

Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile

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Abstract. Understanding the processes that drive kelp forest communities is critical for management and conservation of these productive ecosystems. As a way to advance in this direction, we explored the effects of fishing pressure and upwelling intensity over kelp forest communities along the central coast of Chile. We sampled kelp communities in different upwelling conditions associated with contrasting management regimes, namely Territorial User Rights for Fisheries (TURFs) and open-access (OA) areas. In TURF areas, we found a 2.6-fold increase in reef fish biomass, higher diversity of all fish trophic groups, mainly dominated by benthic carnivore feeders, and a 1.8-fold reduction in the number of kelp grazers. On the other hand, upwelling regimes evidence a 1.6-fold increase in abundance and recruitment of the dominant kelp (*Lessonia trabeculata*), and also an increase in biomass of planktivorous reef fishes. We found that grazers were capable of reducing kelp condition (measured as canopy foliage index) in OA areas outside the influence of upwelling. Enclosure experiments in the field revealed the effect of grazers on kelps, reducing kelp growth (i.e., blade elongation) and increasing blade tissue loss. Results provide evidence that TURF areas could be important ancillary conservation instruments in kelp forest ecosystems, if key processes of the subtidal community assemblages (e.g., interactions between grazers and reef fish) are maintained. We conclude that human impact interplays with the influence of upwelling in structuring kelp communities.

Key words: gastropod; herbivory; overfishing; reef fish; *Tegula tridentata*.

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INTRODUCTION

Increasing evidence suggests that no-take marine reserves can play a key role in enhancing ecosystem function and resistance to natural and human disturbances, particularly fisheries (Menge

2000, Lester et al. 2009, Navarrete et al. 2010). In a global analysis, partially protected areas (e.g., Territorial Use Right for Fisheries; hereafter TURFs) show similar responses in species richness and abundance than no-take areas, suggesting that together they may contribute to marine

conservation (Lester and Halpern 2008, Gelcich et al. 2012, Afflerbach et al. 2014). In fact, recent studies have evidenced the potential of TURFs, on type of partial protection that is globally promoted as a best practice for coastal management, to provide benefits for both management and conservation (i.e., increased biomass and diversity, see Gelcich et al. 2012). The response of key biological assemblages and communities to partial closure varies among TURFs, depending on the level of protection (Gelcich et al. 2012). However, inherent site-specific differences to natural environmental variation such as wave exposure, temperature, and nutrient/resource supply may also affect the response to protection. Understanding patterns of geographic variation in community structure in relation to nearshore oceanographic conditions is a first step to elucidate the key functional players and their responses to different management scenarios (e.g., Guenther et al. 2012, Reed et al. 2011).

Eastern boundary upwelling areas, such as the southeast Pacific Humboldt Current System, are among the most productive ecosystems of the world, and at the same time, heavily used by coastal fisheries (Thiel et al. 2007). Most upwelling areas are characterized by strong heterogeneity, with spatially persistent differences in oceanographic conditions that determine the local supply of nutrients that in turn affect primary production (e.g., Bustamante and Branch 1995, Wieters et al. 2003, Navarrete et al. 2005, Wieters 2005). Upwelling-driven variation in resource supply rates (nutrients, plankton, and/or larvae) can also alter the strength of trophic interactions that influence benthic algal biomass and community structure (e.g., Bustamante and Branch 1995, Menge 2000, Wieters et al. 2003, Nielsen and Navarrete 2004, Aquilino et al. 2009). In addition to direct trophic pathways, upwelling can also control individual algal traits that determine habitat modification and relative importance of facilitation in regulating local benthic communities (e.g., Wieters 2005). Understanding how geographic patterns in community structure may relate to upwelling variation is a first step to identify testable hypotheses and integrative frameworks at scales useful for management.

The coast of central Chile offers unique opportunities to evaluate the interplay between levels of fishing efforts (by restrictions imposed in

TURFs) and meso-scale oceanographic processes on nearshore community structure and key functional players. First, large and consistent meso-scale spatial variation (sites 10s–100s km) in the intensity of upwelling drives thermal variability and nutrient availability onshore (e.g., Wieters 2005, Tapia et al. 2009, 2014). In rocky intertidal habitats, numerous studies highlight the important consequences of such upwelling heterogeneity on spatial patterns of community structure and regulation (Nielsen and Navarrete 2004, Wieters 2005, Broitman et al. 2011). However, such quantitative information across meso- to large spatial scales is lacking for shallow subtidal communities, where most of the coastal fisheries harvest is derived. Second, the main species targeted by artisanal fishers in these subtidal kelp forests environments correspond to relatively large benthic herbivores (limpets, sea urchins) and carnivores, such as muricid gastropods, crabs, and predatory fishes (Worm et al. 2006, Pérez-Matus et al. 2007, Gelcich et al. 2012). Some of these same carnivore species have already been identified as key predators exhibiting strong top-down regulation in adjacent rocky intertidal habitats (Castilla 2000), suggesting that they may play important structuring roles in subtidal kelp forest communities.

Along the coast of Chile, a TURF system was established to manage inshore benthic species generating a mosaic of fishing pressure that allows combining management regimes with variation in the key environmental conditions (e.g., upwelling) dominating the region. Individual TURFs are relatively small (<250 ha) and are immersed in a landscape of open-access (OA; no access restriction) areas. Therefore, spatial variability is expected in relation to the quality of fishing grounds for the principal target resources (Orenzanz et al. 2005, Thiel et al. 2007). The TURF policy applies directly to a diverse assemblage of species such as the carnivore whelk *Concholepas concholepas*, the predatory crabs *Cancer* spp. and *Homalaspis plana*, numerous herbivorous keyhole limpets *Fissurella* spp., and the red sea urchin *Loxechinus albus* (Gelcich et al. 2010). Densities and individual sizes of exploited species are larger in comparison with those observed in adjacent OA areas (see Gelcich et al. 2012). However, TURFs have secondarily benefited to other non-target resources (Gelcich et al. 2010).

Spearfishing by hookah, scuba, or snorkeling is still allowed in TURFs, but because of the way fishers regulate the access to benthic species, no fishing activities other than targeted benthic resources take place within TURFs. In fact, reef fishes in TURFs show five- to 10-fold higher biomass and 1.5-fold higher species richness than in OA areas (Gelcich et al. 2010).

Here, we describe geographic patterns in near-shore kelp bed community structure in relation to contrasting management regimes and upwelling conditions as a first step to understand the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities. Field surveys in TURFs and OA areas (no access restriction) along the central coast of Chile (spanning 450 km) were conducted to estimate changes in key ecological components, including (1) kelp foliage, density, and size; (2) total and trophic group biomass of exploited and non-exploited reef fish species; (3) density and habitat use of dominant grazing invertebrates; and (4) understory cover and richness of sessile species. In order to better understand the potential role of consumers in controlling kelp growth and tissue loss, we also conducted a field experiment to determine observed patterns in kelp canopy foliage in the field.

