Plant Species Diversity in a Marine Intertidal Community: Importance of Herbivore Food Preference and Algal Competitive Abilities

Jane Lubchenco

PLANT SPECIES DIVERSITY IN A MARINE INTERTIDAL
COMMUNITY: IMPORTANCE OF HERBIVORE
FOOD PREFERENCE AND ALGAL COMPETITIVE ABILITIES

JANE LUBCHENCO*

Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138

Since Hutchinson (1959) drew attention to the question "Why are there so many kinds of animals?" investigation of the causes of species diversity has proven to be a fertile area of ecological endeavor. A major current emphasis is on mechanisms creating and/or maintaining diversity (Connell 1971, 1975; Dayton 1971, 1975; Dayton et al. 1974; Jackson and Buss 1975; Janzen 1970; MacArthur 1972; B. Menge and Sutherland 1976; Paine 1966, 1971, 1974; Pianka 1967, 1969; Ricklefs 1973). One such mechanism, the predation hypothesis, suggests that predators, by keeping the abundance of their prey in check, prevent competitive exclusion and thus permit or maintain a higher species richness than would occur in their absence (Paine 1966, 1971).

Experimental removals or additions of aquatic carnivores have resulted in changes (decreases or increases, respectively) in the local species diversity of lower trophic levels over ecological time (Paine 1966, 1971, 1974; Hall et al. 1970; B. Menge 1976). In contrast, the effect of herbivores on local species diversity patterns is confusing, in part because few experimental studies have been done. In some instances, herbivores appear to increase plant diversity (Harper 1969; Paine and Vadas 1969), decrease plant diversity (Harper 1969), or both (Harper 1969; Paine and Vadas 1969; Vadas 1968). The key to understanding such variable results may reside in understanding consumer prey preferences and competitive abilities of the food species. A number of authors have suggested that only when a consumer (predator or herbivore) preferentially feeds on the competitively dominant prey can the consumer increase diversity (Hall et al. 1970; Harper 1969; MacArthur 1972; Paine 1971; Patrick 1970; Van Valen 1974). In this paper I present results of an experimental evaluation of the effect of generalized herbivores on plant diversity in a rocky intertidal community. In this system, knowledge of (1) food preferences of the herbivores, (2) competitive relationships between the plants, and (3) how these relationships change according to physical regimes in microhabitats permits an analysis of the importance of the relationship between herbivore food preference and competitive ability of the plants.

TABLE 1

FOOD PREFERENCES OF *Littorina littorea**

Preference Ranking	Chlorophyceae (Greens)	Phaeophyceae (Browns)	Rhodophyceae (Reds)
High	Cladophora	Ectocarpus-Pylaiella	Ceramium
	Enteromorpha	Elachistea	Porphyra
	Monostroma	Petalonia	...
	Spongomorpha	Scytosiphon	...
	Ulva	...	...
	Ulothrix-Urospora	...	...
Medium	Rhizoclonium	Dictyosiphon	Asparagopsis
	...	...	Cystoclonium
	...	...	Dumontia
	...	...	Halosaccion
	...	...	Phycodrys
	...	...	Polysiphonia lanosa
	...	...	P. flexicaulis
Low	Chaetomorpha	Agarum	Ahnfeltia
	Codium	Ascophyllum	Chondrus
	...	Chorda	Euthora
	...	Chordaria	Gigartina
	...	Desmarestia	Polyides
	...	Fucus	Rhodymenia
	...	Laminaria	...
	...	Ralfsia	...
	...	Saccorhiza	...

* Preferences were determined by laboratory two-way choice experiments. Only large indivi-duals of any algal species were used. A group of 20–40 snails was placed in the middle of the bottom of a filled 20-gal aquarium (standing new seawater) and surrounded by equal amounts of two species of algae, with the same species on opposing sides. The probability of any snail's contacting species 1 was equal to that of its contacting species 2. These periwinkles did not appear to detect food at a distance, but relied on tactile-chemical methods once plants were contacted. Once a snail contacted a piece of alga it would either move away or remain there and feed. The numbers of snails on the two species of algae were compared using χ^2 after 30–90 min. All large algae had had micro- and macroscopic epiphytic algae removed from them. Results were usually clear-cut and are arranged here in three preference categories. Most experiments were repeated at least once, rotating positions of algae and using a new group of snails. Further details and discussion of these experiments will be presented in a later paper.

