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Title The Associates of Four Species of Marine Sponges of Oregon and Washington


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Four species of sponge from the coasts of Oregon and Washington were studied and dissected for inhabitants and associates. All four species differed in texture, composition, and habitat, and likewise, the populations of associates of each species differed, even when samples of two of these species were found adjacent to one another. Generally, the relationships of the associates to the host sponges were of four sorts: 1. Inquilinism or lodging, either accidental or intentional; 2. Predation or grazing; 3. Competition for space resulting in "cohabitation" of an area, i. e. a plant or animal growing up through a sponge; and 4. Mutualism. Fish eggs in the hollow chambers of Homaxinella sp. represented a case of fish-in-sponge inqilinism, which is the first such one reported in the Pacific Ocean and in this sponge. The sponge Halichondria panicea, with an intracellular algal symbiont, was found to emit an attractant into the water, which Archidoris montereyensis followed

in behavior experiments in preference to other sponges simultaneously offered. A total of 6098 organisms, representing 68 species, were found associated with the specimens of _Halichondria panicea_ with densities of up to 19 organisms per cubic centimeter of sponge tissue. There were 9581 plants and animals found with _Microciona prolifera_, and 150 with _Suberites lata._ The two specimens of _Homaxinella_ sp. examined harbored a total of four clusters of eggs, each consisting of 20 to 30 eggs.

# The Associates of Four Species of Marine Sponges of Oregon and Washington

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## INTRODUCTION

Sponges provide shelter and a substrate for many organisms to live in or upon because the habitats the animals seek are provided by the oscula, channels, chemical products, and textures of the sponges. Gudger (1955) stated the fact that crustacea living within sponges was recorded in 1850, but did not cite a reference. Accounts of fish-sponge inquilinism (lodging) began when Radcliffe (1917) recorded Garmannia spongicola, a goby, within unidentified sponges off North Carolina. Since then various investigators have reported on the associates of sponges.

One of the earliest accounts of sponge associates was that of Vosmaer (1911) in the Siboga-Expedition Reports in which he listed several annelids and an ophiuroid living in the canals of Spirastrella purpureum of tropical waters. He also observed that the barnacle Balanus declivis and the coelenterate Stephanyscyphus mirabilis caused deformation of the sponge surface.

Much later, A. S. Pearse (1935) described the inhabitants of the logger-head sponge (Speciospongia vesparia) at Dry Tortugas, where he found up to 17,128 animals in a single sponge. Nearly every phylum present in that marine situation was represented.

Crozier (1963) found a cirratulid worm living in and upon Microciona prolifera on the Florida coast. He considered their relationship to be very close, perhaps mutualistic or, at least, commensal due to their similar pigmentation and other criteria. Nigrelli et al. (1959), working with biochemical products of Microciona prolifera, found many "epibionts," mostly invertebrates, but did not describe them in detail.

There are indications that the association of animals to sponges is not new in geological time. Gutschick and Perry (1959), for example, have reported finding algal cells and such invertebrates as spiny brachiopods, craniaceans, fenestellids, bryozoans, calcareous tube worms and vermicular Foraminifera in the sponges Scaphiomanon nodulosum and S. hadros of the Mississippian era in Montana. In Germany Eugen and Ilse Seibold (1960) found Foraminifera in sponges of the Upper Jurassic period, some of which were highly species-specific. Some, also, were found to have lived nowhere else but in various sponges.

The greatest percentage of the reports of modern sponge associates involve either fish or crustaccea. The first description of a fish inhabiting a sponge was that of Radcliffe (1917). Other reports of fish-sponge relationships were described by Beebe (1928) who colorfully described his observations of silvery gobies in loggerhead sponges. Pearse (1935) found fish in Dry Tortugas sponges. Breder (1939) outlined the life history and development of Paraclinus marmaratus, an Atlantic sponge blenny that spends nearly all of its life in its host sponge. Gudger (1935) found seven gobies, two blennies, and four other fish living within the loggerhead sponge (Sleciospongia vesparia) and other, tubular, vase-shaped sponges. Caullery (1952), Dales (1957), Yonge (1957) and Nicol (1964) have summarized the symbiotic relationships of marine animals and included in their descriptions previous reports of fish-sponge inquilinism. Such relationships require small, slender fish and sponges that are tubular (e. g. Homaxinella sp.) or with large internal cavities.

The shrimp Synalpheus brooksi spends part or all of its life cycle in the loggerhead sponge (Dobkin, 1965). Khandler (1964) found many Panulirus argus lobsters and a few Mitrax verrucosus crabs in the sponge Callyspongya sp. in Venezuela. Several investigators have found that crabs attach sponges to their carapace as camouflage (Dales, 1957). This association has distribution and survival benefits for the sponge, indicating a tryly symbiotic and mutualistic relationship. That is, both animals are benefitted by the association.

Of the many reports of sponge associates only a handful have attempted to describe or classify the exact relationship of the animals involved. It appears that the majority of the associates are inquilines or, perhaps, commensals, and very few are truly obligate. With respect to fish-sponge associations Gudger (1955) has stated: "The phenomenon herein considered is in all cases one-sided - the sponge gives lodging to the fish which makes no return whatever to the sponge." Caullery (1952) regarded the association of the considerably modified crustaceans Pontonia, Typton, Spongicola and Aega to sponges as inquilinism. He regarded inquilinism as a phase of parasitism, in which the inquilines undergo some modifications and malformations, reminiscent of parasitic adaptations. He believes that the inquilines may feed on the food of the host before it reaches the host or while it is being processed.

Such modifications of the associates to the host should, ideally, vary directly with the relative closeness of the relationship. This idea is supported by the highly modified copepod Clionophilus vermicularis which inhabits the sponge Cliona celata in Ireland. The copepod has lost some appendages, or their use, and has evolved a suctorial mouth structure. This copepod may be parasitic (Gotto, 1965). In contrast to Clionophilus vermicularis is the shrimp Synalpheus brooksi that inhabits many substrata, including several species of sponge, and is not obviously modified.

A sponge-mollusc association was reported by Forbes (1964) in which the oyster, Ostrea permollis, was found to live on or embedded in the sponge Stellata grubii in the Gulf of Mexico. The oyster has not been found naturally occurring on any substrata other than this species of sponge, therefore the distribution of the oyster depends upon that of the sponge.

In a later paper Forbes (1966) described the relationship of the two animals. He found that the oyster can survive when away from the sponge, but it eventually becomes so heavily infested with boring and fouling organisms that it dies. Thus, by living embedded in the sponge, the oyster was provided substrate, shelter and elevation, the latter preventing siltation, overgrowth and fouling of the inhalant region. Forbes found that the oyster spat preferred the Stellata grubii substrate over others offered, although the spat would set on other surfaces if Stellata grubii was not offered or available. When the spat and sponge come in contact with each other, the sponge grows around the oyster in such a way that the exhalant region is directed into a chamber of the sponge which leads to the osculum. The sponge, then, may receive some benefit from the association by increasing its water flow and by receiving the excretory products of the oyster.

The associates of sponges, of course, are not limited to the animal kingdom. In fact, Ridley and Dendy (1887) reported finding a very abundant oscillatorian alga in Halichondria panicea, especially in sponges with a chocolate, brown color. The authors stated they did not know if the brown color was due to the alga. Yonge (1935) has described several symbiotic, parenchymatous algae within certain sponges. Zahl and McLoughlin (1959), McLoughlin and Zahl (1962), and Sara and Liaci (1964) have described zooxanthellae symbiotic in Porifera as well as Coelenterata, and the cultivation of these symbionts.

This paper will attempt to describe qualitatively and quantitatively the associates of the four sponges Halichondria panicea, Microciona prolifera, Suberites lata, and Homaxinella sp. The flora and fauna of each sponge will be listed and compared with those of the other sponges. The habitat of each sponge will be described and related to the associates found with the sponge. An attempt will be made to describe the relationships of the more important associates to their sponge hosts, and to point out the commoner associations.

# METHODS AND MATERIALS

Because these sponges occupy varied varied habitats, the methods of collection varied. Microciona prolifera, Suberites lata, and Homaxinella sp. were subtidal in the locations studied, and their collection required use of SCUBA and trawling.

Microciona prolifera and Suberites lata were pulled or scraped off their substrate and immediately placed in zippered plastic bags, which were sealed underwater. The sponges were then brought to the surface for examination in the laboratory under a binocular microscope (at 120X). Sponges that were brought to the surface and then placed in bags showed a loss of 50% to 70% of their inhabitants by comparison to other specimens of the same size which were sealed in bags under water; therefore, they were not included in the study. These collections were made while SCUBA diving.

Homaxinella sp. was initially trawled up from 15 fathoms by an otter trawl operated by Lyndall Bryxius of the OSU Marine Science Laboratory, Newport, Oregon. Later, unsuccessful attempts were made to SCUBA dive for the species, but visibility was usually zero at the depths at which this species occurs, below 70 feet, and specimens could not be located.

Halichondria panicea normally occurs in rocky, unprotected areas of the lower intertidal to upper, littoral regions. Because this area was too violent and shallow for SCUBA and trawling, collecting there could be accomplished only on rather low tides; thus, collection of this species was somewhat limited by tidal conditions. However, when collection was possible, this species was scraped off the rocks with ones' fingernails. This method proved to be far superior to scrapers or other techniques. The collector normally had but a few seconds to pry some of the sponge off the rocks and dash to safety before the surf crashed over and all around the area; there was not time to manipulate scrapers or other devices.

During examination of all sponges, their inhabitants were recorded and counted and then preserved in AFA for final classification and stomach content analysis. The sponges were torn into small pieces to recover the larger animals therein. Many animals embedded within the sponge were detectable from the surface of the sponge. Sponge sizes were measured roughly by use of a metric rule. No biomass data were taken because the purpose of the study was limited to determining what associates were in the sponges, and, hopefully, what they were doing there.

