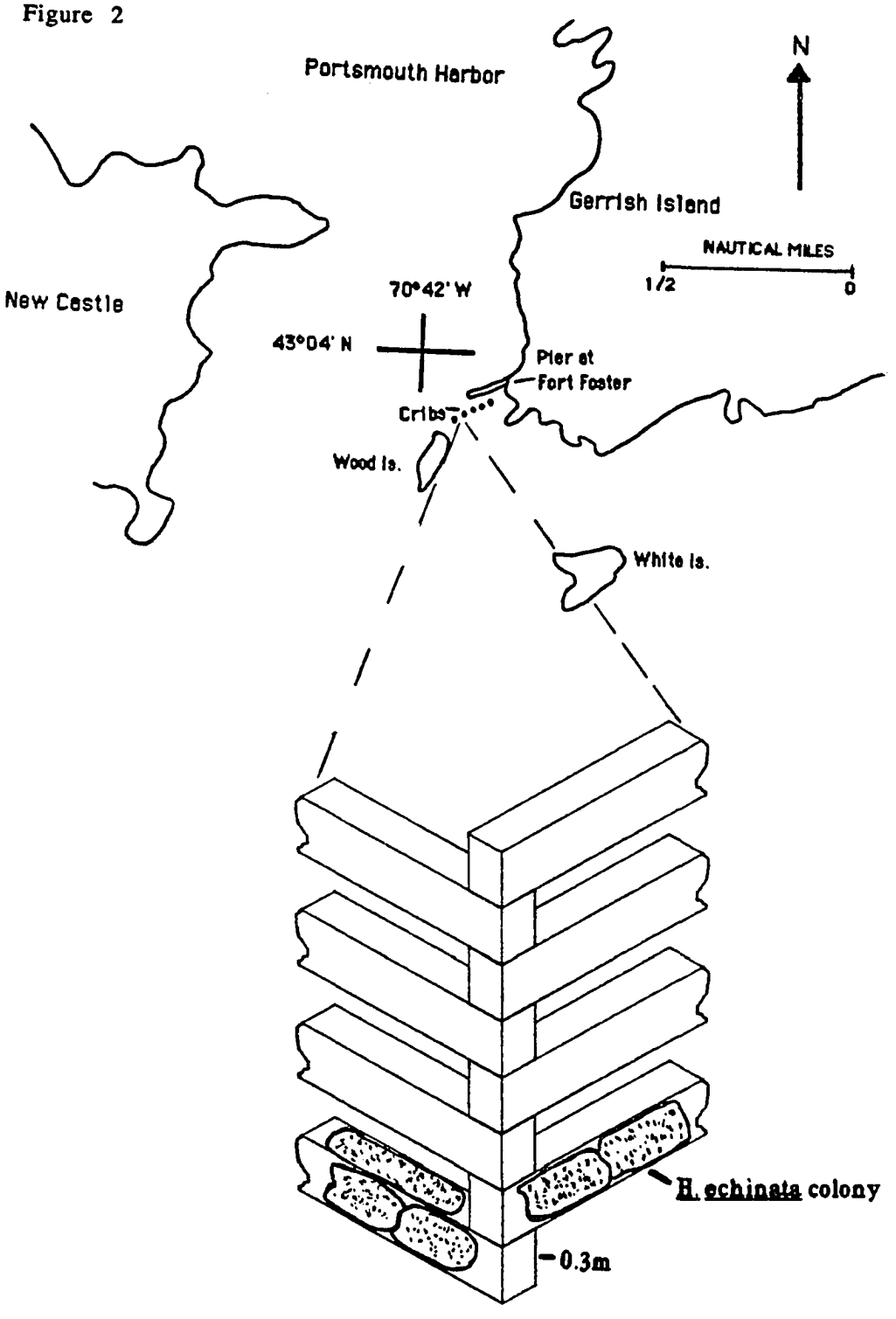


Fig. 3. Map of the Isles of Shoals, Maine. The star indicates Haley Cove, the collection site of hermit crabs with Hydractinia echinata and Cuthona nana in Gosport Harbor (modified from Hulbert, 1980).

Figure 3

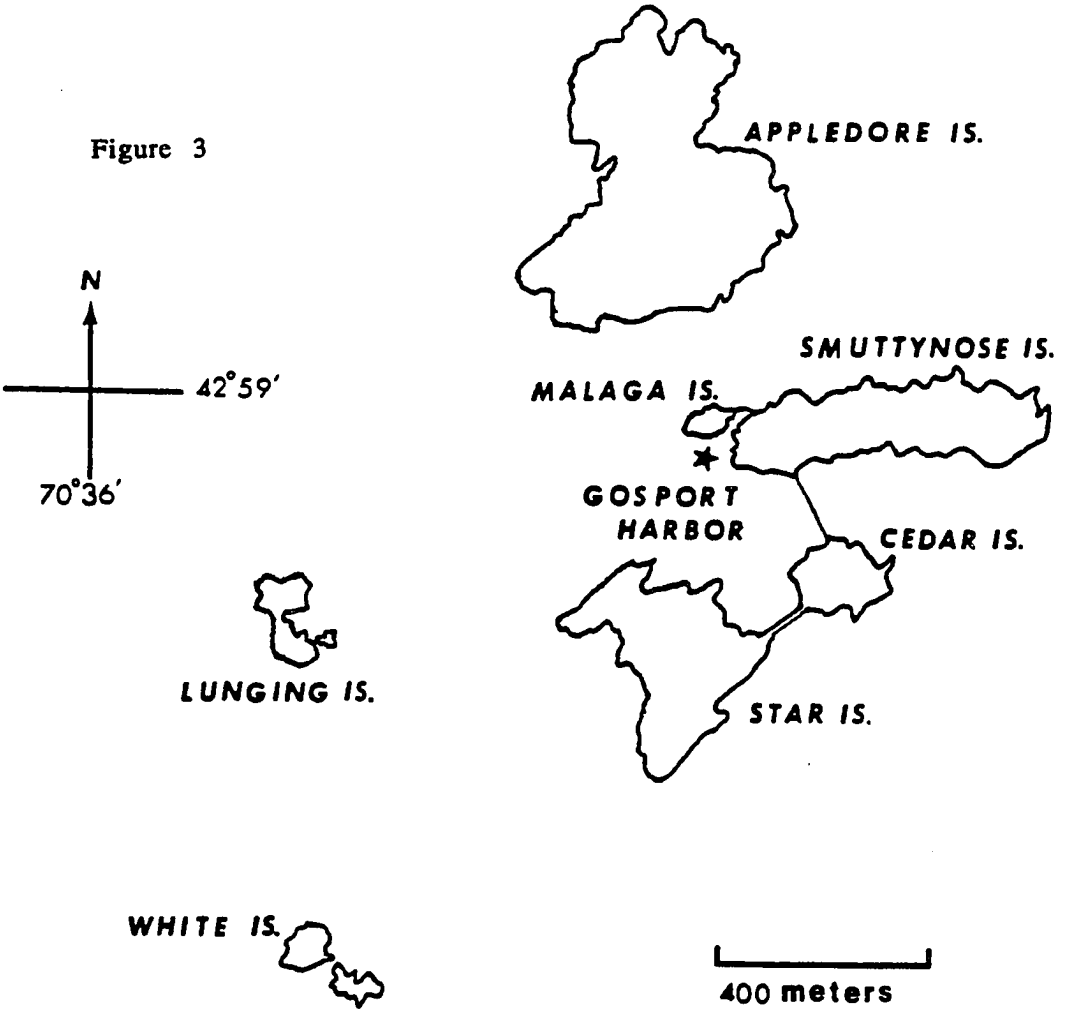


Fig.4. A. Temperatures for Gerrish Island from September 1986 to May 1988.

B. Bottom temperatures for Gosport Harbor, Isles of Shoals, Maine from May 1986 to May 1988.

Figure 4

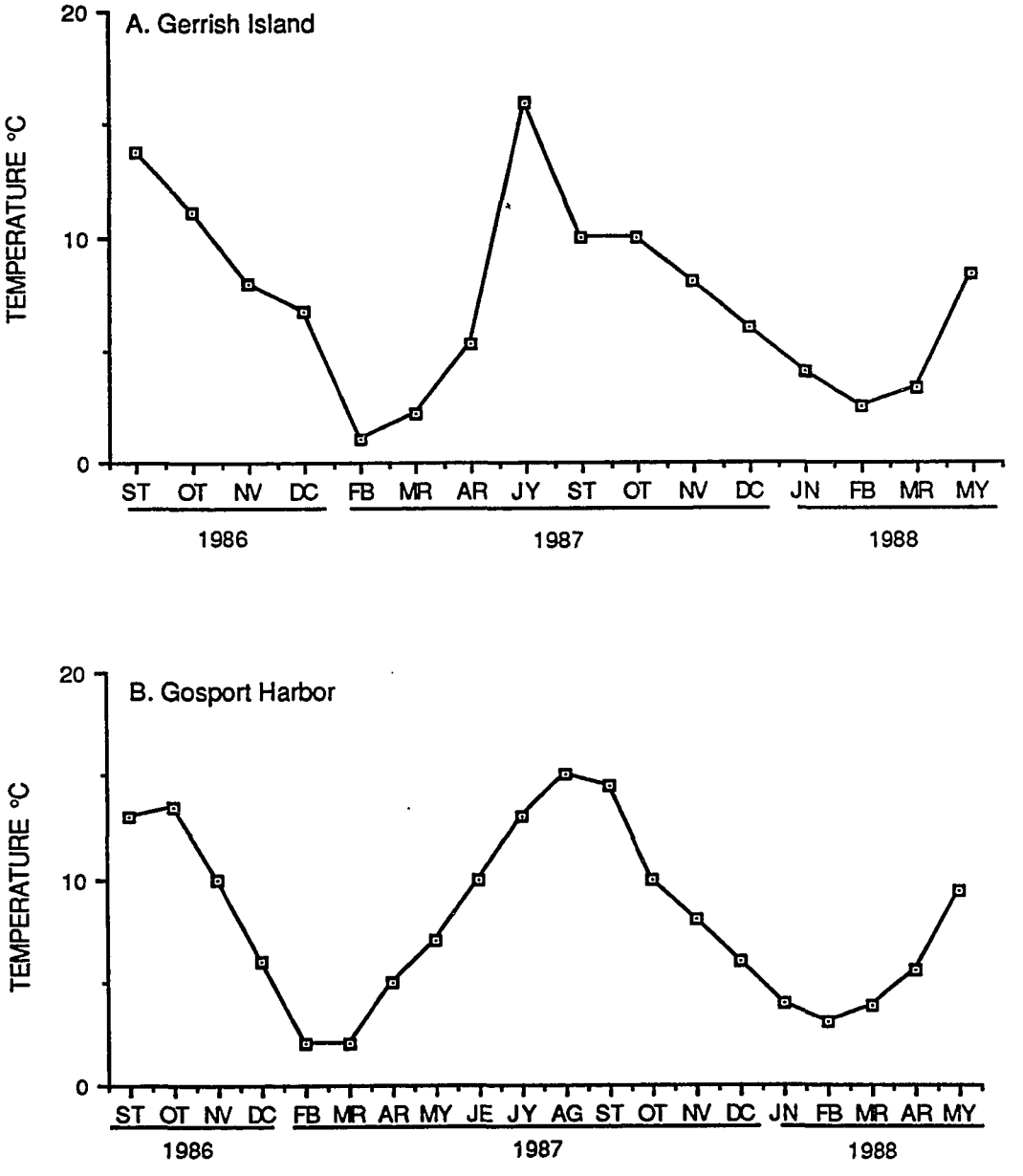


Fig. 5. A. The mean number of hermit crabs/.153m^2 from cofferdam sampling. The bars represent standard error for each mean.N equals the number of cofferdams taken per month.

B. The mean densities of hermit crabs at Gosport Harbor from February, March, April and May of 1988 determined by taking 10 m^2 band transects. The bars represent standard error for each mean. N equals the number of transects taken per month.

Figure 5

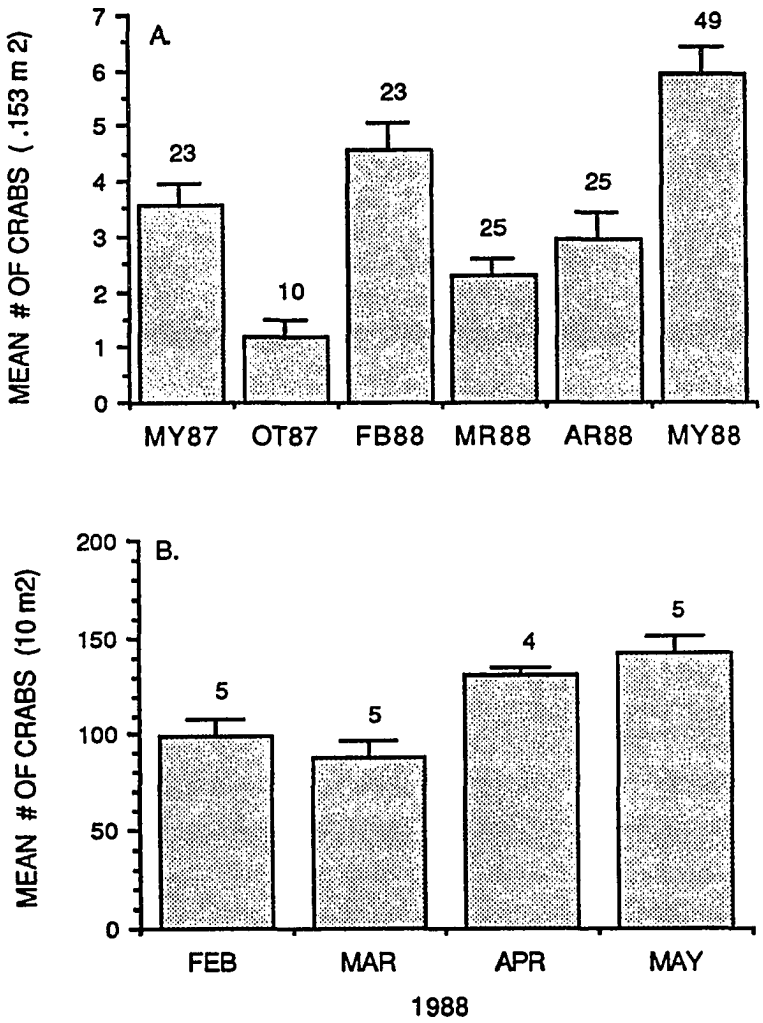


Fig.6. The percentage of grab-sampled hermit crab shells with Hydractinia echinata. Percentages are lower in the colder months and are somewhat greater at least in the fall months although the data are insufficient to speculate about seasonal trends. At leasty 20 % of all shells collected each month had H. echinata colonies.

