

AN ABSTRACT OF THE THESIS OF

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The interaction between the acmaeid limpet, Collisella instabilis and the subtidal laminarian, Pterygophora californica involves positive effects on the limpet population and subtle positive or null effects on the kelp. Collisella, which is found only on Pterygophora and another kelp, Laminaria dentigera (Kjellman, 1889), may exploit several features of the stipe of Pterygophora. The long, cylindrical stipe is used as a habitat which provides food and possibly a refuge from seastar predation and interspecific competition. Much of the food source is the epiphytic algae that grow on the stipe of Pterygophora. The epidermis of the stipe is grazed after the epiphytes are removed. There were no significant differences in stipe diameter growth rate between tagged plants with and without limpets suggesting that grazing does not affect the plant negatively. Moreover, none of the limpet-occupied plants with blades that I observed (>150) had any deep scars on the stipe which might weaken it and increase its susceptibility to breakage.

The limpet may have positive effects on its host by preventing the negative effects of epiphytes. These epiphytes often include juveniles

of Pterygophora and Laminaria, which may cover over 80% of the stipe. Observations suggest that when these epiphytic laminarians are abundant, they may greatly increase the drag that the holdfast of the host plant must withstand. This increased drag may increase the probability of holdfast dislodgement, which appears to be an important source of Pterygophora mortality.

Field manipulations and descriptive transects indicate that the limpets may be the single most important factor affecting the establishment and maintenance of epiphyte abundance and diversity. Host plant blade whiplash and factors which fluctuate seasonally may also affect epiphytes. Limpets may thus have positive effects on their host plant by preventing the establishment and/or growth of drag-increasing epiphytes.

This interaction appears to be either mutualistic or commensalistic. Of these, only mutualism has been modeled. Mutualistic models are thus far not sufficiently complex to account for many important aspects of this interaction. The association between C. instabilis and Pterygophora involves several complexities, such as asymmetrical obligateness, interaction with a third species, and environmental variability.

A LIMPET KELP INTERACTION:
DESCRIPTION AND DEFINITION

by

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A LIMPET-KELP INTERACTION:
DESCRIPTION AND DEFINITION

INTRODUCTION

Ecologists have directed much of their recent theoretical and empirical efforts towards understanding the role of biotic interactions in the dynamics of natural communities. These studies have shown that interactions such as competition, predation, mutualism and commensalism are often responsible for the maintenance of community structure (e.g., Dayton, 1971, 1975; Estes, Smith and Palmisano, 1978; Glynn, 1976; Janzen, 1967; Menge, 1972, 1976; Lubchenco and Menge, 1978; Paine and Vadas, 1969; Vance, 1978; Woodin, 1978). Biological interactions are defined as follows: predator-prey interactions (including plant-herbivore and host-parasite interactions) involve a positive effect on the consumer and a negative effect on the consumed, (+,-); competitive interactions have a negative effect on both species (-,-); mutualistic interactions have a positive effect on both species (+,+); commensalistic interactions involve positive effects on one species and no effect on the other species (+,0); amensalism is an interaction which affects one species negatively and the other not at all (-,0; May 1973). Actual associations may fall between some of these definitions. For example, many competitive relationships may actually be closer to amensalism because of a very small negative effect of one competitor on another. In several studies of competition in insects,

one species was either not affected or affected so little that the effect was unmeasurable (Lawton and Hassell, 1981). Furthermore, real interactions may be facultative: the signs of the interaction may change under different circumstances. The relationship between the Chestnut-headed Oropendula and the Giant Cowbird is an example of this type of interaction (Smith, 1968). Where the Oropendula nests are close to wasp nests, bot fly larvae, which may cause increased mortality of Oropendula young unless picked off by cowbird young, are rarely a problem. Apparently, wasps prevent adult botflies from laying eggs on the Oropendula young. In areas close to wasp nests, Oropendula adults eject the eggs of the Giant Cowbird from their nests. In areas away from wasp nests, the Oropendula adults do not eject Giant Cowbird eggs, but allow the young cowbirds to develop, which reciprocate by keeping the bot fly larvae off the Oropendula young. In the presence of wasp nests, the interaction is parasitic (+,-) and in the absence of wasps it is mutualistic (+,+).

Until recently, the emphasis in ecology has been on theoretical and empirical studies of predator-prey and competitive interactions. Subtler interactions such as commensalism and mutualism have received relatively little attention and often are treated as interesting but ecologically unimportant phenomena (for further discussion, see Risch and Boucher, 1976; May, 1976; Williamson, 1972; Duggins, 1981; Addicott, 1981; Vance, 1978). This attitude may require alteration; there is increasingly strong evidence that mutualistic and commensalistic associations such as plant-pollinator, plant-seed dispersers, mycorrhizal fungi-plant, ant-acacia and tubeworm-infauna play important

roles in determining the abundance and distribution of marine and terrestrial organisms (e.g., Risch and Boucher, 1976; Janzen, 1976; Woodin, 1978; Heithaus, Culver and Beattie, 1980; Duggins, 1981).

Theoreticians have just recently begun to examine the dynamics and stability of subtler biological interactions such as mutualism. Most of this theoretical work has involved mathematical analysis of the stability properties of Lotka-Volterra derived models of mutualism. Commensalistic interactions have not yet been modeled. Three types of stability have been examined: 1) global versus local stability, which are properties of the landscape of neighborhood stability analysis (see May, 1973b); 2) return-time stability (resilience), which refers to the time a system takes to return to a previous equilibrium point following a perturbation; and 3) persistence stability, which is the variability of the system over time (May, 1973b; Menge, 1977). The analyses of May (1976) and Goh (1979) predict that mutualistic interactions would be less "globally stable" than models of competition and predation. From this, both May (1976) and Goh (1979) predicted that mutualism would be less frequent in natural communities and therefore less important in community dynamics. This prediction agrees with the assertion of Williams (1972) that mutualism is a "fascinating biological topic, but its importance in populations in general is small...". May (1976) argues that if obligate mutualistic interactions are subjected to extreme environmental fluctuations, both species in the interaction will probably go extinct because densities of one or the other of the species are likely to fall below the level necessary to allow reproduction and continuation of the population. May (1976) uses this reasoning to

explain why obligate mutualisms in which there is an unstable equilibrium at low densities are less frequent in temperate and boreal systems than in the tropics.

More recent theoretical work and consideration of biological realities cast doubt on the generality of these predictions. These models do not seem to be robust when the assumption of an exclusively two-species system is relaxed. Heithaus, Culver and Beattie (1979) demonstrated that a Lotka-Volterra model of mutualism would be stabilized by the addition of a term which represented the effects of a predator on one of the two mutualists. They further argue that predation on one of the mutualists may happen frequently in natural systems.

Addicott (1981) presents additional evidence which suggests that the stability of two-species models of mutualism may involve inappropriate assumptions. The first criticism by Addicott of these predictions is that Goh's (1979) models will exhibit both local and global stability under certain sets of interaction coefficients only if it is assumed that the only factor affecting the equilibrium density of the two populations is the mutualistic interactions, i.e., the equilibrium density is not affected by density-independent or density-dependent factors. When this assumption is relaxed the model is no longer robust; i.e., a locally unstable equilibrium does not always lead to global instability (Travis and Post, 1979). May's (1976) prediction that the persistence stability of mutualistic interactions is lower in more variable environments (e.g. in temperate versus tropical regions) is criticized by Addicott as not being unique to mutualistic systems. The

tendency of obligate mutualistic systems to be more likely to suffer extinction in a variable environment than in a constant environment is shared by most other kinds of systems as well (Addicott, 1981).

Addicott suggests that more relevant questions are: 1) "is a mutualistic system more or less likely to suffer extinction than other types of (biological) interactions?"; and 2) "as mutualistic systems become increasingly dependent upon each other, do they become more or less sensitive to environmental variation?". A third criticism is that the predictions of May (1976) that mutualistic interactions have a lower rate of return to equilibrium than other types of interactions are based upon a qualitatively restricted model of mutualism. In May's model the equilibrium density of the two populations is affected by the interaction but the maximum possible growth rates are unaffected. Addicott (1981) presents a stability analysis of six combinations of three types of models of mutualistic interactions. These types include mutualistic interactions which affect the equilibrium density alone, the maximum possible growth rate alone, and interactions in which both equilibrium density and maximum growth rate are affected. When compared to an appropriate null model without mutualism, four out of six of these combinations showed greater return time stability and all models showed higher persistence stability. It appears this above evidence that the view of mutualism as inherently unstable relative to predation or competition should be revised. More generalized predictions may be possible if the range of qualitative differences in the effects of mutualism are addressed.