HERBIVORE FOOD PREFERENCES

Along the rocky shores of New England, the most abundant and important herbivore in the mid and low intertidal zones is the periwinkle snail *Littorina littorea* (J. Menge 1975). Often attaining a length of 2–3 cm, this snail forages primarily when under water or during cool, humid low tides. It is a generalist with respect to both size and species of food, consuming most local species of microscopic and macroscopic algae (J. Menge 1975). Laboratory choice experi-ments indicate that *L. littorea* has strong food preferences (table 1). In general, the preferred algae are primarily ephemeral small and tender species (like the green *Enteromorpha* spp.), which appear to lack either structural or chemical means of deterring herbivorous snails. Algae in the lowest preference category are either never eaten by *L. littorea* or are eaten only if no other food has been
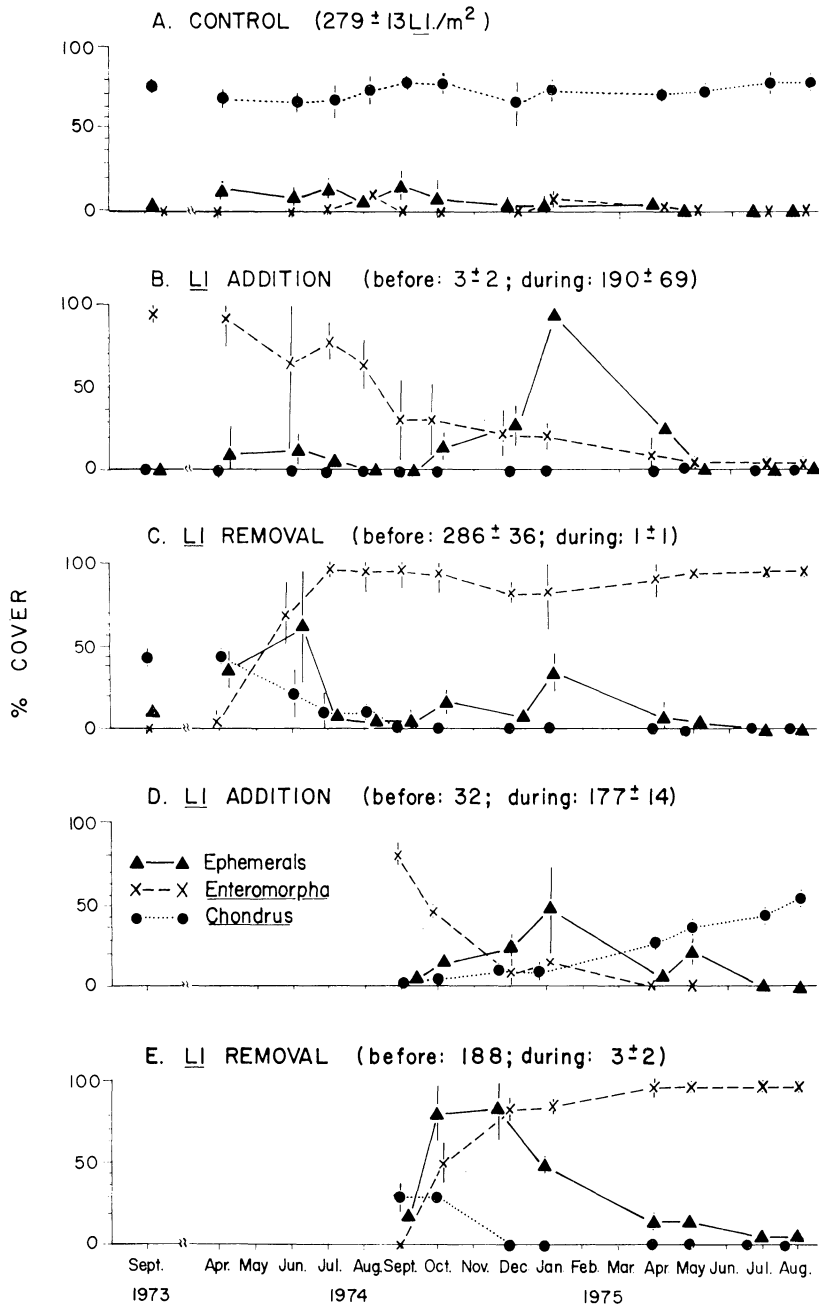
available for a considerable length of time. These plants (like the perennial red *Chondrus crispus* [Irish moss]) are all tough compared to those in the high category. More detailed information on these preferences and how they correlate to potential antiherbivore mechanisms of the algae will be published later. The snails and many of the algae occur both in tide pools and on emergent substrata, i.e., rock exposed to air at low tide. Since different mechanisms and relationships exist in these two different habitats, the effects of the herbivores on the algae will be considered separately for each habitat.

EFFECT OF *Littorina littorea* ON COMPOSITION OF TIDE POOL ALGAE

Normally there is considerable variation in the algal composition of tide pools in the upper half of the rocky intertidal region ($+5.9$–$+12.0$ ft or $+1.8$–$+3.7$ m). Comparable variation exists for European pools where a classification scheme of tide pools based solely on the dominant type of algae present has been suggested (Gustavsson 1972). Algal composition of high tide pools (hereafter called pools) in New England ranges from the extremes of almost pure stands of the opportunistic green alga *Enteromorpha intestinalis* or of the perennial red alga *Chondrus crispus* with a variety of intermediate situations (i.e., pools inhabited by many different types and species of algae). *Littorina littorea* appears to colonize these pools primarily by settlement from the plankton as newly metamorphosed snails (≤ 0.2 cm long). Experimental manipulations and subsequent monitoring of snail density (described below) indicate that immigration and emigration of adult *L. littorea* (≥ 1.2–1.5 cm long) are rare despite the pools being inundated approximately every 6 h. There is wide variation in *L. littorea* density between but not within pools. In any single pool, the snail density remains relatively constant over time. To examine the role of *L. littorea* in controlling the macroscopic algal composition of these pools, periwinkle densities were experimentally altered. In September 1973, three pools of similar height, salinity, size, depth, and exposure to light at the Marine Science Institute, Nahant, Massachusetts, were selected which subjectively appeared to represent the two extremes of the continuum in types of algae present. One pool was dominated by an almost pure stand of *Enteromorpha* (97% cover, see initial point in fig. 1*B*) and had a low density of *L. littorea* (four per m^2). The other two pools were dominated by *Chondrus* (85% and 40% cover; see initial points in fig. 1*A* and 1*C*, respectively) and had high densities of *L. littorea* (233 and 267/m^2).

