REVIEW

Herbivore-kelp interactions in Chilean subtidal communities: a review

Interacciones alga-herbívoro en comunidades
submareales chilenas: una revisión

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ABSTRACT

This paper reviews the literature evidence on the herbivore-kelp interactions along the Chilean coast, basically the role of sea urchins and gastropods in the structure of rocky shallow subtidal marine communities. Due to the morphology of the Chilean coast, we divided our analysis in two large zones. In northern Chile, between 18° - 42° S, the Cordillera de la Costa runs close to the coast generating extremely exposed habitats. In this zone two species of *Lessonia* are dominant in intertidal and subtidal habitats. Here, the sea urchin *Tetrapygus niger* is the most abundant grazer producing extensive intertidal and subtidal barren grounds. South of 42° S to Cape Horn, *Macrocystis pyrifera* forms the most conspicuous kelp association in a fjord zone, where hundreds of islands produce protected habitats. Four species of sea urchins and the gastropod *Tegula atra* graze on *M. pyrifera*. However, their effects are spatially and temporaly restricted. The foraging behavior of the principal herbivore, the sea urchin *Loxechinus albus*, is influenced by the degree of wave action, restricting its effect to exposed areas. In very protected areas *Tegula atra* affects the population dynamics of *M. pyrifera*.

Key words: Chile, benthic herbivores, kelp, subtidal habitats.

RESUMEN

Este trabajo revisa la literatura de las interacciones alga-herbívoro, especialmente el efecto de erizos y caracoles gastrópodos en la estructura de comunidades submareales someras en las costas de Chile. Por la morfología de la costa de Chile, nuestro análisis está dividido en dos grandes zonas. En el norte, entre los 18° y los 42° S, la Cordillera de la Costa Chile se distribuye muy cerca de la costa, generando hábitats extremadamente expuestos. En esta zona dos especies de *Lessonia* son dominantes en hábitats intermareales y submareales someros. Aquí, el erizo negro *Tetrapygus niger* es el pastoreador más abundante, generando extensos "fondos blanqueados". Al sur de los 42° S y hasta el Cabo de Hornos, cientos de islas forman fiordos protegidos del movimiento de agua donde *Macrocystis pyrifera* es el alga dominante. Cuatro especies de erizos y *Tegula* spp. son los pastoreadores más conspicuos asociados a estas comunidades. Sin embargo, el efecto de su pastoreo está delimitado espacial y temporalmente. La conducta de pastoreo del herbívoro más abundante, *Loxechinus albus*, está restringida a áreas expuestas al oleaje. En áreas muy protegidas, *Tegula atra* afecta significativamente la dinámica poblacional de *M. Pyrifera*.

Palabras clave: Chile, hábitats submareales, herbívoros bénticos, huirales.

INTRODUCTION

Shallow subtidal rocky-bottom areas in warm and cold temperate seas are dominated by large brown algal associations (Dayton 1985). The orders Laminariales and Fucales, form extensive kelp forests and dominate in cover and biomass to a depth of 25-30 m in the northern and southern hemispheres (Dawson et al. 1960, Druehl 1970, 1978, Kain 1962, 1977, 1979, North 1971, Barrales & Lobban 1975, Velimerov et al. 1977, Choat & Schiel 1982, Villouta & Santelices 1984, Santelices & Ojeda

1984a, 1984b, Schiel & Foster 1986, Harrold & Pearse 1987, Vásquez 1989, 1991, 1992, Camus & Ojeda 1992). These kelp forests provide the habitat for many invertebrates and fishes, and constitute one of the major factors in their distribution and abundance (Jones 1971, 1972, 1973, North 1971, Duggins 1980, 1981, Santelices & Ojeda 1984 a, b, Vásquez & Castilla 1984, Harrold & Pearse 1987, Vásquez 1993a, 1993b). Large brown algae also provide areas for spawning and larval settlement where exposure to water movement and predation is reduced (Ghelardi 1960, Moore 1971, 1972, 1973, Cancino & Santelices 1984, Vásquez & Santelices 1984, Ojeda & Santelices 1984, Snider 1985).