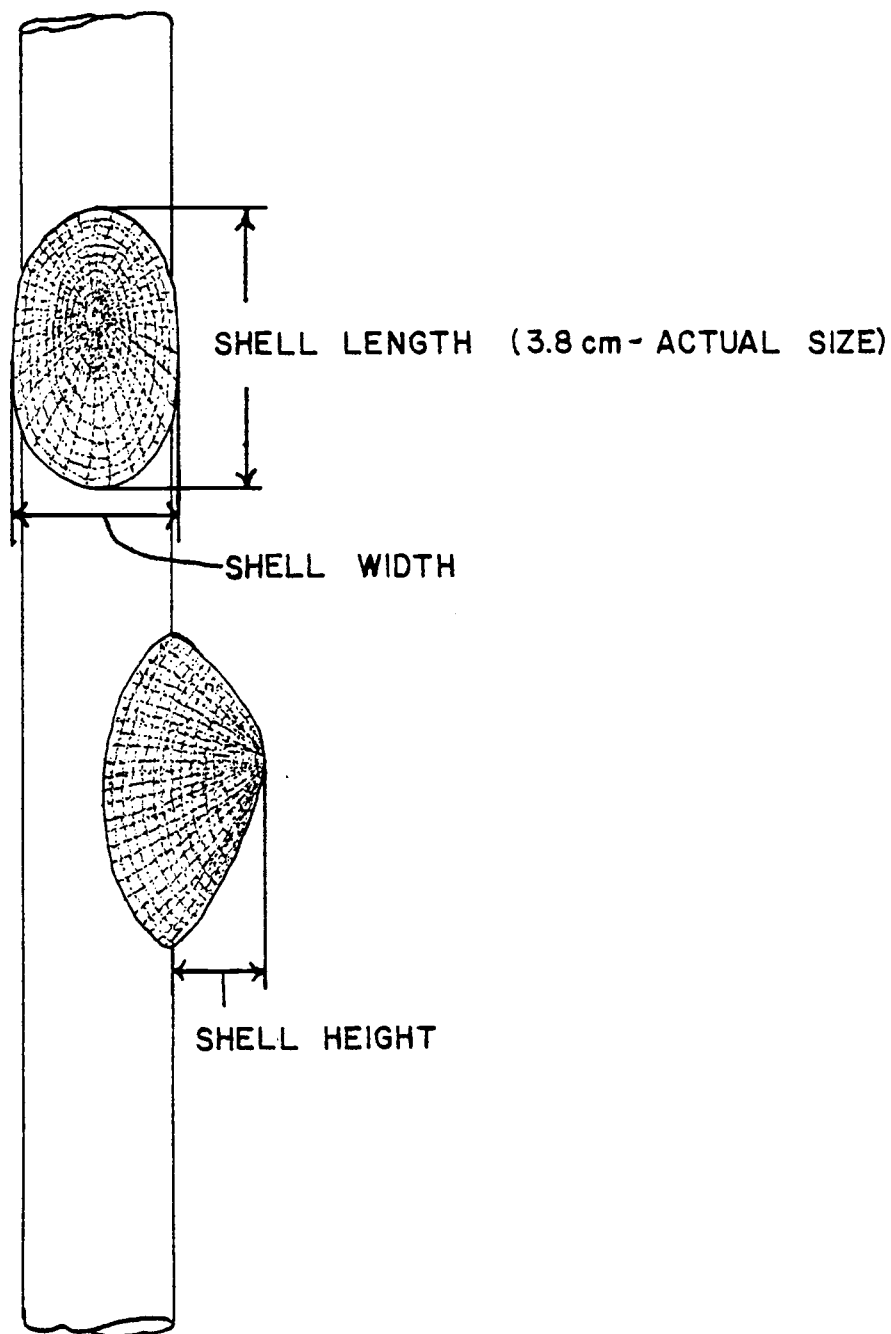
The role of the empirical ecologist in this controversy is to gather information on qualitative differences between mutualistic interactions and to test predictions of the theoreticians by gathering information on patterns of stability properties of real-world mutualistic interactions.

The goal of this thesis was to contribute information about subtler types of interactions such as mutualism or commensalism. Specifically, I have investigated the relationships between the acmaeid limpet, Collisella instabilis and its host kelp, Pterygophora californica, and Laminaria dentigera. In this study, I attempted to define the nature of the relationship between C. instabilis and Pterygophora and to gather inferential data about the nature of the association between C. instabilis and Laminaria. The definition of an interaction involves determining the signs of the effects of the two species on each other, (i.e., positive, negative or zero). Obvious positive effects that the plants have on the limpets is to provide them with a habitat and food in the form of the epidermis of the stipe and epiphytes which grow on the stipe. Less obvious are the effects of the limpet on the host plant, which may include structurally weakening the stipe (-) or reducing negative effects of epiphytes by removing them (+). To determine the effects of the limpet on the plant, four aspects of the association were examined: 1) the ability of the limpets to prevent the establishment of epiphytes on stipes; 2) any negative effects, such as increased drag, of epiphytes on host plants; 3) effects of limpet grazing on the stipe diameter growth of host plants; 4) the presence of visible damage to the stipe caused by limpet grazing which may weaken the stipe and increase its susceptibility to breakage.

