

THE DIET AND PREDATOR-PREY RELATIONSHIPS  
OF THE SEA STAR PYCNOPODIA HELIANTHOIDES (BRANDT)  
FROM A CENTRAL CALIFORNIA KELP FOREST

A Thesis

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## ABSTRACT

The diet of Pycnopodia helianthoides from a kelp forest in central California is dominated by gastropods (79%). Calliostoma ligatum and Tegula pulligo are the most important prey species. There is a 3 to 1 ratio of C. ligatum to T. pulligo in Pycnopodia stomachs, whereas a 2 to 1 ratio exists for their field abundances. This apparent preference occurs despite T. pulligo containing more than four times as many calories as an individual C. ligatum. Pycnopodia digests C. ligatum in half the time required to digest T. pulligo. Pycnopodia selects all sizes of C. ligatum but ignores small T. pulligo. Both the opportunistic Pycnopodia and its prey appear to utilize a chemotactile exchange of information rather than distance chemoreception in their predator-prey relationships. Calliostoma ligatum displays a violent somersaulting escape response when contacted by Pycnopodia, whereas T. pulligo does not move. Neither species is able to adhere to the substratum strongly to prevent predation. Although T. pulligo contains more calories than C. ligatum, C. ligatum appears to be preferred by Pycnopodia. The results of this diet study from the northern end of the California range of the sea otter are very similar to the diet of Pycnopodia from the southern end of the otter's range (Dayton et al., 1980). Otters probably influence the diet of Pycnopodia, since the sea star consumes sea urchins

and bivalves outside the range of Enhydra lutris.

Balanophyllia elegans provides protection to C. ligatum from Pycnopodia predation by stinging advancing sea stars with its nematocysts. When C. ligatum was tethered in an area with B. elegans and an area without the coral, Pycnopodia produced significantly greater C. ligatum mortalities in the coral-free area. Calliostoma ligatum benefits in a second manner while on non-horizontal surfaces by releasing itself from the substratum and dropping to safety below. Calliostoma ligatum are not significantly more abundant around B. elegans but large snails are more common on steep sloping rocks. These two refugia (coral patches and vertical walls) may allow the gastropod to maintain its density despite heavy predation pressure by Pycnopodia.

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## Introduction

Asteroids have important ecological roles in subtidal, temperate waters along the west coast of North America (Mauzey et al., 1968; Landenberger, 1968; Birkeland and Chia, 1971; Rosenthal and Chess, 1972; Birkeland, 1974; Van Veldhuizen and Phillips, 1978; Vance, 1978; Dayton et al., 1980; Sloan, 1980; Watanabe, 1980; Harrold, 1981; Birkeland et al., 1982; Kastendiek, 1982; Schmitt, 1982). As major predators within a community, subtidal sea stars are capable of influencing the distribution and abundance of local prey populations (Mauzey et al., 1968; Birkeland and Chia, 1971; Rosenthal and Chess, 1972; Rutherford, 1973; Birkeland, 1974; Dayton et al., 1980; Sloan, 1980; Watanabe, 1980; Tegner and Dayton, 1981; Birkeland et al., 1982; Kastendiek, 1982).

Pycnopodia helianthoides (hereafter Pycnopodia) is a major carnivore in kelp forests along the west coast of North America. It is the largest and heaviest sea star known, individuals having been recorded with a diameter of 130 cm (Mauzey et al., 1968). Possession of thousands of tube feet promotes quickness and makes this predator probably the fastest (Feder and Christensen, 1966) and most active Pacific asteroid (Ricketts and Calvin, 1968). Small prey items are digested internally within the alimentary tract while larger prey may be digested extra-orally.

Following complete digestion of the prey's soft tissue, nondigestible parts (e.g., mollusk shells and small sea urchin tests) are egested or discarded.

Pycnopodia ranges from the Aleutian Islands to San Diego. In Alaska and California, its distribution and diet overlap that of the sea otter, Enhydra lutris. Where sea otter predation has reduced the numbers of abalone and urchins in central California (McLean, 1962; Ebert, 1968; Lowry and Pearse, 1973), Pycnopodia may be an important competitive predator by consuming small abalone and urchins which have not yet attained a refuge in size (Dayton et al., 1980).

There is only one report (Dayton et al., 1980) of the diet of subtidal Pycnopodia within the range of the sea otter, Enhydra lutris. At Point Piedras Blancas, California, where densities of urchins and abalone are low due to sea otter predation, Dayton et al. (1980) found that 72% of the diet of Pycnopodia was gastropods. Their report differs markedly from other diet studies outside the range of E. lutris where researchers have found subtidal Pycnopodia feeding primarily on Strongylocentrotus spp. in southern California (Hopkins and Crozier, 1966; Leighton, 1971; Tegner and Dayton, 1981; and pers. obs.), Washington (Mauzey et al., 1968), and Alaska (Duggins, 1981). Pycnopodia also consumed bivalves in Washington (Mauzey et al., 1968) and Alaska (Paul and Feder, 1975; Van Blaricom, pers. comm.) in

other habitats without otters. With urchins reduced and bivalves generally absent from rocky substrata at the Hopkins Marine Life Refuge, one of the purposes of this study was to examine the prey of subtidal Pycnopodia from the northern end of the California range of E. lutris in a Monterey Bay kelp forest.

Laboratory studies involving Pycnopodia feeding biology have been limited. Greer (1961) performed feeding observations in aquaria and examined the morphology of the digestive system of Pycnopodia. Breen (1979) looked at selective feeding rates for Pycnopodia held in aquaria with clams, urchins, and oysters. Aquarium conditions are unnatural and such diet studies may not accurately reflect the diet of the sea star in the field.

The importance of Pycnopodia in influencing the distribution and abundance of local prey populations is supported by its interactions with a variety and number of organisms which display avoidance and/or escape responses to contact with the sea star (Bullock, 1953; Feder, 1963; Feder and Christensen, 1966; Montgomery, 1967; Mauzey et al., 1968; Robilliard, 1972; Rosenthal and Chess, 1972; Dayton, 1975; Getting, 1976; Margolin, 1976; Phillips, 1976, 1977, 1978; James and Nolen, 1978; Moitza and Phillips, 1979; Nance and Braithwaite, 1979; Hoffman, 1981; Schmitt, 1981; Palmer et al., 1982). Steroid saponins have been implicated as the chemical cues released by predatory sea stars that elicit

such avoidance and escape responses in prey (see Mackie and Grant, 1974 for review; Phillips, 1980).

Predator-prey interactions are fundamental in determining availability and utilization of prey items to asteroids. The methods sea stars employ in capturing prey are complicated and involve factors other than prey defensive responses. The choices made by Pycnopodia between the two most calorically valuable prey were observed relative to their densities, defensive responses, sizes, handling times, adhesion to the substratum, microhabitat distributions, and possible prey refugia at the Hopkins Marine Life Refuge during 144 hours (194 dives) of SCUBA observation.

The objectives of this study were to determine the diet of Pycnopodia from a kelp forest at the northern end of the California range of the sea otter, examine interactions between the asteroid and its prey, investigate the factors affecting prey selection by Pycnopodia, and examine possible prey refugia.

## Materials and Methods

### Site Description

Pycnopodia was studied at the Hopkins Marine Life Refuge (HMLR) on Point Cabrillo, Pacific Grove, California (Figure 1) using SCUBA. A lush understory of red algae and

Cystoseira osmundacea on a gently sloping rock bottom dominate the shallow subtidal at HMLR. Deeper areas are inhabited by a diverse invertebrate assemblage on large granite boulders and bedrock interspersed with sand channels. Macrocystis pyrifera is the only brown alga in deeper waters at HMLR. A detailed description of the study site may be found in Pearse and Lowry (1974).

