REVISTA CHILENA DE HISTORIA NATURAL

Revista Chilena de Historia Natural 84: 241-261, 2011

REVIEW ARTICLE

The functional roles of herbivores in the rocky intertidal systems in Chile: A review of food preferences and consumptive effects

Los roles funcionales de los herbívoros en sistemas intermareales rocosos en Chile: Una revisión de las preferencias alimenticias y efectos de consumo

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ABSTRACT

This paper reviews recent knowledge about the functional roles that herbivores have in intertidal communities in Chile. Specifically, I review field and laboratory studies dealing with the food preferences of herbivores, the responses of algae to herbivore attacks and reports of negative and positive functional effects of herbivores on algal populations and communities. Most herbivores studied are characterized as generalist species. Green ephemeral and a few corticated algae dominate diets, while all species considered ingest larvae and post-metamorphic stages of invertebrates challenging classical characterizations of the herbivore guild. Functional redundancy and complementarity within the herbivore guild is discussed in relation to both quantitative and qualitative evidence. The magnitude of consumptive per capita effects of herbivores on algae can be related, although not entirely, to body size. Feeding mode can determine differential species participation in different phases and stages of community succession. Positive effects of herbivores on algae via spore dispersion, and also compensatory potential after consumption, appear to match the classical model of the "grazing optimization hypothesis". Only one species that form "gardens" is reported, suggesting a lack of information regarding behavioural aspects of abundant taxa from intertidal habitats in Chile. According to variation in oceanographic conditions and thermal regimes along the coast of Chile, geographical variation in functional effects of herbivores and thereby shifts in the herbivore-algae balance is expected. Future studies should consider the functional relationship within the herbivore guild at different temporal and spatial scales, and compensatory potential after species loss. Whether herbivore species have either redundant or complementary roles in intertidal communities can help us to understand the intensity and direction of human impacts in both community structure and ecosystem functioning.

Key words: Chile, herbivores, functional role, guild, intertidal.

RESUMEN

Este trabajo revisa el conocimiento reciente sobre los roles funcionales que los herbívoros tienen en comunidades intermareales en Chile. Específicamente, se revisaron estudios sobre preferencias tróficas de los herbívoros, respuestas de las algas al ataque de estos y reportes de efectos negativos y positivos de los herbívoros sobre poblaciones y comunidades de algas. La mayoría de los herbívoros estudiados se caracterizan por ser generalistas tróficos. Las algas verdes efímeras y pocas algas corticadas dominan la dieta, mientras que todas las especies consideradas ingieren larvas y postmetamórficos de invertebrados lo cual desafía la caracterización clásica del gremio. La ocurrencia de redundancia funcional y complementariedad al interior del gremio de herbívoros, es discutida en relación a las evidencias cuantitativas y cualitativas presentadas. La magnitud de los efectos de consumo per cápita de los herbívoros sobre las algas puede estar relacionada, aunque no completamente, al tamaño corporal. Los modos de forrajeo pueden determinar la participación diferencial de las especies en distintas fases y estados de la sucesión comunitaria. Los efectos positivos de los herbívoros sobre las algas a través de dispersión de esporas, y potencial de compensación luego del consumo, parece coincidir con los modelos clásicos de la "hipótesis de optimización del forrajeo". Solo una especie que forma "jardines" ha sido reportada en Chile, lo cual muestra la falta de información sobre los patrones de comportamiento de taxa abundantes presentes en estos hábitats en Chile, los cuales muestran comúnmente este tipo de comportamientos en otras costas. De acuerdo a la variación en las condiciones oceanográficas y régimen termal a lo largo de la costa de Chile, se espera que existan variaciones geográficas en los efectos funcionales de los herbívoros y en el balance herbívoro-alga. Futuros estudios deberían considerar las relaciones funcionales al interior del gremio a diferentes escalas espaciales y temporales, y el potencial de compensación en funciones luego de la pérdida de especies. Si los herbívoros tienen roles redundantes o complementarios en la comunidad intermareal, puede ser de gran interés para entender la intensidad y la dirección que tienen los impactos humanos en la estructura comunitaria y funcionamiento ecosistémico.

Palabras clave: Chile, gremio, herbívoros, intermareal, rol funcional.

INTRODUCTION

Herbivory is commonly defined as the consumption of living plant tissue by animals, and herbivores are considered all those animals adapted to live solely consuming plant tissue. Thus, herbivory is related to the consumptive effects that animals can cause on populations or communities of plants, and is considered one of the most important ecological processes in marine as well as in terrestrial ecosystems around the world (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Huntly 1991, Schmitz 2008). In marine systems, herbivores can determine temporal and spatial distribution of algae in both intertidal and subtidal habitats (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983). Through consumption of mature algae and spores, different intertidal and subtidal herbivores can affect successional pathways, determining algae species composition and abundance (Lubchenco 1978, Hawkins & Hartnoll 1983). Almost every dimension of algal life history and performance can be influenced by marine herbivores (e.g., succession, Sousa 1979; chemical defences, Duffy & Hay 1994). But although many species can cause negative effects on algae, positive direct and indirect effects are also important mechanisms recently considered as relevant factors in the structure of intertidal communities (Branch et al. 1992, Plaganyi & Branch 2000). As herbivores are also consumed by high-level carnivores, including humans, they also have a central importance in food web dynamics and ecosystem function (Schmitz 2008).

Diverse studies have been conducted in rocky intertidal systems, but lack of replication has hindered testing hypotheses regarding the effect of herbivores on community structure. Widespread negative effects on algal biomass are common features. On the other hand, information from the diet of herbivores suggests positive interactions between grazers and algae may occur in some intertidal habitats and recent studies reporting frequent invertebrate consumption by generalist grazers challenges the basic definition of this guild.

In Chile, an important number of studies dealing with the effect of herbivores on community structure have been conducted in subtidal habitats examining for example the dynamics of kelp forests (see Vásquez & Buschmann 1997 for review). Some of the most abundant herbivores in Chilean subtidal habitats are amphipods (Lancelloti & Trucco 1993), sea urchins, fishes and some molluscs (e.g., Vásquez et al. 1984, Santelices 1990). In intertidal habitats, a similar pattern is seen with amphipods (Lancellotti & Trucco 1993) molluscs (Otaíza & Santelices 1985, Santelices et al. 1986, Valdovinos 1999, Rivadeneira et al. 2002), some crustaceans, fish (Muñoz & Ojeda 1997, Horn Ojeda 1999) and two common species of sea urchins (Vásquez & Buschmann 1997, Vásquez 2007) as the most abundant and diverse herbivore species. Of all the taxonomic groups, molluscs are one of the most diverse in intertidal habitats (Rivadeneira et al. 2002) and are common in experimental studies because they can be easily manipulated.

In this paper, I review the status of marine intertidal studies conducted in Chile dealing with effects of herbivores on algae. Specifically, I consider studies on food preferences and algal responses to herbivore attack, experimental approaches evaluating community-level effects of herbivory and discuss studies reporting positive effects of herbivores on algae. Finally, I highlight the importance of experimental approaches, as well as consideration of natural history for better understanding the diversity of functional roles herbivores play on Chilean intertidal rocky shores.

In general, studies dealing with the role of herbivores in intertidal systems in Chile can be separated into three categories; (a) studies that characterize diet or food preferences of herbivores and relate them with effects on algae populations; (b) studies that through field or lab experiments explicitly evaluate the consumptive effects (commonly negative) of herbivores on algae and other sessile populations and communities and; (c) studies that observe positive relationships between herbivores and algae (mutualistic interactions). Considering these studies altogether, they give us relevant information about the functional role that herbivores play in intertidal ecosystems.

FOOD PREFERENCES OF HERBIVORES

From a functional perspective, the food preferences of herbivores are relevant to understand the impacts that different species exert on algae community structure (e.g., Lubchenco & Gaines 1981, Steneck & Dethier 1994). Whether herbivores are generalist or specialist consumers, could be of interest to understand the role that these species have on the successional pathways of the system, increasing or decreasing the rate of succession (e.g., Lubchenco 1978).