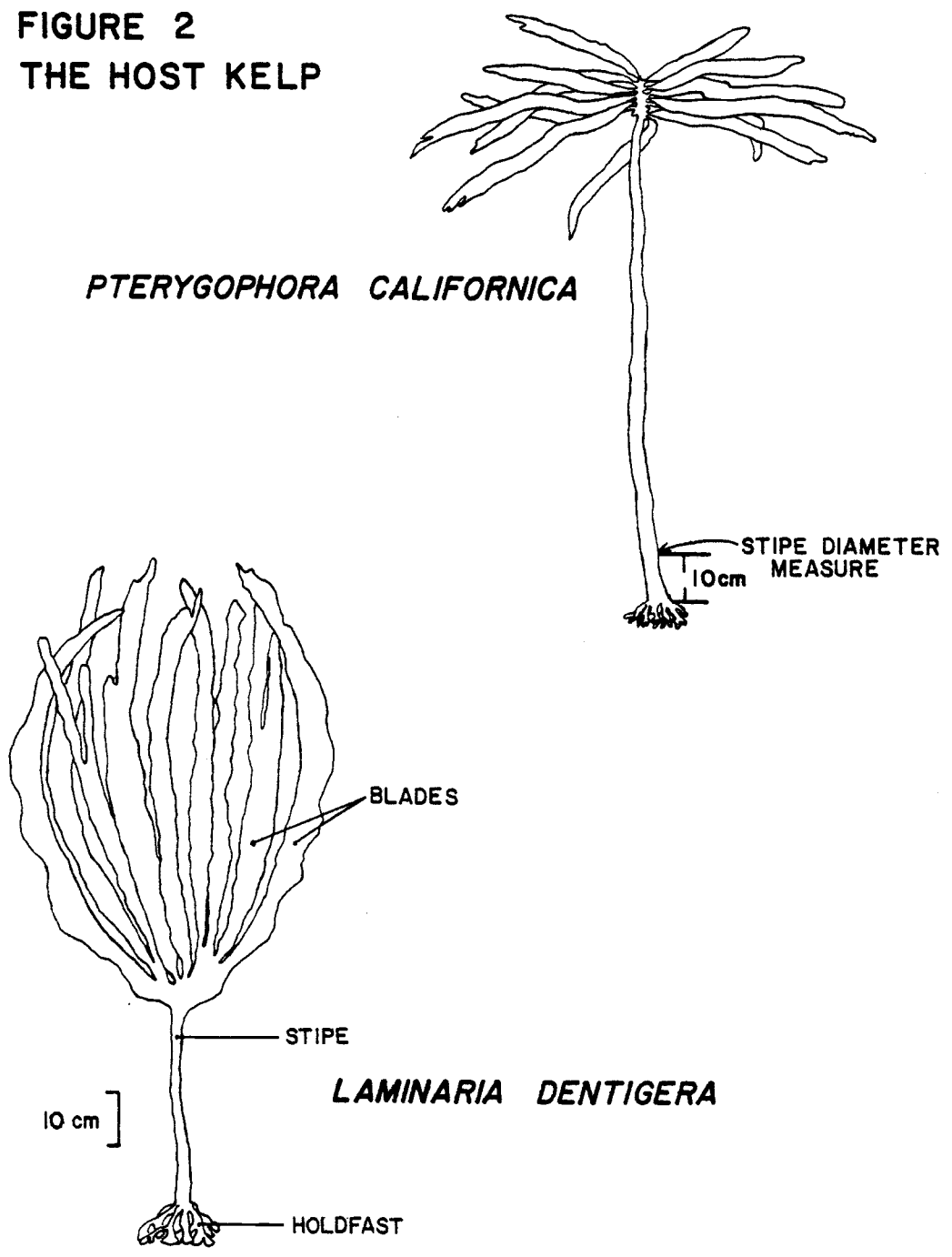
Natural History

Collisella instabilis, the unstable limpet, is found exclusively on the stipes of two species of laminarian algae, Pterygophora californica and Laminaria dentigera (Test, 1945; MacGinitie and MacGinitie, 1968; K. Yates, personal observations). This brownish limpet has a shell which curves upward anteriorly and posteriorly (Smith and Carlton, 1975; see Figure 1). Both of the kelps have a root-like holdfast, a long, cylindrical stipe and blades which emerge from an intercalary meristem at the top of the stipe (see Figure 2). The sporophytes of Laminaria and Pterygophora, which are the most prominent stage in the life cycle of the Laminariales, are perennial. The blades partially or totally disintegrate, beginning in September and October. Then new blades begin to grow in February (Bold and Wynne, 1979; K. Yates, personal observations). Both Pterygophora and Laminaria have growth rings that are easily distinguishable in a cross-section of a stipe. The growth rings of Pterygophora appear to be produced annually (McKay, 1933). The rings of Laminaria dentigera may also represent yearly growth increments, although this has not been investigated. Laminaria hyperborea, which in morphology and geographic range is similar to L. dentigera, has been shown to have annual growth rings (Kain, 1963). Pterygophora occurs primarily in the subtidal zone from Vancouver Island, British Columbia to Bahia de Rosario, Baja California (Abbott and Hollenberg, 1976). Laminaria is found in the lower intertidal and shallow subtidal zones from the Bering Strait to Ensenada, Baja California (Abbott and Hollenberg, 1976). Laminaria is much more

FIGURE 1 SHELL MEASUREMENTS
AND MORPHOLOGY OF
COLLISELLA INSTABILIS



**FIGURE 2
THE HOST KELP**



abundant in the low intertidal than Pterygophora (Abbott and Hollenberg, 1976; Bold and Wynne, 1978). While Pterygophora is more abundant subtidally than Laminaria, neither species occurs deeper than 9 meters at any of the study sites. This may be due to the increasing abundance of the red sea urchin, Strongylocentrotus franciscanus, below this depth (K. Yates, personal observation). Other species of algae that grow beneath the host plants include Botryoglossum farlowianum, Cryptopleura spp., Plocamium cartilagineum, Odonthalia sp., Ectocarpus sp., Corallina spp. (both upright and crustose forms), Bossiella spp., and young sporophytes of Pterygophora and Laminaria.

Several species of algae are epiphytic on Pterygophora stipes. The fleshy red algal epiphytes include Cryptopleura sp., Membranoptera weeksiae, Iridaea cordata, Plocamium cartilagineum, Hymenena cuneifolia, Hymenena smithii and Polysiphonia sp. Brown algal epiphytes include Ectocarpus sp., and small (<20 cm stipe length) plants of Pterygophora and Laminaria dentigera. Many diatom genera are also epiphytic on Pterygophora, including Triceratium spp., Navicula spp. and Licmophora spp. Laminaria dentigera occasionally is a host to Ectocarpus sp. and diatom epiphytes, but even these are rare, as will be explained later.

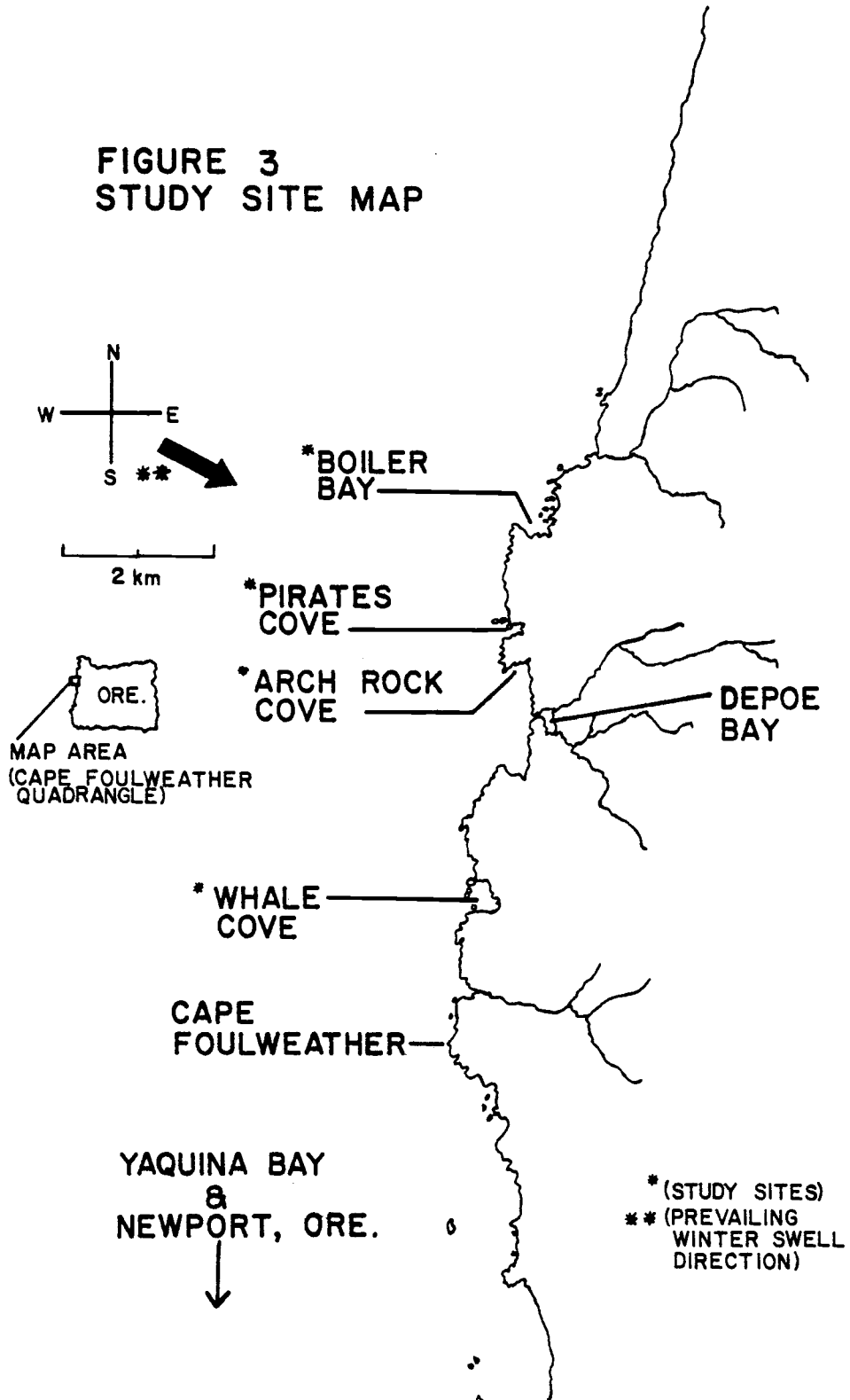
Herbivorous molluscs that are often found on the substratum around the host plants include Tegula brunnea and Cryptochiton stelleri. Predatory invertebrate species such as the seastars Evasterias trochelii and Pycnopodia helianthoides, and the brachyuran crabs, Pugettia producta, Cancer antennarius and C. productus are also found near host plants. Molluscivorous demersal fishes, such as Hexagrammos decagrammos

(kelp greenling), Hexagrammos superciliosus (rock greenling), and Scorpaenichthys marmoratus (cabezon) are often observed on the substratum around the host plants.

Study Sites

Four coves along the Central Oregon coast occurring within 15 miles of the Oregon State University Marine Science Center in Newport, Oregon, were used as study sites. Ranked in order of decreasing exposure to wave action, the sites are: Boiler Bay, Arch Rock Cove, Pirates Cove and Whale Cove (see Figure 3). This exposure hierarchy is a subjective judgement which is based upon how often ocean conditions were safe enough to dive, how much surge was experienced during successive dives at all the coves on the same day, and by determining the direction the mouth of each cove faced relative to the prevailing wave direction during winter storms. At all coves Pterygophora and Laminaria occurred on mudstone, basaltic outcrops and basalt boulders. The mudstone was heavily bored and weakened by pholad clams and other boring organisms. All of the plants that were used in this study were attached to mudstone approximately 3-4 meters below mean low low water. Some plants attach to basalt, but due to their relatively scarcity, these plants were not included in this study.

**FIGURE 3
STUDY SITE MAP**



MATERIALS AND METHODS

All field work was done in 3-5 meters of water using scuba. This study began in June of 1979, ended in March 1981 and involved over 130 dives for over hours underwater. All dive entries were from the shore. Study areas were chosen so that they were within swimming distance. Water temperature during these dives ranged from 8°C to 14°C.