Kelps appear unique among the world's macrophyte communities because almost the entire plant can be heavily grazed by one type of herbivore: the sea urchin (Dayton 1985). Not all species of sea urchin have this potential but in most temperate areas at least one species does (Lawrence 1975). In the northern hemisphere sea urchins are among the major grazers structuring kelp communities in shallow waters (see reviews by Lawrence 1975, Schiel & Foster 1986, Harrold & Pearse 1987). On the contrary, the results of several studies in southern South America suggests sea urchin herbivory is not an important structuring factor of these communities. Barrales & Lobban (1975) documented the absence of large and abundant grazing echinoid population along the coast of Chubut in Argentina. Three species of echinoids occur in this area, but individuals are too small and not in sufficient number to graze intensively (Barrales & Lobban 1975). Likewise, Dayton (1985) found kelp forests where sea urchins do not graze actively. Vásquez et al. (1984) found a similar situation in the kelp forests of Isla Navarino, southern Chile, where algal species are apparently regulated by interspecific competition and substratum availability (Santelices & Ojeda 1984b). This was confirmed experimentally by Castilla & Moreno (1982), who artificially increased the densities of four species of echinoids in enclosures in the same kelp forest, and found no effect of the herbivores on the algal abundance.

The situation described above would be rather different north to 42°S where *Macrocystis pyrifera* (L.) C.Ag. is not the dominant kelp species. Instead areas are dominated by *Lessonia trabeculata* Villouta et Santelices. In subtidal shallow rocky areas of central and northern Chile, *Tetrapygus niger* (Molina) is the most abundant sea urchin (Viviani 1975, Vásquez personal observation). The high population density of this species impedes the settlement of macroalgae propagules and maintains extensive barren areas. As discussed by Vásquez (1989), the ecological impact of *T. niger* in areas dominated by subsurface kelp forests of *L. trabeculata* would not appear to be all-or-none (sensu Harrold & Pearse 1987) as reported for some northern hemisphere kelp communities. *T. niger* modifies algal morphology and produces two morphotypes that are affected differently by bottom surges. These morphological modifications have important consequences for the persistence of *L. trabeculata* populations (Vásquez 1992).

This paper reviews the literature on the ecological role of herbivores associated with kelp stands along the Chilean coast. We discuss and compare the evidence from northern and southern Chilean kelp communities on the following topics: herbivore diversity and distribution, predator-herbivore interactions, and relevant biological and physical factors in the structure of these South American kelp communities. We contrast these results with the evidence that has emerged from the northern hemisphere kelp communities.

DIVERSITY AND DISTRIBUTION OF THE SEA URCHIN AND OTHER HERBIVORES ALONG CHILEAN COAST

Seven genera with fifteen species of sea urchin inhabit the Chilean coast (Mortensen 1952, Larrain 1975). Five of these species are associated with kelp communities. *Tetrapygus niger* (Molina) and *Loxechinus albus* (Molina), two sympatric species, are associated with *Lessonia* spp and *Macrocystis integrifolia* Bory kelp forests in subtidal and intertidal areas between 18° and

42° S (Viviani 1979, Brattström & Johansen 1983, Contreras & Castilla 1987, Vásquez 1989). *L. albus* is the most conspicuous sea urchin in the fjord zone (south to 42° S), where *Macrocystis* is the dominant kelp species (Dayton 1985). Nearby, in the coastal kelp forest at Isla Navarino in the Beagle Channel, *Loxechinus albus*, *Arbacia dufresnei* (Blainville), *Pseudechinus magellanicus* (Philippi), and *Austrocidaris canaliculata* (Agassiz) coexist in areas dominated by *M. pyrifera* (Vásquez et al. 1984, Castilla 1985). However, in some southern Chilean areas, the gastropod *Tegula atra* (Lesson) seems to be the most important grazer in *M. pyrifera* beds (Moreno & Sutherland 1982, Buschmann 1992, Buschmann 1995).

KELP COMMUNITIES IN NORTHERN AND CENTRAL CHILE

In comparison to the data accummulated in the northern hemisphere, the southwestern Pacific and particularly the subtidal communities of central and northern Chile have received little attention. Some studies in the south part of Chile (Alveal et al. 1973, Dayton et al. 1973, Dayton 1974, Dayton et al. 1977, Dayton 1985, Moreno & Sutherland 1982, Ojeda & Santelices 1984a, Villouta & Santelices 1984, 1986, Vásquez et al. 1984, Vásquez & Castilla 1984, Moreno & Jara 1984, Contreras & Castilla 1987) generally provide accurate descriptions of the structure of subtidal communities dominated by *M. pyrifera*. Exceptional are the experimental manipulations of sea urchin densities in southern Chile (Castilla & Moreno 1982) and the exclusion of the canopy of dominant algae in Valdivia (Moreno & Sutherland 1982), and in the Beagle Channel (Santelices & Ojeda 1984 a).