### Diet

To determine the diet, a total of **forty-one** Pycnopodia were collected from HMLR from June 1980 to June 1981. Thirty-six dives, searching a total bottom area of **1654** m<sup>2</sup>, were made during diet sampling. Sampling consisted of extending a meter tape with attached weights (which allowed the tape to conform to the substrata) through the kelp forest on random compass bearings between depths of 0-13 m (MLLW). A temporary buoy was placed at the end of each sampling transect to allow continuation of sampling along the same bearing on future sampling dives. When a depth of zero meters (MLLW) or the edge of the kelp forest was reached, a new random compass bearing was chosen to re-enter the Macrocystis pyrifera forest.

The method of using a meter tape set at random compass bearings to provide a belt transect through the kelp forest gives a truer representation of the diet of the HMLR

Pycnopodia population than haphazard sampling where researchers turn over the most obvious (and hence larger) individuals. The method used in this study also allowed all habitats (sand channels, crevices, exposed areas, etc.) to be sampled in their correct proportions.

Sampling was conducted during day and night (five of 41 Pycnopodia were collected at night) and all substrata were searched within 1 m of both sides of the transect line. For each Pycnopodia encountered, date and time of collection, distance along the meter tape, maximum diameter of the sea star to the nearest centimeter, depth, substratum type (rock or sand), substratum slope (0-90 degrees), and stomach position (internal or everted) were recorded. The sea stars were lifted from the substratum and the tube feet were cleaned of any attached material. Pycnopodia was transferred to clear plastic bags and sealed underwater. Any prey being extra-orally digested by the sea star's everted stomach were also placed into the bag.

To fully assess the diet of Pycnopodia, in situ sampling must be accompanied by a method for complete stomach inspection since the asteroid can digest prey either extra-orally or internally. The stomach contents can be analyzed without sacrificing individuals by examining material discharged or regurgitated by Pycnopodia. This form of diet analysis can be used with other organisms where permanent removal could significantly affect population size and

community interrelationships.

Sea stars were taken to the Moss Landing Marine Laboratories where the aboral surface was lightly pressed, sometimes enabling a portion of the prey to be removed without injuring the asteroid. Each Pycnopodia was then placed into a separate plastic bucket (18.9 l), covered with a lid, and supplied with a constant source of fresh running seawater. The buckets were checked frequently and any material regurgitated or discharged was identified and preserved. The sea stars were returned to HMLR one to two weeks following collections.

Five of the forty-one (12.2%) Pycnopodia were dissected within five to nine hours after collection to determine the presence or absence of entirely soft-bodied prey that would have been completely digested and thus missed by analyzing only material discharged. In addition, two of the forty-one (4.8%) were dissected following the one to two week period they were held in buckets in the laboratory to determine whether or not all hard parts of digested prey had been discharged.

Additionally, qualitative underwater feeding observations were made in kelp forests along the central California coast in Santa Cruz and Monterey counties. Sea stars were overturned and their diameter measured to the nearest cm. Prey being extra-orally digested by the animal were identified, and if no prey were visible near the oral opening, the

aboral surface was lightly pressed to force out the portion of prey from the stomach which could be removed without injuring the asteroid. Occasionally, Pycnopodia were taken to the surface where the stomach was dissected and placed in 10% buffered formalin for later laboratory analyses.

### Prey Densities and Defensive Responses

Densities of all Calliostoma and Tegula species from depths of 6-10 m below MLLW at HMLR were estimated from May to June 1982. Twenty-eight 0.25 m<sup>2</sup> quadrats were placed at random distances along transect lines set at random compass bearings. Since Pycnopodia had access to all areas within the kelp forest, both sand and rocky substrata were sampled. Gastropods of the two genera were removed from within the quadrats and placed into bags underwater.

In addition to collecting the obvious large individuals, small gastropods of both genera were found by carefully removing algae and intensely combing all substrata within the quadrat. The average time spent searching a quadrat was 12 minutes.

Interactions between Pycnopodia and other organisms were recorded while observing moving sea stars at HMLR. Contacts between Pycnopodia and its prey were observed during day and night surveys within the kelp forest.



### Prey-Size Selection

Vernier calipers were used in the laboratory to measure the maximum basal diameters (to the nearest 0.1 mm) of Calliostoma ligatum and Tegula pulligo from 41 HMLR Pycnopodia stomachs and 18 of the 28 0.25 m<sup>2</sup> density quadrats. An unpaired t-test was performed on comparisons between stomachs and quadrats for each species.

### Prey Handling Times

Handling times for Calliostoma ligatum and Tegula pulligo were determined by placing one adult gastropod in an aquarium with a Pycnopodia that had been starved for one week (to ensure that the digestive tract was empty). The time from contact to egestion was recorded. Individual Pycnopodia were never used in more than one trial and only one gastropod of either species was given to a sea star. Sizes of Pycnopodia used ranged from 23-59 cm in diameter and averaged 34.4 cm. To compare values for C. ligatum and T. pulligo, an unpaired t-test was performed on the mean handling time for each trial.

### Prey Adhesion

A laboratory experiment was conducted to compare the

ability of Calliostoma ligatum and Tegula pulligo to adhere to the substratum when contacted by Pycnopodia. If the force required to remove a gastropod was significantly different between prey species and that force was large, then prey adhesion might be an important prey defensive response which could influence prey selection by Pycnopodia. However, if there was no significant difference in the adhesion between prey species or if either force was small, then prey adhesion may not be important in prey selection by Pycnopodia.

Metal rings were epoxied to the apices of seven adult C. ligatum and five adult T. pulligo with underwater epoxy (Brolite Splash Zone Compound A + B A-788-66 by Koppers Co., Inc.). Gastropods were allowed to attach underwater to the surface of the aquarium. A spring scale was used to measure the amount of vertical force (measured in grams to the nearest 25 g) required to lift each species slowly from the water table while in contact with the tube feet of a live Pycnopodia.

#### Tethering of Calliostoma ligatum

After observing Pycnopodia retreat from contact with Balanophyllia elegans, a field experiment was designed to test the ability of B. elegans to protect Calliostoma ligatum from Pycnopodia predation. A granite substratum at 8 m

(MLLW) with a slope of 30 degrees (shaded by a nearby wall) and densely populated with B. elegans was chosen as the site for a gastropod tethering experiment at HMLR conducted from May to August 1981 (Figure 2). The right half of a 0.5 x 1 m rectangular area was cleared of all flora and fauna including B. elegans. Only macroalgae were removed from the left side of the rectangle leaving 500 B. elegans polyps in the control area. Two threaded brass bolts were cemented into the substratum using a pneumatic drill and Brolite Splash Zone Compound. The shells of live C. ligatum (ranging from 13.3-20.5 mm basal diameter with an average of 16.2 mm) were affixed by epoxy to a monofilament or nylon line 8-17 cm long. Each gastropod was tied to a separate nail (8-10 individuals per replicate) spaced 2.5-3.0 cm apart on a 31 x 4 cm piece of wood. The entire apparatus was affixed to the substratum with a brass nut and washer onto the threaded bolt on the cleared side of the site. An identical tethering apparatus was bolted to the control side.

Both the control and cleared sides of the experimental site were sampled every one to five days (average = 2.3 days), including sampling at night. Sampling consisted of checking tethered snails for mortalities and untangling tethers. At each sampling time, all possible asteroid predators other than Pycnopodia (Pisaster giganteus, Dermasterias imbricata, Pisaster ochraceus, Orthasterias koehleri, and Patiria miniata) were removed from within five m of the

site during three replications of the experiment. P. giganteus and P. miniata had to be removed from the tethering area because they were found digesting tethered snails on both sides of the site during a preliminary trial run. Replications ran between seven and 12 days, averaging 9.3 days.

