

AN ABSTRACT OF THE THESIS OF

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Title: Diverse Consumer Guilds in Intertidal Communities of Oregon
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Low intertidal communities of Oregon and Panama have many predator and herbivore species. This diversity of consumers is important to the organization of both communities because of qualitative differences among the consumer species in their ability to circumvent specific prey defenses. In Oregon, the red alga Iridaea cordata is protected by its cuticle from damage by the isopod Idotea wosnesenskii; however, the cuticle does not prevent feeding by three other common herbivores - Strongylocentrotus purpuratus (sea urchin), Katharina tunicata (chiton), and Collisella pelta (limpet). In Panama, limpets are protected from predators by their shells, but different shell forms deter different predators. Flat, thin shells are difficult for large, shell-crushing predators (Diodon hystrix [fish], Ozius verreauxii [crab]) to seize, yet they are easily drilled by gastropods (Thais melones, Acanthina brevidentata). Thicker, more conical limpet shells pose a barrier to drilling, but are easily grasped and crushed by fishes and crabs.

In both systems variability in defense effectiveness, in conjunction with high feeding intensities, greatly influences prey distribution and diversity. Two mechanisms are important. (1) When discrete habitats.

harbor dissimilar consumers, feeding enhances between-habitat prey diversity (= spatial variance in species composition). Enhancement of diversity occurs when different prey species fall victim to consumption in different habitats. Via this mechanism, the Rhodophyte Iridaea is frequently restricted to vertical rock surfaces when adjacent horizontal areas harbor many cuticle-impartial herbivores. Similarly, among Panamanian limpets the opposing effects of drilling and crushing predators restrict flat limpets to smooth surfaces where predaceous gastropods are rare, and conical limpets to crevices and holes where larger predators cannot penetrate. (2) When dissimilar consumers co-occur in the same habitat, their feeding can depress within-habitat prey diversity by reducing the chance of prey escapes. A reduction in diversity occurs through complementary effects when weaknesses of one consumer are partly or wholly counteracted by strengths of another. This mechanism is especially important in Panama in specific habitats exposed to both crushing and drilling predators. Under such conditions all limpet species are rare since no shell shape deters both predator groups.

Diverse Consumer Guilds in Intertidal Communities
of Oregon and the Republic of Panama
and Their Effects on Prey Assemblages

by

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TABLE OF CONTENTS

	Page
I. Introduction.....	1
II. Consumer Guild Structure and the Organization of Prey Assemblages.....	4
Introduction.....	4
Study Areas and Species.....	18
Methods and Results.....	22
Discussion.....	40
III. Herbivory and Between-Habitat Diversity: The Differential Effectiveness of a Plant Defense.....	44
Abstract.....	44
Introduction.....	46
Study Organisms.....	49
Methods.....	52
Results.....	57
Discussion.....	77
IV. Herbivory and Algal Diversity in a Tropical Intertidal Community.....	84
Introduction.....	84
Species and Study Areas.....	86
Methods.....	89
Results & Discussion.....	91
V. General Discussion.....	108
VI. Literature Cited.....	114

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Stylized communities with four herbivores and four habitats.....	8
2. Shell form for four Panamanian limpets	21
3. Mortality rates of Panamanian limpets exposed to different predators in the laboratory	24
4. Densities of herbivores and predators in boulder fields on Taboga Island, Panama.....	28
5. Densities of flat limpets on boulders of varying surface textures.....	32
6. Mortality rates of Panamanian limpets following transplants in the field.....	35
7. Stylized summary of effects of predation on limpet distribution and diversity patterns.....	39
8. Distribution of <u>Iridaea cordata</u> and five common herbivores in Boiler Bay, Oregon.....	59
9. Photograph of herbivore damage to manipulated <u>Iridaea cordata</u>	65
10. Responses by <u>Iridaea cordata</u> and herbivores to removal of <u>Katharina tunicata</u>	74
11. Distribution of Panamanian limpets as a function of distance from crevices.....	93
12. Patterns of crustose algal cover adjacent to limpet home scars.....	98
13. Distribution of erect algae relative to crevices and holes.....	101
14. Changes in crustose algae following removal of <u>F. virescens</u>	104
15. Algal species richness at different distances from crevices.....	106
16. Graphical depiction of the divergent effects of qualitative variation in consumption with different consumer distributions.....	110

LIST OF TABLES

<u>Table</u>	<u>Page</u>
I. Damage observed for <u>Iridaea cordata</u> in different reproductive conditions.....	61
II. Densities of herbivores on <u>Iridaea cordata</u>	62
III. Damage in field transplants of manipulated <u>Iridaea cordata</u>	66
IV. Laboratory feeding rates for five common herbivores on <u>Iridaea cordata</u>	68
V. Feeding by <u>Lacuna marmorata</u> on blades of <u>Iridaea cordata</u> in different reproductive conditions.....	69
VI. Damage in field transplants of manipulated <u>Iridaea cordata</u> on horizontal surfaces.....	72
VII. Densities of Panamanian limpets on boulders of different surface texture.....	94
VIII. Percent cover of algae on smooth low zone surfaces with no limpets.....	96

DIVERSE CONSUMER GUILDS IN INTERTIDAL COMMUNITIES OF OREGON AND THE REPUBLIC OF PANAMA AND THEIR EFFECTS ON PREY ASSEMBLAGES

Chapter I

GENERAL INTRODUCTION

Much of the early interest in predator-prey interactions was stimulated by the observation of regular cycling in predator and prey populations (Elton 1924, 1942, MacLulich 1937). Contemporary mathematical treatments predicted oscillations in predator-prey interactions (Lotka 1925, Volterra 1926) and this correspondence with empirical observations helped focus attention on the importance of predators as regulators of prey population densities. Topics such as the frequency of population control by predators (e.g., Hairston et al. 1960, Murdoch 1966, Ehrlich and Birch 1967, Caughley and Burk 1970), the factors promoting predator-prey coexistence (Huffaker and Kennett 1956, 1969, Utida 1957, Huffaker 1958, Dodd 1959, Rosenzweig and MacArthur 1963, Maly 1969), and the component responses of predators to changes in prey density (Holling 1959, 1965, Ivlev 1961) have helped define the interactions between a single prey and its predator.

The extension of this interest to single-predator multiple-prey interactions addressed the effects of predators on the structure of communities. The specific areas drawing the most attention -- the impact of predators on patterns of local prey diversity and distribution (Tansley and Adamson 1925, Doult 1960, Gillette 1962, Paine 1966, Harper

1969, Parrish and Saila 1970, Janzen 1970, Connell 1975, Menge and Sutherland 1976, Lubchenco 1978) -- have noted the importance of prey defenses and predator feeding preferences. Somewhat independently, these two factors have also been the focus of attention for studies of evolutionary interactions between predators and their prey. This area documents the role and patterns of heritable variation in the ability of predators to capture and consume prey and in the ability of prey to avoid being eaten (Utida 1957, Pimentel and Al-Hafidh 1963, Fenner and Ratcliffe 1965, Pimentel 1968, Fenner 1971, Rosenzwing 1973).

In this thesis I examine variation in defense effectiveness and feeding preferences in multiple-predator multiple-prey systems. Here, variation in the ability of predators to circumvent individual defenses may be present both within predator populations and among individuals of different predator species (Ricklefs 1970, Janzen 1981, Lubchenco and Gaines 1981, Menge and Lubchenco 1981, Fox 1981). My coverage of this topic is presented in three distinct manuscripts to be published separately. They are bound together by their treatment of similar questions, but can be read independently. Chapter II is a general discussion of the effects of predation and herbivory in diverse communities that subsumes to some degree the less general treatments in Chapters III and IV. Chapter II includes an extensive introduction to the problems involved, their general significance, and the treatment they have received in the literature. This information gives the general framework for the entire thesis. Two predictions are generated for the effects of herbivores or predators that are unique to diverse communities. The utility of these predictions is then examined for

predation on a guild of herbivorous marine snails from the Republic of Panama.

Chapter III and IV cover similar questions but for interactions among different species. In Chapter III, I discuss herbivory on a marine alga (Iridaea cordata) common along the Oregon coast. Here, one of the predictions from Chapter II is examined for a plant-herbivore interaction. In Chapter IV, I return to the Panama system to discuss herbivory on algae. This study extends the empirical work from Chapter II to interactions among three trophic levels -- predation on limpets and herbivory by limpets on algae. The results obtained in all three empirical studies are similar, even though the studies occur in different places, involve different species, and describe interactions among different trophic levels. This concordance suggests that the ideas developed in Chapter II may be robust. Finally, Chapter V summarizes the salient features of the thesis in a brief graphical model of consumption in diverse communities.

CONSUMER GUILD STRUCTURE AND THE ORGANIZATION OF PREY ASSEMBLAGES

Chapter II.

INTRODUCTION

Most natural communities are inherently complex. Hence, their study requires reductionist approaches. The simplifications used commonly take two forms. Processes are either studied (1) within a small component of the system (e.g., a guild of consumers or a predator and its prey) or (2) in simple communities used as model systems for more complex assemblages. These two approaches, however, will successfully describe entire, diverse communities only if no important organizational characteristics are unique to more complex systems. Here, I suggest this requirement is often not met for one well-studied community level process -- the effect of consumers on patterns of prey abundance, distribution and diversity.

Interest in consumer-prey interactions (hereafter to include feeding by carnivores or herbivores) covers a broad range of questions. These include consumer effects on: the dynamics and regulation of prey populations; community stability; prey morphological, chemical, and life-history characteristics; and the coexistence and distribution patterns of prey species (see Krebs 1978, Ricklefs 1979, Roughgarden 1979). Despite this diversity of topical interest, however, the approach to these problems is bound by a common thread. In general,

mathematical and empirical studies involve either a single consumer species or treat consumption as a single, cumulative, group effect (some noteworthy exceptions will be discussed later). A potential limitation of such approaches is that neither can directly examine the impact of consumer diversity, an important characteristic specific to complex consumer assemblages. With a single consumer species consumer diversity has no appropriate analogue (other than intraspecific phenotypic or age class variation, to which I will return), whereas lumping consumer species into large groups may mask any complementary or compensatory effects of different species within the group. It is thus important to ascertain what specific contribution consumer diversity makes to patterns of community structure. To this end this paper has two parts. First I develop two hypotheses for the effects of consumer diversity in complex assemblages. Subsequently I provide support for them with data on predation in a rocky intertidal community in Panama and from the literature.

Qualitative Variation In Consumption

From the point of view of a prey individual, the selective pressures exerted by consumers have two components: 1) a quantitative component that deals with variation in consumption due to changes in feeding intensity or magnitude (i.e., changes in consumer density or individual foraging rates relative to prey recruitment and production), and 2) a qualitative component (i.e., the direction of selective pressures exerted) determined by the identity and foraging characteristics of the

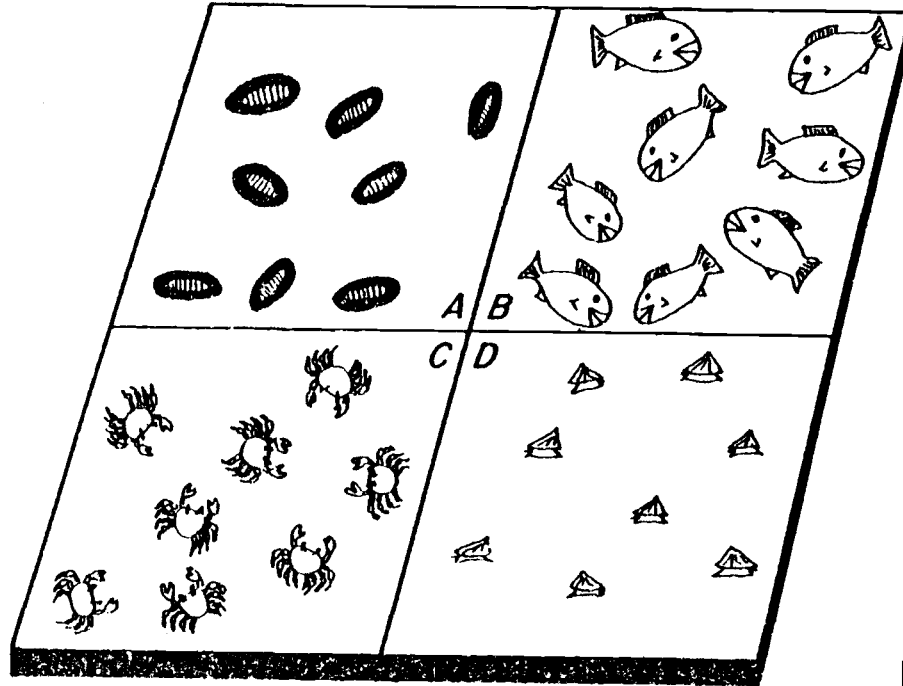
consumer species. Because most theoretical and empirical systems studied have low consumer diversity, most analyses of the effects of "variation in consumption" on the distribution and diversity of prey have in effect been analyses of the quantitative component in isolation (Tansley and Adamson 1925, Paine 1966, 1977, Harper 1969, Parrish and Sailer 1970, Connell 1975, Menge and Sutherland 1976, Day 1977, Fretwell 1977, Lubchenco 1978, Hastings 1978). However, unless the effects of consumption magnitude are independent of changes in the number of consumer species, models based solely on variation in feeding intensity may have limited predictive value in complex systems where qualitative variation in consumption can be an important variable.

For example, consider two hypothetical situations with four habitats and four consumers (Figure 1a, b). Though I use herbivores, the following discussion should be equally applicable to carnivores. Assume, for the sake of clarity, that the magnitude of consumption is high in all four habitats and that individuals of all four species have equal foraging rates. If densities are equal, the magnitude of consumption is the same in all habitats, allowing examination of the effects of qualitative variation in consumption. Two extreme consumer distributions are illustrated. In Figure 1a there is complete spatial segregation of the consumer species. Consumer diversity is low within each habitat, but variance in the identity of consumer species between habitats is high. At the other extreme (Figure 1b) all the consumer species live in all four habitats. Consumer diversity is therefore high in all habitats, but variance between habitats in the quantity and quality of consumption is absent.

Figure 1. Stylized communities with four herbivores (chiton, fish, limpet, and crab) and four habitats to contrast the effects of spatial segregation (A) versus spatial overlap (B) of the consumer species.

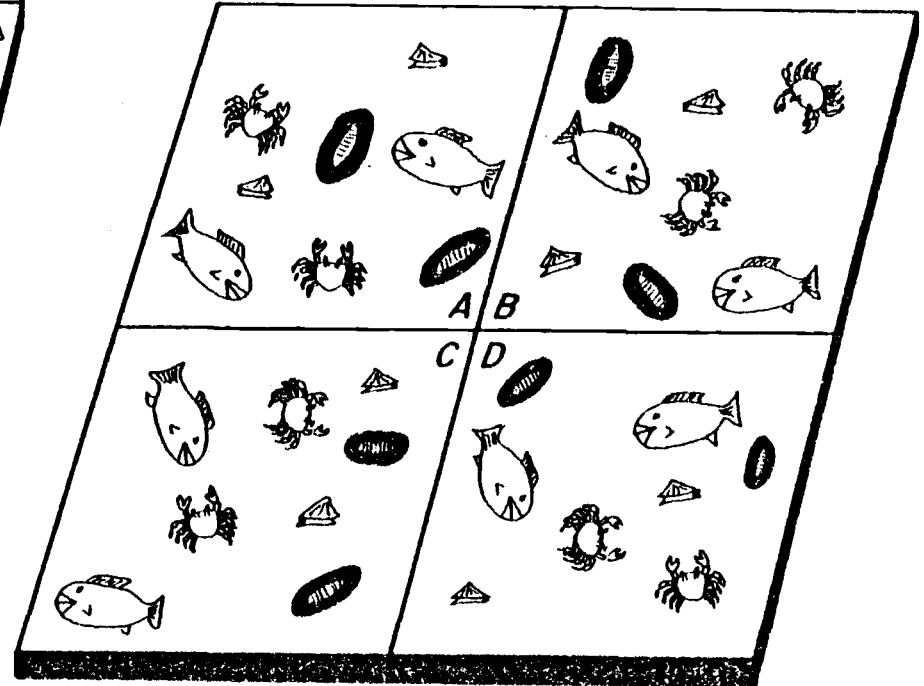
Figure 1.

A.



Low Within Habitat Consumer Diversity
High Between Habitat Consumer Diversity

B.



High Within Habitat Consumer Diversity
Low Between Habitat Consumer Diversity

What if the consumer species are qualitatively different? For example, they may vary in their ability to circumvent specific defensive mechanisms of prey. Structural toughness may inhibit feeding by one herbivore, but have little influence on other species. Toxins may deter one predator, but not another. Alternatively, consumers may vary in their feeding preferences as a response to different nutritional requirements or digestive capabilities. If these types of qualitative differences occur, the effects of consumption in the two situations illustrated should differ despite constant magnitudes of consumption.

With spatial segregation of consumers and high rates of consumption (Figure 1a), the only prey likely to persist in each habitat are those with an effective defense against or of little nutritional value to the specific consumer in that habitat. The word specific is important here, because the prey species persisting in each habitat may differ, reflecting the qualitative differences between the consumers. Spatial segregation, coupled with qualitative differences between the consumers, should therefore enhance between-habitat or beta species diversity (MacArthur 1965, Whittaker 1972) by decreasing the overlap in prey species composition. This diversifying effect of qualitative variation in consumption is a direct consequence of spatial variance in the direction of selective pressures imposed by the consumers. I do not imply here that qualitative variation in consumption will be the sole determinant of between-habitat species diversity. Rather, when consumer species are spatially segregated, variance in consumption is superimposed on other differences between the habitats (e.g., in the physical regimes). Hence, feeding should amplify the spatial variance

in species composition that would otherwise arise from other deterministic and stochastic factors. The larger the qualitative differences between the consumers, the larger the expected magnification of beta diversity.

Where consumer species overlap in their distributions, qualitative differences among them should play a very different role. In Figure 1b prey individuals in any habitat are subjected to all four consumers. Therefore, to persist despite high intensities of consumption, prey must be simultaneously defended against or of little nutritional value to all of the consumers. Here, qualitative differences between the consumers should decrease within-habitat, or alpha prey diversity, by decreasing the probability that specific defenses will be effective against the entire array of consumers (i.e., consumers can have complementary effects when the deficiencies of one coincide with the strengths of another). In addition, since quantitative and qualitative characteristics of consumption do not vary between habitats, feeding in Figure 1b will not enhance between-habitat prey diversity. In fact, consumption may depress beta diversity if mortality by consumers is a primary determinant of individual fitness, since the spatial component of its variance is low.

These two simple cases suggest two hypotheses for the effects of qualitative variation in consumption that are independent of changes in feeding intensity.

- (1) When consumers are spatially segregated, qualitative variation in consumption should increase between-habitat prey diversity by increasing spatial variance in selective pressures.
- (2) When consumers overlap spatially in their foraging, consumer diversity should decrease within-habitat prey diversity by decreasing the probability of prey escapes.

These hypotheses do not represent alternatives. Rather they predict the effects of qualitative variation in feeding given two different consumer distribution patterns. For both predictions, the magnitude of the hypothesized response should correlate positively with the magnitude of qualitative differences between the consumers.

Supporting Evidence for Two Assumptions

The proposed relationships between qualitative variation in consumption and prey diversity are critically dependent on two conditions.

- (1) Qualitative differences between consumer species in their ability to circumvent prey defenses and in their feeding preferences are common.
- (2) The probability of one prey species being simultaneously defended against a group of consumers decreases with an increase in the number of consumers in the group.