In northern and central Chile (18°- 42°S) *Lessonia trabeculata* forms extensive subtidal kelp beds on rocky bottoms in areas exposed and semiexposed to heavy surge. As this is the type of subtidal habitat most commonly found along this portion of the Chilean coast, this is the most important kelp in this area.

In the latitudes mentioned above, *Tetrapygus niger* is the most abundant sea urchin associated with *L. trabeculata* kelp forests (Vásquez personal observation). Dense populations of this sea urchin species impede the settlement of macroalgal propagules and maintain extensive barren grounds (Vásquez 1993 b).

In these communities the abundance, distribution patterns and diets of the most conspicuous organisms associated with *L. trabeculata* were studied by Vásquez (1989, 1990, 1992, 1993b). The organisms included were selected because of their direct (benthic herbivores) or indirect (benthic predators and carnivorous fishes) relationships with the stability (sensu Dayton et al. 1984) of the *L. trabeculata* kelp forest in northern Chile (Vásquez 1993a, 1993b). The sea urchin *T. niger* and the gastropod snail *Tegula tridentata* Potiez et Michaud were the benthic herbivores considered. The herbivorous fish *Aplodactylus punctatus* Valenciennes has also been abundantly found in central and northen Chile (Cáceres et al. 1993, 1994). The sea star *Meyenaster gelatinosus* (Meyen) and three carnivorous fishes (*Cheilodactylus variegatus* Molina, *Mugiloides chilensis* Cuvier et Valenciennes, and *Semicossiphus maculatus* (Pères) were evaluated as the most abundant predators.

The benthic herbivores, *Tetrapygus niger* and *Tegula tridentata*, are most the abundant and frequently found in *L. trabeculata* kelp beds at Playa El Francés, northern Chile. *T. niger* is discontinuously distributed throughout the kelp bed forming patches on stable rocky bottom. The distributional patterns of this sea urchin are correlated with the abundance and distribution fluctuations of *Meyenaster gelatinosus* (Vasquez 1993b). Large *T. niger* comprise c.a. 40% of the diet of this sea star. The average size of *T. niger* indicates that the population at Playa El Francés is mainly formed by large individuals. During the study period, sea urchin recruitment was not recorded and it has been shown that regular recruitment may be necessary to maintain the population densities in the presence of predators (Kenner 1992). The analysis of gut contents of *T. niger* shows that crustose calcareous algae were the

most frequent and abundant food item in the diet (Vásquez 1993 b).

Tetrapygus niger forms high density groups in areas with strong water movement (sea bed and coastal currents). The causes that provoke the formation of sea urchin fronts have seldom been studied in subtidal macroalgae communities (Schiel & Foster 1986). It has been asserted that the front formed mainly by strongylocentrotid individuals is the principal factor generating the destruction of kelp beds (see review by Harrold & Pearse 1987). Bernstein et al. (1983) stated that the sea urchin fronts are defense mechanisms against predators. Nevertheless, Vadas et al. (1986) demonstrated that the results obtained by Bernstein et al. (1983) were the results of their experimental design and that the sea urchin grouping was produced by food concentration. Harrold & Reed (1985) proposed that drifting algae constitute an important food resource and their abundance and predictability release the benthic macroalgae from grazing pressure. Apparently the strongylocentrotids of the northern hemisphere have morphological adaptations that allow them to capture and incorporate this resource in their diet. However, in the southern hemisphere *T. niger*, the most abundant sea urchin in rocky subtidal communities in northern and central Chile, is unable to use drift algae as an important food item. Vásquez (1986)[1] and Contreras & Castilla (1987) demonstrated that the feet are not efficient in capturing drift algae. In this context, this morphological constrain of the urchins can be compensated, partly by aggregation. The formation of high density groups of *T. niger* in zones with strong bottom currents should increase the probability of retaining drifting algal material among the sea urchin spines. Therefore the data presented by Vásquez (1989, 1993b) support the results obtained by Vadas et al. (1986), relative to the cause of the formation of sea urchin groups. However, even though groups of sea urchins appear to respond in a certain degree

to trophic necessities in both hemispheres, the evidence suggests that the principal causes of *T. niger* grouping in subtidal kelp beds of *L. trabeculata* are the bottom coastal currents (Vásquez 1989, 1993b).