I identified many of the associates and sponges by use of the publications of Hartman and Reish (1950), Light, et al. (1954), Ricketts and Calvin (1952), and deLaubenfels (1954).

# OBSERVATIONS AND EXPERIMENTS

## Suberites lata

The most striking thing about Suberites lata is its extreme toughness and seemingly impenetrable composition. In the calm waters of Hood Canal, Washington, the sponge occurs as either large clumps, flat and spreading masses, or as narrow and highly contorted strips. On the unprotected rocks of Yaquina Head, Oregon, it occurs as tough mounds on the bottom in small protected caves of the mid-tidal zone, which is in contrast to Hood Canal sponges. Hood Canal specimens appear with more surface contortions, often taking on a "whipped cream" form, whereas Yaquina Head sponges are more streamlined and thinner.

In Hood Canal Suberites lata attaches to flat rocks that are lightly covered with fine mud at a depth of 5 to 10 meters (MLLW). This mud is colloidal in nature and supports a very sparse macroscopic biota.

Suberites lata harbored only a small number of organisms. The one organism that occurred most commonly in Suberites lata was the small spionid, Polydora socialis. As seen in Table 1, it was found on virtually every specimen of sponge inspected in Hood Canal. However the worm is also commonly found embedded in substrates other than

Table 1. The organisms found associated with *Suberites lata* and the numbers found in each sample of sponge.

| | Sample Number | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Hood Canal, Wn. | | | | | | | | | | | | | Yaquina Head, Ore. |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| *Platynereis agassizi* | 2 | | | | | | | | | | | | 2 | |
| *Polydora socialis* | 8 | 3 | 7 | 8 | 1 | 1 | 1 | 9 | 2 | 4 | 1 | 2 | 8 | |
| *Aoroides columbiae* | 3 | 1 | | | | | | | | | | | | 1* |
| Misc. Polychaetes[a] | 2 | | 1 | | | 1 | | | | 1 | 1 | | | |
| Nematodes | 1 | | | | | | | | | | | | | 1 |
| Anomura | 1 | | | | | | | | | | | | | |
| Caprellids | 2 | | | | | | | | | | | | | |
| *Cancer antennarius* | | | 3 | | | | | | | | | | | |
| *Crago stylirostris* | | | | | | | | | | | | | 1 | |
| Crab Megalops | | | | | | | | | | | | | | 1 |
| Misc. molluscs[b] | | | | 4 | | | | 2 | | 1 | | | | 3 |
| Sabellids[c] | | | | | | | | | | | | | | 25 |
| Bryozoans | | 1 | | | | 1 | | 1 | | | | | | |
| *Crisia* sp. | | | | | | | | | | | | | | |
| *Membranipora* sp. | | | | | | | | | | | | | | 2 |
| Hydroids[d] | | X | | | | X | | | | | | | | X |
| Chlorophyta | | | | | | | | | | | | | | |
| *Enteromorpha* sp. | 2 | | | | 1 | | | | | | | | | |
| Rhodophyta | | | | | | | | | | | | | | |
| *Platythamnion* sp. | | | | | | | | 1 | 1 | | | | | |

*Not identifiable.

[a] Opheliidae: *Armandia bioculata* #1, #6, #10; unidentifiable Nereid #3; unidentifiable Phyllodocid #11.

[b] *Saxicava arctica* #4; miscellaneous gastropods #8, #10; unidentified small white bivalves #14.

[c] Sabellidae: *Pseudopotamilla ocellata* (majority).

[d] *Eudendrium* sp. #2 ; *Syncornye* sp. #6; *Eudendrium* sp. #14. Individual hydranths of these hydroids cannot be counted as individuals as they are simply members of an entire colony that proliferates through the sponge.

Table 2. The thickness and volume of Suberites lata and the total number, density, and most common groups of organisms in each sample.

| Sample number | Thick-ness(cm) | Volume ($cm^3$) | Total animals | Density ($/cm^3$) | Predominant groups of animals |
|---|---|---|---|---|---|
| | | Hood Canal, Washington | | | |
| 1 | 7 | 686 | 21 | 0.03 | Polydora socialis - Aoroides columbiae |
| 2 | 4 | 480 | 6 | 0.01 | Polydora socialis - Crisia sp. |
| 3 | 4 | 360 | 8 | 0.02 | Polydora socialis |
| 4 | 5 | 630 | 9 | 0.01 | Polydora socialis |
| 5 | 5 | 463 | 2 | 0.002 | Polydora socialis |
| 6 | 6 | 822 | 7 | 0.01 | Polydora socialis |
| 7 | 5.5 | 616 | 1 | 0.001 | Polydora socialis |
| 8 | 4 | 676 | 15 | 0.02 | Polydora socialis - Crisia sp. |
| 9 | 4 | 480 | 3 | 0.006 | Polydora socialis |
| 10 | 3 | 210 | 6 | 0.03 | Polydora socialis |
| 11 | 4 | 288 | 2 | 0.007 | Polydora socialis |
| 12 | 3 | 195 | 2 | 0.01 | Polydora socialis |
| 13 | 4 | 416 | 9 | 0.02 | Polydora socialis |
| | | Yaquina Head, Oregon | | | |
| 14 | 3 | 721 | 59 | 0.08 | Tubularia sp. - Misc. Polychaetes |

sponge. . Polydora socialis excavated small burrows in the sponge and often was found with its head extended just out of the burrow. The burrow was filled with fine mud, debris, and feces; and was usually shallow. The worm was curled up within the burrow.

It is significant that organisms other than Polydora socialis were not found in large numbers with Suberites lata. This indicated that the relationships of these other organisms to the sponge were very haphazard and loose. Many were probably there as a result of random wanderings. Polydora socialis was the only organism actually burrowing in the sponge; the remainder were either sitting on top, passing by, hiding beneath or within a convolution of the sponge, or attached to the sponge surface. Polydora socialis probably used the sponge as a place of shelter and concealment. It can feed by extending only its head above the sponge surface. The mud surrounding the sponge is most likely rich in plankton and other suspended matter.

Other organisms found with Suberites lata include: Algae: Enteromorpha sp., Platythamnion sp.; Arthropoda: Aoiroides columbiae (Amphipoda), unidentified caprellids, Cancer antennarius (Brachyura), unidentified Brachyura and Crago stylirostris (Caridea). Annelida: Platynereis agassizi (Nereidae), Polydora socialis (Spionidae), Pseudopotamilla ocellata (Sabellidae), Armandia bioculata (Opheliidae), unidentified Phyllodocidae, and various

Nereids.

Mollusca: Saxicava arctica, unidentified small gastropods and bivalves; Nematoda; Coelenterata: Tubularia sp., Eudendrium sp., Syncoryne sp. (Hydroidea); Ectoprocta: Crisia sp., and Membranipora sp.

The arthropods found associated with Suberites lata were observed upon the sponge surface, hiding beneath contortions of the sponge. Those annelids other than Polydora socialis were found burrowed beneath the sponge or lying within tubes of mud deposited upon the sponge surface. They were never found within the sponge. The nematodes were found upon the surface or partially protruding into the top centimeter of the sponge between its spicules. Those hydroids, bryozoans, and algae found associated with the Suberites lata in Hood Canal were usually attached to the very surface and only rarely were they attached to embedded parts.

Regardless of what was associated with particular specimens of Suberites lata, there appeared to be no correlation between sponge size or thickness and the number of associates per unit volume of sponge. Pearse (1935) found an inverse relationship between sponge size and number of associates per cubic centimeter of Speciospongia vesparia. This relationship did not appear with Suberites lata. However, the nature of the sponge consistency, the growth position, and the organisms involved differed greatly between Speciospongia vesparia and Suberites lata. The associates of Speciospongia vesparia were able to burrow deep into that sponge because of its many open chambers and soft consistency. Whereas, the associates of Suberites lata were not able to burrow deeply, if at all, into the hard, compact sponge, and consequently they were restricted to numbers and species that could occur on the sponge surface except for Polydora socialis. The nature and consistency of S. lata were probably the factors that limited the number of organisms found associated with it.

The general area surrounding the zone inhabited by Suberites lata in Hood Canal were densely inhabited with large algae (Laminarians), sea cucumbers (Stichopus californianus), sea anemones (Metridium senile), surf grass (Zostera), fish (Sebastodes, etc.) and various encrusting animals. However, in the immediate vicinity of Suberites lata there was invariably a noticeable sparcity of growth and a thin layer of fine ooze covered the bottom. The limited distribution of Suberites lata may help avoid fouling. The large laminarian algae reached lengths of up to 50 to 20 meters and widths of up to 1-1/2 meters in the areas just below the Suberites lata zone, and vast, tangled forests of Sargassum nuttalli occurred well above the Suberites lata zone. If these algae covered the bottom in the S. lata zone due to dislodging, death, falling over, or some other mechanism; then the sponge would conceivably be smothered if it occurred in the same zone.

Competition for space above the zone in which Suberites lata occurred appeared to be intense. Barnacles, bryozoans, serulids, small red algae, and stalked tunicates crowded the few rocks that projected above the layer of suspended mud. Suberites lata may not be able to compete with these organisms for substrate, especially when it is clean of suspended mud. No other sponge species was ever found in the general area of S. lata.

When I returned to sites of collection a month or so after previous collections, the fringes of, and the areas adjacent to, parts of sponge collected appeared decomposed, gray, and dying. Death was most likely due to the previous removal and disruption of the water current system and its canals.

The one specimen of Suberites lata found on Yaquina Head, Oregon, was inspected for associates. The organisms found are compared to those of adjacent specimens of Halichondria panicea on page 38.

The Yaquina Head specimen showed a greater total number, density, and diversity of associates than Hood Canal specimens. A sabellid polychaete, Pseudopotamilla ocellata, was the most common organism found. Some of these worms had their tubes, within the sponge; however, most of their tubes extended beneath the sponge or they were in excavated or eroded areas that had collected debris. The cause and effect relationship between the tubes and excavated areas was not clear.