Feeding modes

Food preferences of herbivores are linked to algal handling mode and effects on algal communities. Diverse classifications of feeding modes have been proposed by some authors who utilize ingested food size (see Hawkins & Hartnoll 1983 for review). Thus, they separate the different species into microphagous (mainly feeding in microalgae) and macrophagous (feeding on macroalgae). For example, considering microphagous and macrophagous feeding modes in limpets Branch (1981) proposed four basic foraging patterns; (i) species feeding on microalgae and detritus, (ii) species feeding on macroalgae, (iii) territorial species closely linked to a particular food plant, and finally (iv) epiphytic specialist species feeding on their host plant and microalgal epiphytes. Despite ingested food size, almost all molluscan herbivores are considered "grazers", in the sense that they mainly feed on microalgae and plantlets of green ephemeral algae, and some fish and crustaceans are considered "browsers" in that they can bite large pieces of adult algae (Hawkins & Hartnoll 1983, Horn 1992).

Feeding modes appear more variable in trophic generalist than in specialist species, because it has been observed some generalist herbivores can alternate the feeding on microalgae with feeding on pieces of adult macroalgae (e.g., fissurelids limpets and fish, see Horn & Ojeda 1999 and see below). According to a most general classification, it could be more appropriate to consider "grazers" these species able to scrap the substratum removing spores, plantlets of macroalgae, epiphytes, microalgae, and recently settled invertebrates (see below). Meanwhile, "browsers" could be considered all those species removing pieces of adult or established algae through "biting" on their fronds. These categories of feeding are similar to those which are commonly used for fish (Horn 1992) and for terrestrial herbivores (McNaughton 2001).

In particular, modes of feeding are directly related to the morphology of the buccal apparatus of herbivores (Steneck & Watling 1982, Horn & Ojeda 1999). Different feeding structures can constrain the capacities of herbivores to remove large pieces of macroalgae or to deeply scrape the rocky substratum to ingest epilithic microalgae, but they can't determine specific food choice (see below). Feeding modes (browsing, grazing, and two alternating strategies) are important characteristics that could help to understand qualitative effects of herbivores on either algae developmental stages or morphologies, but poorly determine quantity of algae removed which is mostly a matter of body size (see below).

Molluscs' food preferences

One of the most diverse and locally abundant groups of herbivores present in the rocky intertidal habitat in Chile are molluscs (Santelices et al. 1986, Valdovinos 1999, Rivadeneira et al. 2002). Most species are generalist grazers, and show considerable similarity in the items they consume. The most frequent items consumed by molluscan grazers are diatoms, ulvoids, and calcareous crusts (Santelices & Correa 1985, Santelices et al. 1986, Camus et al. 2008). Seasonal variations in the diet of grazers correlate with food availability (Santelices et al. 1986), suggesting that most species have an opportunistic strategy in their feeding patterns.

Despite the fact that most molluscan herbivores present in the intertidal habitat in Chile consume microalgae and microscopic stages of green ephemeral algae (i.e. plantules, spores), the browser/grazer *Fissurella picta* appears to be also capable of consuming adult corticated algae like *Mazzaella laminarioides* (hereafter *Mazzaella*, Moreno & Jaramillo 1983, Godoy & Villouta 1986). Similarly, the Pulmonate limpet *Siphonaria lessoni* has been reported to consume adult stages of *Mazzaella*, and according to Jara & Moreno (1984) populations of this limpet can cause important reductions in biomass of this alga (but see below). Interestingly, very low ingestion of corticated *Mazzaella* by *Siphonaria* or fissurellid limpets was reported by Santelices et al. (1986)'s study conducted in central Chile contrasting with the high availability of *Mazzaella* in this region (Santelices 1990).

Previous studies dealing with diet composition were not able to separate consumption on adult or microscopic stages of algae thus constraining information on consumptive effects of herbivores. In order to establish the ability of molluscan herbivores to ingest adult stages of both ephemeral and corticated algae, Aguilera (2010) conducted short term laboratory trials (replicate trials for 7-10 days) evaluating consumptive effects of the species *F. crassa*, *S. lessoni*, *C. granosus* and *S. araucana* on ephemeral (ulvoids, *Porphyra*) and corticated (i.e. *Mazzaella*) algal biomass. In general, it was observed that *S. lessoni* and *F. crassa* were the only species capable of consuming adult stages of corticated *Mazzaella* and the ephemeral *Ulva rigida* and *Porphyra columbina* (Aguilera 2010). The pulmonate limpet *S. lessoni* eats some portion of cystocarpic fronds, and can only consume tiny pieces of adult gametophyte of *Mazzaella*. The ability to consume adult stages of algae was related to feeding modes (see above), whereas quantity of algae consumed showed a linear relationship with herbivore body size (see below). In general, body size correlates with consumption rates, handling times and the time animals spend foraging (Mittelbach 1981) thereby suggesting a scaling relation of food intake and body size in consumer assemblages (see below). In the field, in the higher intertidal zone, *S. lessoni*, together with the periwinkle *Nodilittorina peruviana*, is able to feed upon bleached fronds of *Mazzaella* (author personal observations). The key-hole limpet *F. crassa* can consume entire fronds of adult plants of *Mazzaella*, and because of its large size (5.0-7.0 cm shell length, see also Oliva & Castilla 1986) this herbivore can have strong effects on natural populations of this alga (see below). In consequence, both *F. crassa* and *S. lessoni* have the potential to affect microscopic as well as adult plants of both ephemerals and corticated algae. These herbivores apparently can alternate grazing and browsing provoking an apparent differentiation in their trophic niche and their functional role compared with other herbivores.

Are molluscan grazers omnivorous?

Many studies dealing with the diet of herbivores report the presence of invertebrates, mainly barnacles, in the gut of molluscan grazers (Santelices & Correa 1985, Santelices et al. 1986, Aguilera 2005, Aguilera & Navarrete 2007). These herbivores may be considered omnivores owing to their ability to feed (i.e. ingest, digest and assimilate) in more than one trophic level (Pimm & Lawton 1978), in this case a basal (algae) and intermediate (animal) species. The ingestion of barnacles (i.e. cyprid larvae and post-metamorphics) by grazers occurs when they scrape the substrate in a "bulldozing-like" fashion. This foraging mode is an important mechanism of post-settlement mortality for diverse invertebrates, widely reported in other systems (e.g., Dayton 1971, Chan & Williams 2001).

Studies conducted in northern Chile (20° S-70° W) (Aguilera 2005) report that the species *Chiton granosus* frequently consume cyprid larvae (Frequency = 67 % of guts analysed) and post-metamorphic spat (100 %) of chthamalid barnacles beside other invertebrates (e.g., dipteran larvae, Aguilera 2005). Previous authors suggested cyprids are the main item ingested by *C. granosus* (see Jara & Moreno 1984), but these larvae are able to pass undamaged through the gut and the caecum of this chiton (Aguilera 2005). The proportion of cyprids found in the faecal pellets of *C. granosus* is commonly high (e.g., Santelices & Correa 1985, Aguilera 2005) suggesting these larvae may not be digested properly by this chiton.

Recently, an extensive study dealing with trophic relationships among molluscan herbivores present in intertidal systems of northern Chile (from 21°00' S to 30°06' S) (Camus et al. 2008) showed that 29 of the most representative species of molluscan herbivores ingest invertebrates. The animal items account for around 60 % of the food consumed by these herbivores. In general, the chitons *C. granosus* and *Enoplochiton niger* and the scurrinid limpets *Scurria viridula* and *S. ceciliana* include barnacle larvae and post-metamorphic spat besides other invertebrate items in their diet (Camus et al. 2008, Sanhueza et al. 2008). Camus et al. (2009) showed that fissurellid limpets (formerly *Fissurella limbata* and *F. picta*) and *C. granosus* are able to digest and also assimilate animal items. This finding appears to indicate the generality of animal consumption by molluscan grazers, pointing out that most species behave like omnivores rather than strict herbivores (Camus et al. 2009). This information highlights the importance of these species for trophic web dynamics and their broader functional roles in intertidal systems (Camus et al. 2008, Camus et al. 2009). Likely, consumption of barnacles (larvae and post-metamorphics) may supply herbivores with both proteins and minerals not present in algae especially during their reproductive peaks (J. Lubchenco personal communication). In this context, studies on the diet of chitons (conducted in Siberia), suggest a selective shift in feeding patterns of some species from herbivore to omnivore according to seasonal changes in environmental conditions (Latyshev et al. 2004). Thus, ingestion of animal items by herbivores may vary in response to changes in the physiological requirements of herbivores (e.g., development stages, reproductive peaks) and also seasonal variation in both algal spores (Santelices 1990) and animal settlement (e.g., barnacles, Aguilera 2005, Aguilera & Navarrete 2007). Therefore, information on both animal ingestion and assimilation analysis suggest consumption of invertebrates may not be entirely incidental and nutrient requirements of these herbivores, not present in algae, might account for this kind of intake (see Bozinovic & Martinez del Río 1996) which deserve further studies. For example, food choice experiments could be conducted in order to determine whether generalist herbivores are able to select animal items and how environmental variability can modify this feeding behaviour.