On the other hand, the causes of the sea urchin aggregations in northern Chilean waters differ from those in shallow coastal areas in the northern hemisphere. In these environments, strong water movement produces high sea urchin mortalities (Lissner 1980, 1983). Russo (1977), Cowen et al. (1982) and Ebert (1982), have demonstrated that the exposure to intense water movement diminishes the abundance and modifies the sea urchin trophic behavior. Furthermore, the wave motion and coastal currents can limit feeding (Himmelman & Steel 1971, Mann & Breen 1972, Mann 1973, Lissner 1980, Choat & Schiel 1982) and greatly affect the annual rate of survival and the body size of many sea urchin species (Ebert 1982). In subtidal kelp beds of *L. trabeculata* where a high density of *T. niger* occurs, the vegetation coverage is greatly reduced, generating patches dominated exclusively by crustose calcareous algae (Vásquez 1989, 1991).

Even though the intensity of water movement promotes the aggregation of *Tetrapygus niger*, in contrast to that documented for other types of sea urchins in the northern hemisphere, the acummulative effect of the phenomenon appears to have similar ecological consequences. Therefore, the reduction of benthic grazers (due to migration or mortality) in subtidal areas, or a decrease in sea urchin grazing abilities due to water movement, have significant effects on hard bottom benthic communities. Thus, the effect of water movement (waves and currents) can generate temporal and spatial grazing refuges analogous to those proposed by Lubchenco and Gaines (1981) allowing the settlement and growth of macroalgal propagules.

Tegula tridentata was found by Vásquez (1993b) throughout the kelp bed of *L. trabeculata*, associated with stable rocky seabeds and small rocks on sandy bottom, and the analysis of its size suggests recruitment during the entire year in the northern Chilean coast. *T. tridentata* gut content

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[1] Vásquez JA (1986) Morfología de estructuras alimentarias como factores en la organización de comunidades submareales. Biota (Chile) 1: 104.

analysis shows that this gastropod snail is an omnivorous organism including many prey items in its diet, including algae and benthic invertebrates.

The effect of predators upon populations of herbivores associated with subtidal kelp communities of macroalgae (see reviews by Schiel & Foster 1986, Harrold & Pearse 1987) is profusely documented. Sea otters (*Enhidra lutris*), fishes (*Semicossiphus pulcher*, *Centrostephanus coronatus*), sea star (*Pycnopodia heliantoides*, *Patiria miniata*) and lobsters (*Homarus americanus*, *Panulirus interruptus*) have received special attention as natural controls of population densities and diets of strongylocentrotids in the northern hemisphere. In northern California, *E. lutris* is one of the most important predators in the control of the sea urchin densities (Estes & Palmisano 1974, Estes 1980, Estes et al. 1978, 1981, 1982). In southern California, predation of *S. pulcher* and *C. coronatus* is also an important factor in the regulation of sea urchin populations (Himmelman & Steel 1971, Nelson & Vance 1979, Tegner & Dayton 1981, Cowen 1983). The asteroids *P. miniata* and *P. heliantoides* are important in the regulation of echinoids (Mauzey et al. 1968, Paine & Vadas 1969, Dayton et al. 1984). In California, *P. interruptus* predation produces the greatest effect on the abundance, distribution, size frequency and feeding behavior of various species of *Strongylocentrotus* (Tegner & Dayton 1981, Tegner & Levin 1983). However the abundance of urchins cannot only be affected by predators, as but also by factors affecting recruitment such as larval abundance and early post-settlement survival (Watanabe & Harrolld 1991).