There is substantial evidence for the first assumption. Large variability in effectiveness has been shown for chemical defenses (Thompson 1963, Rothschild and Kellett 1972, Schoonhoven 1972, Freeland and Janzen 1974, Anstey and Moore 1976, Levin 1976, Rosenthal et al., 1976, 1977, 1978, Fox and McCauley 1977, Morrow and Fox 1980, Maxwell and Jennings 1980), structural defenses (Norris and Kogan 1980, Lubchenco and Gaines 1981), behavioral defenses (Neill and Cullen 1974), and for defenses where the mechanism is presently unclear (see Chapter III). In fact, if we include pathogens under the collective term of consumers, even substantial intergenotypic variance in defense effectiveness has been found within a long list of plant (c.f. Callow 1977, Day 1974, Sequeira 1978, Vanderplank 1975, 1982) and animal species (Groves et al. 1980, McDevitt and Bodmer 1973, Rager-Zisman et al. 1980). As Janzen (1981) states, "... One herbivore's poison is another herbivore's food. 'Toxic' is not an intrinsic trait of any chemical or defense structure ... Each defense is breached by some herbivore(s); no herbivore can breach all. There is enormous variation in the size of herbivore loads among plant species, but they all have them. Likewise, some herbivores can eat a very large number of plant species and parts ..., but none can feed on all, and many specialists feed on only one."

Interspecific variation in feeding preferences is documented even better (c.f., Schoener 1974, Harper 1977, Fox and Morrow 1981). This variance may be caused by numerous factors such as specializations as an evolutionary response to competition (c.f. Diamond 1978, Roughgarden 1979), differences in nutritional requirements, differences in digestive

capabilities (e.g. Montgomery and Gerking 1980), dissimilar constraints imposed by different feeding structures (see examples in Harper 1977), or even differential susceptibilities to prey defenses (see references cited above). Variation in feeding preferences is common, and when coupled with variation in defense effectiveness, they provide an ample source of differences to drive qualitative variation in consumption.

Condition 2 is more complex. Three different mechanisms could decrease the probability of prey escapes as the diversity of consumers increases. These are (1) combinations of defensive characteristics may be unattainable, (2) combinations of traits may be attainable but evolutionarily unstable, and (3) evolutionary forces may retard the rate of attainment of defenses simultaneously effective against a collection of consumers. Mechanisms two and three will not be important in the specific empirical studies I discuss later. Therefore, I will treat the existing support for these two processes in more detail here.

Mechanism (1): Design Constraints and Opposing Selective Pressures. If structural characteristics are the primary determinants of an individual's fitness when exposed to different consumers then design constraints may make certain simultaneous defenses unattainable. For example, to be both large and small, or erect and prostrate simultaneously is impossible. Therefore, where structural characteristics are important, increases in consumer diversity will, on average, decrease the probability that any single prey will have an effective, collective escape. This mechanism plays an important role in two of the empirical studies discussed below. Such design constraints may further have important evolutionary consequences. If qualitative

differences between consumers are large, then the evolution of anti-consumer defenses may be hindered by balanced or opposing selective pressures. Whenever factors that defend an individual from mortality by one consumer enhance susceptibility to others, then consumer diversity can impose limitations on the evolution of prey defenses to even a subset of the entire consumer guild.

Mechanism (2): Pleiotropic Effects. If genes coding for anti-predator or anti-herbivore defenses interact pleiotropically to reduce the relative or the absolute fitness of the prey, then multiple defenses will not increase in frequency within the prey population. Limited direct evidence is available on the costs of defenses (but see Kerfoot 1977b), especially when they occur in combinations. Nevertheless, such costs are often inferred (Fox 1981). Predator-prey and herbivore-plant studies therefore currently afford few opportunities to evaluate this blockade to multiple defenses. However, a clear demonstration of this mechanism comes from studies of plant-pathogen interactions if the traditional labels of consumer and prey are reversed. By way of analogy, consider the pathogen as a prey exposed to plant resistance mechanisms (= consumers). This analogy is not completely unrealistic since the mechanism of resistance in the examples I will discuss involves a hypersensitivity "attack" by the plant on recognized pathogens. Susceptible plants unknowingly accept the pathogen without reacting since the pathogen is not recognized as a foreign body. Resistance occurs when a pathogen is recognized and is killed or isolated by a non-specific reaction (the hypersensitivity response). Recognition for a large number of host-pathogen systems is determined on

a gene for gene basis (VanderPlank 1982), frequently with a large number of pseudoalleles in both the host and the pathogen. In such cases plants with a specific suite of resistance genes will react to pathogens unless they have an exact matching set of virulence genes.

The most intensively studied plant-pathogen system of this type involves Canadian wheat and the stem rust Puccinia graminis tritici (Vanderplank 1975, 1982). Virulence by stem rust on wheat varieties containing either the Sr6 or the Sr9d resistance genes is common in Canada. However, the cultivar Selkirk, which contains both the Sr6 and Sr9d resistance genes, has been protected in Canada from major rust damage for more than 25 years. Rust strains with combined virulence to both resistance genes (i.e., multiple defenses) have been found in Canada in two different years (1960 and 1975); however, they were unaggressive and unable to persist under natural conditions (Katsuga and Green 1967, Green 1971, Vanderplank 1982). Subsequent work with this plant-pathogen system suggests there are two groups of resistance genes (an ABC group and a XYZ group) that invoke the hypersensitivity response. Virulence (= defense of the pathogen from attack) is strongly associated for genes within each group but strongly dissociated between groups (although there is an environmental interaction component - Roelfs et al. 1979, Vanderplank 1982). That is, individual pathogen strains frequently have several virulence genes within one of the two groups. Strains containing virulence genes from both groups simultaneously, however, are very rare. This dissociation, apparently driven by pleiotropic reductions in pathogen fitness, means that a diversity of resistance genes (= mortality agents to pathogens) greatly

decreases the probability of pathogen (= prey) success if genes from both the XYZ and ABC groups are present. The importance of this mechanism for other consumer-prey systems awaits further research on the costs of specific defenses in isolation and in combination (Levin 1976).

Mechanism (3): Improbable Evolutionary Changes. Increasing the diversity of consumers means that escapes from consumption are more likely to require either: (1) a quantum evolutionary change in the prey phenotype, or (2) the inheritance of several individual defensive characteristics. Both requirements decrease the probability of the evolution of successful defenses to diverse sets of consumers. The first case requires the simultaneous occurrence of several mutations, the second requires the simultaneous inheritance of several single defenses. The second mechanism will be particularly important if individuals with an incomplete set of defenses gain little selective advantage over undefended individuals. Two studies of evolutionary responses to toxins clearly demonstrate the potential evolutionary blockade posed by multiple mortality agents. Klein and Schorr (1953) demonstrated that although Staphylococcus aureus readily developed resistance to three antibiotics when applied singly, resistance did not increase when the drugs were used in combination. Similarly, Pimentel and Bellotti (1976) showed rapid rises in resistance to six single toxins by Musca domestica, but no increases were found when the flies were collectively exposed to all six toxins. The importance of these mechanisms for consumer-prey interactions may be even greater since

consumers represent potentially coevolving gene pools rather than static mortality agents.

Thus, at least on theoretical grounds there are reasons to expect that the ecological and evolutionary consequences of consumption should be dependent on the diversity of consumer species. If any of the three mechanisms operates, the realm of probable prey escapes decreases with increases in the diversity of consumer species (Condition 2).

To test the hypothesized effects of consumer diversity on prey I worked with predators of rocky intertidal molluscan herbivores (limpets) from the Pacific coast of Panama. Several characteristics of this system facilitate these tests. First, the diversity of herbivores and predators is high, but manageable. Second, the predation intensity on these herbivores is sufficiently great (Bertness et al. 1981, Menge and Lubchenco 1981) that if the proposed effects of consumer diversity are important, they ought to be easily demonstrated. These features allow several consumer species to be studied individually and in combination.

STUDY AREAS AND SPECIES

The rocky intertidal community of the Bay of Panama experiences a large semi-diurnal tidal fluctuation (ca. 6m), pronounced seasonal variation in water temperature and wave intensity, and conspicuously lacks large populations of sessile invertebrates and erect macroalgae (Lubchenco et al. in preparation). Crustose algae, however, are very abundant, as are a diverse array of herbivores and predators. The rocky shoreline consists of a mixture of continuous rocky benches and large boulder fields. All of the field experiments to be discussed were run on the south sides of Taboguilla and Taboga islands, situated approximately 10 km south of the Pacific entrance to the Panama canal (see Garrity and Levings 1981, Menge and Lubchenco 1981, Lubchenco et al. in preparation for more detailed descriptions of the physical and biotic environments and maps of the study areas).

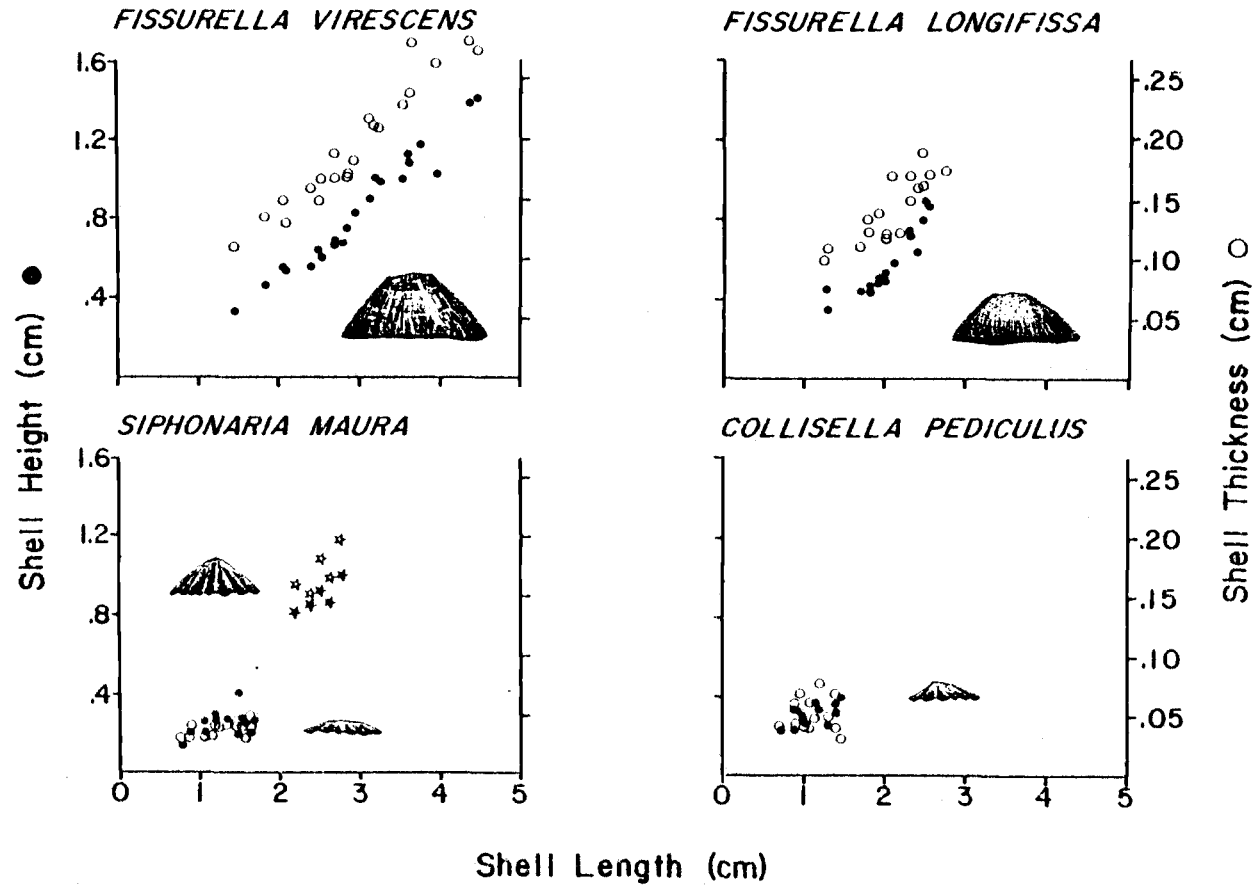
Four major predators eat limpets in the low zone (+.6 m to +2.4 m) of this community: the porcupine fish Diodon hystrix, the crab Ozius verreauxii, and two gastropods, Thais melones and Acanthina brevidentata (hereafter called by their generic names). All four predators have broad diets, but limpets are frequently a major component (Menge et al. in press, L. West personal communication). On the basis of their feeding modes these predators can be divided into two groups. Diodon and Ozius crush using jaws and chelae, respectively, whereas the gastropods use a toothed radula to drill holes in the shells of their prey.

The four common limpet species in the low zone include the acmaeid limpet Collisella pediculus, the pulmonate limpet Siphonaria maura, and two keyhole limpets, Fissurella virescens and F. longifissa. On the basis of shell shape, these four limpet species can also be divided into two groups (Figure 2). The two keyhole limpets have a pronounced conical shape with thick shells, while Collisella and Siphonaria tend to be fairly flat with thinner shells. (The five large S. maura in Figure 2 are very atypical individuals collected from man-made pillars. Their significance will be addressed later.)

These groupings of predators and herbivores were made on the presumption that the two limpet groups ought to be differentially susceptible to feeding by the two predator groups. Thin shells should be easily drilled by snails, yet when combined with a flat shape may be inaccessible to the large foraging apparatus of fish (jaws) and crabs (claws). By contrast, the conical shape of the keyhole limpets should make them readily accessible to crushing predators, however their thick shells may inhibit drilling. Thus, the two predator groups should vary qualitatively in the success of their feeding on the two limpet groups.

Figure 2. Shell height (●) and shell thickness (○) versus shell length for four common limpet herbivores from the Pacific coast of Panama. Individuals were chosen to cover the normal range of shell sizes, and are not a random sample of field populations. Starred points for S. maura are very atypically large individuals but show distinctive changes in shell form from smaller individuals.

Figure 2.



METHODS AND RESULTS

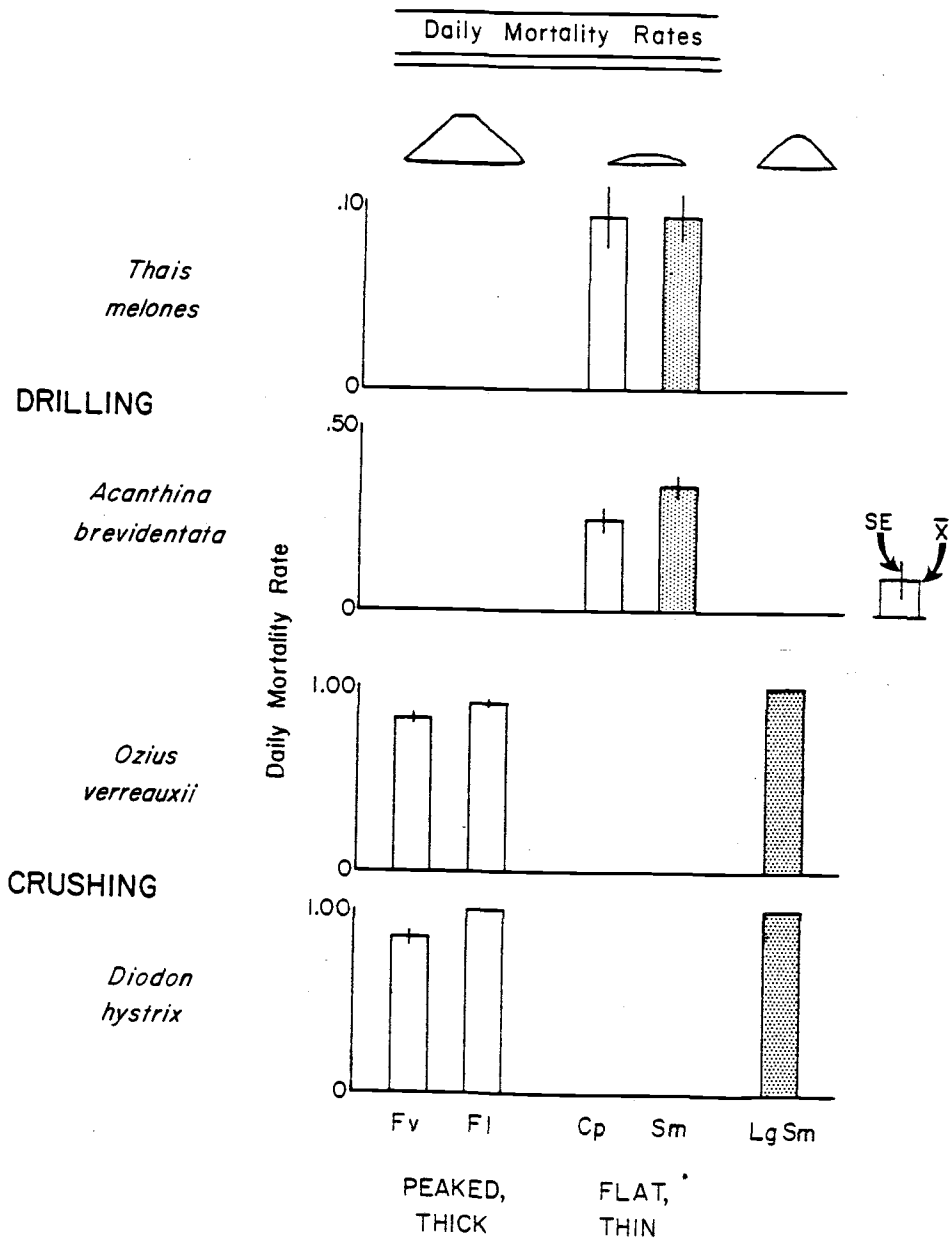
Laboratory Experiments

Each of the limpet species was offered singly and in multiple species combinations to each of the four limpet predators. Between 20 and 25 limpets were kept with either one (Diodon or Ozius) or five (Thais or Acanthina) predators in seawater tables at the Naos Marine Laboratory of the Smithsonian Tropical Research Institute for three months in dry season 1981. There were four replicates for each predator-prey combination and four replicates with a mixture of limpet species exposed to each predator. All tanks were monitored twice daily for mortalities and dead prey were replaced. Tanks with limpets but no predators served as controls. Limpets were collected by chiseling off sections of rock with resident limpets from the low zone. This left individuals attached to their home scars when exposed to predators. These experiments are not meant to estimate feeding rates since such values would depend on the number of predators and prey present. Rather, they examine which prey are defended from consumption by which predators.

Results of these laboratory experiments support the prediction that the limpet groups are differentially susceptible to the predator groups (Figure 3). Drilling predators ate many flat limpets but not conical limpets. Crushing predators frequently consumed the conical Fissurella but rarely killed the flat limpets. Several other observations help elucidate the mechanisms involved. First, there are no significant

Figure 3. Mortality rates for limpets exposed to four different predators. All values are laboratory measurements using the facilities of the Naos Marine Lab of the Smithsonian Tropical Research Institute. Fv = Fissurella virescens, Fl = F. longifissa, Cp = Collisella pediculus, Sm = Siphonaria maura, LgSm = large S. maura. Rates are the proportion of available limpets consumed. Values depicted are means of daily mortality rates for single and mixed limpet species replicates. Offering limpets singly or in combination did not affect the mortality patterns.

Figure 3.



differences between the mortality rates obtained when limpets are offered singly or in combinations (MANOVA, $F_{4,155} = 1.12$, $P > .25$). Therefore, these patterns are not merely an expression of feeding preferences. Second, since the limpets were held with the predators over two months, the absence of mortality, especially in one-predator one-prey tanks, strongly suggests the flat limpet species are well defended against crushing predators, and the conical limpet species are well defended against drilling predators.