Because *Enteromorpha* is one of *L. littorea*'s preferred food species (table 1) and *Chondrus* is not eaten by the snails, I hypothesized that the observed correlation between littorine abundance and algal composition was causal. It appeared that intense snail grazing may be eliminating ephemeral algae such as *Enteromorpha* and allowing inedible *Chondrus* to persist. To test whether *L. littorea* was responsible for the algal differences between pools, I removed all *L. littorea* from one *Chondrus* pool, added them to the *Enteromorpha* pool, and left the second *Chondrus* pool undisturbed as a control. These experiments were

EFFECT   OF   LITTORINA   LITTOREA   ON

ALGAL   COMPOSITION   OF   TIDE   POOLS

A. CONTROL   (279 ± 13 L.I./m^2)

B. LI ADDITION   (before: 3 ± 2 ; during: 190 ± 69)

C. LI REMOVAL   (before: 286 ± 36; during: 1 ± 1)

D. LI ADDITION   (before: 32; during: 177 ± 14)

▲——▲ Ephemerals
✗——✗ Enteromorpha
●······● Chondrus

E. LI REMOVAL   (before: 188; during: 3 ± 2)

% COVER

Sept.   Apr. May Jun. Jul. Aug.Sept. Oct. Nov. Dec Jan Feb. Mar. Apr May Jun. Jul. Aug.

1973   1974   1975

initiated in April 1974 after the samples shown for that date had been taken (fig. 1*A*–*C*). The percentage of cover of algae and density of herbivores were monitored throughout the following $1\frac{1}{2}$ yr. The few species of encrusting algae (*Ralfsia, Hildenbrandia,* and encrusting corallines) are not included here because of sampling and/or field identification problems. Their distribution in the various pools appears uniform. Percentage of cover of upright algae was estimated by observing what species was under each of 100 dots on a 0.25-m^2, $\frac{1}{2}$-inch Plexiglas quadrat placed over the area. The coordinates of the dots were obtained using a table of random numbers. As many quadrats as could be fit onto the bottom of each pool were sampled. Three quadrats fit in pools A, D, and E and four quadrats in pools B and C.

In the control pool, *Chondrus* abundance remained high throughout this monitoring period (fig. 1*A*); *Enteromorpha* and other ephemeral algae were present but never abundant. In *Chondrus* pools, the periwinkles feed on microscopic plants and sporelings and germlings of many ephemeral algae that settle on *Chondrus*. In the *L. littorea* addition pool (formerly *Enteromorpha* dominated, fig. 1*B*), *Enteromorpha* gradually declined in abundance to < 5% cover by April 1975. Snails could be seen actively ingesting *Enteromorpha* throughout this time period. Comparison of this experimental pool to the control (compare fig. 1*B* with 1*A*) supports the hypothesis that *L. littorea* is the cause of this decline in *Enteromorpha*. Note that ephemeral algal species (e.g., *Ectocarpus confervoides, Petalonia fascia,* and *Scytosiphon lomentaria*) became seasonally abundant even in the presence of *L. littorea*. Periwinkles are less active during the winter (J. Menge 1975), and as a result, ephemeral algae can temporarily swamp them (e.g., in January 1975). From January to April, periwinkles became increasingly active and eliminated nearly all edible algae from the pool. (Inedible algae include *Chondrus* and crusts.) No *Chondrus* has yet appeared in this pool. However, my observations in the low intertidal suggest that *Chondrus* recruits slowly (J. Menge 1975). I therefore predict that this alga will eventually settle and become abundant in the *L. littorea* addition pool. In the *L. littorea* removal pool (formerly with 40% cover of *Chondrus,* fig. 1*C*), *Enteromorpha* and several seasonal, ephemeral species immediately settled or grew from microscopic sporelings or germlings and became abundant. These include *Cladophora* sp., *Rhizoclonium tortuosum, Spongomorpha lanosa, Ulva lactuca* (all green algae), *Chordaria flagelliformis, Petalonia, Scytosiphon* (browns), *Ceramium* spp., *Dumontia incrassata* (reds), and filamentous diatoms. In spite of the presence of these species, *Enteromorpha* quickly became

FIG. 1.—Effect of *Littorina littorea* on algal composition of high tide pools at Nahant, Massachusetts. Means ±95% confidence intervals of angularly transformed (Sokal and Rohlf 1969) percentage of cover data are indicated. All pools are 1–2 m^2 in surface area and 10–15 cm deep. Three to four permanent quadrats (0.25 m^2) were sampled per pool. The mean density of *L. littorea* (1974) is indicated after each caption. "Before" percentage of cover and density data were taken in September and April for *A, B,* and *C* and in September for *D* and *E*. Removals or additions were begun immediately after April (*A, B, C*) or September (*D, E*) sampling. See legend in *D. Chondrus* is deemed "present" only when upright thalli occur.

the most abundant alga in this pool. Although individuals of *Enteromorpha* are ephemeral, the species appears able continually to monopolize space by reproducing and recruiting throughout the year. Hence, individuals of *Entero-morpha* initially colonizing this pool are probably not still present a year later, but have been replaced by other individuals. I have often observed *Entero-morpha* in tide pools releasing swarmers (spores or gametes) during low tide which may increase the probability that offspring will recruit near their parents (e.g., Dayton 1973).

Careful examination of the *L. littorea* removal pool revealed that the disappearance of upright thalli of *Chondrus* was not simply the result of its being hidden by the canopy of *Enteromorpha*. *Enteromorpha* settled on *Chondrus* and on primary substratum and appears to have outcompeted the long-lived *Chondrus*. Following settlement of *Enteromorpha* on *Chondrus*, the thalli (upright portions) of the latter became bleached and then disappeared. However the encrusting holdfasts of *Chondrus* remain.

A second set of *L. littorea* addition and removal experiments were initiated in September 1974 to determine the effect of seasonal differences on these results, since many ephemeral algal species in tide pools are different in spring-summer and fall-winter (J. Menge 1975). These experiments demonstrated that upon removal of *L. littorea* (fig. 1E), ephemerals (primarily the brown algae *Ecto-carpus*, *Scytosiphon*, and *Petalonia*) are initially more abundant. However, *Enteromorpha* eventually prevails, as in the removal experiments initiated in April. Notes (but no data) taken on other pools lacking *L. littorea* indicated that *Enteromorpha* had continually covered about 80%–100% of the pool sub-stratum for at least 3 yr.