#### Microhabitat Distribution of Prey

If the results of the tethering experiment showed that corals provided protection for gastropods, the distributions and interrelationships of two prey species and other associated organisms would be examined. The microhabitat distribution of species of Calliostoma, Tegula, Balanophyllia elegans, Corynactis californica, Astrangia lajollaensis, and red algae was sampled from 49 0.25 m<sup>2</sup> quadrats placed at random distances along transects established at random compass bearings on the rock bottom of the HMLR kelp forest from February 1982 to October 1982. If the quadrat landed on a non-flat rock face and/or on a very heterogeneous surface, the next randomly selected quadrat was used. (This helped reduce additional variables so that variation in the slope of the rock could be the primary focus). Depth, substratum type, substratum slope (using an underwater inclinometer), number of individuals of all species of Calliostoma and Tegula, number of B. elegans polyps, and

percent cover (visual estimate) of B. elegans, C. californica, A. lajollaensis, and red algae were recorded. Gastropods from 13 microhabitat quadrats (127 Calliostoma ligatum and 21 Tegula pulligo individuals) were placed into bags underwater and basal diameters were measured in the laboratory. Correlation coefficients were calculated between all combinations of microhabitat categories mentioned above using an alpha level of 0.05 (two-tailed).

During microhabitat sampling, it was evident that percent cover of red algae decreased from the tops of rock outcrops to the bases of boulders. It was thought that in areas where the percent cover of red algae was reduced (possibly due to low light levels) this might allow habitation by corals, perhaps providing protection for gastropods. To determine if light might be one factor responsible for the inverse relationship between percent cover of red algae and increasing rock slope, subsurface light was measured within the HMLR kelp forest on a single date in June 1982. A diver-held, flat, cosine-corrected light collector on a 50 m cable [used in conjunction with a surface sensor (Li-Cor model LI-185A Quantum meter, Lambda Instruments Corp.)] was placed at the top of five vertical rock outcrops (facing different directions) and moved two meters down the exposed wall (9-11 m below MLLW) while recording depth. The methods were also repeated in open water away from rocks within the kelp forest as a control.

## Observations and Results

Diet

The average density of Pycnopodia in the HMLR kelp forest was 0.03 per m<sup>2</sup> with 80.5% occurring on rocky substrata. The sizes of Pycnopodia sampled ranged from 4-50 cm in diameter and averaged 30 cm. Only three of 41 (7%) were not feeding.

Occasionally live prey were released by Pycnopodia enroute to the laboratory and during the first 24 hours in aquaria (probably due to stress). The remains of digested prey were generally released within the first two days in the laboratory.

Stomachs of five individuals dissected before they were allowed to discharge stomach material revealed no new soft-bodied prey species not already discharged by another individual. In addition, no prey item was found to be composed entirely of digestible parts. No prey were found in the two Pycnopodia dissected following the laboratory holding period. Since the five dissections conducted before prey were discharged showed nothing that would have been missed, and since all prey remains were discharged while Pycnopodia was held in the laboratory, this method of diet inspection appears to provide a valid representation of what the sea star consumes.

Of 353 total prey items from 41 stomachs, only two were unidentifiable (Table 1). Although a variety of taxa were found, gastropods dominated with 279 individuals total, comprising 79.0% of the diet based on number of prey. The gastropods Alia carinata and Calliostoma ligatum were the most numerous prey. Of the 48 Crustacea (13.6% of the diet) 25 individuals were hermit crabs. The remaining taxa (26 items) consisted of Echinodermata (10), Bivalvia (5), Polychaeta (3), Bryozoa (2), fishes (2), Porifera (1), and Sipuncula (1).

The average number of individual prey per Pycnopodia was 8.7 with a maximum of 43. The average number of prey species per Pycnopodia was 3.9 with a maximum of 13.

One of the 41 Pycnopodia contained seven Conus californicus in its stomach; two shells were observed being partially extruded through the aboral surface. Predation on C. californicus was observed only during May and June from 1980 to 1982 when aggregations of mating and egg-laying C. californicus were observed. Pycnopodia were observed on the aggregation site with several empty C. californicus shells directly beneath the sea stars. Other individuals contained shells in the stomach. Aggregations of C. californicus were not observed during months other than May or June.

In central California locations other than HMLR, C. ligatum was the most abundant prey and gastropods were also the dominant prey items. On one occasion, a large adult

Crepidula adunca (which had been attached to a Tegula brunnea), was being digested by a Pycnopodia (Table 2). However, none of the C. adunca from the 41 individuals sampled at HMLR were digested. Only three random field observations found abalone in the Pycnopodia diet. In each case, Pycnopodia was digesting a single abalone less than 13 cm total length. On a few occasions Pycnopodia were seen feeding on Pacific hake, Merluccius productus. These fish were probably diseased, injured, or discarded by commercial fishermen returning to port since large numbers were found dead or dying on the kelp forest bottom at HMLR during July 1981. Large sea stars (Orthasterias koehleri, Pisaster giganteus, and Pisaster ochraceus) were consumed by Pycnopodia with diameters greater than 40 cm. Tegula montereyi was represented in the diet by a single individual. Other observations showed that Pycnopodia rejected T. montereyi in the field and laboratory.

### Prey Densities

Calliostoma ligatum and Tegula pulligo were the two most abundant species of the two genera found at HMLR (Table 3). Calliostoma ligatum (7.2 ind./0.25 m<sup>2</sup>) were twice as abundant from density quadrats as T. pulligo (3.6 ind./0.25 m<sup>2</sup>). This two-to-one ratio of C. ligatum to T. pulligo in the field differs from the three-to-one ratio in the diet of



Pycnopodia. Gastropods as small as 3.7 mm basal diameter were found in random quadrats.

#### Prey Defensive Responses

Calliostoma ligatum displays a violent escape response when contacted by Pycnopodia. The shell is rotated back and forth while the snail changes direction and moves rapidly away from the sea star. Often the foot is thrown against the substratum, somersaulting the gastropod from the predator. These escape responses were never observed to be effective against Pycnopodia predation. On non-horizontal surfaces, C. ligatum, were observed on several occasions to display substratum release as an effective escape response from Pycnopodia.

When Tegula pulligo was contacted by Pycnopodia, it simply withdrew its body under the shell and clamped down on the substratum, and made no attempt to move from the sea star. Tegula pulligo and C. ligatum both display running, shell rotation, and eventually substratum release (usually resulting in escape) when contacted by Pisaster giganteus (Harrold, 1981). Only when the tube feet of P. giganteus are firmly attached to the shell of T. pulligo will the gastropod clamp down to the substratum.

Field contacts between Pycnopodia and C. ligatum and T. pulligo indicated that T. pulligo would occasionally be

passed over while the sea star selected C. ligatum. Moreover, Pycnopodia will pass very close to gastropods but not consume them unless the animal is contacted.

### Prey-Size Selection

Size comparisons of Calliostoma ligatum gathered from Pycnopodia stomachs (average = 12.85 mm) and those obtained from density quadrats (average = 12.46 mm) showed no statistically significant difference ( $P > 0.5$ , unpaired t-test, Table 4). Tegula pulligo gathered from Pycnopodia stomachs (average = 16.39 mm) were significantly larger than T. pulligo gathered from density quadrats (average = 12.13 mm) [ $P < 0.001$ , unpaired t-test, Table 4].

### Prey Handling Times

From 22 trials (16 with Calliostoma ligatum and 6 with Tegula pulligo), the average time required for a Pycnopodia to capture, digest, and egest a single C. ligatum was 25 hours; the same process averaged 54 hours for T. pulligo (Table 5). Pycnopodia required a significantly longer time to consume C. ligatum as opposed to T. pulligo ( $P < 0.001$ , unpaired t-test, Table 5). It was difficult to get Pycnopodia to eat a T. pulligo during the trials. Tegula pulligo had to be offered many times and was often rejected even in

the sea star's starved condition. Calliostoma ligatum was always consumed immediately and never rejected.

