

Seasonal variation in epifaunal communities associated with giant kelp (*Macrocystis pyrifera*) at an upwelling-dominated site

NATALIA S. WINKLER,^{1*} ALEJANDRO PÉREZ-MATUS,¹ ÁLVARO A. VILLENNA^{1,2}
AND MARTIN THIEL^{2,3,4}

¹Subtidal Ecology Laboratory & Center for Marine Conservation, Estación Costera de Investigaciones Marinas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago,

(E-mail: natalia.s.winkler@gmail.com) ²Facultad Ciencias del Mar, Universidad Católica del Norte,

³Millennium Nucleus Ecology and Sustainable Management of Oceanic Island (ESMOI), ⁴Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

Abstract Kelp forests are highly productive and species-rich benthic ecosystems in temperate regions that provide biogenic habitat for numerous associated species. Diverse epifaunal communities inhabit kelp sporophytes and are subject to variations in the physical environment and to changes experienced by the kelp habitat itself. We assessed seasonal variations in epifaunal invertebrate communities inhabiting giant kelps, *Macrocystis pyrifera*, and their effects on this seaweed. Six seasonal samplings were conducted over a year at an upwelling-dominated site in northern-central Chile where physical conditions are known to fluctuate temporally. More than 30 taxa were identified, among which peracarid crustaceans stood out in both diversity and abundance. Species richness and abundance differed among sporophyte sections (holdfast and fronds) and throughout the year. The frond community was dominated by two grazers (the amphipod *Peramphithoe femorata* and the isopod *Amphoroidea typa*), while suspension feeders, grazers, and omnivores (the amphipod *Aora typica*, the isopod *Limmoria quadripunctata*, and polychaetes) dominated the holdfasts. Abundances of the dominant species fluctuated throughout the year but patterns of variation differed among species. The most abundant grazer (*P. femorata*) had highest densities in summer, while the less abundant grazer (*A. typica*) reached its peak densities in winter. Interestingly, the area of kelp damaged by grazers was highest in autumn and early winter, suggesting that grazing impacts accumulate during periods of low kelp growth, which can thus be considered as ‘vestiges of herbivory past.’ Among the factors determining the observed seasonal patterns, strong variability of environmental conditions, reproductive cycles of associated fauna, and predation by fishes vary in importance. Our results suggest that during spring and early summer, bottom-up processes shape the community structure of organisms inhabiting large perennial seaweeds, whereas during late summer and autumn, top-down processes are more important.

Key words: associated epifauna, kelp, *Macrocystis pyrifera*, seasonal fluctuations, temperate regions.

INTRODUCTION

Large kelps are widely distributed in temperate coastal areas of both hemispheres (Dayton 1985; Graham *et al.* 2007), providing a broad range of ecosystem services, including wave protection, habitat for diverse organisms, essential habitats for coastal fishes (such as spawning and nursery, feeding, and migration grounds), and biomass production, among others, thus having a crucial importance for the ecology of associated algae and fauna and for the economy of local fishing communities (Steneck *et al.* 2002; de Juan *et al.* 2015). Kelp forests are considered one of the most productive and diverse benthic

ecosystems of the world acting as ecosystem engineers, crucial for the co-existence of hundreds of species (Steneck *et al.* 2002; Graham *et al.* 2007). Habitat-forming kelps provide environmental heterogeneity and high structural complexity (Dayton 1985; Graham *et al.* 2007), hosting diverse and abundant assemblages of algae, fish fauna, and sessile and motile epifauna of invertebrates (Ebeling *et al.* 1980; Ojeda & Santelices 1984; Thiel & Vásquez 2000; Pérez-Matus *et al.* 2007; Villegas *et al.* 2008). Depending on their utilization of vegetative structures (holdfast, stipes, or blades), epifauna may partition their activities among and within kelps in relation to their differential requirements, and consequently, the community found in the canopy may differ from that living in the bottom parts of kelps (Christie *et al.* 2003).

*Corresponding author.

Accepted for publication May 2016.

Temperate reefs worldwide are exposed to considerable seasonal variation. Seasonal change in environmental conditions associated with solar irradiance, seawater temperature, salinity, water movement, storms (Edgar 1983; Reed *et al.* 2011), sedimentation (Geange *et al.* 2014), and nutrient availability has been shown to control seaweed population dynamics (Buschmann *et al.* 2004; Nielsen & Navarrete 2004; Wieters 2005; Vásquez *et al.* 2006; Graham *et al.* 2007; Kraufvelin *et al.* 2010). Several seaweed species show higher biomass and per-capita growth rate during summer–spring, while limited growth and loss of tissue is observed during winter due to lower light intensities, temperature, and nutrient availability (Edgar 1983; Buschmann *et al.* 2004; Tala & Edding 2005). How these changes influence the assemblage of mobile epifauna and how they in turn affect their host seaweed remain unknown.

It has been reported that the abundance and composition of associated epifaunal assemblages (Edgar 1983; Ojeda & Santelices 1984; Taylor 1998; Adami & Gordillo 1999; Ríos *et al.* 2007), as well as grazing damage (Viejo & Åberg 2003), significantly vary due to the seasonal fluctuations of annual seaweeds. Both annual and perennial seaweed populations are common ecosystem engineers in coastal temperate environments. Nonetheless, there is limited information on the dynamics of epifaunal communities associated with large perennial seaweeds, which maintain dense biomass throughout the year with minor seasonal fluctuations in abundance (Tuya *et al.* 2011). In addition, most studies on kelps have focused on the holdfast community, and few have been conducted on the upper kelp sections (for an exception, see Coyer 1984). Holdfasts are important structures in large brown seaweeds as they modify the heterogeneity of subtidal substrata (Moore 1972; Tuya *et al.* 2011). However, the holdfast size and morphology is substantially different from that of fronds, which are characterized by extensive blade biomass.