In the second set of experiments, addition of *L. littorea* resulted in an immediate increase in ephemeral algal abundance (fig. 1D). These algae were apparently able to settle because the *Enteromorpha* abundance had been reduced by grazers. However, both the ephemerals and *Enteromorpha* were eventually eaten. Contrary to the first addition experiment, encrusting hold-fasts of *Chondrus* were present in this pool. Upright *Chondrus* thalli began to appear after grazers removed the ephemerals and *Enteromorpha*. Thus *Chondrus* increased in abundance in pool D via vegetative growth whereas it had not yet appeared in pool B, probably because of slow recruitment. Excepting these variations in *Chondrus* abundance, the outcome of both sets of experiments was the same. Removal of *L. littorea* resulted in a near pure stand of *Enteromorpha* (fig. 1C and E), while addition of this snail resulted in elimination of *Enteromorpha* and, in one case, eventual dominance by *Chondrus* (fig. 1D).

These experiments suggest that in tide pools *Enteromorpha* is the dominant competitor for space. However, because it and most of the ephemeral seasonal algae are preferred species of *L. littorea* (table 1), their abundance decreases when this grazer is common and active. *Chondrus* persists in tide pools where *L. littorea* is dense because it is not eaten. In such pools, the periwinkles feed on microscopic plants, sporelings, and germlings of many ephemeral algae that

RELATIONSHIPS BETWEEN ALGAL COVER, CRABS, AND NEWLY SETTLED L. LITTOREA IN TIDE POOLS
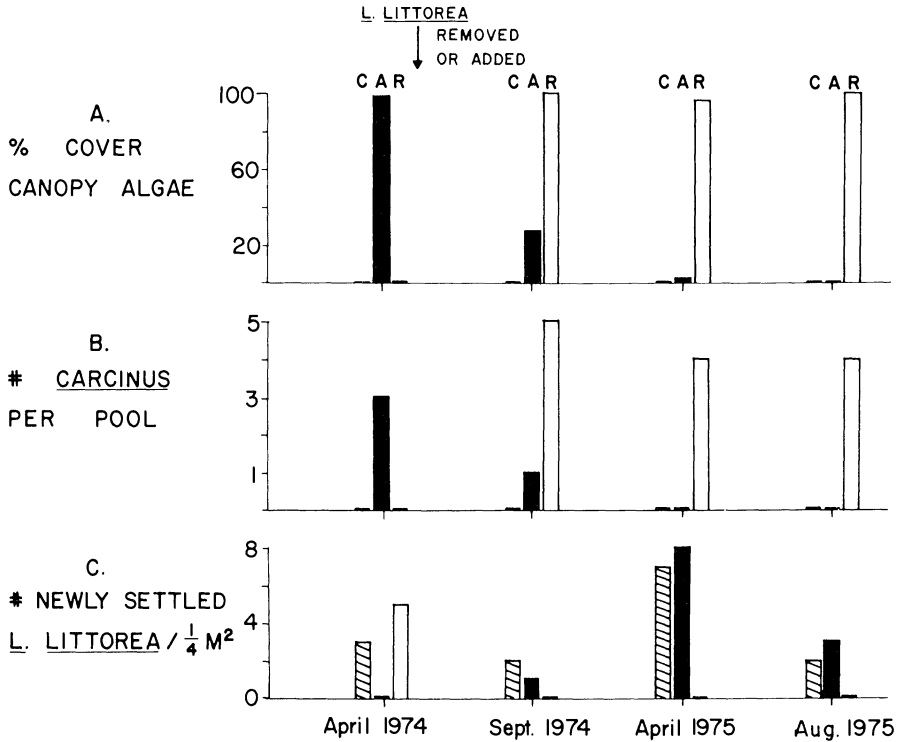

FIG. 2.—Changes in canopy algae, abundance of green crabs, and abundance of newly settled *Littorina littorea* following periwinkle manipulations in tide pools. *L. littorea* settles primarily during the spring and early summer. *C* (control, cross-hatched bars), *A* (*L. littorea* addition, solid bars), and *R* (*L. littorea* removal, blank bars) pools are the same as in figure 1*A*, *B*, and *C*, respectively. The other two experimental pools show similar changes. Canopy algae ($\geq$ 10 cm tall) is primarily *Enteromorpha* but may also include up to 5% total of *Scytosiphon* and/or *Rhizoclonium*. Percentage of canopy algae (X) and no. *Carcinus*/pool (Y) are positively correlated (linear regression: $Y = -0.02 + 0.04X$, $r^2 = .96$). No. *Carcinus*/pool (X) and no. newly settled *L. littorea* are negatively correlated ($Y = 5.69 - 1.59X$, $r^2 = .73$ for spring data).

settle on *Chondrus*. Thus *L. littorea* exerts a controlling influence on the algal composition of these pools.