### Prey Adhesion

In seven trials with seven separate Calliostoma ligatum the force required to remove the mollusk when touched by Pycnopodia was less than 25 grams. This force was measured as the gastropod lifted its foot, turned, and started running. The force required to lift Tegula pulligo from the substratum when touched by Pycnopodia was between 150-250 g each for four individuals that made no attempt at locomotion away from the sea star.

### Tethering of Calliostoma ligatum

An advancing Pycnopodia elevates its rays while moving forward. When it contacts the tentacles of Balanophyllia elegans, the asteroid quickly raises its arms from the contact and moves rapidly away. Pycnopodia were observed to give the same response when apparently stung by the nematocysts of Corynactis californica and Astrangia lajollaensis.

Twenty-five of the 31 mortalities in the Calliostoma ligatum tethering experiment were from the cleared side of the experimental site (Table 6). A chi-square goodness of fit test with the Yates continuity correction showed that a

significantly greater number of mortalities occurred in the B. elegans removal treatment when compared to mortalities in the control area ( $0.001 < P < 0.005$ , Table 6).

During one observation of the actual experiment, a Pycnopodia was found on the cleared side of the site with a single tethered snail in its stomach. On another occasion, a Pycnopodia was found on the cleared side digesting three tethered snails at the same time.

#### Microhabitat Distribution of Prey

Significant correlations (Table 7) revealed the following relationships: The average size of Calliostoma ligatum, but not the total number of individuals, increased with increasing substratum slope. There was a positive relationship between the number of C. ligatum and percent cover of Corynactis californica but no correlation existed between C. ligatum and Balanophyllia elegans or Astrangia lajollaensis. As depth increased within the kelp forest, substratum slope also increased (becoming more vertical), adding more vertical rocks to the bottom. The percent cover of red algae decreased relative to both depth and increasing substratum slope. The percent cover of B. elegans also increased with depth.

Significant correlations involving Tegula species (Table 7) showed inverse relationships. The number of

Tegula pulligo decreased with increasing size of C. ligatum and increasing slope. Numbers of Tegula brunnea decreased with increasing depth and slope.

During microhabitat sampling, qualitative observations revealed that Calliostoma supragranosum and smaller C. ligatum were often found clumped at the base of red algal holdfasts or in pockets in rock. Small T. pulligo were found interspersed with shell fragments which form coarse sand around rocky areas.

Light decreased along vertically faced rocks at an average rate of 63% from the tops of the outcrops to the bases of the rocks two meters below (71 to 26 microeinsteins/m<sup>2</sup>/sec). With identical sky conditions one hour later, the light level at comparable depths in open water directly adjacent to the kelp forest, decreased 26% (61 to 45 microeinsteins/m<sup>2</sup>/sec) over the same two meter depth interval measured on rock outcrops within the kelp forest.

## Discussion

### Diet

The diet of HMLR Pycnopodia is very similar to that of Pycnopodia studied at Point Piedras Blancas by Dayton et al. (1980), an area where sea otters are also present. Diets in both areas are dominated by gastropods (79% at HMLR, 72% at

Point Piedras Blancas) with Calliostoma ligatum predominating at HMLR and Calliostoma spp. at Point Piedras Blancas. The virtual absence of sea urchins and bivalves from the diet of central California Pycnopodia is probably due to sea otter predation which has greatly reduced the numbers of these potential prey. All other subtidal Pycnopodia diet studies have been done outside the range of Enhydra lutris and have shown the dominant prey to be bivalves and sea urchins (Hopkins and Crozier, 1966; Mauzey et al., 1968; Leighton, 1971; Paul and Feder, 1975; Duggins, 1981; Tegner and Dayton, 1981; pers. obs.; Van Blaricom, pers. comm.). Only two Pycnopodia feeding reports outside the otter's range list other major prey besides bivalves and urchins [Hopkins and Crozier (1966) also list Tegula spp. as prey of southern California Pycnopodia but do not mention any numbers and Yates (pers. comm.) has reported that Pycnopodia in Oregon feed on Cryptochiton stelleri]. The similarity of the diets of Pycnopodia from the northern and southern ends of the California range of E. lutris and Pycnopodia diet studies outside the range of the sea otter suggest that E. lutris may not only determine community structure but may also influence the diet of Pycnopodia where the two organisms coexist.

Dayton et al. (1977) have stated that the caloric "value" of prey is one of many factors which influence the foraging biology of carnivores. Alia carinata is a very

abundant gastropod at HMLR (Pearse and Lowry, 1974), however, the small size of A. carinata (shell length to 11 mm; Abbott and Haderlie, 1980) implies that it is not as calorically important in the diet of Pycnopodia as the larger Calliostoma ligatum (shell diameter to 25 mm; Abbott and Haderlie, 1980). Caloric measurements of Alia (= Mitrella) spp. (lumped with other "medium-sized" gastropods) were done by Ellison et al. (1979) and a value of 36 calories per individual was reported. Calliostoma ligatum, however, has a much greater caloric content of 321 calories per individual (Harrold, 1981). The 29 A. carinata individuals found in one HMLR Pycnopodia stomach (which accounted for nearly half of all A. carinata from 41 Pycnopodia) were probably clumped together when encountered by the predator. Large numbers of these gastropods are required to yield the same equivalent nutrition as one C. ligatum.

Amphissa versicolor (shell length to 17 mm; Abbott and Haderlie, 1980) is smaller than C. ligatum and T. pulligo and appears to be less calorically important to Pycnopodia although it is the third most abundant gastropod in the diet. Using the value of 5154 cal/g as an average established by Thayer et al. (1973) for 10 species of gastropods, the small size of A. versicolor indicates that it would probably yield fewer calories than C. ligatum or T. pulligo.

Tegula pulligo (shell diameter to 30 mm; Abbott and Haderlie, 1980) also contributes significantly to the

caloric intake of Pycnopodia due to the greatly increased caloric value per individual (1356 cal/snail) over that of C. ligatum (321 cal/snail) which in turn is due to the increased amount of tissue in similar sized shells (wet weight is 0.99 vs. 0.28 g for C. ligatum, Harrold, 1981). From a strictly caloric view, T. pulligo should dominate in the diet, however, they were present in only 11 of the 41 Pycnopodia stomachs (26.8%).

With 5380 calories per gram of tissue (ash free dry weight), Nassarius mendicus contains only 79 calories per individual (Harrold, 1981) and is not as important in the diet as other more calorically rich prey (T. pulligo and C. ligatum). It is smaller and more slender than C. ligatum and T. pulligo with a shell length of 15-25 mm (Abbott and Haderlie, 1980).

### Prey Densities

Since Calliostoma ligatum is the most common large gastropod at HMLR, random foraging by Pycnopodia would seem to account for its numerical rank in the diet (Table 3). While Tegula pulligo is the second most common large gastropod at HMLR, it is not represented in the diet in proportion to its caloric importance nor in proportion to its field abundance. Tegula pulligo is apparently less preferred by Pycnopodia or exercises some anti-predator adaptation to



discourage predation. Tegula montereyi appears to be avoided even more, or is less susceptible to capture by Pycnopodia since none were present in the diet, yet their density was equal to Tegula brunnea, which were found 7 times in the 41 Pycnopodia stomachs.

It is difficult to compare density estimates with those of other researchers who generally found lower density values because, in this study small Calliostoma and Tegula were actively searched for in addition to the large-sized individuals. Lowry et al. (1974) looked at the distribution of Calliostoma and Tegula species within HMLR, but their collections were made only on algae.

