Revista Chilena de Historia Natural
60: 153-158, 1987

Marine herbivory studies. The South American contribution

Estudios de herbivoría marina. La contribución sudamericana

BERNABE SANTELICES

Departamento de Biología Ambiental y de Poblaciones, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT

No more than 20 contributions dealing with marine plant-herbivore relationships have been produced in temperate South America. All the studies have been done on Chilean coasts and most have been published in the last seven years. Therefore, the interest for the subject in the area is quite recent and fragmentary, comprising just a few habitats and species. A review of these contributions indicates that some of these studies, while repeating findings already described elsewhere, have either increased the general biological background required to understand several types of ecological relations or have called attention to species with unique ecological roles in these systems. Other studies question the validity of generalizations concerning defense and escape mechanisms while still others have characterized a different type of marine plant-herbivore relationship dealing with the algal capacity to survive digestion.

Key words: Marine grazing, plant-herbivore relationships, escape/defenses in macroalgae, digestion survival.

RESUMEN

El número de contribuciones orientadas a entender las relaciones planta-herbívoros en ambientes marinos templados de Sud América alcanza a menos de 20 trabajos. Todos estos estudios han sido realizados en las costas de Chile y la gran mayoría ha sido publicado sólo en los últimos años. Así, el interés por el tema en esta área geográfica es reciente y el conocimiento acumulado es fragmentario, incluyendo sólo unos pocos habitats y unas pocas especies. Una revisión de estas contribuciones indica que, aunque algunos estudios han repetido hallazgos ya realizados en otras latitudes, ellos han incrementado el conocimiento biológico requerido para entender varios tipos de relaciones ecológicas o han llamado la atención a especies con funciones ecológicas bastante únicas en estos sistemas. Otros estudios han contribuido a cuestionar la validez general de algunos conceptos relacionados con mecanismos de defensa y escape en las algas mientras que algunas contribuciones recientes han permitido caracterizar un tipo diferente de relación planta-herbívoro, la que se refiere a la capacidad de macro-algas para resistir digestión por invertebrados.

Palabras claves: Herbivoría marina, relaciones planta-herbívoros, mecanismos de escape y defensa en macroalgas, supervivencia a digestion.

INTRODUCTION

The following is a review of the current status of marine plant-herbivore studies developed in temperate South America. Included in this review are all the descriptive and experimental studies dealing with macroalgae. Planktonic algae and their grazers have not been included here, nor have studies of coral reefs.

Less than 20 contributions dealing with the subject have been produced in temperate South America. All the studies have been done in Chile and most have been published in the last seven years. Thus, interest in the subject is quite recent and as yet fragmentary, and the studies comprise just a few localities and species. In spite of this, the results have increased our understanding of the following five main topics: 1) Distribution and diet of herbivores, 2) escape and defense mechanisms of algae, 3) population effects of grazers, 4) community effects of grazers, and 5) digestion susceptibility of algae and the role of grazers in spore production and dispersal. The present contribution reviews the progress achieved along each one of these topics.

Distribution and diet of herbivores

Some insights into distribution and diets of herbivores in a few coastal habitats along Chile have been obtained from studies principally aimed at evaluating the importance of interspecific competition as a density regulation factor. For example, in

(Received 2 October 1986. Accepted 20 October 1987)

the *Macrocystis pyrifera* beds of the Beagle Channel area no predator was found controlling population densities of four species of sea urchins. Therefore, studies on diets and microhabitat uses of these four species were performed in order to test the hypothesis that regulation of sea-urchin density may result from competitive interactions (Vásquez *et al.* 1984). With the exception of *Pseudoechinus magellanicus* and *Austrocidaris canaliculata,* the remainder pairs of species did not overlap in microhabitat utilization. Diet overlap was high but the algal resource being used by all the sea urchins (fronds of *Macrocystis pyrifera*) did not appear to be limiting. The authors concluded that even though experimental manipulation was still needed to rule out definitively the importance of interspecific competition as maintaining the present pattern of distribution, the available data suggested that it was negligible. Field observations and measurements indicated that differences in intensity of water movement was the factor most likely determining population density of these sea urchins.

Water movement and frequency of water exchange also appeared as a significant factor affecting the distributional patterns of a chiton assemblage on rocky walls and boulder fields in central Chile (Otaíza & Santelices 1985). In both types of habitat the small-sized individuals were found in places least exposed to wave impact, whereas large individuals of large-sized species occurred at the most exposed levels.