In both of the *L. littorea* removal experiments (pools C and E), the green crab *Carcinus maenas* became abundant after a canopy of *Enteromorpha* was established (fig. 2*A* and *B*). Thereafter, very few tiny, newly metamorphosed *L. littorea* (0.2–0.3 cm long) were counted in the pools, in contrast to an abundance of them in the *L. littorea* addition and control pools (fig. 2*C*). Examination of numerous nonexperimental pools confirms that *Enteromorpha*-

dominated pools harbor many *Carcinus*, while *Chondrus*-dominated pools lack this crab. A dense canopy probably provides protection for this crab from sea gull (*Larus argentatus* and *L. marinus*) predators. Laboratory experiments demonstrate *Carcinus* readily preys upon small (but not medium or large) *L. littorea*. Thus, once *L. littorea* is absent from a pool long enough for *Enteromorpha* to become abundant, *Carcinus* may invade and prevent young *L. littorea* from recruiting from the plankton into the pools. Such a mechanism would explain the continued existence of low periwinkle density pools filled with highly desirable food. Hence, gulls probably indirectly affect the type of algae in pools. The pools may represent two alternative stable nodes (Lewontin 1969): (1) pools dominated by *Chondrus* because a dense contingent of herbivores continually removes superior competitors, and (2) pools dominated by the competitively superior *Enteromorpha* because predators prevent herbivores from being established. In this situation such alternative stable points may exist because the pools are essentially islands for which immigration and emigration are limited.

EFFECT OF *L. littorea* ON DIVERSITY OF ALGAE

When Competitive Dominant Is Preferred

The relationship between *Littorina littorea* density and the diversity of algae in tide pools can be seen in figure 3*A* and *B*. These data are from September 1974 after *L. littorea* grazing and competition between algal species have eliminated heavy spring and early summer recruitment of many short-lived algal species (Lubchenco and Menge 1978). Because the food preferences of *L. littorea* are known (table 1), and because this herbivore has been demonstrated to have a controlling effect on algae in tide pools (fig. 1), the source of between-pool variations in algal compositions and diversity can be interpreted as follows: When *L. littorea* is absent or rare, *Enteromorpha* outcompetes other algal species in pools, reducing the diversity. When *L. littorea* is present in intermediate densities, the abundance of *Enteromorpha* and various ephemeral algal species is reduced, competitive exclusion is prevented, and many algal species (ephemerals and perennials) coexist. At very high densities of *L. littorea*, all edible macroscopic algal species are consumed and prevented from appearing, leaving an almost pure stand of the inedible *Chondrus*. (New microscopic algae probably continue to settle and provide food for *L. littorea*.) Both the number of species (*S*) and *H'*, an index of diversity based on both species number and the relative abundances, reveal the same unimodal relationship of macroscopic algal diversity to *L. littorea* density. A similar relationship was found for sea urchins grazing algae (Vadas 1968; Paine and Vadas 1969) and is suggested by qualitative results in certain terrestrial systems (Jones, cited in Harper 1969). These results support the theoretical predictions of Emlen (1973).

When Competitive Subordinate Is Preferred

Other workers have suggested that the effect of consumers on prey species diversity depends on the relationship between food preferences of the poten-
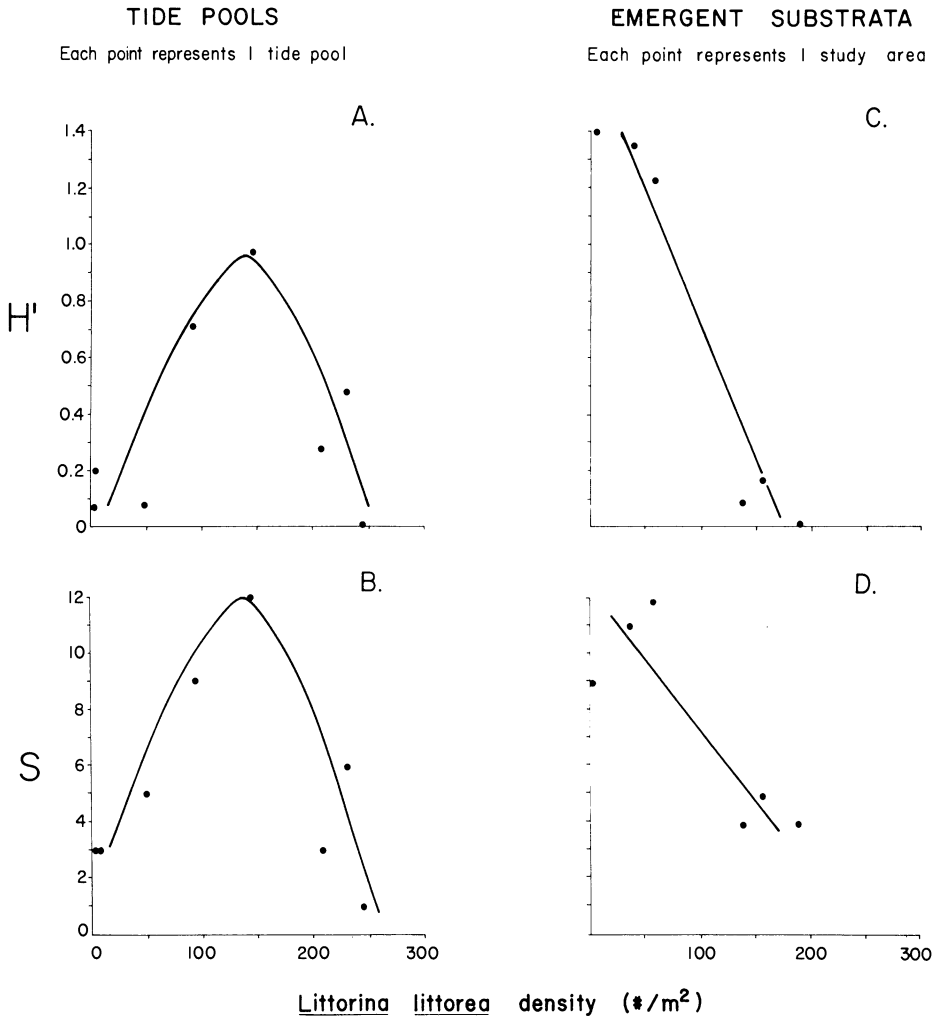
EFFECT OF <u>LITTORINA LITTOREA</u> ON THE DIVERSITY OF ALGAE