Third, limpets of extreme sizes show atypical mortality patterns. Once S. maura individuals become very large, their shell form more closely resembles the two keyhole limpets than smaller individuals of the same species (Figure 2). When these large S. maura are kept with predators, their pattern of mortality similarly parallels that seen for the Fissurella species and contrasts sharply with that of smaller conspecifics (compared stippled bars of Figure 3). This strongly argues that shell form, and not some covarying factor, is the key determinant of susceptibility to these predators. As further evidence, if the limpets are overturned so that shell form is irrelevant, all predators readily eat all limpets.

The two predator groups in this system thus differ qualitatively. In fact, with respect to limpet shell form, they represent opposing selective agents. Those shell characteristics that provide nearly complete immunity to consumption by one predator group, enhance an individual's susceptibility to the other.

Field Observations and Experiments

Knowledge of the spatial distributions of the predators is necessary to assess the impact of these qualitative differences (Figure 1). Porcupine fish forage primarily and very successfully on smooth rock surfaces (personal observation). Their large size (range: up to 1 m in standard length; Bertness 1981, Menge et al. in press) and wide, blunt head (Thomson et al. 1979) preclude feeding in crevices, cracks, or holes. The crab Ozius is generally rare at my study sites and its foraging habits are less well known. In contrast, the predaceous gastropods are much more abundant on heterogeneous surfaces than on smooth surfaces (Figure 4a). This pattern of gastropod abundance is partly due to the fact that the predaceous gastropods are themselves preyed upon by fish; however, the diminished physical rigors of crevices are also apparently important (L. West personal communication, Gaines unpublished data).

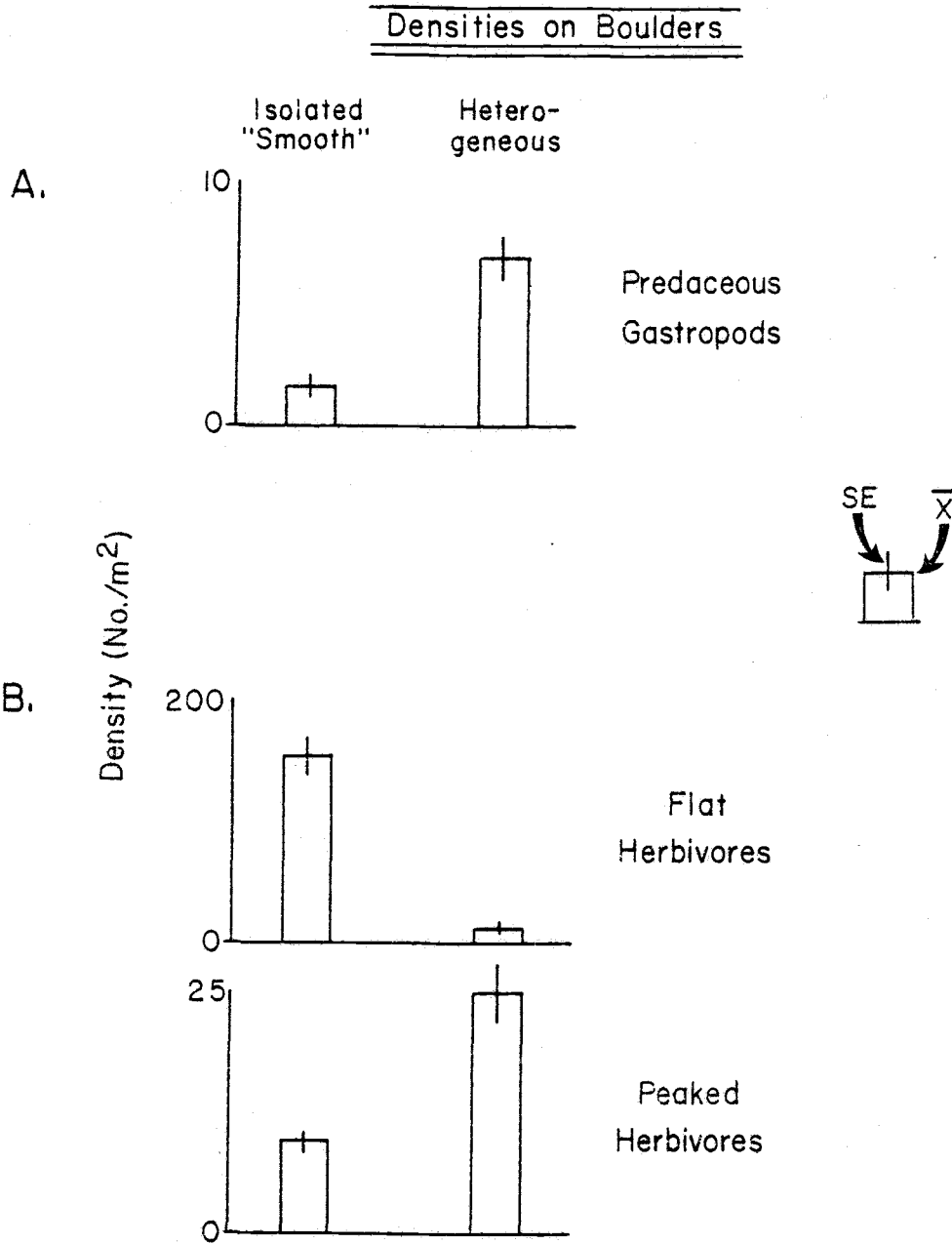
This component of the system therefore resembles the first hypothetical situation discussed above (Figure 1a). Qualitatively different predators are spatially segregated into different habitats. (Microhabitat is probably a better term here, but for consistency I define habitat throughout this discussion as physically different areas regardless of their size.) Smooth surfaces are readily exposed to fish, but have few predaceous gastropods heterogeneous surfaces are inaccessible to fish, but may harbor many predaceous gastropods. Does spatial segregation of these qualitatively different predators enhance between-habitat limpet diversity (Hypothesis 1)?

Figure 4. a. Densities of predaceous gastropods (Thais + Acanthina) on heterogeneous and smooth boulders. Boulders served as replicates of fairly uniform surface texture.

b and c. Densities of flat and conical limpets (same species as in Figure 3) on the same boulders as in a.

Values presented are means and standard errors for samples taken throughout the year from January 1979 through September 1981.

Figure 4.



I assessed the distributions of the four limpet species via comparisons of their abundances on large boulders (>1 m diameter) that were either very heterogeneous in surface texture or fairly smooth (no boulders were completely devoid of surface irregularities). Boulders were used since they provide discrete habitats of a given surface texture and since limpets would not move through the shallow subtidal areas separating replicate boulders. Surveys of >30 marked boulders of each type throughout the year show that the distribution of limpets is consistent with the prediction of the first hypothesis (Figure 4b, c). On smooth boulders, where predaceous gastropods are uncommon but foraging by fish foraging is unimpeded, flat limpets are abundant and conical limpets are scarce. By contrast, on heterogeneous boulders, where predaceous gastropods are abundant but the foraging of fishes is restricted, the pattern of limpet abundances is reversed -- flat limpets are rare, conical limpets are relatively abundant. In the former case the relative difference in flat versus conical limpet abundances is a conservative estimate, because all of the conical limpets surveyed resided in isolated surface depressions on these otherwise smooth surfaces (see Chapter IV). Therefore, when the two predatory groups feed in different habitats, between-habitat variance in limpet diversity is correspondingly high.

An evaluation of the second hypothesized effect of qualitative variation in consumption (i.e. decreased within-habitat prey diversity with increased consumer diversity) requires habitats where the consumers overlap in their foraging. This criterion is met in Panama by a special type of smooth rock surface. Both smooth boulders that closely abut

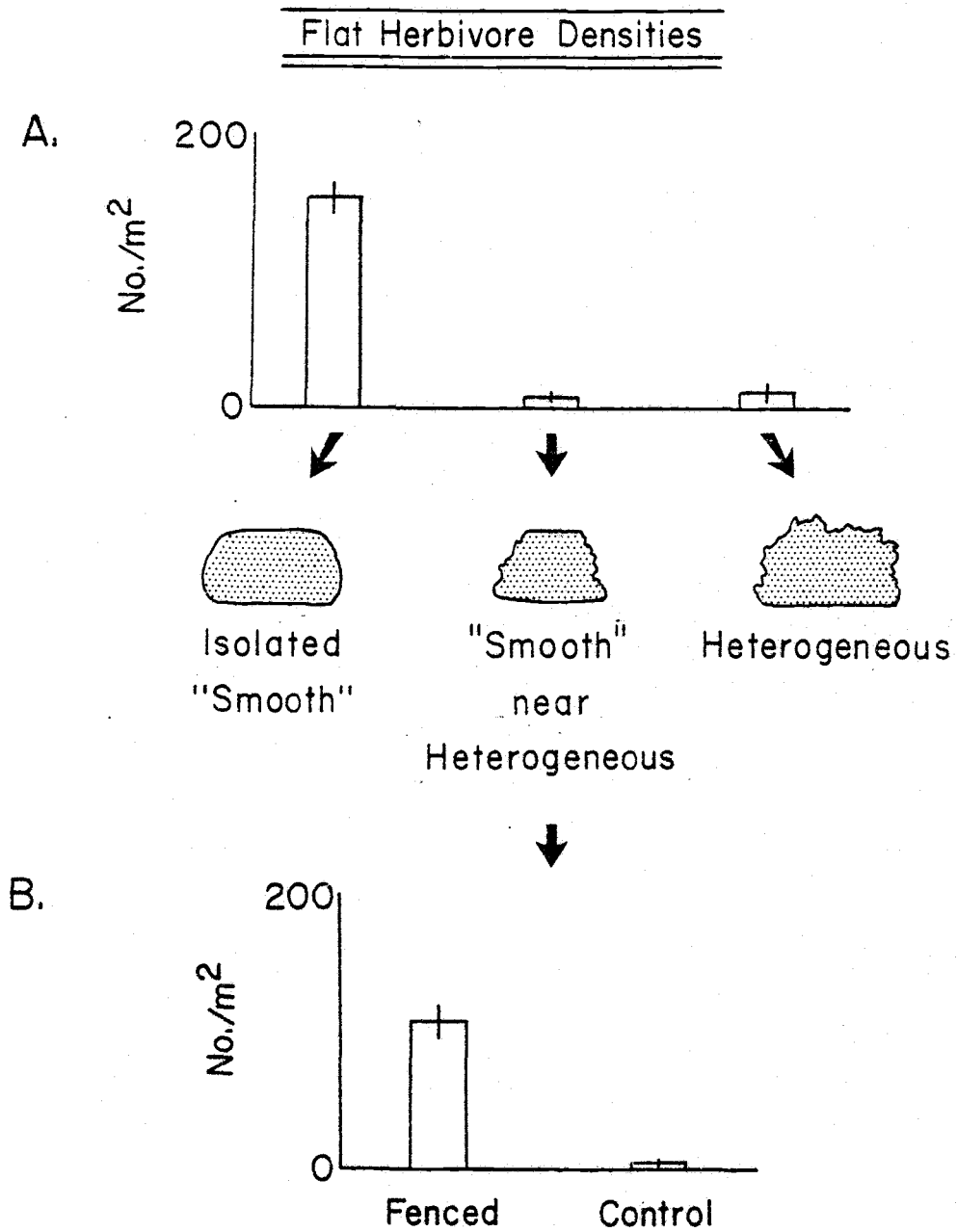
heterogeneous boulders and boulders with smooth tops but heterogeneous sides are exposed to both predaceous fishes and predaceous gastropods residing in nearby surface irregularities. (Thais, the more abundant of the two predators, has a mean daily foraging range on the order of 1 m; L. West personal communication.) These areas with overlap of qualitatively different consumers (as in Figure 1b) are thus different from the isolated smooth and heterogeneous areas previously discussed.

The limpet distribution patterns on these "smooth near heterogeneous" boulders are consistent with those hypothesized (Figure 5a). Conical limpets, as noted above (Figure 4b), are rare on all smooth surfaces. However, smooth surfaces that are near heterogeneous areas have few flat limpets despite their textural similarity to isolated smooth boulders (where flat limpets are extremely common; Figure 5a). Thus, no limpets are common in those habitats exposed to both predatory groups.

Although these limpet distributions are consistent with the two predictions based on qualitative variation in consumption, the correlations could also be driven by other factors that differ among the habitats. To test whether predation accounts for these limpet distributions, I ran three field experiments that specifically addressed the impact of predation on: (1) the distribution of the conical limpets, (2) the distribution of the flat limpets, and (3) the distribution of both limpet groups in smooth areas abutting heterogeneities. The first two experiments involved a series of transplants. To measure predation rates in the field, >200 marked individuals of each limpet species were transplanted to two low zone

- Figure 5. a. Densities of flat limpets on boulders of different surface textures and spatial location. Smooth near heterogeneous includes smooth boulders abutting heterogeneous boulders and boulders with smooth tops and heterogeneous sides.
- b. Densities of flat limpets in September 1981 for smooth boulders fenced to block movement by gastropod predators and unmanipulated controls. Half of each boulder was enclosed by a 10 cm high stainless steel mesh fence. The unenclosed halves of each boulder served as a fence control by their close proximity to the fence.

Figure 5.



microhabitats: smooth rock surfaces and crevices or holes. Both Fissurella species could be successfully transplanted by collecting individuals as they were moving during incoming or receding tides. If pried from their home scars however, these limpets were invariably damaged. Siphonaria and Collisella were never successfully transplanted as individuals. Therefore, small pieces of rock with resident limpets were removed with a chisel and reattached elsewhere with marine epoxy.

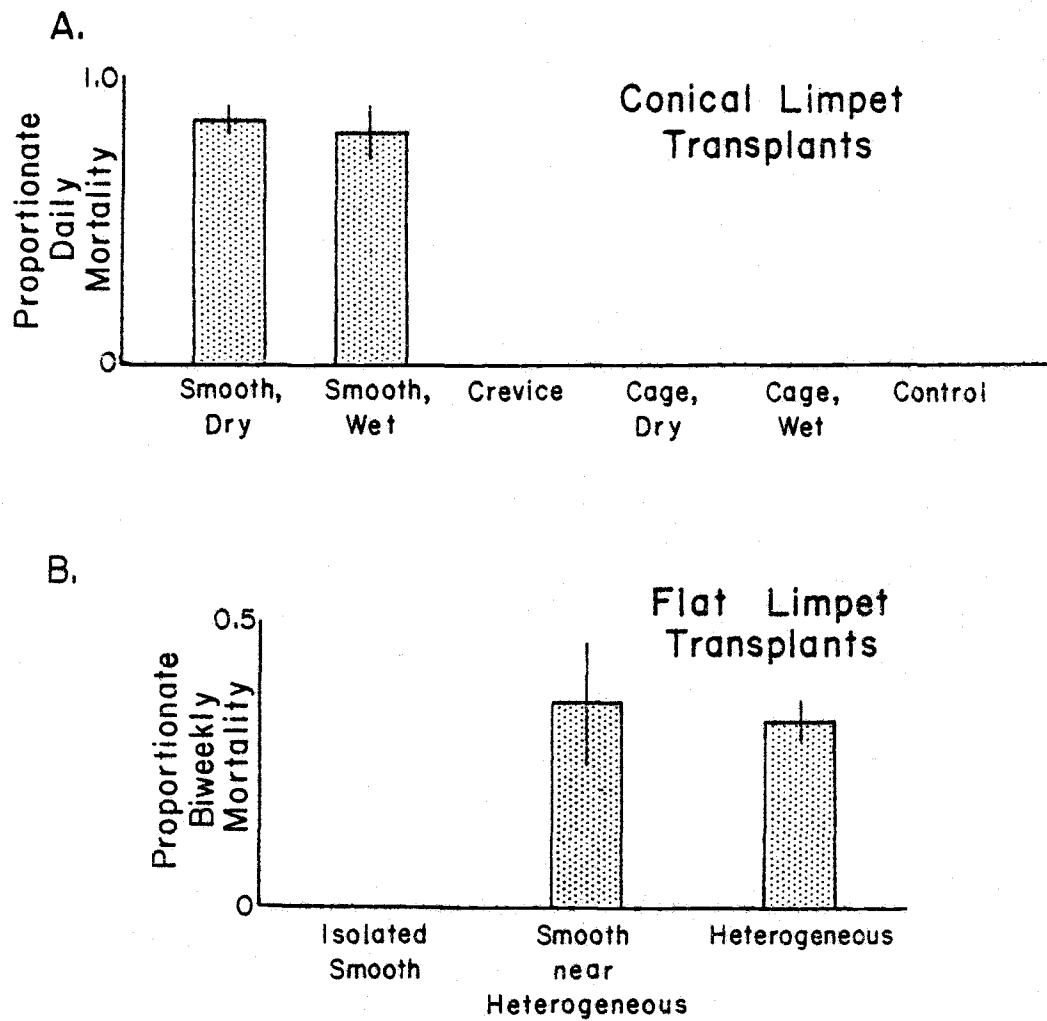
If the conical species are transplanted to smooth surfaces, they experience extremely high mortality rates (Figure 6a; mean life expectancy = 1.1 days). This pattern is obtained regardless of whether the limpets are kept wet or allowed to dry out during low tide. If, however, the conical limpets are: (1) not transplanted, (2) moved to another crevice (to control for mortality induced by the transplantations), or (3) transplanted to smooth surfaces and left exposed during low tides but protected from fish during high tides by stainless steel mesh cages, few limpets died. Therefore, where either natural or artificial physical barriers to foraging fish are absent, conical limpets have a very low probability of survival.

Similar transplants of the flat limpet species show the reversed pattern of mortality (Figure 6b). When individuals are transplanted to areas where predaceous gastropods are rare (isolated smooth areas), there is no limpet mortality. If, however, flat limpets are exposed to large numbers of predaceous gastropods (heterogeneous areas or smooth areas that are not isolated) mortality is relatively high.

Finally, smooth surfaces adjacent to crevices and holes can be effectively "isolated" by building a fence around the smooth surface to

- Figure 6. a. Mortality rates for transplants of conical limpets to various habitats. Wet = limpets had buckets of seawater poured over them at 15 minute intervals throughout low tides. Dry = limpets were exposed to all of the normal physical rigors of the habitat. Cages were removed during daytime low tide exposures. 10 marked limpets were transplanted daily (for 21 low tide periods) into each habitat during the dry season of 1981 and mortality rates were recorded over a two month period. Control individuals were not moved. Cages were placed over smooth substrata. Values are means and standard errors.
- b. Mortality rates for transplants of flat limpet species. Transplants back to isolated smooth surfaces served as controls for the transplanting technique. Mortality rates were assessed as in a.

Figure 6.



impede intrusions by gastropod predators residing nearby. I isolated half of the smooth tops of each of four boulders with heterogeneous sides in this manner in March 1981. The unfenced half of each boulder served as a control for treatment effects of the stainless steel mesh. Within six months, the densities of flat limpets increased dramatically on these artificially isolated smooth surfaces relative to the unmanipulated controls (Figure 5b; $P < 0.001$, paired t-test). Even in this short period of time, the flat limpet densities approached those found on naturally isolated smooth boulders (compare Figures 5a and b).