MATERIALS AND METHODS

The kelp forest ecosystem

Shallow subtidal hard-bottom habitats along the open coast of central Chile are commonly characterized by lush monospecific kelp beds (*Lessonia trabeculata*) with an understory dominated by crustose macroalgae (predominantly calcareous *Lithothamnion* and non-calcareous *Hildenbrandia*) and patchy, intermixed assemblages of foliose (predominantly brown algae such as *Dictyota kunthii*, *Halopteris* spp.) and turf (predominantly *Gelidium* spp.) algae. Sessile invertebrates are not commonly abundant, though bryozoans, sponges, and barnacles can reach more than 10% of the cover (Pérez-Matus et al. 2007, Villegas et al. 2008). A diverse array of mobile macroinvertebrate predators and grazers inhabit these kelp beds, with numerical abundance and biomasses dominated by sea stars (*Meynaster gelatinosus*; *Heliaster helianthus*), crabs (*Cancer* spp.; *Homalaspis plana*), red sea urchins (*Loxechinus albus*), and muricid whelks (*Concholepas concholepas*), mostly

abundant in TURF sites (Fernández and Castilla 1997, Gelcich et al. 2008, 2012). The predominant grazers in OA areas are the black sea urchin (*Tetrapygus niger*) at shallow depths (0–5 m) and the snail *Tegula tridentata* (hereafter *Tegula*) at intermediate depths (8–20 m; Vásquez and Buschmann 1997). Along northern and central Chile, benthic predators such as sea stars (*M. gelatinosus*; *H. helianthus*) and crabs (*Cancer* spp.) appear to limit sea urchins to the shallow subtidal, where they are known to control recruitment of the kelp *L. trabeculata* (Vásquez 1993, Vásquez and Buschmann 1997, Perreault et al. 2014). Fish predators such as *Graus nigra*, *Semicossyphus darwini*, *Cheilodactylus variegatus*, and *Pinguipes chilensis* occur across shallow and deep zones, patrolling not only shallow urchin barrens but also the deeper kelp beds. Similarly, omnivorous and herbivorous fishes such as *Scartichthys viridis* and *Aplodactylus punctatus*, respectively, are also abundant through different depths of the kelp beds (Angel and Ojeda 2001, Pérez-Matus et al. 2007, 2012).

Study sites

Studies were carried out over ~450 km of the open coast of central Chile, from 29°41' to 33°21' SL (Fig. 1). Surveyed sites were chosen according to their proximity to major upwelling centers and contrasting management regimes (TURFs vs. OA). Within each of four oceanographic locations characterized by either strong or weak coastal upwelling, we selected adjacent TURF and OA management conditions for a total of eight study sites. The two main upwelling centers in the region are Punta Lengua de Vaca (Talca) located at 31° S and Punta Curaumilla (Quintay) located at 33° S, where we established our “upwelling” locations, whereas warmer areas only weakly or indirectly influenced by upwelling (here referred to as “non-upwelling” locations) were Guanaqueros (Toralillo 30° S) and El Quisco-Algarrobo (33° S). The localized nature of upwelling is easily observed in thermal imagery (e.g., Broitman et al. 2001, Navarrete et al. 2005), and the thermal manifestation of coastal upwelling at these same study sites has been quantified from time series of in situ temperatures measured in shallow near-shore waters (see Tapia et al. 2009, 2014). Further, onshore nutrient concentrations are tightly correlated with temperatures in the study region (e.g., Nielsen and Navarrete 2004, Wieters 2005). Each

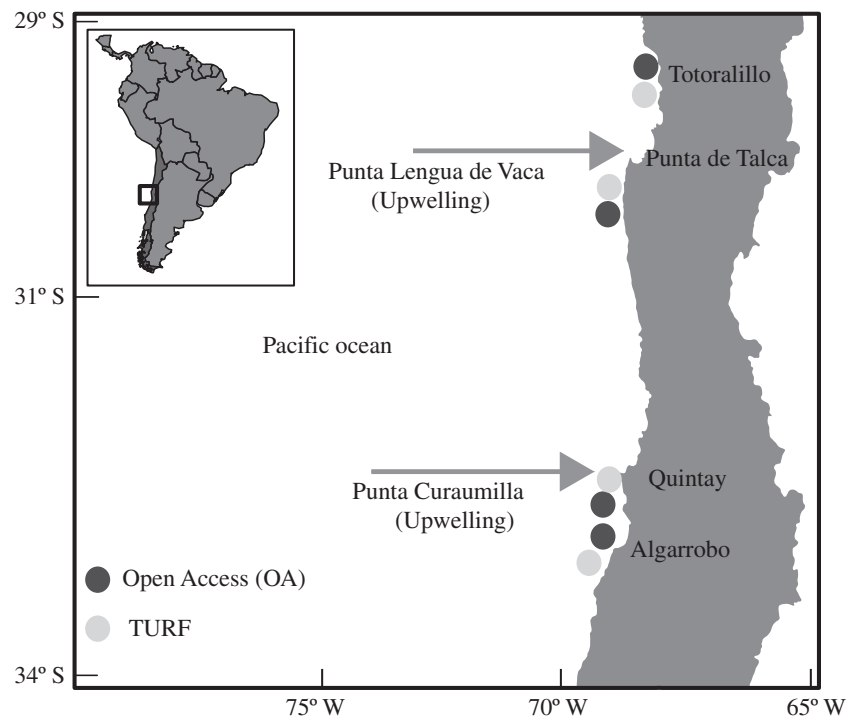


Fig. 1. Map of the sampling locations and sites. Arrows indicate the two upwelling centers (following Tapia et al. 2014). Territorial User Rights for Fisheries (TURF) sites are represented in gray circles and open-access (OA) in black circles.

of these oceanographic locations contained a well-enforced TURF (24-h surveillance) and adjacent OA fishing grounds (see Fig. 1). Previous studies have recognized that enforcement is strongly dependent on costs and proximity to fishing coves (Gelcich et al. 2010) and that TURFs with different enforcement levels have important differences in macroinvertebrate species richness, density, and biomass, suggesting the important implications of management over time (Gelcich et al. 2012). In order to standardize management conditions, we selected TURF sites with identical ages (time since they were established). Totoralillo and Punta Talca were decreed in September 1997, Quintay was established in March 1997, and Algarrobo in October 1999 (SERNAPESCA 2017). Thus, all of them exhibit nearly 18 yr of well-enforced management. Open-access sites were selected to be as similar as possible to TURFs with respect to dominance of kelp beds, bottom topography, wave exposure, and depth. We considered that at these sites, traditional fishing grounds, with no access restrictions, were found.

All study sites were chosen to be as similar as possible in coastal orientation and wave exposure, as quantified following a fetch index (Thomas 1986). Before sampling a fixed location, we determined the global positioning system coordinates (accuracy ± 3.3 m) using a handheld Garmin GPS 72 H. From the GPS (global positioning system) information, a physically derived exposure index was calculated based on the total mean of the fetch, which was set as the sum of fixed radial distances of 1 km with 5 degrees intervals (72 radii in total). The distance to the point of the first intersection with land substratum was measured, and the fetch was the distance of open water over which waves can be generated by winds, a proxy of wave exposure. Fetch calculations were made using similar protocols of the program Fetch Effect Analysis (see Burrows et al. 2008 for more details). The rationale for this variable is that as more enclosed (wave protected) a site is by land, the lower the level of wave action to which it is likely to be exposed (Thomas 1986). The average fetch varied among sites but no clear pattern was

observed between treatments (upwelling and management). Mean fetch was higher in the Totoralillo OA followed by the Totoralillo TURF, Punta de Talca (both treatments), Quintay OA, Algarrobo OA, and the TURF at Quintay, Algarrobo (see Appendix S1: Fig. S1).

Variation in kelp-dominated communities

To characterize the variation in the structure of kelp-dominated communities under contrasting upwelling and management regimes, underwater surveys were performed during late austral spring (November) to late austral summer (March) 2013–2014 at all sites (Fig. 1). Two 100-m transects, with 10 systematically spaced monitoring stations each, were stretched perpendicular to the coastline at each site. At all sites, transects covered from the upper to the lower edge of kelp bed distribution, stretching from 5 to 16 m depth, respectively. Replicate transects were placed approximately 200 m apart. Sampling was conducted on rocky outcrops of similar slope and wave exposure by the same team of four divers in order to minimize observer errors. Thus, each taxon/group (i.e., reef fish, kelp, grazers, and understory species) was evaluated exclusively by the same diver (see details below). All surveys were conducted between 10:00 and 14:00 hours. Abiotic variables such as visibility ranged from 5 to 10 m and bottom temperature ranged from 13.3° to 14.6°C among all the study sites and sampling times.