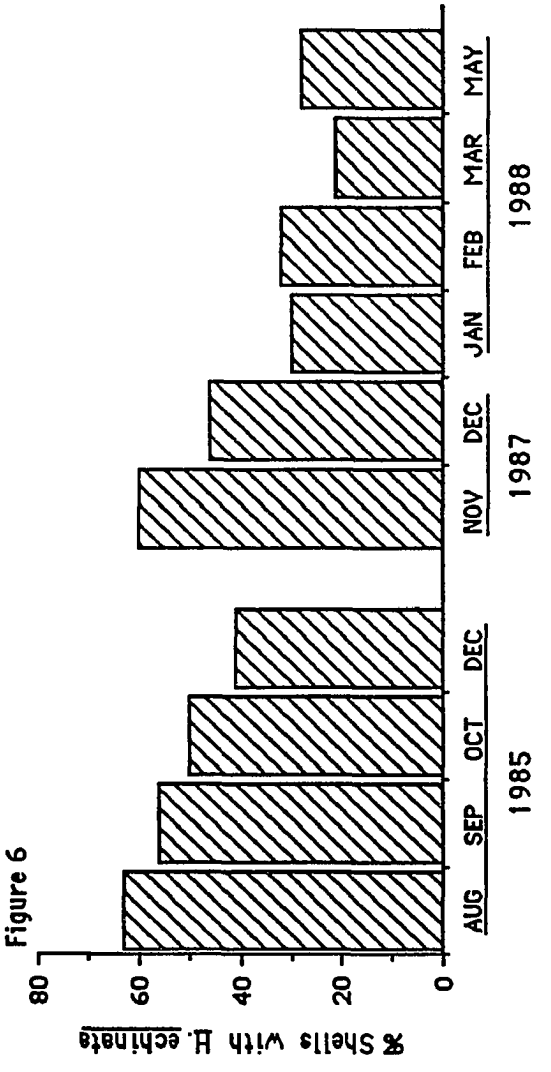


Figure 6

Fig.7. The percentage of grab-sampled shells with small and large colonies of Hydractinia echinata. Small colonies are those covering less than 20% of the shell, while larger colonies cover 80% or more of the shell. There are more smaller colonies present for all months sampled than larger colonies.

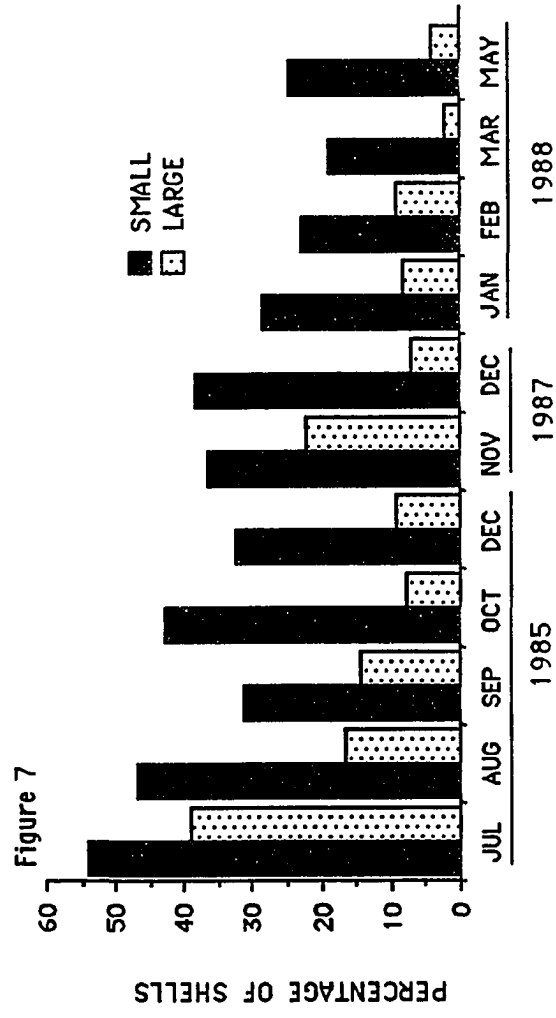


Figure 7

Fig. 8. The percentage of colonies with reproductive structures for the grab-sampled shells. The percentage tends to decrease in the colder months.

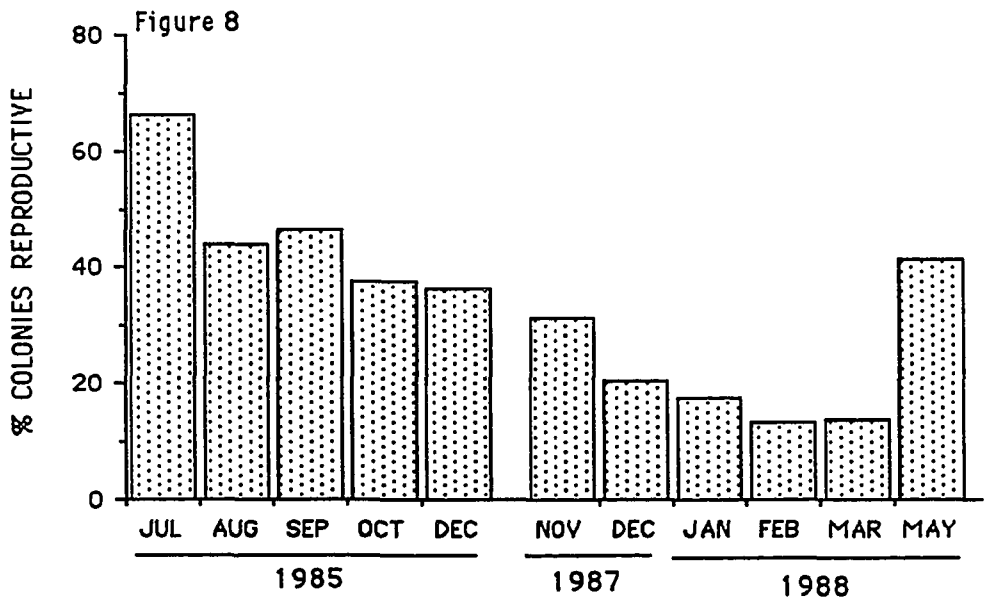


Fig.9. The percentage of grab-sampled shells with 1 or more colonies of Hydractinia echinata. The highest percentage is in July 1985, although all months have less than 11%.

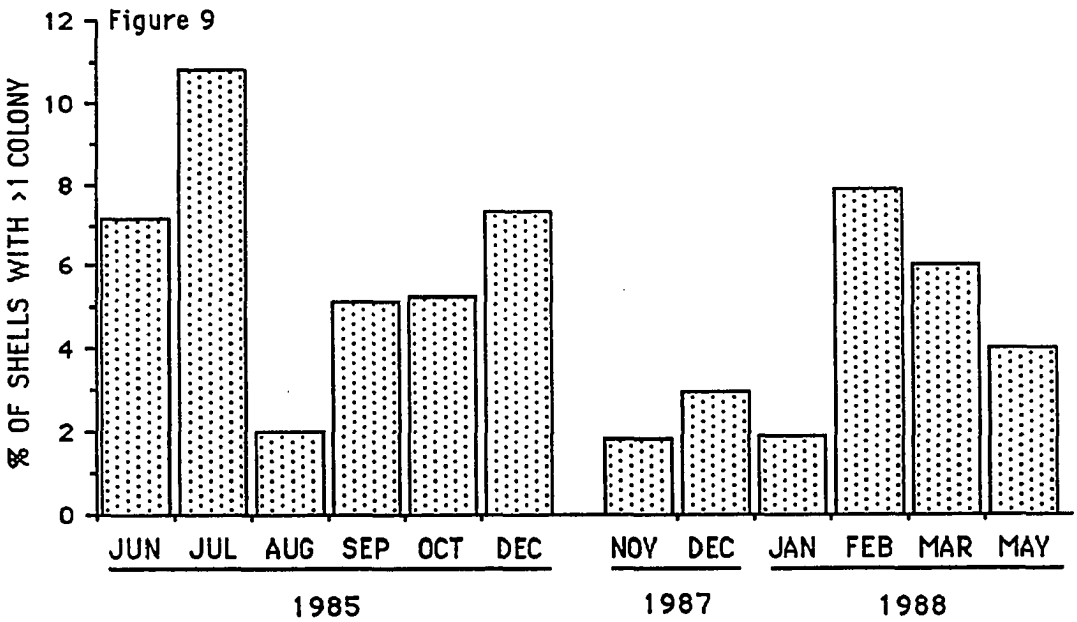


Fig.10 A.The percentage of grab-sampled shells inhabited by P. acadianus. The numbers above the bars represent the total number of crabs collected for each month.

B.The percentage of P. acadianus with H. echinata on their shells. The numbers represent the actual numbers of P. acadianus with colonies on their shells.

C. The percentage of grab-sampled shells inhabited by P. arcuatus. The numbers above the bars represent the total number of crabs collected for each month.

D. The percentage of P. arcuatus with H. echinata on their shells. The numbers represent the actual number of P. arcuatus with H. echinata on their shells.

Figure 10

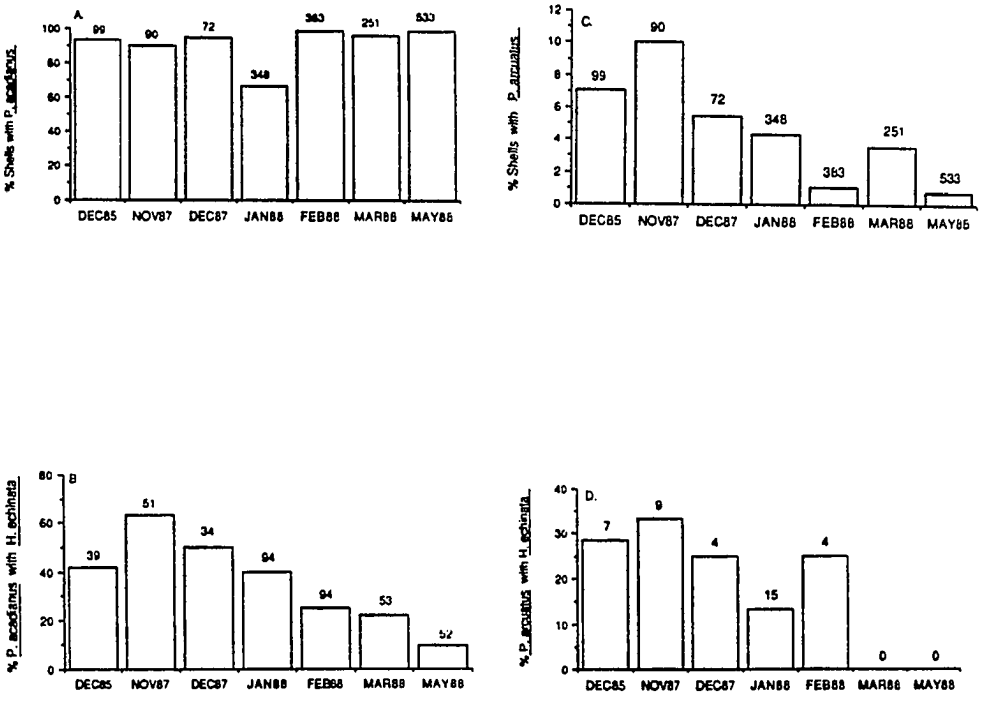


Fig.11. A.The percentage of shell types for the crabs by grab sampling. The numbers in parentheses are the total number of crabs collected for each year. The category labeled 'other' includes Thais, Colus and Buccinum shells.

B. The percentage of shell types for crabs with shells covered with Hydractinia echinata by year. The numbers in the parentheses are the total number of shells collected.