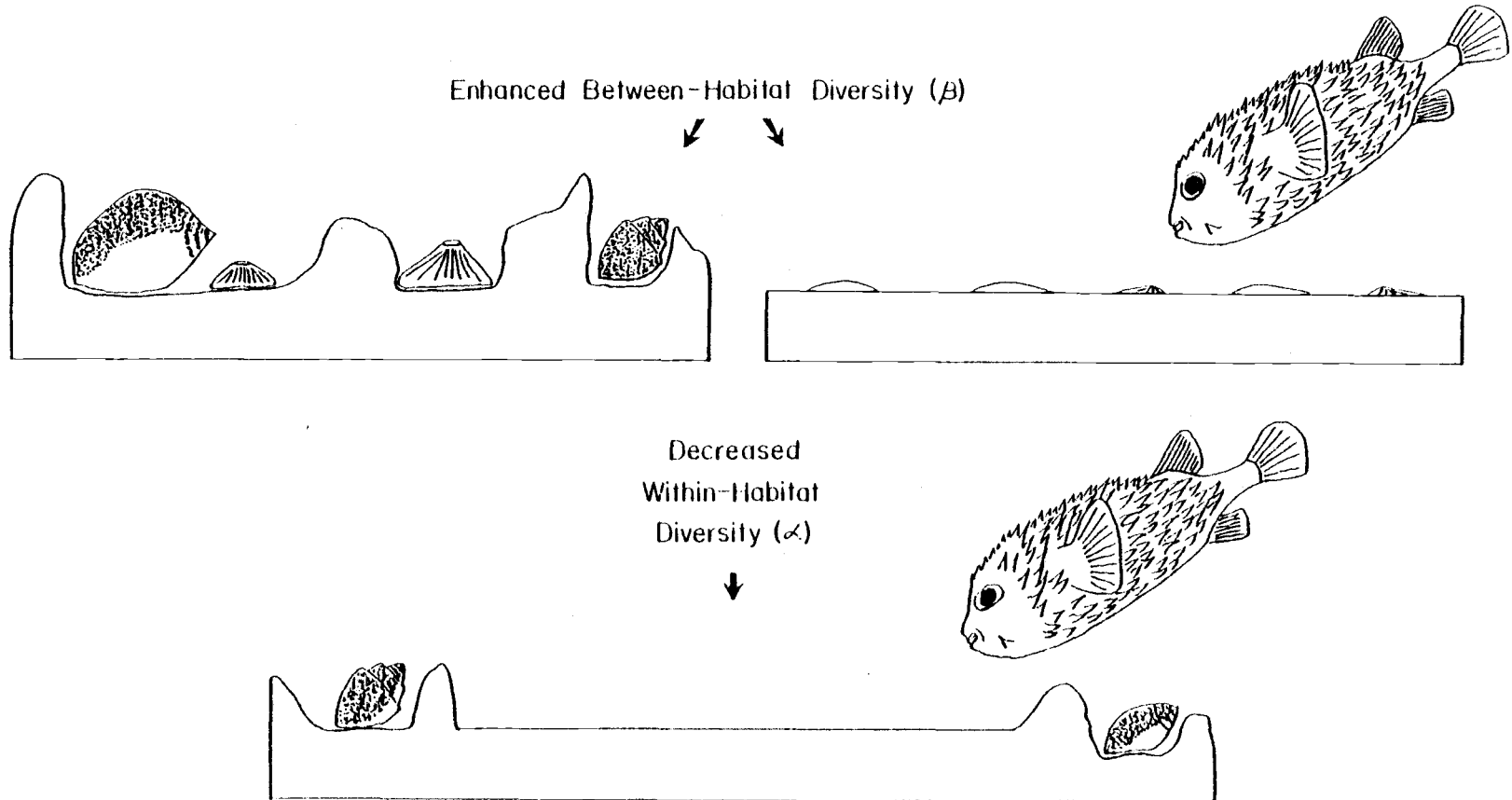
One potentially confounding factor in these comparisons is that the magnitude as well as the qualitative aspects of predation vary spatially. I have not measured feeding intensity, and ideally it would be worthwhile to look at the marginal effects of consumption magnitude with a variety of different consumer diversities (i.e., hold feeding intensity constant and vary the identity and diversity of consumers). Nonetheless, I would argue for this system that any variance in the intensity of consumption probably has little effect on the observed limpet diversity patterns. The magnitude of predation is very high in all habitats whenever a limpet has the "wrong" shell shape relative to the predators of that habitat. Recall that the mean life expectancy for conical limpets on smooth surfaces was 1.1 days. Therefore, even an order of magnitude change in consumption intensity in either direction would only alter expected survivorship to .1 or 11 days. Since limpet life cycles undoubtedly require well over 11 days for completion, such

differences would have little influence on the pattern of limpet distributions.

These experiments illustrate two points. First, a simple measure of the quantity of consumption alone would not predict the impact of predation on limpet diversity patterns. The magnitude of predation is universally high but the effects of predation in the three habitats differ greatly. The key factor is that the system is characterized by a diverse set of predators. From the standpoint of the limpet herbivores, this predator diversity has functional significance since the predator groups represent opposing selective agents on shell shape. Ultimately, this qualitative variation is an important determinant of limpet distribution and diversity patterns as is stylized in Figure 7. When the predator types are spatially segregated they enhance between-habitat limpet diversity by restricting conical limpets to heterogeneous surfaces and flat limpets to smooth, homogeneous surfaces. In contrast, when the feeding of the predator types overlaps, they depress within-habitat limpet diversity since neither shell shape effectively deters both predator groups (see mechanism 1 above).

Figure 7. Stylized summary of effects of predation on limpet distribution and diversity patterns. Segregation of crushing predators (porcupine fish) and drilling predators enhances limpet diversity between heterogeneous and isolated smooth areas. Overlap of the two predators (coiled snails) depresses limpet diversity in smooth areas adjacent to heterogeneities since no limpet is defended against both predators simultaneously.

Figure 7.



DISCUSSION

Other Empirical Support for the Hypotheses

Hypothesis 1: Spatially Segregated Consumers

There are several examples of qualitative variation in consumption enhancing between-habitat diversity. The best studied cases come from freshwater lakes. Here, the predators include fish (adults and fry) and invertebrates (primarily copepods). Largely due to differences in the mode of prey detection used (visual versus tactile) and in the size of the respective predators, these two groups of freshwater consumers select for differences in a suite of structural, life-history, and behavioral characteristics (see Kerfoot and Peterson 1980 for review). When fish were restricted to the center of lakes (Brooks and Dodson 1965, Milsson and Pejler 1973, Werner and Hall 1977), or when fry predominated in the periphery of the lake (Zaret 1972, Kerfoot 1975, Zaret and Kerfoot 1975, Kerfoot and Peterson 1979), they selected for slow growth, early maturation, low visibility (Brooks 1965, Zaret 1965) and escape behaviors of their zooplankton prey (Confer and Blades 1975). In contrast, where fish predation was decreased (e.g., open-water areas of holarctic lakes), copepods preyed heavily on smaller zooplankton and increased the success of larger and long-featured zooplankton (Kerfoot 1975, 1977a, b, Confer and Cooley 1977, Kerfoot and Peterson 1979). These qualitative differences between the predators can

thus maintain between habitat clonal and species diversity (see Kerfoot and Peterson 1980).

For marine systems, I have shown that the cuticle of the red alga Iridaea cordata is an effective deterrent to feeding by some herbivores in the area but has little influence on others (Chapter III). When the herbivores are spatially segregated, as occurs in many low intertidal areas of the Oregon coast, Iridaea is excluded from habitats with high densities of the herbivores against which the cuticle is ineffective. When the herbivores are experimentally removed, between-habitat algal diversity decreases as the distribution of Iridaea expands (Chapter III). Similarly, Brawley and Adey (1981) suggest on the basis of laboratory experiments, that the spatial segregation of amphipods and herbivorous fish between the crests and slopes of coral reefs may be important in the generation of the high between-habitat algal diversity of these habitats.

Finally, this mechanism promoting between-habitat species diversity strongly parallels that proposed for the maintenance of allelic polymorphisms through genotype by environment interactions for individual fitness (Levene 1953, Dempster 1955, Maynard Smith 1970, Karlin and McGregor 1972, Gillespie 1974, Christianson and Feldman 1975, Gliddon and Strobeck 1975, Hedrick et al. 1976, Slatkin and Charlesworth 1978). Indeed, qualitative variation in consumption over space could promote the maintenance of polymorphisms at loci coding for anti-herbivore and anti-predator defenses if sufficient heritable variation in defensive abilities exists within a prey population, and if there are prey genotype by consumer species (or by consumer genotype) interactions

in defense effectiveness (as suggested for several plants and animals -- see Vanderplank 1975, 1982, Rice 1983 for reviews). Large qualitative differences between the consumers, however, diminish the probability that sufficient variation will be present within any prey population for defensive capabilities necessary to persist in all habitats. Under these circumstances consumption will enhance between-habitat species diversity. The degree of diversification will be an increasing function of the extent of differences between the consumer species.

Hypothesis 2: Overlapping Consumers

Evidence relating to the second hypothesis is less extensive. Three sources, however, provide qualified support. Menge and Lubchenco (1981) suggest that the diversity of predators and herbivores in an intertidal community of the Pacific coast of Panama helps lower diversity of both sessile invertebrates and algae. Species richness increases following the removal of consumer groups and the size of the increase correlates with the number of groups excluded. Whether these changes accrue primarily from increases in within or between-habitat diversity, however, and the relative contributions of qualitative and quantitative changes in consumption remain to be addressed (Menge and Lubchenco in preparation).

The effectiveness of multiple consumers in decreasing the probability of prey escapes has received the greatest attention in the control of pests of agricultural crops. Two successful techniques rely on a diversity of mortality agents to reduce the probability of pest

escapes: biological control with multiple predator introductions and integrated control. First, some early workers postulated that the most effective strategy to control pests was to introduce only the single "best" predator or parasite (Turnbull and Chant 1961, Turnbull 1967). A single predator, it was argued, should avoid interspecific competition which might hinder regulation of the pest. Subsequent empirical work, however, suggests that even severe competition does not interfere with pest regulation (see case studies in van den Bosch 1968, Huffaker 1971, DeBach 1974). Rather, multiple consumers enhance regulation. Theoretical work with multiple parasitoid systems similarly suggests that consumer diversity augments the effectiveness of pest control (Hassel and Varley 1969, Hassel 1978). One of the better successes of pest control via multiple consumers has been regulation of the California red scale on citrus (DeBach 1974). Four parasites currently coexist and maintain the red scale at very low population sizes by attacking different host stages in a complementary manner. Second, integrated control of pests uses combinations of biological and chemical control agents. The underlying rationale is that a diversity of control tactics can greatly decrease the probability of pest escapes if the application of pesticides is coordinated to complement the individual weaknesses of biotic mortality agents. Numerous successes with this approach (see DeBach 1974) further support the second hypothesized effect of qualitative variation in consumption.

HERBIVORY AND BETWEEN-HABITAT DIVERSITY:
THE DIFFERENTIAL EFFECTIVENESS OF A PLANT DEFENSE

Chapter III.

Abstract

The effects of consumers on prey populations are traditionally considered to be primarily a function of the intensity or magnitude of consumption. Interactions between the intertidal alga Iridaea cordata (Turner) Bory and five common herbivores of the Oregon coast suggest that the diversity of consumer guilds can be as important in determining the effects of consumers as is the intensity of consumption. Laboratory and field experiments show that the five herbivores in this system can be divided into two functional groups with respect to feeding on Iridaea. 1) Katharina tunicata (chiton), Strongylocentrotus purpuratus (sea urchin), and Collisella pelta (limpet) readily feed on both reproductive and non-reproductive Iridaea. In contrast, 2) Lacuna marmorata (coiled snail) and Idotea wosnesenskii (isopod) feed on reproductively mature plants, but avoid non-fertile individuals. Idotea is deterred from eating immature plants by the alga's cuticle. Lacuna, while impartial to the presence of the cuticle, avoids non-fertile plants for an unidentified reason.

When these herbivores are abundant and spatially segregated, Iridaea has a restricted distribution (isolated on vertical walls) which is explainable on the basis of the above qualitative feeding differences among the five herbivores. Iridaea persists with Idotea and Lacuna

(although reproductively mature blades are heavily damaged), but is rare or absent when there are high densities of either Katharina or Strongylocentrotus. Herbivore removal experiments show that when Katharina is removed from isolated rocky benches, Iridaea establishes in areas where it was previously absent, although it does not reach densities as high as those found where the alga normally occurs. Thus, qualitative variation in herbivory as a result of feeding by different species, enhances between-habitat algal diversity by restricting the distribution of Iridaea. If the effects of the herbivores are experimentally reduced, Iridaea shows a more uniform distribution.

These interactions emphasize that between-habitat species diversity is partly an expression of spatial variation in selective regimes. The greater the selective differences between two habitats the smaller the probability that they will share species in common. Spatial variation in physical characteristics can lead directly to enhanced between-habitat diversity. In addition, if differences in consumer distribution patterns are superimposed on habitat patterns, the effects of physical differences can be greatly magnified by variation in consumption. This diversifying effect of consumers can be mediated either through variation in the quantity (i.e. magnitude) or quality of consumption (i.e. as a result of feeding by different species).

INTRODUCTION

Consumer pressure has a quantity and a quality component. Most studies of the impact of consumers on their prey have focused on quantity, emphasizing either a single consumer species or lumping consumers together in one or more groups and analyzing their cumulative effects (but see Dodson 1970, Birkeland 1974, Kerfoot 1979). These simplifications have enhanced our understanding of patterns of variation in consumption intensity (Connell 1975, Menge and Sutherland 1976, Paine 1977, Fretwell 1977, Lubchenco 1978); however, the role of qualitative variation in consumer pressure has received considerably less attention (Inouye, et al. 1980, Lubchenco and Gaines 1981).

Here I address one aspect of heterogeneity in consumption: the effect of qualitative variation in consumer pressure (as a result of feeding by different species) on between-habitat patterns of prey abundance and diversity. The rationale for this emphasis is if consumer species have different effects on community structure, and feed in different habitats then consumption can induce between-habitat variation in the expected fitness of specific prey individuals even when the magnitude of consumption (i.e. intensity) does not vary. The greater the differences between the consumer species, the greater the probability that the prey species composition of the two habitats will be dissimilar. Thus, heterogeneity in consumption can increase between-habitat or beta species diversity (MacArthur 1965) by enhancing the variance in selective pressures between two habitats.

To examine these predictions I focused on interactions between the red alga Iridaea cordata (Turner) Bory and a guild of consumers along the coasts of Oregon and Washington. The latter includes the sea urchin Strongylocentrotus purpuratus (Stimpson), the chiton Katharina tunicata (Wood), the limpet Collisella pelta (Rathke), the coiled gastropod Lacuna marmorata Dall, and the isopod Idotea wosnesenskii (Brandt). Hereafter these species will be called by their respective generic names.

The stimulus for this work came from the observation (Gerwick and Lang 1977) that reproductively mature blades of Iridaea are generally more heavily damaged than non-fertile blades of similar size. One hypothesis accounting for this differential damage is that reproductive maturity is associated with an increase in the attractiveness of the plant as a food source (e.g., calorific value of Iridaea increases with fertility; Himmelman and Carefoot 1975). Alternatively, at maturation there may be a decline in the effectiveness of anti-herbivore defenses. For example, Gerwick and Lang (1977) noted that the outer cuticle layer of the alga is ruptured around mature reproductive structures. The coincidental timing of this structural change with increased plant damage and the purported deterrent role of cuticles in terrestrial plants (Anstey and Moore 1954, Lupton 1967, Martin and Juniper 1970) suggested that the cuticle may perform a comparable defensive function for Iridaea. However, there are several common, but very different herbivore species in this system (see above). In addition, on the Oregon coast these herbivore species are often spatially segregated into different low zone habitats. In these areas

Iridaea has a very restricted distribution, while on shores where the herbivores are more intermingled or rare, Iridaea is less habitat specific. Thus, I deemed it important to determine how herbivore-specific the cuticle might be as a deterrent to grazing. Specifically, in this paper I ask:

- 1) Why does plant damage increase upon reproductive maturation of Iridaea?
- 2) Is Iridaea an equally attractive food source to the five herbivore species in this system?
- 3) If not, how does heterogeneity in consumption influence the distribution of Iridaea when the herbivores are spatially segregated (i.e. does qualitative variation in herbivore pressure enhance between-habitat plant diversity)?

STUDY ORGANISMS

Iridaea cordata is a foliaceous red alga (20-120 cm tall, 12-24 cm wide) noted for its conspicuous iridescence. It is common in the low intertidal and subtidal zones of rocky coastlines from Alaska to Baja California (Abbott 1971, Abbott and Hollenberg 1976). Several blades are borne on short stipes from a perennating holdfast. Juvenile blades are first evident in spring and in Oregon the onset of fertility is in early to mid summer (personal observation), although fertile and non-fertile blades co-occur throughout the summer and early autumn. A large proportion of adult blades are lost by late fall and most plants persist through the winter as a crustose base (Hansen and Doyle 1976). When mature, tetrasporangial plants (asexual) have numerous small sori (clusters of sporangia) spread across the blade. The distal portions of the blades mature first and sorus development progresses basally (personal observation). Similarly, mature cystocarpic blades (female) have a uniform distribution of numerous small reproductive structures. Spermatangial blades (male) were rare at my study areas and will not be considered further. The thallus of the alga is covered by a multilaminated cuticle of alternating electron opaque and translucent layers which causes the plant to be iridescent. The cuticle is composed of protein (50%), carbohydrates (40%), inorganic salts (5%) and fatty acids (<10%) (Gerwick and Lang, 1977).

The herbivores in this system are diverse in both taxonomy (four classes in three phyla) and foraging characteristics. The purple sea urchin Strongylocentrotus purpuratus (Echinoidea; Echinodermata) is

fairly large (commonly 50 cm in diameter) and feeds by biting or tearing with five teeth. Its diet is generalized although it feeds preferentially on several large brown kelps (Paine and Vadas 1969b, Vadas 1977). Numerous studies have shown that this herbivore can have dramatic effects on algal abundance and diversity (Paine and Vadas 1969a, Leighton 1966, Dayton 1975a, b, Duggins 1980, Sousa et al. 1981). Three of the remaining herbivores are molluscs and feed by scraping with a toothed radula. The chiton Katharina tunicata (Polyplacophora; Mollusca) ranges in size up to 12 cm (Morris et al. 1980), and occurs in the low intertidal zones of Oregon and Washington somewhat above the distribution of Strongylocentrotus on exposed horizontal surfaces (Dayton 1975b). Its impact on algal distribution appears to vary with location (Paine 1980). Collisella pelta (Gastropoda; Mollusca) is a common limpet of middle to low intertidal zones which reaches a size up to 40 mm (Morris et al. 1980). It commonly occurs associated with large brown algae or in mussel beds and frequently feeds on erect macroalgae (Craig 1968). By comparison, Lacuna marmorata (Gastropoda; Mollusca) is fairly small (shell to 7 mm long), and it is most abundant on low intertidal algae and surfgrass (Morris et al. 1980). The impact of this species on the algal community has received little attention, although population outbreaks of a related species on the East coast of North America (L. vincta) have been suggested to occasionally cause extensive damage to subtidal algae (Fralick et al. 1974). Finally, Idotea wosnesenskii (Malacostraca; Arthropoda) is a common, moderately large (to 35 mm) isopod found in intertidal and subtidal habitats from Alaska to Central California

(Morris et al. 1980). This crustacean bites with small mandibles (Naylor 1955) and its effect on algal patterns is unknown.

METHODS

Study Areas

The majority of the field experiments were conducted at an exposed rocky point at the southern end of Boiler Bay, Oregon (44°50'N, 124°03'W). The low zone at this site consists of numerous horizontal, hard mudstone benches of varying tidal heights separated by sharply vertical surfaces (e.g., channels and crevices). Two additional, secondary sites (Mar Vista Cove and Limestone Kiln) are located on San Juan Island, Washington (48°32'N, 123°05'W). These two areas have gently sloping intertidal surfaces and are well protected from waves.