Reef fish biomass and trophic groups.—Underwater visual censuses and photography were used to quantify local density and biomass of larger benthic, demersal, and pelagic fish species. Cryptic species were not quantified. A first diver registered the identity and size (total length; TL) of each fish encountered within a 4 m wide “tunnel” along each transect. Visual estimates of size were more than 90% accurate, as determined by comparisons of in situ estimates with direct measurements of captured individuals. Body mass for individual fishes (weight; W) was calculated using species-specific length:mass conversions ($W = aL^b$, where L is the body length of each individual from visual estimates, and the parameters a and b are constants for each species [Pérez-Matus et al. 2014]).

In order to determine whether management affected species composition of different fish

trophic groups under different upwelling regimes, fish were categorized into five trophic groups based on published dietary information of the local species. Fish species were labeled as (1) herbivores (browsers, macroalgal eaters, scrapers, territorial herbivores, and turf algal eaters), (2) planktivores, (3) benthic carnivore (invertivores), (4) omnivores, and (5) piscivores (Angel and Ojeda 2001, Pérez-Matus et al. 2012). Additionally, fishes were grouped as non-commercial and exploited species (including all species that are subjected to spearfishing or are economically important; see Godoy et al. 2010). We used biomass data as response variable, analyzing total fish biomass (sum of biomass from all species) and economically important species biomass (sum of biomass from exploited species only) separately, in addition to biomass of different trophic groups (as above).

To explore total variation in exploited reef fish biomass, a split-plot design was implemented using generalized linear mixed models (GLMM) because the response variable was based upon counts (number of fish converted to biomass) that showed unequal variances and non-normally distributed errors (Crawley 2007, Zuur et al. 2009). Specifically, we used a split-plot design in which management experimental units were nested within those for the upwelling conditions to account for the larger oceanographic influence. Each combination of upwelling and management condition was replicated twice, which was limited by natural availability of conditions along the central coast. Sites were treated as random effects and two experimental factors (upwelling and management) were treated as fixed effects in a fully (two-factor) complete split-plot design experiment (Crawley 2007). The variance partition coefficient (VPC) was calculated as the degree of clustering of the random parameters (Zuur et al. 2009). Therefore, VPC was measured by dividing the variance of the higher-level random parameters (site nested within TURF and upwelling) with the variance of site and variance of the higher-level random parameters. This model was used in all further analyses. All analyses were conducted using R (R Development Core Team 2015).

Kelp forest.—A second diver estimated the density, individual size (using a measuring tape), and canopy foliage of *L. trabeculata* in two 1-m² quadrats placed on each side of the transect (i.e.,

left and right) at each monitoring station ($n = 20$ quadrats per transect). All sporophytes found in each quadrat were measured with a measuring tape, counted, and assigned a foliage category based on visual estimates of the percentage of stipes with healthy blades per sporophyte. The “kelp canopy foliage index” ranged from 1 (virtually no blades on the stipe, leaving a “skeleton” sporophyte) to 5 (almost all stipes having blades, a full canopy) and was based on the following percentages of blade-to-stipe ratio: 1 < 10%; 2 = 10–30%; 3 = 30–50%; 4 = 50–80%; 5 = 80–100% (see Appendix S1: Fig. S2).

To evaluate whether kelp density differed by management and upwelling regimes, we used analysis of variance (ANOVA) as in the model described above. Shapiro and Fligner–Killeen tests were used to evaluate normality and homoscedasticity of variance to meet ANOVA assumptions, respectively. Variation in canopy foliage index was evaluated using GLMM. To evaluate the size distribution of kelp, we ranked individuals into size classes as recruits and juveniles (<10 cm holdfast diameter) and adult sporophyte (>10 cm holdfast diameter) and conducted a permutation multivariate analysis of variance (PERMANOVA).

The herbivorous grazers and the cover of understory species.—A third diver estimated the density of the most predominant benthic herbivores: turban snails (*Tegula*) and black sea urchins (*T. niger*), using 1-m² quadrats on each side of the transect, as above ($n = 20$). All snails within each quadrat were counted and their microhabitat location (e.g., kelp holdfast, stipe, blade, substratum) was recorded. We used GLMMs under the model explained above because the response variable was based upon counts (number of snails, urchin). Since we found urchins in only two sites (Totoralillo OA and Quintay OA) and in one transect station, we did not include them in the analysis. The proportion of *Tegula* density on each microhabitat location (i.e., over kelp or substratum) was analyzed using GLMM specifying a binomial distribution.

Finally, a fourth diver quantified the percent cover of all sessile species in the algal understory in two 0.25-m² quadrats placed on each side of the transect (i.e., right and left) at each monitoring station ($n = 20$ quadrats/station per transect). Percent cover was estimated using random point

contact with 81 intersection points per quadrat recording primary and secondary cover. We categorized sessile species into one of the different functional groups (i.e., leathery macrophytes, articulated calcified, corticated, foliose, filamentous, crustose) following Steneck and Dethier (1994), where sessile invertebrates were grouped according to trophic categories: filter feeders (predominantly sponges, mussels, tunicates) or sessile scavengers (anemones). Using the same model as above, we analyzed all functional groups using ANOVA (see Appendix S1). Shapiro and Fligner–Killeen tests were used to evaluate normality and homoscedasticity of variance to meet ANOVA assumptions, respectively.

Manipulative experiments

Effects of grazers on kelp growth in the field.—Since the field survey revealed that (1) grazers density tends to be higher in OA areas and (2) canopy foliage index tends to be lower in OA, we designed a field experiment to test the potential influence of grazing by the snail *Tegula* on kelp foliage, evaluating kelp growth and loss of kelp tissue. The field experiment was run at Punta de Tralca, Chile (33°25' S, 71°42' W; see Fig. 1), during the austral summer (February–March 2013). We selected this OA site because it was dominated by kelp beds of *L. trabeculata* and can be easily accessed from shore. Prior to the experiment, a preliminary sampling was done to estimate local densities and size of snails inhabiting adult kelp individuals in order to implement natural densities in the experimental setup. Both variables were obtained by counting the number of snails found on 10 randomly selected *L. trabeculata* sporophytes (including holdfast, stipes, and blades) at a standardized depth of 8 m. All snails from each of the 10 sporophytes surveyed were carefully removed and placed in a mesh bag (0.5 mm mesh size) and measured in the laboratory (maximum length: anterior to posterior) to the nearest 0.01 mm using vernier calipers. The number ($n = 53$) and size (mean: 13 mm; range: 10–17 mm) of snails were chosen to represent average abundance observed in the field survey during our initial removal of *Tegula*.

To evaluate kelp growth (measured here as blade elongation), naturally established *L. trabeculata* sporophytes free of epibionts and with no sign of deterioration (e.g., grazing marks, wounds, and

bleached tissue) were exposed to three experimental conditions, determined by the density of *Tegula*. The following three treatments were used: (1) enclosed snails (hereafter grazing, with mean natural densities of *Tegula*), (2) exclusion of all consumers permanently (no grazing), and (3) all consumers allowed access to stipes from nearby areas (manipulated control). For the grazing and exclusion (no grazing) treatments, mesh tubes (60 × 80 cm length) were fastened to the upper edge of the holdfast enclosing the whole sporophyte from the base of stipes only; prior the enclosure, all grazers were removed. Eighteen *L. trabeculata* sporophytes were randomly selected from a ~100-m² kelp bed patch. We removed all *Tegula* from the manipulated control ($n = 6$) and disposed them away from the experimental arena. One day after the removal, six sporophytes were randomly assigned to each treatment. For all treatments, our response variables were (1) blade elongation rates (as proxy for kelp growth) and (2) tissue loss.