Although some grazers frequently consume post-metamorphics and larvae of different invertebrate species (e.g., Aguilera 2005, Camus et al. 2008), it is not entirely clear whether this consumption can translate into significant effects in abundance of these invertebrates. Although grazers can remove a considerable number of barnacle cyprids and post-metamorphics from the rock surface (through bulldozing), some authors have observed that pedal mucus of grazers can positively affect the settlement of cyprid larvae (e.g., Johnson & Strathmann 1989). Therefore, positive as well as negative effects of grazers on barnacle settlement have been observed in other systems (e.g., Berlow & Navarrete 1997). Because grazers maintain bare space for new colonizers of barnacles, some species may have indirect positive effects on the abundance of barnacles (see Aguilera & Navarrete 2007 for effects of *C. granosus* on barnacle settlement).

Food preferences by other intertidal herbivores

The most abundant, non-molluscan herbivores present in the low intertidal fringe and intertidal pools are the sea urchins *Tetrapygus niger* and *Loxechinus albus*. These species aggregate underneath the kelp *Lessonia nigrescens* forming "barren grounds" when grazing (see Vásquez & Buschmann 1997 for review). Analysis of the gut contents of *T. niger* showed crustose calcareous algae were the most frequent and abundant food item in its diet, although drift of the kelp *Lessonia nigrescens* and *Macrocystis pyrifera* are also consumed in low intertidal habitats (e.g., Rodríguez 2003, Navarrete et al. 2008). Similar to molluscan grazers, both sea urchins include a wide variety of invertebrates in their diets (González et al. 2008, Navarrete et al. 2008).

Despite the high similarity in the general morphology between *T. niger* and *L. albus*, these species have differential feeding mechanisms which were related to fine differentiation in the buccal apparatus (Contreras & Castilla 1987). These morphological characteristics would appear to constrain their diets; adult *T. niger* can consume significantly more benthic algae attached to rock than *L. albus* which consume more drift algae (González et al. 2008). Ontogenetic shift in the diet of *L. albus* could account for the diverse role this species may play in low intertidal habitats (see Rodríguez 2003); juveniles of this species consume mostly *Ulva* spp. while adult individuals consume drift *Lessonia*.

Other important components from the herbivore guild are fish, which can forage on both microscopic and adult stages of algae

(Horn 1992, Horn & Ojeda 1999). Some authors report that algae consumption by fish is common in the intertidal assemblage present in Chile (Stepien 1990). Nevertheless, this could be due to ontogenetic changes in the diet of many species from omnivores to herbivores (e.g., *Aplodactylus punctatus*; Benavides et al. 1994, Ojeda & Cáceres 1995). The bleniid *Scartichthys viridis* appears to be the only strict herbivorous fish in intertidal habitats (Muñoz & Ojeda 1997, Quijada & Cáceres 2000). The diet of *S. viridis* consists of green ephemeral algae (i.e. ulvoids) and exceptionally corticated algae like *Gelidium* spp. (Cáceres & Ojeda 2000, Muñoz & Ojeda 2000). Even though this fish can remove microscopic stages of macroalgae in a "grazing-like" fashion (Muñoz & Ojeda 1997, Horn & Ojeda 1999), animals are also able to remove large pieces of ulvoids and red algae through browsing of the distal portion of these algae (Ojeda & Muñoz 1999). Therefore, this fish could have consumptive effects on the intertidal algae community via different feeding modes similar to fissurellid limpets (see below).

Omnivorous fish *Girella laevifrons* can consume large proportions of algae in intertidal levels similar to those observed for *S. viridis* (Muñoz & Ojeda 1997). In contrast, *G. laevifrons* needs to complement energy from algae with protein of animal origin. The other common fish in intertidal habitats, the species *S. sanguineous* (Cancino & Castilla 1988), consume commonly ephemeral algae but also animal items (e.g., gastropods, barnacles) showing no clear trophic relationship with any guild (see Muñoz & Ojeda 1997). Regarding body size of adult fish species (commonly larger than 30 cm), they may have large per capita consumption of both ephemeral and corticated algae species suggesting strong effects on mid-to low intertidal populations (see below).

In general, all herbivores studied (grazers and browsers) show dietary changes which indicate opportunistic shifts in their feeding habits, perhaps in response to seasonal changes in algae abundance or/and physical factors or ontogenetic changes related to shifts in energetic demands and body size (Santelices 1990, Cáceres et al. 1993, Muñoz & Ojeda 2000). The algae consumed by intertidal herbivores studied were previously considered independent of calcareous matrices, phenolic compound or caloric contents of the algae (see Santelices 1987 for review). Recently, different chemical and structural algal traits has been considered relevant to understand herbivore-algae interaction because some herbivores can "induce" enhancement in the concentration of chemical compounds (e.g., polypropionates), changing the palatability of algae (i.e. brown algae, see Macaya et al. 2005, Rothausler et al. 2005). Although the food preferences of molluscan herbivores may be related to radular and plant morphologies (Steneck & Watling 1982, Steneck & Dethier 1994), modification of the algal chemical concentration can change the susceptibility of algae to herbivore consumption at very low temporal scales (Macaya et al. 2005, Macaya & Thiel 2008) and likely food preferences of herbivores.

Defensive anti-herbivore mechanisms have been suggested to be important in herbivore-algae interactions in both tropical and temperate systems (Duffy & Hay 1994; Cronin & Hay 1996). Commonly "constitutive" defences of algae (i.e. defences present permanently in algae) predominate over "induced" defences in systems with either large herbivores or high intensity of herbivory, but they tend to be costly to maintain (Cronin & Hay 1996). Induced anti-herbivore defences can be triggered only a few hours after herbivore consumption, and disappear when grazing pressure diminishes (Macaya & Thiel 2008). In this way, algae chemical compounds may alter the food choice of herbivores but only at very low temporal scales likely not altering algal attractiveness for herbivores. In general, induced defences are related to low consumption intensity and both plant and herbivore identity (Rothausler et al. 2005). For example, field and laboratory experiments conducted in central-north Chile showed palatability of brown algae *Glosophora kunthii* and *Dyctiota kunthii* can be reduced by consumption of the amphipod *Parhyalella ruffoi* but not by other herbivores (Macaya et al. 2005, Rothausler et al. 2005). It has been reported that chemical deterrents of herbivores are mostly concentrated in reproductive blades of algae (i.e. *Lessonia nigrescens*) (Pansch et al. 2008). These structures have high fitness value for algae and higher energetic content for herbivores thus ensuring a close co-evolutionary relationship between different herbivore and alga pairs. There is no information, however, whether induced defences can trigger a more sustained or consistent effect on herbivore diet. Furthermore, apparently only herbivores of small body size (i.e. amphipods and isopods), characterized by low consumption rates, are able to induce responses in algae (Cronin & Hay 1996).

Most herbivores studied appear to prefer ephemeral algae that have low chemical compounds or structures resistant to herbivory (see Duffy & Hay 1994, Steneck & Dethier 1994), but others like chitons or species with very strong buccal apparatus like sea urchins prefer calcareous and non-calcareous crusts which have been considered to be tolerant to grazing (e.g., Steneck & Dethier 1994). Sea urchins can also consume drift kelps in pools and low intertidal habitats thereby broaden their feeding niche compared with other herbivores (Rodríguez 2003). Few molluscs appear to be able to consume corticated algae when they reach the adult stage, which may be related to either constraints of the morphology of its buccal apparatus or defensive mechanisms present in these algae (e.g., Steneck & Watling 1982, Duffy & Hay 1994, Steneck & Dethier 1994).

Food preferences of herbivores, feeding modes and reaction of algae to herbivore attack have been correlated with the kind of effects that different species have on community structure (Cronin & Hay 1996, Macaya et al. 2005, Schmitz 2008). Nevertheless, the effect of consumers on resources can not be easily related to either their diet or functional traits (e.g., body size, see below). It is necessary to take into account both direct and indirect effect of herbivores on their food resources, and manipulative experiments are often the only way to test mechanistic hypotheses dealing with both consumptive effects of herbivores on algal communities and functional structure of the assemblages (Paine 1992).