### Prey Defensive Responses

There are distinct differences between the escape responses of Calliostoma ligatum and Tegula pulligo when contacted by Pycnopodia. Although ineffective against Pycnopodia attacks on horizontal surfaces, shell twisting and running escape responses of C. ligatum are highly effective in deterring predation by the slower Pisaster giganteus (Harrold, 1982). The sizable tube foot surface area (due to a large number of arms and overall size) and fast speed of Pycnopodia are responsible for overcoming (on horizontal surfaces) the effectiveness of these C. ligatum escape responses. On non-horizontal surfaces, substratum release

may be an effective escape response from Pycnopodia if C. ligatum falls a considerable distance away from the predator.

Tegula pulligo, unlike C. ligatum, displays a greatly different escape response to contact with Pycnopodia and P. giganteus. Instead of using its shell twisting and running escape response, which reduce P. giganteus predation (Harold, 1982), the gastropod makes no attempt at locomotion away from Pycnopodia and simply clamps to the substratum. Dayton et al. (1977) describe an identical response in the gastropod Concholepas concholepas when contacted by the predatory Chilean asteroid Meyenaster gelatinosus and describe it as an apparent "toughing it out" tactic. Tegula pulligo may rely on its possible distastefulness or the chance that Pycnopodia will select it less often because of a greater digestive time by the asteroid.

Tegula pulligo and C. ligatum appear to be able to distinguish between contact by Pycnopodia and P. giganteus. The escape responses of T. pulligo to the two predators are consistently different and C. ligatum shows an increased intensity in its escape responses with Pycnopodia including the addition of a somersaulting behavior, catapulting the prey from the predator. This somersaulting escape response is also ineffective on horizontal surfaces but is successful when the gastropod is close enough to reach a ledge or other geographic feature where it may roll off and fall to safety.

### Prey-Size Selection

The lack of significance between sizes of Calliostoma ligatum in Pycnopodia stomachs and in density quadrats implies that Pycnopodia is a random forager with respect to size selection of C. ligatum. By contrast, Pycnopodia individuals consume larger Tegula pulligo which are more common on algae and rocky substrata. Smaller T. pulligo individuals are present in the shell fragment sand where Pycnopodia apparently does not actively forage. The sea star may ignore small T. pulligo while crossing sand channels enroute to other rocky habitats with preferred prey (C. ligatum and larger T. pulligo).

### Prey Handling Times

The increased handling time for Tegula pulligo, when contrasted with Calliostoma ligatum, is probably a result of the greater amount of tissue (nearly four times) in a T. pulligo shell and the toughness of the tissue. Schmitt (1981) used acid hydrolysis experiments to show that the tissue of Tegula eiseni from southern California is difficult to digest by sea stars and this may be true for T. pulligo as well.

Another possible explanation for the longer digestive time might be that T. pulligo is better able to withstand

the digestive juices and lack of oxygen inside the Pycnopodia stomach than C. ligatum. Christensen (1970) has stated that certain bivalves were able to withstand anaerobic conditions in stomachs of the sea star Astropecten irregularis, however, this has yet to be shown to occur in gastropods. There is no difference in the capture time between the two Pycnopodia prey species and both are able to withdraw the operculum far back into the shell.

#### Prey Adhesion

Although Tegula pulligo can adhere to the substratum more tightly than Calliostoma ligatum, this defensive response probably does not explain the apparent preference of Pycnopodia for C. ligatum over T. pulligo. An adhesive force of 150-250 g by T. pulligo must be inconsequential to the strength of thousands of Pycnopodia tube feet which easily open mussel valves. Sea stars are able to lift weights greater than 4000 grams (Feder and Christensen, 1966). The incidence of 22 T. pulligo in the diet of the 41 HMLR asteroids attests to the ineffectiveness of substratum adhesion as a completely effective T. pulligo escape response.

Miller (1974) similarly attached hooks to C. ligatum shells and used a pulley system to measure the tenacity (also to the nearest 25 g) of gastropods when touched by

Pisaster ochraceus. She reported a mean value of 51 g/cm<sup>2</sup> foot area, which, when converted to g/adult C. ligatum, is slightly higher than the values obtained in this study for contact with Pycnopodia.

#### Tethering of Calliostoma ligatum and Prey Refugia

It is evident from the tethering experiment that Balanophyllia elegans provides protection for Calliostoma ligatum and most likely this is against Pycnopodia predation. This contention is supported by several studies and observations. The fact that Pycnopodia retreats upon encountering B. elegans further suggests that the coral can serve as a refuge for the gastropod. Following removal of Corynactis californica from pier pilings, Landenberger (1967) observed Pisaster ochraceus and Pisaster giganteus feeding on Mytilus spp. that were previously unavailable to the sea stars due to the barrier of C. californica. Similarly, Wolfson et al. (1979) found that bands of C. californica prevented Pycnopodia and other asteroids from advancing up legs of an offshore platform to consume Mytilus spp. A similar situation is likely here with gastropods.

Calliostoma ligatum does not feed on cnidarians, but primarily consumes detritus and diatoms (Perron, 1975; Sellers, 1977) and is probably not present around the coral for food. In fact, C. ligatum withdraws from contact with B.

elegans, C. californica, and Astrangia lajollaensis. Calliostoma ligatum is apparently stung by the nematocysts of these organisms yet is occasionally found associated with them, again suggesting a refuge.

The six gastropod mortalities from the uncleared side of the tethered site may have been caused by predation by P. giganteus reinvading the site after their removal. Other potential predators are fishes and octopuses. Several kelp forest fishes are known to prey on gastropods [Embiotoca lateralis (Gnose, 1967; DeMartini, 1969; Alevizon, 1975; Haldorson and Moser, 1979), Hexagrammos decagrammus (Dayton et al., 1980), Ophiodon elongatus (Miller and Geibel, 1973; Hunt, 1977), Rhacochilus vacca (Quast, 1968; DeMartini, 1969; Hunt, 1977; Ellison et al., 1979; Haldorson and Moser, 1979), Scorpaenichthys marmoratus (Dayton et al., 1980), and Sebastes chrysomelas and Sebastes carnatus (Hallacher, 1977)]. Since the shell was always present at the end of a tether and only the tissue removed, fishes are not believed to have been predators on tethered snails.

No octopuses were found on the site during night dives and no drill holes were found in the shells [although their method of predation is not limited to drilling (Hochberg and Fields, 1980)]. Small crabs and hermit crabs are preferred in the field (Hochberg and Fields, 1980). Calliostoma ligatum were not eaten when kept in aquaria for two weeks with octopuses. These observations suggest octopuses were

unlikely predators on tethered snails.

In addition to deriving protection from foraging sea stars, C. ligatum may benefit in a second manner when on a non-horizontal rock populated with corals. If the protection of the nematocysts of the coral is insufficient to deter Pycnopodia, C. ligatum can release itself from the vertical substratum, fall, and escape. Feder (1967) observed Calliostoma zizyphinum (and other gastropods) in England and Norway to utilize substratum release from vertical rocky surfaces as a defensive response when contacted by predatory sea stars.

Substratum release may be an effective escape response for C. ligatum on horizontal rocks when strong surge is present. Dayton et al. (1977) reported "being showered with escaping prey items" in strong surge when the presence of a predatory Chilean asteroid would elicit substratum release by prey.

Watanabe (1980) has shown that algae are a refuge for Tegula spp. from asteroid predation. The mean lengths of Gigartina blades are longer in shallow water at HMLR and strong surge makes it difficult for sea stars to capture gastropod prey under these conditions (Watanabe, pers. comm.).

Pycnopodia are more common in deeper waters at HMLR where the percent cover of red algae (Table 7) and surge decrease with depth. Calliostoma ligatum is more likely to

encounter a foraging Pycnopodia in these areas. Therefore, vertical rock walls with a high percent cover of corals would appear to be the most beneficial refugium for C. ligatum and allow the gastropods to maintain their density despite heavy predation pressure by Pycnopodia.