To measure growth and tissue loss, five blades were randomly selected from each selected sporophyte and tagged by looping cable ties of different colors to follow growth since initial measurement of the same blade. Growth was estimated by the hole-punch technique (Parke 1948). At day 0, a 3 mm diameter hole was punched in the central part of the blade at a distance of 10 cm from the stipe/blade transition using a cork borer. Apical blades were used because of their active growth. After 32 d in the field, caged sporophytes ($n = 12$) were collected for the evaluation of tagged blades and estimations of the remaining number of snails (when necessary). The five-tagged blades of each caged and uncaged sporophyte ($n = 6$) were removed and transported to the laboratory for final measurements. Kelp growth of each sporophyte, estimated as blade elongation rate based on hole displacement distance, was calculated using the mean values of the five blades and expressed as daily growth (mm/d). Tissue loss was calculated by estimating the difference between expected length (summing the initial length at day 0 and the displacement of the hole during the experiment) and realized final length (at day 32) of the tagged blade (see Tala et al. 2004, Rothäusler et al. 2009).

To evaluate whether grazing effects (i.e., tissue loss) and macroalgae growth (i.e., blade elongation)

varied according to the different treatments, one-way ANOVA was used, followed by a Tukey's honestly significant difference post hoc tests when appropriate. Shapiro and Fligner-Killeen tests were used to evaluate normality and homoscedasticity of variance to meet ANOVA assumptions, respectively.

RESULTS

Reef fishes

Reef fish consistently presented significantly higher diversity and abundance of species in TURF areas, regardless of upwelling condition (Fig. 2). A total of 13 fish species from five trophic groups were observed during our surveys. Species observed at all sites included the planktivore *Chromis crasma*, the herbivore *Aplodactylus punctatus*, the omnivore *Scartichthys viridis*, and the benthic carnivore *Pinguipes chilensis*. Total reef fish biomass was significantly higher at TURF sites compared to OA sites (Fig. 2a, Table 1). Likewise, biomass of reef fish species exploited by recreational and artisanal fishers, such as *Graus nigra*, *Cheilodactylus variegatus*, *Paralabrax humeralis*, *P. chilensis*, and *Prolatilus jugularis*, was significantly higher at TURFs than at OA sites (Fig. 2b, Table 1). We observed large individuals of *G. nigra*, *P. chilensis*, and *C. variegatus* only at TURF sites (except in Punta de Talca), which predominantly explained differences in biomass. There was no significant effect of upwelling on total or exploited fish biomass (Fig. 2, Table 1). The VPC revealed a positive influence of the random parameters over our predictors in both total fish biomass (0.85) and exploited fish biomass (0.7).

In terms of fish trophic groups, biomasses of benthic carnivores and herbivores were higher at TURFs than at OA sites. Planktivore biomass was higher at upwelling-dominated sites. Finally, biomass of omnivores was similar among all sites, regardless of upwelling or management regime (see Table 1).

Kelp density and canopy foliage index

Kelp density was significantly higher at upwelling sites (i.e., Quintay and Punta Talca; Fig. 3a, Table 1), regardless of the presence of TURFs. The canopy foliage index was overall lower in non-upwelling areas (Fig. 3b, significant interaction in Table 1) and particularly low in

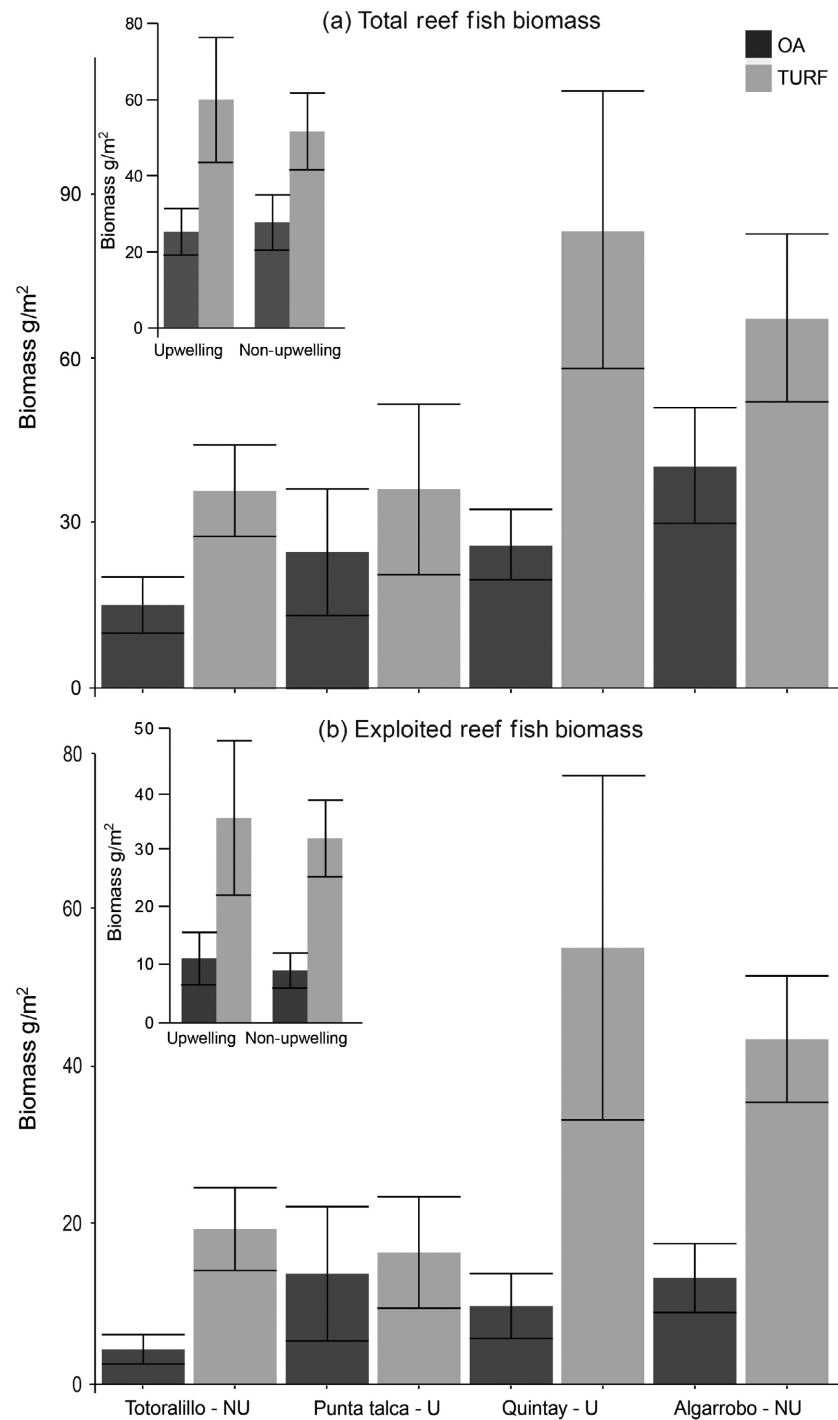


Fig. 2. Mean ($\pm$ standard error) for (a) total reef fish biomass (g/m^2) of 15 species and (b) exploited reef fish biomass (g/m^2 ; i.e., *Semicossyphus darwini*, *Graus nigra*, *Cheilodactylus variegatus*, *Pinguipes chilensis*, *Paralabrax humeralis*, *Prolatilus jugularis*) under different upwelling conditions and management regimes (Territorial User Rights for Fisheries [TURF] in gray bars and open-access [OA] in black bars). The figure inside represents the sum of site means per categories (upwelling and non-upwelling sites). U refers to upwelling sites and NU to sites with no upwelling influence.