Recently, Santelices *et al.* (1986) studied the seasonal diet variation of a guild of grazers, formed by the numerically most important middle intertidal herbivore molluscs on exposed rocky habitats of central Chile. This guild included two species of *Fissurella* (*crasa* and *limbata*), two of *Collisella* (*zebrina* and *ceciliana*), plus *Littorina peruviana, Siphonaria lessoni,* and *Chiton granosus.* All these grazers show extended, often overlapping patterns of distribution and all are supposed to be trophic generalists.

Food content analyses indicated marked interspecific differences in diets for any given pair of species and clear seasonal changes in the diet of any given grazer. Dietary changes indicated opportunistic shifts in feeding habits of these grazers, perhaps in response to changes in algal abundance. Any close diet similarity that may have occurred between any given pair of species by no means appeared permanent in time (Santelices *et al.* 1986).

Overall, the above studies on distribution and diet of herbivores have provided us with a basis to understand species coexistence. In so doing these species have provided general knowledge on diets and trophic relationships of grazers, a type of information which is a requisite to understand many different ecological relations in marine systems. From this perspective, much needs to be done in intertidal and subtidal communities of the southern hemisphere.

Escape and defense mechanisms of algae

The gut content analysis of the above guild of molluscs if complemented with other field and laboratory studies should give an idea of the effectiveness of escape and defense mechanisms of algae. The literature predicts that seaweeds should either escape in space or time, or show several types of defenses. These include caloric contents, secondary compounds, presence of calcareous matrices or defensive aspects of external morphology including size or crustose morphology. Because the herbivore group under study was constituted by molluses, differences in bucal apparatuses should be considered. Steneck & Watling (1982) predicted that the differences in radular structure should determine the type of algal morphology to be consumed. Therefore, in looking for patterns of escape and defense mechanisms of the algae, this prediction can also be tested.

A combination of field and laboratory data (Santelices, unpublished) indicates that time-space escape mechanisms do not seem to be common among most of the numerically important algal species on rocky intertidal habitats of central Chile. Further, frequency of algal consumption by herbivores as measured from gut content analysis, does not keep any relationship with presence or absence of calcareous matrices, increased or reduced caloric contents of the algae, or presence or absence of phenolic compounds. Although some species with secondary compounds rank low in frequency of consumption, others such as *Ralfsia,* which also has phenolic compounds, appears as one of the most consumed species. If algal morphologies are grouped into morphofunctional as-

semblages (*sensu* Littler & Littler 1980 and Steneck & Watling 1982), a close relationship is found with the type of grazer consuming them. Some grazers, with a given type of radula, can consume only some types of algae whereas other molluscs can attack other morphologies. Some morphologies, such as microalgae and crusts, are susceptible to almost all types of radula whereas others, such as saccate forms, are unaffected by these grazers. Through laboratory experiments offering different types of algae to several types of grazers after experimentally modifying the algal morphology, it has been possible to evaluate further the importance of external morphology versus calcareous inclusions, presence of secondary compounds, or reduced caloric contents. All these yet unpublished experiments have suggested that algal external morphology is a most significant character determining consumption by grazing molluscs.

In summary, the research results which are being gathered along this line of study are not supporting some of the earlier predictions regarding defensive and escape mecanisms of algae. Rather, they are consistent with morpho-functional approaches to the study of plant-herbivore relationships. Overall, they stress the importance of considering the type of grazer under study before making generalizations on the subject. Certainly, the limitations to attack a given type of plant or to resist a given type of toxin should be different among different types of grazers.

Population effects of grazers

Although not a single study has been specifically devoted to the study of population effects of grazing, some of the data provided by Santelices *et al.* (1980) on the effects of the selective grazing of *Scurria scurra* on *Lessonia nigrescens* could be analyzed under this perspective. The kelp *L. nigrescens* is the dominant canopy-former in low intertida/shallow subtidal belts of exposed rocky habitats along Chile. The stipes of *L. nigrescens* constitute the habitat of the limpet *Scurria scurra,* which feeds on and lives inside cavities bored in the proximal parts of the stipes. As the limpet increases in size and weight, so does the volume of the cavity. Larger and heavier stipes are therefore increasingly weakened and are eventually removed by water impact. This reduces the risk for *L. nigrescens* individuals infested with *Scurria scurra* to become so heavy as to be susceptible to detachment by water drag, and increases their longevity as compared to uninfested individuals.