The associates of the Yaquina Head sponge were markedly different from those of Hood Canal, indicating that the composition of the community living with *S. lata* was not constant nor predictable; but, rather, it was dependent upon the local ecology and community of organisms. The density of the associates also seemed to depend upon the local conditions as shown by the relatively constant densities exhibited by Hood Canal specimens and by the generally lower populations in the Hood Canal specimens as a group compared to the larger number of organisms in the Yaquina Head sponge.

## *Microciona prolifera*

The idea of investigating the inhabitants of local sponges first occurred to me when *Microciona prolifera* was observed in the shallow waters of the Nahcotta jetty in Willapa Bay, Washington. When the beautifully colored, large, red-orange clumps of *Microciona prolifera* were brought to the surface, hordes of shrimp, amphipods, crabs, nereids, and nudibranchs either jumped, swam, or wriggled out of the branches of the sponge.

There are at least two reports of inquilinism or symbiosis with Microciona prolifera. In the first of these Nigrelli et al. (1959) reported finding such worms as Clymenella, Lepidonotus, and Spirorbis; the crustacea Carcinides maenas, Panopeus, Balanus and isopods; clumps of mussels (Modiolus); sea anemones (Sagartia); some bryozoans and gobies.

As mentioned previously, Crozier (1963) described a close relationship between a red cirratulid worm and Microciona prolifera. A very dark red cirratulid was found a few times here, but the worms were subsequently lost. Therefore, it remains unknown if these worms were the same as those reported by Crozier in Florida. They superficially resembled his descriptions of the worms.

Crozier described M. prolifera as a "thin sheet covering numerous objects below the piers" and with some erect areas. His description indicates that the gross morphology of the species varies from place to place because Nigrelli et al. (1959) described its form as erect and branching; and the specimens found in this investigation were also branching, erect, and originated from a basal trunk and branched out to form a clump with a diameter of up to one foot or more. Most specimens reached a height of 6 to 7 inches. Many adjacent branches often fused, and thereby, formed a large mass of sponge.

*Microciona prolifera* was found only in Willapa Bay, Washington, on mud-covered rocks at a depth of 2 to 5 meters (MLLW). This area was generally quite barren of life; very few plants occurred at this depth, though there appeared to be plenty of light. Tidal fluctuations caused the only significant movements of water in the area, sometimes creating 2 knot currents.

The form taken by the sponge was often related to its position in the tidal currents. Sponges on the top of the rocks were not bushy and large, but, instead were shorter, branched only a few times, and small in diameter. They also had few associated organisms, perhaps because they trapped less mud and debris in which many of the organisms were frequently found. Those sponges that were attached under over-hanging rocks or were otherwise relatively sheltered were heavily cluttered with hydroids, algae, sea anemones and all of the rest of the associates that will presently be described.

As shown in Table 3 the associates of a number of specimens of *M. prolifera* were relatively constant in population density and community composition. Four groups of animals were most numerous: I. Polynoidae (*Halosydna brevisetosa*, *Harmothoë imbricata*, *Eunoë nodosa*, *Lepidonotus caeloris*, and *Harmothoë lunulata*); II. Sabellidae (*Schizobranchia insignis*, *Pseudopotamilla ocellata*, and *Sabella media*); III. Amphipoda (Gammaridae: *Corophium*

Table 3. The height and volume of Microciona prolifera and the total number, density, and most common groups of organisms in each sample.

| Sample number | Thick-ness(cm) | Volume ($cm^3$) | Total animals | Density ($/cm^3$) | Predominant groups of animals |
|---|---|---|---|---|---|
| 1 | 4 | 684 | 965 | 1.49 | Corophium - Bugula sp. - Caprellids |
| 2 | 5 | 964 | 385 | 0.31 | Corophium - Harmothoë imbricata - Platynereis agassizi |
| 3 | 2 | 24 | 21 | 0.90 | Corophium - Halosydna - filamentous algae |
| 4 | 3 | 36 | 131 | 3.64 | Corophium - Sabella media - Caprellids |
| 5 | 3 | 90 | 273 | 3.03 | Corophium - Nematodes - Platynereis agassizi |
| 6 | 6 | 576 | 248 | 0.43 | Corophium - Harmothoë imbricata - Sabella media |
| 7 | 13 | 2340 | 1820 | 0.79 | Corophium - Diadumene - Sabellids - Caprellids |
| 8 | 5 | 200 | 76 | 0.38 | Corophium - Harmothoë imbricata- Platynereis agassizi |
| 9 | 5 | 546 | 145 | 0.27 | Corophium - Diadumene - Caprellids |
| 10 | 5 | 350 | 238 | 0.68 | Corophium - Sabella media - Platynereis agassizi |
| 11 | 6 | 1440 | 1885 | 1.31 | Corophium - Harmothoë imbricata - Caprellids - Munna chromatocephala |
| 12 | 5 | 400 | 652 | 1.63 | Corophium - Schizobranchia insignis - Caprellids - Munna chromatocephala |
| 13 | 7 | 490 | 956 | 1.90 | Corophium - Caprellids - Munna chromatocephala |
| 14 | 8 | 1248 | 939 | 0.70 | Corophium - Caprellids - Munna chromatocephala |
| 15 | 5 | 520 | 847 | 1.63 | Corophium - Caprellids - Munna chromatocephala - Platynereis agassizi |

acherusicum; Caprellidae: Caprella angusta, C. equilibra, C. pilipalma, C. californica, Tritella laevis, Duetella californica), and IV. Isopoda (Munna chromatocephala).

Of the array of organisms found on Microciona prolifera, the amphipods by far outnumbered the other groups. These amphipods were identified by Dr. J. Laurens Barnard of the Smithsonian Institution to be Corophium acherusicum. The amphipods were most often attached to the lower areas of the sponge, particularly in the junctions of branches that had collected mud and debris. Corophium acherusicum was found within the sponge matrix occasionally. In such cases the amphipods had formed burrows in the sponge and backed into them. These burrowing individuals were capable of completely withdrawing themselves into their burrows.

Other organisms that were found embedded within the sponge included some tube worms and terebellids. Many of these worms positioned themselves at the apex of a branch of the sponge in such a manner that their tubes ran directly down the middle of the branch, partially blocking the osculum. The centers of these branches were composed of very thick and elongate spicules that extended the length of the branch. The large size and tubular arrangement of these spicules allowed enough space for these worms to form their tubes. No disfiguration of the sponge was observed in branches inhabited by these worms, although the excurrent streams of the oscula of these branches were nearly plugged (Fig. 1).

Many of the sabellids and terebellids were found wrapped around the sponge branches or embedded in the mud collected in the junctions of the sponge. The terebellids, particularly, were associated with mud in these junctions. Often the sabellids formed their tubes through this mud and extended them up and around the sponge branches above. A sabellid tube was never found to enter a branch laterally. On some occasions the tubes entered a short, stunted branch. The stunted condition of these branches may have been caused by the presence of the worm, or the worm may have entered the main stem laterally and the sponge subsequently formed a stunted branch around the tube.

Many Polynoidae were associated with _Microciona prolifera_. These included large specimens of _Harmothoë imbricata_, which were found deep among the branches of the large clumps of sponge, particularly when the branches were very close together. The distribution of the various species of the group Polynoidae appeared to be entirely random.

The sea anemone _Diadumene luciae_, which is often found in marine muddy areas, was rather common on the branches of _M. prolifera_. The greatest number of these animals were also

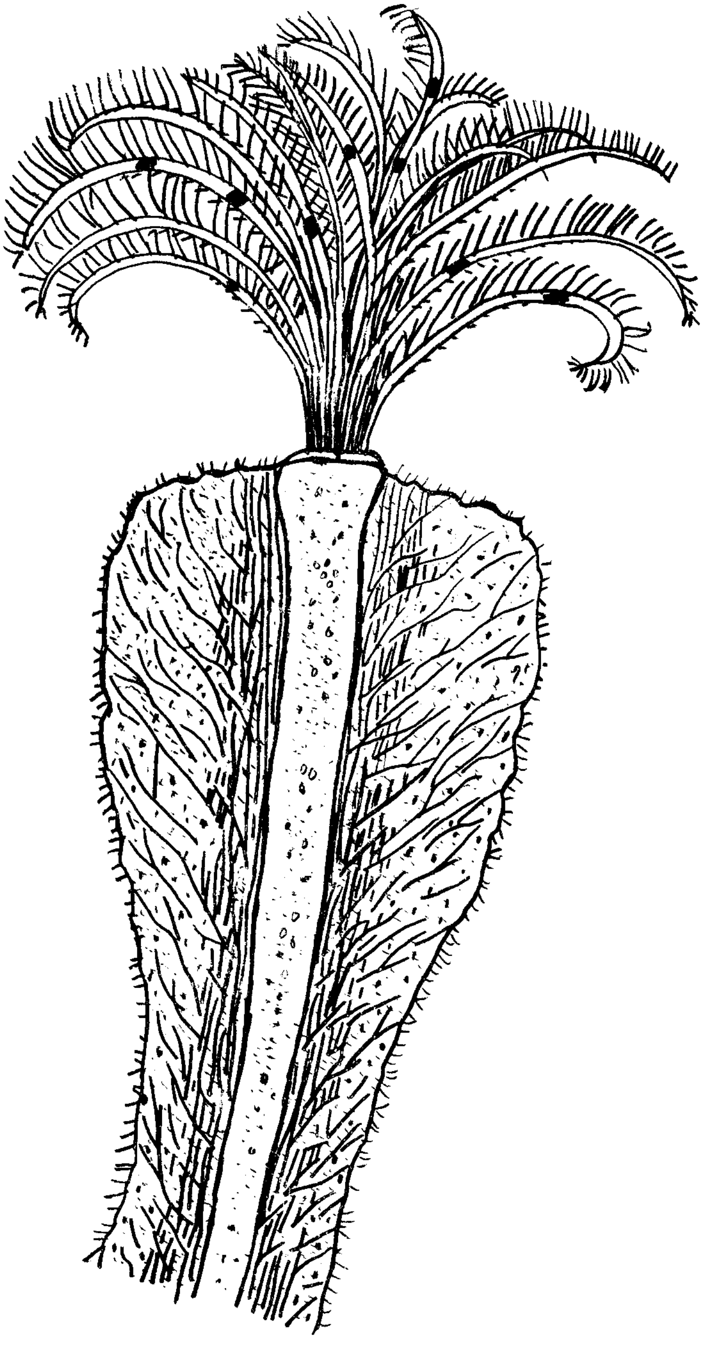


Figure 1. A branch of *Microciona prolifera* showing the orientation of the Sabellid *Pseudopotamilla ocellata* within the sponge.

found burrowed in the mud of the junctions of the branches, but never embedded within the sponge itself.