The star fish *Meyenaster gelatinosus*, and the carnivorous fish *Mugiloides chilensis*, *Cheilodactylus variegatus* and *Semicossyphus maculatus*, are the most important predators in the community dominated by *L. trabeculata*. All these carnivores include *Tetrapygus niger* and *Tegula tridentata* in their diets. In this way, these species would have an additional effect on the regulation of the main herbivores associated with *L. trabeculata*. *M. gelatinosus* preys on large *T. niger*, whereas the dimensions of the oral structures of carnivorous fishes restrict

them to small prey. This is evident for *M. chilensis* and *C. variegatus*, where the maximum sizes of *T. niger* in their gut contents do not exceed a test diameter of 20 mm. Considering the abundance of carnivorous fish the selective predation of these organisms on small size prey could explain the absence of small of *T. niger* in the area studied (Vásquez 1989, 1993b).

Although the analysis of carnivores gut content does not allow inference regarding the regulation of their prey population, the results suggest that the herbivore abundance notably associated with *L. trabeculata* is affected by the predation of a carnivorous guild (sensu Root 1967). This hypothesis differs from that proposed for the subtidal kelp beds of the northern hemisphere, where just one key predator (sensu Paine 1966, however see Power et al. 1996 for a new definition) regulates the population density of its prey items (Lowry and Pearse 1973, Mann 1977, Estes et al. 1978, 1982, Duggins 1980, Tegner & Dayton 1981, Bernstein et al. 1982, Tegner & Levin 1983). Nevertheless, the evidence presented by Foster and Schiel (1988) strongly indicates that the concept of the sea otter as a keystone species is applicable only to a relatively small number of sites and thus does not constitute a general explanation of kelp community structure in California.

A number of factors have been reported to determine the abundance, distribution, physiology and reproduction of benthic marine algae (Schwencke 1971, Santelices 1977, Norton et al. 1982). Among physical factors, water motion is of particular importance in the morphological expression and distribution of benthic macroalgae (Connell 1972, Koehl 1977, 1982, 1984, Jackson 1977, Menge 1978, Lubchenco & Menge 1978, Druehl 1978, Sousa 1979, 1984, Gerard & Mann 1979, Paine & Levin 1981, Denny et al. 1985). On the other hand, herbivory is the main biological factor affecting their abundance and distribution (see reviews by Lawrence 1975, Lubchenco & Gaines 1981, Gaines & Lubchenco 1982, Schiel & Foster 1986, Johnson & Mann 1988).

Despite possible interrelations between physical and biological factors, the general

trends of the experimental ecological studies, with the exception of those by Velimerov and Griffiths (1979), Santelices & Ojeda (1984 a, 1984b) and Dayton et al. (1984), have been to consider them as two independent forces. In this context, herbivory, water motion and spacing between plants, have been analyzed as independent structural factors that influence intertidal macroalgal populations.

Experimental studies conducted in northern Chile (Vásquez 1989, 1991, 1993a, 1993b, Vásquez & Santelices 1990) reveal that benthic herbivores, sea urchins and gastropod snails modify algal morphology, producing two morphs: plants that grow in the absence of herbivores, with numerous flexible stipes ("bushy form"), and plants in the presence of grazers, with one or few stipes of little flexibility ("arborescent form") in the presence of grazers. Water motion (bottom surges) generates selective mortality which affects significatively the arborescent form.

On land, plants growing at high densities of plants have low rates of growth, reproduction and survivorship compared to plants growing in similar environments but with low population densities (Harper 1977). In this context, evidence related to marine macroalgae differs. Schiel & Choat (1980) indicated that *Ecklonia radiata* and *Sargassum sinclairii* reach a larger size when part of a dense population in semi-exposed environments. These authors suggested that plant gregariousness decreases the mortality produced by water movement. Black (1977) found that mortality and growth rates of juvenile *Egregia laevigata* Setch. are density-dependent, at least during the first three months of age. Santelices & Ojeda (1984b) suggested that distance between adult plants of *Lessonia nigrescens* Bory is a critical factor influencing the recruitment of juveniles at intertidal habitats of central Chile. In subtidal bottom kelp forests of *Lessonia trabeculata* in northern Chile, the distance between plants (high densities) is a mechanism that favors the persistence of *Lessonia*, primarily reducing herbivory (increasing the whiplash effect of the fronds) and secondarily reducing the dredging effect of the bottom surges (Vásquez 1989, 1992).