Figure 11

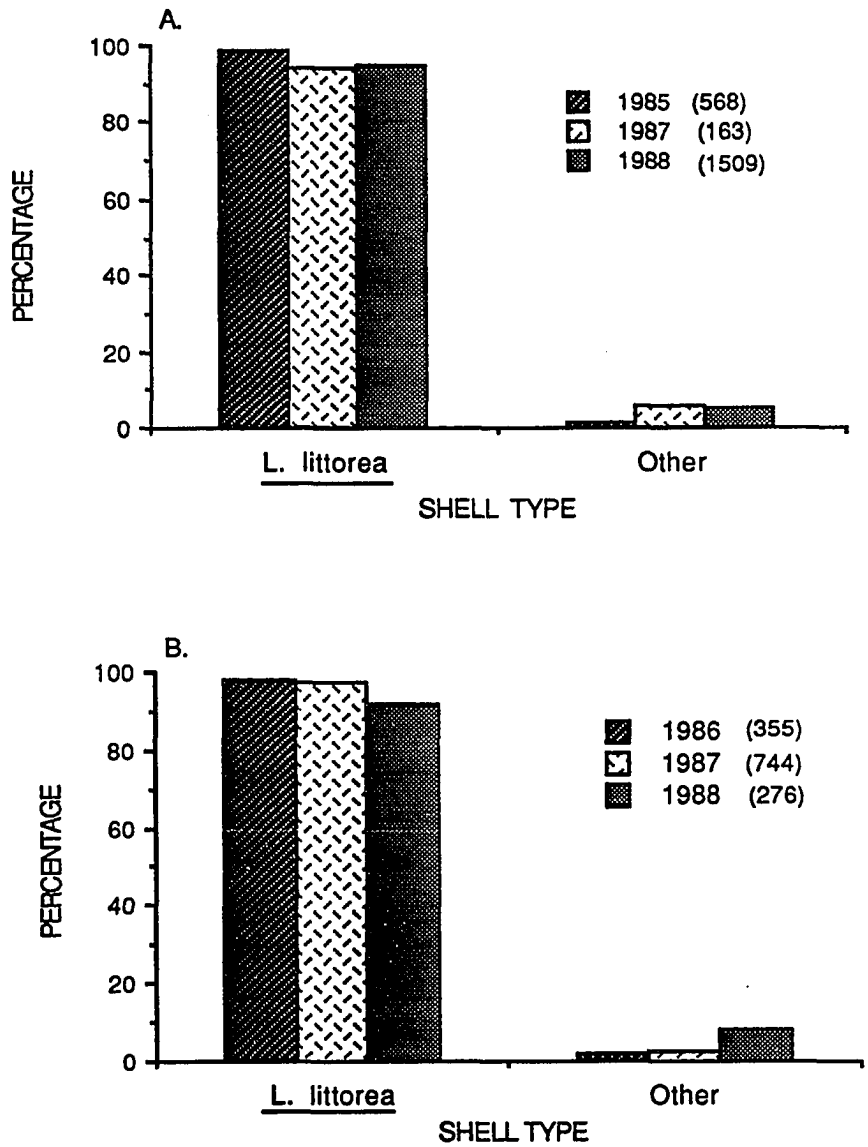


Fig.12. Size frequency histograms for shell size (LxW) of shells covered with Hydractinia echinata collected from May 1986 to May 1988. N represents the total number of shells measured.

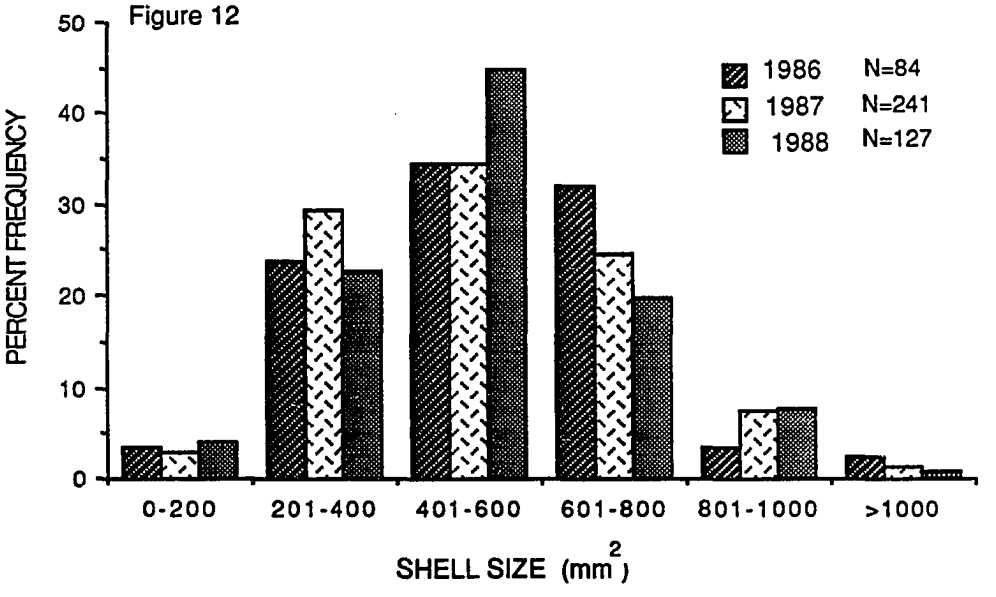


Fig.13. Percent frequencies for Cuthona nana collected from May 1986 to May 1988. Animals collected are grouped as non-reproductive (<1-9mm) and reproductive (>10mm) individuals. The * indicates months when sampling was not possible due to rough seas.

Figure 13

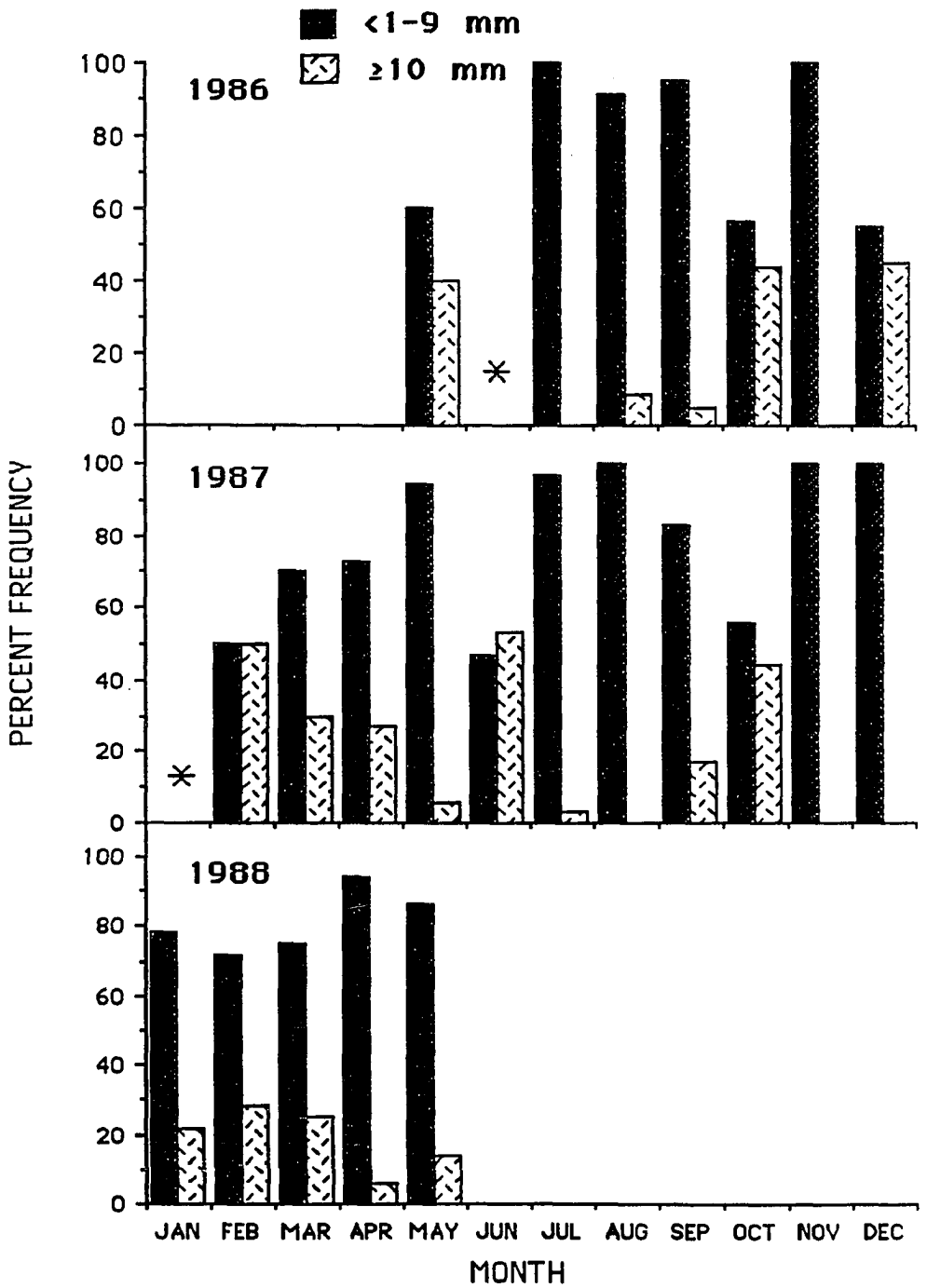


Fig.14. The percentage of hermit crab shells covered with Hydractinia echinata having 1 or more Cuthona nana present plotted with temperature.

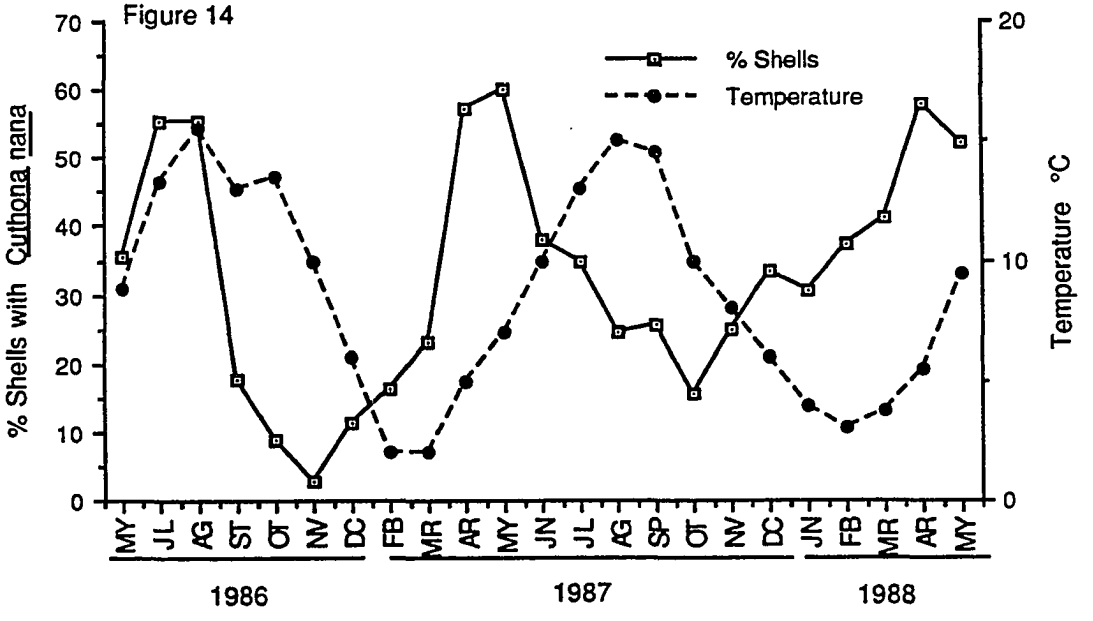


Fig.15. The mean number of Cuthona nana per hermit crab shell covered with Hydractinia echinata for each month sampled from May 1986 to May 1988. The bars for each mean represent standard errors.

Figure 15

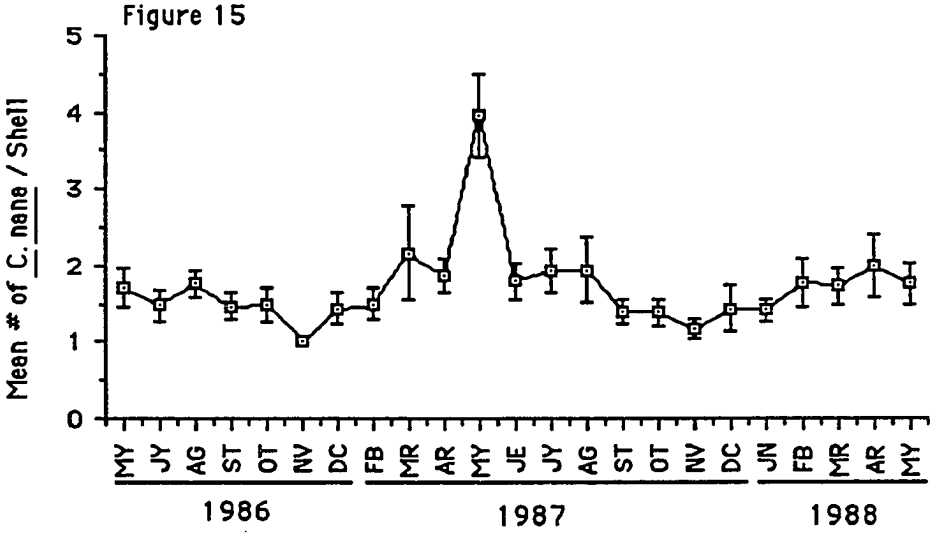


Fig.16. The mean size of Cuthona nana on Hydractinia echinata colonies covering hermit crabs shells graphed with temperature. The bars for the mean sizes represent standard errors.

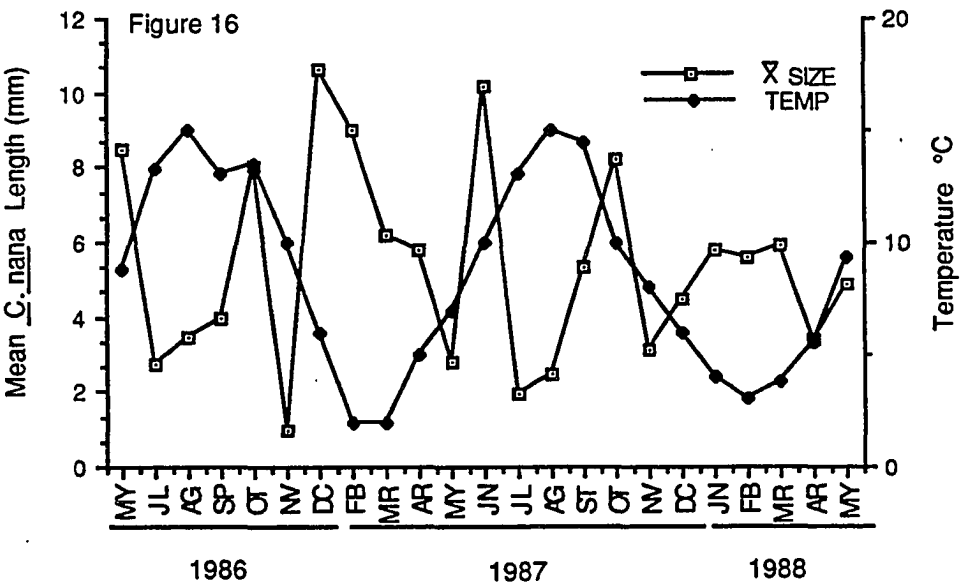


Fig. 17. The percentage of non-reproductive (<1-9mm) and reproductive (>10mm) Cuthona nana scored as being alone, paired or with 3 or more individuals on a hydroid-covered hermit crab shell from May 1986 to May 1988. Chi-square tests indicate a significant difference among the 3 categories for non-reproductive (P<.0001,df2) and nonsignificant differences for reproductive individuals.

