

Functional identity and functional structure change through succession in a rocky intertidal marine herbivore assemblage

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Abstract. Despite the great interest in characterizing the functional structure and resilience of functional groups in natural communities, few studies have examined in which way the roles and relationships of coexisting species change during community succession, a fundamental and natural process that follows the release of new resources in terrestrial and aquatic ecosystems. Variation in algal traits that characterize different phases and stages of community succession on rocky shores are likely to influence the magnitude, direction of effects, and the level of redundancy and complementarity in the diverse assemblage of herbivores. Two separate field experiments were conducted to quantify per capita and population effects and the functional relationship (i.e., redundancy or complementarity) of four herbivore species found in central Chile during early and late algal succession. The first experiment examined grazer effects on the colonization and establishment of early-succession algal species. The second experiment examined effects on the late-successional, dominant corticated alga *Mazzaella laminarioides*. Complementary laboratory experiments with all species and under natural environmental conditions allowed us to further characterize the collective effects of these species. We found that, during early community succession, all herbivore species had similar effects on the ephemeral algae, ulvoids, but only during the phase of colonization. Once these algae were established, only a subset of the species was able to control their abundance. During late succession, only the keyhole limpet *Fissurella crassa* could control corticated *Mazzaella*. The functional relationships among these species changed dramatically from redundant effects on ephemeral algae during early colonization, to a more complementary role on established early-successional algae, to a dominant (i.e., keystone) effect on late succession. This study highlights that functional relationship within consumer assemblages can vary at different phases and times of community succession. Differentiation in herbivore roles emphasizes the need to evaluate consumer's impacts through different times of community succession, and through experimental manipulations to make even broad predictions about the resilience or vulnerability of diverse intertidal assemblages to human disturbances.

Key words: Chile; ephemeral algae; functional redundancy; functional roles; grazing; herbivores; human impact; interaction strength; keystone species; rocky shore.

INTRODUCTION

Subtle functional similarity or dissimilarity among species within functional groups have been observed to drive large changes in community composition as well as profound alterations of multiple ecosystem processes (Walker 1992, Loreau et al. 2001, Naeem and Wright 2003, Heemsbergen et al. 2004). Human impacts on the environment, from local to global scales, can cause not only a general decline in biodiversity, but also functional shifts, as sets of species with distinct effects in an ecosystem function are replaced by others (Grime et al. 2000, Hughes et al. 2003, Myers and Worm 2003,

Perrings et al. 2010). Species functional identity is thus a key component of biodiversity (e.g., Hooper and Vitousek 1997, Downing and Leibold 2002, Díaz et al. 2003, Bruno et al. 2005, Burkepile and Hay 2010). The challenge is then to understand, predict, and manage functional alteration of ecosystems, identifying the mechanisms associated with different functional relationships among species (i.e., redundancy, complementarity) within assemblages (Díaz and Cabido 2001, Petchey and Gaston 2002, Bellwood et al. 2003). In a functional perspective, it has been considered that different assemblages can be characterized by the presence of either complementary (e.g., facilitative) or redundant (i.e., equivalent) species (e.g., Walker 1992, Naeem and Li 1997, Loreau 2004). These functional relationships determine different ecosystems responses to natural or human-caused disturbances. In the case of

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redundant species, evidence from experimental studies suggests that functionally identical species can potentially compensate each other after species loss, providing some degree of ecological insurance (see Bellwood et al. [2003] for coral fish assemblage, and Thibault et al. [2010] for rodent guild). In turn, complementary species perform distinctive roles by means of differentiation in functional traits (e.g., feeding modes), which can foster facilitation among species (e.g., Schmitz 2009), ecosystems resilience, and persistence of multiple functions (Loreau and Hector 2001, Cardinale et al. 2002, Bellwood et al. 2004).

Probably because determining the functional structure of complete consumer assemblages in marine and terrestrial ecosystems is a major task all by itself (Paine 1992, Chalcraft and Resetarits 2003a), it has been generally assumed that individual functional relationships, i.e., redundancy or complementarity, remain approximately constant in a given system as long as the number of species and species identity do not change. Abundant experimental evidence in different systems has demonstrated that overall functional effects of consumers vary widely with changes in diversity of both assemblages of resources and consumers (Duffy et al. 2001, Aquilino et al. 2004, Hillebrand and Cardinale 2004, Bruno et al. 2008). In addition, recent evidence strongly suggest that functional relationships within guilds can also vary through developmental stages of community (Burkepile and Hay 2010). The presence or absence of differential biological traits among the species composing the resource assemblage (i.e., functional diversity) are thus expected to influence the magnitude or strength of consumer effects (Berlow 1999, Duffy et al. 2001, Brose et al. 2005, Stachowicz et al. 2008, Hillebrand and Matthiessen 2009). For example, it has been observed that the strength of marine herbivore effects on algal biomass and abundance is highly dependent not only on resource species richness but also on phenological diversity and developmental stages (e.g., Díaz et al. 2001, Edwards et al. 2010). Plant traits, such as resistance and tolerances to herbivore consumption, growth rate, productivity, and plant size can change considerably through the lifetime of individual plants, changing edibility and palatability to herbivores. Similarly, herbivore feeding modes can change during development and likely cause different effects on plant assemblages (see Schmitz 2008). Several models assume that changes in herbivore control over plant biomass and composition are caused by changes in vegetation characteristics (e.g., Price 1991, Chase et al. 2000, Wise and Abrahamson 2007). Thus, in a consumer assemblage with homogeneous resource acquisition, functional similitude or redundancy could switch over time or space to a complementary functional relationship due both to changes in resource traits and consumers' feeding modes (Bellwood et al. 2003, Hillebrand et al. 2007, Hoey and Bellwood 2009). One important process causing continuous changes in

vegetation characteristics is community succession: the semi-orderly replacement of populations of different species over time (Connell and Slatyer 1977). Thus, succession in plant assemblages could have profound consequences on consumer functional roles and relationships, even though the consumer species composition might remain unaltered. Although succession characterizes terrestrial and marine community dynamics (e.g., Connell 1978, Farrell 1991, Berlow 1997, Navarrete and Berlow 2006), few experimental studies have directly addressed changes in consumer functional roles and relationships over different successional stages (see Burkepile and Hay 2010).

Generally, characterization of species in functional groups and functional relationships is based on the identification of morphological, taxonomic, or feeding traits of the species, commonly using multivariate methods that tease apart the different functional groups based on sets of correlated traits (Petchey and Gaston 2002, 2006, Micheli and Halpern 2005). Although useful to address some dimensions of the problem, this coarse functional classification has important limitations (Naeem and Wright 2003). Several studies have shown that there is a weak relationship, if any at all, between taxonomic diversity and functional diversity (Possingham et al. 2000, Naeem and Wright 2003). Furthermore, poor correlations between consumers' diet and their direct and indirect impacts on a given ecosystem function is common in many assemblages (Paine 1969), and especially when consumers also have large sublethal (e.g., behavioral) effects on prey (e.g., Sih and Wooster 1994). Therefore, the experimental approach is often the best or the only tool to provide reliable information about functional identity and functional relationships (Menge et al. 1994, Berlow et al. 1999, Duffy et al. 2001, Díaz et al. 2003, Resetarits and Chalcraft 2007).