Several species of caprellids were found associated with M. prolifera. No particular one seemed to be predominant, and the distribution of these species appeared to be entirely random. The caprellids attached themselves to the branches of the sponge over the entire height of the sponge and probably preyed on organisms passing by or caught on the sponge surface. One species of isopod (Munna chromatocephala) was found on Microciona prolifera. As shown in Table 4, this isopod was found in about half of the samples.

The worms of the group Nereidae were always present in small numbers, usually crawling in the mud collected by the sponge. However, the nereids were more numerous in the last group of specimens collected. Of the nereids, Platynereis agassizi was most common. Nereis mediator and N. vexillosa were also found a few times. Since these worms are found commonly elsewhere in the marine situation, their association with Microciona prolifera does not have any significance. They feed on the debris in the mud collected by the sponges.

The organisms found with Microciona prolifera include the Arthropoda: Amphipoda: Corophium acherusicum (Gammaridae); Caprella angusta, C. equilibra, C. pilipalma, C. californica,

Table 4. The organisms found associated with Microciona prolifera and the numbers found in each sample of sponge.

| | Sample number | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Willapa Bay, Wash. | | | | | | | | | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| Corophium acherusicum | 788 | 309 | 15 | 100 | 244 | 160 | 1540 | 60 | 70 | 149 | 1650 | 500 | 761 | 797 | 655 |
| Sabellidae[a] | 9 | 1 | | 18 | | 15 | 80 | | 3 | 37 | 24 | 34 | 18 | 8 | 7 |
| Caprellidae[b] | 36 | | | 7 | 4 | | 36 | 2 | 40 | 4 | 50 | 40 | 56 | 40 | 15 |
| Diadumene luciae | 6 | 6 | 1 | | | 2 | 55 | 1 | 9 | 2 | 4 | | | 6 | 5 |
| Annelidae: | | | | | | | | | | | | | | | |
| Polynoidae[c] | 11 | 19 | 3 | 1 | 3 | 26 | 43 | 3 | 7 | 6 | 28 | 11 | 4 | 7 | 8 |
| Terebellidae[d] | 6 | 7 | | | | 10 | 22 | | 3 | 1 | | | | 4 | 1 |
| Sabelariidae[e] | | | | | | | | | | | 1 | | | 1 | |
| Cirratulidae[f] | | | | | | | | | | | | 6 | 3 | | |
| Nereidae[g] | | 14 | 2 | 1 | 3 | 3 | 1 | | 2 | 20 | 20 | 8 | 18 | 25 | 21 |
| Misc.[h] | 4 | 6 | | 2 | 3 | 3 | | 7 | 3 | 10 | 2 | 2 | 1 | 3 | |
| Bugula sp. | X | X | | X | X | X | | | | | X | | X | X | X |
| Nematoda | 3 | 6 | | 4 | 10 | 6 | 6 | 2 | | 3 | 3 | 11 | X | X | |
| Mytilus californianus | 1 | 3 | | 1 | 2 | 3 | 3 | 1 | 3 | | | 1 | | | |
| Munna chromatocephala | | | | | | | | | | 11 | 90 | 41 | 91 | 41 | 125 |
| Misc. Arthropoda[i] | | *' 2 | + 2 | | +@ 4 | +@ 5 | *@ 3 | | | '+ 4 | *c 11 | | h 1 | *c 3 | |
| Misc. Mollusca[j] | | 2 | | | | 2 | 1 | | 1 | 2 | 2 | | 1 | 2 | |
| Misc. algae[k] | 1 | 4 | | X | | | | 1 | | 2 | 2 | | 3 | | |
| Misc. Echinodermata | | 1 (Ophiuroid) | | | | | | | | | | | | | |
| Sipunculida | | | | | | | 2 (Sipunculus nudus) | | | | | | | | |

[a]Sabellidae include: Pseudopotamilla ocellata, Schizobranchia insignis, Sabella media.

[b]Caprellidae include: Caprella angusta, C. equilibra, C. pilipalma, Tritella laevis, Deutella californica.

[c]Polynoidae include: Halosydna brevisetosa, Harmothoë imbricata, Harmothoë lunulata, Lepidonotus caeloris, Eunoe nodosa.

[d]Terebellidae include: Amphitrite robusta, Strebolosoma sp.

[e]Sabellariidae include: Sabellaria cementarium.

[f]Cirratulidae include: Cirriformia spirobranchia.

[g]Nereidae include: Nereis mediator, N. vexillosa, Platynereis agassizi.

[h]Miscellaneous annelids include: Arabella sp. (Arabellidae), Polydora cardinale (Spionidae), various Syllidae, Eteone longa and Genetyllis castanea (Phyllodocidae).

[i]Arthropods include: *Crago sp., 'Anomura crab, +ostracods, @barnacles, cCancer anntenarius, hhermit crab.

[j]Mollusca include: a cockle, oyster, Saxicava arctica, and other unidentified bivalves; and unidentified gastropods (#6).

[k]Algae include: Scytosiphon sp. (#1), Aglaophenia sp. (#2), Ceramium eatonianum (#2), Chaetomorpha sp. (#8), and various filamentous reds and greens (#2, 3, 4, 10, 13), and various browns (#10, 11).

Tritella laevis, and Deutella californica (Caprellidae); Brachyura: Cancer antennarius; Caridea: Crago sp., unidentified hermit crab and spider crabs; unidentified barnacles; ostracods; and Isopoda: Munna chromatocephala.

Mollusca: Mytilus californianus, M. edulis; unidentified oyster, Saxicava arctica, various bivalves, and Archidoris montereyensis.

Annelida: Schizobranchia insignis, Sabella media, and Pseudopotamilla ocellata (Sabellidae); Sabellaria cementarium and Idanthryus sp. (Sabellariidae); Lepidonotus caeloris, Harmothoe imbricata, H. lunulata, Halosydna brevisetosa, and Eunoë nodosa (Polynoidae); Neoamphitrite sp., Strebelosoma sp. and Polycirrus calendrum (Terebellidae); Cirriformia spirobranchia (Cirratulidae); Polydora cardinale (Spionidae); Platynereis agassizi, Nereis vexillosa, N. mediator (Nereidae); Arabella sp. (Arabellidae); Genetyllis castanea and Eteone longa (Phyllodocidae).

Nematoda; Coelenterata: Diadumene luciae (Anthozoa), Aglaophenia sp. (Hydrozoa); Sipunculoidea: Sipunculus nudus; Echinodermata: unidentified ophiuroid; and Ectoprocta: Bugula sp.

Algae: Scytosiphon sp., Ceramium eatonianum, Chaetomorpha sp., and various filamentous reds and greens.

Less than half of these animals and plants were firmly attached or embedded in the sponge; and most of the animals could be seen swimming among or running upon the branches of the sponge when observed by a diver. Many of the amphipods, shrimp, crabs, and fish were scared away by a diver. No fish was ever collected from the sponges, although fishes were observed several times.

As is the case with most of these organisms, their distribution and dispersal is accomplished by means of planktonic larvae and spores. These larvae probably became caught in the spicules of the sponge and the maturation and growth of the young organism continued in the sponge. All growth stages of many animals were found in these sponges. However, this is shown much better in *Halichondria panicea*, as described on page 34.

## *Homaxinella sp.*

This sponge has much the same shape as *Microciona prolifera* but it is branched fewer times and, more important, its branches are hollow. The diameter of the hollow chambers was generally about one-half cm. or less. The color was a drab brown to cream, sometimes with blotches of red. *Homaxinella* sp. normally occurs at a depth of 20 to 30 meters on hard rock bottom off the Oregon coast. It was obtained with an otter trawl.

The sponge was identified by the author to be of the genus

*Homaxinella*, according to the description of deLaubenfels (1954). However, no species description proved adequate, and other references used did not offer a satisfactory description of such a sponge; therefore, no species name was assigned.

At the base of the chambers of two of these sponges clusters of fish eggs were found. These clusters consisted of 20 to 30 eggs solidly cemented together in a shape that fit snugly into the base of the chamber. The fish embryos were always found to be alive and thriving; with well developed eyes and fins.

No adult fish was found. In an attempt to identify the fish whose eggs I found, some of the eggs were placed, still within the sponge, in a well-aerated marine aquarium. But they died within a month, probably because either the sponge slowly died and deteriorated; or because the adult fish were not present to fan the eggs. Breder (1939) observed such fanning of eggs with the sponge blenny *Paraclinus marmaratus*.

At a depth of 20 meters where *Homaxinella* sp. was found, it was dark and efforts to collect the sponge and fish with SCUBA gear were unsuccessful.

Gudger (1955) has reported many fishes as inquilines in sponges. Most of these fish were gobies or blennies, their slender body form being ideal for fitting into the sponge chambers, where they orient themselves facing into the excurrent stream. This present case of fish-sponge inquilinism is most likely one involving such a blenny or goby. If so, it is the first report of such a relationship from the Pacific Ocean. Fish-sponge inquilinism has never been reported anywhere other than the Atlantic Ocean, and the literature includes no further information than given by Gudger (1955) on this subject.