Figure 17

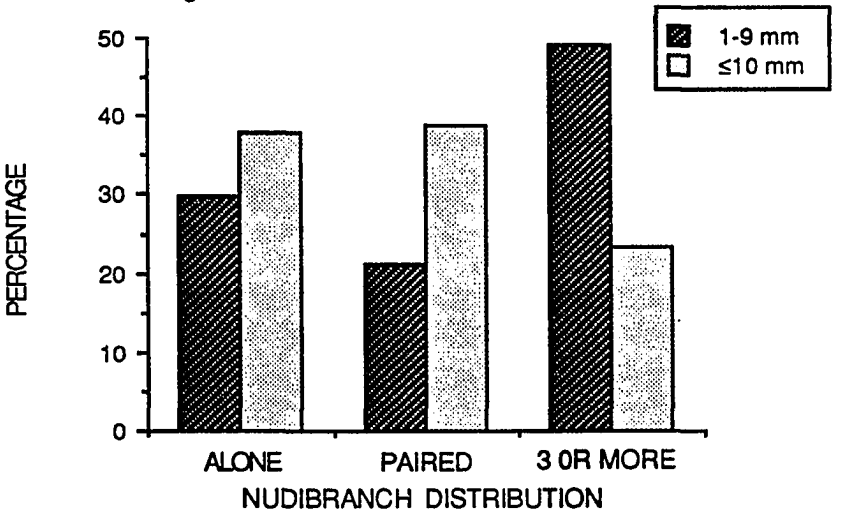


Fig. 18. The growth plots for the viney morph from Gerrish Island in the first trial of the hydroid transplant experiment. Significant differences exist for mat area and stolon area with greater areas occurring in the control or high current colonies (A,B).

Figure 18

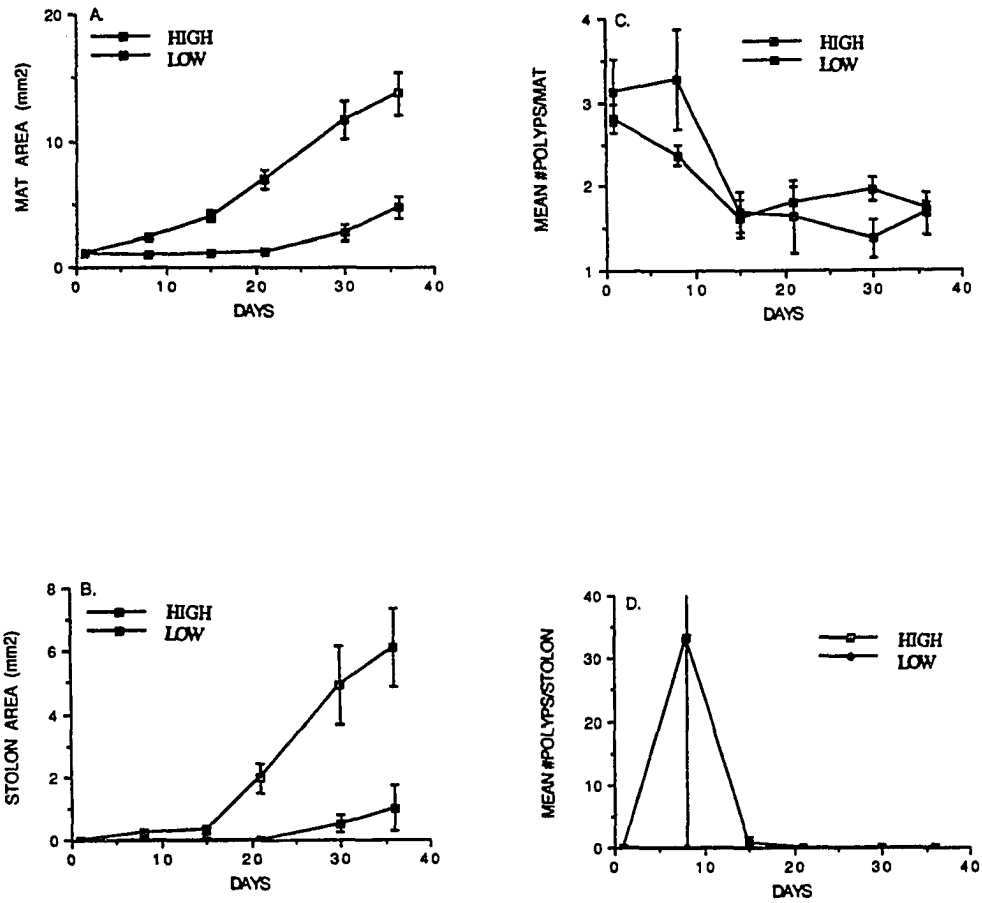


Fig. 19. The growth plots for the viney morph from Gosport Harbor in the first trial of the hydroid transplant experiment. The only significant difference exists in stolon area with the colonies grown in the high current having the greater stolon area (B).

Figure 19

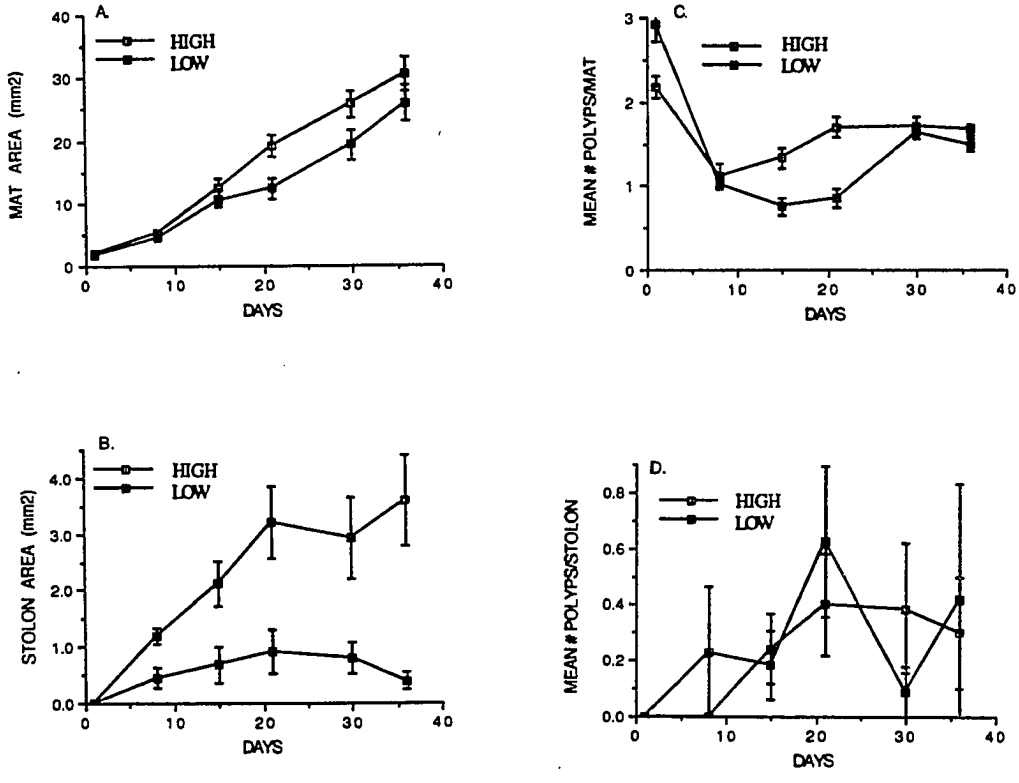


Fig. 20. The growth plots for the viney morph from Gerrish Island in the second trial of the hydroid transplant experiment. A significant difference exists only for the number of polyps per stolon area with a greater ratio occurring in the control or high current colonies (D).

Figure 20

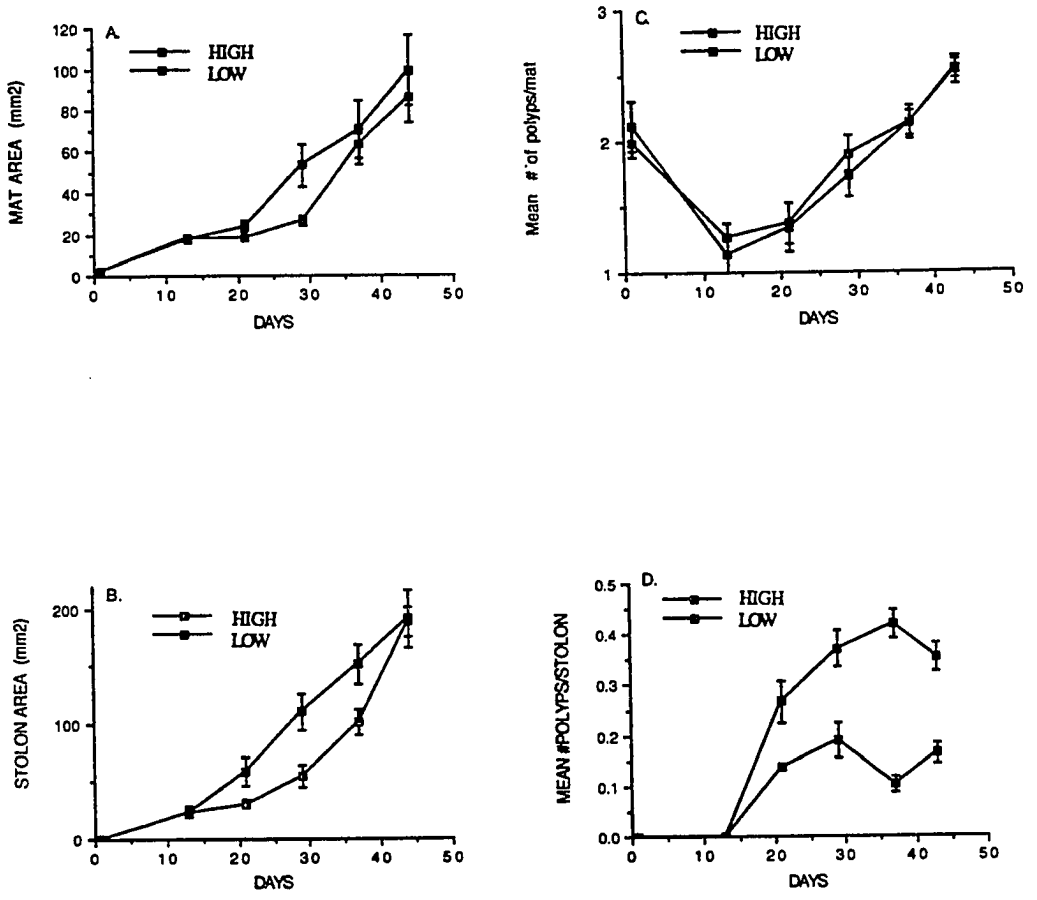
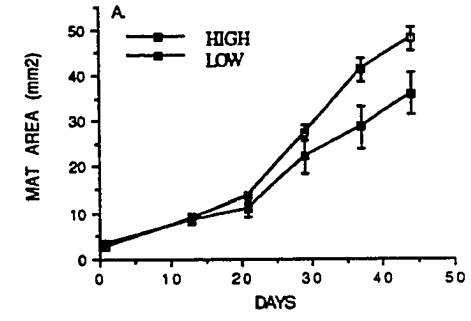


Fig. 21. The growth plots for the matty morph from Gosport Harbor in the second trial of the hydroid transplant experiment. A significant difference exists only for the number of polyps per mat area with a greater ratio occurring in the high current colonies (B).

Figure 21



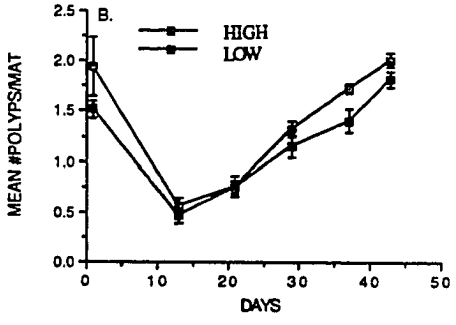
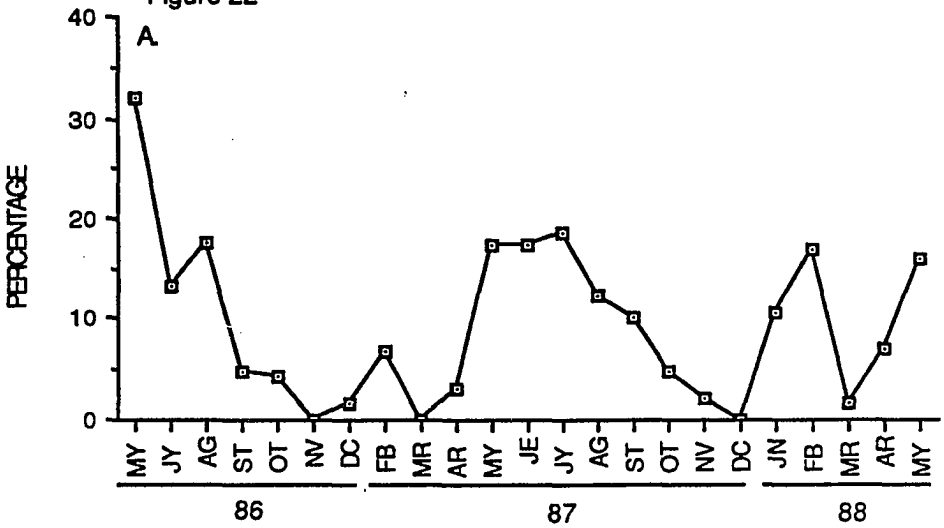


Fig. 22. The percentage of shells with colonies having tentaculozooids for: A. hermit crab shells with hydroid-covered of Hydractinia echinata and, B. grab-sampled hermit crabs.