#### Microhabitat Distribution of Prey

My initial hypotheses (based on qualitative subtidal observations) were that as the substratum slope increased from 0 to 90° the percent cover of Balanophyllia elegans, Corynactis californica, Astrangia lajollaensis, and number of Calliostoma ligatum increased.

The lack of uniform association of C. ligatum with B. elegans, C. californica, and A. lajollaensis is surprising. The tethering experiment in this study has shown that B. elegans is capable of providing protection for C. ligatum against Pycnopodia predation and it would seem that the abundances of the gastropod and B. elegans would be positively correlated. Instead, the percent cover of C. californica is positively associated with the number (all sizes) of C. ligatum (Table 7). Perhaps C. californica provides an even better refuge for C. ligatum from asteroid predation with its large nematocysts. It can be easily argued that aggregations of C. californica and A. lajollaensis seem too closely spaced to provide a refuge for C. ligatum. There



must be a limit to the number of gastropods which can inhabit a cnidarian area because of the stinging and crowding. Another possibility may be that the gastropods are more common at the periphery of the C. californica aggregation. Calliostoma ligatum retreats from contact with B. elegans, C. californica, and A. lajollaensis and it is unclear why the snail is only correlated with the often densely packed C. californica.

Adult B. elegans appear to be randomly distributed throughout rocky areas within the Hopkins kelp forest (Fadlallah, pers. comm.). This random distribution of B. elegans is supported by the lack of significance in relationships between B. elegans and substratum slope (Table 7). McLean (1962) listed B. elegans, C. californica, and C. ligatum as organisms abundant on vertical rock surfaces in a kelp forest at Granite Creek in central California, but these appear to be qualitative observations as well. Perhaps because there is less light on vertical faces (as evidenced from the in situ light measurements), under overhangs, and in crevices, algal cover is significantly reduced with increasing slope (Table 7), thereby making B. elegans "seem" more common on vertical faces.

One possible explanation for the increased abundance of B. elegans in deeper areas at HMLR, may lie with the decreased cover of red algae with depth (Table 7). Fadlallah (1981) has stated that B. elegans is more common in

areas without algae where the polyps are not subject to thrashing, although there was no inverse relationship found between B. elegans and red algae in this study.

The reason only large sized C. ligatum are significantly more common on increasing substratum slopes (Table 7) is revealed when refugia from predation for each size group are examined. Small C. ligatum are more commonly found clumped under red algal holdfasts or in pockets in rock where they are probably afforded a refuge from Pycnopodia predation. Small C. ligatum are not significantly abundant on rocks with steep substratum slopes (Table 7) where there are fewer algal holdfasts and pockets in rock. The decreased size, weight, and foot area of a small C. ligatum may be insufficient to allow the animal to fall, or push itself a safe distance from a predator unless it is on a nearly vertical wall. Large C. ligatum, on the otherhand, may release themselves from the substratum and if their movement and momentum are blocked by an encrusting organism, they may more easily push off and tumble to safety, even if they are on less than vertical surfaces.

The correlation of large C. ligatum occurring with steep slopes (where there is less red algae, Table 7) is supported by an inverse relationship between the size of C. ligatum and percent cover of red algae (Table 7). The qualitative observation that small C. ligatum are more common around red algae is also confirmed by this inverse

relationship (Table 7).

Even with field manipulations it is difficult to experimentally test whether the gastropod is responding to vertical surfaces, coral patches, both, or neither. The current study does not permit establishing whether large C. ligatum knowingly seek vertical surfaces and/or coral patches as a refuge, or are more abundant in these areas because of reduced predation pressure here (although the latter interpretation seems more plausible). Solaster stimpsoni are more common on vertical substrata at San Juan Island, Washington, and avoid horizontal areas where densities of Solaster dawsoni (the chief predator of S. stimpsoni) are five times greater (Birkeland et al., 1982). Birkeland et al. (1982) suggest that contact between the two Solaster species on vertical surfaces would probably result in both sea stars falling from the wall, breaking contact, and allowing S. stimpsoni to escape.

Tegula pulligo are significantly less common in areas with large C. ligatum and steep substratum slopes (Table 7). These correlations imply a different niche utilization for the two species which may be based on food. Tegula pulligo are more common on lower substratum slopes where they feed on macroalgae. Calliostoma ligatum is not an herbivore and large individuals are significantly less abundant around red algae and low slopes (Table 7).

Tegula brunnea is more common at shallow depths and on

low substratum slopes because of algal protection against predators (Watanabe, 1983; Riedman et al., 1981). A dense stand of red algae, proliferating at HMLR with increased light at shallow depths and full exposure on horizontal surfaces, covers gastropods in still water. Large-bladed red algae move back and forth in surge, preventing predatory sea stars from attaching to a stationary object (Watanabe, pers. comm.).

#### Chemoreception vs. a Chemotactile Response

One critical factor which regulates predator-prey interactions between asteroids and gastropods is conveyance of chemical information between the two organisms. The results of my field study appear to contradict results of laboratory studies on the ability of Pycnopodia and their prey to detect each other at a distance due to chemoreception (Phillips, 1976; 1977; 1978; Moitza and Phillips, 1979; Hoffman, 1981). My subtidal observations indicate that a tactile exchange of information is more important than chemoreception, as many gastropod species that are found in the diet pass close to the sea star and both ignore each other unless contact is made.

Occasionally, Calliostoma ligatum will contact a stationary (presumably inactive) Pycnopodia and the gastropod will exhibit a violent escape response which would appear

unnecessary when the sea star does not pursue the gastropod. This observation contradicts the lab results (Phillips, 1978) that suggest some prey are able to detect Pycnopodia from a distance and differentiate foraging and inactive sea stars.

Laboratory work on Pycnopodia by Phillips has suggested interpretations of predator-prey interactions that may not be characteristic of animals in the field. Phillips used (sometimes admittedly) abnormal conditions such as high flow rates and high concentrations of sea star scent producing a "super-stimulus" in aquaria (Phillips, 1976; 1977; 1978; Moitoza and Phillips, 1979), sprinkling salt on Pycnopodia to make them move and presumably become foraging predators (Phillips, 1978), and unnaturally high densities of 10 Pycnopodia/m<sup>2</sup> to assess the diet with respect to sea urchins (Moitoza and Phillips, 1979). Hoffman (1981) has followed the examples of Phillips in a laboratory study using a similar Y-trough with conditions that are nonexistent in the field, perpetuating Phillips' foraging and defensive hypotheses. It must be emphasized that laboratory experiments are simply tools used to elucidate possible behavior in the field. When experimental lab conditions are far removed from nature, the biological meaning of the resulting data must be interpreted with caution.

### Foraging Strategy

Moitoza and Phillips (1979) cite literature to state that Pycnopodia is a generalist, but a better description would be that Pycnopodia is an opportunist. Although Pycnopodia have been found with prey species from a wide variety of taxa in their stomachs, they appear able to take advantage of locally dense prey such as gastropods at HMLR. Mauzey et al. (1968) report that the diet of Pycnopodia varies by habitat and their conclusion is supported by data from this study and other Pycnopodia diet studies from Alaska to California. The seasonal use of aggregations of Conus californicus and large numbers of dead Merluccius productus also suggest that the asteroid is an opportunistic forager. Wobber (1973) documents a similar use, by Pycnopodia, of dead or dying Loligo opalescens following their spawning, although Pycnopodia were not observed feeding on L. opalescens in central California kelp forests in this study.