## *Halichondria panicea*

*Halichondria panicea* is a green sponge that forms sheets one to five cm. thick over the unprotected rocks of the midtidal zone. The green color occurs only in the upper layer of the sponge. The sponge abruptly becomes yellow just below the surface. The green coloration is most likely due to an intracellular alga that is restricted to the surface where it receives sufficient light. I have observed green algal cells under a phase microscope from preparations of the green portions of the sponge. This alga-sponge relationship has not been studied; however Sara and Liaci (1964) have suggested that there is a relationship between the sponges *Cliona copiosa* and *C. viridis* and the autotrophic characteristics, needs and by-products of their symbiotic flagellates.

Halichondria panicea invariably occurs where the surf is the most violent, attached to the seaward side of the most seaward rocks that receive the full force of the surf. It is also found in surge channels where the action of passing waves is amplified.

When rocks covered with H. panicea were dislodged and placed in protected tidal pools, the sponges gradually became yellowish, covered with sand, and were preyed upon by hermit crabs, shrimp, and large isopods (Idothea sp.). These predators were not commonly found on the sponge in the areas where it naturally occurred. It is possible that the sponge requires a high oxygen tension provided by the intracellular algae, and that the algae cannot survive when covered with sand which accumulates in protected areas. The eventual fate of these transplanted sponges was not determined due to winter storms and a lack of low tides. Those sponges that occurred on the underside of rocks were usually yellow and more rubber-like in consistency than the sponges exposed to light, indicating that the sponge does not absolutely require the alga but does somewhat better with it.

Halichondria panicea was found to have many and varied associates. The total numbers and densities of these associates varied greatly from sponge to sponge, suggesting that ecological factors other than the sponge itself may determine a particular sponge community. However, several species of plants and animals were nearly always found in sponges collected at different places.

Collections were made in Oregon at Seal Rocks, Yaquina Head, and Boiler Bay. Seal Rocks was divided into three areas for collections: (1) The South and (2) North ends which were similar but 100 meters distant and (3) the "Outside", which received the most violent surf possible. Yaquina Head was originally divided into two areas: (1) The Outside, and (2) the Surge channels, but the associates found did not differ between the two areas; consequently, the divisions were dropped. Boiler Bay sponges were not examined in the laboratory with the thoroughness given Seal Rocks and Yaquina Head sponges and will not be included in the data. However, it is significant that the organisms hastily observed with *Halichondria panicea* at Boiler Bay were similar to those found at the other stations, both in generic composition and in proportions represented.

Attempts were made to determine if the organisms associated with the sponge would take up residence in any sponge material other than *H. panicea*. Other species of encrusting sponges occurred in the same zone as *H. panicea*, but they were only rarely found with any associates. These sponges included *Haliclona* sp. and *Plocamia* sp., which is bright red and often had the tiny, bright red nudibranch *Rostanga pulchra* crawling on it, but neither species of sponge commonly had the associates found on adjacent *H. panicea.*

Artificial, cellulose sponges were attached by concrete nails to the rocks in areas of *H. panicea* in an effort to determine if they would attract organisms similar to those found on *H. panicea.* However, these sponges were washed away within days and no information at all was gained as to the specificity of the associates.

Another behavioral experiment was set up in the laboratory to determine what attracted some of the motile animal associates. The nudibranch *Archidoris montereyensis* is a characteristic associate of *H, panicea* and was found very often near or upon the sponge. It was only rarely found on other species of sponge, whether or not the species had a consistency or coloration similar to that of *Halichondria panicea*.

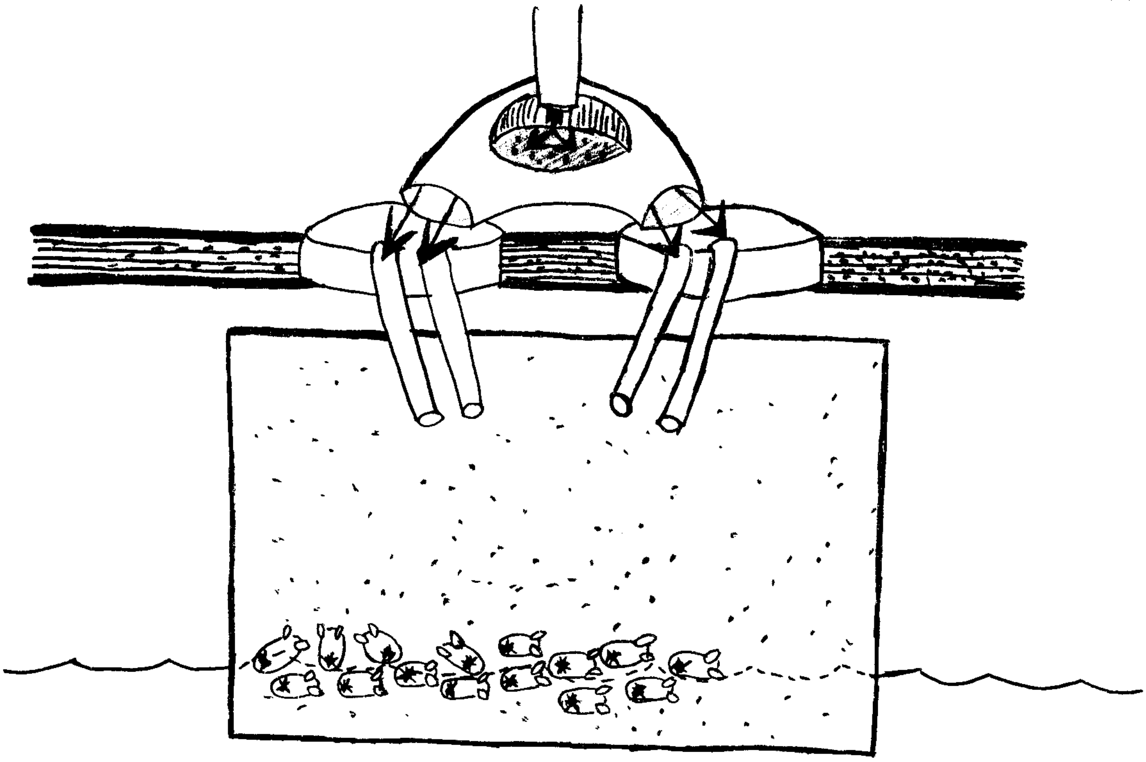
When several *Archidoris montereyensis* were placed upon *Suberites lata* downstream from a chunk of *Halichondria panicea* in the laboratory, the nudibranchs immediately crawled off the former and onto the latter. This suggested that a chemotaxis was involved.

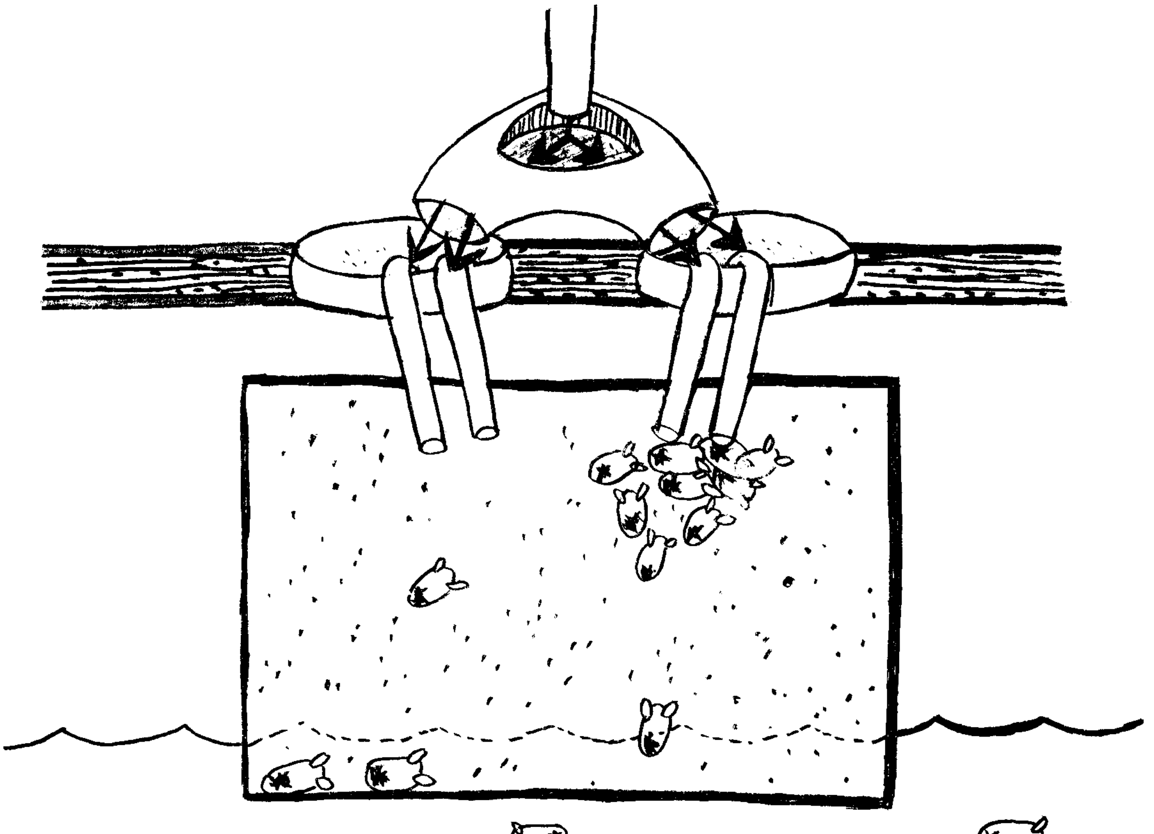
To establish somewhat more objective evidence of chemoreception in this relationship a system of water ways was set up involving *Suberites lata*, *Halichondria panicea* and *Archidoris montereyensis*. The simple apparatus, as shown in Fig. 2 was

Figure 2. The apparatus used to illustrate the chemical attraction of the nudibranch *Archidoris montereyensis* to *Halichondria panicea*. The left water outlet is from *Suberites lata*, the outlet on the right is from *Halichondria panicea*.