Field Observations

The distribution of I. cordata and the five herbivores in the lower intertidal zone of Boiler Bay, Oregon was determined by locating 30 randomly designated quadrats along 50 m transect lines through each of three habitats (horizontal surfaces in two tidal ranges - +0.3m to +0.6m and +0.8 m to +1.0 m, and vertical surfaces between these horizontal benches). Densities were measured using .25 m² quadrats; percent cover of Iridaea was determined using .25 m² vinyl quadrats with 100 randomly placed dots as described in Menge (1976). Densities of those herbivores which reside on the surface of Iridaea (Idotea, Lacuna) were determined by noting the abundance of each herbivore species relative to the surface area of individual blades.

Field and Laboratory Tests of the Cuticle as an Anti-Herbivore Defense

To test the role of the cuticle as a feeding deterrent, I removed the cuticle layer from Iridaea by carefully scraping the surface of the alga with a razor blade (Gerwick and Lang [1977] used this method to study the structure of the cuticle). Intact non-fertile blades were collected and traced to determine their premanipulation size. The cuticle was then removed from both sides of one half of each blade. These plants were threaded between the strands of braided nylon rope, individually tagged with colored yarn, and transplanted in August, 1978 (at Mar Vista Cove) back to positions close to those from which they were originally collected by tying the ropes to stationary boulders. After 10 days, all blades were retrieved and the percentage of damaged tissue on each half was calculated as the number of randomly plotted dots on a clear vinyl sheet falling over damaged areas, divided by the total number of dots falling on the entire blade. If the blade edges were damaged I approximated the outline of the blade (Iridaea has a fairly predictable lanceolate shape). These experiments could not run longer than this time period since the cuticle frequently regenerates within 14 days (Gerwick and Lang 1977, personal observation).

To control for physical damage directly induced by removal of the cuticle, parallel sets of manipulated blades were transplanted (a) into cages made of a fine mesh (0.318 cm opening) which excluded herbivores (but also altered the physical regime somewhat due to increased shading), and (b) onto ropes tied between pilings at a similar tidal height at the Oregon State University Marine Science Center in Newport,

Oregon. These blades were exposed to air for similar time periods and were likely subjected to even more intense desiccation stress than those blades returned to the outer coast due to the lack of wave activity near these docks. But the blades were physically removed from the normal constellation of herbivores of more exposed shores no herbivores were found on or near these blades at the end of the experimental period.

To gain some insight into species specific effects of the cuticle, a series of laboratory experiments was run with each herbivore species from March 1979 to October 1980. Initially, individual herbivores were offered two 25 cm² segments of non-fertile Iridaea; one segment had the cuticle removed, while the other had an intact cuticle. For each trial, both squares of the alga were cut from the same blade to reduce possible confounding effects from blade-specific preferences. The number of herbivores used per trial and the length of each trial differed between species because of variation between individual herbivore feeding rates and differential reactions of the herbivores to laboratory conditions. Therefore, comparisons between species are limited to analyses of differences in the relative amounts of consumption of tissue on the cuticle-intact and cuticle-removed squares (i.e., the pattern of consumption) rather than the overall quantity of tissue consumed.

Treatments consisted of offering paired squares of Iridaea to 15 Lacuna or to one individual of all of the other herbivore species. One pair of blade samples of Iridaea was offered to Idotea, Collisella and Lacuna while two pairs were offered to Katharina and Strongylocentrotus. Individual feeding trials ran for one (Katharina), three (Strongylocentrotus), or seven days (Idotea, Collisella, and Lacuna).

These time periods, herbivore numbers and algal amounts were chosen to guarantee sufficient time to detect feeding differences while ensuring that food was never in limited supply. All herbivores were held for three days without food prior to each experiment. The percentage of blade area eaten was measured by a random dot method as described above. Feeding trials were run in the circulating seawater systems at Friday Harbor Laboratories or Oregon State University. Individual herbivores were never used in more than one feeding trial. All comparisons of feeding rates on the two blade treatments were made using Wilcoxon's signed-ranks test.

Field Tests of Spatial Variation in Herbivory

The pattern of spatial variation in feeding on Iridaea was determined by a more extensive series of transplants of blades with the cuticle removed from one-half of the surface. The experiments used methods exactly parallel to those previously discussed, except that the blades were transplanted from vertical walls into several low-zone habitats characterized by different herbivore species [horizontal benches at two tidal levels (+0.3 m to +0.6 m and +0.8 m to +1.0 m) and vertical surfaces between these levels]. After 7 days, the patterns of herbivore damage were quantified, as before, in each habitat and compared with those from the laboratory feeding experiments on the five common herbivore species. This comparison should indicate whether there are any correlations between variation in the qualitative

characteristics of herbivory in the field and the restricted distribution of Iridaea.

Finally, to directly test whether the absence of Iridaea from certain low-zone habitats was causally related to the qualitative characteristics of herbivory, I altered the herbivore distribution patterns by periodic removals of herbivore individuals. For logistic reasons, these manipulations focused on higher horizontal benches in the low zone characterized by high densities of Katharina. I removed all individuals of this chiton from two small, isolated benches (each approximately 2 m² surface area) in January 1979 at Boiler Bay, Oregon. The density of Iridaea was monitored periodically for the ensuing 2 years. Although the isolation of these areas by surge channels kept immigration of chitons at fairly low levels, the experiment was maintained by approximately bimonthly removals of chitons. Two nearby areas of similar size were monitored as unmanipulated controls.

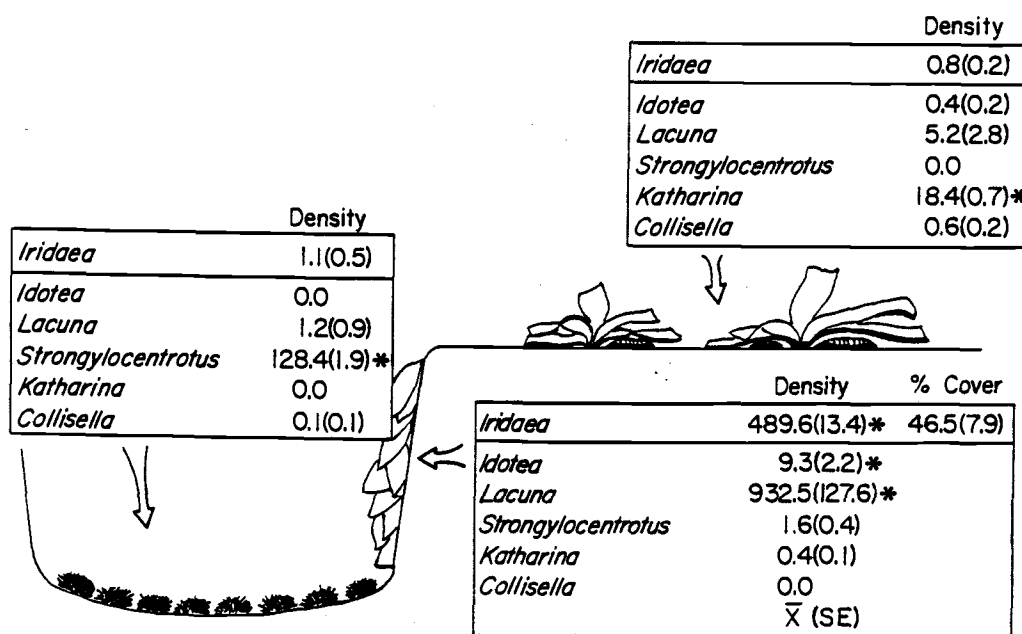
RESULTS

Field Observations

Iridaea is not uniformly distributed throughout the low intertidal zone. At Boiler Bay, Iridaea is extremely abundant on vertical surfaces but rare on adjacent horizontal substrata at similar tidal levels (Figure 8). This restricted distribution is characteristic of several other exposed rocky points along the central Oregon coast (personal observation) and is correlated with variance between these habitats in the abundances of the different herbivore species (Figure 8). While these herbivore patterns are from a single sampling date (August 1980) they are indicative, for all species except Lacuna, of the herbivore abundance patterns I have recorded at this site from March 1979 through October 1981. Lacuna shows dramatic seasonal density fluctuations with peaks of abundance in late summer (D'Antonio personal communication, personal observation). Low horizontal surfaces (+0.3 m to +0.6 m), have high densities of Strongylocentrotus, yet few other herbivores. Algal individuals other than calcified crustose species are rare in this habitat. Slightly higher horizontal areas (+0.8 m to +1.0 m) have high densities of the chiton Katharina, no sea urchins and very low densities of the other herbivores. The brown alga Hedophyllum sessile (C. Agardh) Setchell constitutes most of the algal biomass on these higher surfaces with an understory of erect and crustose coralline algae. These herbivore and algal distribution patterns on horizontal surfaces are similar to those described by Dayton (1975) for the outer coast of

Figure 8. Distribution of Iridaea cordata and five common herbivores for three habitats at Boiler Bay, Oregon. Upper horizontal surfaces were between +.8 m and +1.0 m. Lower horizontal surfaces were between +.3 m and +.6 m and were not tide pools at low tide. Densities are number of individuals per m². Values for Lacuna are undoubtedly low due to the difficulty of locating extremely small individuals in the field. Asterisks indicate the numerically predominant species in each habitat.

Figure 8.



Washington. In contrast, vertical surfaces have very low densities of Strongylocentrotus and Katharina. However, Idotea and Lacuna, which generally both occur on algae at low tide, are present in all three habitats but are much more abundant on the algae of vertical walls. They frequently occur on blades of Iridaea and significantly, they are both found almost exclusively on fertile blades (Table II). This distribution parallels the pattern of enhanced herbivore damage on reproductively mature plants (Table I).

Thus, there is large between-habitat variation in algal species composition in the low intertidal zone at Boiler Bay. Iridaea is one of the major variants, ranging from dense stands on vertical walls to near complete absence elsewhere. These algal patterns correlate with between-habitat differences in the numerically dominant herbivore species. Iridaea persists with Idotea and Lacuna (although reproductively mature blades are heavily damaged), but it is rare when there are high densities of either Katharina or Strongylocentrotus. Interestingly, in many other areas along the Oregon coast where Strongylocentrotus and Katharina are rare on horizontal benches, Iridaea is fairly abundant on horizontal as well as vertical surfaces. For example, at the northern end of Boiler Bay, Iridaea has a mean density on horizontal surfaces of 377.3 individual blades per m^2 and covers 28.9% ($N = 25$ quadrats, August 1980) of the substratum. These algal abundances are more comparable to the values for vertical surfaces at sites where Katharina and Strongylocentrotus occur abundantly (Figure 8). Similar, less restricted distributions of Iridaea are apparently found in protected areas of Washington (Hruby 1976) and California

Table I. Percent damage for individual fertile and non-fertile blades of Iridaea cordata. The Washington samples are from August 1978 while the Oregon data are from August 1980. No distinction is drawn between tetrasporangic and cystocaspic blades since the patterns are qualitatively similar. Percent damage was calculated by a random dot point intercept method as described in the text. Values are \pm (S.E.). All comparisons are by a Wilcoxon two sample test. Henceforth, * = $P < .05$, ** = $P < .01$, *** = $P < .001$, NS = $P > .05$.

	% Damage	
	<u>Fertile</u>	<u>Non-Fertile</u>
Washington		
Mar Vista Cove (N = 88)	44.7 (4.2) ***	15.2 (3.2)
Limestone Kiln (N = 80)	38.8 (5.4) *	7.4 (2.5)
Oregon		
Boiler Bay (N = 160)	39.6 (4.6) ***	11.2 (3.1)

Table II. Herbivore densities on fertile and non-fertile blades of *Iridaea*. Values are \bar{x} (S.E.). All comparisons are by a Wilcoxon two sample test.

	No. of Individuals/m ² of Blade Area		
	<u>Fertile</u>		<u>Non-Fertile</u>
Washington			
Mar Vista Cove (N = 88)			
August 1978			
<u>Lacuna</u>	51.1 (9.6)	***	3.6 (1.1)
<u>Idotea</u>	3.0 (0.9)	*	0.0
Limestone Kiln (N = 80)			
August 1978			
<u>Lacuna</u>	29.8 (4.1)	***	0.0
<u>Idotea</u>	0.0	NS	0.0
Oregon			
Boiler Bay (N = 70)			
August 1980			
<u>Lacuna</u>	36.4 (5.2)	***	0.0
<u>Idotea</u>	1.1 (0.3)	*	0.0
October 1980			
<u>Lacuna</u>	889.0 (31.9)	***	0.0
<u>Idotea</u>	2.4 (0.6)	**	0.0

(Hansen and Doyle 1976). The reasons for the expanded distribution of Iridaea and the scarcity of the two herbivores on some horizontal surfaces are not known. Nonetheless, these differences suggest that the pattern of herbivory and the distribution of Iridaea may be linked.

The Cuticle as an Anti-Herbivore Defense

The field transplants of Iridaea with the cuticle removed from half of the blade surface clearly demonstrate that the cuticle deters herbivory by at least some herbivores in the system (Figure 9). While the intact half of transplanted blades remained largely unchanged, nearly 10 percent of the cuticle-free surface was removed after 10 days (Table III). Considering only those blades with greater than 0.5 percent damage, the effectiveness of the cuticle is supported even more strongly. Over 25 percent of the cuticle-free surface of damaged blades was consumed (Table III). This analysis suggests that those blades encountered by herbivores during the 10 day experimental period sustained major damage if the cuticle was removed. There were no treatment effects in either of the control groups of transplants, i.e. caged or suspended in water column (Table III). Furthermore, there is a high degree of similarity between damage patterns on transplanted manipulated blades and blades offered to herbivores in the laboratory (personal observation). Taken together, these results support the contention that the Iridaea blades were damaged by herbivores. However, these field experiments do not permit identification of the herbivore(s) responsible for the damage.

Figure 9. Herbivore damage on a manipulated blade of Iridaea. The cuticle was completely removed from the right half of the blade. This photograph was taken at the end of the two week experimental period.

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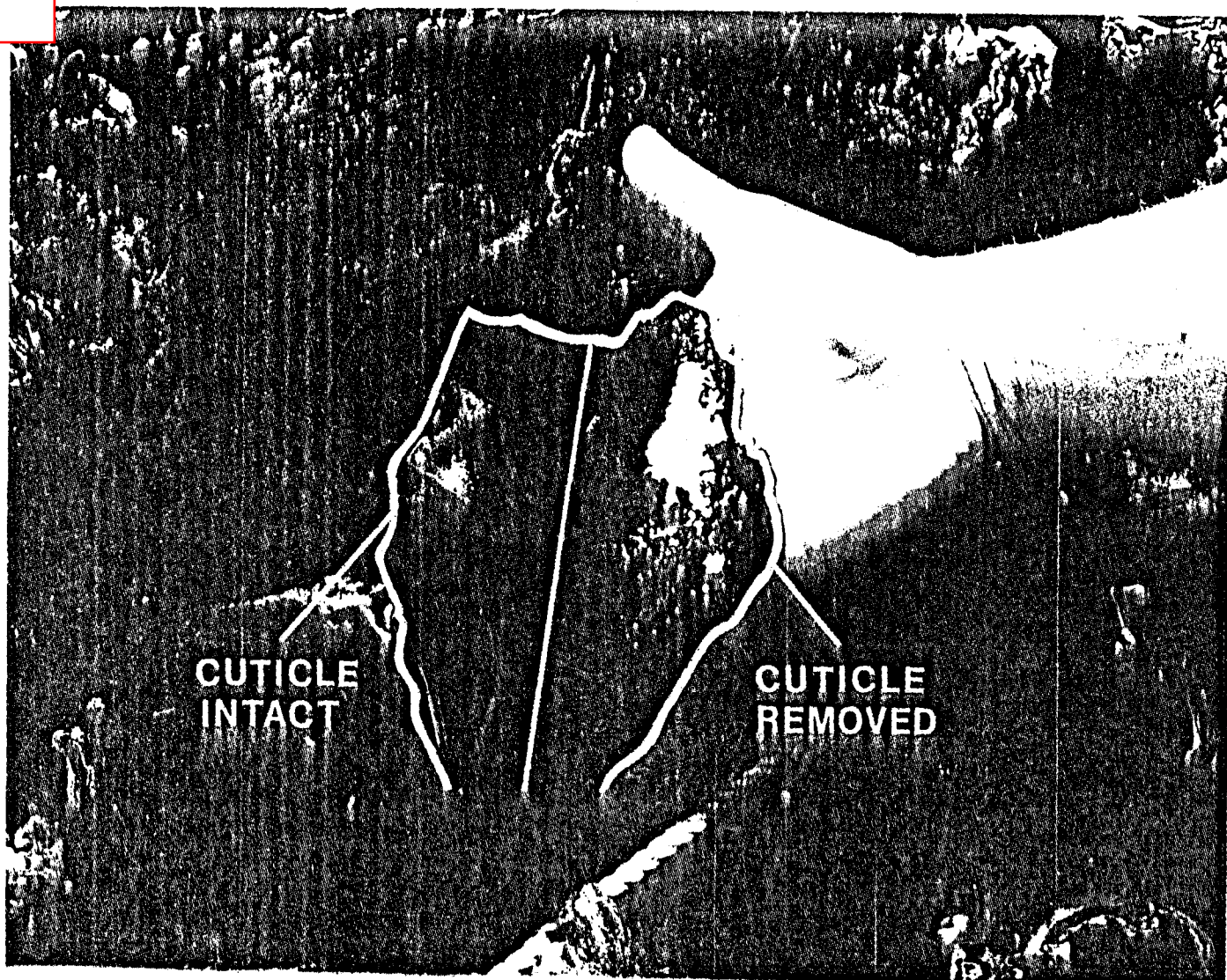


Figure 9.

Table III. Percent damage in field transplants (August 1978) of cuticle-manipulated Iridaea. Values are \bar{x} (S.E.). The comparison including all blades is by a Wilcoxon's signed ranks test while that for blades with major damage uses a Wilcoxon two sample test since the observations are not paired.

<u>% Damage</u>			
Transplants on Vertical Surfaces			
All Blades			
Cuticle Intact 1/2 of Blade	(N = 28)	0.2 (0.1)	***
Cuticle Removed 1/2 of Blade		9.8 (4.1)	
Blades with >0.5% Damage			
Cuticle Intact 1/2 of Blade	(N = 2)	0.6 (0.1)	**
Cuticle Removed 1/2 of Blade	(N = 9)	25.5 (5.1)	
Controls			
1. Within Cages			
Cuticle Intact 1/2 of Blade	(N = 16)	0.0	NS
Cuticle Removed 1/2 of Blade		0.0	
2. Between Pilings			
Cuticle Intact 1/2 of Blade	(N = 25)	0.3 (0.1)	NS
Cuticle Removed 1/2 of Blade		0.1 (0.1)	

The results of laboratory feeding experiments with specific herbivores show that the cuticle is an effective defense against only one herbivore species (Idotea; Table IV). The other four species (Katharina, Strongylocentrotus, Collisella and Lacuna) are impartial to the cuticle and feed at comparable rates on intact and cuticle-free segments of the alga. Hence, both laboratory feeding experiments and field transplant experiments suggest that the cuticle is a deterrent to herbivory. However, the effectiveness of this deterrent evidently varies with the herbivore species.