Variation in per capita and population impacts (*sensu* Navarrete and Menge 1996) of the same consumer species has been experimentally measured in different guilds or taxonomic assemblages and has been usually related to spatial variation in environmental conditions or density-dependent factors (Paine 1992, Navarrete and Menge 1996, Wootton 1997, Ruesink 1998, Berlow et al. 2004). These estimates provide a means of comparing the effects of widely different species in a manner that relates to the dynamics of a measured response variable. Using this general approach and through a series of field and laboratory experiments, we investigated quantitative and qualitative variation in functional effects of molluscan herbivores as characteristics of the algal assemblage change over succession. All herbivore species show generalist diets, composed mostly of epilithical microalgae and green ephemeral algae, mostly ulvoids (Santelices et al. 1986), but also significant fractions of small stages of several invertebrate species, which are ingested while grazing on the rock surface (Aguilera 2005, Camus et al. 2008). Thus, species in this guild

(sensu Root 1967, Jaksic 1981) are usually classified within a single functional group (commonly as grazers). Small differences in diet are only loosely correlated to differences in buccal morphology among these mollusks (Santelices et al. 1986). Several studies have shown that some of these species can remove spores and algal germlings, especially of ephemeral algae, but they cannot control algal abundance once plants reach adult size (Otaíza 1986, Nielsen and Navarrete 2004, Aguilera and Navarrete 2007). From experimental studies conducted in central and southern Chile, it has been suggested that only a subset of species can have effects on adult established macroalgae (Moreno and Jaramillo 1983, Jara and Moreno 1984, Oliva and Castilla 1986), but no studies have simultaneously evaluated the role of the different species in the same assemblage and latitude. In this system, we evaluated the general hypothesis that despite the ample diet overlap, the strength and functional identity of herbivores change between early and late algal succession stages. We predicted that early during succession the herbivore assemblage presents high levels of redundancy and therefore resilience to species loss, while late in succession, when algal species are usually tolerant or resistant to herbivory (Lubchenco and Gaines 1981, Duffy and Hay 1994, Steneck and Dethier 1994), few herbivore species can control algal biomass, conforming more to a keystone pattern of functional structure.

METHODS

Intertidal community succession and focal species

Community structure of the wave-exposed mid-intertidal fringe at the site of Pelancura, central Chile (33°33' S, 71°37' W), where experiments were conducted, is characterized by the dominance of the mussel *Perumytilus purpuratus* and the corticated red alga *Mazzaella laminarioides*, which grows directly on the rock surface and onto the shells of mussels and barnacles. The fleshy crustose red alga *Hildenbrandia lecanellieri* can also cover large extensions of rock surface, interspersed with seasonally variable patches of foliose ephemeral algae, mostly ulvoids (Santelices 1990, Fernández et al. 2000, Broitman et al. 2001). Carnivore predators, such as the sea star *Heliaster helianthus*, the muricid gastropod *Concholepas concholepas*, and to a lesser extent crabs and birds, are common at the site and can create patches of bare substratum in the mid-intertidal zone (Castilla 1981, Navarrete and Castilla 2003). These patches are quickly colonized by periphyton (bacteria, diatoms, and microscopic stages of macroalgae), early-successional filamentous and foliose algae (green ephemerals, mostly *Ulva* spp., *Blidingia minima*, as well as the red alga *Porphyra columbina*), and, depending on the time of the year, barnacle spat (Santelices 1990, Fernández et al. 2000). The late-successional *Mazzaella laminarioides* becomes established only after 12–14 months from clearing the rock surface (Nielsen and Navarrete 2004, Aguilera and

Navarrete 2007). The herbivore guild in mid-intertidal levels includes about nine species of generalist mollusks belonging to four major distantly related taxa (by their common names; keyhole limpets, scurrinid limpets, pulmonate limpets, and chitons [Santelices et al. 1986, Espoz et al. 2004]). Two fish species, the blennid *Schartichtys viridis*, and the clingfish *Sicyases sanguineus*, have also been shown to consume macroalgae in channels and boulders of the low intertidal zone and on vertical walls (Cancino and Castilla 1988, Muñoz and Ojeda 1997). Unpublished studies (J. Escobar and S. A. Navarrete, *unpublished manuscript*) show that on occasion, fish also venture into mid-level platforms next to channels and pools, where they consume fronds of the corticated alga *Mazzaella laminarioides*. Therefore, we included fish in the design of the experiments to avoid potential confusion with mollusk grazing, even though their effect is expected to be less important on the ample wave-exposed platforms used in the experiments.

For our experimental studies we chose the most abundant species of each of the four different molluscan taxa in the mid-intertidal zone of wave-exposed platforms (Santelices et al. 1986), namely, the chiton *Chiton granosus*, the scurrinid limpet *Scurria araucana*, the pulmonate limpet *Siphonaria lessoni*, and the keyhole limpet *Fissurella crassa*. Differences in spatial distribution, activity patterns, and foraging excursions among these species have been described (Aguilera and Navarrete 2011). Of all the focal species, only *F. crassa* is collected for human consumption, which reduces the abundance of large adults in open-access areas as compared to marine reserves (Oliva and Castilla 1986, Castilla 1999). Therefore, population impact of this species should be different inside and outside marine reserves. Based on per capita effects, we provide estimates of population-level effects for this species under both conditions. According to morphological characterization of buccal apparatuses (see Steneck and Watling 1982), the focal species comprise a fairly diverse group of foragers. Chitons and scurrinid limpets have strong radular apparatus with the highest excavating ability (i.e., polyplacophoran and docoglossan radula, respectively), while keyhole limpets and *Siphonaria* present more fine teeth, with low excavating potential (i.e., rhipidoglossan radula).

Field experiments to quantify interaction strengths

Grazer effects on early succession.—To determine the effects of each species on the early colonization of spores, germinating plantules, and established stages of early-successional algal species, we set up an enclosure/exclusion experiment in the mid-intertidal shore at Pelancura. We selected 28 plots 25 × 25 cm in size, with a crevice (~3.0 cm wide, 3.0 cm deep) where animals could find shelter. The rock surface was scraped clean with drill-mounted brushes and manual chisels, removing all organisms, including encrusting algal fragments. In this manner, we reset community succession to the

initial colonization of bare rock surface. The general result of this brushing procedure, in terms of eliminating crustose algae that could regrow vegetatively, was similar to that obtained when using a propane torch to burn the rock surface (see Aguilera and Navarrete 2007). The following treatments were then randomly assigned to experimental plots (see Appendix A: Fig. A1): enclosure of (1) six individuals of *C. granosus*, (2) 12 individuals of *S. lessoni*, (3) one individual of *F. crassa*, and (4) two individuals of *S. araucana*. The number of individuals used in experimental enclosures attempted to match the natural densities of the species in the field (Santelices et al. 1986, Aguilera 2010) as well as their gregarious or individual habits (Aguilera and Navarrete 2011). In addition, we also set up (5) exclusions of all benthic grazers, (6) exclusion of benthic grazers and fish, and (7) control plots to which all benthic grazers and fish had unrestrained access (see details in Appendix A: Fig. A1). All treatments were replicated four times in a completely randomized design. Enclosures were made of stainless-steel wire fences (8 cm high, 7-mm mesh openings) fastened to the rock with stainless-steel screws. Gaps between the substratum and the fence were sealed with plastic mesh. Animals were collected from nearby areas, individually marked with bee tags glued to the shells, and transplanted into the plots. Previous studies have shown that fences are effective in keeping animals enclosed and produce little disturbance to animal movement and foraging, especially when they include crevices that provide shelter against heat stress (Garrity 1984, Aguilera 2010, Aguilera and Navarrete 2011). Nevertheless, we evaluated the potential impact of enclosures on animal behavior by following the “manipulated” (handled, marked, and transplanted into experimental plots) and randomly chosen “unmanipulated” (marked but not handled) individuals outside the experimental plots. Activity rhythms, movement, and crevice use of manipulated and unmanipulated animals were compared. The exclusions consisted of a fence with the same characteristics as enclosures, which prevented access to all benthic grazers, but fishes could still feed inside the plots. To exclude benthic grazers and fish (total exclusion), we put a colored nylon mesh (1.2 mm diameter, ~4.0 cm separation) atop the fences. This nylon mesh impeded access of fishes while keeping shading effects to a minimum. Finally, control plots were marked with stainless-steel screws in the corners, but otherwise unmanipulated.