Table 1. (a) Reef fishes, total, exploited, and trophic group biomass, (b) density and canopy foliage index of kelp *Lessonia trabeculata*, (c) abundance of the grazer *Tegula* and (d) abundance of understory functional groups such as crustose algae (*Hildenbrandia* sp., *Lithothamnium* sp.), articulated algae (i.e., *Gelidium* spp., *Cladophora* spp., Ceramiaceae), filter feeders (poriferans, ascideans, mussels), and species richness as number of understory species.

Source of Variation	Upwelling			Management			Upwelling × Management		
	df	Z	<i>P</i> (> z)	df	Z	<i>P</i> (> z)	df	Z	<i>P</i> (> z)
(a) Reef fishes									
Total	1	0.32	0.75	1	−3.23	0.001	1	−0.28	0.77
Exploited	1	0.08	2.5	1	−3.4	0.001	1	0.68	0.49
Planktivores	1	2.5	0.01	1	−0.02	0.99	1	−0.4	0.77
Herbivore	1	−0.58	0.5	1	−2.63	0.001	1	−0.45	0.05
Omnivore	1	0.54	0.6	1	0.09	0.9	1	−1.3	0.2
Benthic feeder	1	0.06	0.75	1	−3.45	0.001	1	−0.8	0.43
Piscivore	1	0.3	0.7	1	−0.6	0.5	1	0.43	0.2
(b) Kelp									
Density	1	4.3	0.001	1	1.9	0.06	1	−0.3	0.77
Canopy foliage	1	0.5	0.7	1	−1.01	0.3	1	0.8	0.4
(c) <i>Tegula</i>									
Density	1	0.34	0.73	1	1.91	0.05	1	−1.7	0.08
On kelp	1	9.8	0.03	1	−4.6	0.0001	1	5.8	0.0001
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
(d) Understory									
Crustose	1	1.18	0.30	1	6.5	0.01	1	6.1	0.01
Turf	1	141.7	0.35	1	9.8	0.004	1	13.3	0.001
Filter feeder	1	1.3	0.3	1	0.1	0.07	1	12.7	0.07
Richness	1	25	0.03	1	21	0.04	1	2.8	0.23

Note: Bold values indicate significance at $P > 0.05$.

OA sites of non-upwelling areas. Kelp canopy foliage index was consistently higher in upwelling-dominated sites (Punta Talca and Quintay), exhibiting higher values of stipe-to-length ratio, regardless of management regime (Fig. 3b, Table 1). In OA sites in non-upwelling areas, we observed an almost total absence of fronds in a high percentage of sporophytes. This was visually striking, as live kelp plants stripped of their canopy foliage appeared as “skeletons” and occurred in patchy distributions on a scale of 1–10s of meters (see Appendix S1: Fig. S2). The VPC revealed no influence of the random parameters over our predictors for both kelp density and canopy foliage index (~0).

Lastly, average kelp size was lower in upwelling centers due to the abundance of small kelp individuals (PERMANOVA, $df = 7$; pseudo- $F = 2.86$; $P > 0.0001$). The proportion of recruits (i.e., holdfast diameter <10 cm) was higher in upwelling than in non-upwelling areas, regardless of management regime (Fig. 4).

Density and use of kelp by grazers

Density of grazers was significantly higher at OA sites particularly in non-upwelling locations (Fig. 5a, Table 1). However, higher grazer (*Tegula*) density in OA management was also observed in upwelling locations but the magnitude of the effect was weaker (Fig. 5a; Table 1). Individual *Tegula* were frequently found actively grazing along of kelp sporophytes (i.e., blades) in most OA sites of non-upwelling areas (Fig. 5b). The sea urchin *Tetrapygus niger* was absent at most study sites, or found only in low abundance (Quintay OA [mean ± standard error (SE) = 6.75 ± 6.8 ind/m²] and Totoralillo TURFs [mean ± SE = 3.5 ± 3.5 ind/m²]). The VPC revealed a positive influence of the random parameters over our predictors in total number of *Tegula* (VPC = 0.9).

Cover of understory species

Understory species richness showed no interaction between upwelling and the effects of management regime. Sessile species richness that

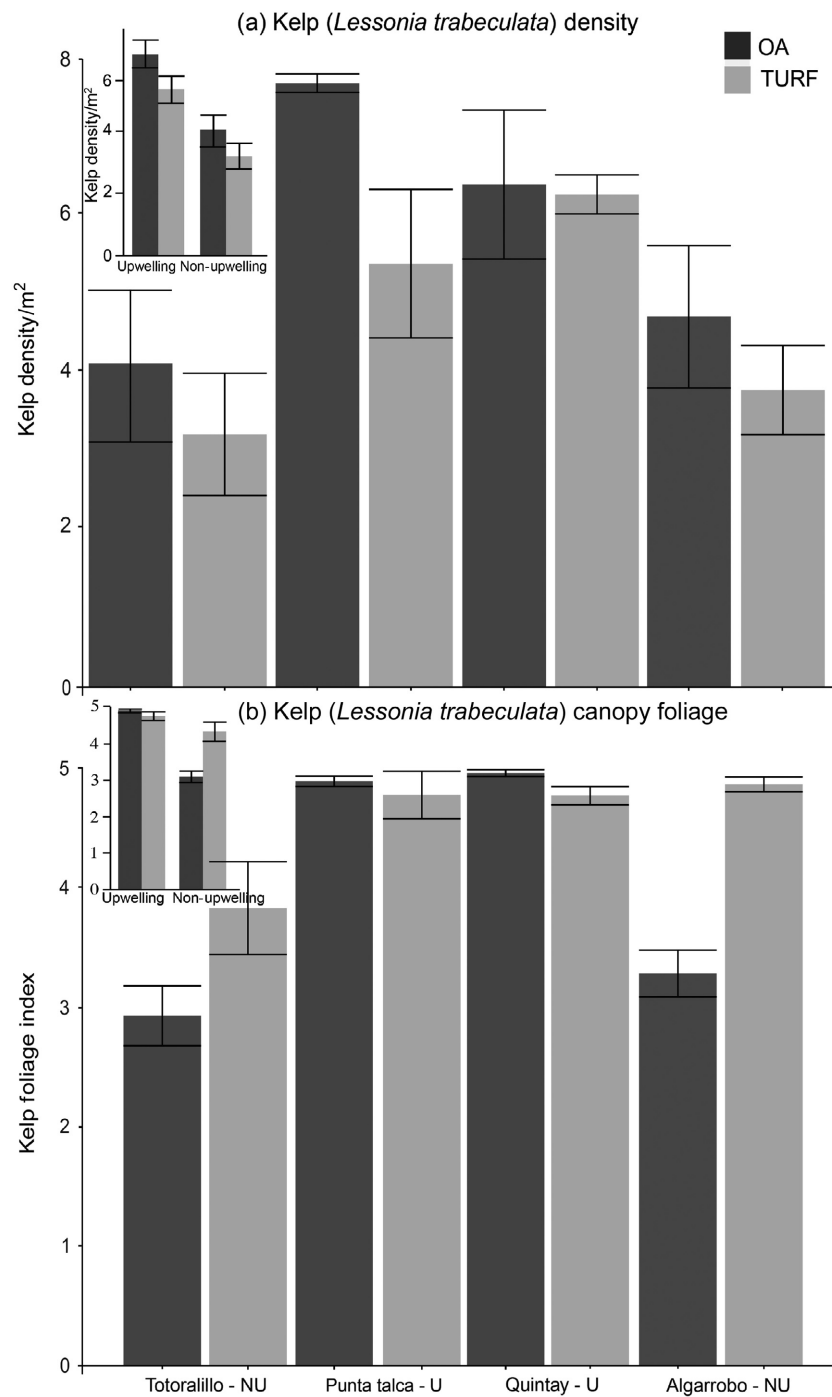


Fig. 3. Characterization of the kelp forest based on the mean ($\pm$ standard error) for (a) density of kelp *Lessonia trabeculata* and (b) kelp canopy foliage index under different upwelling conditions and management regimes (Territorial User Rights for Fisheries [TURF] in gray bars and open-access [OA] in black bars). The figure inside represents the sum of site means per categories (upwelling and non-upwelling sites). U refers to upwelling sites and NU to sites with no upwelling influence.