Figure 22



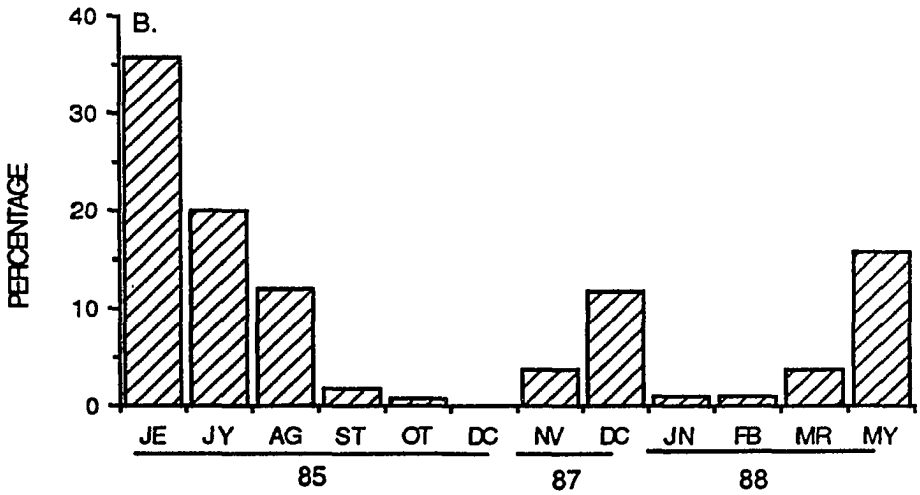


Fig. 23. There were no significant differences in egg and shell size ($p<.197$; $p<.440$, respectively) between Gerrish Island and Gosport Harbor. Egg capsule sizes did differ ($p<.015$) with Gerrish Island capsules being larger with a mean size of 259 um. The bars represent standard errors.

Figure 23

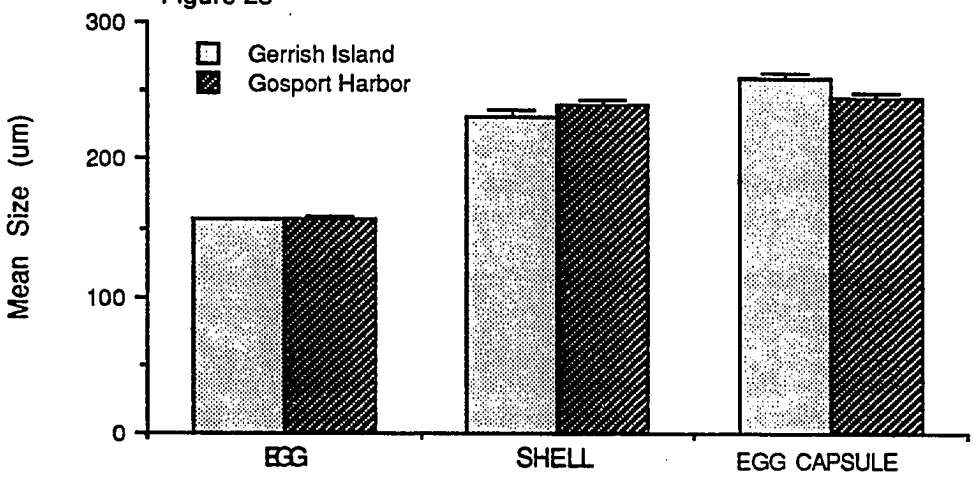


Fig. 24. A. Mean egg mass diameters for Gerrish Island and Gosport Harbor Cuthona nana. No significant differences exist between the two sites.

B. The mean number of eggs/egg mass for Gerrish Island and Gosport Harbor Cuthona nana. No significant differences exist.

Figure 24

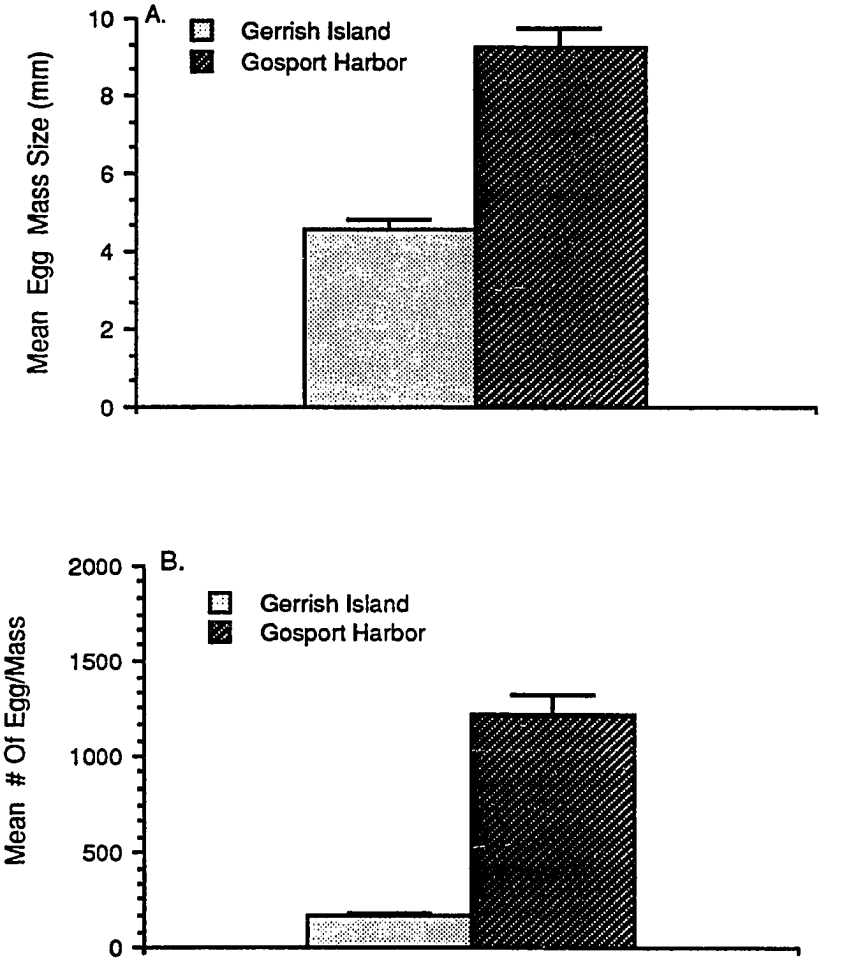


Fig. 25. A.The relationship between time and the growth of Gosport Harbor animals is best described by a quadratic equation. As animals reach 20 mm in size, growth begins to level off and decreases slightly followed by death.

B.The percent change in body length of Cuthona nana (all initially 3 mm) from Gosport Harbor is linear and decreases with time.

Figure 25

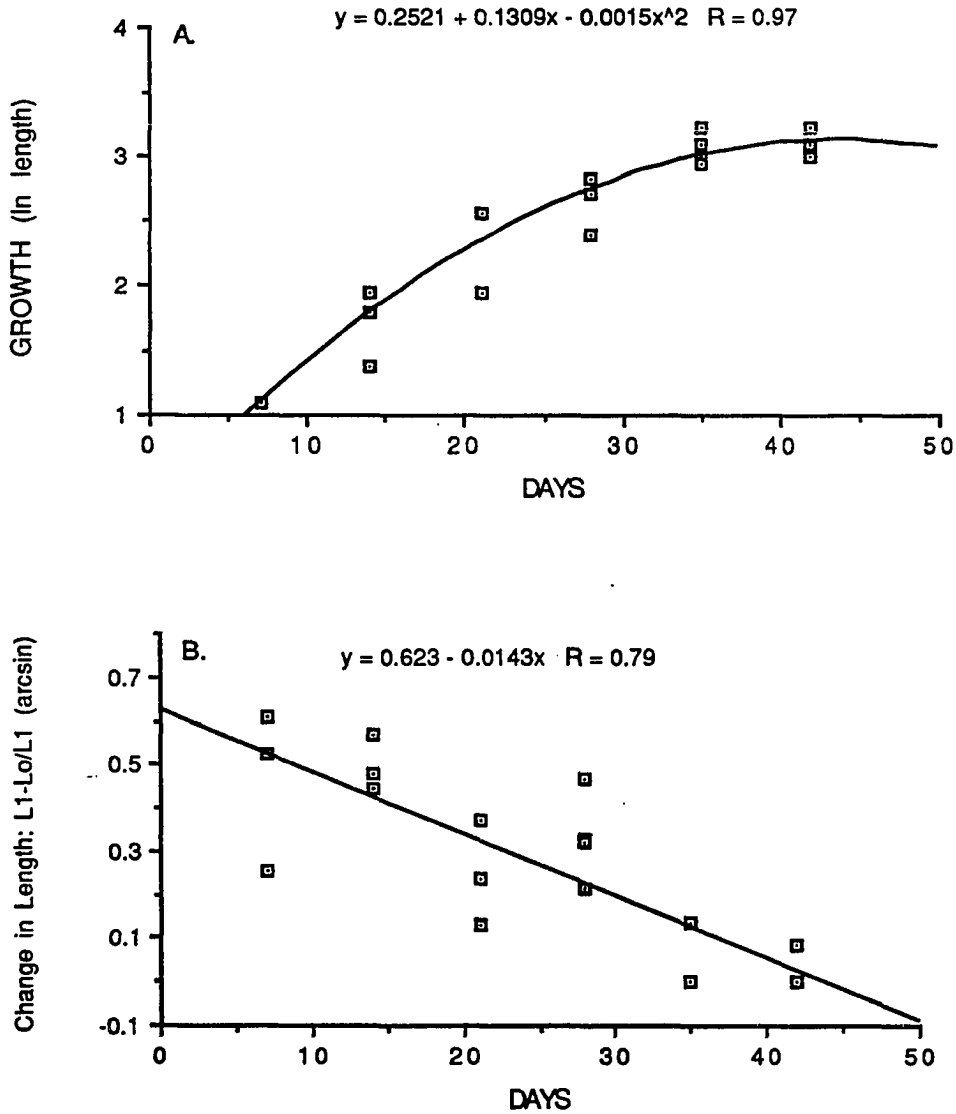


Fig. 26. A.The mean lengths for Cuthona nana hatched from a Gosport Harbor egg mass. The study period was 122 days at 12 °C. The bars and numbers represent standard error and the number of replicates, respectively.

B.The percent change in body length ($L_{T2} - L_{T1}/L_{T2}$) per day for Cuthona nana from the same egg mass from Gosport Harbor. The bars and numbers represent standard errors and the number of replicates for each mean, respectively. The change in body length increases for the first 86 days with the exception at 73 days, and begins to decrease after 86 days when animals average 9-10mm in length.

Figure 26

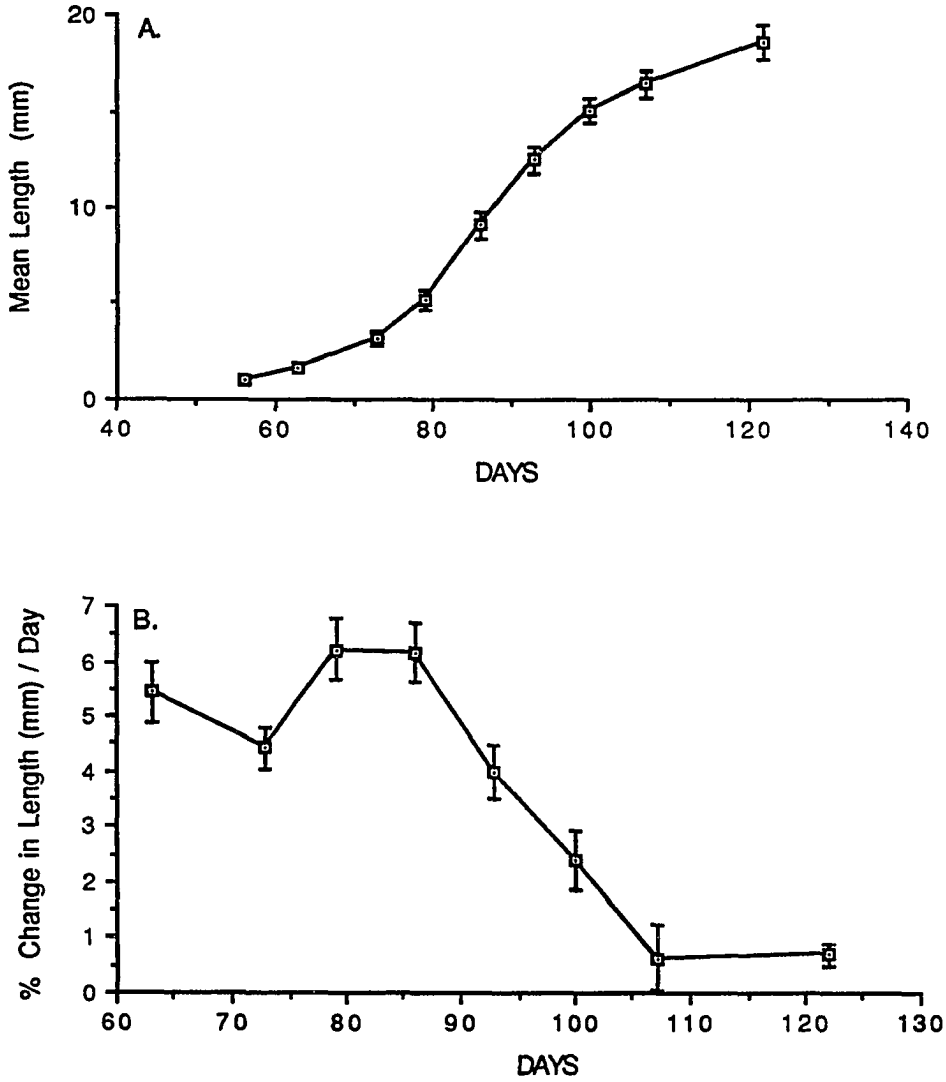


Fig. 27. A positive relationship exists for nudibranch length and the total tissue eaten (mg) in a 24 hour period (r_s = 0,340, N=35, $p<0.04$).