Because enclosing all focal grazer species together (i.e., additive design) was impractical in the field due to the size of experimental areas (increasing plot size increased dislodgement by waves), the control areas provided the only information about total effects of grazers at natural densities in the study area. Because fish had no effects on early-successional stages (see *Results*; Appendix C), total effects can be attributed to

benthic grazers that were recorded inside the plots throughout the study.

Monthly from April through August 2008 we recorded the cover of sessile organisms (i.e., primary cover, no species grew on other sessile species during the course of the experiment) using a 25×25 cm quadrat with 81 uniformly spaced intersection points (see Steneck and Dethier 1994). Every 10–15 days we counted the number of marked and unmarked grazers in the plots during day and nighttime low tides, replacing lost individuals from enclosures when necessary. Natural density of benthic grazers at the study site was recorded through replicated transects parallel to shoreline with 40 25×25 cm contiguous quadrats. In addition, every month from March through September 2008 we collected individuals of all species to examine their diet through gut content analyses (see Appendix D for details).

Grazer effects on late succession.—Because the late-successional algal assemblage at mid-intertidal levels is characterized by the dominance of the red corticated alga *Mazzaella laminarioides* (Jara and Moreno 1984, Santelices 1990, Broitman et al. 2001, Nielsen and Navarrete 2004), we used this competitive dominant species as a means to compare per capita and population effects among grazer species (see Paine 1992, Navarrete and Castilla 2003, for similar approaches). This alga typically becomes established only after 12–13 months following rock clearance (Nielsen and Navarrete 2004, Aguilera and Navarrete 2007). Therefore, to standardize initial conditions among experimental treatments, we used transplants of fronds (adult plants) of *M. laminarioides*. This procedure simplified somewhat the late-succession community structure as compared to the natural system (Appendix F: Fig. F1), but allowed us to make more straightforward comparisons among grazer effects (see *Discussion*). New 25×25 cm areas were scraped clean and new grazer individuals were transplanted into experimental plots to guarantee independence between this and the experiment on early succession. Grazer enclosure treatments, exclusions of benthic grazers, total exclusions, and controls were the same as described previously (1–4; see Appendix A: Fig. A1), except that because fish have been shown to browse on *Mazzaella* frond (J. Escobar and S. A. Navarrete, *unpublished manuscript*), we used a colored nylon mesh atop all enclosure fences. In addition, to better isolate the potential effect of fish from benthic grazers, we also incorporated a fish exclusion treatment in four additional plots in which we used a partial fence with nylon mesh atop to exclude fish, but allowed benthic grazers through cuttings in all four sides (Appendix A: Fig. A1e). All experimental plots received a number of both cystocarpic and immature fronds of *Mazzaella* to complete 4.4 ± 1.7 g wet mass per plot. Frond length of every plant was measured in the laboratory and then the basal disc was glued to a $8.7 \times 5.0 \times 0.2$ cm acrylic plate with superglue “*la gotita*” (AKAPOL S.A., Buenos

Aires, Argentina). Plates were affixed to the rock inside each experimental plot with a flat head stainless-steel screw adjusted to the plate surface. Plants were replaced with new ones every 20–25 days. The experiment was conducted from 8 October to 7 November, and repeated two times from 15 November to 5 December 2008 and from 8 December 2008 to 24 January 2009. Treatments were haphazardly relocated and new animals and algal transplants were added between these trials. Data from the different repetitions of this experiment were pooled before analysis. At the end of the experiment, plants were weighed and frond length was measured in the laboratory. Any frond damage was recorded to help differentiate herbivore feeding marks.

Laboratory experiments with early- and late-successional algae

To complement field experiments and evaluate whether grazer effects on early and late succession were additive, synergistic, or antagonistic, we conducted consumption experiments in the laboratory of the Estación Costera de Investigaciones Marinas (ECIM) under ambient conditions (see Appendix A: Fig. A2). The design consisted of enclosures with individuals of each focal species alone in separate experimental “arenas” and in mixture or “polyculture” of all species together (see Bruno et al. 2008). Experimental arenas consisted of 40 × 40 cm concrete blocks with a crevice (20 cm long × 8.0 cm wide × 4.0 cm deep) carved in the center to provide a “natural” shelter for individuals. The arenas were surrounded with a barrier of antifouling paint, and a 10 cm high fence of coarse plastic mesh to prevent animals from abandoning the blocks (Aguilera 2010). All arenas were placed in aquaria with running seawater and air and were placed outdoors under ambient light and air temperature. High and low tides were simulated by immersing and exposing experimental arenas to air, following the natural tidal cycle observed at the time of the experiments. The following treatments were applied (see Appendix A: Fig. A2): (1) 3–4 individuals of *C. granosus* (total biomass per plot = 25.2 ± 1.39 g, mean ± SE), (2) two individuals of *S. araucana* (4.2 ± 0.57 g), (3) 6–7 individuals of *S. lessoni* (1.71 ± 0.07 g); (4) one individual of *F. crassa* (45.5 ± 5.7 g), (5) “all-herbivores” polyculture with three *C. granosus* + six *S. lessoni* + two *S. araucana* + one *F. crassa*, in which biomass of each species was adjusted to those present in individual species enclosures, and (6) a control for autogenic changes in algae, which was a similar experimental arena with no grazers. Experiments started after four days of acclimation of individuals, when mature (carposporic) measured fronds of the early-successional ephemeral *Porphyra* (~5.5 g), or late-successional *Mazzaella* (~10.0 g) were glued directly to the block surface inside experimental arenas. The red alga *Porphyra* sp. was chosen as a representative of early-successional species because of the ease of transplant and because it was common in field experiments.

Trials with early- and late-succession algae were run separately with different animals, and all treatments were replicated three times and randomly reassigned for each trial. Experiments were conducted for around 10 days, from 2 to 12 December 2008 and from 17 to 24 January 2009. Plants were then removed, counted, measured, and weighed, and frond damage was recorded.