Damage generated by epifaunal herbivores (mesograzers) varies depending on the distribution, density, and composition of the herbivore assemblage. The effects of epifauna on seaweeds range from no variation in host growth (Poore *et al.* 2009) to reduction in reproductive output, growth rates, and impacts on algal morphology (Duggins *et al.* 2001; Coleman *et al.* 2006; Poore *et al.* 2014). By consuming large amounts of algal biomass, epifaunal communities can affect the abundance and distribution of their host seaweeds (Dayton 1985; Chess 1993; Vásquez & Buschmann 1997; Haggitt & Babcock 2003). In addition, seasonal changes in seawater temperature can affect seaweed chemical composition (lipid, carbohydrate, and protein content) (Himmelman & Carefoot 1975), alter feeding behavior of herbivores (Sotka & Giddens 2009), and modify the structure

and activity of fish predator communities (Ebeling *et al.* 1980). In general, the relationship between seasonal fluctuations of epifauna and grazing intensity in perennial seaweeds is still poorly understood (Viejo & Åberg 2003). Temperate perennial seaweeds are exposed to strong seasonal variation in their physical and biological environment, and thus, it is expected that their associated epifaunal communities and the influence of associated organisms on seaweed hosts will fluctuate seasonally.

Similar to many other temperate regions of the world (including northern California, South Africa, and New Zealand), the dynamics of the coastal South-East Pacific are characterized by strong upwelling, nutrient-rich waters, and high biological productivity that vary seasonally (Broitman *et al.* 2001; Steneck *et al.* 2002; Wieters 2005; Thiel *et al.* 2007; Bravo *et al.* 2013). In Chile, the two large kelps *Lessonia trabeculata* and *Macrocystis pyrifera* dominate temperate subtidal rocky reefs which are subject to intense inter-annual and seasonal fluctuations in biotic and abiotic variables. Both kelp species present seasonal growth and productivity patterns linked to the availability of nutrients and solar radiation (Brown *et al.* 1997; Buschmann *et al.* 2004; Tala & Edding 2005).

We focussed on the perennial giant kelp *M. pyrifera* to examine the seasonal variation in epifaunal communities and grazing damage. In particular, we studied the temporal variability in within-sporophyte distribution, the composition, and abundance of epifaunal assemblages inhabiting *M. pyrifera*, as well as herbivore-inflicted damage on the host seaweed. We expected to find differences in the composition of epifaunal assemblages among sporophyte sections (fronds–holdfast) in relation to their trophic requirements; specifically grazers in higher abundances on fronds while other trophic groups (e.g. carnivores, detritivores) should be more common in holdfasts. As kelp productivity varies over the year reaching maximum growth during the austral spring and summer, we hypothesized that epifaunal abundances on fronds would increase in summer and diminish during the winter, hence reducing the grazing impact on blades and stipes during the cold season. However, holdfast communities are expected to show reduced seasonal variations in epifaunal abundances due to constant attachment of the structurally complex holdfast of *M. pyrifera*.

METHODS

Macrocystis pyrifera and study area

Kelp forests of *M. pyrifera* occur along the entire Chilean coast (Vásquez & Buschmann 1997; Graham *et al.* 2007; Thiel *et al.* 2007). Holdfasts are attached via multiple root-like haptera to the substratum, while fronds (blades and stipes) form a dense canopy extending from the

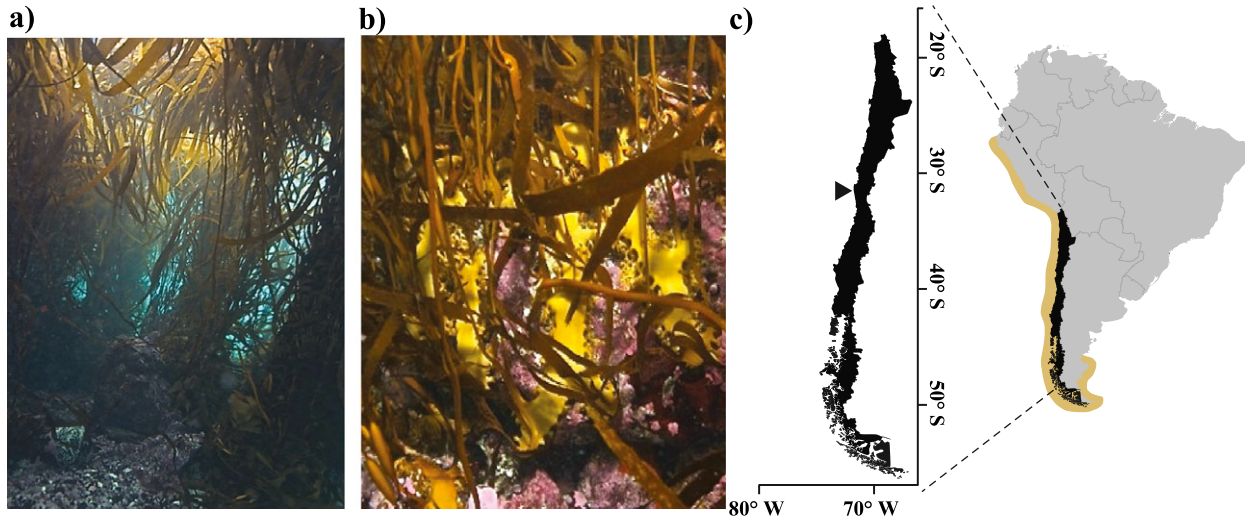


Fig. 1. Example of (a) *Macrocyctis pyrifera* forest and (b) holdfast at study site. (c) Map of Chile showing the localization of the subtidal kelp systems dominated by *M. pyrifera* at the study site (Punta de Talca is marked with a black arrow), and distribution of the giant kelp *M. pyrifera* along the coasts of South America (indicated as light brown area) (adapted from Graham *et al.* 2007).

holdfast to the upper tip of the long stipes (Fig. 1a,b). Both kelp sections (fronds and holdfasts) create a complex three-dimensional habitat structure in coastal subtidal areas (Graham *et al.* 2007).

This study was conducted on the northern-central coast of Chile in a kelp forest at Caleta Talquilla, Punta de Talca ($30^{\circ}52'37.55''\text{S}$, $71^{\circ}40'57.95''\text{W}$) (Fig. 1c). The bottom has low rugosity, and the substratum is dominated by small cobbles and boulders (10–30 cm diameter). The kelp forest growing at this site is characterized by monospecific stands of *M. pyrifera*, extending from the intertidal zones to 150–200 m distance from the shore and up to 5–8 m depth; farther beyond the outer limit of the *M. pyrifera* forest, the bottom is dominated by extensive stands of *L. trabeculata* down to about 30 m depth (A. Pérez-Matus, unpubl. data, 2012).