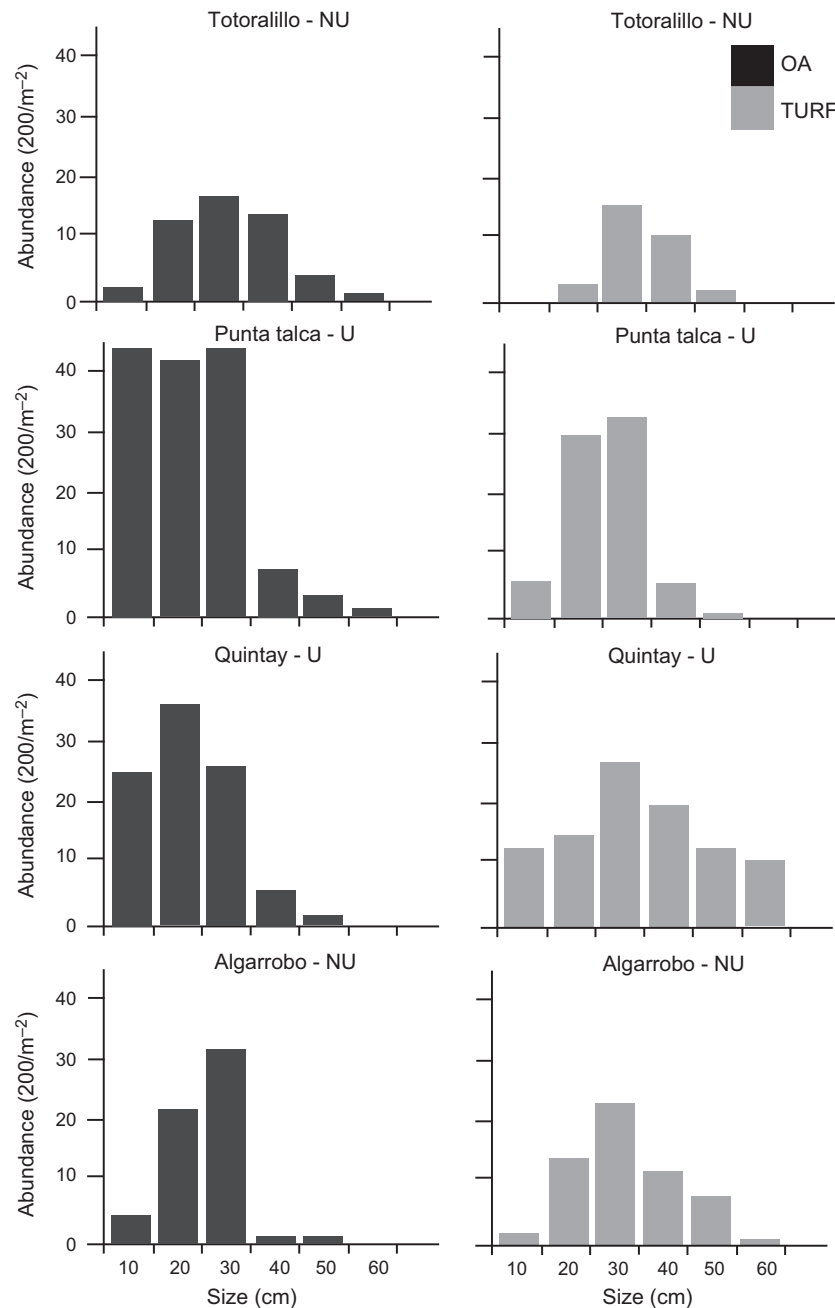


Fig. 4. Total abundance (200 m^{-2}) and holdfast size (cm) distribution of kelp (*Lessonia trabeculata*) under different upwelling conditions and management regimes (Territorial User Rights for Fisheries [TURF] in gray bars and open-access [OA] in black bars). U refers to upwelling sites and NU to sites with no upwelling influence.

covered substratum was significantly higher in all TURF sites compared with OA sites, regardless of upwelling regime (Table 1). We observed that underneath the kelp canopy (i.e., understory), the rock surface was mostly dominated by

crustose calcareous algae, *Lithothamnium* spp., and non-calcareous crustose, *Hildenbrandia* spp., which together covered more than 65% of the substratum at all sites. In TURF sites, either turf algae or filter feeders covered the remaining 30%