Community effects of grazers

Most studies dealing with the community roles of grazers have attempted either to evaluate the impact of gastropods (Moreno & Sutherland 1982) or sea urchins on kelp recruitment (Castilla & Moreno 1982, Ojeda & Santelices 1984, Santelices & Ojeda 1984a, 1984b, Dayton 1985), or to measure the effects of molluscs on the temporal and spatial distribution pattern of middle intertidal algae (Santelices *et al.* 1981, Moreno & Jaramillo 1983, Jara & Moreno 1984, Moreno *et al.* 1984, Otaíza 1986). While these studies have reproduced general ecological phenomena already described elsewhere, often they have identified species which in Chile have important ecological roles and no parallel development in equivalent habitats elsewhere. In some cases, conspicuous differences in community effects have resulted from a single difference in the foraging behavior of a given ecologically important grazer. For example, previous experimental urchin removal in California resulted in a great increase in the number of juveniles of *Macrocystis pyrifera,* a community response that was also expected in the Chilean beds (Dayton 1974). However, when equivalent experiments were performed in *M. pyrifera* beds in the Beagle Channel area, no significant differences in kelp recruitment were found between experimental areas with and without sea urchins (Castilla & Moreno 1982). The sea urchin species (*Loxechinus albus*), which supposedly overexploited the kelp, was found to normally consume drifting fronds, senescent blades, and debris. Therefore the sea urchins were not attacking live kelp plants and consequently allowed the existence of large kelp beds, despite their high densities. Recently, Dayton (1985) stated that *Loxechinus* foraging behavior is influenced by the degree of wave surge and by hunger. He stated that some habitats in southern Chile

(46-54°S) semi exposed to oceanic waves were characterized by situations in which *Loxechinus* overexploits the kelps and maintains urchin-coralline algae barren grounds.

In other cases, growth attributes of algal species have also affected the resulting landscape. This is the case, for example, of *Codium dimorphum,* a non-calcareous, crustose Chlorophyte that occupies most of the mid and low intertidal space in wave exposed roky habitats of central Chile. Experimental field manipulation has shown (Santelices *et al.* 1981) that *C. dimorphum* is able to overgrow, exclude, and therefore limit, the lowermost extent of most other intertidal algal species. However, every year summer bleaching disrupts crust continuity creating new borders which are then susceptible to attack by grazers. Herbivore exclusion experiments have indeed shown that grazing plays a major role in the seasonal reduction of *Codium* after initial summer bleaching of the colony. These results illustrate well-known ecological phenomena gathered in equivalent studies in North America, namely the importance of grazers in the time-space distributional patterns of algae, and the relationships between abiotic and biotic disturbance and competitive dominance. But, in addition, Chilean studies have called attention to the special characteristics of *Codium* for becoming a dominant in these systems. Algal crusts are generally characterized as having slow growth rates, great longevity, and being persistent through times and conditions of high disturbance, including high grazing pressures. *Codium dimorphum,* by contrast, is grazer-susceptible, but has a notorious regeneration capacity and fast growth. As a crust, *C. dimorphum* is a unique example and only in the Chilean coasts this type of crust has been reported to reach high ecological importance as primary space user, especially in areas devoid of larger herbivores.

Some studies, while illustrating grazing effects on algal distribution, have simultaneously called attention to the effects of human predation on the system. For example, in Mehuin, near Valdivia (*ca* 40°S), experimental removal of *Fissurella picta* led to a rapid increase in the cover of the middle intertidal dominant *Iridaea laminarioides* (Moreno & Jaramillo 1983). From 1978 to 1982 some of these study sites were protected from human interference, resulting in a spectacular increase in the abundance of *Fissurella picta* coupled with a dramatic decline of *Iridaea laminarioides* (Moreno *et al.* 1984). Increased grazing pressure in the absence of human predation was considered the reason for the macroalgal decline. While these results parallel equivalent studies in other latitudes, they have the additional merit of bringing attention to the effects of human predation on the system. As Moreno *et al.* (1984) have suggested, perhaps anthropic influences have been more important than previously thought in shaping and maintaining the structure of these communities.

Overall the combination of results gathered in the above studies stresses the importance of community studies in ecological systems with a large number of ecologically important, endemic species. Such studies are likely to provide the basis for understanding how similar is the organization of geographically disjunct communities and how important are past history and evolutionary constraints in setting these organizational patterns.