A. The positions of the nudibranchs upon release.

B. The positions of the nudibranchs after one-half hour.





similar to that used by Davenport (1966) in his behavioral experiments involving symbionts. Essentially, two water currents ran over the two elevated sponges separately and then converged on a slanted board partly immersed in sea water. The sponges were placed in separate glass bowls, and the water currents out of the sponge bowls were run through glass capillary tubes. The nudibranchs were placed at the bottom of the board and released.

Archidoris montereyensis crawled upstream and concentrated around the outlets from Halichondria panicea often and around that of Suberites lata rarely. In the first run, 9 of the 15 nudibranchs released congregated around the H. panicea outlet, and 6 were randomly dispersed. In the second run, 10 of the 15 moved up the Halichondria panicea stream and positioned themselves under the outlet. When left overnight the nudibranchs assumed an entirely random distribution, indicating that they had become habituated to the stimulus and confused, or that they became confused after finding no sponge.

The nudibranchs showed their dependence upon water currents in detecting and finding Halichondria panicea in the next experiment conducted. Two wire mesh buckets were placed at opposite ends of a 4 ft. laboratory tank, and the nudibranchs were placed in the center of the tank in 4 inches of water. A control test was run with no sponges, and the result was either complete lack of movement or confusion.

When Suberites lata and Halichondria panicea were placed in the buckets, the nudibranchs did not respond. When water currents were directed over the sponge, the nudibranchs moved toward the end with H. panicea. Within three hours 13 of the 15 were within the immediate vicinity of, or on top of, H. panicea. After 24 hours 9 were on the sponge and the remainder were scattered. Archidoris montereyensis was never found on or near Suberites lata in any of the experiments.

To test the idea that the nudibranchs were merely following a water current regardless of its origin, the animals were placed again on the slanted current board when the sponge bowls were vacant of sponges. Only two nudibranchs followed the currents, the remainder (13) scattered randomly.

It is apparent from the above results that the nudibranchs were following a chemical exudate from the sponge. The nudibranchs moved faster when copious amounts of exudate were squeezed from the sponge.

What do these animals do once they find the sponge, or what is their relationship to the sponge? Stomach content analyses showed that the nudibranchs were preying upon the sponge, sometimes to the point of completely devouring a mass of sponge. In most examinations there were green, and sometime red, algae; and always some amount of sponge spicules. A few times the stomachs of these nudibranchs were packed full of clumps of sponge, the spicules of which were identified as those of Halichondria panicea.

Also, in the laboratory Archidoris montereyensis was a voracious eater of H. panicea. Evidence of this was also seen while collecting. Some nudibranchs were found crawling on the rock surface and eating a tunnel through the sponge.

Predation is not an uncommon relationship among these associates. Sponge spicules were found in the stomachs of Acmaea asmi, Mopalia lignosa, larger Oedognathus rudus, Pachycheles sp., Cancer productus; and in some large amphipods and isopods pieces of spicules were found. Thus, predation represents one of the major categories of relationships of the sponge associates.

However, far exceeding predation in importance is the relationship that might be called "accidentalism" in which the sponge merely represents something handy to stand on or hang onto. Bakus (1962) in his Ph.D. thesis, concerning Puget Sound sponges, stated: "There appears to be little or no correlation between local sponge hosts and species of invertebrates found under, within, or on the surface of the host species. No clear-cut cases of symbioses were observed with the dubious exception of Suberites ficus (Johnston) and the hermit crab Pagurus brandti (Benedict). Dr. Gunnar Thorsen (personal communication) recently found a small prosobranch snail (Carithiopsis stephansae Bartsch) at Garrison Bay, San Juan Island, that may be a symbiont of Halichondria aff. panicea (Pallas)."

Examples of accidentals include: The fish Pholis ornata; the amphipod Jassa falcata; the crabs Oedignathus rudis, Pachycheles sp., Cancer productus, and C. magister; the mussel Mytilus californianus; the chiton Tonicella lineata; most of the annelids and the flatworm Leptoplana chloranota.

Similar to accidentalism is a relationship that could be termed "cohabitation", i.e. in this case two organisms grow and proliferate simultaneously in the same place. The best examples of this with Halichondria panicea were the algae Microcladia borealis and Corallina gracilis, the gooseneck barnacle Mitella polymerus, and, perhaps, the acorn barnacles Balanus nubilis and B. glandula. This phenomenon was seen many times, particularly among the algal associates. The sponge occurred around the bases of the algae over large areas of rock, and the algae were attached to the rock.

Since the method of initiating this relationship was never actually observed, the mechanism is a matter of speculation. Another method besides simultaneous growth may involve the trapping of spores of the algae and larvae of crabs, barnacles, bivalves, and other organisms in the lower chambers of the sponge with a subsequent lack of digestion of these planktonic forms by the sponge cells. Many instances, particularly with *Mytilus californianus* and *Balanus glandula*, were observed in which the animals were very small (apparently stunted), and often dead. Death may have occurred due to smothering by the sponge. In such cases the larvae may have become caught, settled, begun development and then were smothered by the sponge after a certain point in development. In some cases hundreds of very small, empty *Balanus glandula* shells were found on the rock under *Halichondria panicea*. In such instances it was possible that the sponge could have spread over the previously settled young barnacles. However, among the dead barnacles there usually occurred living specimens of a size equal to, smaller than, or larger than the dead ones, which indicates that the larvae were continually arriving via the incurrent sponge streams.

Regardless of their method of finding their host sponges, many varied organisms were found as associates of *Halichondria panicea*. They included: Arthropoda: *Jassa falcata*, and *Pontogeneia* sp. (Gammardiae); *Caprella equilibra* and *Tritella laevis* (Caprellidae); *Dynamene sheareri*, *D. dilata* and *Munna chromatocephala* (Isopoda); various copepoda; *Balanus glandula*, *B. nubilis*, and *Mitella polymerus* (Cirripedia); *Pachycheles* sp., *Oedognathus rudis*, *Cancer productus*, and *C. magister* (Decapoda); various mites; and Insecta: Telmatogeton sp. larvae and Liparocephalus cordicollis (Staphylinidea).

Mollusca: Acmea asmi, Leptothyra bacula, Archidoris montereyensis, Onchidiella sp., and Thais lamellosa (Gastropoda); Mytilus californianus, Saxicava arctica and various bivalves (Lamellibranchia); Mopalia lignosa and Tonicella lineata (Amphineura).

Annelida: Halosydna brevisetosa and Harmothoe imbricata (Polynoidae); Nereis mediator, N. vexillosa, Platynereis agassizi and Neanthes brandti (Nereidae); Sabellaria cementarium (Sabellariidae); Pseudopotamilla ocellata, Sabella media, Schizobranchia insignis and Chone mollis (Sabellidae); Typosyllis pulchra, Odontosyllis phosphorea and various syllids (Syllidae); Neoamphitrite sp. (Terebellidae); and various Cirratulidae.

Platyhelminthes: Leptoplana chloranota (Polycladida). Nematoda. Coelenterata: Hydractinia sp., and Syncoryne sp. (Hydrozoa). Ectoprocta: Membranipora sp. Pycnogonidea. Sipunculoiea: Sipunculus nudus. Pisces: Pholis ornata (Saddleback gunnel).

Algae: Corallina gracilis, Gigartina cristata, Constantinea simplex, Halosaccion glandiforme, Odonthalia floculosa and Microcladia borealis.

Quite consistently, the most common organisms were Jassa falcata (Amphipoda), Balanus nubilis and B. glandula (Cirripedia), Dynamene sheareri and D. dilata (Isopoda), nematodes, and Corallina gracilis (Rhodophyta). The amphipods were generally found upon the sponge surface when examined in the laboratory. However, when the sponges were examined in their habitat the amphipods were hidden in the holes of the sponge or within small burrows they had formed. These amphipods, both gammarids and caprellids, are conveniently equipped with chelate appendages for holding onto the sponges in the surf. The Dynamene isopods were found in small depressions in the sponge surface. The majority of the barnacles were found underneath the sponges, and few were found on the sponge surface. The algae found were generally attached to the rock substrate and protruded up through the sponge.

The annelid worms occurred in a random manner throughout the sponge, but most were found underneath. Sabellid tubes often ran along the substrate-sponge interface and angled up near their anterior end to clear the sponge surface. The nereids and other Errantia usually were found in excavated tunnels or tubes within the sponge situated so that their anterior ends protruded from the sponge. The nematodes were located throughout the sponge, crawling among the various chambers. The large crabs inhabited cavities and pockets in the rock beneath the sponge. In some instances they were completely sealed within their sponge-rock shelters. The stomachs of these crabs were filled with the sponge that was providing them shelter.

Sipunculus nudus was found within the sponge itself. The single Pholis ornata was found in a crab shelter underneath a mass of sponge. Hydroids were attached to the sponge surface or to stems embedded within the sponge, as were some of the algae, i. e. Microcladia borealis (Rhodophyta). Liparocephalus cordicollis (Insecta) was found crawling on the dry sponge surface at low tide. Fly larvae (Telmatogeton sp.) were within the sponge partly protruding from it. Mytilus californianus were often attached to the rock substrate by their byssal threads, but well embedded within the sponge.

In general, Halichondria panicea exhibited a varied and rich biota. This was particularly noticeable when a comparison was made between the associates of immediately adjacent masses of Suberites lata (#14) and H. panicea (#21). The predominant associates of the S. lata specimen were Tubularia sp. and miscellaneous sabellids; while those of H. panicea were Jassa falcata, Corallina gracilis and Oedignathus rudis. The population density of S. lata was 0.08 organisms per cubic centimeter and that of H. panicea was 0.26 organisms per cubic centimeter, which is very low for H. panicea. S. lata had none of the Corallina gracilis, Oedignathus rudis, Mitella polymerus, Mytilus californianus, nor terebellidae that were found on H. panicea. Similarly, H. panicea had none of the Tubularia sp., annelids, nor bivalves that were associated with S. lata. Thus, the associated organisms of the two sponges differed markedly and the population density of the two varied by a factor of more than three times. The two sponges had only a couple of species of animals in common, namely Jassa falcata and the megalops stage of Pachycheles sp.