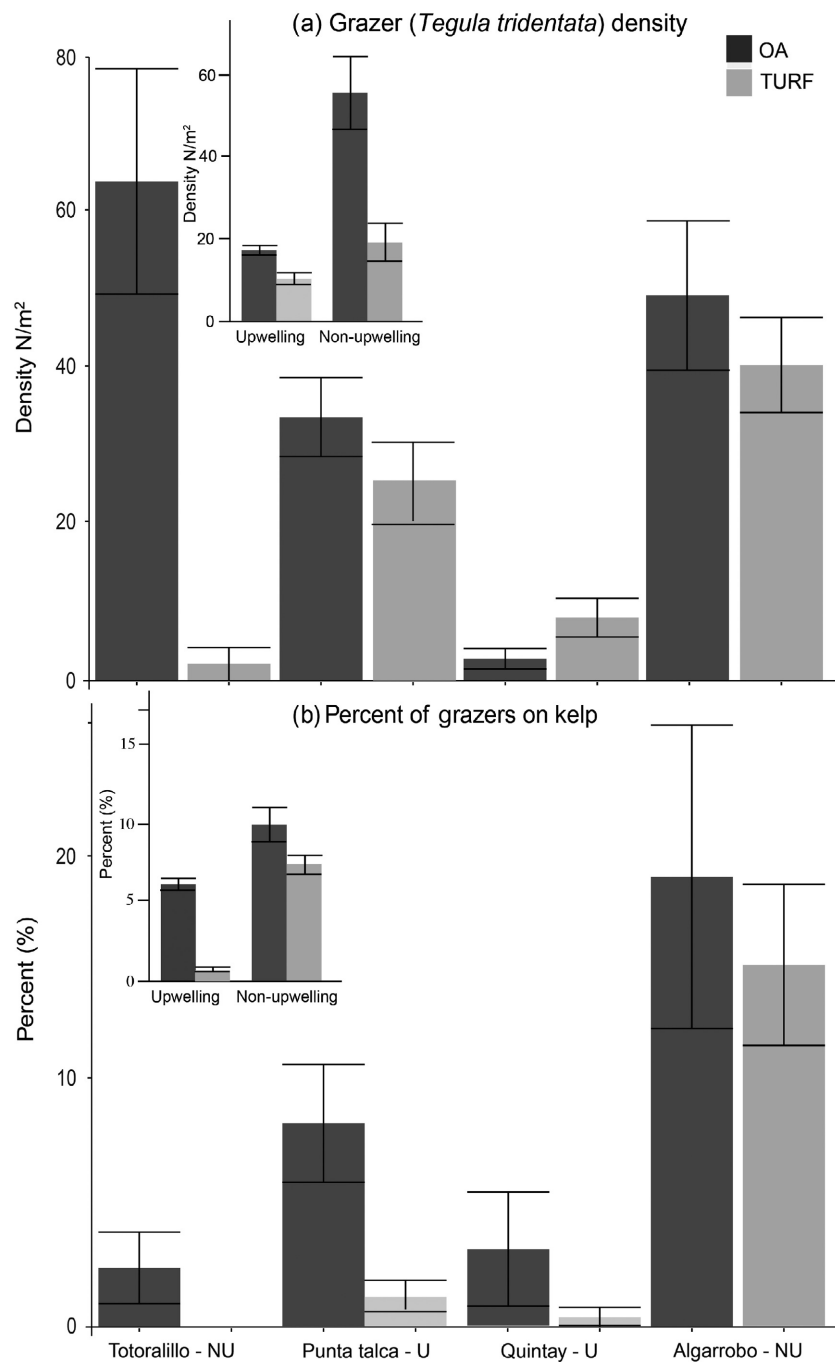


Fig. 5. Mean ($\pm$ standard error) for (a) density and (b) proportion in percent (%) of *Tegula* on kelp (holdfast, stipes, blades) under different upwelling conditions and management regimes (Territorial User Rights for Fisheries [TURF] in gray bars and open-access [OA] in black bars). The figure inside represents the sum of site means per categories (upwelling and non-upwelling sites). U refers to upwelling sites and NU to sites with no upwelling influence.

of the substratum, whereas the two crustose algal species covered more than 85% of all OA sites.

Effects of snails on kelp growth in the field

Our field experiment showed significant difference among treatments in kelp blade elongation growth (one-way ANOVA, $df = 2$, $F = 30.69$, $P < 0.001$; Fig. 6a) and tissue loss (one-way ANOVA, $df = 2$, $F = 9.60$, $P < 0.001$; Fig. 6b). Blade elongation growth was negative when grazing snails (*Tegula*) were added in natural densities to our enclosure treatment. Significantly higher and positive blade elongation growth was observed in snail exclusion and manipulated control treatments (Tukey's post hoc test, $P = 0.035$). No differences were observed between our manipulated control and snail exclusion treatments (Tukey's post hoc test, $P = 0.18$; Fig. 6a). Similarly, kelp tissue loss (cm/d) was significantly

different among treatments (one-way ANOVA, $df = 2$, $F = 9.60$, $P < 0.001$; Fig. 6b). Greater kelp tissue loss was observed, where *Tegula* were added (i.e., grazing; Tukey's post hoc test, $P = 0.01$). Significantly lower tissue loss was observed either when kelp was exposed to natural density of snails (manipulated control) or when snails were experimentally removed (grazing; Tukey's post hoc test, $P = 0.49$; see Fig. 6b).

DISCUSSION

Our results allow understanding patterns reported in numerous previous studies conducted at single or restricted locations and shedding light onto local variability in relation to dominant management scenarios (i.e., TURFs vs. OA) and near-shore oceanographic conditions (i.e., upwelling). Our quantitative and manipulative approaches provide new insights into the causes of changing community structure at different trophic levels in kelp forest ecosystems of central Chile. On the one hand, we observed a reduction in biomass of herbivores and benthic carnivorous reef fishes driven by a substantial removal of individuals from non-protected, OA sites, regardless of upwelling conditions. On the other hand, upwelling is shown to be extremely important in our system, affecting density, recruitment, size distribution, and foliage of habitat structuring kelp (*Lessonia trabeculata*), regardless of management condition and reducing the intensity of modifying top-down processes. Planktivorous fish may respond to the enhanced conditions in upwelling locations, as higher biomass of this trophic group was also found. We also observed an increase in abundance of small herbivores (i.e., *Tegula*), particularly in non-upwelling areas, that can lead to a reduction in foundation species (i.e., *L. trabeculata*), which appears to be slowly being overgrazed. These findings provide a first step toward a better understanding of coastal kelp ecosystems of South-eastern Pacific Ocean, considering interspecific trophic interactions. Our results show the relevance of considering multi-specific approaches to manage coastal fisheries in the productive eastern boundary ecosystems as humans, via fisheries, impact community and food web structure (see Pérez-Matus et al. 2017).

Although our study is based on hard-won data from multiple sites along a large extent of

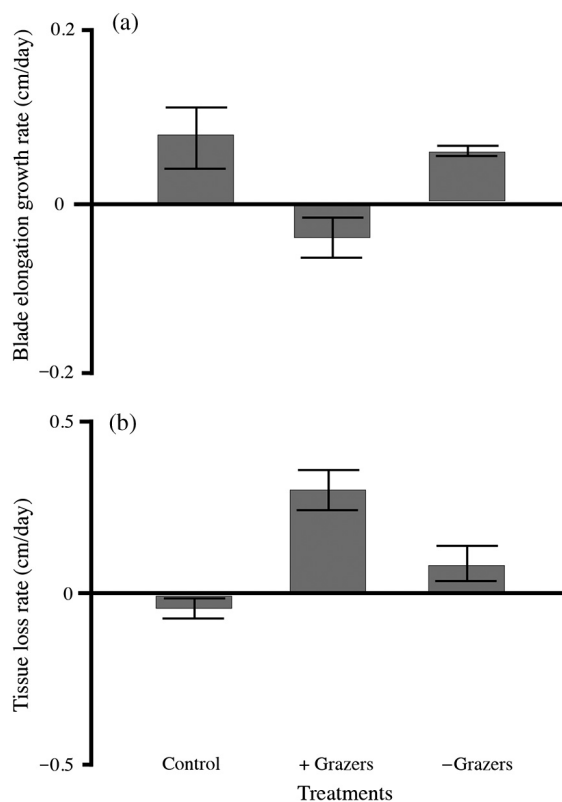


Fig. 6. Results from field experiment showing mean ($\pm$ standard error) blade elongation (cm/d), used as a proxy of growth rate, and tissue loss (cm/d) among treatments (manipulated control, added grazers [grazing], and grazers excluded [no grazing]).

coastline (that allows us to match relevant scales to oceanographic processes and management scenarios), our statistical tests suffer from lack of power, as we were only able to achieve minimum replication (there were only two large upwelling centers that contain well-established TURFs along this region). Thus, it was surprising that we observed such strong, significant differences in some variables, providing confidence to our interpretation of these effects, whereas the lack of observed differences in others must be interpreted with greater caution.

We found that TURFs consistently maintained higher total and exploited fish biomass, higher biomass of invertivore fishes (i.e., benthic carnivores), higher kelp density, and higher richness of sessile species in the kelp understory, irrespective of the upwelling regime. Because no biological diversity data were collected before TURF implementation, it is impossible to know with certainty whether such changes are associated exclusively with management or with fishers' ability to choose more productive and biologically diverse sites. Due to the diverse priorities that drive fisher's selection of coast for TURF petition, the latter seems unlikely, as accessibility is one of the most limiting factors on this wave-exposed coast. Further, key case studies in which specific TURFs were followed through time document critical influence of fisher practices (Castilla and Duran 1985, Lester et al. 2009). Because access to spearfishers is limited in the studied TURFs due to fisher-lead enforcement that prohibits other divers from entering the TURF, the direct effects of reduced fishing intensity seem most plausible explanation for higher fish biomass.