Transect Data

To quantify various aspects of the limpet-kelp association, I ran subtidal transects at all sites. A 20 meter brass chain marked at 1 meter intervals was stretched out on the surface of the water. The chain was unrolled parallel to the shore over an area known to contain host algae. The chain was lowered into the water and pulled taut on the bottom. Data were recorded from plants that were closest to randomly chosen meter marks along the chain. When transects were run to compare Pterygophora to Laminaria, data were taken from a plant of each species closest to a random mark. The data that were taken for each plant usually included: (1) the frequency of limpets in five size classes, (2) a subjective estimate of percent cover of epiphytes on a host plant stipe, (3) epiphyte type richness, and (4) the presence of other invertebrate species on the plants. Limpet size classes were the shell lengths (1) 0-1 cm, (2) 1.1-2 cm, (3) 2.1-3 cm, (4) 3.1-4 cm, and (5) 4.1-5 cm. Epiphyte species richness could not be recorded accurately

due to the difficulty of identifying some algal species underwater. The epiphytes were classified into 3 types. These were 1) Ectocarpus scuz, which included Ectocarpus spp. filamentous red algae and diatoms; 2) fleshy red algae; 3) laminarian epiphytes.

The data on limpet size class frequency per plant were converted to limpet biomass per plant by multiplying the limpet size class frequency by an estimate of the biomass of a limpet with the average length of a size class. This estimate was obtained from a regression equation with limpet length as the independent variable and limpet biomass as the dependent variable. Fifty limpets of a variety of sizes were collected from Arch Rock Cove and Whale Cove. The limpet bodies were then separated from their shell and both parts were dried at 80°C for approximately 1 week. Shell length, height and width were measured (see Figure 1). The shells and bodies were weighed separately on a Sartorius 2842 electric balance. A regression equation was then estimated using the least squares method.

Whale Cove Manipulations

Field manipulations were used to test whether limpets could prevent the establishment of epiphytes on host plants. These experiments were also designed to see if limpets could affect stipe diameter growth or weaken the stipe by grazing through the epidermal layer into the cortex. Since these experiments involved manipulating the densities of limpets upon individual plants, it was first necessary to establish whether the limpets remained on a single plant or moved readily from one

plant to another. The limpet movement study was initiated in July of 1979 and was monitored at least once a month through September of 1979. Plants were tagged with a Dennison Mark IISS tagging gun which inserted numbered anchor tags through the top of the stipe. The limpets were marked with numbered tags. They were pulled off tagged plants by hand, placed into numbered plastic bags and taken back to shore. A portion of their shell was scraped free of encrusting organisms and dried with acetone. Numbered plastic tags were applied with Super Glue®. The tagged limpets were then put into the same plastic bag and taken back to their original host plants. Each limpet was carefully observed after placing it back on the stipe of the host plant to make sure its foot regained its adhesion to the plant.

The limpet density manipulations were initiated in July 1980. These experiments were designed to show the effects of four densities of limpets on the establishment of epiphytic algae and stipe diameter growth. Initially, a rope grid was secured to the bottom of Whale Cove so that experimental plants could be easily found on successive dives. Nylon webbing loops were secured to the bottom by placing a surveyors P-K® nail through a brass grommet in the loop and pounding it into a prepared area on the mudstone. This area was prepared by scraping off all organisms down to bare rock. Splash Zone® underwater epoxy-putty compound was then molded around the nail to provide additional surface area for adhesion to the soft mudstone. Brass clips secured the bright yellow polypropylene rope to the nylon loops.

To initiate the experiment, thirty plants along the rope grid were gently rubbed free of epiphytes by gripping the stipe with a gloved hand

and rubbing up and down the stipe until all visible epiphytes were gone. These plants were thus denuded of epiphytes and will hereafter be called cleaned plants. All limpets were also removed from the stipes by hand. An area of the rock adjacent to the denuded plants was scraped free of organisms with a rigid putty knife and a numbered piece of nylon webbing was nailed to the prepared area with masonry nails. Clearing the rock was necessary to be able to see the tag and provide a more solid substratum into which the nail could be driven. These tags were used to locate individual plants on later dives.

The plants were then divided into five groups using random numbers and each group was assigned one of five different treatments; 0, 1, 2, 3, or 4 limpets per plant. The limpets were between 2.5-4.0 cm in shell length. Six haphazardly chosen plants initially lacking epiphytes were also tagged to control for the effects of epiphyte removal. These plants initially had limpets on them which were removed at the beginning of the experiment. Thus these plants will be called 0-limpet control plants hereafter. Significant differences in epiphyte establishment between experimental and control plants would indicate that my method of epiphyte removal had some effect on epiphyte establishment since both groups theoretically began the experiment with no epiphytes on the stipe. Stipe diameter of all plants was measured 10 cm above the highest haptera as illustrated in Figure 2. Limpet number per plant was checked one week after the experiments were initiated and lost limpets were replaced. This process was repeated each time the experiments were monitored.

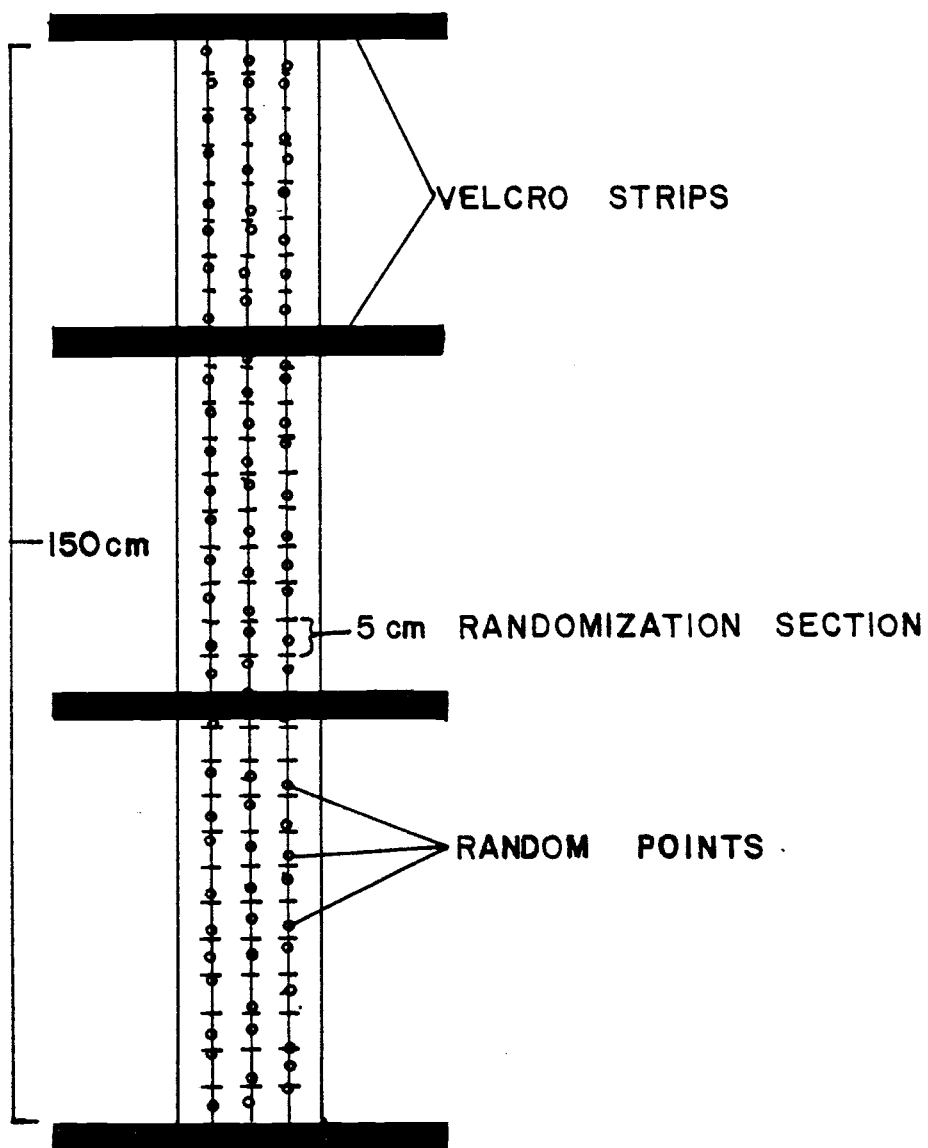
Epiphyte establishment was measured by estimating the percent cover of epiphytes on the stipes of denuded and control plants after initiating the experiment. A cylindrical quadrat was used to estimate percent cover of epiphytes. The lengths of the plant stipes were unequal so a complicated quadrat design was necessary to ensure unbiased estimation of percent cover on stipes of unequal lengths. Three lines along this 150 cm long quadrat were sectioned into 5 cm lengths. One point was randomly placed within each of the 5 cm lengths on each of the three lines. When the quadrat was secured around a plant, the number of dots over epiphytes and the total number of dots on the plant were recorded. The total number of dots recorded was 3X the number of whole 5 cm sections that fell along the stipe. Figure 4 illustrates this quadrat design.