TIDE POOLS

Each point represents 1 tide pool

EMERGENT SUBSTRATA

Each point represents 1 study area

A.   C.

B.   D.

Littorina littorea density (#/m²)

FIG. 3.—Effect of *Littorina littorea* density on the diversity of algae in high tide pools (*A, B*) and on emergent substrata in the low intertidal zone (*C, D*). S = no. species, H' is an index of diversity, here based on the percentage of cover of each species. Each point in *A* and *B* is from four (0.25 m²) quadrats. Each point represents a different pool at Nahant, Massachusetts, September 1974. Each emergent substratum point was from 10 (0.25 m²) quadrats in the low zone at six different areas in Massachusetts and Maine, June and July 1974 (see J. Menge [1975] for descriptions of areas). Regression equations: (*A*) tide pool $H' = -0.0409 + 0.01250X - 0.00005X^2$, $r^2 = .65$; (*B*) tide pool $S = 1.64 + 0.1357X - 0.00056X^2$, $r^2 = .73$; (*C*) low emergent substratum $H' = 1.58 - 0.0089X$, $r^2 = .94$; (*D*) low $S = 11.58 - 0.0415X$, $r^2 = .72$. For mid-zone regressions (not illustrated), density of *L. obtusata* was converted to units of *L. littorea* density where 1 g wet weight *L. obtusata* is presumed to be equal to 1 g wet weight *L. littorea*. X, then, = "units of *L. littorea*," i.e., actual density of that snail plus presumably equivalent units of *L. obtusata*. Mid $H' = 1.65 - 0.004X$, $r^2 = .91$; mid $S = 8.03 - 0.017X$, $r^2 = .81$.

tially controlling consumer and competitive hierarchies of the food species (Paine 1969; Harper 1969; Patrick 1970; MacArthur 1972). The importance of this relationship can be seen when the effect of *L. littorea* on diversity of algae in tide pools is compared to its effect on diversity of algae on emergent substrata. In the New England rocky intertidal zone the competitive dominance of the most abundant tide pool plants is actually reversed when they interact on emergent substrata. Perennial brown algae (*Fucus vesiculosus, F. distichus,* and *Ascophyllum nodosum*) are competitively superior to other algae in the mid zone, while the perennial red alga *Chondrus* is competitively dominant in the low zone (J. Menge 1975; Lubchenco and Menge 1978). *Littorina littorea's* preferences remain the same in and out of tide pools. Consequently there is an inverse correlation between periwinkle abundance and algal species diversity on emergent substrata (fig. 3C and D). Specifically where *L. littorea* is scarce or absent (e.g., at areas exposed to wave action, or in experimental removals at protected sites) at least 14 ephemeral species coexist with *Fucus, Ascophyllum,* and *Chondrus.* (These include *Enteromorpha, Spongomorpha spinescens, S. arcta, Rhizoclonium tortuosum, Ulva lactuca* [greens]; *Chordaria flagelliformis, Dictyosiphon foenicularis, Ectocarpus* spp., *Elachistea fucicola, Petalonia fascia, Pylaiella littoralis, Scytosiphon lomentaria* [browns]; and *Ceramium* spp. and *Dumontia incrassata* [reds].) Although the ephemeral species are all eventually outcompeted by the perennials on primary space, the former can coexist with the latter by occupying patches of primary space cleared by disturbances or by settling and growing epiphytically upon the perennials. If no such refuge were possible, there would be no relationship between *L. littorea* density and algal diversity, and the herbivores would simply increase the rate at which the eventual dominance by competitively superior plants was attained. On emergent substrata in New England, when *L. littorea* is abundant, it preferentially eats the ephemerals, leaving the more unpalatable fucoids and *Chondrus,* thus decreasing diversity. *Littorina obtusata* has the same effect as its congener in the mid zone (J. Menge 1975). Similar results have been suggested by Patrick (1970) for freshwater snails grazing diatoms (based on unpublished laboratory data of K. Roop) and by Harper (1969) for Milton's data on sheep grazing pastures.

<div align="center">DISCUSSION</div>

Space has been shown to be a primary limiting resource in many rocky intertidal communities (Connell 1961, 1971, 1972; Dayton 1971, 1975; Lubchenco and Menge 1978; B. Menge 1976; J. Menge 1975; Paine 1966, 1974). This resource is modified by physical conditions that may determine the outcome of competitive interactions. Thus in tide pools in New England, ephemeral algae like *Enteromorpha* are competitively superior while on emergent substrata the more hardy perennials dominate primary space. Spatial and temporal heterogeneity in physical conditions are undoubtedly important in maintaining the coexistence of these competing species.

The result that in some habitats an opportunistic species can continually outcompete perennials is worth emphasizing. Evidently in the absence of

herbivores, ephemerals such as *Enteromorpha* can outcompete the perennial fucoids and Irish moss in tide pools but probably not on emergent substrata. In the latter habitat, ephemerals like *Enteromorpha* can temporarily "outcompete" perennials on newly opened primary substrata by growing faster (J. Menge 1975). However, these ephemerals are eventually replaced by perennial species (e.g., *Fucus* in the mid zone), which can recruit slowly and take over when the ephemerals die. The key difference between the ephemerals' performance in the two habitats appears to be that they can continually recruit and replace themselves in tide pools but not on emergent substrata. The brown alga *Postelsia* is another short-lived species which appears to outcompete later successional species, barnacles and mussels, by virtue of its ability to recruit offspring near parent plants (Dayton 1973). Thus in microhabitats where ephemerals outcompete perennials, the successional sequence does not progress except where herbivores remove the ephemerals.