Our results suggest that upwelling conditions appear to set the scene, favoring higher overall abundance of kelp in different ontogenetic stages (e.g., adults and recruits). Prior studies at many of these same study sites have documented consistent among-site differences in onshore temperature and nitrate concentrations that follow spatial patterns of upwelling intensity along the coast (Wieters 2005, Tapia et al. 2009, 2014). Thus, the lower temperatures and higher nutrients at sites of intense upwelling could enhance critical attributes of kelp performance (e.g., growth, reproduction, survival) critical to maintain higher abundance. Indeed, variation in upwelling explains among-site differences in growth rates of other benthic

macroalgae (e.g., corticated turfs) along central Chile (Wieters 2005) and kelps elsewhere (e.g., Field et al. 1980, Tegner and Dayton 1991). The relatively high proportion of small, new recruits (<10 cm diameter) at upwelling centers, and their near-absence at non-upwelling areas, suggest that propagule supply and early survival may be limiting factors in local population size at non-upwelling locations. On the other hand, it is remarkable how the influence of upwelling propagates to planktivorous fishes influencing the fish assemblages. Upwelling may directly or indirectly enhance abundance of food availability for planktivorous fish–phytoplankton productivity, which seems unlikely since chlorophyll concentrations are persistently lower at some upwelling centers, apparently due to strong offshore and alongshore advection that transports blooms away from upwelling centers to maintain consistently lower phytoplankton abundance (Wieters et al. 2003). Similarly, onshore settlement and recruitment rates of key benthic invertebrates (mussels, barnacles) tend to be lower at areas of strong upwelling (Navarrete et al. 2005), suggesting that there may also be relatively reduced availability of planktonic larvae. We suspect that the abundance of planktonic reef fish may be related to upwelling-enhanced kelp productivity that may result in augmented detritus, essential to planktivorous fishes, as has been documented for other suspension feeders elsewhere (Field et al. 1980, Krumhansl and Scheibling 2012).

Our analyses provide information on the interplay between management effects and nearshore oceanographic conditions such as upwelling intensity. Territorial Use Right for Fisheries presence appeared to reduce damage and loss of kelp foliage, as well as to restrain abundance of kelp grazers, where upwelling was weak or absent. In contrast, TURFs had no such effects at upwelling centers. These results suggest that herbivory could have a strong influence on adult kelp canopy and morphology at spatially identifiable areas along the coast. Here, we often observed large aggregations (>200 individuals) of snails (*Tegula*) that were foraging high in the canopy of near-defoliated sporophytes. Our field observations and experiments suggest that *Tegula* climb onto blades and stipes principally for feeding and not as an escape response from other benthic predators (e.g., fish, sea stars, crabs). This could

potentially reduce individual kelp growth and augment tissue loss. Other herbivores, including sea urchins commonly restricted to shallower habitats, were infrequently found. One hypothesis of the higher abundance of snails in OA, as well as the strata of the kelp they use, may be related to the lower abundance of large fish predators such as *Semicossyphus darwini*, *Cheilodactylus variegatus*, and *Graus nigra* (see fig. 1 in Godoy et al. 2010), which are known consumers of important grazers including *Tegula* (Pérez-Matus et al. 2012). In addition, fishing efforts are persistently high on other potential *Tegula* predators such as the muricid gastropod (*Concholepas concholepas*) and carnivorous crabs (e.g., *Homalaspis plana*, *Cancer* spp.) at most OA sites (Gelcich et al. 2008, 2012), which might limit snail mortality and lead to increased snail (*Tegula*) abundance. Unfortunately, our surveys do not provide adequate estimates of alternative invertebrate predator abundance because their relatively high-mobility use of refuges and nocturnal behavior require separate sampling methods. The lack of predators (e.g., reef fish and crabs) may have reduced top-down effects in OA areas in comparison with TURFs causing a twofold increase in abundance of *Tegula*. In our non-upwelling sites, where nutrient input is lower, the increases in the abundance of *Tegula* have the potential to affect kelp sporophyte foliage as it can be derived from our field experiment. Additionally, reduced nutrients in non-upwelling conditions may limit growth and physiological condition that interacts with top-down processes, leaving individuals more vulnerable to herbivory by altering chemical and/or structural defenses. In this scenario, structural defenses generated by dense foliage and water motion that creates a whiplash effect have been documented as an important mechanism to prevent grazing in intertidal *Lessonia* (Konar 2000, Thiel et al. 2007).

Snail grazing and associated damage with kelp morphology through reduction in the blade-to-stipe ratio (kelp canopy foliage index) were clearly evident in our experiment. In the OA sites (but only in non-upwelling conditions), snails were active and feeding on kelp, leaving some patches without blades (i.e., reducing the kelp canopy foliage) and suggesting important numerical and behavioral changes in *Tegula*. Snail grazing most likely explained the observed kelp

morphologies and the presence of vast parts of the kelp forest in a defoliated state. However, snails directly “devouring” an entire kelp sporophyte (i.e., stipes and holdfast) were not observed. It is plausible that the recorded changes in kelp canopy foliage reflect either sublethal effects of this mesograzers or additional influences of other herbivores in the system. Indeed, Gelcich et al. (2012) reported consistently higher abundance of the non-commercial black sea urchin *T. niger* in OA locations, and Perreault et al. (2014) experimentally evaluated the effect of the black sea urchin *T. niger* in shallower habitats at one of our study sites (i.e., Totoralillo OA), suggesting the ability of sea urchins to trigger shifts from kelp to barrens in depths between 2 and 6 m, where other factors such as wave action and whiplash of fronds and stipes may have also reduced *Tegula* impacts (Vásquez 1991).

Another important aspect in Chile, and especially in northern areas from 18° to 32° S, is the social, ecological, and economical important influence of the benthic fisheries (Vásquez 2008, Navarrete et al. 2010). Economically, landings of kelps reach up to 350,000 dry tons per year, representing close to US\$90 million for the industry (Vásquez 2008). Until 2002, the Chilean brown seaweed fishery was mainly sustained by collecting stranded kelp on the shore that is taking advantage of natural kelp mortality. Since then, four kelp species have been intensively harvested as a source of raw material for the extraction of alginic acid, generating negative impacts in the regional abundance of subtidal kelp species (Krumhansl et al. 2016). Although we did not visually record the effect of subtidal kelp harvesting in our study sites, kelp harvest is quite common around our northern sites, particularly in Punta Talca and Totoralillo. Kelp fishery removes entire sporophytes, thus generating space for recruitment, and this may be observed at Punta Talca (Vásquez 2008). Ecologically, the effect of this fishery in the subtidal environment has not yet been evaluated, but certainly may introduce additional effects of fishing that might cascade to the entire community.

Species assemblages are expected to respond in different ways to oceanographic processes (Smith and Witman 1999, Wieters et al. 2003, Witman and Smith 2003). In the eastern boundary upwelling ecosystems, the localized nature of coastal

upwelling affects community configurations by enhancing recruitment and growth of epifaunal and algal communities (Menge 2000, Wieters et al. 2003, Aquilino et al. 2009). Our results demonstrated that kelp beds responded positively in upwelling areas, highlighting the important role of bottom-up effects (nutrient enrichment) on the food web, and in the intensity of biological interactions, particularly top-down effects. We observed impacts of grazing on kelp in OA sites (possibly due to top-down processes); however, our results highlighted that kelp condition was further reduced at sites without the influence of upwelling (nutrient-rich waters). In well-enforced TURF (i.e., 24-h surveillance), our results further support the ancillary and unexpected role of TURFs for conservation of coastal fishes, which are not the target group of this management strategy (Gelcich et al. 2008, 2012). Moreover, we showed that TURFs played an important role in enhancing fish biomass regardless of environmental conditions, and we hypothesized that this enhancement effect generated important consequences in maintaining the kelp forest community. Our results show similar patterns to studies conducted in semi-protected areas in coral reefs, showing that collaborative management (e.g., TURF) maintains a greater fish biomass than areas lacking local management (Cinner et al. 2012). Our results also highlight the need of developing and supporting complementary management schemes, namely TURFs and MPAs (marine protected areas), to preserve exploited and non-exploited biomass and ecosystem functioning.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1808/full>