Epiphyte Drag Experiments

An experiment to investigate the effects of laminarian epiphyte drag on the uprooting mortality of host plants was initiated at Pirates Cove. Nineteen plants with heavy loads of laminarian epiphytes and nineteen plants without epiphytes or with only small (<5 cm long) fleshy red algal epiphytes were tagged in the same manner as the experimental plants at Whale Cove. Heavy loads were defined as plants with 20% or more of their stipe surface covered by laminarian epiphytes. This was estimated subjectively. These plants were located along a rope grid like that described for Whale Cove. I recorded both the number of laminarian epiphytes and the length of the stipe covered by the

holdfasts of these epiphytes. These plants were monitored as often as possible during lulls between winter storms to determine plant losses during winter 1980-81. The plants were monitored for the last time at the end of March 1981.

FIGURE 4
DESIGN OF EPIPHYTE COVER
ESTIMATION QUADRAT



RESULTS

The Limpet-Kelp Association: Description

The relationship between total dry limpet biomass and shell length is very close to what would be predicted from typical surface area to volume ratios. Correlation coefficients and regression equations were computed for limpet shell length versus limpet body dry weight, limpet shell dry weight and total dry limpet biomass (both shell and body dry weights). The regression equation between limpet shell length and total dry limpet biomass, which yielded the highest correlation coefficient ($Y = .04 X^{3.55}$, $r = .98$, $n = 50$) was used to estimate limpet biomass from field shell length measurements. The lengths used to predict the average biomass of each size class were, in order, as follows: (1) .5 cm; (2) 1.5 cm; (3) 2.5 cm; (4) 3.5 cm; (5) 4.5 cm. Most of the limpets found in transects were in the two lowest size classes, which have a mean biomass of .0034 grams and .1687 grams (see Table 1). A chi-squared test for unevenness of distribution among the five size classes was highly significant ($\chi^2 = 53.83$, $p \ll .005$).

The data gathered from subtidal transects suggests patterns of the presence and abundance of limpets and epiphytes on Pterygophora host plants (see Table 2). The percentage of plants occupied by limpets appeared to be similar for all three coves. Approximately 71% of the Pterygophora plants observed in all of the transects were occupied by one or more limpets (Line 5, Table 2). The mean number of limpets per plant was significantly higher at Boiler Bay than at either Whale or

Pirates Coves (Line 6, $p < .005$). In addition, striking differences in these patterns between Pterygophora and Laminaria host plants were also revealed (see Table 3).

Pirates Cove appeared to have the highest incidence of host plants with both limpets and epiphytes, with 100% of the observed host plants having epiphytes (Line 1, Table 2). Fewer of the host plants at Boiler Bay and Whale Cove were occupied by epiphytes. The number of plants with laminarian epiphytes appeared to be lower at Boiler Bay than at either Pirates or Whale Coves, although this may also be an artifact of the small sample size at Boiler Bay (Line 2, Table 2). The mean percent cover of epiphytes on epiphyte-occupied host plants appeared to be lowest at Whale Cove the difference between Whale Cove (Line 4, Table 2). This other study sites was statistically significant (one-way ANOVA; $p < .05$). When all transects from all coves are examined, 69% of the Pterygophora plants observed had epiphytes.

One of the more interesting patterns to emerge was the difference in estimated epiphyte percent cover between plants with and without limpets. Although cover on plants with limpets was always less than on plants without limpets for all of the transects at all study sizes, this difference was not significantly different (see Table 2). However, the mean percent cover of epiphytes on plants with a limpet biomass less than or equal to the average size class 1 limpet ($\leq .0034$ grms) was significantly higher than the mean percent cover of epiphytes on plants with an estimated limpet biomass of greater than .0034 grms (see Table 4). The correlation coefficients for linear, exponential, and power equations for a correlation between limpet biomass and percent cover of

epiphytes were all less than .20. These correlations are not significantly different from zero at the .1 two-tailed significance level. In addition, epiphyte-type richness was significantly higher on plants with a limpet biomass less than or equal to .0034 gms than on plants with a higher biomass.

Transect data that were taken to compare patterns of the limpet-kelp association between the two host species suggest differences in epiphyte cover and limpet numbers between Pterygophora and Laminaria (Table 3). The mean percent cover of epiphytes on Pterygophora stipes was significantly higher on Pterygophora than on Laminaria (t-test; $p < .05$). In addition, the mean number of limpets was significantly lower on Laminaria than on Pterygophora.

Whale Cove Manipulations

Of the 27 limpets tagged in the limpet movement study, 26% (i.e. $n = 7$) were lost. However, with the exception of one case of a limpet moving between two plants whose bases were in contact, no tagged limpets were ever found on nearby plants. Hence this loss was probably not due to movement to other plants. Collisella was never observed moving on the rock substrate around or between plants. In addition, the limpets were never observed in any other habitat besides kelp stipes. The movement study established that limpet densities could be maintained on plants relatively easily by compensating for limpet loss due to mortality.

The density manipulation experiments were monitored three times: August and September 1980 and February 1981. In August and February, percent cover of epiphytes was zero for all plants. However, in September, significant differences in percent cover of epiphytes occurred among the treatment means ($P < .005$; one-way ANOVA). The mean percent cover of the 0-limpet treatment plants was significantly different from the means of the 1, 2, 3 and 4 limpet treatments using both a t-test and a Student-Newman-Keuls non-parametric test for multiple comparisons ($p < .01$ in both tests). The means and the individual plant percent cover data are given in Table 5. The 0-limpet denuded plant treatment mean was also significantly different from the 0-limpet control plants (t-test, $p < .05$). Thus, denuding either has a positive effect on the establishment of epiphytes or was ineffective in removing the initial epiphyte cover. The differences between the 0-limpet treatment and the 1-limpet treatment are even more pronounced if the surface area of individual plants is taken into account. Plant #17 (Table 5) is the only one of the 1-limpet treatment plants with any epiphyte cover. This plant also has the lowest density of limpet biomass per stipe surface area.

Furthermore, if only those treatments showing epiphyte percent cover are included in the regression (i.e., 0, 1, and 2 denuded limpet plants), there is a significant inverse linear correlation between limpet biomass per stipe area and epiphyte percent cover ($Y = -4.69X + 31.14$, $r = .58$, $p < .05$). The low correlation coefficient could be due to variability in individual limpet grazing rates, variation in the susceptibility of individual plants in epiphyte establishment, or

variability in the effectiveness of epiphyte removal. Variability in the susceptibility of plants to epiphyte establishment may occur if whiplash from surrounding plants is a factor in epiphyte establishment and individual plants experience different amounts of whiplast from surrounding plants. Limpet grazing rates may vary among individuals due to phenotypic or genetic differences. Initial epiphyte removal may have been variable due to differences in the duration of force or rubbing on individual plants or differences in the resistance of different epiphytes to removal by rubbing.

Stipe diameter was measured on the experimental and control plants at the beginning and the end of the experiments. There was no consistent pattern in the gains and losses of stipe diameter (see Table 6). The differences in diameter change between the limpet treatments did not follow any trends and were not significant at the .05 level (one-way ANOVA). Apparently, the error involved in the measurement method was greater than any changes in stipe diameter.

In summary, it appears that grazing by limpets affects the establishment of epiphytes on denuded host plants, but does not affect the growth rate of the host stipe (within experimental error). Epiphyte removal was either imperfect or promoted the establishment of epiphytes. This could be checked by microscopic examination of the stipe surface for sporelings or holdfasts. In addition, the effect of the limpet on epiphyte establishment appears to be limpet biomass-dependent; i.e., higher biomass had a more pronounced effect on epiphyte establishment.

Epiphyte Drag Experiments

Many of the plant tags at Pirates Cove could not be found following winter, 1980-1981. Only 10 plants with laminarian epiphytes and 11 plants without laminarian epiphytes could be located the last time this experiment was monitored. It appears that the tags for one gridline of plants were covered or destroyed by the movement of cobbles and gravel into part of the cove. Bad visibility and wave surge prevented thorough winter monitoring. Of the plants that were located, 2 plants with laminarian epiphytes and 1 plant without laminarian epiphytes were uprooted. Overall, 22% of the tagged plants found from this experiment and other tagged plants at Pirates Cove were uprooted and 8% of the tagged plants at Whale Cove were uprooted.

DISCUSSION

Defining the Interaction

This limpet-laminarian association appears to be midway between mutualism and commensalism. The Whale Cove experiments reveal no measurable negative effects of the limpets on the stipe diameter growth or survival of Pterygophora within the time span of this study. The limpets do not appear to damage the structural integrity of the stipe or produce scars on the stipe even at the highest limpet density: no stipes of tagged plants were broken. Similarly, the secondary meristem of the stipe is apparently not damaged by the grazing of the limpets because there were no significant differences in mean stipe diameter growth between any of the treatments (Table 6). However, the grazing of the limpet on the epidermis may cause enough damage to produce an energy drain on the host plant. If the diversion of this energy from other important plant functions such as holdfast growth, blade growth or reproduction is significant, then the limpets may have subtle negative effects on the host plant. However, the damage caused by limpet grazing on host stipes in the time span of this research appears small and any energy drain was probably negligible relative to the photosynthate produced by the host plant.