Figure 27

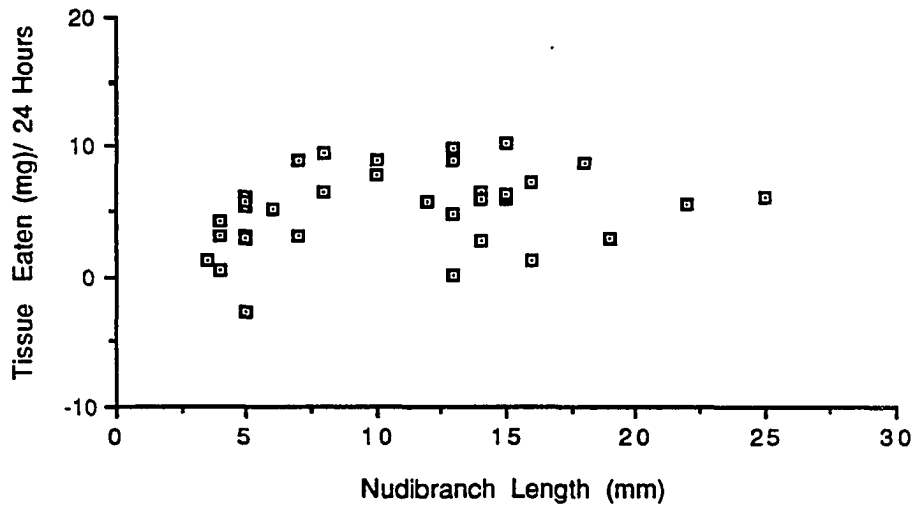


Fig. 28. A. A scattergram for polyp tissue wet weights for small Cuthona nana, 3-8mm. No positive relationships exists for the amount eaten and the size of the nudibranch ($p<0.683$).

B. A scattergram for polyp tissue wet weights for large Cuthona nana, 9-25mm. No positive relationship is present between nudibranch size and the amount of polyp wet weight eaten ($p<0.228$).

Figure 28

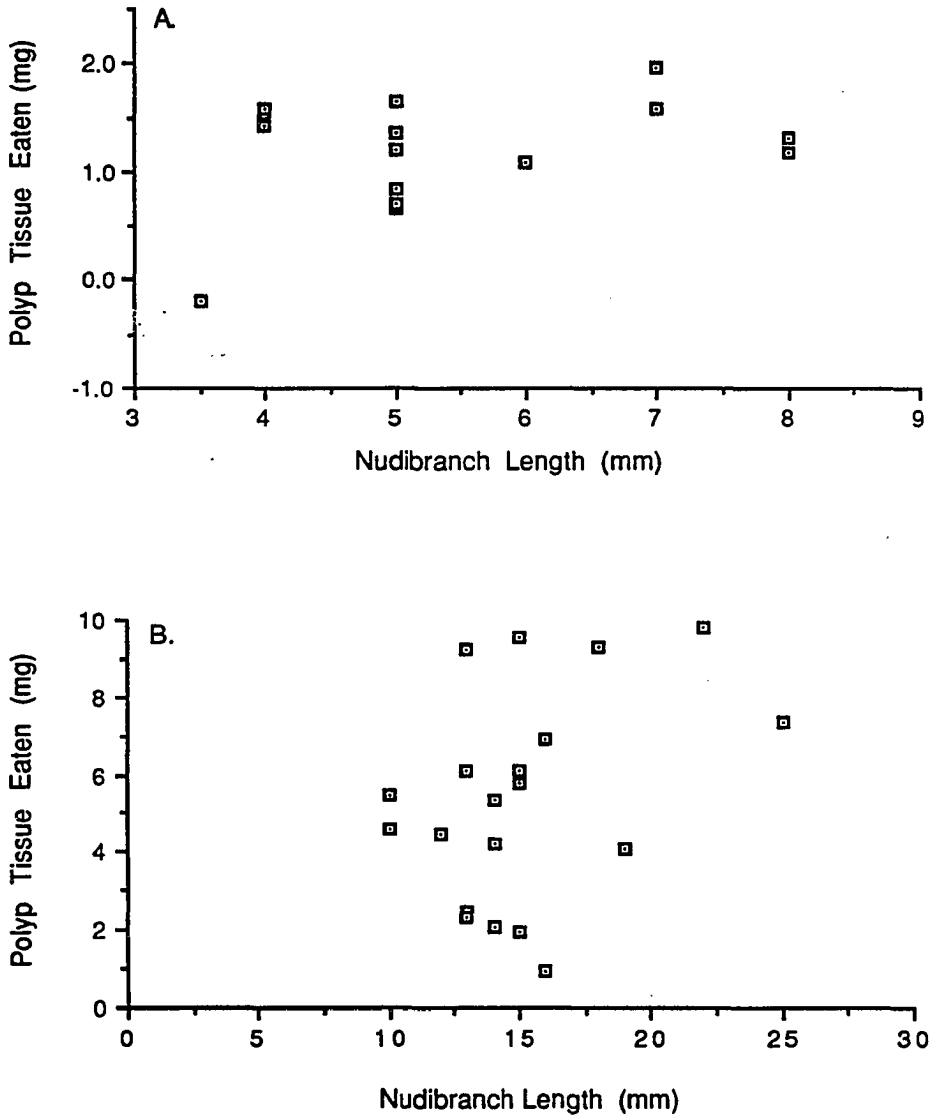


Fig. 29. A. A positive relationship exists for small nudibranchs (3-8mm) and the amount of mat tissue eaten (mg) in a 24 hour period ($p<0.009$).

B. A negative relationship exists for larger nudibranchs (9-25mm) and the amount of mat tissue consumed in a 24 hour period ($p<0.019$), supporting the observations that larger nudibranchs feed on polyps more than mat tissue.

Figure 29

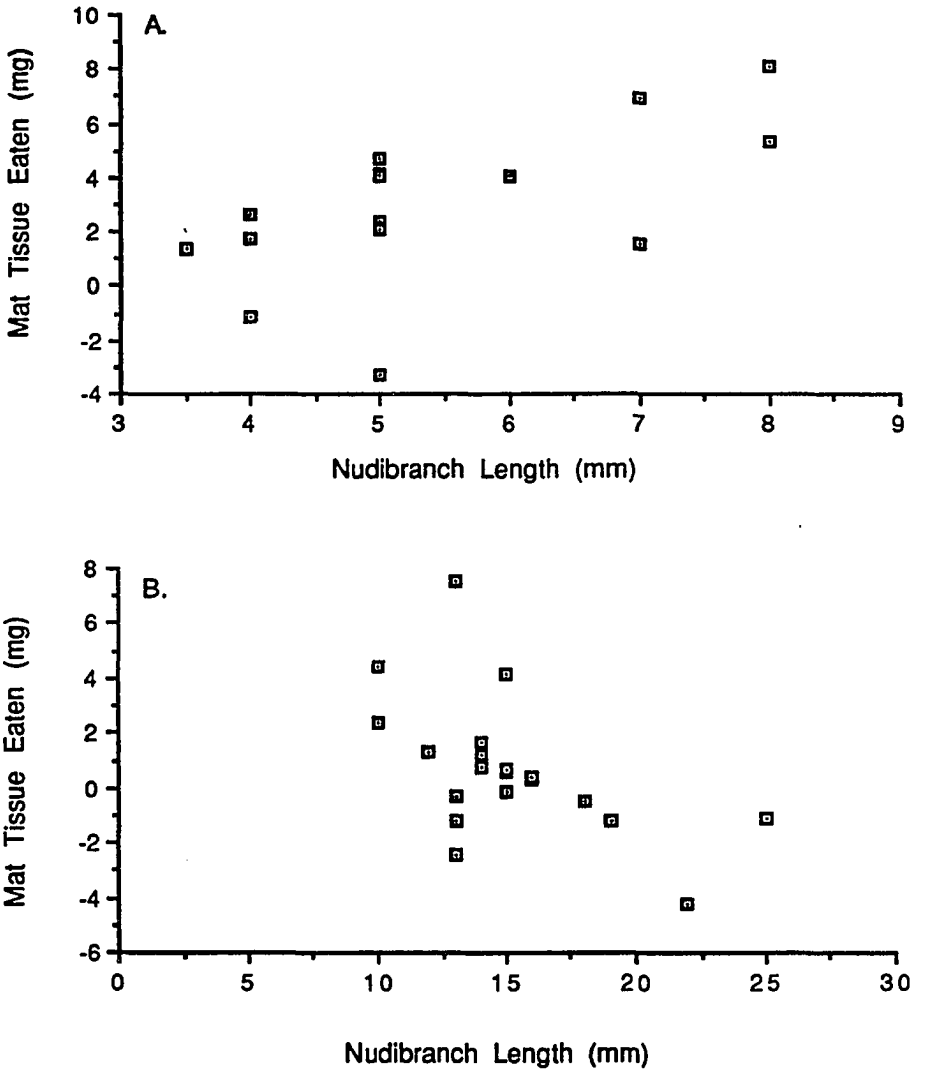


Fig. 30. The percentage of colony grazed from field collections of hydroid-covered shells. The number above each bar represnets the number of shellls with grazed patches measured for that month.

Figure 30

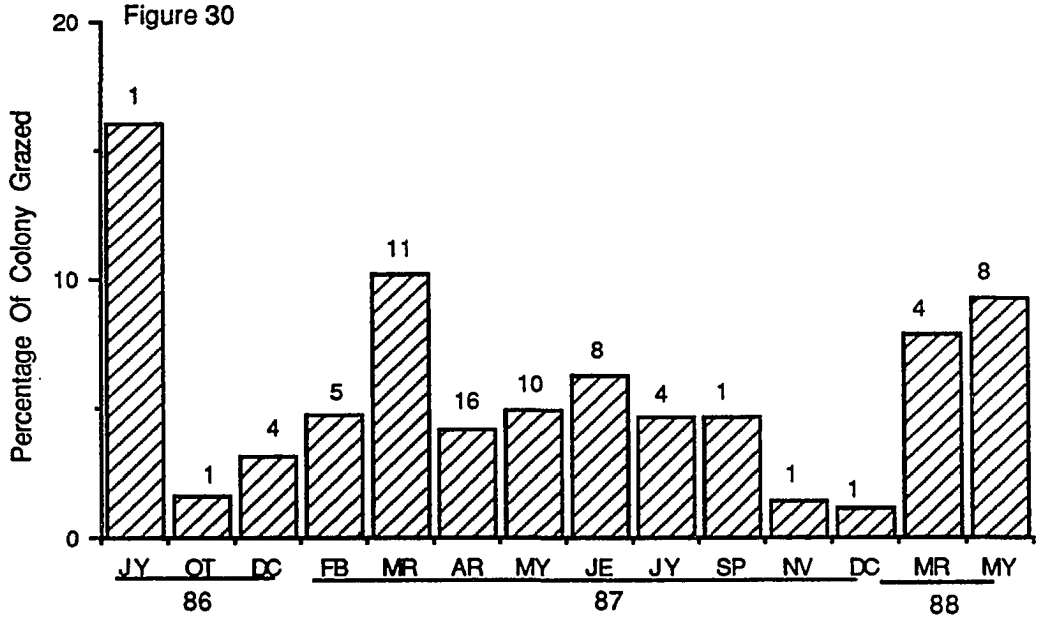


Fig. 31. The percentages of predation shown by the presence of a grazed patch and by the presence of a nudibranch and/or a grazed patch. The percentages of grazed patches are especially greater during the spring and early summer when the percentages of shells with nudibranchs are greater.

Figure 31

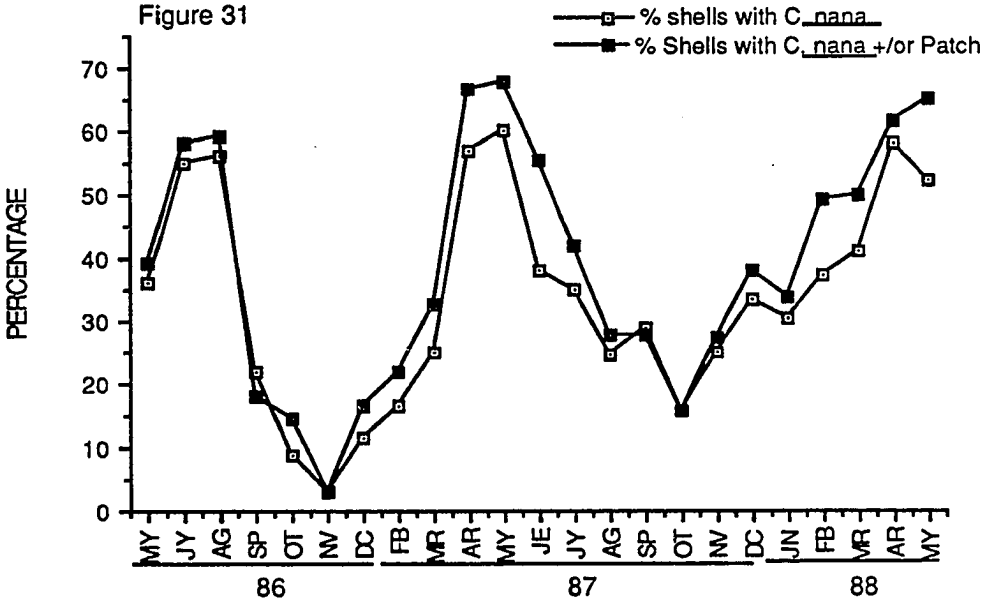


Fig. 32. One trial with four replicates indicated that juvenile Cuthona nana (2-4mm) do not leave colonies of Hydractinia echinata during a 21 day period. On the other hand, adults (12-20mm) climbed on and off colonies an average of 1-2 times per day. Bars represent the standard deviations of the means.