Digestion susceptibility of algae and the role of grazers in spore production and dispersal

Up to 1983 most ideas about benthic algal adaptations to surviving herbivory had focused mainly on defense and escape mechanisms of settled plants. The possibility that algal sexual or asexual reproductive bodies may survive digestion by invertebrates and fish was not considered. However, in terrestrial plants the capacity to survive digestion has been regarded as a coevolutionary development of special importance for seed dispersal, and in planktonic communities the differential capacity of diatoms and unicellular algae to survive digestion is known to result in significant changes of community structure.

Studies developed in Chile with the black sea urchin *Tetrapygus niger* indicated that as many as 42% of the algal species consumed by the sea urchin were able to survive digestion, originating new thali in cultures started from faecal pellets. No significant relationship was found between the frequency of algae in the urchins' gut and their frequency of occurrence in the cultures. Therefore, algal survival did not

appear to be a function of frequency of consumption by the urchin. However, the relative importance of opportunistic algal forms changed from 63% in the gut contents to over 85% in the culture dishes, indicating that the capacity to survive digestion was greater among opportunistic algae than among late successional forms (Santelices *et al.* 1983).

The general validity of this phenomenon was tested with the guild of grazing molluscs referred to above. In addition to being among the most important grazers in the mid-shore, molluscs have a complex digestive system and a buccal apparatus not only different from that of sea urchins, but also one that differs among molluscs themselves. On average, 56% of the 27 algal species found in the gut contents of these grazers could survive digestion, being able to grow in cultures started from the grazer's faecal pellet. As in the case of sea urchins, opportunistic algal species had a much greater ability to pass alive along the digestive tract than late successional forms (Santelices & Correa 1985).

Recent studies with controlled feeding experiments (Santelices & Ugarte 1987) indicate that two types of response can be found when mollusc grazers are fed with foliose opportunists. Some algal fragments surviving digestion show tissue regeneration. More frequently however, the cytoplasm of the surviving cells condenses towards one side of the cell, the wall disintegrates, the tissue looses integrity and the protoplasts are set free in the culture medium. In the Chlorophyta studied the protoplasts developed flagella, behave like swarmers and settled on the bottom of the culture vessel originating new thalli. In *Porphyra* the protoplasts arising from the cells either formed a callus or developed into the alternate (*Conchocelis*) filamentous phase.

Grazers can significantly influence the type of response shown by algae. Indeed, the number of tissue fragments of two Chlorophyta species releasing swarmers was significantly higher than the controls (uningested) thalli when consumed by *Siphonaria* or *Fissurella*, thus implying that the digestion process of these grazers stimulates spore production in these algae. In addition, these results suggest that 100% mortality of many opportunistic algal species may be a rare event, rather than the norm.

Swarmer and protoplast release from partially digested algal remains does not occur among algal species with differentiated reproductive structures. Survival in this case is wholly dependent on the capacity of meristematic cells to pass alive through the digestive tract of grazers. When the growth is by the activity of apical cells, as in filamentous opportunists, the probabilities to survive digestion increase for densely branched morphologies.

In structurally more complex algal forms, digestion survival capacity is reduced and varies among reproductive and vegetative cells. Perhaps more interesting than digestion survival capacity is the possibility in this type of algae that grazers may play important roles in dispersing algal reproductive propagules. This seems to be the case of some amphipod grazers (*e.g., Hyale media*) with strong feeding preference for mature cystocarps of *Iridaea laminarioides*. When the amphipod grazes, it tears up the cystocarps thus helping the release of spores (Buschmann & Santelices 1987), even transporting some of them on their body and legs. This type of grazing activity may therefore contribute to spore dispersal in algal groups which otherwise have been traditionally characterized as having restricted dispersal capacities.

Overall the research conducted along this line in South America has stressed the non-detrimental effects of grazing, suggesting in some cases that it may increase algal fitness. Likewise, these results are calling attention to the possibility that some grazers may have important ecological roles beyond those classically described in most studies on plant-herbivory interactions. Some of these grazers may be important in dispersing, redistributing and, in some cases, even increasing the number of macroalgal propagules. Obviously, much more research is required in order to document fully these ideas.

Conclusions

In summary, the small number of plant-herbivore studies so far conducted in South America can be accommodated into three categories:

a) Some studies, while repeating findings already described from other latitudes, have either increased the general biological background required to understand several

types of ecological relations, or have called attention to species with unique ecological roles in these systems.

b) Other studies have contributed to question the validity of some general concepts on defense and escape mechanisms. They have stressed the need of considering the evolutionary constraints of the grazers under study as well as the life history of the algae, before generalizing about the outcome of these interactions.

c) Still other studies have characterized a different type of marine plant herbivore relationship, dealing with the algal capacity to survive digestion and the non-detrimental effects of grazers which may even increase the reproductive output and perhaps the fitness of some algal species.