Collisella does seem to prevent the establishment of epiphytes which may have negative effects on the host plants (Table 5). Transects suggest that, high limpet densities in particular prevent the establishment of laminarian epiphytes (Table 4). The mean epiphyte type

richness of plants with a limpet biomass $>.0034$ gms was 2.3. A mean richness of >2 indicates the presence of laminarian epiphytes. Other factors may also affect the establishment or maintenance of epiphytes on the host plants. Several of the 0-limpet control plants never became covered with any observable epiphytes, even though limpets were never present. Moreover, when epiphytes did establish on experimental plants, the top third of the stipe usually remained bare. Host plant blade whiplash may have provided enough physical disturbance to prevent the establishment of epiphytes on the stipe immediately below the blades on the same plant, or may also have acted in conjunction with blades from surrounding host plants to prevent epiphyte establishment all along the stipe. Other stipe conditions, such as high concentrations of anti-epiphyte secondary plant compounds or excessive mucous possibly could have prevented the establishment of epiphytes. However, I have no data or observations on the existence of or the effectiveness of these conditions. Such conditions would have to be extremely variable between plants to account for the observed variability in the establishment of epiphyte cover between the control plants.

Seasonality also appears to affect the establishment or presence of epiphytes. Epiphyte percent cover was essentially zero on all experimental plants in August, 1980 and February, 1980, but was much higher on 0-limpet and epiphyte removal control plants in September, 1980. Apparently, too little time had elapsed since the initiation of experiments for epiphytes to establish by August. It is also likely that the experiments were initiated after the period of most active algal colonization and growth. Observations from the spring of 1981

support this. During late May and early June I observed new epiphytes, especially small laminarians, on the stipes of experimental and surrounding plants at Whale Cove. I also observed many small laminarian epiphytes at Arch Rock Cove during this period which were obviously established during 1981. Newly established epiphytic laminarians are easily distinguished from epiphytes settling the previous year by size. The tags at the base of experimental plants were also overgrown by Ectocarpus sp. during late May and early June of 1981, sometimes to the point of total obliteration of the tag and effective tag loss.

The decrease in epiphyte cover from September to February may have been due to a decrease in factors promoting algal growth, such as nutrient or light levels relative to limpet grazing rates, which may have remained constant. However, this would not explain the low percent cover on the plants without limpets. Wave action, which increases in magnitude in the stormy winter months may have been responsible for decreasing the epiphyte percent cover during the winter. Ectocarpus sp. and its associated diatoms and filamentous red algae would probably be most susceptible because they are so loosely attached. Lubchenco and Menge (1978) observed a similar removal of epiphytes from host plants (Chondrus crispus) by excessive wave action shock at one of their more exposed study sites in New England.

The significant difference between mean percent cover of epiphytes on the 0-limpet plants and on the control plants suggest that epiphyte removal either somehow promoted the establishment of epiphytes or that the denuding of the 0-limpet plants was not effective in removing all of the holdfasts or microscopic sporelings of epiphytes. Epiphyte estab-

lishment may have been promoted by epiphyte removal if this action removed some kind of anti-epiphyte compound (I know of no such compound from Pterygophora). However, the data from the 1, 2, 3, and 4 limpet treatment plants indicate that any epiphyte-promoting effects of stipe denuding were overpowered by the effects of limpet grazing.

Even though other factors may affect the establishment of epiphytes, the data from the Whale Cove manipulations and the data from transects at all study sites indicate that limpet grazing may be the most important single factor affecting epiphytes on host plant (see Tables 2, 4, and 5). The variability in the establishment of epiphytes on 0-, 1-, and 2-limpet plants may have been partially due to differences in the efficiency in removal of epiphyte holdfasts or microscopic epiphyte sporelings.

Epiphytes appear to increase the drag of wave surge on the host plants. Although the kelp loss study was inconclusive, I have observed that plants with heavy loads of laminarian epiphytes are bent over much more in wave surge than are host plants without laminarian epiphytes. Increased drag caused by laminarian epiphytes may increase the uprooting mortality of host plants. Since 8% of the tagged plants at Whale Cove and 22% of the tagged plants at Pirates Cove were uprooted, this appears to be an important source of mortality for the host plants. These results suggest that uprooting mortality is more frequent at more exposed sites, such as Pirates Cove.

Negative effects of epiphytes on host plants have been suggested by others. G. Van Blaricom (personal communication) suggested that increased drag caused by Nereocystis (a laminarian alga) epiphytes may

increase the uprooting mortality of Pterygophora. He also proposed that these negative effects of Nereocystis epiphytes may be partially responsible for patterns of algal dominance in some nearshore communities at Pt. Piedras Blancas in central California. J.L. Menge (1975) has data which suggests that in New England Fucus host plants with epiphytes may be uprooted more by storm wave action than plants without epiphytes. Furthermore, she suggested that Littorina littorea, a periwinkle which eats epiphytes of Fucus, may tend to prevent these negative effects. Similar adverse effects of epiphytes on Chondrus crispus in New England were suggested by Prince (1971) and Lubchenco and Menge (1978).

If epiphytes increase the probability of being uprooted, my field observations indicate that this effect is not uniform in space and time. For example, many tagged plants with heavy epiphyte loads were not uprooted while several host plants with no epiphytes were uprooted. In addition, many of the host plants that were cast up on shore were free of epiphytes (K. Yates, pers. obs.). These observations suggest that other factors need to be taken into account in considering uprooting of these laminarians. The strength of attachment of the host plant probably varies with the number of haptera attached to the substratum, the surface area of these attachment points, and the amount of bioerosion of the holdfast by boring organisms. The strength of the substratum itself and spatial differences in the amount of whale surge introduces additional variability. The holdfasts of many of the drift plants that were collected were still attached to fragments of mudstone. For example, 32% of the drift plants with holdfasts collected

on one day from the beaches at Arch Rock and Whale Coves had fragments of mudstone attached to the bottom of the holdfast. Apparently failure of the substratum is at least partially responsible for the mortality of some of these plants. All of the experimental plants and the majority of the total number of plants at the study sites were attached to mudstone, which is eroded by boring organisms such as pholad clams and sipunculids.

Benefits to *Collisella instabilis*

The question of what benefit the limpet receives from the host plant is essentially the question of why the limpet evolved to its specialized habitat. The effects of the plants on the limpet population are hard to investigate experimentally because the association is obligate for the limpet. The saddle-shaped shell of the limpet conforms perfectly to the cylindrical surface of the stipe when the anterior-posterior axis of the shell is parallel with the longitudinal axis of the stipe (see Figure 2). Once the limpet is large (> 2 cm) and the shell has a pronounced saddle shape, it is difficult for the limpet to move on non-cylindrical (i.e. non-stipe) surfaces. The shell shape is probably phenotypically plastic. I have observed that shells often bear evidence of conformation to a wider or narrower stipe. However, once the shell is saddle-shaped the limpet may not be able to survive long enough to adapt to a flat surface because the shell may not be used to bear against the substratum to resist dislodgement forces. Other limpet species which live on flat surfaces can clamp down their pallial muscles and use their

foot muscles and shell edges to brace themselves against the rock.

Collisella shells are often found cast up on the beach and in gravel and shell debris accumulations subtidally (K. Yates, pers. observ.). Since seastar predation, which does not damage the shell, was never observed in the field, and other forms of predation (e.g., crabs, demersal fish) probably involve breaking of the shell, I assume that most of these intact limpet shells represent mortality from other natural causes, such as dislodgement from the stipe. From repeated observations of individually marked limpets on their host stipes, I have evidence that limpets are lost from host plants and do not move to other plants. Thus, since dislodgement is probably an important source of limpet mortality, a limpet that moves off its cylindrical habitat to a flat surface may be strongly selected against due to its increased susceptibility to dislodgement. This potential selective force may cause C. instabilis to be essentially obligately associated with its host plant once its shell conforms to the stipe. Additional evidence that the association is obligate for the limpet is that limpets with the curved brown shell and subdued radial and concentric sculpture lines of C. instabilis were never found off the stipes of Laminaria dentigera or Pterygophora californica in this study, and have never been reported elsewhere to be found in any other habitat (Smith and Carlton, 1975, Kozloff, 1976).