Concomitant with the reversal of competitive dominance in different micro-habitats is the alteration of effects of herbivores. The plants that seem best suited to cope with the physical rigors of the intertidal zone, the perennials, are also least attractive to periwinkle herbivores. Thus these herbivores have a negative or small effect on algal species diversity on emergent substrata. In tide pools, however, because the preferred algae are also competitively dominant, herbivores determine the algal composition and species diversity in this microhabitat. This shift in competitive dominance in different microhabitats and consequent alteration of effects of consumers may be widespread, but it needs additional documentation.

The effects of *Littorina littorea* on plant species diversity in New England are complex. The key to understanding these effects lies in knowledge of the food preferences of the herbivore. These results may typify the effects of many generalized consumers: When the competitively dominant species is preferred by the consumer, there is a unimodal relationship between prey diversity and consumer density, with the highest diversities at intermediate consumer densi-ties. When the competitively inferior species are preferred, there is an inverse correlation between prey diversity and consumer density (e.g., fig. 3). Under the former conditions, effects of consumers counteract competitive dominance. In the latter situation, feeding reinforces effects of competitive dominance.

As indicated earlier, the general effects of herbivores on plant species diversity have not been clear. After reviewing a number of case studies of effects of terrestrial herbivores on plant species diversity, Harper (1969) concluded that the results were too variable and inconsistent to warrant any generaliza-tions. In view of the results presented here, it is possible to reinterpret the studies cited by Harper. I believe knowledge of three critical factors is necessary to obtain the proper insight into these studies. These factors are (1) the relationship between herbivore preferences and competitive ability of the plants, (2) the length of time the experiment was monitored after the manipulation, and (3) the initial relative abundance of the herbivores. The importance of the second and third factors can be seen in the following example. In figure 3, if the initial density of *L. littorea* were 250/m², its removal

would result in an initial increase in species richness followed by a decrease as competitive interactions occurred. In contrast, if the initial density were only 100/m², snail removal would result in a decrease in algal diversity. Thus the initial relative intensity of grazing or predation and the amount of time the experiment is monitored will determine what effect removal of the consumer has.

The importance of all three of the above factors is indicated by numerous studies. First, experimental manipulations of predators or herbivores that selected competitively superior food species conform to either the left half of the or the whole unimodal curves in figure 3A and B, depending on the range in abundance of consumers (Hall et al. 1970; Harper 1969; Paine 1966, 1971, 1974; Paine and Vadas 1969; Vadas 1968). Second, studies in which consumers preferred competitively inferior species comply with results in figure 3C and D (Harper 1969; Patrick 1970). Third, examples of overgrazing (i.e., the right half of fig. 3A and B curves) caused by a high density of consumers abound (Bartholomew 1970; Dayton 1971, 1975; Earle 1972; Harper 1969; Kitching and Ebling 1961, 1967; Leighton et al. 1966; Lodge 1948; Ogden et al. 1973; Paine and Vadas 1969; Randall 1965; Southward 1964; Vadas 1968). Taken together, these results suggest that generalized herbivores can have the same effect on species diversity as do generalized predators. This effect appears to depend primarily on the relationship between the consumer's food preferences and the competitive interactions of the food species.

The effects of periwinkles on algae presented here are the result of local manipulations of herbivores over ecological time. To what degree consumers affect broadscale biogeographic patterns of species diversity of lower trophic levels over evolutionary time remains to be seen. However, I believe the effects may be comparable. In the following example, regional differences in plant species diversity perhaps caused by the effects of an herbivore may be intermediate between local and broadscale patterns.

There is a striking difference in the low intertidal algal species diversity of New England rocky coasts and that of the rocky shores in the Bay of Fundy, which may be a function of the abundance of the herbivorous sea urchin *Strongylocentrotus droebachiensis*. Unlike *L. littorea*, this urchin readily eats *Chondrus*, and several lines of evidence suggest it has an effect on low-zone algal diversity comparable to the periwinkle's effect in tide pools.

In the low zone of New England, this urchin is rare and *Chondrus* outcompetes most other algae and dominates the zone (cols. 1, 2 in table 2; Lubchenco and Menge 1978). Changes in algal species diversity at different New England areas are caused by varying densities of periwinkles affecting algal epiphytes on *Chondrus* (fig. 3). Sea urchins are common in the low zone at rocky areas in the Bay of Fundy. Field experiments done with this urchin indicate it readily eats *Chondrus* and can prevent this plant from monopolizing space in the low zone (fig. 4; Lubchenco and Menge 1978). Thus sea urchins may prevent *Chondrus* from dominating the low zone in the Bay of Fundy and allow many other algae to coexist there (col. 3, table 2). This example would parallel the results of Dayton (1975) and Vadas (1968) for the Pacific northwest

TABLE 2

Effect of Sea Urchins on Algal Species Diversity in the Low
Intertidal Zone in New England and the Bay of Fundy

	NEW ENGLAND		BAY OF FUNDY	
	Chamberlain, Maine (1)	Canoe Beach, Cove, Nahant, Mass. (2)	Cape Forchu, Yarmouth, Nova Scotia (3)	Quoddy Head, Maine (4)
Herbivore densities:*				
Strongylocentrotus	0	0	4.2 ± 2.6	26.4 ± 13.8
Acmaea	0	.1 ± .2	.5 ± .8	21.2 ± 7.1
L. littorea	0	126.8 ± 60.0	0	0
Algal diversity and percentage of cover:				
No. species†	8	3	27	6
H'_e	1.20	.23	2.03	1.14
$\bar{X}\%$ cover canopy	0	0	78.6 ± 19.7	.4 ± .7
$\bar{X}\%$ cover understory ..	80.6 ± 17.0	89.9 ± 10.2	125.6 ± 20.7‡	2.6 ± 2.1
$\bar{X}\%$ cover Chondrus ... (= in understory) ...	74.5 ± 18.2	83.3 ± 11.4	14.6 ± 10.2	0

Note.—Data are from June–July 1975–1976.