The coastal zone between 28° and 32°S is characterized by an extensive upwelling zone, resulting in highly dynamic oceanographic conditions where organisms are exposed to intensive seasonal variations in nutrients and temperature over the year (Thiel *et al.* 2007; Bravo *et al.* 2013). Specifically, Narváez *et al.* (2004) identified homogeneity of the water column in the autumn and winter, whereas a strong thermocline caused by the increase in solar radiation characterized coastal waters up to 10 m depth during spring and summer. In addition, maximum upwelling-favorable winds occur during the austral spring (Bravo *et al.* 2013), and the intensity of nutrient supply through upwelling varies both seasonally and latitudinally (Nielsen & Navarrete 2004; Thiel *et al.* 2007). Water temperatures range between 13°C (winter) and 18°C (summer), while salinity shows no seasonal variation with a mean value of 33‰ (Buschmann *et al.* 2004; Tapia *et al.* 2014).

Sampling design and field collections

Surveys were conducted bimonthly in February, April, July, September, November 2012, and January 2013. Samples

from each season (summer, autumn, winter, and spring) were obtained over a year of sampling. Temperatures during the study year followed a normal seasonal pattern without any particular anomalies (Table S1). The sampling period did not present extreme deviations in water temperatures, indicating that each sampling season could be considered as representative for the study site, following a similar pattern as in other years.

At each survey date, six randomly selected kelp individuals were sampled from the kelp forest. Field collections were made by SCUBA diving at depths ranging from 3 to 5 m. Sporophytes ranging from 1.5- to 2.5-m stipe length were selected. Due to natural variation in environmental conditions, seaweeds at the study site do not grow much larger and selected sporophytes represent the average sporophyte size at the local and adjacent kelp populations (Graiff *et al.* 2016). There was no difference in plant size among sampling months.

In order to avoid loss and mixing of the respective associated epifauna, fronds and holdfast structures were collected separately using large mesh bags (0.5 mm mesh opening) before they were cut off. The mesh bag was carefully placed over the frond, which was separated from the holdfast with a diving knife before closing the bag. A second bag was then quickly held over the holdfast, which was detached from the substratum with the diving knife and rapidly placed in the mesh bag together with all associated organisms. During sampling, we could see that the occasional amphipod, isopod, or polychaete was lost while prying off the holdfast from the substratum and placing it in the sampling bag. However, these were isolated cases, and we are confident that they did not affect the main results herein. Once on the shore, both sporophyte sections were labeled, fixed in a 5% formalin solution, and then transported to the BEDIM laboratory (Biology Ecology & Diversity of Invertebrates from Marine Environment) at Universidad Católica del Norte where sporophyte sections were measured and weighed, and epifauna was identified.

Taxa identification

Fronde and holdfast samples were washed with freshwater and sieved through a 0.5-mm sieve to retain the associated epifauna of each sporophyte section. Additionally, the washed kelp samples were carefully examined for any remaining fauna and then returned to the 5% formalin solution. Taxa were identified to species level whenever possible, with the exception of polychaetes, which were classified as one large group. Species were identified and counted using dissecting (Zeiss Stemi 2000-C) and light microscopes (Zeiss Primo Star), and systematic catalogs (Nordenstam 1930; Carvacho 1982; Myers & Moore 1983; Winkler 1992, 1994) together with help from specialists on different taxonomic groups.

Organisms inhabiting *M. pyrifera* holdfasts ($n = 36$) and fronds ($n = 36$) were classified into taxonomical groups, such as Amphipoda, Isopoda, Decapoda, Polychaeta, and Mollusca among others. In addition, based on their trophic characteristics, species were classified into large trophic functional groups, such as suspension feeders, grazers, omnivores, and carnivores (Thiel & Vásquez 2000; Sepúlveda *et al.* 2003; Taylor & Brown 2006). Bryozoans or hydrozoans were not considered for this study as benthic sporophytes of *M. pyrifera* in semi-exposed environments are usually free of sessile epibionts (A. Graiff & M. Thiel, unpubl. data, 2016).

Condition and damaged area of blades

The condition of blades was measured by scoring all blades from each sampled frond, as either 'complete' with no signs of herbivore damage on the blades or 'damaged by grazing' with clear signs of herbivory (including mesograzers) and damage caused by mesograzers. A blade was categorized as 'complete' when the maximum width was not at the end of the blade, while the category 'damaged by grazing' included internodes with the blade and/or the pneumatocyst missing as well as severely shortened blades where the maximum width was always at the end of the blade (absent and incomplete blades).

In addition, to determine the damaged area per blade, three upper and three lower blades of each frond were randomly selected and photographed. The percent of damaged or missing area on each blade was estimated from the projected total area using Image-Pro, version 4.0 software (Media Cybernetics Inc., Bethesda, MD, USA). Damage on blades included damage by *Peramphithoe femorata* nests and grazing damage such as missing areas or surface damage (lighter grazed regions).

Statistical procedures

Univariate and bivariate analyses

Species richness was calculated as the total number of taxa collected in both holdfasts and fronds and then compared to assess the existence of ecological differences among

sporophyte sections. Additionally, diversity and similarity indices (Shannon–Wiener and Sorenson's coefficient, respectively) were calculated.

Relative abundance for each species and taxon was calculated as the numerical proportion of each species or taxon from the total number of sampled individuals and expressed in percentage. Mean abundances were standardized to numbers as the individuals per kilogram of algal wet weight. The effect of sporophyte section (holdfast and fronds) and sampling month (February, April, July, September, November, and January) on total abundance (mean number of individuals per kilogram algal wet weight) was analyzed using a two-way analysis of variance (ANOVA). To meet ANOVA assumptions, abundance data were tested for normality and homogeneity of variances using Shapiro–Wilk's test, Q–Q plots, and Levene's test, respectively. Log-transformation achieved normality and homogeneity of variances for the dependent variable. After all significant ANOVA tests, post hoc Tukey HSD tests were performed to assess which sampling months differed significantly from others at a significant level of $P < 0.05$. In addition, to test for the effect of water temperature on total abundance of organisms on both plant sections, a simple linear model (lm)/regression analysis was performed independently. Monthly temperature values were obtained from the CEAZA website (<http://www.ceazamet.cl/>).

As above, damage on fronds was measured as (i) proportion of blades damaged by grazing from the total number of blades per frond, (ii) proportion of area damaged by *P. femorata* nests from the projected total area per blade, and (iii) proportion of grazed area from the projected total area per blade. In order to test for the effect of sampling month on frond damage, three independent linear models (lm)/regression analyses were performed.