Another seasonal but very important factor in the structure of bottom kelp forests in northern Chile is the use of *L. trabeculata* as the substratum for the settlement of elasmobranch fish egg capsules (Vásquez 1989). This event produces high rates of mortality in large plants during summer months. Notwithstanding, this reproductive behavior facilitates the settlement of propagules and the growth of *L. trabeculata* through the reduction of intraspecific interaction with parental plants.

KELP COMMUNITIES IN SOUTHERN CHILE

The most conspicuous kelp associations are formed by the giant kelp *Macrocystis pyrifera*, whose geographical distribution in the Pacific Ocean includes the west coast of North America and southern Chile (Neushul 1972). In contrast to the situation in the north Pacific, few ecological studies have been done in giant kelp forests from southern South America. These works has been focused on: 1) the influence of the sea urchins on the distribution and abundance of *M. pyrifera* (Dayton 1974, 1975, 1985, Castilla & Moreno 1982, Vásquez et al. 1984, Castilla 1985); 2) population dynamics and community structure of *M. pyrifera* (Moreno & Sutherland 1982, Moreno & Jara 1984, Santelices & Ojeda 1984 a b, Ojeda & Santelices 1984, Dayton 1985) and 3) regulation patterns of sea urchin populations (Dayton et al. 1977, Vásquez & Castilla 1984, Vásquez et al. 1984, Dayton 1985, Castilla 1985).

In the kelp forests of Isla Navarino, Santelices & Ojeda (1984 a) tested the effects of three sets of ecological factors on the distribution and organization of the *M. pyrifera* populations: 1) the possibility of competitive exclusion of *Macrocystis* by *Lessonia vadosa* Searles by removing specimens of *L. vadosa* at the upper side of the giant kelp forest; 2) the possibility of survival of transplanted plants, growth in deeper water and adequacy of the substratum; 3) the possibility of interspecific interference on density and distributional patterns removing the floating canopy of large *Macrocystis* plants.

Their results indicate that the importance of the factors determining the population structure and distribution patterns of *Macrocystis* differ according to the section of the bed. They pointed out that the nearshore edge of the belt appears to be set by interspecific competition with *L. vadosa*. Experimental results indicated than even though *M. pyrifera* could recruit under the *L. vadosa* canopy, densities and growth rates are lower than in absence of *L. vadosa*. If *L. vadosa* is removed, the *Macrocystis* belt extended 1 to 2 m further into shallower water. However, these experimental data provide no information on which to base an evaluation of the factors restricting *L. vadosa* to shallower waters.

The deepest edge of the *M. pyrifera* bed in the Puerto Toro area appears primarily set by substratum availability (Santelices & Ojeda 1984). However, during winter, decreased light intensities and temperatures perhaps limit apical elongation. Field observation indicated that interspecific competition between *M. pyrifera* and *Lessonia flavicans* Bory, result from conditions of unlimited substratum availability. In the few areas with solid substrata extending into deeper waters, it would appear that monospecific stands of *L. flavicans* often limit the seaward border of *M. pyrifera* (Santelices & Ojeda 1984).

Four species of sea urchins (*Loxechinus albus*, *Arbacia dufresnei*, *Pseudechinus magellanicus*, *Austrocidaris canaliculata*) occur in the coastal kelp forest of *Macrocystis* at Puerto Toro in the Beagle Channel. The distribution patterns and diets of the four species suggest a clear separation of the microhabitats used and the diet (Vásquez et al. 1984). The localization of the sea urchin species was noted in relation to four types of microhabitat: on boulders, in holdfasts of *Macrocystis* and under boulders and crevices. The number of observations and the probability of occurrence of each sea urchin species in each of the four microhabitat categories showed that *Pseudechinus* and *Austrocidaris* were found in the four microhabitat categories but with different probabilities. *Pseudechinus* occurred more frequently inside the holdfast of *M. pyrifera*, while *Austrocidaris* was found more frequently under boulders. *Loxechinus* was commonly found on boulders, less frequently found in rock crevices or under boulders, and never found inside the holdfast of *Macrocystis pyrifera*.

Gut content analysis indicated that *Loxechinus* had the most diversified diet of benthic algae, *Macrocystis* being the most frequent item. *Pseudechinus* consumed mainly *Macrocystis*, whereas *Austrocidaris* and *Arbacia* contained others frondose benthic algae and sessile invertebrates. *Arbacia* was particularly notable with over 50% of the gut content consisting of serpulids and barnacles.