* Densities are $\bar{X}$ ± 95% confidence intervals/0.25m² for 10 quadrats at each area; see Lubchenco and Menge (1978) or J. Menge (1975) for methods.

† Includes both canopy and understory species. In the low zone, L. littorea grazes and affects only epiphytic algae on Chondrus; sea urchins graze and affect Chondrus and most other understory and canopy species.

‡ Percentage of cover > 100% reflects the dense multilayer arrangement of the understory at Cape Forchu.

coast of North America. In New England, urchins occur only in the subtidal region; in the Bay of Fundy they are both subtidal and intertidal. It is not clear why urchins are more abundant in the low intertidal zone in the Bay of Fundy. Possible factors are (1) a lower level of gull predation, (2) less desiccation stress, and (3) less wave action in Fundy. When urchins are exceedingly abundant, e.g., at Quoddy Head, Maine (on the Bay of Fundy), algal species diversity and abundance are very low (col. 4, table 2). In such areas, only encrusting coralline algae, a few unpalatable species (Desmarestia and Agarum; Vadas 1968), and some recently settled ephemeral species are present. Thus there is evidently a unimodal relationship between low intertidal algal species diversity and sea urchin density similar to that in figure 3A and B (see also Vadas 1968). That this correlation is causal can be demonstrated only through experimental manipulations.

Throughout this paper I have emphasized the importance of preferential predation on the competitively dominant prey. However, it may be possible for nonselective predation to have comparable effects on prey species diversity. This could be accomplished with differential recruitment and/or growth rates of the prey such that with nonselective predation the competitively dominant prey are prevented from outcompeting other prey. For example, Chondrus may

EFFECT OF STRONGYLOCENTROTUS
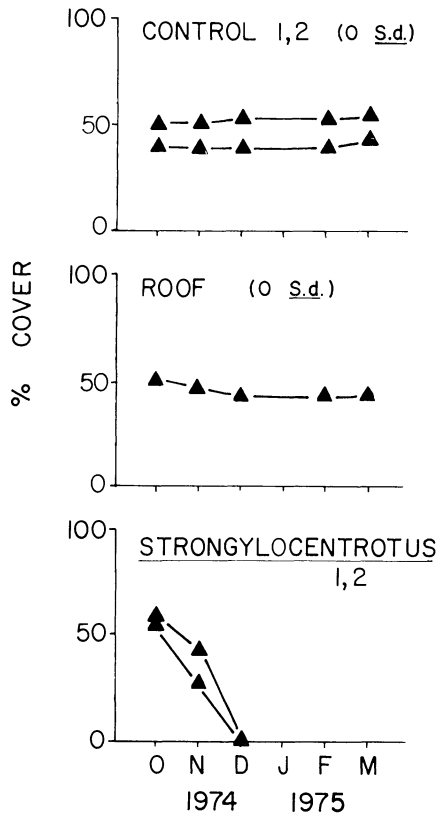## ON CHONDRUS

FIG. 4.—Effect of sea urchins on *Chondrus* in the low zone at Grindstone Neck, Maine, where urchins are normally absent. Two 10 × 10 × 4-cm stainless steel mesh cages containing one (3.5 cm test diameter) and two (both 3.2 cm) urchins were placed over *Chondrus*. Two unmanipulated controls and one stainless steel mesh roof indicate the normal percentage of cover of *Chondrus* without urchins. In the urchin enclosures, urchins completely removed *Chondrus*, including the encrusting holdfast.

be prevented from dominating the low zone by urchins in the following manner. If urchins graze most plants present in proportion to their abundance (except for certain unpalatable algae), and many of these plants have higher recruitment and/or growth rates than does *Chondrus*, *Chondrus* could not take over. In other words, the critical factor is the effect the consumer has on the competitive dominant (here, prevention of competitive exclusion), not the means (selective or nonselective grazing) by which it is accomplished.

From the above discussion, it is obvious that not all herbivores have similar effects on plant species diversity. If the sea urchins are removing *Chondrus* and preventing it from outcompeting other low zone algae in the Bay of Fundy, they have a very different effect on the emergent substratum community than

do the periwinkle snails that do not graze *Chondrus*, but only its epiphytes. The size, manner of feeding, degree of food specialization, and mobility of herbivores may be important determinants of their effects on vegetation. For example, spatial escapes of seeds and young trees from their specialized and less mobile herbivores may provide an important mechanism of maintaining tropical rain forest tree diversity (Connell 1971, 1975; Janzen 1970). Nonetheless, it appears that a critical determinant of the effect many generalized consumers have on their food resources is the relationship between consumer food preferences and food competitive ability.

SUMMARY

Field experiments demonstrate that the herbivorous marine snail *Littorina littorea* controls the abundance and type of algae in high intertidal tide pools in New England. Here the highest species diversity of algae occurs at intermediate *Littorina* densities. This unimodal relationship between algal species diversity and herbivore density occurs because the snail's preferred food is competitively dominant in tide pool habitats. Moderate grazing allows inferior algal species to persist and intense grazing eliminates most individuals and species. In contrast to pools, on emergent substrata where the preferred food is competitively inferior, this herbivore decreases algal diversity. Thus, the effect of this consumer on plant species diversity depends on the relationship between herbivore food preference and competitive abilities of the plants. These results may apply to most generalized consumers and provide a framework within which previously confusing results can be understood.

Thus predators or herbivores do not simply increase or decrease species diversity of their food, but can potentially do both. The precise effect a consumer has probably depends both on the relationship between its preferences and the food's competitive abilities and on the intensity of the grazing or predation pressure.

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