Multivariate analysis

Seasonal variations in epifaunal communities and trophic groups from both holdfast and fronds were assessed using permutational analysis of variance (PERMANOVA). PERMANOVA analyses used the Bray–Curtis similarity index to build the resemblance matrices and were run with 9999 permutations. Later, the SIMPER routine was used to determine which functional group contributed most to either the similarity or dissimilarity among sampling months. In addition, nonmetric nMDS plots were constructed from the resemblance matrices and used to visualize how the succession of the sampled communities followed a trajectory or sequential changes over time. The analysis was performed by the seriation with replication test of the RELATE analysis using PRIMER v6 software (Clarke & Gorley 2006) for both holdfast and frond communities independently.

Subsequently and separately for both holdfast and fronds, the most abundant species from the holdfast and fronds were selected to test for the effect of sampling month on their abundances using one-way ANOVAS. Both univariate and multivariate analyses were conducted using R software (R Development Core Team 2010, www.R-project.org).

RESULTS

Species richness

Throughout the entire study period (February 2012 to January 2013) and across all samples, more than 30 taxa were found in the community associated with giant kelps *M. pyrifera* at Punta de Talca. The community was dominated by three phyla, with the

Arthropoda (Crustacea) being the most species-rich and abundant group in both holdfasts and fronds. This phylum contributed with 21 species and three orders (Amphipoda, Isopoda, and Decapoda), with Amphipoda being the most species-rich taxon. The phyla Annelida and Mollusca were also identified as abundant groups. The phylum Annelida was represented by the class Polychaeta, which contributed with species from the nereid and syllid families, while the phylum Mollusca comprised four species (Table 1).

Table 1. Taxa of marine invertebrates, functional group, relative abundance (%), and abundance (mean number of individuals per kg algae (wet weight) \pm SE) found on *Macrocystis pyrifera* holdfast ($n = 36$) and fronds ($n = 36$) from Caleta Taquilla

| Classification | Taxa | Functional group | Holdfast | | Fronds | |
|-----------------------------|--------------------------------|------------------|------------------------------------|------------------|----------------------------------|-----------------|
| | | | Rel. ab. | Ab. \pm SE | Rel. ab. | Ab. \pm SE |
| Crustacea | | | 77.5% | | 99.2% | |
| Amphipoda | | | 22.1% | | 87.6% | |
| | <i>Aora typica</i> | S-G | 10.9% | 44 \pm 8.3 | 0.0% | 0 |
| | <i>Bircenna fulva</i> | G | 2.0% | 8.8 \pm 1.4 | 4.0% | 2.2 \pm 0.5 |
| | <i>Caprellidea</i> | S | 0.05% | 0.1 \pm 0.1 | 0.0% | 0 |
| | <i>Elasmopus</i> sp. | ? | 1.5% | 6.6 \pm 2.5 | 0.0% | 0 |
| | <i>Erichthonius</i> sp. | S | 2.3% | 9.4 \pm 4.4 | 0.0% | 0 |
| | <i>Hyale</i> sp. | G | 0.02% | 0.1 \pm 0.1 | 0.0% | 0 |
| | <i>Maera</i> sp. | ? | 0.9% | 4.1 \pm 2.2 | 0.0% | 0 |
| | <i>Paramoera</i> sp. | ? | 1.7% | 5.6 \pm 2.1 | 3.7% | 1.9 \pm 0.5 |
| | <i>Parhyalella penai</i> | G | 0.1% | 0.5 \pm 0.5 | 0.0% | 0 |
| | <i>Peramphithoe femorata</i> | G | 2.6% | 11.1 \pm 2.1 | 79.9% | 34.3 \pm 4.0 |
| | <i>Ventojassa</i> sp. | S | 0.1% | 0.5 \pm 0.3 | 0.0% | 0 |
| Isopoda | | | 51.5% | | 11.3% | |
| | <i>Amphoroidea typa</i> | G | 0.2% | 1 \pm 0.5 | 9.4% | 4.6 \pm 0.9 |
| | <i>Ianiropsis</i> sp. | G | 0.4% | 2.1 \pm 1 | 0.0% | 0 |
| | <i>Limnoria quadripunctata</i> | G | 50.6% | 171.5 \pm 29.5 | 1.9% | 1.2 \pm 0.6 |
| | <i>Paranthura porteri</i> | ? | 0.2% | 0.9 \pm 0.4 | 0.0% | 0 |
| | <i>Uromunna</i> sp. | ? | 0.1% | 0.5 \pm 0.2 | 0.0% | 0 |
| Decapoda | | | 3.9% | | 0.1% | |
| | <i>Taliepus</i> sp. | G | 1.4% | 5.9 \pm 1.3 | 0.1% | 0.1 \pm 0.04 |
| | <i>Pagurus</i> sp. | | 0.4% | 0.8 \pm 0.3 | 0.0% | 0 |
| | Shrimp | | 0.1% | 0.3 \pm 0.2 | 0.0% | 0 |
| | Other decapods | | 2.1% | 7.1 \pm 1.3 | 0.0% | 0 |
| Others | | | 0.0% | | 0.1% | |
| | <i>Tanais marmoratus</i> | S | 0.0% | 0 | 0.05% | 0.01 \pm 0.01 |
| | Mysidacea | | 0.0% | 0 | 0.1% | 0.05 \pm 0.05 |
| Polychaeta | | | 20.7% | | 0.7% | |
| | Polychaetes | O-S | 20.7% | 83.8 \pm 12.3 | 0.7% | 0.4 \pm 0.2 |
| Mollusca | | | 1.5% | | 0.0% | |
| | Gastropoda | | 0.3% | 1.1 \pm 0.7 | 0.0% | 0 |
| | <i>Patella</i> sp. | G | 0.1% | 0.1 \pm 0.1 | 0.0% | 0 |
| | <i>Tegula tridentata</i> | G | 1.2% | 4 \pm 1 | 0.0% | 0 |
| | Polyplacophora | G | 0.02% | 0.1 \pm 0.1 | 0.0% | 0 |
| Others | | | 0.2% | | 0.0% | |
| | Actinia | S | 0.05% | 0.2 \pm 0.1 | 0.0% | 0 |
| | Echinodermata | G | 0.1% | 0.4 \pm 0.3 | 0.0% | 0 |
| | Digenea | | 0.1% | 0.3 \pm 0.2 | 0.0% | 0 |
| Total abundance | | | 371.3 \pm 40.0 | | 44.8 \pm 3.8 | |
| Total number of individuals | | | 4407 | | 1987 | |
| Diversity (H) | | | 1.679 | | 0.785 | |
| Similarity (CC) | | | 38.0% | | | |

Functional groups are described as follows: (S) suspension feeders, (G) grazers, and (O) omnivores. Diversity (Shannon–Wiener index, H) and similarity (Sorenson’s coefficient, CC) of the invertebrate community for comparison between plant sections. The relative abundance (%) of each classification group shows in bold. ? stands for ‘unknown functional group.’