One curious result of these experiments is the extremely low feeding rates of Lacuna on both cuticle-free and cuticle-intact blades (Table IV) given its high densities on Iridaea in the field (Table II). There are at least three explanations for this low feeding rate. First, Lacuna may not actually feed upon Iridaea but may subsist on microscopic epiphytes growing on the surface of the blade. Second, Lacuna may prefer fertile blades for reasons which are independent of the state of the cuticle. For example, Lacuna may be selecting on the basis of plant quality, (which may vary with the reproductive condition of the plant), or it may be deterred from feeding on non-fertile plants by some mechanism other than the cuticle. Third, Lacuna may not feed well under laboratory conditions. To investigate these alternatives, I ran paired feeding trials to compare consumption by Lacuna on fertile and non-fertile blades using methods identical to those given above for testing the effectiveness of the cuticle as a defense. These experiments reveal that Lacuna readily feeds on Iridaea, but primarily on fertile blades (Table V). In fact, most of the small holes characteristic of feeding

Table IV. Herbivore feeding experiments on cuticle-manipulated blades of *Iridaea*. All blades are non-fertile. Values are \bar{x} (S.E.). All comparisons are by Wilcoxon's signed-ranks test. *Katharina* would not feed in the laboratory so all feeding trials with this herbivore were run in stainless steel enclosures in the field similar to those used by Himmelman and Carefoot (1975). N = the number of replications.

	Percent Eaten	
	<u>Cuticle Intact</u>	<u>Cuticle Removed</u>
1. Cuticle Impartial Species		
<u>Katharina</u> (Field, N = 16)	38.8 (6.1)	NS 40.4 (6.0)
<u>Strongylocentrotus</u> (Lab, N = 20)	35.9 (9.4)	NS 41.9 (10.1)
<u>Collisella</u> (Lab, N = 8)	20.3 (11.4)	NS 24.7 (15.5)
<u>Lacuna</u> 2.3 (0.6) (Lab, N = 29)	NS	2.1 (0.8)
2. Cuticle Inhibited Species		
<u>Idotea</u> 15.9 (1.8) (Lab, N = 24)	***	46.5 (3.1)

Table V. Feeding by Lacuna in the lab on fertile versus non-fertile blades of Iridaea. Values are \bar{x} (S.E.) per 25 cm². All comparisons are by Wilcoxon's signed-ranks test.

		<u>% Damage</u>	
Experiment A			
Fertile	19.3 (6.1)		
	(N = 12)		***
Non-Fertile, Cuticle Intact		2.7 (1.2)	
Experiment B			
Fertile	20.7 (8.0)		
	(N = 8)		***
Non-Fertile, Cuticle Removed		3.4 (1.9)	

by Lacuna were centered over reproductive structures (personal observation). This preference is strong regardless of the condition of the cuticle (Table V).

Thus, the five herbivores in this system sort into two functional groups. 1) Katharina, Strongylocentrotus and Collisella, which feed freely on Iridaea in all reproductive conditions, and 2) Lacuna and Idotea, which prefer fertile plants. The reasons for this avoidance apparently differ: Idotea prefers cuticle-free plants regardless of the plant's reproductive state; Lacuna prefers fertile plants regardless of the presence or absence of the cuticle.

Field Tests of Spatial Variation in Herbivory

The observations of Iridaea abundance at Boiler Bay (Figure 8) showed that Iridaea was rare in habitats with high abundances of some herbivore species (Katharina and Strongylocentrotus), yet coexisted in dense stands, until reproductive maturity, with other herbivore species (Lacuna and Idotea). These algal distribution patterns are consistent with the qualitative differences in foraging found between the five herbivore species in the laboratory. A causal basis for the association between lab and field results is supported by the field transplants of Iridaea into different habitats. The pattern of herbivore damage in these experiments changed as a function of the prominent consumer species in each habitat. There was little variance in damage between the cuticle-free and cuticle-intact halves of blades when either Strongylocentrotus (low horizontal areas) or Katharina (high

horizontal areas) was abundant (Table VI). These results differ from those when the blades were transplanted onto vertical surfaces where Iridaea is normally common (Table III). Thus, the pattern of herbivory in the field parallels the pattern of the distribution of Iridaea. The cuticle is an effective defense against herbivores found where Iridaea normally occurs, yet is completely ineffective against herbivores found where Iridaea is rare.

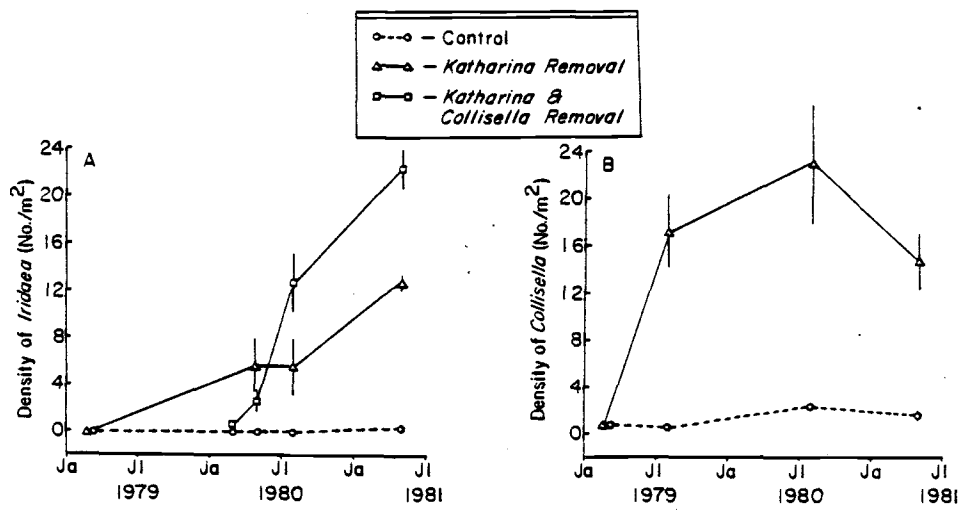
Definitive evidence for the effect of variation in herbivory on Iridaea comes from the manipulations of herbivore densities on horizontal benches. Removal of Katharina led to a highly significant increase in the density of Iridaea relative to control areas over the two-year experimental period (Fig. 10a). This supports the contention that between-habitat variation in herbivore pressure enhances the restriction of Iridaea to vertical walls. However, the abundance of Iridaea after removal of Katharina is still small relative to the densities which normally occur on vertical walls (compare Figures 8 and 10). A confounding effect that explains part of this discrepancy is that the removal of Katharina apparently released Collisella from interspecific competition, allowing this species to reach higher than usual densities (Figure 10b). Paine (1980) has observed similar results in Washington. Since this limpet species is also impartial to the presence of the cuticle (Table IV), and has been shown elsewhere to feed heavily on Iridaea (Craig 1968), the large increases in its density may have partially compensated for the absence of Katharina. To examine these potentially compensatory effects, a parallel set of two removal areas was initiated in November 1979 from which both Katharina and

Table VI. Field transplants of cuticle-manipulated Iridaea from vertical onto horizontal surfaces. Values are \bar{x} (S.E.). All comparisons are by Wilcoxon's signed-ranks test. Transplants onto vertical surfaces and controls are presented in Table III.

<u>Habitat</u>		<u>Percent Damage After 7 Days</u>	
<u>Hedophyllum - Katharina</u> Zone (+0.8 m to +1.0 m)			
Cuticle Intact	(N = 10)	96.5 (0.3)	NS
Cuticle Removed		95.5 (1.1)	
<u>Strongylocentrotus</u> Zone (+0.3 m to +0.6 m)			
Cuticle Intact	(N = 10)	94.8 (0.7)	NS
Cuticle Removed		94.9 (0.6)	

Figure 10. A. Response by Iridaea to experimental removal of cuticle-impartial herbivores on high horizontal benches. The Katharina removals and controls were initiated in January 1979, while the combined Katharina and Collisella removals commenced in November 1979. B. Densities of Collisella for control and Katharina removal areas. Vertical bars are standard errors.

Figure 10.



Collisella were continuously removed. The methods used were comparable to those described above.

The response by Iridaea to the absence of both Katharina and Collisella was significantly greater than to the absence of Katharina alone (Figure 10a). This supports the contention that increased densities of Collisella partially compensated for the removal of Katharina. Nonetheless, the densities of Iridaea in the total removal areas are still far below those of vertical surfaces in the low zone. There are at least two further factors which may account for this difference. First, two years may not be sufficient time for Iridaea to reach high densities. The steady increase in blade densities throughout the two-year experimental period is consistent with this suggestion. However, the rapid response of Iridaea to manipulations of competitors in other areas (Dayton 1975a, Hruby 1976) suggests that this explanation may be inadequate (although the studies cited were done at lower tidal heights where rates of recruitment and growth may be higher). Second, other differences between the habitats (e.g., physical characteristics, competitive interactions) may be acting in concert with variation in herbivory. Therefore, while removal of herbivores may expand the distribution of Iridaea, the absence of variation in this single factor is insufficient to remove all of the between-habitat variation in plant abundance.

Although I did not alter the abundance of herbivores on low horizontal surfaces, Dayton (1975a) has shown that Iridaea (and many other algal species), become established upon removal of Strongylocentrotus along the coast of Washington. Eventually, though,

the abundance of these species declined with increases in the large brown alga Hedophyllum sessile. Therefore, herbivory also seems to play a major role in the exclusion of Iridaea from low horizontal areas although it is not the sole factor affecting between-habitat variation in algal abundance.

In summary, although it may serve several other functions, the cuticle of Iridaea can be an effective anti-herbivore defense. Since the cuticle is ruptured around mature reproductive structures, it can partly account for the high herbivore damage seen in fertile individuals of the alga. However, the success of the cuticle as a deterrent varies against different herbivore species. Feeding by the isopod Idotea is significantly depressed by the cuticle, while the other four common herbivores are unaffected by the presence of the cuticle. Similar variation among the herbivores is shown by the pattern of consumption by Lacuna. Although this coiled gastropod is impartial to the presence of the cuticle, it feeds almost exclusively on fertile blades of Iridaea for an unidentified reason. In the field, these differences between herbivores mean that the success of Iridaea will vary as a function of the identity, as well as the density of herbivore individuals. When the five herbivore species studied here are abundant, but have contiguous spatial distributions, Iridaea does not co-occur with either Katharina or Strongylocentrotus, yet it grows in dense stands in areas with high abundances of Lacuna and Idotea. If the effects of the cuticle-impartial herbivores are experimentally reduced, Iridaea shows a more uniform distribution. Thus, heterogeneity in herbivory as a result of consumption by different species, enhances between-habitat variation in species composition by restricting Iridaea to vertical substrata.

DISCUSSION

Although many studies of marine communities have shown dramatic effects of herbivores on patterns of community structure (see Lubchenco and Gaines 1981 for review), we have little information on algal characteristics which act as anti-herbivore defenses. The field and laboratory studies presented here of feeding by Idotea on Iridaea demonstrate that the cuticle should be added to the small, but growing list of potential plant deterrents to grazing by marine herbivores. Furthermore, the structural similarities noted in the cuticle layers of many other red algal species (Gerwick and Lang 1977) warrant additional studies on how widespread these protective attributes may be. Previous work on algal defenses has implicated both structural (Menge 1975, Lubchenco and Cubitt 1980, Littler and Littler 1980, Hay 1982) and chemical (Irvine 1973, Geiselman 1980, Geiselman and McConnell 1981) characteristics of the plant as determinates of feeding preferences by other marine herbivores. Currently, I do not know which of these two categories best accounts for the deterrent effects of the cuticle in Iridaea. More widespread attention has been given to structural and chemical characteristics of plants as they affect feeding by terrestrial herbivores (e.g., Tanton 1962, Ehrlich and Raven 1964, Mooney and Dunn 1976a, b, Feeny 1970, 1975, Janzen 1974, Freeland and Janzen 1974, Futuyma 1976, Rhoades and Cates 1976, Rausher 1981). This wealth of information from higher plants should be valuable in suggesting "prime candidates" for undocumented defenses in marine algae.

Variation in Defense Effectiveness

Despite this broad interest in anti-herbivore (and anti-predator) mechanisms, relatively little attention has been given to two areas which are addressed by the feeding of the five herbivores in this system: 1) What is the scope of effectiveness of specific defenses?, and 2) When qualitative variation exists between consumer species, what are its effects on patterns of community structure? Others have cautioned that defenses against consumers are not necessarily universally effective. For example, Orians and Janzen (1974) state "...that no defense is likely to provide complete protection and that something effective against one set of predators may be ineffectual against others." The experiments presented here provide a clear demonstration of the differential effectiveness of a plant defense mechanism against the normal set of herbivores which encounter the plant. How general are these results? A definitive resolution of this question is hampered by the paucity of studies which explicitly consider the effects of foraging by the entire range of consumers in diverse systems.

Some evidence, largely drawn from comparisons of consumers from different localities (and thus naive to many prey items offered), suggests that the pattern of variation presented here may be widely applicable. A broad range of detoxification abilities have been shown in mammals (reviewed in Freeland and Janzen 1974) and insects (see references in Maxwell and Jennings 1980) for plant-borne toxins.

Rothschild and Kellett (1972) have similarly documented a variety of responses to the potentially toxic effects of feeding by mostly naive invertebrate and vertebrate predators on insects which sequester cardiac glycosides. In marine systems, Hay (1981) has shown that a profusely branching morphology in an alga may decrease the foraging success of sea urchins and fish, yet this shape encourages feeding by amphipods (Brawley and Adey 1981). Finally, analogous to the fate of the cuticle of Iridaea (reported above), the waxy cuticle of the sprouting broccoli, Brassica oleracea var. italica, inhibits attack by the cabbage flea beetle, Phyllotreta albioneca (Anstey and Moore 1976). In contrast, in another variety of this same plant (B. oleracea var. acephala) the cuticle enhanced attack by the cabbage aphid, Brevicoryne brassicae, and the whitefly, Aleurodes brassicae (Thompson 1963).

Thus, the defensive attributes of a particular prey characteristic must often be defined with respect to specific consumers. Resistance to one consumer does not necessarily imply resistance to all. Some of this interspecific variation in defense effectiveness may ultimately be predictable on the basis of characteristics shared within taxonomic or functional groups of consumers. For example, there have been many recent predictions that different types of chemical defenses will be the most effective deterrents to specialist versus generalist herbivores (Feeny 1970, 1975, 1976, Rhoades and Cates 1976, Futuyma 1976, Rhoades 1977, Fox 1981). However, as seen in the herbivores in this study, variation may still be common even among broadly generalized consumers.

Between Habitat Diversity

As demonstrated by the feeding of the five herbivores on Iridaea, these types of qualitative differences between consumers gain added significance since they can have important effects on spatial variation in community structure. Between-habitat diversity (or the degree of difference in species composition among habitats) will be a function of 1) the influence of stochastic processes generating random spatial differences in species composition, and 2) the largely deterministic effects of variation in the selective regimes of the respective habitats. In the second case, any characteristic which enhances the between-habitat variance in selective forces will tend to reduce the probability that similar species will coexist in each habitat (i.e. it will increase between-habitat diversity). The greater the magnitude of the selective differences, the smaller the expected overlap in species composition.

Physical differences between two areas may directly prevent a given species from persisting in both habitats. This is one hypothesized basis for the association of enhanced species diversity with greater habitat heterogeneity (Simpson 1964, MacArthur 1965, 1969); however, these direct effects can be greatly magnified if the physical differences among the habitats ultimately lead to between-habitat variation in consumption (herbivory or carnivory). By superimposing differences in consumer distributions on the pattern of habitat distributions, between-habitat prey diversity can be dramatically

enhanced due to the amplification of selective differences between the respective habitats.

Between-habitat variation in the quantity of consumption has received fairly widespread attention for marine systems. Studies of the role of consumers in setting the upper or lower limits of the distribution of sessile organisms (Connell 1961, Paine 1966, 1964, Dayton 1971, Lubchenco and Menge 1978, Underwood 1980, Sousa et al. 1981) can be interpreted as demonstrations of between-habitat variation in consumption intensity (although the variation is often along a gradient rather than between two discrete habitats). Similarly, between-habitat diversity has been shown to be maintained between microhabitats such as crevices or holes and smooth surfaces by the restriction of consumers to the refuges provided by substratum irregularities (J. Menge 1975, B. Menge 1976, Vance 1979, Menge and Lubchenco 1981). In each of these studies the disparity in the species composition of the two habitats (i.e. between-habitat diversity) declines when the amplifying effect of changes in consumption intensity is experimentally removed.

As shown here, between-habitat variation in the qualitative characteristics of consumption can play a similar diversifying role. While qualitative differences (e.g., in susceptibility to defenses) are possible within a species (Rothschild and Kellett 1972), they are likely to be larger and more frequent between consumer species. Iridaea is quite successful on vertical surfaces where it is defended by the cuticle from Idotea or by some unknown mechanism from Lacuna. In contrast, it is rare or absent from those surfaces with moderate to high

densities of herbivores against which it is poorly defended. Experimental removal of these herbivore effects decreases between-habitat algal diversity since the distribution of Iridaea expands.

These results do not imply that variation in herbivory is the only factor influencing the distribution of Iridaea. In fact, my experiments suggest that several factors are important. Horizontal and vertical surfaces undoubtedly have different physical characteristics and they support a different array of potential competitors. Each of these factors may contribute to the noted disparity in the abundance of Iridaea in the herbivore removal experiments relative to normal densities found on vertical surfaces. Further, quantitative differences between the herbivore pressure exerted in these habitats certainly occurs. However, while density changes in Collisella may partly compensate for the removal of Katharina (Figure 11), such compensation through density changes is not possible between either Idotea or Lacuna and any of the other three herbivores since they are differentially susceptible to the defenses of Iridaea. Thus, qualitative variation in consumption seems to play a fundamental role in the maintenance of the restricted distribution of Iridaea by augmenting the effects of spatial differences in both physical parameters and the magnitude of consumption. If these patterns are characteristic of species-rich systems in general, then the role of consumers in community organization changes with increased consumer diversity since the potential for qualitative variation in consumer pressure is increased. Ecologically, such qualitative variation in feeding over space or time can alter prey distribution or diversity patterns even when the magnitude of

consumption is constant. Furthermore, non-uniformity in the effectiveness of anti-herbivore or anti-predator defenses implies that consumer species may frequently act as qualitatively different selective agents. Thus, evolutionary responses to predation by diverse consumer guilds may be fundamentally different from responses to mortality by a single predator since feeding by different consumer species may impose strong disruptive or diversifying selection.

HERBIVORY AND ALGAL DIVERSITY IN A TROPICAL INTERTIDAL COMMUNITY

Chapter IV

INTRODUCTION

Refuges and defenses are key determinants of the success of a prey individual in regimes of intense predation. Defenses decrease the chance that a prey individual will be eaten if it is encountered by consumers, whereas refuges provide a means of escape for those individuals that would otherwise be killed or damaged. The interplay between predation and these two mechanisms of prey persistence can generate predictable patterns of community structure.

Intense predation can reduce the number of species coexisting in a habitat by excluding prey with no effective defense (Harper 1969, Paine 1977, Lubchenco 1978). On the other hand, the restriction of poorly defended species to refuges increases between-habitat prey diversity by creating a mosaic of prey species that reflects the underlying distribution of habitats.

In Chapters II and III, I considered the added significance that accrues when several consumer species are present. In such cases there can be high variability in what comprises a defense to or a refuge from consumers. In this chapter, I present a third empirical example, involving herbivory in the Panama system, to support the hypotheses developed in Chapter II. The main contribution of this last example is its extension of the treatment of variability in refuges and defenses

(Chapter II) to interactions among three trophic levels. The rationale is that if predators influence the within and between habitat diversity of herbivores, then predation can alter the qualitative aspects of herbivory on plants. Here, I address the consequences of predation on limpets in Panama (Chapter II) to the patterns of algal community structure in this system.