CONSUMPTIVE EFFECTS OF HERBIVORES

In Chile, experimental studies dealing with herbivore-algae interactions in rocky intertidal systems have been designed to evaluate the role of molluscan grazers on abundance, distribution, and successional patterns of algae and other sessile organisms (e.g., barnacles). Although many studies reproduce general patterns found in other coasts of the world (Underwood 1980, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Coleman et al. 2006), often they have identified species in Chile that have important roles and apparently no parallel in equivalent habitats. Through either similarity or differentiation in the effects reported for herbivores, it should be possible to examine the functional relationship among different species (i.e. redundant or complementary roles) and the compensatory potential of species. Redundant or equivalent effects of species within assemblages, are hypothesized to provide a high insurance of ecosystem function after species loss (Walker 1992, Naeem 1998). Complementary effects of species are related to the diversity or differentiation of functions that species have on community or ecosystems through niche differentiation and facilitation, thereby, enhancing ecosystem functions (Loreau & Hector 2001). Thus, how functionally related species are is of interest to understand how human disturbances can scale up to alteration of different ecosystem functions (see below).

Effects of herbivores on intertidal community structure

One of the first experimental studies dealing with the effects of herbivores on intertidal communities in Chile was conducted by Moreno and Jaramillo (1983). This study showed the importance of molluscan herbivore assemblages in the structure of sessile communities (algae and barnacles). Through herbivore removal experiments (in non-replicated experimental platforms, 5×5 m) conducted inside a Marine reserve (Mehuín), these authors observed that the browser/grazer *Fissurella picta* has a key role on mid-intertidal algal communities through consumption of the corticated dominant algae *Mazzaella laminarioides* (= *Iridaea boryana* in these study) (Moreno & Jaramillo 1983). Outside the marine reserve, however, consumptive effects of *F. picta* on *Mazzaella* were suppressed by human gathering which drastically reduces the abundance of adult limpets (Jara & Moreno 1984, Moreno et al. 1984). Thus, other grazers like *Siphonaria lessoni* (not consumed by humans) appear to compensate for the absence of *F. picta* in controlling corticated *Mazzaella* (Jara & Moreno 1984). Similarly, in central Chile the fissurellid limpets appear to have key roles on community structure (Oliva & Castilla 1986). Strong effects of the key-hole limpet *F. crassa* on *Mazzaella'* biomass was observed in mid-intertidal levels through field experiments (Aguilera 2010). Although other herbivores, formerly *S. lessoni*, can consume this alga (see above) they can not compensate for *F. crassa* in controlling corticated *Mazzaella* either at per capita or at population level (Aguilera & Navarrete, unpublished data). High consumption of corticated late-succession algae (e.g., *Mazzaella*) by fissurellid limpets can entirely modify the intertidal landscape, especially when abundance of large key-hole limpets is high (as inside the marine preserve of Las Cruces, Oliva & Castilla 1986). Hence, these limpets might be considered keystone herbivores in Chilean intertidal habitats. Poor information, however, is yet available about the role these herbivores play on successional trajectories of the algal community either enhancing or decreasing species diversity.

Small, but locally abundant, molluscan grazers (i.e. chitons, scurrinid limpets) appear to have important roles in removing ephemeral algae, maintaining bare rock, and indirectly enhancing barnacles and calcareous algae during colonizing phases of the emergent community (Moreno & Jaramillo 1983, Jara & Moreno 1984, Aguilera & Navarrete 2007, Aguilera 2010, see Fig. 1 for summary of effects of these herbivores on early succession). Studies dealing with the grazing effect of one of the most abundant grazer species in intertidal habitats in central Chile, the chiton *Chiton granosus*, (Otaíza & Santelices 1985, Otaíza 1986, Aguilera & Navarrete 2007) show this species can reduce ephemeral algae abundance and have positive effect in the production of bare rock (see Fig. 1). Through scraping the substratum, chitons can affect recently colonizing spores, plantlets, and sessile invertebrates (see above) accounting for patchiness in ulvoids and bare rock distribution (Otaíza 1986, Aguilera & Navarrete 2007, Aguilera 2010). Owing to high densities of *C. granosus* in mid-to high intertidal levels (i.e. both juvenile and adult ~600 individuals m^{-2} Otaíza & Santelices 1985), this chiton can have important population-level effects during the colonizing phase of the algal community (see Fig. 1, Otaíza 1986, Aguilera & Navarrete 2007, Aguilera 2010). Other grazers, the limpet *S. araucana*, also have important roles similar to those observed for *C. granosus* (Aguilera & Navarrete, unpublished data). Due to the high similarity in foraging effects between these species, they could be considered functionally redundant (i.e. equivalents, see Walker 1992) in the role they play during early community succession (Aguilera 2010). In this context, the redundancy model (Walker 1992, Naeem 1998, Rosenfeld 2002) suggests that the more similar in morphology, behaviour or diet two species are, they tend to be most similar and interchangeable in their functional roles. Chitons and Scurria limpets may be similar in the mode they handle algae, because both species have tough buccal apparatuses (i.e. polyplacophoran and doccoglossan respectively, see Steneck & Watling 1982) allowing deep scraping of the substratum. This foraging mode allows ingestion of microalgae, spores and recently settled invertebrates during the colonizing phase of community succession (see Fig. 1). Nevertheless, the morphology of buccal apparatuses impede *C. granosus* and *S. araucana* from removing pieces of adult algae, even green algae, resulting in a similar reduction in the magnitude of their effects during the establishment phase of ephemeral algae at early succession (see Fig. 1, Aguilera 2010). Interestingly, contrary to the classic view of the guild, some studies suggest *C. granosus* and some *Scurria* species may have short time positive effects on *Mazzaella* abundance (Aguilera & Navarrete 2007, Aguilera & Navarrete, unpublished data, Aguilera et al., unpublished data) which await further confirmation (see Fig. 1, punctuated arrows). According to the similarity of niches among these species it is suggested that redundant species should have higher levels of inter-specific competition and thus local coexistence would be restrictive (Leibold 1998). These species have a comparatively similar diet (Santelices et al. 1986), but some form of habitat segregation at the micro-scale has been observed in the mid-intertidal (Aguilera & Navarrete 2011) which might explain local coexistence.

In the same context, high levels of redundancy are expected within taxonomically similar species in the role they play in the community (e.g., by niche conservatism, see Webb et al. 2002). Contrary to this view, studies dealing with the grazing effect of scurrinid limpets in Chile (see Espoz et al. 2004 for a general phylogenetic structure of the group) show both similar and dissimilar effects of different species of this assemblage. For example, in northern Chile Correa et al. (2000) show that joint (i.e. additive) grazing by the species *Scurria araucana* and *S. viridula* is the key factor controlling ephemeral algae abundance and diversity. Similarity in diet (Santelices et al. 1986, Camus et al. 2008), and feeding behaviour between these grazers (not explored by Correa et al. 2000) might account for the additive effects reported. In turn, the other abundant scurrinid limpet *Scurria*