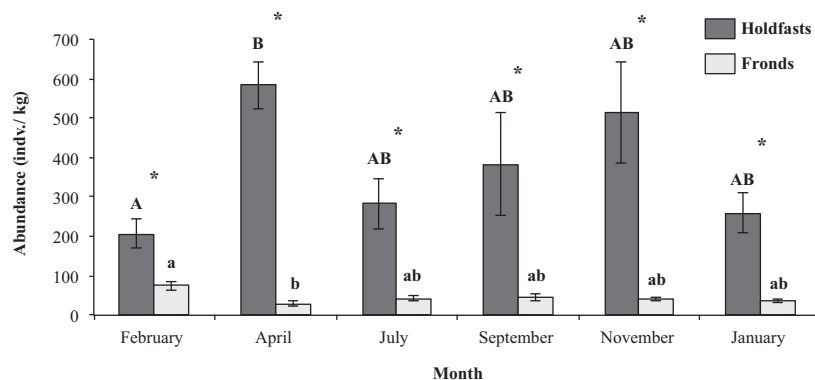


Fig. 2. Abundance (mean number of individuals per kg algae (wet weight) \pm SE) of epifauna in *Macrocystis pyrifera* holdfasts and fronds during sampling months ($n = 6$ per month). Significant differences between holdfast and frond abundances within a single month are represented by '*'. Within holdfasts, monthly means that do not share an uppercase letter (A, B) are significantly different, while within fronds, monthly means that do not share a lowercase letter (a, b) are significantly different from each other.

The invertebrate assemblages differed among sporophyte sections. Diversity (H) was two-fold higher in holdfasts than on fronds. In the holdfasts, a total of 4407 individuals from 28 species were registered over a year, while on fronds, a total of 1987 individuals from nine species were registered. Species richness varied among the two invertebrate communities, sharing 38% similarity (according to Sørensen's index). The most represented groups in the holdfasts were Isopoda (51.5%), Amphipoda (22.1%), and Polychaeta (20.7%), while the assemblage on the fronds was dominated by Amphipoda (87.6%) and Isopoda (11.3%) (Table 1 for relative abundance of each group).

Abundance

Holdfasts contained on average 371.3 individuals per kg, while on fronds, the average abundance was 44.8 individuals per kg (Table 1). In addition, for the epifaunal abundances, there was an interactive effect between algal section and sampling month (ANOVA, $F_{1,60} = 5.635$, $P < 0.0001$; Table S2). There were significant differences in total abundances among fronds and holdfasts, and also over time: for each sampling month, the abundances in holdfasts differed from those on fronds (Fig. 2). Additionally, within the holdfasts, the total abundances differed significantly among sampling months, with the lowest abundances in February (summer) and the highest in April (autumn). Abundances on fronds also differed among months, but contrary to abundances in holdfasts, here the highest abundances were registered in February and the lowest in April (Fig. 2). Finally, there was a significant effect of water temperature on epifaunal abundances of both holdfasts (LM, $P = 0.025$; Table S3a) and fronds (LM, $P = 0.005$; Table S3b), further

confirming the differences in epifaunal abundances among sampling months.

When species were grouped according to their functional group (Table 1), the multivariate analysis showed that the abundances of communities inhabiting both holdfasts (PERMANOVA, Pseudo- $F_{5,30} = 3.93$, $P(\text{Perm}) < 0.0001$; Table S4a) and fronds (PERMANOVA, Pseudo- $F_{5,30} = 0.25$, $P(\text{Perm}) = 0.035$; Table S4b) varied seasonally. The SIMPER analysis revealed seasonal variations in holdfasts mainly influenced by grazers (61.4%) and omnivores (21.4%), while the suspension feeders were the group that contributed least to the community variation among months (17.2%) (Table S5). The variation of frond communities over the year was driven by grazers, which contributed about 96% to the observed similarities among months (Table S6). In addition, the ordination nMDS plots indicate that frond communities were similar within summer (i.e. January and November) and within winter (i.e. April–September–November) while holdfast communities appeared to be more different among months (Table S7).

The most abundant species from each relevant functional group within holdfast communities were *Aora typica* (suspension feeder and grazer), *Limnoria quadripunctata* (grazer), and polychaetes (omnivore). However, the fronds were dominated by two grazers: the amphipod *P. femorata* and the isopod *Amphoroidea typa* (Table 1).

The abundance of *A. typica* did not change throughout the year (Table S8a, Fig. 3a), but sampling month did have an effect on the abundances of *L. quadripunctata* (ANOVA, $F_{5,30} = 6.52$, $P < 0.001$; Table S8b) and polychaetes (ANOVA, $F_{5,30} = 5.23$, $P = 0.001$; Table S8c) in *M. pyrifera* holdfasts. The abundance of the isopod *L. quadripunctata* from holdfasts reached an average of 171.5 individuals per