Data analyses

Inspection of trends in algal cover following rock denudation in the early-succession field experiments allowed us to differentiate between two distinct phases (see Appendix B). The first phase (phase 1: “colonization”) was characterized by colonization, germination, and rapid growth of algae as they became established in the experimental plots (see *Results*). This colonization phase took about 2–4 months depending on algal species (see Appendix B: Fig. B1). In the case of the green alga *Blidingia minima*, separation between the two phases was less clear, as algal cover in some treatments continued to grow (e.g., in benthic exclusion) while in others had reached a plateau. Therefore, we used two different ending dates (June and July; see Appendix B: Fig. B1) to define phase 1 and calculate herbivore effects. Comparisons of different treatments in this stage allowed us to estimate mostly direct effects of grazers on plant colonization and before the propagation of indirect effects through the local species assemblage (Wootton 1993, Menge 1995, Berlow et al. 1999). The second phase (phase 2: “establishment”) corresponded to the phase when algal growth leveled off reaching the adult stage or even declined (see Appendix B: Fig. B1). Therefore, comparisons among treatments in this phase measured both direct and indirect effects of grazers on fronds of a target algal species already established in the plots (Berlow 1999). Besides grazer effects on target algal species, we quantified the grazers’ ability to generate or maintain bare rock (see Appendix B: Fig. B1d), which by itself represents an important function played by grazers and carnivores in rocky shores (Navarrete and Castilla 2003).

To quantify the strength of per capita grazer–plant interactions in field and laboratory experiments, we used the method proposed by Osenberg and Mittelbach (Osenberg and Mittelbach 1996), and Wootton (1997), referred to commonly as “dynamic index” (DI; see Berlow et al. 1999). This index is recommended when resources exhibit exponential growth and when prey is far from equilibrium (Berlow et al. 1999). The index was calculated as

$$DI = \left(\ln(\text{COV}_{\text{EN}}/\text{COV}_{\text{BE}}) \right) / Nt$$

where COV_{EN} is the specific algal cover in the herbivore enclosures, COV_{BE} is the algal cover in the benthic grazer exclusions, N is the density of herbivores in the experimental plots, and t is the elapsed time. We used

mean algal cover in the benthic grazer exclusion plots as the reference state because fish effects were negligible during the experiments as compared with the molluscan exclusion (see Appendix C). Estimates of population interaction strength were obtained as $DI \times$ natural density of herbivores in the field (Navarrete and Menge 1996, Berlow et al. 1999). In the case of *Mazzaella*, we considered the pooled data of three and two repetitions of the field and laboratory experiment, respectively. As before, we calculated per capita and population (collective in laboratory) interaction strengths using the DI index, but using adult plant biomass (grams) as the response variable. Based on our experimental estimates of per capita grazing effects for the commercially exploited *F. crassa*, we estimated population effects of this species inside the marine reserve of ECIM, where densities are higher because the species has been protected from humans for over 28 years (Castilla 1999). Confidence intervals (95%) for mean interaction strength estimates were obtained through a bootstrapping procedure (Efron and Tibshirani 1991, Manly 1997) considering all replicates of the experiment (see also Paine 1992). Additionally, we performed paired comparisons of effects between the two phases of early succession and for effects recorded in field and laboratory experiments (for *Porphyra* and *Mazzaella*) for each grazer species using a bootstrap *t* test as described by Manly (1997; see details in Appendix G).

RESULTS

Herbivore effects on early-succession community

Our experiments did not detect significant effects of fish on any of the species of algae that composed the early stages of succession (Appendix C). Therefore all results regarding early succession were based on herbivore enclosures, benthic grazer exclusions, and controls. The per capita and population effects of benthic herbivores on early-succession algae varied depending on algal species and to a lesser extent, between the two phases (colonization and establishment) of the early succession (Fig. 1; Appendix B: Fig. B1). Thus, we present results separately for the three main algal species observed during early succession.

In general, all molluscan herbivores except *Siphonaria lessoni* had strong, significantly negative per capita effects on the colonization of ulvoids (phase 1, white symbols in Fig. 1a), the most abundant species observed in early succession (Appendix B: Fig. B1a). Of these, *Fissurella crassa* had the largest negative per capita effect, but not significantly different from that exerted by *Chiton granosus* and *Scurria araucana*. After three months from initiating the experiment, when algae reached adult size (phase 2, solid symbols in Fig. 1a), all herbivores reduced their per capita effects on ulvoids. In the case of *C. granosus*, per capita effects were indistinguishable from zero (Fig. 1a; Appendix: Fig. B1a), and *S. araucana* had small but still significantly negative effects on ulvoid fronds. The keyhole limpet *F.*

crassa maintained strong but highly variable (across replicates) per capita effects on established ulvoids (Fig. 1a). Accordingly, bootstrap tests of significance showed that only per capita effects of *C. granosus* changed between the two phases of early succession (Appendix G: Table G1).

At the population level, effects on ulvoids were significant for *C. granosus* and *S. araucana* during the colonizing phase (phase 1 in Fig. 1b). The naturally high densities of these mollusks in the study site (which resemble densities observed at other sites of central Chile; see Santelices et al. 1986, Rivadeneira et al. 2002), account for strong population effects. In contrast, the strong per capita effects of *F. crassa* became comparatively negligible due to the low population density of this species in fishery-open areas. Using densities of *Fissurella* observed inside the ECIM marine reserve of Las Cruces makes the population effect of this species more comparable (population effect was -0.458 day^{-1} during colonization) to that of *C. granosus* and *S. araucana*. Indeed, the effect of *F. crassa* on ephemeral algae is predicted to be over five times higher inside the ECIM reserve than at the immediately adjacent study platforms in Las Cruces (see Appendix E: Fig. E1).

In the control treatment, to which all herbivores had access, we found a strong negative and significant effect on colonization by ulvoids and a smaller but still significant effect on established fronds. Expected herbivore effects based on an "additive" model of the four individual species effects (arrows in Fig. 1b) were within the 95% CI of the grazing effects observed in controls (all species acting together) during the field experiment, both during ulvoid colonization (open circle and arrow in Fig. 1b) and on established fronds (solid circle and arrow in Fig. 1b).

Taken together, these results suggest an important contribution of most but not all benthic grazers in controlling abundance of ulvoids during colonization, and weak to moderate effects once these algae get established. Three out of the four species had significant effects on colonization and two of the four species once plants were established. Furthermore, according to high densities of *S. araucana* and chitons and despite their moderate per capita effects, these two species can modulate ulvoid colonization, which appears to compensate the high per capita but low population effect of keyhole limpets on this alga in the fishery-open areas. Within reserves, where *Fissurella* is protected, all three species would have comparatively similar population effects on ulvoids, which could account for the low abundance of these algae inside the marine reserve (see Appendix E: Fig. E2).