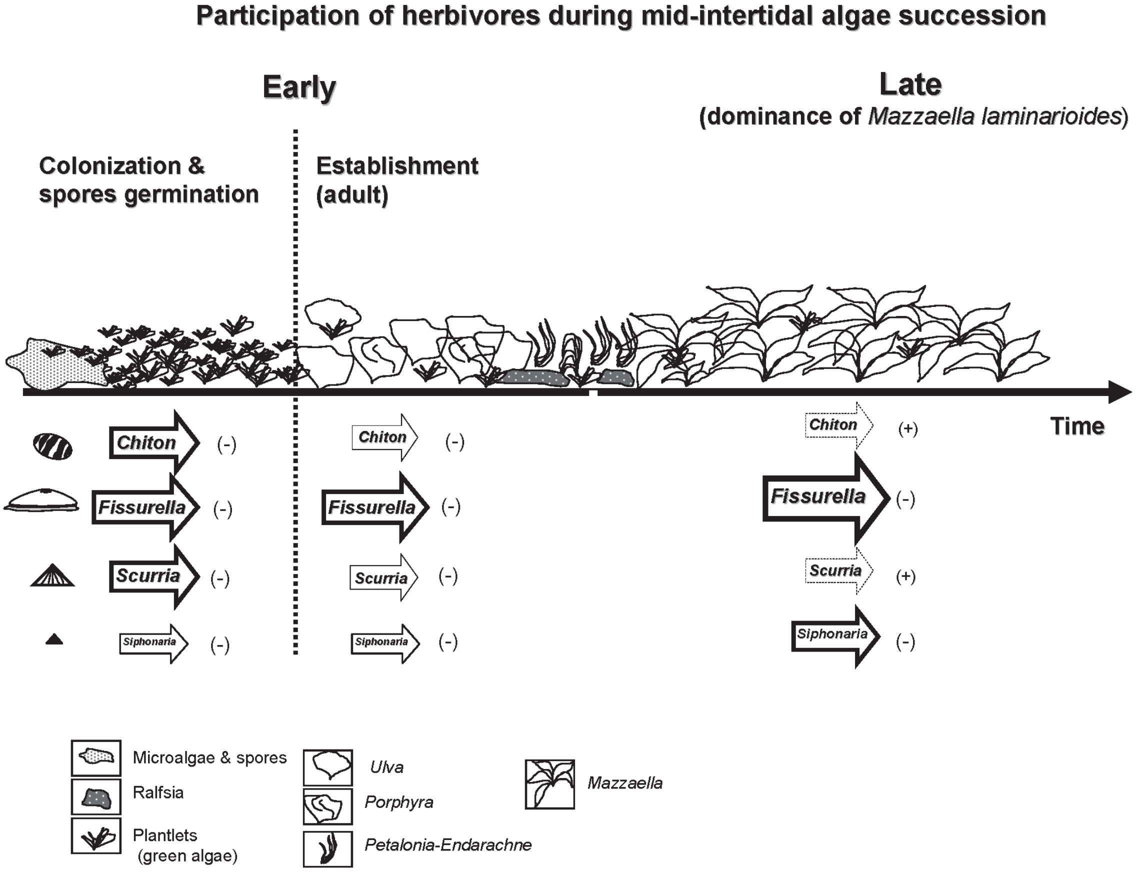

Fig. 1: Scheme of the relative participation of molluscan herbivores during early and late algae community succession in the mid-intertidal zone. Early community succession is separate in a colonization phase and establishment of the adult plants. Magnitude of per capita effects (recorded through field and laboratory experiments, see Aguilera 2010) of different molluscan herbivores are presented as solid arrow of different size. Potential effects (those awaiting further confirmation) are presented as punctuated arrows. Direction of effects is presented in front of each arrow (- negative; + positive). Key of algal groups are presented below.

Esquema de la participación relativa de moluscos herbívoros durante la sucesión algal temprana y tardía en la zona intermareal media. La sucesión temprana es separada en una fase de colonización y establecimiento de plantas adultas. La magnitud de los efectos per cápita (registrados a través de experimentos de terreno y laboratorio, ver Aguilera, 2010) de los diferentes moluscos herbívoros son presentados como flechas de distinto tamaño. Efectos potenciales (en espera de confirmación) se presentan como flechas punteadas. La dirección de cada efecto es presentada en frente de cada flecha (- negativo; + positivo). La clave de identificación de los grupos de algas es presentada en la parte inferior.

ceciliana (see Espoz et al. 2004), can have locally important effects on intertidal habitats through grazing on the shells of the mussel *Perumytilus purpuratus* (Santelices & Martinez 1988). Field experiments conducted by Santelices and Martinez (1988) suggests that, although mussels can trap spores of algae while immersed, feeding of *S. ceciliana* on spores and plantlets during the period of emersion prevents *P. pupuratus* being overcrowded by green algae which can diminish food availability for this mussels. This effect may be constant through time because limpets tend to forage persistently on the same mussel (author personal observation). Despite the potential phylogenetic inertia (see Webb et al. 2002) in either diet or morphology among scurrinids (Espoz et al. 2004), limited redundancy in effects would be expected in this limpet group because they could have differential habitat use likely related to different physiological and/or behavioural responses accounting for "functional niche" differentiation (Rosenfeld 2002). Both direct and indirect effects, commonly related to differences in behaviour and habitat use at micro-scales (cm) observed in some grazers present in the mollusc assemblage (Aguilera & Navarrete 2011), can contribute to the differences in the roles scurrinid limpets play in intertidal community. Further investigation is required to explore contribution of behavioural traits and the spatial niche of herbivores on the magnitude and also direction of their effects.

In contrast to most molluscs, sea urchins commonly exert strong per capita and population level effects on algal communities, and some studies conducted in Chile corroborate information recorded in other systems about the magnitude of impacts (see Vásquez & Buschmann 1997, Vásquez 2007 for review). Contreras and Castilla (1987) experimentally tested the effects of two sympatric sea urchins, *Tetrapygus niger* and *Loxechinus albus*. Utilizing intertidal rock pools (60 to 70 cm long; 45 to 50 cm wide) as experimental arenas, these authors found the two sea urchin species have differential feeding mechanisms accounting for differential effects on the algae community. The species *T. niger* consumes both benthic algae (e.g., *Gelidium*) and drift kelp (e.g., *L. nigrescens*), but when kelp drift availability is low (see Rodríguez 2003), juvenile and adult individuals can generate "halos" (i.e. bare rock patches) in the bed of intertidal pools. In turn, only juveniles of *L. albus* can produce small halos similar to *T. niger* while adult individuals (> 3 cm diameter) consume mostly floating algae (i.e. *Lessonia*, *Macrocystis*) (Contreras & Castilla 1987). Previous studies (e.g., Dayton 1985) suggest populations of the two sea urchins can shift the algae assemblage to an "alternate state" (sensu Sutherland 1974) in the low intertidal and subtidal community. One state in the presence of these grazers is dominated by calcareous crusts ("barrens"); meanwhile in the absence of these grazers kelp forest develop. In contrast, Contreras and Castilla (1987) found *T. niger* is the only species capable of forming barren grounds. These authors suggest that differences in effects may be related directly to the different feeding apparatuses of these urchins; the Aristotle's lantern in *T. niger* is twice as long as that in *L. albus*, and this last species possesses modified aboral podia ("suckers") which help mostly in the capture and transport of food (algal drift) to the mouth. In general, both species commonly aggregate forming dense patches in low-tidal pools (mainly juveniles in the case of *L. albus*, see Vásquez 2007) generating high small-scale (cm) impacts in benthic habitats. According to differentiation in their feeding patterns, sea urchin species might have dissimilar even complementary ecological roles in low intertidal and subtidal habitats.

Although it was previously suggested that herbivorous fish play minor roles in temperate shores (Lubchenco & Gaines 1981), field experiments conducted in Chile suggest they can have enormous effects on both colonization and establishment of different functional groups of algae (see Muñoz & Ojeda 1997, Horn & Ojeda 1999, Ojeda & Muñoz 1999). The blennid fish *Scartichthys viridis* commonly ventures into mid-to low intertidal habitats grazing selectively on ephemeral algae and epilithic microalgae (Muñoz & Ojeda 1997, Ojeda & Muñoz 1999). Therefore, this fish can reduce biomass of ulvoids and other ephemerals, drastically affecting algal composition of early successional community (Ojeda & Muñoz 1999, Muñoz & Ojeda 1997).

The effect of *S. viridis* resembles the effect that molluscan grazers have on algal communities (Moreno & Jaramillo 1983, Aguilera 2010). Contrary to most molluscan grazers, the browser/grazer *Girella laevifrons* and the browser *Aplodactylus punctatus* can quickly remove large pieces of algae by cutting the distal portion of adult plants (Stepien 1990, Cáceres et al. 1993, Horn & Ojeda 1999). In this context, experimental exclusion of fish, molluscs and both taxa conducted in the mid-intertidal of a wave exposed platform in central Chile (see Aguilera 2010), showed that the effect of the fish assemblage (un-identified browser species) was concentrated in the distal portion of blades of both ephemeral (i.e. ulvoids) and corticated (i.e. *Mazzaella*) algae (Aguilera & Navarrete, unpublished data). A recent study suggests the effect of browsing fish on corticated *Mazzaella* could be common even in the mid-intertidal zone during the immersion period of the rock platforms (Escobar & Navarrete, unpublished data).