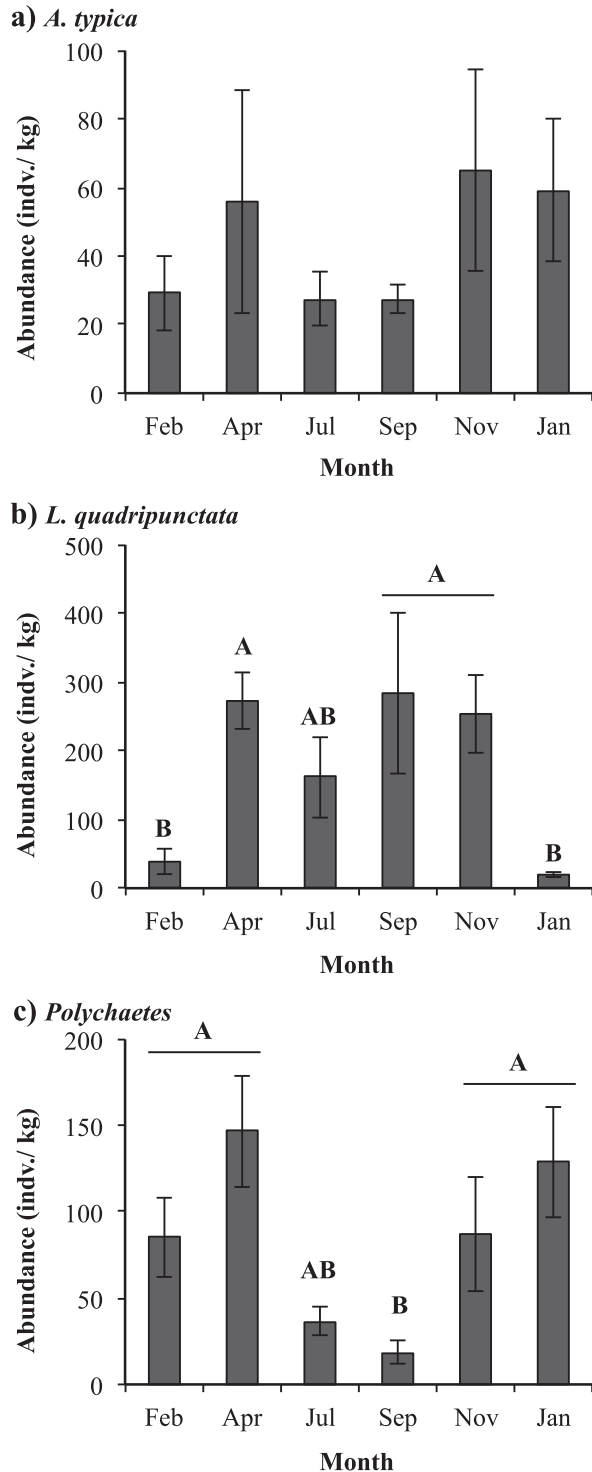


Fig. 3. Abundance (mean number of individuals per kg algae (wet weight) \pm SE) of (a) *Aora typica*, (b) *Linnoria quadripunctata*, and (c) Polychaetes during sampling months (February, April, July, September, November, and January) in *Macrocystis pyrifera* holdfast ($n = 6$ per month). Means that do not share a letter (A, B) are significantly different.

kg, being the highest abundance for a single species registered during this study (Table 1); low abundances were registered during January and February and higher abundances during April, September, and November (Fig. 3b). Polychaete abundances were high during February, April, November, and January, reaching a minimum in September (Fig. 3c). Finally, the most abundant species found on fronds was the amphipod *P. femorata* followed by the isopod *A. typa* (Table 1). Sampling month significantly affected the abundances of *P. femorata* (ANOVA, $F_{5,30} = 3.39$, $P = 0.015$; Figure S9a) and *A. typa* (ANOVA, $F_{5,30} = 10.48$, $P < 0.0001$; Figure S9b). The highest abundances of *P. femorata* were registered during February (summer), while the lowest were reached during autumn and winter (April and July; Fig. 4a). Abundances of *A. typa* were low throughout the year

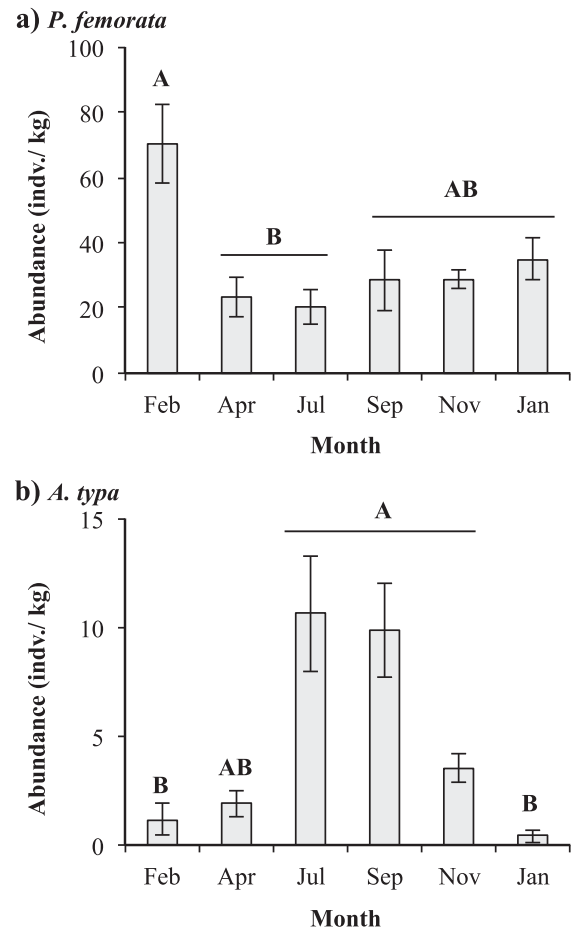


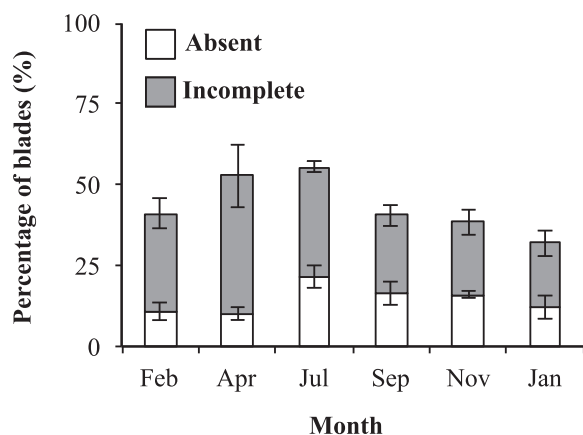
Fig. 4. Abundance (mean number of individuals per kg algae (wet weight) \pm SE) of (a) *Peramphithoe femorata* and (b) *Amphoroidea typa* during sampling months (February, April, July, September, November, and January) on *Macrocystis pyrifera* fronds ($n = 6$ per month). Means that do not share a letter (A, B) are significantly different.

with the highest numbers observed during late winter and beginning of spring (July, September, and November) and the lowest during January and February (Fig. 4b).