From a caloric view, Pycnopodia apparently is not an optimal forager, since it will choose prey species with a lower caloric yield. Twice as many Calliostoma ligatum as Tegula pulligo are present in the field, but three times as many C. ligatum were taken compared to T. pulligo. Yet, a single T. pulligo is calorically equivalent to more than four C. ligatum. The greater caloric yield of T. pulligo is

possibly reflected in the handling times, since it took roughly twice as long to digest T. pulligo.

Palatability is an important factor in determining the degree of predation and may not involve escape reactions of prey (Mackie and Grant, 1974). Calliostoma ligatum may simply taste better than T. pulligo. Tegula montereyi may be the most distasteful of all HMLR gastropods because Pycnopodia observed in the laboratory brought the gastropod to the oral area where it was always released and never taken into the stomach in an attempt at digestion. Watanabe (pers. comm.) offered equal numbers of Tegula brunnea, T. pulligo, and T. montereyi to two Pycnopodia in aquaria and out of 50 snails consumed, only one was T. montereyi. Some other anti-predator defense may have been involved, but distastefulness seems likely. These observations imply that Pycnopodia could be displaying a preference for C. ligatum.

The view of Pycnopodia foraging strategy gained from this study is that the predator moves nonrandomly through the kelp forest (avoiding corals and spending less time in sand channels) searching for food, and finding primarily C. ligatum on rocky substrata. If the sea star encounters other, possibly less desirable prey (such as Alia carinata) it takes them into the digestive tract and continues its search. The energy expended by Pycnopodia for selecting a small prey item must be minimal. Other prey items such as T. pulligo, may be found in the diet as a consequence of an

extended search period in which preferred prey are not found.



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Table 1. Diet of 41 Pycnopodia helianthoides from the Hopkins Marine Life Refuge, Pacific Grove, California, from June 1980 to June 1981.

<u>PREY ITEM</u>	<u>NUMBER</u>	<u>% OF TOTAL</u>
GASTROPODA		
<u>Alia carinata</u>	67	
<u>Calliostoma ligatum</u>	67	
<u>Amphissa versicolor</u>	34	
<u>Tegula pulligo</u>	22	
<u>Nassarius mendicus</u>	21	
<u>Mitrella tuberosa</u>	17	
<u>Barleeia acuta</u>	8	
<u>Conus californicus</u>	7	
<u>Tegula brunnea</u>	7	
<u>Calliostoma supragranosum</u>	6	
<u>Lacuna unifasciata</u>	5	
<u>Calliostoma canaliculatum</u>	4	
<u>Tricolia pulloides</u>	3	
<u>Anisodoris nobilis</u>	1	
<u>Balcis thersites</u>	1	
<u>Balcis sp.</u>	1	
<u>Bittium sp.</u>	1	
<u>Collisella ochracea</u>	1	
<u>Collisella sp.</u>	1	
<u>Megatebennus bimaculatus</u>	1	
<u>Ocenebra minor</u>	1	
<u>Seila montereyensis</u>	1	
<u>Triphora pedroana</u>	1	
Unident. dorid nudibranch	1	
TOTAL GASTROPODA	279	79.0
CRUSTACEA		
Hermit crabs	25	
<u>Pugettia richii</u>	7	
<u>Paracerceis cordata</u>	5	
<u>Pachycheles pubescens</u>	4	
<u>Alpheus spp.</u>	2	
<u>Cancer branneri</u>	1	
<u>Cancer productus</u>	1	
<u>Cancer sp.</u>	1	
<u>Cymadusa uncinata</u>	1	
Unident. crab megalops	1	
TOTAL CRUSTACEA	48	13.6



Table 1 (continued). Diet of 41 Pycnopodia helianthoides from the Hopkins Marine Life Refuge, Pacific Grove, California, from June 1980 to June 1981.

<u>PREY ITEM</u>	<u>NUMBER</u>	<u>% OF TOTAL</u>
ECHINODERMATA		
Ophiuroid pieces	5	
<u>Strongylocentrotus purpuratus</u>	4	
Unidentified holothuroid (Molpadiida or Dendrochirotida)	1	
TOTAL ECHINODERMATA	10	2.8
BIVALVIA		
<u>Hinnites giganteus</u>	2	
<u>Modiolus carpenteri</u>	2	
<u>Spisula planulata</u>	1	
TOTAL BIVALVIA	5	1.4
POLYCHAETA		
<u>Autolytus</u> sp.	1	
<u>Phragmatopoma californica</u>	1	
Scale worm (Lepidonotinae)	1	
TOTAL POLYCHAETA	3	0.8
BRYOZOA		
Cheilostome colonies	2	
TOTAL BRYOZOA	2	0.6
FISHES		
<u>Eptatretus stoutii</u> egg case	1	
<u>Liparis mucosus</u>	1	
TOTAL FISHES	2	0.6
PORIFERA		
<u>Leucosolenia eleanor</u>	1	
TOTAL PORIFERA	1	0.3
SIPUNCULA		
<u>Phascolosoma agassizii</u>	1	
TOTAL SIPUNCULA	1	0.3
TOTAL UNIDENTIFIED SOFT TISSUE	2	0.6
GRAND TOTAL	353	100.0

Table 2. Additional prey of Pycnopodia helianthoides from other central California field feeding observations.

PREY

Calliostoma annulatum  
Crepidula adunca ^  
Haliotis rufescens  
Haliotis walallensis  
Merluccius productus  
Ophiopholis aculeata var. kennerlyi  
Orthasterias koehleri  
Patiria miniata  
Pisaster giganteus  
Pisaster ochraceus  
Stenoplax fallax  
Tegula montereyi  
Unidentified holothuroid

Table 3. Comparison of density of Calliostoma and Tegula species from 5 to 11 m at HMLR, May to June 1982 using 0.25 m<sup>2</sup> quadrats (N=28) and incidence of each species in the diet of Pycnopodia (N=41) from HMLR, June 1980 to June 1981.

Species	Mean Density per 0.25 m <sup>2</sup>	Number in diet
<u>C. ligatum</u>	7.2 (SD 8.4)	67
<u>C. supragranosum</u>	0.8 (SD 1.5)	6
<u>C. canaliculatum</u>	0.2 (SD 0.4)	5
<u>C. annulatum</u>	0 (SD 0)	0
<u>T. pulligo</u>	3.6 (SD 5.0)	22
<u>T. brunnea</u>	0.1 (SD 0.4)	7
<u>T. montereyi</u>	0.1 (SD 0.4)	0
<u>T. funebris</u>	<0.1 (SD 0.2)	0
	N=28 0.25 m <sup>2</sup> quadrats	N=41 <u>Pycnopodia</u> stomachs

Table 4. Mean sizes of Calliostoma ligatum and Tegula pulligo from Pycnopodia stomachs (N=41) and density quadrats (N=18) from HMLR.

	<u>C. ligatum</u> from <u>Pycnopodia</u> Stomachs	<u>C. ligatum</u> from Density Quadrats
N	64	125
Mean size (in mm)	12.85	12.46
S.D.	4.36	3.72

alpha = 0.05  
 t-calculated = 0.647  
 t-critical = 1.973  
 P > 0.500  
 No significant difference

	<u>T. pulligo</u> from <u>Pycnopodia</u> Stomachs	<u>T. pulligo</u> from Density Quadrats
N	21	58
Mean Size (in mm)	16.39 **	12.13 **
S.D.	3.2	5.00

alpha = 0.05  
 t-calculated = 3.642  
 t-critical = 1.992  
 P < 0.001  
 \*\* Significantly different

Table 5. Handling time required for Pycnopodia to capture, ingest, digest, and egest Calliostoma ligatum and Tegula pulligo in the laboratory.