In functional terms, the fish *S. viridis* may have similar, even redundant, roles to those observed for most molluscan grazers (i.e. chitons, scurria limpets) during early succession. Browsing fish may entirely compensate (according to their potential high per capita consumption, see below) the effects of fissurellid limpets on adult established algae (both corticated and ephemerals). Commonly, molluscan herbivores forage during the low-tide period (when rock is wet, Aguilera & Navarrete 2011) while fish venture onto flat platforms when they are completely immersed. Thus, these herbivores could have more complementary than redundant roles on the algae community due to temporal niche differentiation (Carothers & Jaksic 1984) which needs to be further explored.

In general, because body size is related to consumption rate, handling times and foraging range (Mittelbach 1981), this could greatly determine the magnitude of consumers' effects. The magnitude of per capita effects of different species has been positively related to body size in different assemblages (e.g.,Wood et al. 2010). For example, data on the per capita effect of herbivores on green ephemeral algae measured through field experiments in the mid-intertidal in central Chile, during the colonizing phase of early succession (0 to 3 months of field experiments, see Aguilera 2010), show a linear relationship between per capita effect and body size (see Fig. 2, grey circles). The magnitude of effect of different herbivores appears to be also related to body size at different times of community succession (early v/s late succession see Fig. 1, Aguilera 2010). Although little published data are available, based on reported body size of some herbivore species per capita effects may be estimated/predicted (see Fig. 2). This estimation, however, must be considered with caution because other traits (e.g., foraging behaviour) of the different species may well modify this picture (see below). Thus the fish *Scartichthys viridis* (body size = 75.67 ± 97.44 g, Muñoz & Ojeda 1999) and the chiton *Enoplochiton niger* (body size = 75.26 ± 2.58 g, Broitman et al. unpublished data), can be predicted to have a large mean per capita effect on ulvoids compared with most molluscan grazers (see Fig. 2 black square and diamond respectively). The medium size species *Scurria viridula* is predicted to have moderate effects compared with other scurrinids (i.e. *S. araucana*) and chitons (see Fig. 2 black triangle). In this context, field experiments by Ojeda & Muñoz (1999) report larger effects for *S. viridis* on ulvoid abundance than the present analysis suggests (see Fig. 2 black square). Therefore, analyses based solely on body size may underestimate real per capita effects of large herbivores and need to be considered with caution.

Both theoretical and experimental studies suggest body size is positively related to foraging range (e.g., displacement length at foraging) (see Mittelbach 1981, Wood et al. 2010). Range of movement during foraging could explain the importance of body size of herbivores on the magnitude of their effects. In contrast to this, studies by Aguilera & Navarrete (2011) showed that *S. lessoni*, the smallest herbivore considered (0.97 cm ± 0.07 cm shell length), had intermediate foraging excursions of 24.6 cm (± 3.7 cm) from resting areas (i.e. crevices) with low effects on ulvoids (see Fig. 1 and 2). In turn, *S. araucana* a medium sized species (2.6 cm ± 1.2 cm shell length) had shorter excursions (6.5 cm ± 3.9 cm) from its homing scars and an intermediate size effect on ulvoids (Fig. 1 and 2). Therefore, other behavioural traits related to consumption rate and/or responses of herbivores to predator pressure (for molluscs responses, see Espoz & Castilla 2000, Escobar & Navarrete 2011) may also be of interest to understand changes in the magnitude of effect of different herbivores on algae biomass.

It is worth noting that humans can act as selective herbivores harvesting different algae species (i.e. clipping, trimming or detaching entire plant), thereby modifying both intertidal and subtidal algal community structure (see Branch & Moreno 1994, Moreno 2001 for review). As presented above, some herbivores are able to consume competitively dominant algae species (e.g., *Mazzaella*) enhancing intertidal community diversity. Since humans also harvest keystone herbivores (e.g., fissurellid limpets) they can reduce algal diversity through increasing the abundance of dominant algae species (Moreno et al. 1984, Oliva & Castilla 1986). When harvesting is concentrated on the dominant alga, community diversity can be enhanced again because abundance of non-exploited species rise (Branch & Moreno 1994). Therefore, human impacts in both herbivores and algae abundance (acting as predator and herbivore respectively) can provoke dramatic alterations of herbivore-algae interaction strengths and thus food web structure (Moreno et al. 1984, Oliva & Castilla 1986, Branch & Moreno 1994). Future studies should take into account the direction and magnitude of human effects on consumer-resource interactions, because this could shed light on the contribution of specific interactions (e.g., *Fissurella-Mazzaella*) to ecosystem resilience.

Physical regulation of herbivores' effects

There is evidence that the abundance and composition of both herbivores and algae are strongly affected by bottom up processes such as coastal upwelling (Broitman et al. 2001, Camus 2001, Nielsen & Navarrete 2004, Thiel et al. 2007). Commonly, onshore larval transport is

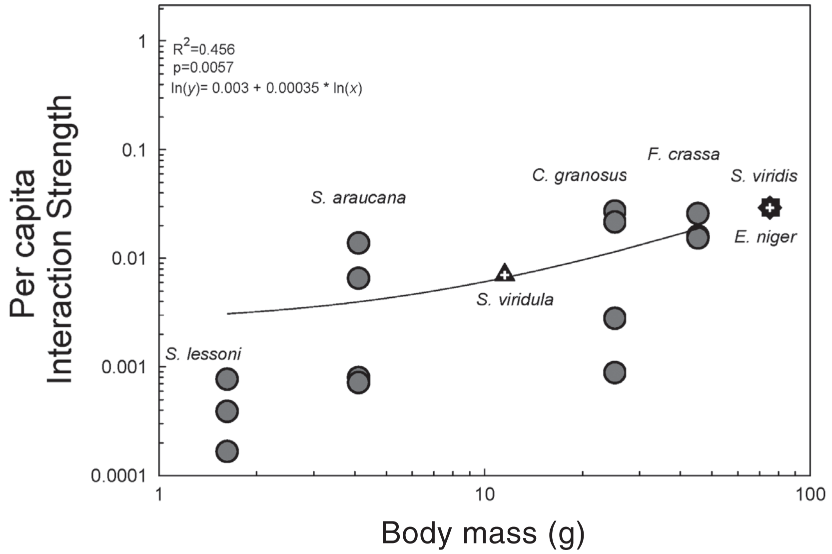

Fig. 2: Linear regression between magnitudes of per cápita effect, recorded through field experiments at the colonizing phase of intertidal succession, and body size (g) of molluscan herbivores: *Siphonaria lessoni*, *Scurria araucana*, *Chiton granosus*, *Fissurella crassa*. Each circle represents a replicate plot. Expected mean effect are presented for *Scurria viridula* (black crossed triangle), *Enoplochiton niger* (black crossed diamond) and for intertidal fish *Scartichthys viridis* (black crossed square) (individuals mean size from Sanhueza et al. 2008, Ojeda & Muñoz 1999 and Broitman et al., unpublished data).

Regresión lineal entre la magnitud de los efectos per cápita, estimados a través de experimentos de terreno durante la fase de colonización de la sucesión intermareal, y el tamaño corporal (g) de los siguientes moluscos herbívoros: *Siphonaria lessoni*, *Scurria araucana*, *Chiton granosus*, *Fissurella crassa*. Cada círculo corresponde a una réplica experimental. Se presentan los efectos promedio esperados para *Scurria viridula* (triángulo negro-cruzado), *Enoplochiton niger* (diamante negro-cruzado) y para el pez intermareal *Scartichthys viridis* (cuadrado negro-cruzado) (tamaño individual promedio tomado de Sanhueza et al. 2008, Muñoz & Ojeda 1999 y Broitman et al., datos no publicados).

affected by different oceanographic conditions like upwelling which can alter the abundance of benthic species with free living larvae (e.g., Shanks et al. 2000). Additionally, nutrient loading can greatly account for variation in biomass and growth rates of different functional groups of algae affecting herbivore-algae interactions (Nielsen & Navarrete 2004). Therefore, differences in the magnitude of per population effects of herbivores at large spatial scales (e.g., sites separated by 10s of kilometers) are expected according to different oceanographic processes operating along coastal ecosystems (e.g., Bustamante et al. 1995, Thiel et al. 2007). In this context, through excluding small-non fissurellids molluscan grazers in sites with different upwelling intensity in central Chile, Nielsen & Navarrete (2004) showed that abundance of molluscan grazers (chitons, scurrinid limpets and *S. lessoni*) and both composition and abundance of different functional groups of algae differs with levels of seashore productivity. Both the abundance of green ephemeral algae (formerly ulvoids) and the biomass of molluscan grazers were observed to be high in zones of low upwelling intensity (i.e. Las Cruces and El Quisco); meanwhile the cover of corticated algae (formerly *Mazzaella*) was low. In turn, abundance of corticated algae increases in sites of high upwelling intensity (i.e. Matanzas and Pichilemu). This information suggests consumptive effects of herbivores on algae may be compensated by increases in tolerances of algae to consumption. For example, despite the high densities of grazers in low upwelling localities the magnitude of their effects (at the population-level) on green ephemeral may be dampened by high growth rates of these algae. Furthermore, since the growth rate of corticated algae are enhanced by upwelling (Nielsen & Navarrete 2004, Wieters 2005), biomass and even composition of these algae could be regulated by oceanographic conditions rather than herbivores (see Wieters 2005). Thus, "herbivory intensity", which is a function of herbivore consumption relative to plant growth rates (Lubchenco & Gaines 1981), could be modified, but not completely altered by, local oceanographic conditions. Some generality, however, in the foraging pattern of molluscan grazers (i.e. patellid limpets), over broad geographical scales, has been reported in other coasts (i.e. European) (e.g., Jenkins et al. 2001). Therefore, it is necessary to explore potential geographic variability in consumption effect of different herbivores in order to disentangle their role in different communities.