Damage on blades

The proportion of blades damaged by grazing (absent + incomplete blades) did not differ among the sampling months (Figure S10a) (Fig. 5a). However, the percentage of grazed area per blade (probably caused by herbivorous species, such as *Bircenna fulva*, *Hyale* sp., *Parhyalella penai*, *P. femorata*,

a) Blades damaged by grazing



b) Damaged area on blades

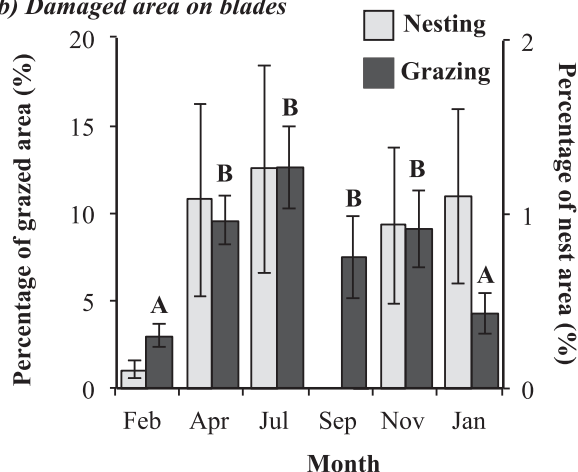


Fig. 5. Percentage (% \pm SE) of (a) blades damaged by grazing (categories 'absent' and 'incomplete' blades) scored from *Macrocystis pyrifera* fronds ($n = 6$ fronds per month) and (b) grazed and nested area on blades ($n = 36$ blades per month) during sampling months (February, April, July, September, November, and January). Means that do not share a letter (A, B) are significantly different within the factors.

A. typha, and *Taliepus* sp.) was significantly different among sampling months (LM, $P = 0.002$; Figure S10b), reaching the highest grazed area (11% damage on average) in April (autumn) and July (winter) and the lowest (<5% damage) during the summer (January and February; Fig. 5b). The area damaged by *P. femorata* nests did not vary significantly over time (Figure S10c) (Fig. 5b).

DISCUSSION

In temperate regions, physical and chemical seawater variables fluctuate seasonally, determining growth and reproductive dynamics of kelp sporophytes and the ecology of associated species (Dayton 1985; Buschmann *et al.* 2004; Graham *et al.* 2007; Thiel *et al.* 2007). Herein, although observations only covered a single seasonal cycle, strong seasonal differences were observed in the diversity and abundance of associated species within sporophytes (holdfast and fronds) of *M. pyrifera*. Moreover, abundances of organisms differed asynchronously over time in each sporophyte section. Fronds and holdfasts harbored different species and trophic groups. A combination of bottom-up and top-down processes determines the ecology of the kelps and their associated fauna. It is likely that the observed patterns of species distribution, abundance, richness, and effect on kelps result from a seasonal shift in the strength of those processes.

Differences among frond and holdfast communities

Previous studies had already reported strong differences in the epifaunal assemblage from different seaweed sections (Christie *et al.* 2003, 2009), as well as a lower number of species in the kelp canopy than in holdfasts (Coyer 1984; Adami & Gordillo 1999; Christie *et al.* 2003). In our study, species richness on fronds was only a third of that found in holdfasts. Total abundance of macrofauna was also higher in holdfasts than on fronds, even though the canopy has a substantially larger total surface area than the holdfasts. While in most benthic habitats the number of species increases with the amount of area or volume available for organisms (species-area relationship, SPAR), there are two major components in habitat architecture that affect the structure of associated assemblages, namely surface area and structural complexity. Biogenic habitats offer a complex arrangement of living structures providing different microhabitats and habitat heterogeneity that permit species co-existence and greater abundances. The higher species richness and abundance in kelp

holdfasts may be partly due to the complex holdfast structure with hapteron layers growing in different directions and overlapping to create a three-dimensional habitat with interstitial spaces that can be inhabited by many organisms. Furthermore, detritus and sediment accumulating around holdfasts provide additional habitat and food for diverse organisms (Moore 1972).

Even though the holdfast community was diverse, richness was lower than reported from previous studies in southern Chile (Ojeda & Santelices 1984; Adami & Gordillo 1999). The difference can be explained, as in Chile invertebrate diversity increases with latitude (Rivadeneira *et al.* 2011), a trend that is stronger for species with direct development such as amphipods, isopods, and some gastropods. In addition, the presence of carnivorous fish predators decreases south of 40°S (Navarrete *et al.* 2014) while fish predation in northern-central Chile is strong (Muñoz & Ojeda 1997; Pérez-Matus *et al.* 2007), possibly also contributing to the apparent latitudinal differences in species richness within these kelp communities.

Seasonal variation of environmental conditions affects species abundances

Bottom-up processes control photosynthetic organisms such as kelps as they largely depend on incoming solar radiation, which in temperate regions varies seasonally. Both light intensity and coastal upwelling events are stronger during spring–summer (Bravo *et al.* 2013; Tapia *et al.* 2014), promoting canopy growth and reproduction of kelp sporophytes (Buschmann *et al.* 2004; Thiel *et al.* 2007). There was a strong interaction in density of epifauna among seasons and sporophyte sections, suggesting contrasting changes in abundance of invertebrates in both sporophyte sections throughout the year.

On fronds, highest epifaunal abundances were recorded during summer while at the same time holdfasts held the lowest abundances. Interplay of bottom-up forces and biotic interactions may explain the observed patterns. For example, on fronds, the most abundant organisms found were grazers (such as amphipods and isopods), which rely on algal tissue to grow and reproduce. Therefore, strong seasonal fluctuation in primary production (food quality and quantity) (Himmelman & Carefoot 1975) supports high densities of these invertebrates during summer, which decrease substantially in autumn and winter (e.g. Edgar 1983). Kelp canopies are extremely vulnerable to damage or detachment when water motion exceeds the mechanical performance of fronds or the attachment strength of holdfasts, resulting in natural

decline of canopy and individuals being removed from the population (Seymour *et al.* 1989; Graham *et al.* 2007; Reed *et al.* 2011). Our results are in accordance with the dynamics of kelp epifauna reported from other regions where low abundances of frond epifauna during autumn and early winter are explained by canopy loss and therefore lower biomass available for epifaunal consumers (Coyer 1984). However, the seasonal variation of the epifaunal community in our study was not as pronounced as that observed in other regions (e.g. Edgar 1983; Taylor 1998; Christie *et al.* 2003), possibly because the seasonal variation in environmental variables (temperature, light, nutrient availability) is relatively moderate within the Humboldt Current System in northern-central Chile.