SPECIES AND STUDY AREAS

Four herbivorous limpets are commonly found in the low zone (+.6m to +2.4m) of rocky intertidal shores of the Bay of Panama: Fissurella virescens, F. longifissa, Siphonaria maura, and Collisella pediculus. The two Fissurella species (0. Archaeogastropoda) are keyhole limpets with a prominent hole in the apex of their shells that serves as the excurrent opening for the respiratory and urogenital systems. Collisella pediculus is also an archaeogastropod, but is in the superfamily Patellacea, a group containing many common (primarily temperate) limpet genera (Patella, Acmaea, Cellana). Siphonaria maura is a member of the subclass Pulmonata, a largely terrestrial and freshwater group with reduced or absent gills and a vascularized mantle cavity. All four species have prominent scars and are only active while being splashed during incoming and receding tides (Bertness, et al. 1981; Menge and Lubchenco 1981, Menge et al. in press, Gaines unpublished data).

These four limpet species are eaten by a diverse group of predators (Menge et al. in press). The porcupine fish, Diodon hystrix, is a large, teleost predator (up to 1m in standard length; Thomson et al. 1979) that feeds on a variety of gastropods in the intertidal zone (Palmer 1979, Bertness 1981, Bertness et al. 1981, Menge et al. 1983). It crushes shelled prey with massive mouth plates, and few gastropod species ever attain sizes that provide complete immunity from its attack (Bertness 1981, Bertness et al. 1981). The other two common limpet predators are themselves gastropods. Thais melones and Acanthina brevidentata each feed on many mobile and sessile prey (Menge et al.

1983, L. West personal communication) by drilling holes with a toothed radula. The last predator, the crab Ozius verreauxii, is included for comparison with the other crushing predator, Diodon. It is generally rare at my study sites.

The most ubiquitous algae in the low zone of rocky shores of the Bay of Panama are crustose species (Lubchenco et al. in preparation). Several algal divisions are represented. Ralfsia sp. and Mesospora heathiana are members of the Phaeophycophyta (brown algae); Hildenbrandia prototypus is a member of the Rhodophycophyta (red algae); and Schizothrix calcicola is a member of the Cyanobacteria (blue-green algae). Schizothrix calcicola occurs in both calcified and uncalcified morphs. Erect algal species are normally uncommon and largely restricted to protected microhabitats such as crevices and holes (Menge and Lubchenco 1981). The more frequently encountered species are (by division): Chlorophycophyta--Enteromorpha spp., Cladophora spp.; Rhodophycophyta-- Gelidium pusillum, Gelidiella sp., Centroceras clavulatum, Hypnea valentiae, Polysiphonia pacifica, Jania spp.; Phaeophycophyta-- Giffordia mitchelliae; Cyanobacteria-- Microcoleus lyngbyaceus.

All of the work presented here was conducted on the south sides of Taboguilla and Taboga Islands, situated approximately 15 km south of the Pacific entrance to the Panama Canal (see Menge et al. 1983 for map). The main site on Taboguilla Island was a large, continuous, rocky bench, while the Taboga Island site was a region of large (generally >1m diam.) boulders at various tidal heights. The Taboga site was somewhat protected from the large southerly ocean swells characteristic of the wet season (May to November; Glynn and Stewart 1973, Glynn 1976) and

there was no evidence of boulder movement during the three year duration of this work. Briefly, the physical characteristics of these areas are: large tidal excursion (ca. 6m), mean surface water temperature -- 26 to 29°C, daily maximum air temperature range -- 22 to 34°C. More specific details of the physical regime are described in Garrity and Levings (1980) and Menge and Lubchenco (1981).

METHODS

Field Observations

The density and microhabitat distribution patterns of the limpet species were recorded in $.25 \text{ m}^2$ quadrats (30) placed randomly along transect lines on Taboguilla Island. All transects ran parallel to the shore in the low zone (+.6 to +2.4 m). These data were recorded twice each year (mid dry and wet seasons) from 1978 through 1981. The densities of limpets and predaceous gastropods were also monitored on isolated marked boulders (Taboga Is.) of differing surface texture during the same time period.

The algal abundance patterns in the immediate vicinity of individual limpets were monitored with quadrats shaped as concentric bands (2 cm wide) centered on isolated individual limpets. Each band contained 50 randomly positioned dots used to estimate percent cover by a dot intercept method. Quadrats centered in small crevices without limpets recorded the algal patterns in the absence of limpet effects. Fifteen sets of quadrats were scored for each limpet species.

Field Experiments

To test the influence of the limpets in the generation of algal patterns adjacent to their scars, a large reef on Taboguilla Island was partitioned into discrete treatment areas isolated by large crevices or abrupt ridges. Treatments included: Control, S. maura removal, F.

virescens removal, F. longifissa removal, and total limpet removal.

Permanent quadrats were positioned in each treatment area in two microhabitats. One set of 18 cm by 12 cm permanently marked quadrats (8 replicates) was placed adjacent to discrete surface irregularities. These quadrats were divided into bands to measure changes in algal patterns with distance from a crevice or ridge. A second set of quadrats was isolated (by at least 1 m) from surface irregularities greater than 2 cm in relief. All quadrats were monitored photographically at approximately three month intervals from October 1978 through February 1981. Limpets were removed from treatment areas at approximately two month intervals.

RESULTS AND DISCUSSION

Field Observations

As noted elsewhere (Chapter II), the four limpet species are distinctly segregated into two habitats (Figure 11). The two keyhole limpets are largely restricted to crevices or other irregularities in the rock. In contrast, S. maura and C. pediculus generally occur away from large crevices; although they often reside in small depressions in the rock or adjacent to small ridges or cracks. Similar results are evident from the samples of limpet densities on boulders (Table VII). The keyhole limpets are much more common on heterogeneous boulders, whereas S. maura and C. pediculus are far more abundant on boulders with fairly smooth surfaces.

The general effects of predation on limpets in this system (Chapter II) are to restrict the distributions of the limpet species. As a consequence, predators also restrict the potential effects of these herbivores on their algal prey. This creates a mosaic of herbivory that is particularly important if the non-molluscan herbivores are also considered. The other major herbivores that feed in the low zone include both fish (Scarus perrico, Eupomacentrus spp., Kyphosus elegans, Prionurus punctatus, Ophioblennius steindachneri) and crabs (Grapsus grapsus; Menge et al. 1983). As with the piscine and crustacean predators of limpets (Chapter II), the large size of these herbivores limits their activities in crevices, cracks and holes (Menge and Lubchenco 1981). Therefore, individual plants growing on smooth versus

Figure 11. Distribution of limpet herbivores from the nearest large (>1 cm relief) crevices, holes, or ridges. Data are from dry season 1981.

Figure 11.

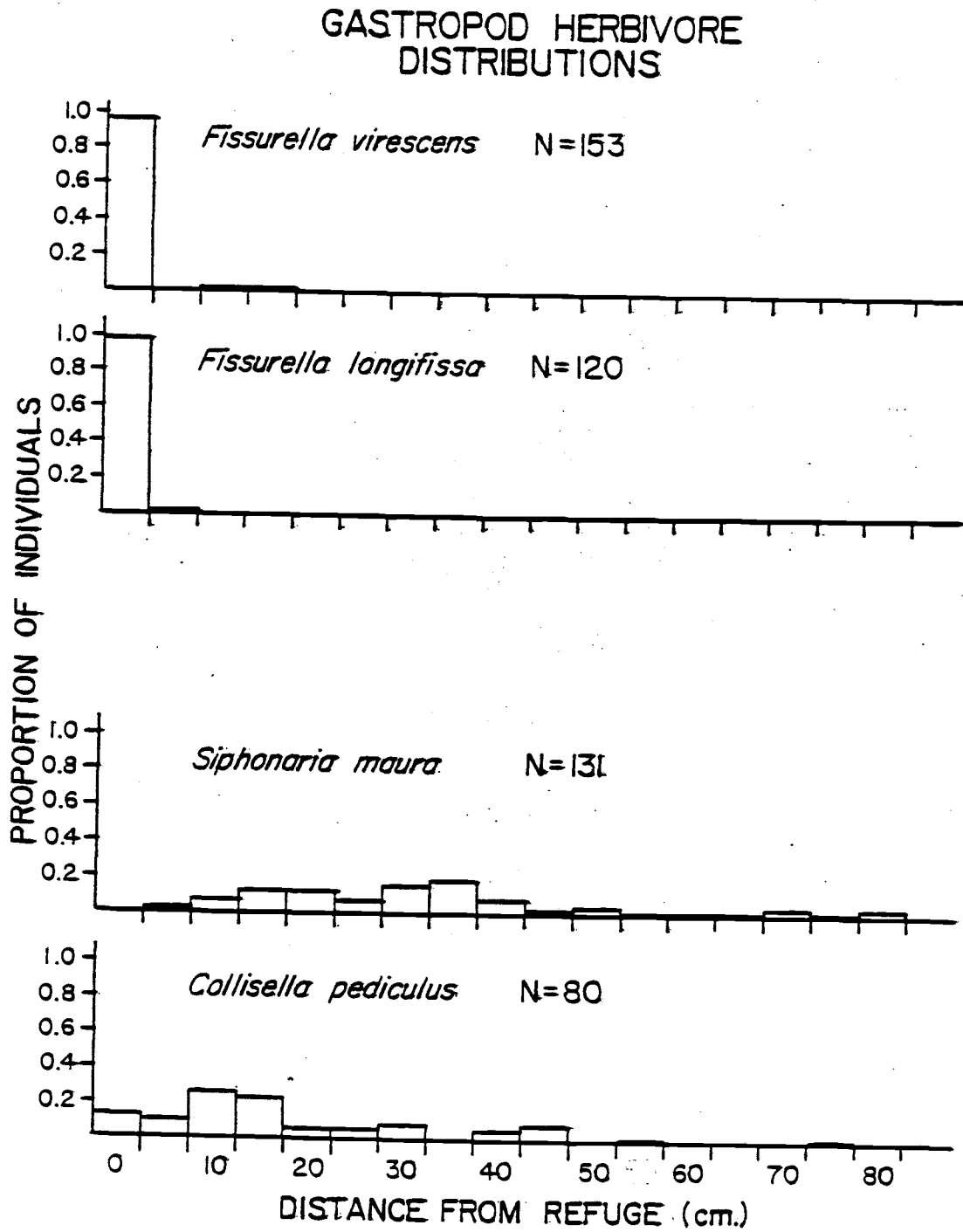


Table VII. Mean densities of limpets on boulders of smooth or heterogeneous surface texture. Values are \bar{x} (S.E.) for number of individuals per m^2 for 6 control boulders of each type.

Date	<u>Densities</u>			
	Smooth		Heterogeneous	
	<u>Fissurella</u>	<u>Siph. &</u>	<u>Fissurella</u>	<u>Siph. &</u>
	spp.	<u>Coll.</u>	spp.	<u>Coll.</u>
	<hr/>	<hr/>	<hr/>	<hr/>
Sept 79	2.7 (1.8)	188.1 (38.0)	20.2 (1.4)	7.8 (0.2)
Jan 80	3.7 (2.7)	88.4 (9.7)	13.9 (0.8)	1.7 (1.0)
Mar 80	4.1 (1.9)	105.6 (22.6)	11.3 (0.7)	8.5 (2.7)
Aug 80	8.1 (1.1)	284.4 (110.0)	16.5 (1.9)	7.8 (2.8)
Jan 81	6.4 (1.7)	153.0 (44.9)	15.4 (2.4)	1.4 (0.7)
June 81	2.2 (0.9)	140.9 (24.3)	12.9 (1.1)	4.7 (0.6)

heterogeneous surfaces must contend with different sets of herbivores. Growth on smooth surfaces exposes plants to all of the larger herbivores as well as the two flat limpets, whereas growth in crevices only exposes a plant to large molluscan herbivores. The situation is thus analogous to the spatial segregation of limpet predators (Chapter II).

Smooth, low zone rock surfaces with no limpets are on average completely covered by three crustose algal species (Table VIII). Erect algae are very rare. When limpets are present these algal patterns change in the vicinity of the home scar (Figure 12). Measured as proportionate similarity to the algal patterns in Table VIII, there is little variance in crust cover and species composition in areas distantly removed (>20 cm) from limpets. However, there are precipitous declines in proportionate similarity approaching the home scar of all limpets. These changes are not seen around crevices when limpets are absent. The primary change that occurs near all limpets is an increase in the amount of bare rock. The specific changes in algal species composition observed, including differences between the limpet species, will be discussed elsewhere (Gaines in preparation). Two points are clear, however, from the data presented in Figure 12. Assuming, temporarily, that the limpets cause the algal changes near their residence:

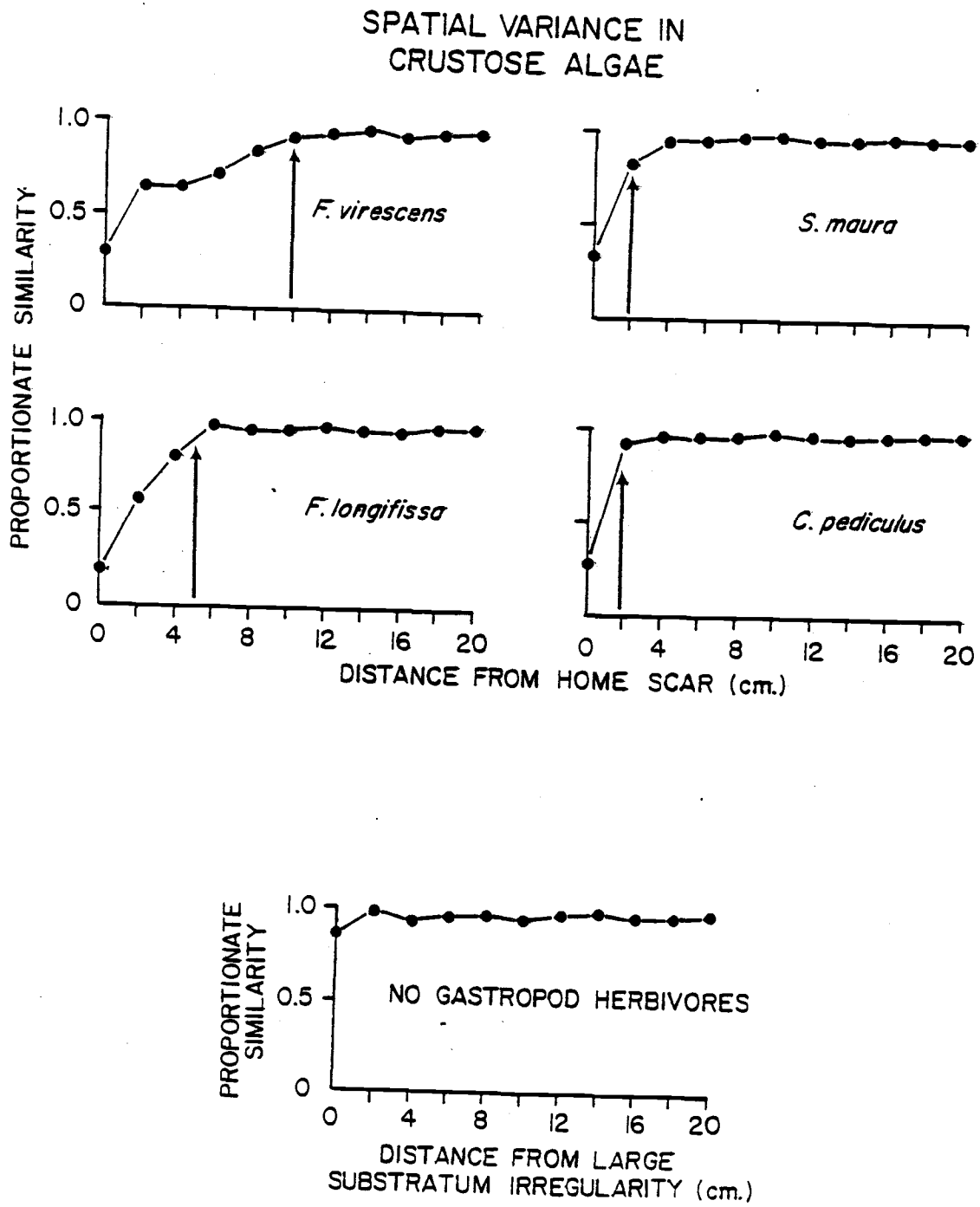
- (1) The limpets as a group have different effects on algal patterns from the larger herbivores. This is supported by the consistently low similarity in algal species composition and relative abundance between areas near limpets and other areas unaffected by limpets. The primary difference among the herbivore groups is in their ability to damage

Table VIII. Percent cover of algae on smooth low zone surfaces with no limpets. Values are \bar{x} (S.E.) from 30 quadrats taken in dry season 1981.

<u>Species</u>	<u>% Cover</u>
<u>Ralfsia</u> sp.	53.0 (3.7)
<u>Hildenbrandia</u> <u>prototypus</u>	1.4 (0.6)
<u>Schizothrix</u> <u>calcicola</u>	
Calcified	14.1 (1.5)
Uncalcified	31.5 (2.8)
Total Crustose Algal Cover	100.0
Total Erect Algal Cover	0.0

Figure 12. Changes in crustose algal patterns with distance from individual limpets. Proportionate similarity is a measure of the crustose algal cover shared between two quadrats. For all comparisons the standard reference was a mean from 20 quadrats isolated by at least 1 m from the nearest limpet. Arrows indicate the mean foraging distance for individuals of each species. Foraging distances were determined by measuring the furthest excursion of individuals from their home scar during receding and incoming tides, their only active periods. Data were taken year round from 1979 through 1981.

Figure 12.



crustose algae. The high similarity between algal patterns in crevices without limpets (isolated from larger herbivores) and smooth surfaces exposed to fish and crabs (Figure 12) obviates their minimal effects on crustose plants. The prostrate shape of these algae probably reduces their accessibility to larger herbivores much as a flat shell for a limpet is an effective defense against crushing predators.

(2) The four limpet species differ quantitatively in the range of their impact on algal patterns. The effects of the two smaller limpets are much more localized than those seen for keyhole limpets. This correlates well with their smaller mean foraging range (arrows in Figure 12). On a per capita basis, the effects of Siphonaria and Collisella are trivial relative to the larger limpets. Such small individual effects could be compensated by high densities; however, these species are only abundant on large expanses of fairly smooth rock (Chapter II). Although such habitats exist, they are fairly rare. More typically, the intertidal zone is a mosaic of crevices, holes and small expanses of smooth rock. Therefore, the segregation of herbivore effects can generally be considered as a comparison of the effects of limpets (crevices) versus larger, mobile herbivores (exposed surfaces).

The distribution of erect algae is the reverse of the pattern seen for algal crusts (Figure 13). Upright plants, although never extremely abundant, are almost completely restricted to protected microhabitats (Menge and Lubchenco 1981). Thus, there are between-habitat differences in algal distributions that coincide with the segregation of herbivore effects. Crustose algae are abundant on exposed surfaces, where they

Figure 13. Distribution of total erect algal cover relative to substratum irregularities.