	<u>Size of <i>C. ligatum</i></u> <u>(basal diam. in mm)</u>	<u>Size of <i>Pycnopodia</i></u> <u>(max. diam. in cm)</u>	<u>Handling Time</u> <u>(in hours)</u>
Mean	17.9	34.8	25.2 **
S.D.	1.7	9.0	7.3
N	16	16	

	<u>Size of <i>T. pulligo</i></u> <u>(basal diam. in mm)</u>	<u>Size of <i>Pycnopodia</i></u> <u>(max. diam. in cm)</u>	<u>Handling Time</u> <u>(in hours)</u>
Mean	17.6	33.2	53.7 **
S.D.	0.7	7.6	6.4
N	6	6	

alpha = 0.05

t-calculated = 8.45

t-critical = 2.09

P < 0.001

\*\* Significantly different

Table 6. Tethered Calliostoma ligatum experiment at HMLR with and without Balanophyllia elegans.

	Number of Mortalities on <u>B. elegans</u> Side	Number of Mortalities on Cleared Side
Replicate 1	2	10
Replicate 2	2	7
Replicate 3	<u>2</u>	<u>8</u>
TOTAL	6 **	25 **

alpha = 0.05

$\chi^2$ -calculated = 10.45

$\chi^2$ -critical = 3.841

$0.001 < P < 0.005$

\*\* Significantly different

Table 7. Microhabitat distribution correlation coefficient analysis from 0.25 m<sup>2</sup> quadrats at HMLR from February 1982 to October 1982.

	Depth	Substratum Slope	Total No. <u>C. ligatum</u>	Total No. <u>T. brunea</u>	Total No. <u>T. pulligo</u>	% Cover <u>B. elegans</u>	% Cover <u>C.</u> <u>californica</u>	% Cover Red Algae	% Cover <u>A.</u> <u>lajollaensis</u>	Avg. Size <u>C. ligatum</u>	Avg. Size <u>T. pulligo</u>
Depth	.....										
Substratum Slope	+	.....									
Total No. <u>C. ligatum</u>	N.S. (49)	N.S. (49)	.....								
Total No. <u>T. brunea</u>	/// (49)	/	N.S. (49)	.....							
Total No. <u>T. pulligo</u>	N.S. (49)	/	N.S. (49)	N.S. (49)	.....						
% Cover <u>B. elegans</u>	+	N.S. (49)	N.S. (49)	N.S. (49)	N.S. (49)	.....					
% Cover <u>C. californica</u>	N.S. (49)	N.S. (49)	+++ (49)	N.S. (49)	N.S. (49)	N.S. (49)	.....				
% Cover Red Algae	//// (36)	//// (36)	N.S. (36)	N.S. (49)	N.S. (36)	N.S. (36)	N.S. (36)	.....			
% Cover <u>A. lajollaensis</u>	N.S. (24)	N.S. (24)	N.S. (24)	N.S. (24)	N.S. (24)	N.S. (24)	N.S. (24)	N.S. (24)	.....		
Avg. Size <u>C. ligatum</u>	N.S. (13)	++ (13)	N.S. (13)	N.S. (13)	/// (13)	N.S. (13)	N.S. (13)	/	N.S. (13)	.....	
Avg. Size <u>T. pulligo</u>	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	N.S. (8)	.....

No. quadrats in parentheses.

+ = 0.01 < P < 0.05 (positive correlation) / = 0.01 < P < 0.05 (negative correlation)

++ = 0.005 < P < 0.01 (positive correlation) // = 0.005 < P < 0.01 (negative correlation)

+++ = 0.001 < P < 0.005 (positive correlation) /// = 0.001 < P < 0.005 (negative correlation)

++++ = P < 0.001 (positive correlation) //// = P < 0.001 (negative correlation)

N.S. = not significant (P > 0.05)

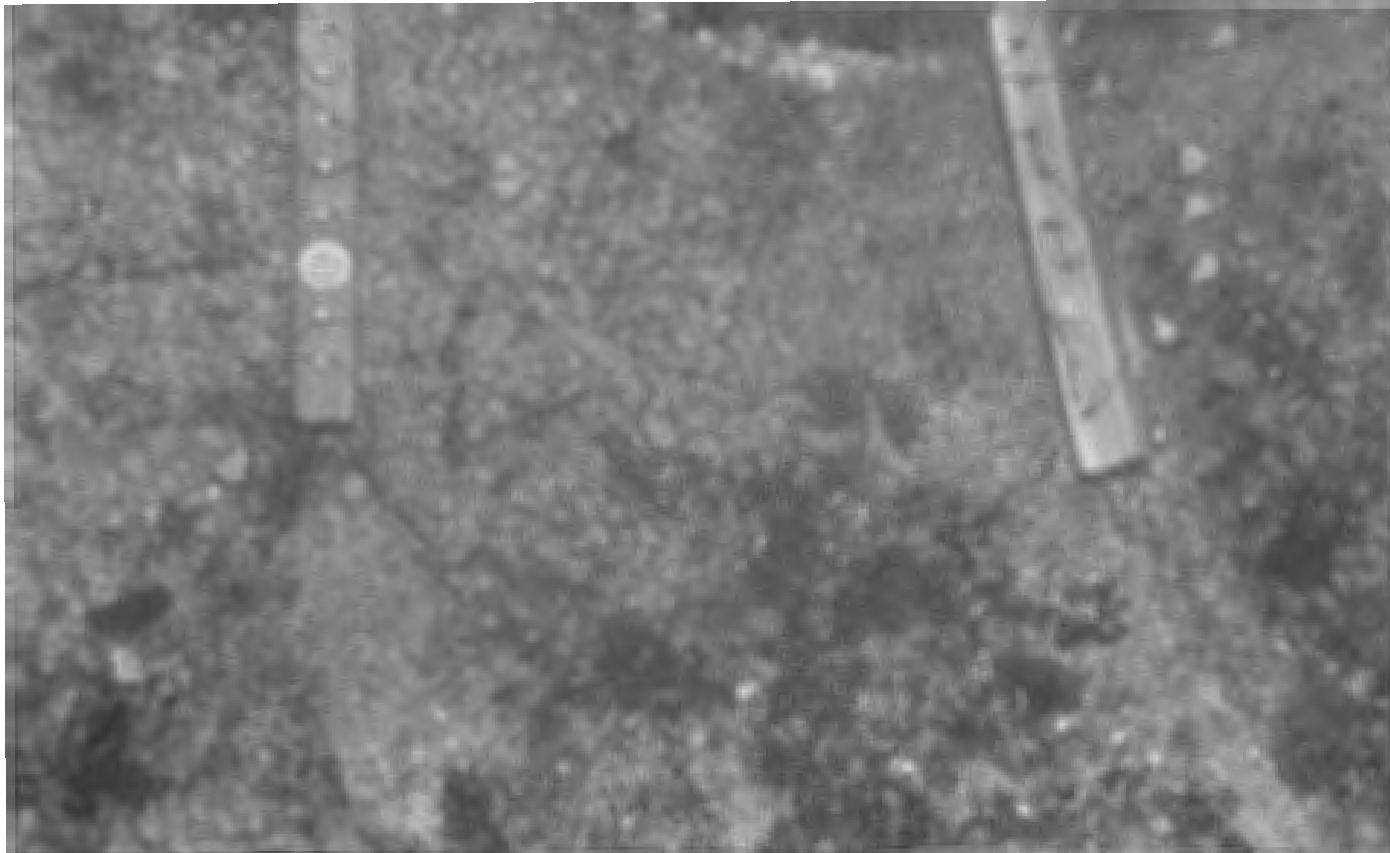


Figure 2. Calliostoma ligatum tethering experiment at HMLR. Gastropods are tied to nails on wooden bar with string. Green epoxy 'cap' cemented string to top of shell for each live individual. Orange spots are Balanophyllia elegans individuals. Coral was removed from right side (cleared). Wooden bars are 31 cm in length.