A different pattern was observed in the case of the other most common green ephemeral alga, *Blidingia minima*. In this case, the per capita effects of *C. granosus* and *S. araucana* and to a lesser extent *S. lessoni* were negative, but too small and variable to be statistically significant either on colonization (phase 1) or when the

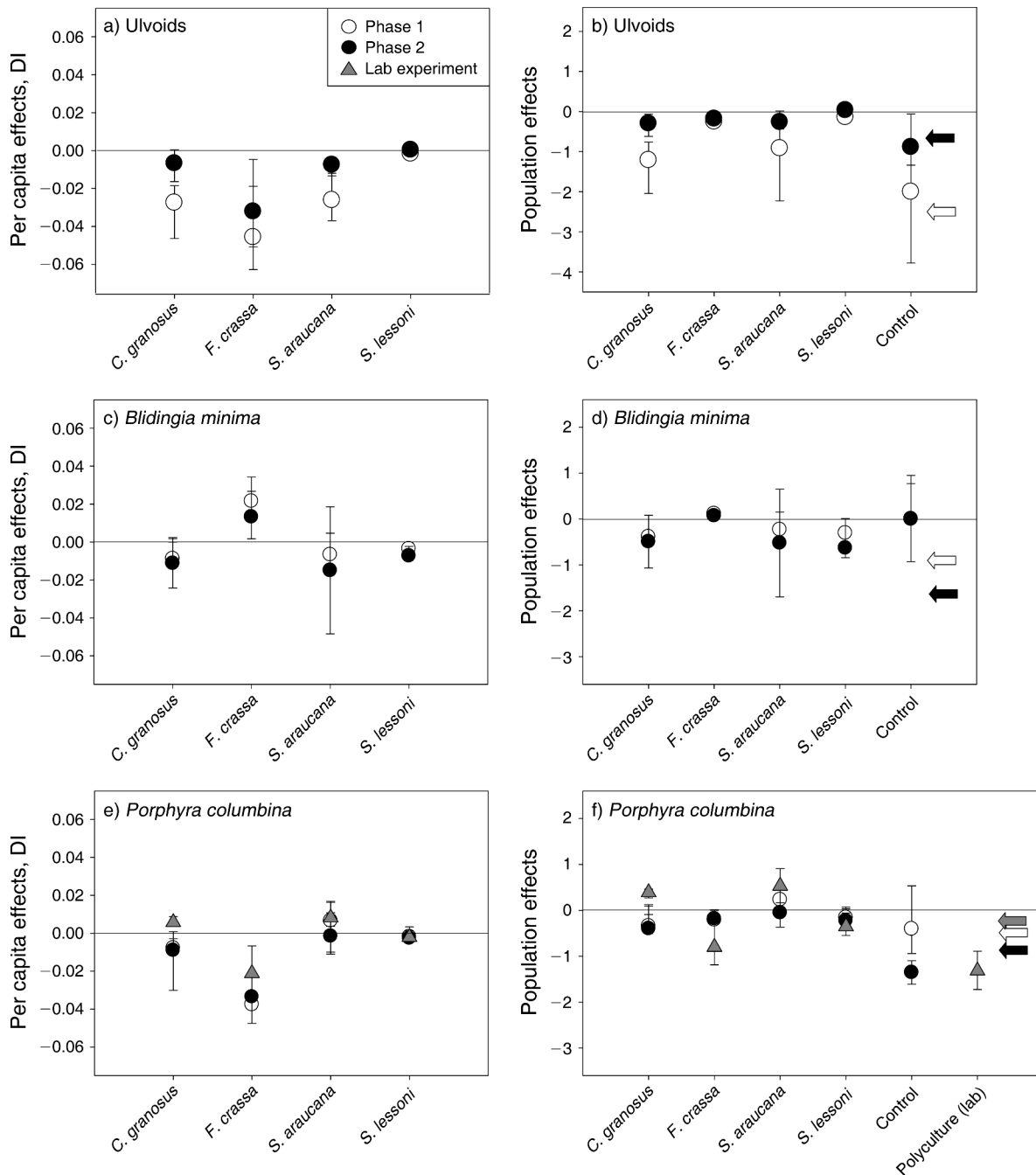


FIG. 1. (a, c, e) Per capita and (b, d, f) population effect of the molluscan herbivores *Chiton granosus*, *Fissurella crassa*, *Scurria araucana*, and *Siphonaria lessoni* on ephemeral algal cover, estimated through field experiments in the colonizing phase (phase 1) and establishment-adult phase (phase 2) during early succession in central Chile. Dynamic index (DI) estimates the differences in percent algal cover present inside each mollusk enclosure plot vs. the mean algal cover recorded in the reference state. In this case the reference state was the benthic grazer exclusion. This index is recommended when resources exhibit exponential growth and when prey is far from equilibrium. Per capita effects were originally measured as impact on algal percent cover per individual per day. Population effects on algal percent cover were originally measured as grams per square meter per day. Ephemeral algae correspond to the (a, b) green *Ulva rigida*-*U. compressa* mix (ulvoids), (c, d) *Blidingia minima*, and (e, f) the red alga *Porphyra columbina*. Effects of herbivores on biomass (originally measured in grams) of the alga *P. columbina* were recorded through laboratory experiments, in which a polyculture treatment (all herbivores enclosed together) was also considered (see *Methods: Laboratory experiments* ... for further details). All data are means and 95% CIs, which were estimated through bootstrapping. Arrows in population effects correspond to the expected additive effect of all herbivores in the different phases considered (white arrow, phase 1; black arrow, phase 2; gray arrow, laboratory experiments).

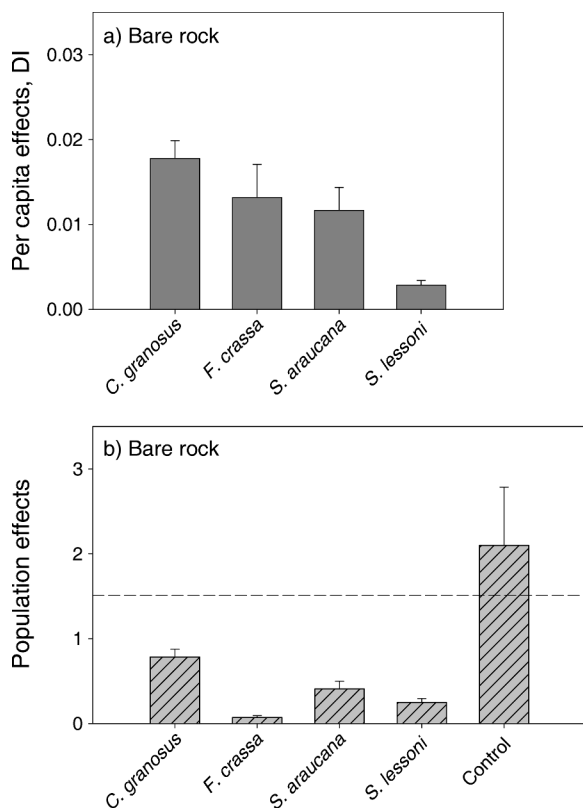


FIG. 2. (a) Per capita and (b) population effects (mean + bootstrapped SE) of molluscan herbivores on bare rock cover, estimated through field experiments during the colonizing (two months) and establishment-adult phases (three months) of early community succession. The dashed horizontal line in panel (b) shows the additive effect of all herbivores. Original measured variables used to calculate the per capita and population indexes are as described in Fig. 1.

small fronds of this species became established in the plots (phase 2 in Fig. 1c). Interestingly, the only significant per capita effect on *Blidingia* was that of the keyhole limpet *F. crassa*, but it was positive, not negative, both during colonization and establishment phases (Fig. 1c). Because this green alga started to colonize the plots only two months after initiating the experiments, the positive effect could be the result of an indirect positive effect of *F. crassa* on *B. minima* by reducing abundance of other space occupants such as ulvoids (see Fig. 1c; Appendix B: Fig. B1c). Calculating grazer effects using a different ending date for phase 1 decreased the estimated DI values for all species, but it did not alter the pattern among species, i.e., the direction and relative magnitudes were maintained. Statistical comparisons showed no significant differences in DI's between the two phases for any of the grazer species (Appendix G: Table G1). At the population level we observed weak negative or positive effects of all species separately, and slightly stronger effects on the established fronds than on colonization (Fig. 1d). The total effect of all benthic grazers at natural densities observed

in the controls was not distinguishable from zero throughout early succession (Fig. 1d). The expected additive effects of all herbivore species overestimated the observed effects in control plots during the established phase but not during colonization, which conforms to an additive effect of herbivores (Fig. 1c, compare symbols and arrows).