If the gut contents obtained for the four sea urchin species are grouped according to their nature, it is possible to distinguish four groups of food: (a) *Macrocystis pyrifera* fronds, wich are the commonest food; (b) other frondose algae (mainly *Gigartina skottsbergii* Setchell et Gardner, *Halopteris hordacea*, *Lessonia* spp., *Epymenia falklandica* Taylor); (c) calcareous algae (crustose coralline); and (d) invertebrates (barnacles, serpulids, sponges). These four categories, together with the four microhabitats considered illustrated the patterns of resource axes utilization. *Loxechinus* and *Arbacia* overlap greatly in their microhabitat distribution. *Pseudechinus* and *Austrocidaris* shared a diversity of rather cryptic microhabitat such as crevices, under boulders and holdfasts of *M. pyrifera*. Nevertheless, even though they had a considerable degree of overlap. *Austrocidaris* was more frequently found in crevices and under boulders while *Pseudechinus* occurred mostly in *Macrocystis* holdfasts.

All four species include *M. pyrifera* fronds in their diets, with a high degree of overlap among several pairs of species. Nevertheless, *Loxechinus*, *Arbacia* and *Austrocidaris* consumed other species of algae (frondose and calcareous) and *Arbacia* consumed mainly invertebrates. Furthermore, according to a related experimental study (Castilla & Moreno 1982) performed in this *Macrocystis* bed, the fronds of *M. pyrifera*, the principal food item in three of the sea urchin species, are not a limiting resource. Indeed, Castilla & Moreno (1982) determined that *L. albus*, one of the most conspi-

cuous sea urchin in the belt, consumed mainly pieces of drifting fronds and had no significant effect on the recruitment or survival of juvenile *Macrocystis*. In addition, Santelices & Ojeda (1984a) found that the recruitment pattern of *M. pyrifera* is determined mainly by the presence of adult canopy rather than by grazers.

Based on a broad geographical survey between 44° and 52°S along southern Chile and the Argentinian coast, Dayton (1985) pointed out that the distribution and abundance of *Macrocystis* is determined by availability of suitable rocky substratum, the interspecific competition with *Lessonia vadosa* (shallow waters) and with *L. flavicans* (deeper waters), entanglement with drift algae and the heavy settlement of bivalves on the kelp fronds, degree of exposure to waves, the grazing of the echinoid *L. albus* and indirectly, the effects of human fishing of *Loxechinus*. He documented that in many areas between 44° - 52° S, *Macrocystis* is overgrazed by *L. albus*. In other areas *L. albus* exist in lower densities or is absent altogether and does not affect the *Macrocystis* population, as suggested by Castilla & Moreno (1982), Castilla (1985), Santelices & Ojeda (1984 a) and Vásquez et al. (1984).

Furthermore, Dayton (1985) stated that *Loxechinus albus* has an important role in the control of *Macrocystis* abundance in wave exposed sites and that its effect on this kelp decreases as the intensity of the wave action also decreases. This explanation is the basis for the general belief that sea urchins only play a major role in harsh environmental conditions with severe storms, low nutrients and warm temperatures (Harrold & Reed 1985). For the above reasons, wave protected environments have long-lived perennial *Macrocystis* populations (North 1971, Rosenthal et al. 1974, Gerard 1976, Kirkwood 1977, Dayton et al. 1984, Druehl & Wheeler 1986). Some Chilean *M. pyrifera* populations also have life spans of 2 to 4 years (Santelices & Ojeda 1984, Moreno & Sutherland 1982, Westermeier & Möller 1990). However, *M. pyrifera* populations found in the northernmost part of the archipelago region in southern Chile have an annual life cycle (Busch-

mann 1992). A new sporophytic cohort of *M. pyrifera* recruit during June-July (Buschmann 1992). In this area the gastropod *Tegula atra* appears to be the most abundant grazer and would seem to explain the decrease in *Macrocystis* abundance during the summer (Buschmann 1995). Nevertheless, although this *M. pyrifera* abundance pattern appears to be related to grazing by *T. atra*, the interactions with environmental variables such as nutrient availability and temperature, that appear to be important in the northern hemisphere (Tegner & Dayton 1987), needs to be studied before further conclusions can be made.