Several hypotheses may account for the evolution of this limpet to the kelp stipe habitat. First, interspecific competition may have led to habitat specialization by Collisella instabilis. Several studies suggest competitive interactions between limpet species (Branch, 1975,

1976; Choat, 1977; Haven, 1973; Stimpson, 1970, 1973; Underwood, 1978; for a review, see Underwood, 1980). This hypothesis has been suggested to be important in driving the evolution of other limpet species, such as Notoacmaea insessa and Patella compressa, which specialize on other laminarian kelp habitats (Choat and Black, 1979). However, although interspecific competition may be reduced or eliminated by specializing on a kelp stipe habitat, intraspecific competition may have been increased or at least not reduced due to a limited availability of suitable stipe habitat, or food. Branch (1975) has suggestive evidence that intraspecific interference competition occurs between individuals of Patella compressa that occur on the same plant of the laminarian species Ecklonia maxima. Aggressive interactions were observed and usually only one large individual of Patella compressa was found on the stipe of Ecklonia maxima (Branch, 1975). In contrast, the mean number of C. instabilis per plant appears to be greater than 1 (see Table 2) and I have observed 5 limpets with shell lengths greater than 2 cm on the same host plant. Intraspecific competition may not be as important in regulating individual plant limpet densities for C. instabilis as it is for Patella compressa.

Second, predation may have been responsible, at least in part, for the specialization of limpets on kelp stipe habitats. The upright stipes of Pterygophora and Laminaria appear to be free of predation by seastars. Seastar species, such as Evasterias troschelii and Pycnopodia helianthoides are often observed on the substrata around the host plants but never, during at least 150 observations of host plant stipes were seastars ever observed on stipes. Pycnopodia helianthoides, the

sunflower star, will eat limpets on stipes that are lying on the bottom of flow-through seawater tanks in the lab (personal observations). Seastars are major predators on limpets (Connell, 1975; Menge, 1972; for a review see Underwood, 1980). The abundance of seastars often increases with depth (Connell, 1975; Watanabe, personal communication) although some species, such as Asterias vulgaris, are more abundant in shallower water (Menge, 1979). Moreover, since most intertidal seastar species forage only at high tide and the foraging activity of seastars may be limited by wave action which decreases with depth, most subtidal limpets may experience more intense predation pressure than intertidal limpets. A refuge from predation such as a kelp stipe may thus be especially important to subtidal limpets. Brachyuran crabs, such as Pugettia producta and Cancer productus have been observed on these stipes and may prey on C. instabilis. A freshly broken C. instabilis shell was found below an experimental plant that had a Cancer productus clinging to the stipe. This was the only observation of a Cancer on a stipe. Pugettia producta is primarily an herbivore and a scavenger, although it will occasionally kill animals (K. Yates personal observations). Demersal fishes, such as cabezon (Scorpaenichthys marmoratus), kelp greenling (Hexagrammos decagrammus) and rock greenling (Hexagrammos superciliosus), are common in and around Pterygophora and Laminaria beds and also eat invertebrates. However, gastropods are rarely eaten, and limpets have never been observed in gut contents (Steiner, 1979).

Specializing on a stipe habitat may involve several disadvantages as well as advantages. The food resources of the stipe, which consist of

epiphytes and the epidermal layer of the stipe, are limited by the surface area of the stipe. This problem may be especially acute at high limpet densities per plant because C. instabilis never leaves its individual host stipe. Transience of the host plant habitat relative to rock habitats may also be a disadvantage. However, Pterygophora is a long-lived kelp. Cross-sections of host stipes often show from 15-20 annual growth rings, which may be yearly growth rings (McKay, 1933). Additional information must be gathered to determine the transience of stipe habitats relative to rock habitats. Data on the sizes and age-specific survivorship of the host plant and the minimum and average age and size of host plants that young limpets settle on would be useful. Stipes would probably not be transient habitats if young host plant mortality was low after the age of preferred limpet settlement and if limpets usually died before old host plants died from uprooting or herbivory.

In contrast to the situation with Pterygophora, there appear to be severe disadvantages to Laminaria dentigera host plants as a habitat. During early spring every year the outside layer, or epicuticle of the stipe of L. dentigera is shed (personal observations; G. VanBlaricom, pers. comm.). During this time the shedding epicuticle, upon which the limpets are found, is very loosely attached to the stipe. A limpet that is pulled off a shedding stipe comes off very easily and often has pieces of the epicuticle attached to its foot. Therefore, during the early spring many limpets may be removed from L. dentigera stipes by wave shock because of the sloughing epicuticle. This is a possible explanation for why limpet numbers are significantly lower on Laminaria

than on Pterygophora, which does not shed an epicuticle (Table 3). There may also be differential settlement of the limpet larvae on the two kelp. Mortality due to epicuticle sloughing and a lack of epiphytic algal food may select against those individuals that settle on Laminaria. When the epicuticle is shed all epiphytes are shed with it so there is little epiphytic food available (K. Yates, pers. obs.). The epicuticle sloughing is also a probable explanation for the significantly lower mean percent cover of epiphytes on Laminaria stipes relative to Pterygophora stipes (see Table 3).

From the data and the observations I have gathered, it appears that the interaction between C. instabilis and Pterygophora involves positive effects on the limpet populations, and slightly positive or null effects on Pterygophora populations. The positive effects of the limpet on the host plants may be patchy in space and time. At this time, the positive effects of the limpet do not appear to be very strong and may be obscured by the host plant attachment variables mentioned above. More data are needed on these positive effects to determine how important they are to the fitness of the host plant.

Other limpet-laminarian associations

Several other prosobranch limpets have specialized in kelp habits. Patella compressa, a South African limpet which is found exclusively on the stipes and lamina of the kelp Ecklonia maxima, has a shell morphology that is very similar to C. instabilis (Branch, 1975; R. Day, pers. comm.). Notoacmaea insessa, is found only on the stipes and

rachis of Egregia laevigata in southern and central California (Black, 1974, 1976). Patina pellucida, which occurs on the thallus of many species of brown algae (Choate and Black, 1979). The acmaeid limpet Scurria scurra, is associated with the laminarian alga Lessonia nigriscens on the Chilean coast (Choate and Black, 1979)

The association between Collisella instabilis and Pterygophora californica is one of the few limpet-laminarian interactions in which the limpet does not appear to damage or form a scar in the tissue of the host plant. Both Patella compressa and Notoacmaea insessa produce scars on their host plant that penetrate into the cortex (Black, 1974, 1976; Branch, 1975). The scars produced by Notoacmaea insessa in the stipes and rachis of its host kelp often cause the plant to break at the scar (Black, 1974, 1976). Black (1976) suggested that the loss of rachises due to limpet grazing may serve to prevent an Egregia plant from becoming so large that it is susceptible to uprooting by wave action. However, this hypothesis was not tested by manipulative experiments. The scars in the cortex of its plant produced by Patella compressa apparently do not have negative effects on the host (Branch, 1974, in Choate and Black, 1979). Patina pellucida, was found to infest and weaken the holdfasts of Laminaria hyperborea (Kain, 1977). Kain (1977) suggests that Patina may cause increased mortality of their host plants through increasing the susceptibility of the holdfast to breakage.

Empirical complexity versus theoretical simplicity

The association I have studied presents some biological complexities that have not been considered in the fabrication of existing models of mutualistic and commensalistic interactions. Most models do not incorporate the effects of interactions with any species other than the two mutualists (e.g., the models of Goh, 1979 and May 1973a, 1973b, 1976). Heithaus et al. (1980) found that the addition of a predator on one of two mutualists stabilized the interaction. In the system I have studied, a third species is involved, but not as a predator. Laminaria, in addition to Pterygophora provides C. instabilis with a substratum and food. The presence of the additional host plant may act to stabilize the system by providing the limpet with an alternative substratum in the event that the populations of Pterygophora are decreased or made locally extinct by some selective environmental agent such as a disease or a specialist herbivore. Moreover, the positive effects of the limpet on Pterygophora, if strong enough, may then reduce the time needed for Pterygophora to return to its former densities by decreasing a source of mortality, uprooting by wave action. The time for the system to return to the densities preceding the action of the perturbation may thus be much lower when the additional species interaction (between C. instabilis and L. dentigera) is present.

An additional complexity of this limpet-laminarian interaction is that it is obligate for only one of the two species. Fluctuations in the abundance of the limpet would probably have much less of an effect on the Pterygophora population than the reverse situation would have on

the limpet population. Few of the mutualistic associations that have been studied are obligate for both species. For example, the mutualistic associations between many species of ants and plants that secrete extrafloral nectar are not obligate for either species (e.g. Inouye and Taylor, 1979; Bentley, 1976, 1977). The associations between ants in the genus Pseudomyrmex and swollen-thorn acacias are not obligate in the strict sense; there are no species-specific associations between ants and acacias (Janzen, 1966). The rock oyster Chama pellucida and several species of sessile invertebrates can exist separately but when they are found together, they evidently form a mutualistic association (Vance, 1978). Notable exceptions are the associations between some fungi and algae (lichens) and the associations between some sea anemones and unicellular algae. Predictions about the persistence stability of models which are based on obligateness for both species or for neither would not apply to the system described here or to the other systems discussed above. The predictions of a model incorporating asymmetrical obligateness may not be intuitively obvious, so I will not attempt to deduce them here.