In the same context, as community composition is also determined by species responses to local environmental stress, they can also determine differential trajectories of community succession. In a grazer exclusion experiment which considered thermal stress amelioration (by seawater drainage), Buschmann (1990) showed that in the presence of grazers but without water drainage green ephemeral algae can persist through different seasons. However, in presence of both grazers and seawater drainage calcareous crusts of *Ralfsia* sp. dominate the substratum, thus outcompeting the ulvoids (Buschmann 1990). Thus, despite different studies showing that green algae are consumed by diverse herbivore species (see above), thermal stress may well modify foraging rates or herbivore effectiveness at low spatial scales (see below) and/or algae growth rates. This can be especially relevant to explain among replicate variability in the effect of herbivores commonly observed in experimental studies. Therefore, Buschmann's experiments suggest desiccation can modify the model used to explain algal successional patterns and that some physical factors are a causal component at the community level and not only a factor modulating the biotic interactions.

Commonly, many experimental studies tease apart variation in "herbivore effectiveness" (number of plants or biomass removed per unit time; Lubchenco & Gaines 1981) by physical condition of the environment (i.e. temperature, desiccation, etc.). Behavioural performances of herbivores such as time they spend foraging, or the amplitude of foraging excursions can be constrained by physical stress, predators or food supply (e.g., Jenkins & Hartnoll 2001, Ng & Williams 2006, Escobar & Navarrete 2011). Indeed, species inhabiting the mid to high intertidal zones are exposed to high thermal stress, because tidal variation exposes animals to substrate heating, freezing and/or desiccation (Williams & Morritt 1995, Finke et al. 2007). In the low intertidal, however, animals are mostly exposed to wave stress which can dislodge both active and resting individuals. This physical gradient may generate a vertical gradient in the effectiveness of herbivores in determining spatial distribution of algae abundance and/or composition (see Underwood 1980). However, recent studies dealing with molluscan grazing in the rocky intertidal showed that the effect of herbivores can not follow a gradient, but instead has a patchy distribution (Díaz & McQuaid 2011). In this context, studies conducted in Chilean coasts have shown that a patchy distribution of resources can resemble the spatial distribution of grazer' abundance generated by behavioural escape, or response, to thermally stressful conditions (e.g., migration, Muñoz et al. 2005, shelter use, Aguilera & Navarrete 2011).

Empirical data shows that the roles herbivores play in intertidal community structure appear to be related to their foraging modes, behavioural responses to the environment and body size. Specifically, "grazers" can free space through feeding on spores and plantlets of macroalgae, thus calcareous and non-calcareous crusts and barnacles persist in areas of intense grazing. Therefore, determination of the levels of redundancy or similarity in the effects of this "sub-set" of species (i.e. grazers) may be of interest. In turn, species with either "browser" or "browser/grazer" mode of feeding (i.e. *Fissurella*, fish), are also capable of consuming adult plants of both ephemeral and corticated algae. Taken together, field experimental studies suggest that these two "sub-sets" of intertidal herbivores may have complementary roles on algae control through differentiation in their feeding modes as reported for other invertebrate species in terrestrial systems (e.g., spiders, Schmitz 2009). At the population level, however, the effect observed for most herbivores may be expected to vary in magnitude modulated by changes in the physical factors affecting algae growth rate, and both abundance and composition of herbivores (Nielsen & Navarrete 2004, Wieters 2005).

POSITIVE EFFECTS OF HERBIVORES ON ALGAE

The potential for positive effects of terrestrial grazers on plant fitness has been discussed extensively in the past (see McNaughton 1986, Belsky 1987). The traditional view that herbivores produce negative effects on plants was challenged by the "Grazing Optimization Hypothesis" (Owen & Wiegert 1976, McNaughton 1986). In a general view, this hypothesis states that primary productivity, or even plant fitness, is maximised at an intermediate level of herbivory. It could happen because plants can compensate or even over-compensate the effects of herbivore consumption at an intermediate level (see Agrawal 2000 for review). Through dispersing seeds of some palatable plants, herbivores can also compensate for the damage they exert on it. In this context, spore dispersion and algae tissue survival following herbivore consumption has been widely reported in Chilean intertidal systems (Santelices 1992).

Algae survival to grazing

Some studies conducted in Chile have reported that sexual and asexual reproductive tissue of some algae can pass alive through the gut of many intertidal invertebrate grazers and fish (apparently not reported in other latitudes!). The validity of the phenomenon was first evaluated by Santelices & Correa (1985) in an assemblage of intertidal molluscan grazers present in central Chile. In this study, on average 56 % of the 27 algal species found in the gut content of these grazers can survive digestion and are able to grow in cultures started from the faecal pellet. Opportunistic or ephemeral algae species (e.g., ulvoids) had a much greater ability to pass alive along the digestive tract of molluscan grazers than corticated species (Santelices & Correa 1985, Santelices 1992).

Diverse mechanisms of algae ingested by grazers have been observed in lab cultures, for example tissue regeneration or protoplast release (see Santelices & Ugarte 1987). In Chlorophyta, for example, the protoplasts can develop flagella and settle in the bottom of the culture vessel originating new talli (see Santelices 1992). Different algae species can have different capacities to survive digestion, but the characteristics of the feeding apparatus and enzymatic compounds of grazers can be of great relevance. For example, Santelices (1992) found that only a small proportion of algae survive the passage through the digestive tract of *Chiton granosus* which have an apparently efficient radular apparatus (see Steneck & Watling 1982 for molluscs' radular characteristics). In contrast some species of littorinid snails can stimulate the protoplast release more than chitons. Furthermore, the gastric compound characteristics of some species of grazers can be of great importance to spore survival. For example only two of 16 species of algae can survive digestion by the fish *Sicyases sanguineus*; this was attributed to the efficient action of different enzymatic compounds (Payá & Santelices 1989).

Other components should also be considered to explain algae survival after digestion, for example the state of hunger of the animals. Clearly if an animal has recently eaten many propagules of some item, other recently ingested items are more likely to survive digestion. But when the animal is hungry few fragment are able to survive. Both enzymatic mechanisms and physiological state of herbivores are thus directly involved in this process (Bozinovic & Martinez del Río 1996).

Spore dispersal by herbivores

Dispersion of propagules of algae by grazers can be considered a positive mutualistic animal-plant interaction in which the animal receives an energy input from algae consumed, or from some parts of it, and the algae gain a potentially effective dispersing mechanism. One example of this mechanism is presented in the amphipod *Hyale media* (Buschmann & Santelices 1988). This species tears up the mature cystocarps of the red algae *Mazzaella laminarioides*, releasing the spores and thus transporting them in their legs and body to other sites (see also Buschmann & Bravo 1990, Buschmann & Vergara 1993). This mechanism could be of great importance for algal species that have restrictive dispersal mechanisms (i.e. unflagellated spores of *Rodophytes*) and that could need this kind of transport to compete with other algae with wide dispersal strategies (see Santelices & Ugarte 1987, Buschmann & Bravo 1990). Despite the documented cases of spore dispersing, no studies have been yet conducted to explore the importance of these mechanisms in plant-plant competitive interactions.