In general, most herbivores except *F. crassa* showed weak nonsignificant, or even positive, per capita effects on the ephemeral red alga *Porphyra columbina* (Fig. 1e). Although *S. lessoni* consumed adult plants of *Porphyra* during the established phase, its per capita effects were indistinguishable from zero. The keyhole limpet showed consistently negative effects of similar magnitude on *Porphyra*, both during colonization and establishment phases. Closely similar per capita effects were obtained in the field and the laboratory experiments for all species (circles vs. triangles in Fig. 1e). Accordingly, no significant differences were observed in grazers' effects between the two phases for any grazer species (see Appendix G: Table G1). At the population level, only *F. crassa* had significant negative effects on *Porphyra* biomass (Fig. 1f). An overall negative effect of all herbivores together (control plots) was observed only on established fronds of *Porphyra* (solid circle in Fig. 1f), and the effect was virtually the same as the collective effect observed in polycultures of the same species in the laboratory (compare solid circle and gray triangle in Fig. 1f). Moreover, the overall effect of all grazer species in the controls was similar to the expected additive effect of the four target species during colonization (compare open circle and arrow in Fig. 1f), but not on established fronds in both field and laboratory experiments (compare solid circle and arrow, and gray triangle and gray arrow, respectively in Fig. 1f).

The pattern of per capita and population effect of grazers on the generation and maintenance of bare rock varied among species (Fig. 2). All species had significantly positive per capita effects on bare rock, but that of *S. lessoni* was significantly lower than the other three species (Fig. 2a). Interspecific differences in population abundance changed the pattern of per capita effects. The chiton *C. granosus* remained as the species with highest impact on bare rock (Fig. 2b), but the population effects of the keyhole limpet *F. crassa* were negligible due to low population density in fishery-open areas, and that of *S. lessoni* was comparable to the effect of *S. araucana*. Furthermore, at the population level, the observed effect of all grazers in the system was slightly higher than, but within the confidence limits of that expected from the additive effects of the four study species (Fig. 2b).

Herbivore effects on late succession

Field estimates of per capita effects of herbivores on the corticated late-successional alga *Mazzaella laminarioides* showed that only *F. crassa* exerted significant negative effects on this species (Fig. 3a). By feeding in a "browsing-like" fashion, the keyhole limpets can reduce

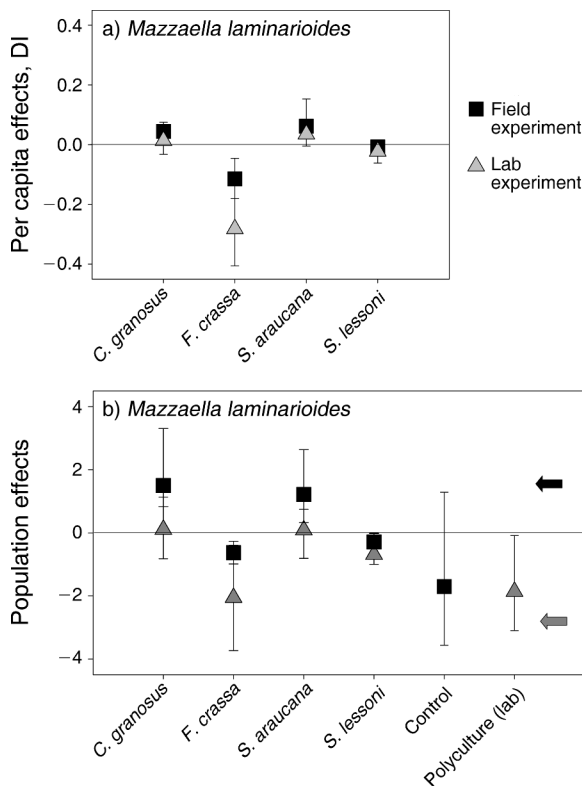


FIG. 3. (a) Per capita and (b) population effect of molluscan herbivores on biomass (originally measured for per capita effects as $\text{g}\cdot\text{individual}^{-1}\cdot\text{d}^{-1}$ and for population effects as $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) of the corticated late-successional alga *Mazzaella laminarioides*, recorded both through field and laboratory experiments. All data are means and 95% CIs. Arrows are as in Fig. 1.

the biomass of this corticated alga at a rate of ~ 0.83 to $2.05 \text{ g}\cdot\text{individual}^{-1}\cdot\text{d}^{-1}$. Although we observed pulmonate limpets, *S. lessoni*, foraging on *Mazzaella*, their per capita effects on frond biomass were negative but not significantly different from zero (Fig. 3a). The other herbivore species had slightly positive per capita effects on *Mazzaella* biomass. Similar per capita estimates were obtained in laboratory experiments (see triangles in Fig. 3a), although per capita effects of *F. crassa* were slightly but significantly overestimated in the laboratory (Appendix G: Table G2). At the population and collective (i.e., laboratory effects) level, *F. crassa* showed the largest negative effect on *Mazzaella* and this species accounted for total herbivore effects in the field and in polycultures in the laboratory (Fig. 3b). Again, collective estimates based on laboratory experiments slightly overestimated the effect of *F. crassa* on *Mazzaella* (Fig. 3b). Because the average effects of *C. granosus* and *S. araucana* on *Mazzaella* were positive, and the effect of the keyhole limpet was sufficient to account for the overall effect observed in the control (Fig. 3b), there were large departures between the observed total herbivore effects and those expected based on the

addition of individual species effects (compare solid arrow and solid square in Fig. 3b). Under laboratory conditions, the collective effects in polycultures were closely predicted by an additive model, which matches the effect recorded by *F. crassa* alone (compare gray arrow and gray triangle in Fig. 3b). Considering densities of *F. crassa* recorded inside the ECIM marine reserve, the population effect of this species is expected to be over six times higher than that observed at nearby platforms exposed to harvesting (see Appendix E).

As body size is predicted to greatly account for consumer effects in different systems (e.g., Wood et al. 2010), we also estimated whether effects of focal herbivores on abundance of algae species were related to their body size (grams). We observed a linear positive relationship between the magnitudes of per capita effects and herbivore body size during the colonization and established phase of early succession (i.e., ulvoids, gray circles in Fig. 4), and for experiments conducted in laboratory conditions (i.e., *Porphyra*, solid triangles in Fig. 4).