DISTRIBUTION OF ERECT ALGAE

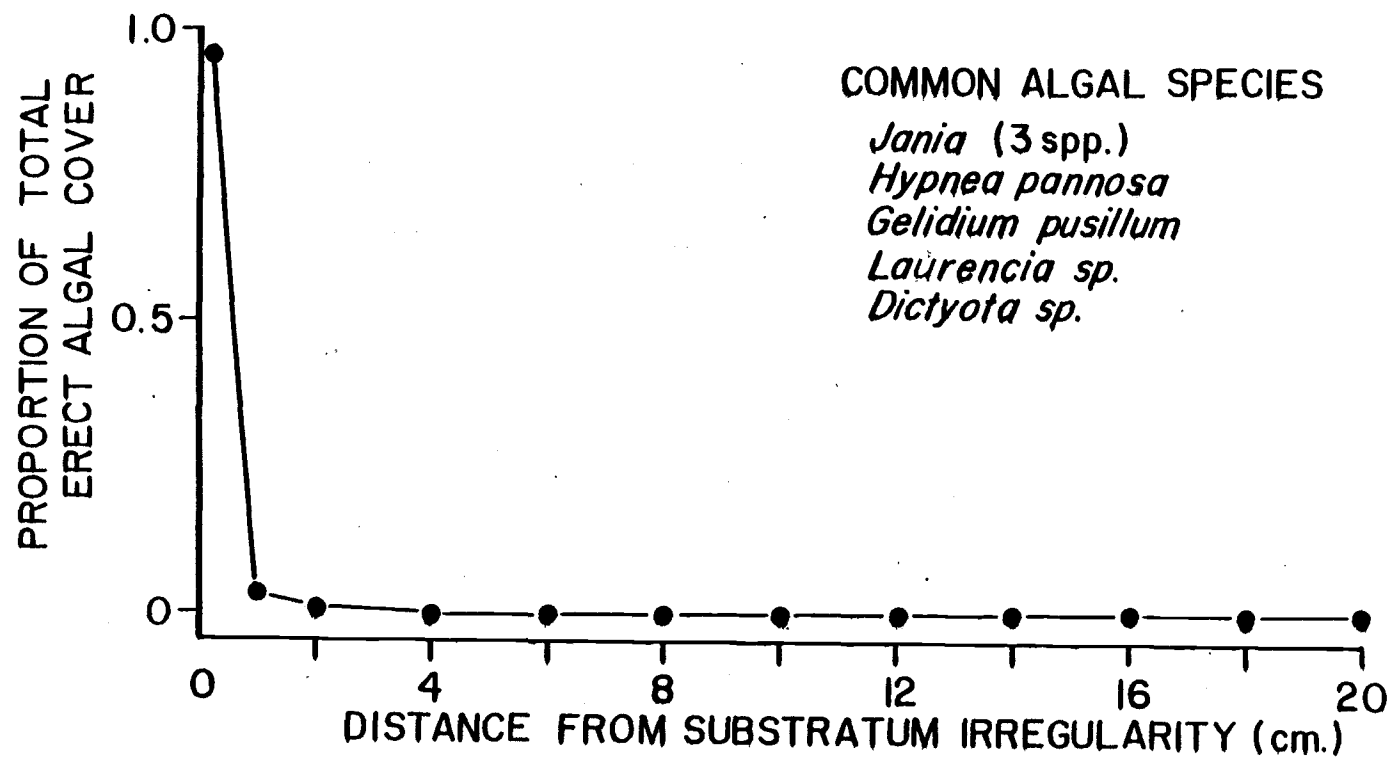


Figure 13.

persist with the larger herbivores. Erect algae are restricted to crevices where they often occur with limpets.

Removal of the two herbivore groups shows that qualitative differences in their effects are important in the generation and maintenance of the algal distribution patterns. Within two years following the removal of the keyhole limpets the differences in crustose algal patterns between crevices and exposed surfaces largely disappears (Figure 14). Similarly, Menge and Lubchenco (1981) have shown that exclusion of herbivorous fish and crabs leads to large increases in the abundance of erect algae. In addition, they noted significant changes in the microhabitat distribution of upright algae as they became established on exposed surfaces. Hence, just as the segregation of crushing and drilling predators enhances between-habitat limpet diversity (Chapter II), the segregation of limpets and larger herbivores enhances between-habitat algal diversity.

Finally, the restriction of keyhole limpets to crevices does not completely isolate their effects spatially from those of the larger herbivores. Areas between 2 and 4 cm from a crevice are not protected from the larger herbivores and they are within the foraging range of resident limpets in the crevice (Figure 15). Therefore, they experience overlap in the foraging of both herbivore groups (analogous to smooth areas near heterogeneities for predation on limpets; Chapter II). The effect of this overlap is to depress algal diversity within this zone of overlap. A plot of algal species richness versus distance from crevices with limpets shows a large depression in the zone of feeding overlap (Figure 15). The drop occurs since neither crustose nor erect plants

Figure 14. Effect of removal of F. virescens on crustose algal patterns. Curves are from comparisons of means of 8 replicates. Removals were initiated in February 1979. Unmanipulated quadrats showed no changes in patterns of similarity throughout the two-year experimental period.

F. virescens REMOVAL

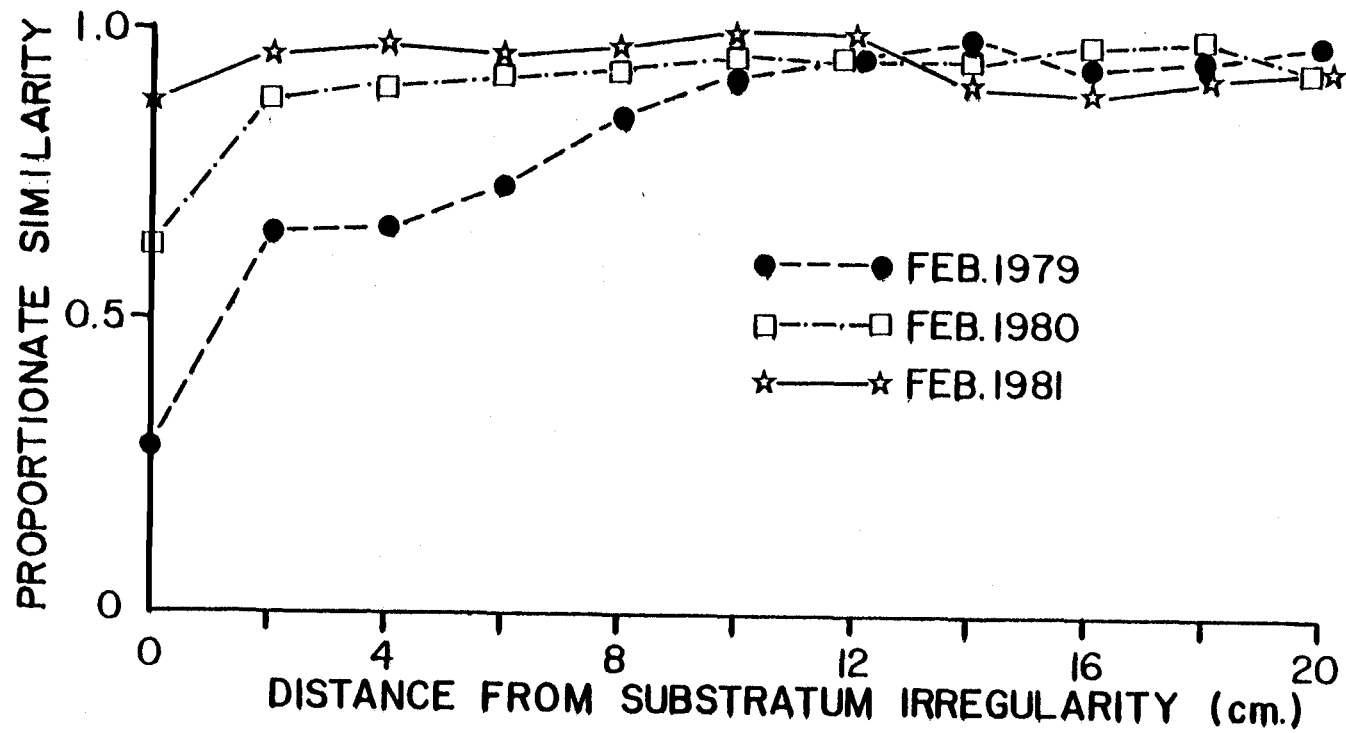


Figure 14.

Figure 15. Algal species richness as a function of distance from substratum irregularities. Solid circles are control quadrats. Open boxes are from the F. virescens removal treatment two years after initial removal.

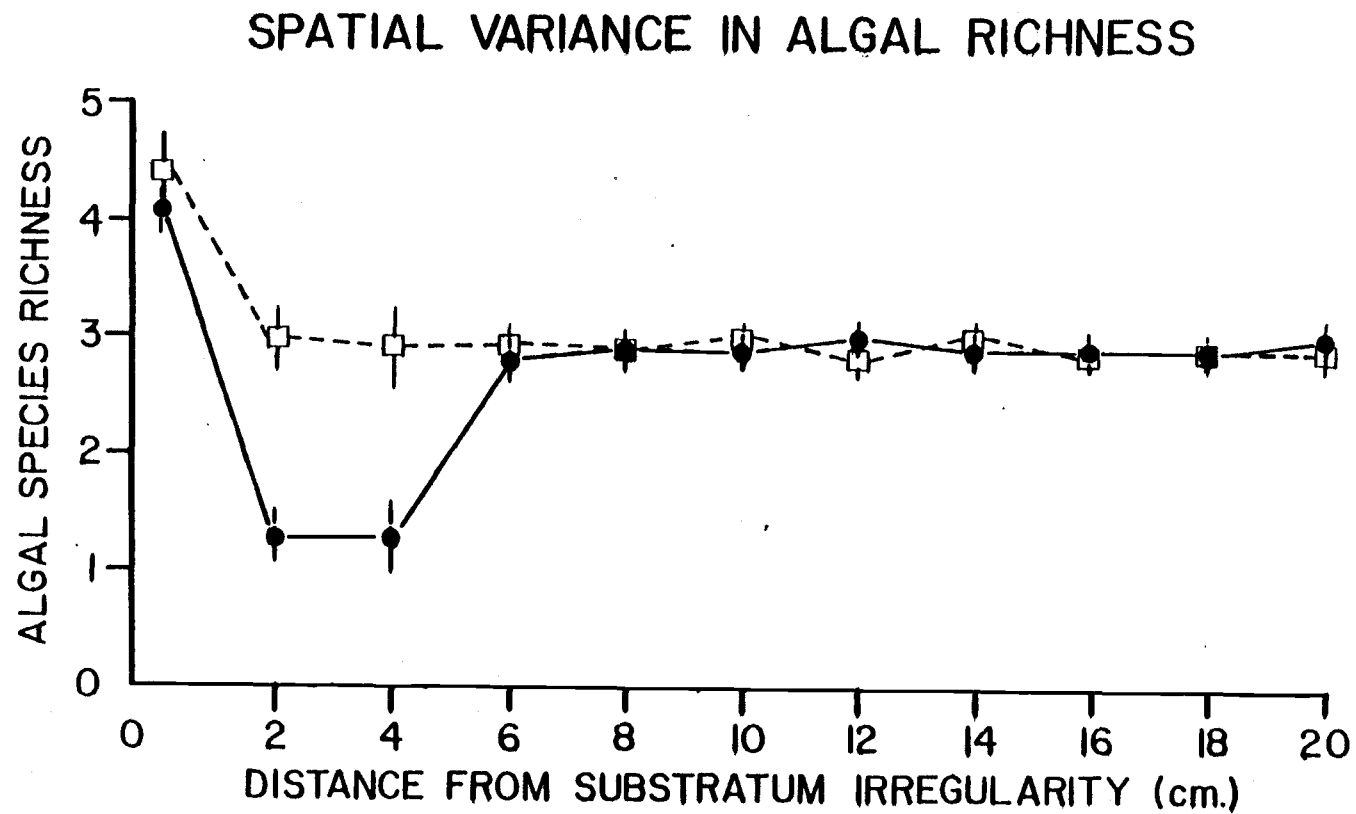


Figure 15.

fare well against both herbivore groups. When the limpets are removed, the depressed diversity disappears within two years (Figure 15). Therefore, overlap of the qualitatively different herbivores depresses algal diversity by decreasing prey escapes.

The effects of predation on prey distributions noted in Chapter II can thus have major impacts on lower trophic levels. When spatial segregation of predator species restricts different limpet types to different habitats (Chapter II), between-habitat algal diversity is indirectly increased. In addition, when overlap in predator foraging decreases within-habitat limpet diversity, a spatial refuge is created for many algal species. Therefore predation, by altering the between and within-habitat patterns of herbivore diversity, can ultimately affect the between and within-habitat diversity of plants.

Chapter V.

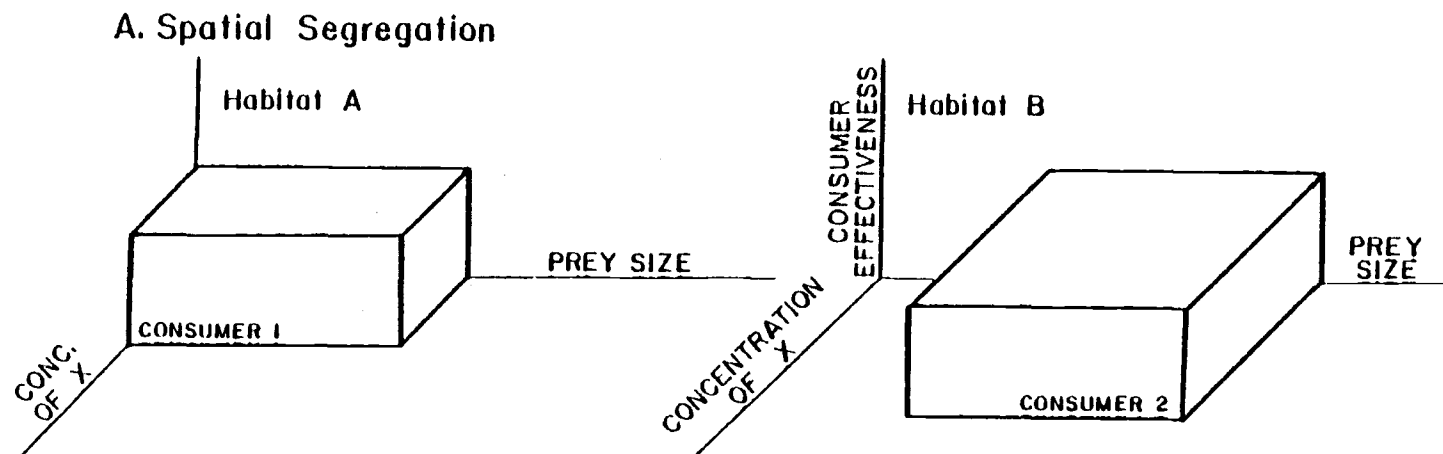
GENERAL DISCUSSION

Complementarity and Compensation:

Unique Properties of Consumer Diversity

The empirical studies of predation and herbivory in Chapters II through IV document the importance of qualitative aspects of consumption in diverse communities. To summarize, the interaction between quantitative and qualitative changes in consumption is probably best depicted graphically (Figure 16). The strengths and weaknesses of individual consumers can be displayed as a plot of some measure of consumer effectiveness versus a series of orthogonal dimensions describing the prey phenotype. For illustration in Figure 16, I use prey size and the concentration of some compound X (e.g., a toxin). I assume solely for clarity of presentation that consumer effectiveness is a step function along all prey characteristic axes. All points in prey character space where consumer effectiveness is zero are potential defenses. Therefore, consumer 1 can feed solely on small prey individuals and its feeding is inhibited by high concentrations of compound X; whereas consumer 2 eats only large individuals and is not influenced by the presence of X. Ideally, consumer effectiveness should be a measure of the expected decrement in prey fitness for a prey individual possessing a given suite of characteristics exposed to a given consumer. The set of prey characteristics where consumer

Figure 16. Graphical depiction of the divergent effects of qualitative differences between two consumers with (A) spatial segregation, and (B) spatial overlap in their foraging. Labels of axes are the same for all three figures. Shaded area in (B) = realm of potential compensation between consumers, unshaded areas demarcate complementary effects of consumption by the two species.



B. Spatial Overlap

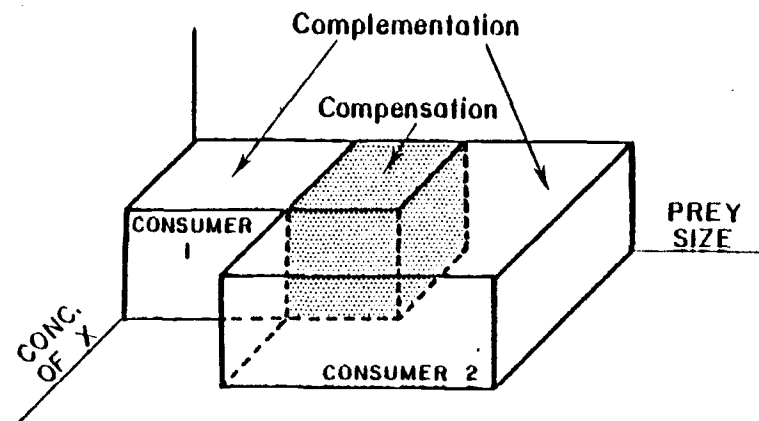


Figure 16.

effectiveness is non-zero is strictly a function of qualitative characteristics of the consumer. However, the height of the curve on the consumer effectiveness axis will be a function of both qualitative and quantitative aspects of the consumer (i.e., the effectiveness of consumer individuals against a given prey phenotype and the number of consumer individuals prey are likely to encounter). There is thus an important interaction between the quantity and quality of consumption. Qualitative differences between consumers will be unimportant unless the magnitude of consumption is at least moderately high, just as variation in the direction of selective pressures is trivial when the magnitude of selective pressures is very low.

The divergent effects of qualitative differences with segregation versus overlap of consumers is easily seen in Figure 16. With spatial segregation of the consumers (Figure 16A), qualitative differences mean that the position of potential prey defenses in character space will shift. To use Wright's (1932) adaptive landscape analogy, qualitative differences between the consumers increase the probability that adaptive peaks will occupy different positions in the two habitats. The larger the differences between the consumers, the more dissimilar the adaptive landscapes will likely be. By contrast, with spatial overlap of the consumers (Figure 16B), qualitative differences lead to complementary effects where the weaknesses of one consumer are partly counteracted by the strengths of the other. Here, qualitative differences should either (1) lead to the diminution or elimination of adaptive peaks which correspond to defenses to only one of the consumers (Mechanisms 1 and 2; Chapter II), or 2) reduce the rate and likelihood of attainment of

adaptive peaks corresponding to simultaneous defenses (Mechanism 3; Chapter II). This does not mean that consumer diversity will always completely eliminate prey escapes (as was true for predation on limpets in Panama; Chapter II). Instead, the range of potential defenses will be decreased. For example in Figure 16B prey individuals that are small but have high concentrations of compound X will be simultaneously defended against both consumers; however, these conditions are much more restrictive than the requirements for persistence with either of the consumer species singly. In general, the greater the complementarity of the consumer species, the greater will be the decrease in prey escapes.

These arguments and empirical studies suggest that the structure of consumer guilds or assemblages can markedly shape the impact of consumption on community structure. While considerable attention has been given to developing a predictive theory for consumer guild structure (see general treatments in Krebs 1978, Ricklefs 1979, Roughgarden 1979), little effort has been devoted to how changes in guild structure alter the impact of consumption on prey dynamics, distribution, and diversity. Clearly these are not completely independent topics. Yet, with the exception of the effects of diversity on community stability (MacArthur 1955, Watt 1964, Hairston et al. 1968, May 1973, Pimm 1980), they have developed largely in isolation. I have argued here that the domain of models based solely on feeding intensity is probably restricted to simple systems or subwebs with few consumer species. As a result, any synthetic approach to more complex systems must simultaneously incorporate the effects of (1) the magnitude of

consumption, (2) the diversity of consumers, and (3) the spatial (and temporal) pattern of their foraging.

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