Figure 32

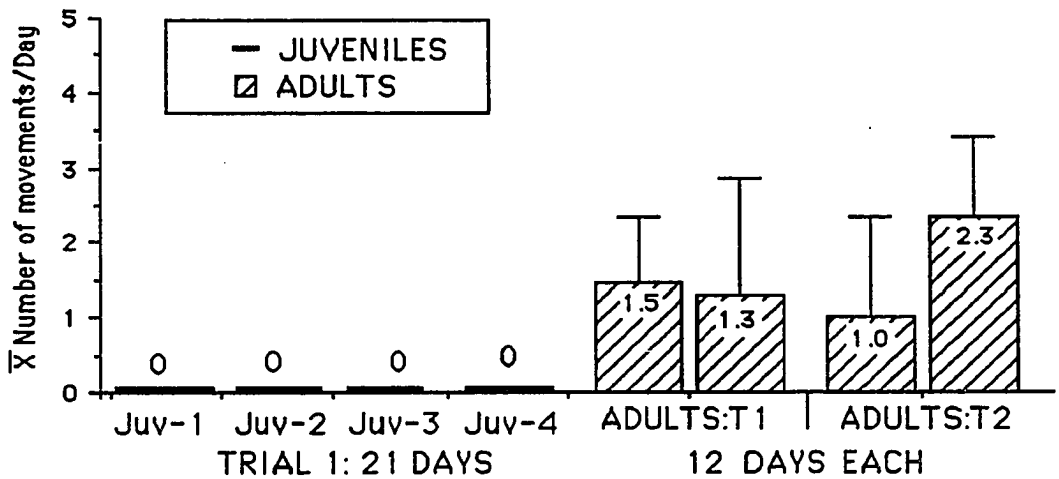


Fig. 33. The results from the pitfall experiment show an average of 3-8 crabs with Hydractinia echinata passing a given area on the bottom of Gosport Harbor in a 24 hour period. Bars represent the standard deviations of the means. The numbers in parentheses are the total number of crabs examined for each month.

Figure 33

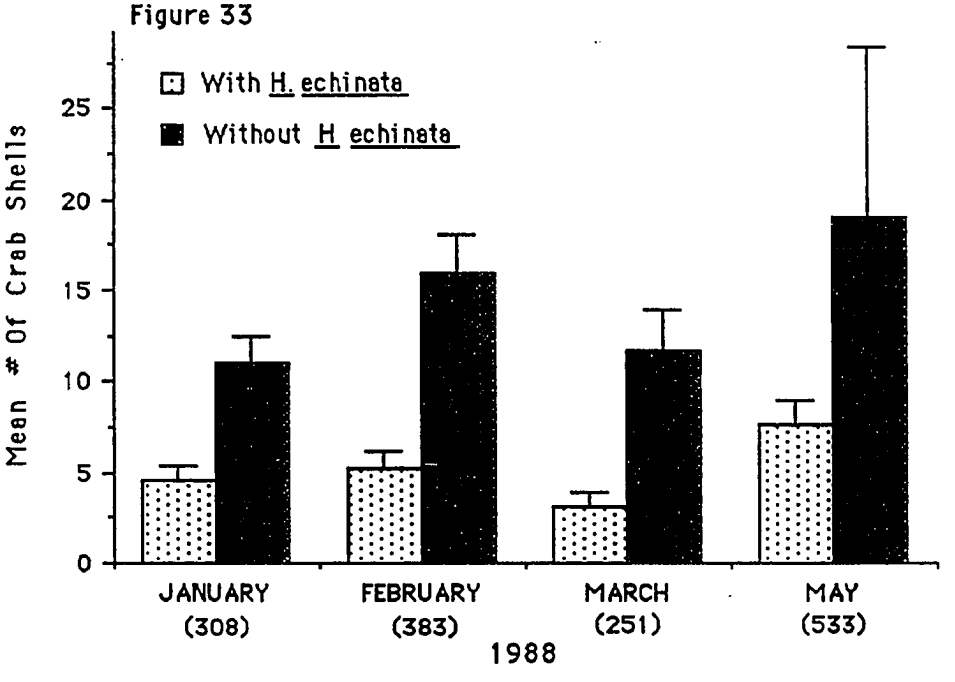
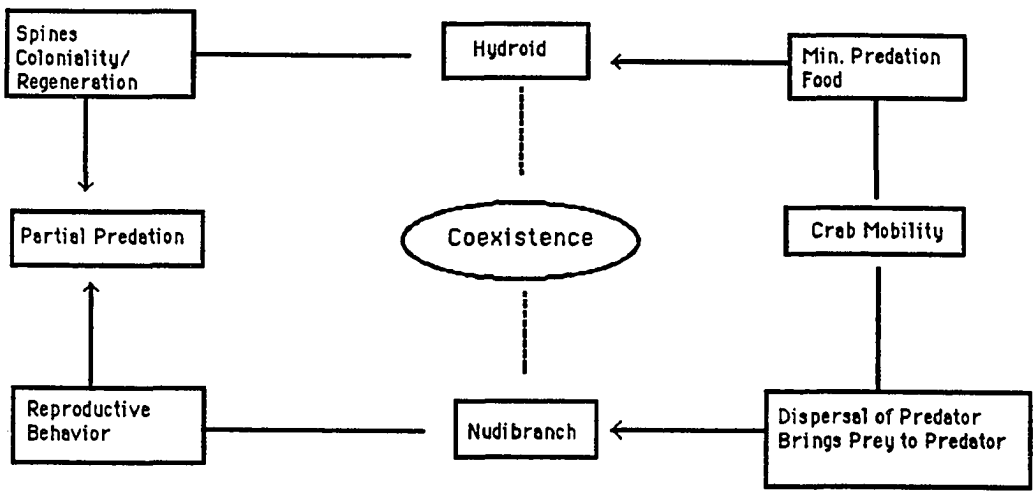


Figure 34. A summary diagram of the interactions between C. nana and Hydractinia echinata and hermit crabs at Gosport Harbor.

Figure 34



APPENDIX

Table 1. The mean number of shells with Hydractinia echinata without a crab in the shell for the band transects (mean number of crabs/10m^2) and the cofferdam samples (mean number of crabs/0.153m^2).N represents the number of band transects or cofferdams taken for each month.

BAND	MONTH	MEAN	STD	SE	N
	FEB 88	2.6	1.67	.748	5
	MAR 88	2.8	2.05	.917	5
	APR 88	1.5	.981	.491	4
	MAY 88	4.0	2.72	1.22	5
COFFERDAM	MAY 87	.130	.458	.095	23
	OCT 87	0	0	0	10
	FEB 88	0	0	0	23
	MAR 88	.20	.408	.082	25
	APR 88	.040	.20	.040	25
	MAY 88	.122	.389	.056	49

Table 2. The percentage of epifauna on grab sampled hermit crab shells and covered shells. N equals the total number of crabs sampled for each month. Coralline algae were recorded in the random samples only for shells with H. echinata also present. The numbers in parentheses following each represent the total number of crab samples while those after the coralline numbers represent the number of shells with H. echinata. Only samples in two months of 1988 were examined for Spirorbis.

		Grab Samples					Hydroid-covered Shells		
	MTH(N)	C. plana	Barnacles	Algae		MTH(N)	C. plana	Barnacles	Algae
	AG(79)	7.6	2.53	8.0(50)	86	MY(26)	0	16.7	0
85	ST(126)	0.79	0	5.2(58)		JL(38)	2.63	10.5	0
	OT(104)	10.2	0	8.3(133)		AG(43)	0	0	0
	DC(99)	16.2	1.01	12.2(41)		ST(84)	1.19	0	4.76
87	NV(53)	13.2	0	3.63(55)		OT(68)	1.47	0	0
	DC(73)	6.85	2.74	2.94(34)		NV(33)	0	0	0
88	JN(40)	5.0	5.0	11.76(17)		DC(63)	1.59	0	0
	FB(383)	0.26	0	9.47(95)	87	FB(73)	6.85	0	1.37
	MR(251)	0.39	0.79	1.89(53)		MR(52)	1.92	0	1.92
	MY(533)	0.18	13.32	0.63(160)		AR(67)	2.99	0	4.48
						MY(92)	1.09	0	6.52
						JE(63)	0	0	4.76
						JL(86)	1.16	0	2.33
						AG(65)	3.08	0	1.54
						ST(98)	2.04	3.06	0
						OT(83)	3.61	2.41	6.02
						NV(44)	2.27	0	0
						DC(21)	0	0	0
					88	JN(41)	0	0	2.44
						FB(59)	3.39	0	10.2
						MR(56)	1.79	0	3.57
						AR(57)	0	3.51	1.75
						MY(63)	0	9.52	1.59

Fig.1. Length frequency histograms for the Cuthona nana population at Gerrish Island from November 1986 to May 1988. Sizes were obtained from field measurements and photographs.

Figure 1

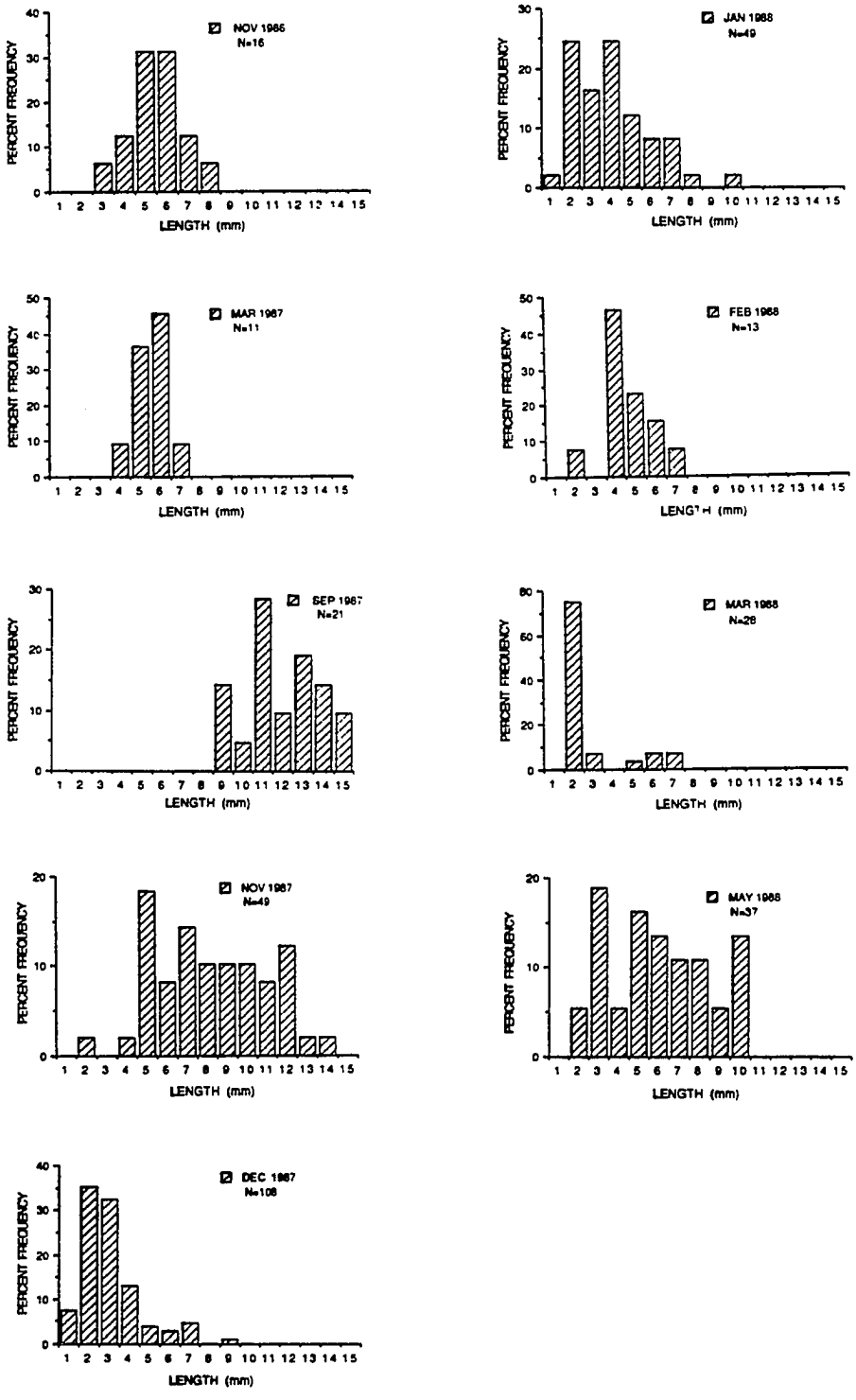
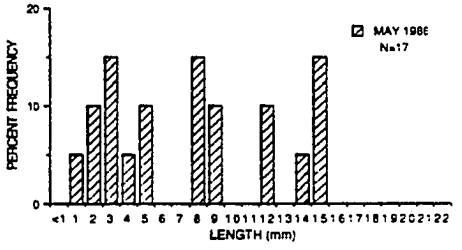
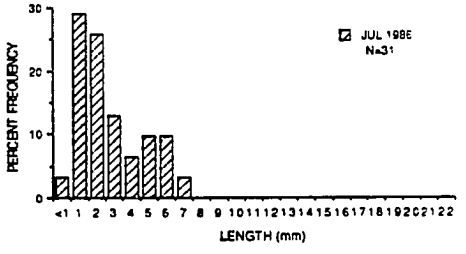
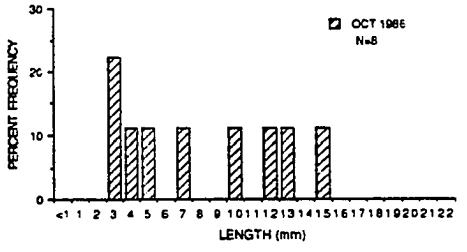


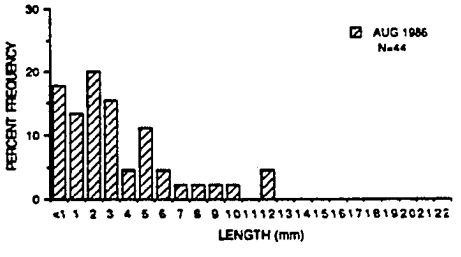
Fig. 2. Monthly length frequency histograms for Cuthona nana collected at Gosport Harbor in seven of eight months beginning in May 1986 to December 1986; sampling was not possible in June. Frequencies are represented as percent; N is the total number of nudibranchs measured for each month.