DISCUSSION

Despite the broad overlap in their diet, our results demonstrate significant functional differentiation among coexisting molluscan herbivore species, and that the pattern of species identity and the functional relationships in the guild varied between early- and late-successional stages of the mid-intertidal community. Furthermore, we detected variation in the magnitude of grazer effects on the ephemeral algal species typical of early succession, depending on the algal species consid-

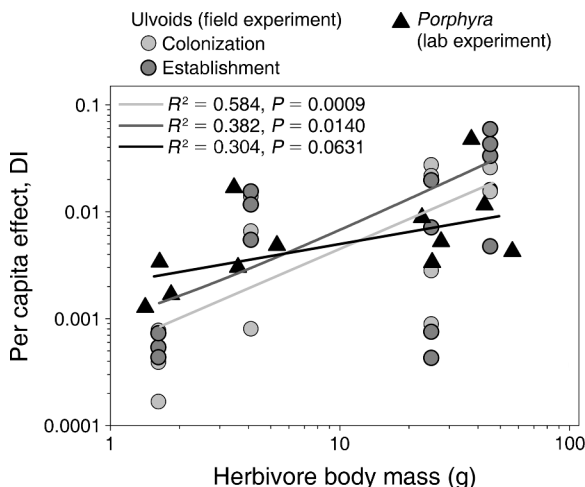


FIG. 4. The relationship between focal herbivore body size (g) and per capita effects for early-successional algal species (note log-log scale). Each point represents a replicate plot for each herbivore species. Different grayscale shades indicate the relationship measured during colonization (light gray) and establishment phases (dark gray) for ulvoids in field experiments and for *Porphyra columbina* (black) in laboratory experiments. Variance explained by linear regression (R^2) and P values are shown.

ered and, to a lesser extent, on whether effects were evaluated during the colonization phase, or on the established fronds. Despite that all manipulated molluscan species had important effects on ulvoids during colonization (except *Siphonaria lessoni*), only *Fissurella crassa* and to a much lower extent *Scurria araucana* had significantly negative effects on the abundance of established adult fronds. Regarding herbivore densities and their functional relationships, compensation in the magnitude of effects (i.e., intensity) may occur only during colonization, but low compensatory effects among species are expected once ephemeral algae are established. On late-successional stages, no compensation is possible as only one species, *F. crassa*, had strong negative effects on algal biomass while most others had weak positive effects. Additionally, most but not all species in the herbivore assemblage play an important role in the maintenance of bare rock. Here we discuss these results and highlight the importance of this knowledge to predict the consequences of diversity loss for intertidal ecosystem functions.

*Functional dissimilitude, trait diversity,
and compensatory potential*

Our results are generally similar to those found in previous studies conducted in other intertidal communities in the world, in which benthic molluscan herbivores have important effects on community structure through consumption of the most palatable algae that typically characterize early succession (Branch 1981, Hawkins and Hartnoll 1983, Jenkins et al. 2005, Coleman et al. 2006). Significant grazer effects on early-successional algae in this study were expected from the high representation of these algal species in the diet of all benthic grazers (Santelices et al. 1986, Camus et al. 2008; see Appendix D: Fig. D1). Yet, *S. lessoni* had no measurable effects on early-successional stages and despite the broad overlap in diet among the other three species (see Appendix D), there were large differences in their effects when comparing the three most common algal species of early succession, as well as between algal colonization and established fronds.

The per capita effects on ulvoids exerted by the keyhole limpet *F. crassa*, the chiton *C. granosus* and the scurrinid limpet *S. araucana* were similar during colonization, but by the time fronds of these species were established, *F. crassa* had a much larger effect than the other species. This pattern may reflect differences in feeding modes and body size among species. While *C. granosus* and *S. araucana* are grazers that scrape the substratum to consume prey, *F. crassa* exhibit a more versatile feeding mode, being able to graze the surface but also browse on established fronds. The keyhole limpet was also the only species having negative per capita effects on *Porphyra* during colonization and on the established fronds. Interestingly, the other herbivore capable of browsing on fronds, *S. lessoni*, had no effects on any of the early-successional algae, which maybe due

to a more limited feeding mode and smaller body size than the keyhole limpets. We did observe individuals of this species feeding on ephemeral algae in the laboratory, but their consumption rate might not keep up with the fast growth rates typical of these early-successional species (Underwood and Jernakoff 1981, Hawkins and Hartnoll 1983, Steneck and Dethier 1994). On the other hand, chitons and *S. araucana* had significant and persistent effects on the generation (or maintenance) of bare rock surfaces within the experimental plots throughout early succession, agreeing well with the mechanical-morphological structure of their radula, which allows them to scrape deep into the surface (Steneck and Watling 1982). However, *F. crassa*, which possesses a less suitable radula for scraping, had similar per capita effects on maintenance of bare rock than these other species, again evidencing the plasticity of feeding behavior in this limpet species. Feeding on late-successional algae always imposes a series of difficulties to most benthic herbivores because these algae are usually large in size and chemically and/or mechanically defended (Gaines 1985, Santelices 1990, Steneck and Dethier 1994, Cronin and Hay 1996). Although large algae can also provide shelter for a diverse array of organisms, it must be noted that many ephemeral algae are not necessarily unprotected from grazing. Indeed, several ulvoid species have been shown to respond to grazing with chemical defenses (Paul and Van Alstyne 1992, Van Alstyne et al. 2001), but their effectiveness as deterrents has been tested with only few grazer species (Van Alstyne et al. 2009). Our results show that more grazer species in the Chilean intertidal assemblage can consume and have effects on ephemeral algae than on late-successional species. In the case of *Mazzaella*, its comparatively large size and the presence of a cuticle (Gaines 1985) seem to effectively reduce edibility to all grazers but *F. crassa*. Again, *S. lessoni* was observed consuming the surface of *Mazzaella* fronds in the laboratory, but the effect was not large enough to significantly reduce algal biomass. Thus, body size, and morphological and behavioral traits (feeding modes) considered together, but not by themselves, could account for differences and similitude among the herbivores in the magnitude and direction of their effects on the successional community. These findings support the general view that species identity is of most importance in consumer assemblages (see Stachowicz et al. 2007, for review) and that their roles are related to multiple traits that differentiate their function in the community (e.g., Díaz et al. 2003). In the intertidal herbivore assemblage studied here, this set of traits interacts with the natural succession that occurs in the community following generation of bare rock.

In general, differences in magnitude of per capita effects can be related to differences in body size among herbivores (Hillebrand et al. 2009, Wood et al. 2010), partly because body size correlates with consumption rates, handling times, and the time animals spend

foraging (Mittelbach 1981, Hairston and Hairston 1993). In our case, the pulmonate limpet *S. lessoni* was the smallest species considered in our study (~1.2 cm, and 0.57 g), and although animals can consume both microscopic and adult stages of ephemeral algae and browse on algal fronds, just like the larger *F. crassa*, the pulmonate limpets had the smallest per capita effects of all herbivores on all algal phases, while *F. crassa* usually (but not always) had the largest effect. Indeed, if we considered only ulvoids, which are consumed by all grazer species, we observed a linear positive relationship between the magnitudes of per capita effects and herbivore body size during the colonization and established phase of early succession (see Fig. 4). Of course, the explanatory power of body size breaks down when considering *Blidingia*, or late-successional species, presumably because morphological/mechanical restrictions take prominence. In many systems body size is inversely related to population densities (Marquet et al. 1990, Navarrete and Menge 1997, and also Wood et al. 2010), which suggests that density could compensate for small per capita effects (see Navarrete and Menge 1997). But this was not the case in our system. Although the pulmonate *S. lessoni* is one of the most abundant herbivores in mid-to-high intertidal levels both per population (at the scale of 1 m²) and collective effects (recorded in laboratory experiments) were still not significant.