Table 5. The organisrr

Yaquina Head

| | 1 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 31 |
|---|---|---|---|---|---|---|---|---|---|
| Arthropoda: | | | | | | | | | |
| *Jassa falcata* & *Pontogeneia* sp.[a] | 4 | 3 | 2 | 24 | 14 | 29 | 51 | 26 | 84 |
| *Balanus glandula* & *B. nubilis* | . | 13 | 106 | 25 | 35 | 10 | 34 | 20 | 21 |
| *Mitella polymerus* | 1 | 2 | . | . | . | 1 | . | . | 1 |
| Caprellidae[b] | . | . | . | . | . | 90 | . | . | 19 |
| Copepoda | . | . | . | . | . | . | . | . | . |
| *Dynamene sheareri* | . | 4 | 5 | 11 | . | . | . | . | . |
| *Dynamene dilata* | . | . | . | . | . | . | 3 | . | 5 |
| *Munna chromatocephal:* | | 4 | . | 8 | 2 | 6 | 8 | 19 | 33 |
| Decapoda (Misc.)[c] | 1 | . | . | 2 | 5 | 4 | 2 | 2 | 12 |
| *Liparocephalus cordicol* | | 2 | 1 | . | . | . | . | . | . |
| *Telmatogeton* larvae | . | . | . | 2 | . | . | . | . | . |
| Mollusca: | | | | | | | | | |
| *Mytilus californianus* | l | 4 | 2 | 90 | . | 13 | 1 | 2 | . |
| *Acmaea asmi* | . | 1 | 1 | 1 | . | . | . | . | 1 |
| *Archidoris montereyensi* | | 1 | 2 | 2 | 2 | 1 | 1 | . | . |
| *Leptothyra bacula* | | . | 1 | 8 | . | 26 | . | . | . |
| Amphineura[d] | | 1 | . | . | 1 | . | . | 1 | . |
| Nematoda | 2 | 21 | 1 | 22 | 3 | 2 | 2 | 5 | 7 |
| Annelida: | | | | | | | | | |
| Nereidae[e] | | 2 | 6 | . | . | . | 1 | 1 | . |
| Sabellidae[f] | | . | . | . | 5 | 14 | 2 | 10 | 11 |
| Terebellidae[g] | l | . | . | . | . | . | . | . | . |
| Syllidae[h] | | . | . | $2^{t}$ | $8^{o}$ | $4^{o}$ | $5^{o}$ | $1^{o}$ | . |
| Miscellaneous[i] | | . | . | . | . | . | . | $3^{s}$ | $1^{s}$ |
| Hydroidae[j] | | X | . | X | . | . | X | X | . |
| Misc. animals | | 21 | 1 | 70 | 5 | 1 | . | 4 | 4 |
| Algae: | | | | | | | | | |
| *Corallina gracilis* | | . | . | . | . | . | 7 | 11 | . |
| *Microcladia borealis* | | 2 | 2 | 23 | . | . | . | . | . |
| Miscellaneous[k] | | . | $1^{H}$ | $4^{P}$ | . | . | . | . | . |

[a] *Pontogeneia* sp. (An

[b] Caprellidae include: a (o), and various unidentified forms (m).

[c] Miscellaneous decap nentarium) and (C)Cirratulidae (unidentified).

megalops stages (uniden nifies that many individual polyps of a large colony

[d] Amphineura include

[e] Nereidae include: N n glandiforme(H), *Constantinea simplex*(C), and

[f] Sabellidae include:

Table 6. The thickness and volume of *Halichondria panicea* and the total number, density, and most common groups of organisms in each sample.

| Sample number | Thick-ness(cm) | Volume ($cm^3$) | Total animals | Density ($/cm^3$) | Predominant groups of animals |
|---|---|---|---|---|---|
| **Seal Rocks** | | | | | |
| | North Side: | | | | |
| 1 | 3/4 | 17.5 | 194 | 10.90 | *Mytilus* - *Balanus* - *Dynamene sheareri* |
| 3 | 1/2 | 84.5 | 589 | 6.97 | *Jassa* - *Balanus* - nematodes |
| 4 | 1 | 28.0 | 40 | 1.42 | *Balanus* - *Archidoris montereyensis* |
| 5 | 1/2 | 4.5 | 51 | 11.40 | *Jassa* - *Balanus* - *Mytilus* |
| 29 | 2 | 124.0 | 133 | 1.07 | *Jassa* - *Balanus* - *Dynamene sheareri* - *D. dilata* |
| 33 | 1 | 90.0 | 98 | 1.09 | *Jassa* - *Balanus* |
| | South Side: | | | | |
| 6 | 1/2 | 24.0 | 115 | 4.80 | *Jassa* - *Balanus* - *Dynamene sheareri* |
| 7 | 1/2 | 33.0 | 94 | 2.85 | *Jassa* - *Leptothyra* - *Dynamene sheareri* |
| 8 | 1/2 | 29.5 | 209 | 7.08 | *Jassa* - *Balanus* - *Corallina gracilis* |
| 9 | 1/2 | 20.5 | 198 | 9.66 | *Jassa* - *Leptothyra* - *Mytilus* |
| 30 | 1 | 48.0 | 180 | 3.30 | *Jassa* - *Balanus* - nematode |
| 32 | 1 | 165.0 | 445 | 2.68 | *Balanus* - *Dynamene sheareri* |
| | Outside: | | | | |
| 12 | 1 | 99.0 | 138 | 1.48 | *Jassa* - *Balanus* - Caprellids |
| 13 | 1 | 110.0 | 117 | 1.07 | *Jassa* - *Schizobranchia insignis* - nematodes |
| 14 | 1 | 84.0 | 50 | 0.60 | *Jassa* - *Corallina gracilis* - nematodes |
| 15 | 1 | 74.0 | 82 | 1.11 | *Jassa* - *Balanus* - *Dynamene dilata* |
| 18 | 2 | 542.0 | 624 | 1.15 | *Jassa* - *Balanus* - *Dynamene dilata* - nematodes |
| 19 | 2 | 385.0 | 673 | 1.74 | *Jassa* - *Balanus* - Caprellids - nematodes |
| **Yaquina Head** | | | | | |
| 10 | 1/2 | 15.5 | 297 | 19.14 | *Jassa* - *Balanus* - Hydroids |
| 11 | 1/2 | 61.5 | 304 | 4.91 | *Jassa* - *Balanus* - Hydroids |
| 16 | 1/2 | 12.0 | 31 | 2.88 | *Acmaea asmi* - *Balanus* - *Gigartina cristata* |
| 17 | 1/2 | 20.0 | 61 | 3.50 | *Jassa* - *Mytilus* - *Corallina gracilis* |
| 21 | 2 | 70.0 | 18 | 0.26 | *Jassa* - *Oedognathus rudis* - *Corallina gracilis* |
| 22 | 1 | 109.0 | 102 | 0.93 | *Odontosyllis phosphorea* - *Balanus* - nematodes |
| 23 | 1 | 148.0 | 130 | 0.88 | *Balanus* - *Dynamene sheareri* - *Corallina gracilis* |
| 24 | 1 | 118.0 | 324 | 2.80 | *Mytilus* - Bivalves - *Corallina gracilis* |
| 25 | 1 | 175.0 | 96 | 0.55 | *Jassa* - *Balanus* - *Corallina gracilis* |
| 26 | 3 | 314.0 | 218 | 0.69 | *Jassa* - Caprellids - *Corallina gracilis* |
| 27 | 1 | 38.0 | 135 | 3.60 | *Jassa* - *Balanus* - Hydroids |
| 28 | 1 1/2 | 171.0 | 153 | 0.89 | *Jassa* - *Balanus* - Hydroids - *Munna chromatocephala* |
| 31 | 2 | 347.0 | 198 | 0.57 | *Jassa* - *Balanus* - Caprellids - *Munna chromatocephala* |

# DISCUSSION

## Overall Comparison of Sponges

The four sponges differed in gross morphology, habitat and consistency. They showed great differences in population composition and densities; and in the amount of variation in these criteria from sample to sample. For example, the population density of *Halichondria panicea* varied from a high of 19.14 organisms to a low of 0.26 organisms per cubic centimeter of sponge. This wide variation was due in large part to the great variation and diversity found in intertidal areas universally. The subtidal sponge *Microciona prolifera* showed far smaller variations in population densities, i.e. from 3.64 to 0.31. *Suberites lata,* which occurred at the greatest depth of the above three species, harbored from 0.001 to 0.03 organisms per cubic centimeter of tissue, which was a somewhat smaller variation than shown by *M. prolifera.* Thus in general, stability and constancy in populations increased with increasing depth. Some of the variation in community densities was due to seasonal fluctuations and changes in the composition of the community. As shown in Table 4, the isopod *Munna chromatocephala* and the nereid worms of *Microciona prolifera* were abundant in about half of the samples, but these samples were from one collecting trip. All collections were made at the same site, hence the incidence of Munna chromatocephala and the nereids associated with Microciona prolifera varied from time to time. That is, some groups may be predominant at one season and insignificant at others; therefore, these groups of organisms may vary independently and simultaneously.

Microciona prolifera had quite an array of organisms associated with it. In Table 4 many taxonomic groups of plants and animals were represented by specimens found with the sponge. Pearse (1935) found a representative of nearly all the groups of local marine organisms in the sponges of Dry Tortugas, indicating that sponges often provide habitats for a large variety of plants and animals.