Field and laboratory studies conducted by Santelices & Bobadilla (1996), report an increase in benthic spore abundance in the presence of molluscan grazers. Pedal mucus of the species *Tegula atra* and littorinid snails can differentially trap propagules of the algae *Ulva rigida*, *Mazzaella laminarioides* and *Lessonia nigrescens* (Santelices & Bobadilla 1996). Because most molluscs lay an inter-individual mucus trails when they move (see Davies & Hawkins 1998), some herbivores could facilitate formation of algal patches at micro-scales (cm) according to their spatial dispersion and scale of movements at foraging. Further studies should consider this mechanism of spatial heterogeneity in algae distribution in intertidal habitats.

Gardening

Through resting in a fixed site some intertidal grazers can affect the micro-space (scale of cm) that surrounds these sites increasing the abundance of algae they commonly consume. The area affected by grazing, some centimetres around the area where grazers rest, is considered a "garden" (Branch 1981, Branch et al. 1992) where the algae consumed by these herbivores (e.g., green algae) persist at higher abundances at micro-scale (cm). Grazers can eliminate competing species of algae that colonize the gardens, defend aggressively these territories against other grazers precluding overexploitation, and maintain low consumption rates (Stimson 1970, Branch et al. 1992, Plaganyi & Branch 2000). Because "gardening" is correlated with systems of poor productivity (Branch et al. 1992), this behaviour drives herbivores to a specialized diet which reflects the degree of adaptation of different species to changes in the physical and chemical environment where they live.

Although "gardening" is common in other systems in molluscs, fish and some Polychaeta (Plaganyi & Branch 2000), in Chile only one study examines the possibility of gardening behaviour and associated territoriality (i.e. in the grazer *Scurria araucana*; Morales & Camus 2005 In: Resúmenes XI Congreso Latinoamericano de Ciencias del Mar, Valparaíso Chile, see also Rojas & Ojeda 2007). Well developed homing behaviour, together with short foraging excursions observed in some species of the scurria genus (i.e. *Scurria plana*, *S. zebrina*, *S. viridula*; author personal observations), could be indicative of this behaviour. However, no aggressive responses associated with territoriality, nor clear "gardens" have been yet reported in these species.

Other positive effects and compensatory potential

A potential positive animal-kelp interaction between the limpet *Scurria scurria* and *Lessonia nigrescens* has been suggested in the past (Santelices 1987). The species *S. scurra* live inside cavities bored in the proximal parts of the stipes of the kelp *L. nigrescens* (Santelices et al. 1980). When the stipe is larger and heavy, the grazing effect of *S. scurra* increases the probability that stipes can be removed by water drag. Thus, this reduces the risk for entire plant of *L. nigrescens* to become so heavy to be susceptible to detachment by water drag increasing their longevity compared with plants where *S. scurra* is absent (see Santelices et al. 1980). Therefore, *S. scurra* appears to have a positive effect on populations of *L. nigrescens* playing a specific, albeit unique, role which could require a thorough re-examination because no recent information is available dealing with this specific grazer-kelp interaction.

In general, few studies have been conducted to evaluate the potential compensatory or over-compensatory growth responses of algae against consumption by herbivores. However, compensatory potential has been reported in subtidal systems. For example, a recent study reports that the subtidal kelp *Macrocystis pyrifera* can compensate for the grazing of the amphipod *Peramphithoe femorata* (Cerda et al. 2009). Through resource allocation to grazed blades, *M. pyrifera* are able to tolerate intermediate intensity of consumption following the main expectation of the "grazing optimization hypothesis". Thus, it is of interest to explore the frequency of compensation of algae to herbivore's consumption in intertidal habitats and also grazing intensity triggering this response. It is also of interest to determine whether positive effects on algae fitness are either sensitive or entirely independent of herbivore identity as the optimization hypothesis suggests.

TABLE 1

Main advances in knowledge about functional roles of herbivores, and future avenues for studies dealing with their effects on intertidal community structure.

Principales avances en el conocimiento de los roles funcionales de los herbívoros, y direcciones futuras para estudios centrados en sus efectos sobre la estructura de comunidades intermareales.

Advances since Santelices' (1987) review	Future avenues, studies focused on:
A. Establishment of clear differentiation in functional roles within different assemblages (i.e. low functional redundancy).	A. Potential for functional compensation among species within assemblages.
B. Characterization of herbivores' contribution during algal succession (identity effect).	B. Factors affecting behavioural strategies (e.g., time spent foraging, home range) of herbivores, and consequences in spatial distribution of resources.
C. Importance of herbivores' functional traits; behavioural patterns, body size and feeding modes in their effects on algal communities.	C. Physiological and behavioural responses of herbivores to local stress.
D. A clear potential for omnivory across different taxa broaden their functional roles in intertidal community	D. Feeding plasticity and animal food selection by generalist herbivores.
E. Importance of physical factors (e.g., nutrient supply, desiccation) modulating herbivore effectiveness and functional effects.	E. Geographic variation in herbivores roles and potential shifts in their functional structure (e.g., from redundancy to complementarity).
F. Relevance of chemical induction of algal defenses by small herbivores in consumer-resource interactions.	F. Algal compensation, or even overcompensation, (e.g., in growth, reproduction) after herbivores' attack.
	G. Human impact as potential mediator of specific herbivore-algae interactions.

CONCLUDING REMARKS

In general, knowledge about the role of herbivores in the intertidal community in Chile is still scarce considering the high diversity of species present in the Chilean coasts (Fernández et al. 2000). Nevertheless, enormous advances have been made since the last review of the topic by Santelices (1987) encouraging future avenues of research on the functional roles of herbivores in intertidal communities (summarized in Table 1).

A number of studies suggest quantitative as well as qualitative differences in herbivore effects in different latitudes (e.g., temperate versus tropical). This may be related to the thermal tolerances, behavioural responses and changes in both composition and abundance of herbivores over geographical scales (Rivadeneira et al. 2002; Rivadeneira & Fernández 2005) (see future avenues Table 1C and 1E). Since both the growth rate and survival of algae are influenced by the interaction of temperature and herbivores (Rothausler et al. 2005), herbivore-algae interactions could vary in a predictive way across latitudes (see future avenues Table 1E).

Studies dealing with effects of herbivores on algae life history, and both algal population and community dynamics (i.e. succession) are of great interest to understand how changes of assemblage composition translate into variation in both food web structure and ecosystem functioning. Through consumption of different primary producers (macroalgae and microalgae), and through generation of bare space, herbivores can perform important functional roles at the community level (see main advances Table 1A and 1D). Likewise, because herbivores are also consumed by other species, including humans, both individual functional traits and population-level information are also of great interest to understand their impacts on ecosystem processes (Schmitz 2008). Whether intertidal herbivores have redundant (= equivalents) or complementary roles (e.g., Walker 1992, Naeem 1998, Loreau 2004) on Chilean intertidal communities has been poorly explored. Future studies should also focus on the potential for functional or numerical compensation among different species and assemblages (Ruesink & Srivastava 2003) (see future avenues Table 1A). Un-explored effects of intertidal herbivores like polychaeta and crustacea, among others, limit predictions about true compensation after potential species extinction or regional contractions of populations (see Jaksic 2003, Rivadeneira & Fernández 2005). According to findings regarding animal diet and differential impacts that herbivores exert on intertidal communities in Chile (see main advances Table 1A, 1D), they might not be properly considered as part of a single “functional group” or “functional guild” (Simberloff & Dayan 1991, Díaz & Cabido 2001). Thus, how herbivores are functionally related through their effects on community structure and the role they play on ecosystem functioning could be a task for the future of herbivore-algae interaction studies in Chilean intertidal communities.

ACKOWLEDGEMENTS: I greatly appreciate the comments and helpful criticism of Bernabé Santelices (CASEB-PUC), Martin Thiel and Bernardo Broitman (CEAZA-UCN) to an early draft of the manuscript. Preliminary ideas of this review were conceived during my PhD training; advice from Sergio Navarrete (ECIM-PUC) during this time is greatly appreciated, and also support from the Andrew Mellon Foundation and CONICYT scholarship. I thank all ‘Chango-LAB’ and ‘ECIMinianos’ for camaraderie and friendship. Financial support for finishing this manuscript was provided by Bernardo Broitman (CEAZA-UCN) through Fondecyt grant # 1090488. Dr. Stuart Jenkins (Bangor-UK) and two anonymous referees greatly improved a final version of this manuscript.

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Associate Editor: Álvaro Palma
Received March 4, 2011; accepted May 12, 2011

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