In general, field and laboratory experiments gave us consistent and complementary information about herbivore effects on both early- and late-successional species. On the late-successional *Mazzaella*, laboratory experiments tended to overestimate the effects of *F. crassa* because in the field there were other food sources present on the rock surface of the experimental plots (see Appendix F: Fig. F1). Thus, although *Mazzaella* was transplanted to bare rock plots, the resulting condition resembled better the complex community found in late-successional stages, where *Mazzaella* and bare rock account for >50% of the cover (Appendix F, Fig. F2). Activity of all species recorded in laboratory conditions was similar to that recorded in field experiments, which was also similar to marked but otherwise unmanipulated animals in the same study site (see details in Aguilera 2010). Although our experimental design did not allow us to evaluate the effect of herbivores on colonization of the late-successional *Mazzaella* (i.e., through grazing on spores and or plantules), previous studies have shown that grazing by the chiton *C. granosus* and the scurrinid limpets *S. araucana* and *S. viridula* can have positive rather than negative effects on its establishment (Aguilera and Navarrete 2007; M. A. Aguilera, B. Broitman, and N. Valdivia, *unpublished manuscript*). We have no clear interpretation, however, for the positive effects of chitons and *S. araucana* on transplanted *Mazzaella* fronds recorded both in field and laboratory experiments. Transplanted fronds were free of epibionts, so that cleaning of fronds by herbivores could not

explain the observed positive effect. We did not examine the potential effect of these grazers on nutrient availability, but it seems unlikely that they could alter nutrient levels in such a wave-exposed upwelling system. However, a recent study suggest that even in exposed, wave-swept rocky shore in a nutrient rich upwelling ecosystem, nutrient enhancement by mussels can facilitate algal growth (Nielsen 2003, Aquilino et al. 2009). Therefore, the mechanisms behind the positive effect of grazers on *Mazzaella*, especially local nutrient enrichment, deserve further experimental studies. In any case, the control of the dominant *Mazzaella* in mid-levels seems to be played only by *F. crassa*.

From redundancy to keystone, compensation potential, and consequences for biodiversity

In general, our results corroborate previous findings in which functional similitude or equivalency is not the norm, even in closely related species (i.e., taxonomic, phylogenetic; Chalcraft and Reseraris 2003b, Reseraris and Chalcraft 2007). Many authors have proposed that as biodiversity increases so does the occurrence of functionally similar species, and that it is this redundancy that provides insurance or resilience against loss of critical processes in ecosystems (McNaughton 1977, Walker 1992, Naeem and Li 1997, Naeem 1998, Yachi and Loreau 1999). Based on the similarity of yield criterion (Loreau 2004), only one pair of species could be judged functionally equivalent or identical in our focal assemblage. We observed high similitude in per capita and population effects on ephemeral algae between the species *C. granosus* and the limpet *S. araucana*. These two species have comparatively similar adult body sizes (Santelices et al. 1986), and although their radular morphology is different due to taxonomic differences (polyplacophoran and doccoglossan, respectively; Steneck and Watling 1982), the two buccal apparatuses are closely similar in their excavating potential (i.e., functional relevance). Therefore, these grazers may be “substitutable” in their effects on ulvoids, especially during colonization. Furthermore, because these species have high densities at the study site, they together may be able to compensate the magnitude of the large per capita effect of *F. crassa* on ulvoids during early succession, especially in fishery-open areas, where the keyhole limpet population size is reduced by humans (Oliva and Castilla 1986). The former two species are also similar in their per capita effect on bare rock maintenance and could also compensate for the low densities of *F. crassa* in maintaining this important community function. Thus, there is “redundancy” of *C. granosus*, *S. araucana*, and *F. crassa* in the magnitude and direction of their effects (Walker 1992, Naeem 1998, Jaksic 2003, Loreau 2004), but this is restricted to ulvoids and bare rock. No clear equivalence in effects was observed for either *Blidingia* or *Porphyra* in any phase of early succession. Instead, herbivores had higher than expected total (additive)

effects on *Porphyra* when they were present at normal abundances in experimental areas (controls in the field) or included together in polycultures, suggesting some level of complementarity through facilitation or resource partitioning in this assemblage (e.g., Loreau and Hector 2001, Cardinale et al. 2002, Bruno et al. 2005).

At the other extreme, the presence of a keystone species, which plays pivotal roles in natural communities (Paine 1969, Power et al. 1996), implies there is low or no compensation after their local extinction (Allison et al. 1996, Navarrete and Menge 1996). This contrasting functional structure is also observed in the same intertidal herbivore guild, but during late-successional stages. Indeed, while the effects of the keyhole limpet *F. crassa* on ulvoids during colonization could be compensated by *C. granosus* and *S. araucana*, its effects on late-successional *Mazzaella* are unique and irreplaceable. Clumps of this dominant alga are characterized by the presence of diverse invertebrate species, which seek shelter under, amid, or upon its canopy (Santelices 1990). Therefore, changes in its abundance can cause important shifts in the community affecting many other species (Oliva and Castilla 1986, Castilla 1999; and see Appendix E). This is particularly evident inside the ECIM marine reserve, where high abundance of large individuals of *F. crassa* can have large population effects on overall cover of both ulvoids and *Mazzaella* at mid-intertidal levels (Oliva and Castilla 1986, Castilla 1999; and see Appendix E: Fig. E1 and E2). Although from previous studies in southern Chile it can be predicted that *S. lessoni* could compensate the effects of fissurellid limpets on this corticated alga (Jara and Moreno 1984), we found low compensatory potential of this pulmonate limpet in our experimental site. Taken together, our field and laboratory results led to the conclusion that *F. crassa* act as a keystone herbivore on intertidal community.

In summary, the functional structure in the herbivore assemblage is characterized by "limited redundancy" (Hoey and Bellwood 2009), with some species exhibiting substitutable roles at the colonization phase and shifting to keystone structure in late succession. Because different sources of biological and abiotic disturbance, operating over scales from a few to hundreds of centimeters can continually generate bare rock surface and reset community succession (Castilla 1981, Santelices 1990, Navarrete and Castilla 2003), the functional structure and relationships within the herbivore assemblage could change over comparatively small spatial scales and over scales of months. Changes in the functional relationships among species have only recently been examined in detail in aquatic ecosystems (Burkpile and Hay 2010; see *Results*), evidencing the overall poor knowledge about how functional groups are organized in space and time. Therefore, if we are to predict the consequences of impinging species loss and the role of biodiversity for ecosystem function (Perrings et al. 2010), it is urgent to determine the degree of

redundancy and potential for compensation within natural assemblages and considering the different phases and stages of community succession.

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SUPPLEMENTAL MATERIAL

Appendix A

Experimental designs (*Ecological Archives* E093-008-A1).

Appendix B

Algal cover through time (*Ecological Archives* E093-008-A2).

Appendix C

Fish effects on early succession (*Ecological Archives* E093-008-A3).

Appendix D

Herbivores diet analyses (*Ecological Archives* E093-008-A4).

Appendix E

Estimated impacts of *F. crassa* inside and outside ECIM marine reserve (*Ecological Archives* E093-008-A5).

Appendix F

Species composition in *Mazzaella*-dominated intertidal community and inside experimental plots (*Ecological Archives* E093-008-A6).

Appendix G

Results of bootstrap *t*-test analyses (*Ecological Archives* E093-008-A7).