It was interesting to observe that occupying an area or zone just below that of Microciona prolifera was a large, globular, yellow sponge of unknown identity, but of a composition very similar to the loggerhead sponge (Speciospongia vesparia) described by Pearse (1935) in Dry Tortugas. This species was examined underwater by the author and in the laboratory for associates, and none was found. The large oscula and chambers, and the soft, spongy consistency should have provided an ideal substrate for the carids, annelids, and so forth that were found on the, seemingly, more inhospitable Microciona prolifera nearby. Yet another seemingly ideal species of sponge with intermingling branches, soft composition and open chambers (probably Leucosolenia sp.) was found encrusting parts of masses of M. prolifera, but was completely devoid of any of the associates crowded onto M. prolifera. Thus it appears that there exists a definite preference for M. prolifera by its associates, even when sponges with a more penetrable consistency are nearby or encrusting upon M. prolifera.

Among the four species of sponge little similarity occurred in population composition. A good example of this dissimilarity was found with the amphipods. Jassa falcata was consistently found, along with a few Pontegenia sp. and Corophium acherusicum, at all of the collecting stations of Halichondria panicea, but J. falcata was never on the other sponges. Aoroides columbiae was associated with Suberites lata and Corophium acherusicum with Microciona prolifera. Thus, the associations of these species seems to be fairly specific. That is, these species usually do not have overlapping associations, and, as with Jassa falcata, their habitat (i. e. shallow burrows in sponges) is consistent within their distributional range. Concerning the distribution and abundance of these amphiphods, Dr. J. Laurens Barnard (personal communication) remarked: "This seems to be a fair sampling of the things you might expect from sponges except for the absence of Leucothoë, a genus that should occur in sponge very abundantly, but perhaps not in these species. *Jassa*, *Corophium* and *Aoroides* build tubes which may be attached to sponges either inside or out, mostly out, I suspect, whereas *Pontogeneia* is a free-living species perhaps nestling in sponges facultatively. In tropical waters genera like *Anamixis*, various Stenothoidae perhaps occur in sponges and in antarctic waters some acanthonotozomatids are believed to live in sponges."

A few animals, however, were observed on two or more species of sponge, such as the cosmopolitan scale worms (*Harmothoe imbricata* and *Halosydna brevisetosa*), the common barnacle *Balanus glandula*, the isopod *Munna chromatocephala*, the carid *Crago* sp., the nudibranch *Archidoris montereyensis*, the crab *Cancer antennarius*, the nereid *Platynereis agassizi* and the sabellid *Pseudopotamilla ocellata*. The occurence of overlaps in community composition of these sponges was rare and the numbers of individuals were very small and insignificant.

Though most of the variation in associate populations of the species of sponge studied was accounted to habitat differences (i. e. intertidal, subtidal and littoral), it was shown (p. 38) that even in the same habitat the sponges differed markedly in the population they harbored. These variations were probably due to the differing consistencies of the sponges and to the differences in the requirements (food, shelter, chemical exudates, etc) of the associates provided by the sponges. As explained on page 30, Halichondria panicea has a characteristic pungent or foul odor, and this odor may be that which the nudibranch Archidoris montereyensis was seeking and following. Suberites lata has no detectable odor, and Archidoris montereyensis was never found on or near it. Pearse (1935) suggested that differences in the odor of sponges may be important in causing great differences in the number of animals inhabiting various species of sponge.

The habitat of Halichondria panicea is characteristically intertidal, free of mud, and an area of extreme turbulence and many species of plants and animals. In contrast, Microciona prolifera, and to an even greater degree Suberites lata, are found in areas of increasing mud deposition around and upon the sponges, decreasing turbulence, decreasing plant life, and decreasing variations and irregularities in plant and animal life from sample to sample. There is, likewise among the symbionts decreasing competition for epifaunal space, and a decreasing tendency or requirement for becoming embedded within the sponge, or otherwise attaching to the sponge in an immovable, permanent manner.

## Effects of Associates Upon the Sponges

The majority of the associates caused little damage to the host sponges. Usually the extent of damage consisted of a tube or burrow excavated through the sponge surface and into the tissue. Archidoris montereyensis with its voracious eating habits, however, was the most damaging associate of Halichondria panicea. All the other organisms together did not eat a fraction of the amount of sponge that the nudibranchs did. In Microciona prolifera the large sabellid worms that bored tubes down the centers of the branches of the sponge caused the most damage of any of the associates; yet this damage appeared to be minimal. Another mechanism of causing damage to the sponges may involve the retention and accumulation of mud and debris by the binding effect of worm tubes, and secretions of some of the associates. This accumulation of compacted mud and debris may sufficiently hinder sponge water currents to cause local damage. Some evidence of this was seen, but not with any regularity. Thus, the physical damage incurred by associates of these sponges may occur via three possible methods, i. e. ingestion and predation, formation of burrows, and deposition of mud.

Many of the sponge associates, particularly the more motile forms, neither harmed nor benefitted the sponges, i. e. they were inquilines hiding among the branches and other structures of the sponges. The fish, crabs, amphipods and shrimp associated with Microciona prolifera were observed to leave the sponge when frightened by a diver; suggesting that they were simply using the sponge as a convenient hiding place, and there was no obligatory relationship to the sponge. Many of the algae and hydroids found with *M. prolifera* were also found on nearby pilings and floats; thus, their occurrence on *M. prolifera* was due to random dispersal of their planktonic stages.

In contrast to organisms causing damage to the sponges, some actually were beneficial. Such organisms include the alga of *Halichondria panicea* and, perhaps, the crustacea of all the sponges. The sponge does not seem to absolutely require the alga, for yellow specimens that were obviously surviving were found on the underside of rocks out of the sunlight. Thus, the alga is probably just a convenience and not a necessity. The crustacea probably serve to clean the surface of the sponges to some degree, feeding on the algae and debris collected there. In no case did any sponge show a necessity for any associate. Whether the reverse is true or not is unknown, though it appears as if the nudibranch *Archidoris montereyensis* depends upon the sponge for a large part of its diet. This dependence may also be true for the amphipods and isopods found.

## Origin and Evolution of Symbiotic Sponge Relationships

The majority of these sponge symbioses, mostly forms of inquilinism, most likely arose as a matter of convenience for the associates. For example, the crustacea could hold onto the sponge surface easily, find food such as algae and debris on the sponge surface and could easily build burrows in the spongy material for protection during rough surf and could still be able to feed from their burrows. Animals such as the sabellids found the sponge to be an easy substrate in which to form their tubes. And finally, organisms such as the algae, barnacles and bivalves were brought to the sponge as larvae and settled on what proved to be a satisfactory surface or else they were trapped in the sponge.

It is quite possible that nearly all the groups of associates represented were carried to the sponges as larvae. This idea is supported by the fact that nearly all stages of development of crabs and amphipods were found in Halichondria panicea. Pachycheles sp. and Oedignathus rudis were found as zooea, megalops and adults. In some samples very small megalops stages and larger adult stages were found together. It is likely, however, that the molluscs such as Mytilus californianus, the barnacles, sabellids, algae, coelenterata, ectoprocta, and other sedentary organisms were carried to the sponge as larvae; and the amphipods, isopods, caprellids, crabs, nereids, scale worms, and nematodes crawled or swam to the sponge as post-larval forms.

In the example of the inquiline fish within Homaxinella sp., as with other examples of fish-sponge inquilinism previously reported; the fish involved were slender and suitable for an existence in small chambers. These chambers provided shelter, water currents for the well-protected, incubating eggs, and a hiding place from which feeding forays could be initiated.

For the foraging associates such as *Archidoris montereyensis*, *Acmaea asmi*, and *Oedignathus rudis* the sponge provided an easy meal. Probably these animals became 'accustomed' to following a chemical emitted by the sponge in order to find their food.

# CONCLUSIONS

Four marine sponges of the Pacific Northwest were studied for symbiotic associates. The relationships exhibited by these organisms fell into the following categories: 1. "Accidentalism" which was most common and a large component of which concerned inquilinism (e.g. Homaxinella sp. - fish, tubes of worms and burrows of amphipods in sponges, etc.); 2. "cohabitation" resulting from competition for space; 3. predation or grazing; and 4. only one distinct instance of a mutual type of symbiosis was observed (i.e. Halichondria panicea-unicellular alga) with a possibility of a second (Suberites lata-Polydora socialis) and a third (sponges-cleaning crustacea). Ecological observations and behavioral experiments indicated that there was a definite attraction of some associates to the sponges (e.g. Archidoris montereyensis to Halichondria panicea). Therefore, the associates were benefitted in one way or another by their sponge relationships; but it is doubted that the sponges benefitted from these relationships except in the association with endozoic algae and in the cleaning of the sponge surfaces by crustacea. It is postulated that many of the animals, particularly the more motile species, were attracted to the sponges and crawled or swam to them as post-larval forms. However, evidence indicates that many sessile species, such as the algae and barnacles, were carried to the sponges as larval forms.

Great differences were found between the population densities and community composition of the different sponges, even when they occurred adjacent to each other. These differences may have resulted from non-overlapping distributions of the associates, differing niches, various sponge consistencies, and different requirements of the associates which were provided by the sponges. The sponges studied were important components of each ecological situation to which they belonged, i. e. in the capacities of providing shelter, food, a possible mating area, a substrate to cling to, and a spongy material in which to build burrows and tubes.

The 32 specimens of *Halichondria panicea* harbored 6098 organisms, representing 68 species, at densities of up to 19 organisms per cubic centimeter of sponge tissue. The 15 samples of *Microciona prolifera* had 9581 organisms at densities of up to 3.64 organisms per cubic centimeter of sponge; and 14 samples of *Suberites lata* had 150 associates at densities of up to 0.03 organisms per cubic centimeter of sponge. The fourth species of sponge, *Homaxinella* sp. harbored clumps of fish eggs. These eggs are probably from an inquiline fish living within the hollow chambers of the sponge. This is the first report of fish-sponge inquilinism in the Pacific Ocean.

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