CONCLUSION

I conclude that the interaction between C. instabilis and Pterygophora californica appears to be either commensalistic or weakly mutualistic. The advantages of the association for the limpet may be that the host plant stipe is a habitat free of interspecific competition and seastar predation. Older half of the host plants observed in transects were occupied by limpets, which graze on the epidermis of the stipe and on epiphytes which settle and grow on the host plant. Although the epidermis of the stipe is grazed on, experiments to detect the effects of limpet grazing on stipe diameter growth suggest that, within the time limits and experimental error of this study, limpets had no effects on this aspect of host plant growth. Transect data suggest that limpets affect the abundance and richness of epiphytes, which occurred on the majority of observed host plants (>90%). Observations suggest that Laminarian epiphytes may grow so large as to cause increased drag on the host plant, which may increase the susceptibility of the host plant to dislodgement by wave shock. This type of epiphyte occurred on over half of the host stipes observed. In field manipulations, limpets appeared to prevent the establishment of epiphytes on initially denuded host plants. Collisella may thus have beneficial effects on its host alga by preventing the establishment of these laminarian epiphytes. However, other factors in addition to epiphyte drag are probably also important in determining the susceptibility of host plants to dislodgement. These other factors, which include holdfast and substratum strength may obscure the effects of

epiphyte drag on the dislodgement mortality of host plants. More data are needed on all of these factors before the importance of epiphyte drag may be determined.

This investigation illustrates the biological complexities that may be involved in mutualistic or commensalistic interactions. These complexities may make the predictions of existing models unrealistic for the system I studied. Although models can never approach the total biological complexity that may be found in nature, adding some complexity is a necessary step to understanding the range of responses that may be expected from a particular system.

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APPENDIX

Table 1. Limpet size class frequency from plants along subtidal transects at Pirates and Whale Coves and Boiler Bay. The biomass values given are for the total biomass in a specific size class at a particular site.

Size Class		<u>1</u> (0-1 cm)	<u>2</u> (1.1-2 cm)	<u>3</u> (2.1-3 cm)	<u>4</u> (3.1-4 cm)	<u>5</u> (4.1-5 cm)	
Estimated							
Biomass (gms)		(.5 cm) .0034	(1.5 cm) .1687	(2.5 cm) 1.034	(3.5 cm) 3.415	(4.5 cm) 8.336	N
Pirates Cove	Frequency	.688	.313	0	0	0	16
	Biomass	.0374	.8435	0	0	0	
Whale Cove	Frequency	.444	.407	.074	.074	0	27
	Biomass	.0408	1.8557	2.068	6.83	0	
Boiler Bay	Frequency	.579	.211	.158	.053	0	19
	Biomass	.0374	.6748	3.1020	3.4150	0	
Total (All Sites)	Frequency	.548	.323	.081	.048	0	62
	Biomass	.1156	3.3740	5.1700	10.2450	0	

Table 2. Summarized data recorded from plants along transects at Whale and Pirates Coves and Boller Bay during Spring, 1980. Values in parentheses are standard deviations. P-values are from comparisons of "all transect" and Boller Bay means using a one-way ANOVA. All percent cover data were transformed by an angular transformation.

	Boller Bay	Pirates Cove			Whale Cove			P-values
	(6/11/80)	5/30/80	6/4/80	All Transects	5/8/80	6/3/80	All Transects	
1. % of plants w/epiphytes	86	100	100	100	86	60	87	
2. % of plants w/laminarian epiphytes	43	86	85	88	86	60	76	
3. \bar{x} % cover of epiphytes on all plants	47(39)	57(20)	62(18)	59 (19)	39(27)	29(37)	35(31)	<.05
4. \bar{x} % cover of epiphytes on plants w/epiphytes	55(36)	57(20)	62(18)	59 (19)	45(24)	48(36)	46(27)	.32
5. % of plants occupied by <u>Collisella instabilis</u>	71	60	71	65	80	60	72	
6. \bar{x} number of <u>C. instabilis</u> on occupied plants	2.71 (3)	.60 (.516)	.71 (.48)	.65 (.49)	1.06 (.79)	1.1 (1.1)	1.08 (.91)	<.005
7. \bar{x} limpet biomass per plant								
all plants (grams)	1.033(1.465)	.376(1.070)	.073(.089)	.252 (.819)	.070(.106)	.975(1.358)	.43 (.95)	.22
occupied plants (grams)	1.446(1.572)	.627(1.369)	.102(.091)	.389(1.007)	.087(.112)	.625(1.433)	.60 (1.081)	.23
8. \bar{x} % cover of epiphytes on occupied plants	32.2(35.9)	45.8(18.8)	57.6 (20.0)	51.2(19.3)	35.9(28.3)	4.3(6.7)	25.4(27.6)	.22
9. \bar{x} % cover of epiphytes on unoccupied plants	83.5(9.2)	74.5(2.9)	72.0 (0)	73.7(2.6)	51.7(22.7)	66.0(30.3)	59.9(26.3)	.24
10. Number of plants sampled	7	10	7	17	15	10	25	

Table 3. Epiphyte cover and limpet abundance per plant of Laminaria dentigera and Pterygophora californica: combined transect data from Pirates Cove and Arch Rock Cove. N = 14 plants of each species. Epiphytes included fleshy and filamentous red algae, filamentous brown algae and laminarian algae. Student's t-test was used to test for differences between means.

	<u>Pterygophora</u>	<u>Laminaria</u>	P-value
\bar{x} transformed epiphyte percent cover	38.57	2.61	p < .005
\bar{x} limpet numbers per plant	.714	.214	p < .05
\bar{x} estimated limpet biomass per plant (grams)	.3441	.0215	NS

Table 4. Differences in epiphyte cover and epiphyte richness as a function of limpet biomass. Combined Data from all sites. All percent data were transformed by an angular transformation. Differences between means for the two limpet biomass groups were significant for both cover and richness at the .005 level (one-way ANOVA).

	Estimated Limpet Biomass Per Plant \leq .0034 gms	Estimated Limpet Biomass Per Plant $>$.0034 gms
\bar{x} % Epiphyte Cover	64.3	23.3
\bar{x} Epiphyte Type Richness	2.3	1.4

Table 5. Whale Cove epiphyte establishment experiments: Individual plant epiphyte percent cover and limpet biomass per stipe area. Replicates were unequal between treatments due to tag or plant loss.

Number of Limpets Per Plant	Plant #	% Epiphyte Cover	Arc-sine Transformed % Epiphyte Cover		Limpet Biomass (grms/cm ² x 10 ⁻³) per Stipe Area
0	14	31	33.8		0
	22	37	37.5		0
	23	14	22.0	x = 33.7	0
	25	28	32.0	Sd = 7.9	0
	27	47	43.3		0
1	03	0	0		4.09
	08	0	0		3.77
	17	55	47.9	x = 8.0	1.61
	18	0	0	Sd = 19.6	6.88
	20	0	0		4.59
	29	0	0		3.54
2	01	0	0		6.10
	02	0	0		6.73
	11	7.6	16.0	x = 3.2	7.45
	12	0	0	Sd = 7.2	8.31
	19	0	0		3.61
3	04	0	0		15.90
	05	0	0		8.18
	15	0	0	x = 0	15.75
	21	0	0	Sd = 0	11.70
	24	0	0		9.02
	30	0	0		6.96
4	09	0	0		15.80
	13	0	0		13.38
	16	0	0	x = 0	10.69
	26	0	0	Sd = 0	9.29
	28	0	0		14.30
0 (Control)	32	0	0		0
	33	24	29.3		0
	34	0	0	x = 12.5	0
	35	0	0	Sd = 17.2	0
	37	30	33.2		0

Table 6. Whale Cove Grazing Effect Experiments: Stipe Diameter Change versus Treatments. Plants #1, 2, 3, 4, 7, 8, 9, 13, 23, 26, 31, 33, and 35 were lost as replicates due to stipe breakage, top loss, uprooting or tag loss. The source of breakage or top loss was the destruction of the rope grid at Whale Cove by winter storm. The linear regression of limpet number and stipe diameter change yielded a r^2 of .01. The mean stipe diameter change for the treatments were not significant at the .05 level (one-way ANOVA).

Plant #	Initial Stipe Diameter (cm)	Stipe Diameter Change (cm)	# of Limpets
14	2.0	0	0
22	2.5	+.2	0
25	2.0	0	0
27	2.1	0	0
32	2.5	+.1	0 (control)
34	2.7	0	0 (control)
37	2.3	0	0 (control)
18	2.8	-.2	1
20	1.9	+.1	1
29	2.6	+.2	1
11	2.6	-.1	2
19	2.8	-.4	2
05	1.8	+.1	3
15	1.9	+.2	3
21	2.4	+.1	3
24	2.4	0	3
30	2.7	-.1	3
16	2.4	0	4
28	2.2	0	4