ACKNOWLEDGMENTS

I appreciate comments and criticisms by Fabián Jaksić, Jane Lubchenco, and an anonymous reviewer on earlier drafts of this paper. Financial support from Dirección de Investigación, Pontificia Universidad Católica de Chile, Grant D.I.U.C. 82/85 is acknowledged with gratitude.

LITERATURE CITED

BUSCHMANN A & B SANTELICES (1987) Micrograzers and spore release in *Iridaea laminarioides* Bory (Rhodophyta: Gigartinales). Journal of Experimental Marine Biology and Ecology 108: 171-179.

CASTILLA JC & C MORENO (1982) Sea urchins and *Macrocystis pyrifera:* experimental test of their ecological relations in southern Chile. In Lawrence JM (ed) International Echinoderm Conference, Tampa Bay: 257-263. AA Balkema, Rotterdam.

DAYTON PK (1974) Kelp communities of southern South America. Antarctic Journal of the United States 9: 22-23.

DAYTON PK (1985) The structure and regulation of some South American kelp communities. Ecological Monographs 55: 447-468.

JARA F & C MORENO (1984) Herbivory and structure in a midlittoral rocky community: a case in southern Chile. Ecology 65: 28-38.

LITTLER MM & DS LITTLER (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. American Naturalist 116: 25-44.

MORENO C & E JARAMILLO (1983) The role of grazers in the zonation of intertidal macroalgae of the Chilean coast near Valdivia. Oikos 41: 73-76.

MORENO C & JP SUTHERLAND (1982) Physical and biological processes in a *Macrocystis pyrifera* community near Valdivia, Chile. Oecologia 55: 1-6.

MORENO C, JP SUTHERLAND & FH JARA (1984) Man as a predator in the intertidal zone of southern Chile. Oikos 42: 155-160.

OJEDA FP & B SANTELICES (1984) Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in central Chile. Marine Ecology, Progress Series 19: 83-91.

OTAIZA R (1986) Patrones de distribución vertical de chitones y efecto de pastoreo de *Chiton granosus* en roqueríos intermareales de Chile central. Monografías Biológicas (P. Universidad Católica de Chile) 4: 173-191.

OTAIZA R & B SANTELICES (1985) Vertical distribution of chitons (Mollusca: Polyplacophora) in the rocky intertidal zone of central Chile. Journal of Experimental Marine Biology and Ecology 86: 229-240.

SANTELICES B & J CORREA (1985) Differential survival of macroalgae to digestion by intertidal herbivore molluscs. Journal of Experimental Marine Biology and Ecology 88: 182-191.

SANTELICES B & FP OJEDA (1984a) Population dynamics of coastal forests of *Macrocystis pyrifera* in Puerto Toro, Isla Navarino, southern Chile. Marine Ecology, Progress Series 14: 175-183.

SANTELICES B & FP OJEDA (1984b) Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. Marine Ecology, Progress Series 19: 73-82.

SANTELICES B & R UGARTE (1987) Algal life-history strategies and resistance to digestion. Marine Ecology Progress, Series 35: 267-275.

SANTELICES B, J CORREA & M AVILA (1983) Benthic algal spores surviving digestion by sea urchins. Journal of Experimental Marine Biology and Ecology 70: 263-269.

SANTELICES B, S MONTALVA & P OLIGER (1981) Competitive algal community organization in exposed intertidal habitats of central Chile. Marine Ecology, Progress Series 6: 267-276.

SANTELICES B, J VASQUEZ & I MENESES (1986) Patrones de distribución y dietas de un gremio de moluscos herbívoros en habitats intermareales expuestos de Chile central. Monografías Biológicas (P. Universidad Católica de Chile) 4: 147-171.

SANTELICES B, JC CASTILLA, J CANCINO & P SCHMIEDE (1980) Comparative ecology of *Lessonia nigrescens* and *Durvillea antarctica* (Phaeophyta) in central Chile. Marine Biology 59: 119-132.

STENECK R & L WATLING (1982) Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Marine Biology 68: 299-319.

VASQUEZ J, JC CASTILLA & B SANTELICES (1984) Distributional patterns and diets of four species of sea urchins in giant kelp forests (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island, Chile. Marine Ecology, Progress Series 19: 55-63.