The *Loxechinus* foraging behavior is influenced mainly by the degree of wave surge and by hunger (Dayton 1985), as in *Strongylocentrotus* spp. (Harrold & Reed 1985). As Dayton (1985) indicated, *Loxechinus* often restricts its local distribution to areas exposed to severe wave action. The importance of hunger is a well known factor influencing the behavior of sea urchins and, in some cases, the formation of the sea urchin grazing fronts, irrespective of density (Lawrence 1975, Harrold & Reed 1985, Harrold & Pearse 1987). With regard to hunger, drift algae are abundant in all areas with large kelp forests (Castilla & Moreno 1982, Dayton 1985). In these areas *Loxechinus* was commonly seen but usually was not very abundant. It is clear that they do not forage far from the food source (Castilla & Moreno 1982, Santelices & Ojeda 1984b). In most protected areas, drift is abundant, and *Loxechinus* is often rare (Vásquez et al. 1984). In most other areas where they are abundant, *Loxechinus* forages actively (Dayton 1985).

Little evidence relates to the regulation of the sea urchin population density in southern South America. Dayton (1985) hypothesized that low larval availability is an important factor related to the relatively low abundance of Tierra del Fuego *Loxechinus* population. These habitats are influenced by the circumpolar Westwind Drift current, and the only source of *Loxechinus* larvae is from the Cape Horn Archipelago. Assuming that *Loxechinus* larvae are similar to other echinoids in spending four or more weeks in the plankton, the

Westwind Drift would carry most of the larvae away, and the only recruitment into these habitats would come from eddies or areas where larvae are trapped (Dayton 1985).

In the northern hemisphere, the abundance of sea urchins is often influenced by predators such as sea otters (Estes & Palmisano 1974, Dayton 1975), fishes and/or lobsters (Mann 1977, Tegner & Dayton 1981, Cowen 1983), crabs (Kitching & Ebling 1961, Bernstein et al. 1983), or asteroids (Mauzey et al. 1968, Paine & Vadas 1969, Rosenthal & Chess 1972). As Castilla & Moreno (1982) and Castilla (1985) indicated, no single, efficient sea urchin predator exists in the *Macrocystis pyrifera* kelp communities of southern Chile. Apparently, the most conspicuous predators of sea urchins are two species of asteroids: *Meyenaster gelatinosus*, which occurred in abundance only north of Golfo de Penas (Dayton 1985), and *Cosmasterias lurida* Philippi, which is the principal predator found in coastal belts of *Macrocystis* at Puerto Toro in southern Chile (Vásquez & Castilla 1984, Castilla 1985). However, *Loxechinus* and the other sea urchin species are very rare in the diet of *Cosmasterias lurida* (Vásquez & Castilla 1984).

Loxechinus has effective defense behaviors, and *Meyenaster* only reduces *Loxechinus* densities on isolated boulders from which the urchins can be stampeded without immediate immigration (Dayton et al. 1977). When the boulders are sufficiently isolated and large, this stampeding phenomenon can result in *Macrocystis* being released from *Loxechinus* predation long enough to recruit and survive to reproduce.

CONCLUDING REMARKS

This review indicate that the northern population of *Lessonia* the sea urchin *Tetrapygus niger* is the main grazer producing extensive barren grounds, but also the effect of the gastropod *Tegula tridentata* and the fish *Aplodactylus punctatus* are important. Water movement can either facilitate or impede the access of benthic grazers to the plants and this herbivores are contro-

lled by a guild of predators and not by a keystone type species. Also, this review show that the *Macrocystis pyrifera* beds in the central-southern coast of Chile are not controlled by sea urchins in exposed sites and the main herbivores are the gastropod *Tegula atra* in protected sites.

As has been pointed out by many authors (Vásquez et al. 1984, Castilla 1985, Dayton 1985, Vásquez 1992), the effects of the herbivores-kelp interaction in southern Chile differs from those in the northern hemisphere. In the last years, it has been a tendency to generalization from the studies done in *Macrocystis* or in *Laminaria*. In this contex, and due to the importance of kelp communities in the southern hemisphere these strong biological interactions must be re-examinated.

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