Figure 2









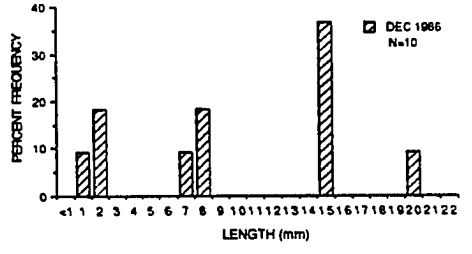


Fig. 3. Monthly length frequency histograms for Cuthona nana from Gosport Harbor beginning in February through December 1987; sampling was not possible in January due to rough seas. Frequencies are represented as percent; N is the total number of nudibranchs measured for each month.

Figure 3

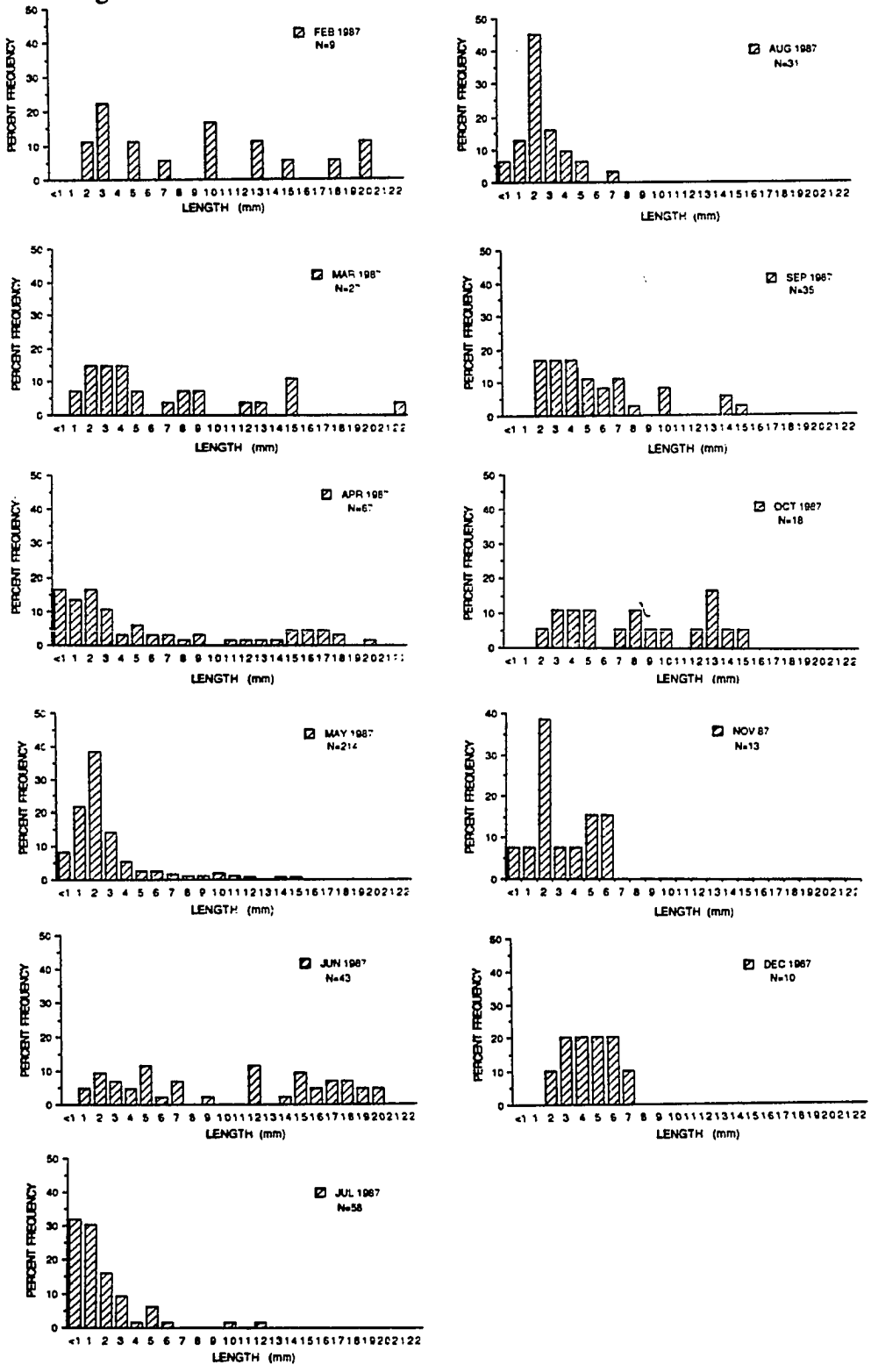
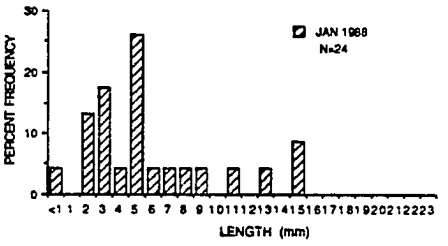
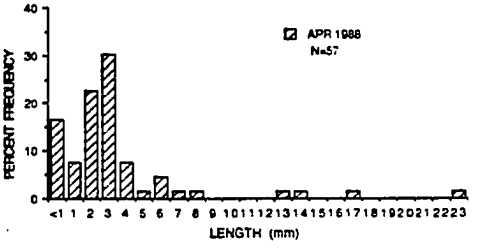
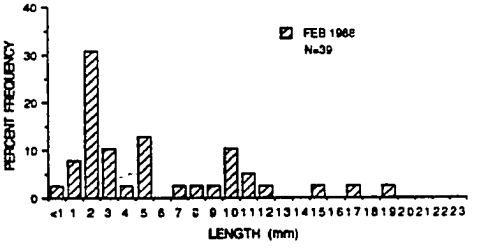


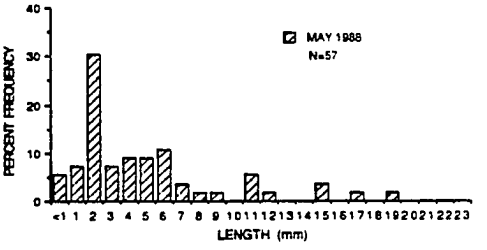
Fig. 4. Monthly length frequency histograms for Cuthona nana from Gosport Harbor for the first 5 months of 1988. Frequencies are represented as percent; N is the total number of nudibranchs measured for each month.

Figure 4









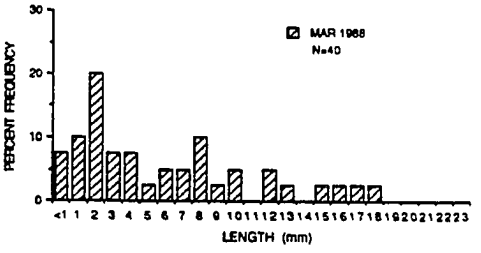


Fig. 5. The cascade arrangement of containers for Gerrish Island nudibranchs to maintain a high-flow habitat.

Figure 5

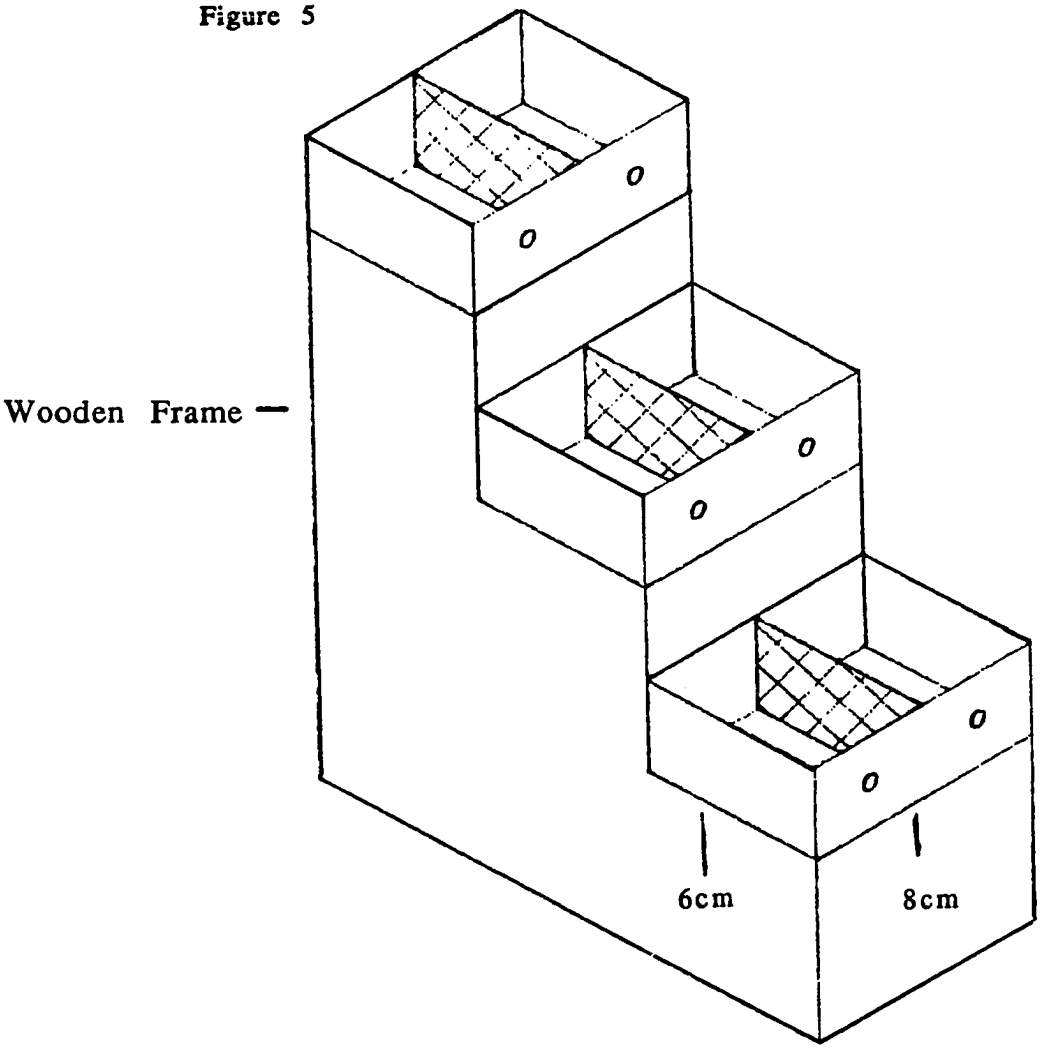
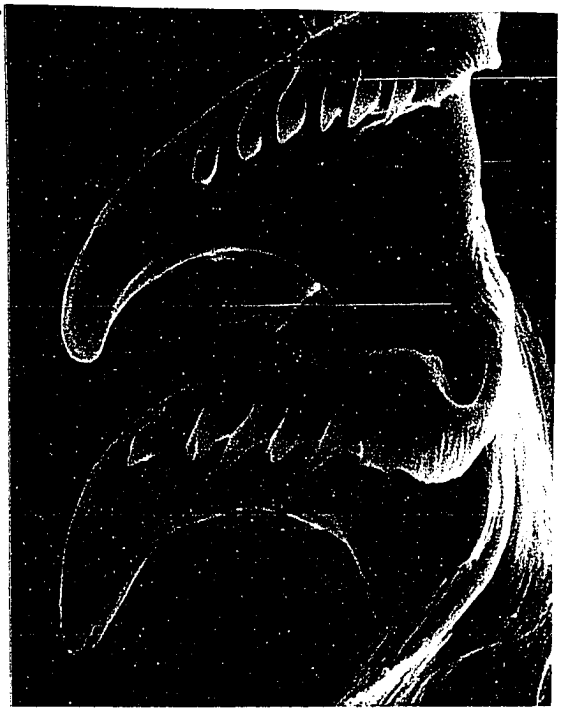


Fig. 6. A. An electron micrograph of a radula from a 11mm Cuthona nana collected from Gerrish Island. The magnification is 2210 X.

B. An electron micrograph of a radula from a 10mm Cuthona nana collected from Gosport Harbor. The magnification is 1100 X.

Figure 6

A.



B.

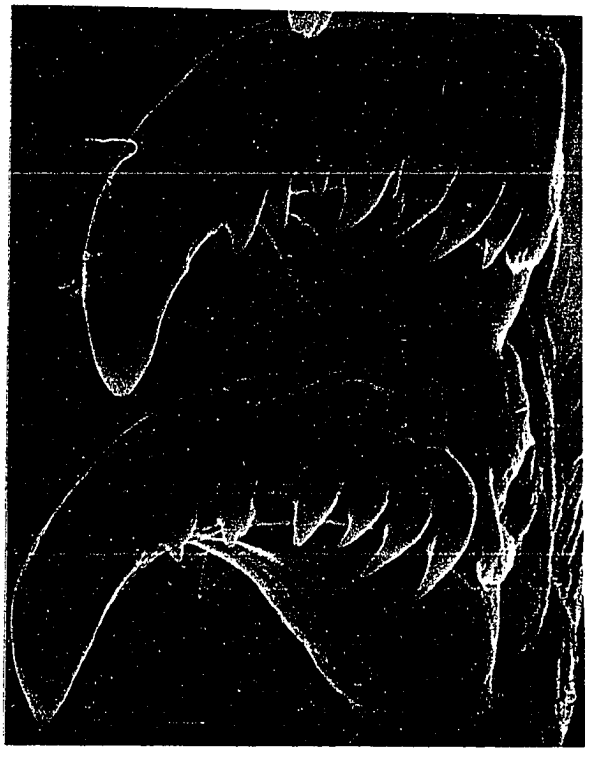


Fig. 7. An electron micrograph of the veliger shell from a Gosport Harbor veliger. The magnification is 260 X. The shell is approximaltey 234 um in length.

Figure 7