The abundances of invertebrates in holdfasts were highest during early winter. Christie *et al.* (2003) suggested that epifauna on fronds migrate down to the holdfast as winter approaches, and fronds are reduced significantly. Furthermore, most holdfast inhabitants abandon the sporophyte within the first minutes after storm-induced detachment (Miranda & Thiel 2008; Gutow *et al.* 2009), and the remaining kelp holdfasts may act as island-like substrata on temperate rocky reefs (Thiel & Vásquez 2000). Thus, we propose that after kelp detachment, which is more common toward the end of summer and autumn (Buschmann *et al.* 2004), invertebrates rapidly recolonize the remaining holdfasts, resulting in higher abundances per holdfast during the winter. Some holdfast inhabitants, such as the isopod *L. quadripunctata*, actively reproduce and grow in holdfasts of giant kelp during the autumn (Miranda & Thiel 2008), thereby contributing to the increasing numbers during autumn and early winter.

Seasonal variation in trophic relationships

Different species may select their seaweed host based on nutritional value, levels of anti-herbivore compounds, or the ability of kelp to provide shelter from predators. It is expected that different trophic groups occupy different parts of individual sporophytes as habitat attributes provided by fronds and holdfast differ. For example, while grazers and some suspension feeders may dominate on sporophyte blades and stipes, predators and detritus- or deposit-feeding species are more likely to occupy the holdfast (Moore 1972; Dayton 1985; Graham *et al.* 2007). Highly mobile grazers, such as peracarid crustaceans, rasp on algal surfaces or excavate galleries in algal thalli, while other species use blades as nesting substratum (Gutow *et al.* 2012). Suspension feeders may only use kelp blades as biogenic substratum and other species are adapted to hide efficiently from predators

in the extensive spaces offered by kelp holdfasts between the haptera (Ojeda & Santelices 1984). Indeed, the trophic structure of the invertebrate community in *M. pyrifera* differed among sporophyte sections, where grazers dominated on the fronds while the holdfast community comprised grazers, omnivores, and suspension feeders, as had also been observed in other regions (Moore 1972; Christie *et al.* 2003).

In holdfasts, the abundances of the herbivorous isopod *L. quadripunctata* and of omnivorous polychaetes varied among months and contributed most to the observed seasonal patterns of the holdfast community. Lowest abundances of *L. quadripunctata* were recorded during late summer. These burrowing isopods are known to be agile swimmers and can also actively migrate between holdfasts (Henderson 2000; Miranda & Thiel 2008), therefore being exposed to predators. Kelps affect the structure of fish assemblages by providing shelter and food (Christie & Kraufvelin 2004), and in return, predators favor kelp growth and health by removing herbivores (Davenport & Anderson 2007; Pérez-Matus & Shima 2010; but see Dolecal & Long 2014).

Fish species richness and abundance is positively correlated with increases in temperature (Pérez-Matus *et al.* 2007). Fishes are important predators of kelp epifauna, especially of peracarid crustaceans (Moore 1981). In northern-central Chile, peracarids are important prey for numerous fish species (Muñoz & Ojeda 1997; Pérez-Matus *et al.* 2012). High fish predation is possibly related to seasonal recruitment pulses of juvenile fishes (Choat & Kingett 1982). Consequently, the lower abundances of isopods during late summer appear to be the result of top-down regulation by direct predation or indirect effects of fish presence (Pérez-Matus & Shima 2010). Abundances of suspension feeders such as the amphipod *A. typica* apparently are not limited by seasonal primary production of their host seaweed (Taylor 1998).

Epifauna grazing on kelps

Effects of mesograzers on seaweed abundance and distribution can be variable (reviewed by Davenport & Anderson 2007; Schiel & Foster 2015). Most studies have reported negligible effects of this group on their host seaweed (Poore *et al.* 2009). However, strong effects of herbivorous epifauna on kelp populations have been observed in stressed seaweeds (particularly after el Niño events), nutrient-deprived areas, or when kelp population reached low densities (Chess 1993; Haggitt & Babcock 2003). Negative impacts of epifaunal grazers include dislodgement of kelp individuals, decrease in algal biomass and

survival of microscopic stages (Sala & Dayton 2011), suppressed growth (Poore *et al.* 2014), and reduced reproductive potential of host seaweeds (Graham 2002).

Damage of fronds can be a result of invertebrates nesting or tissue loss by direct grazing, causing weakened blades to eventually break off and become lost. Mesograzers preferentially consume selected tissue within sporophytes based on their nutritional value, palatability or offered structures (Macaya *et al.* 2005; Pansch *et al.* 2008). Our results show that herbivores are able to reduce up to 10% of the blade area within a sporophyte, but the grazing impact varied seasonally. As in most perennial seaweeds, *M. pyrifera* experience limited growth and loss of tissue during austral winter due to lower light intensities and nutrient availability, while during spring/summer the per-capita growth rate and total biomass is highest (Buschmann *et al.* 2004; Thiel *et al.* 2007). We propose that the observed pattern of grazing on blades, as an analogy of other negative interactions, may be viewed as seasonally persisting ‘vestiges of herbivory past’. Our results show that the impact of grazers on giant kelp became most apparent several months after the summer peak in mesograzer abundance, i.e. during the autumn/winter season when blades are not growing and few new blades are being formed, and consequently grazing damage and blade losses accumulate over time. For example, the amphipod *P. femorata* stands out in abundance being the main mesograzer in frond communities. This species is a semi-sessile nest-dweller (Cerdeña *et al.* 2009, 2010; Gutow *et al.* 2012) that reaches highest abundances in summer, when reproductive activity is high. It is likely that juvenile grazers prefer to feed on new and softer vegetative tissue (Pansch *et al.* 2008; Gutow *et al.* 2012), which in addition might be chemically undefended (Macaya *et al.* 2005; Pansch *et al.* 2008). In contrast, during autumn and winter, grazers on the fronds decrease in density but observed herbivory damage increases as algal tissue are not being regenerated (as in summer).

CONCLUSIONS

Communities in the holdfasts are diverse, possibly facilitated by their architectural complexity, which harbors grazers, suspensivores, and omnivores. Communities associated with fronds were dominated by mesograzers. During the winter, there was a reduction in abundance of epifauna due to kelp detachment via storms and possibly by fish predation during the autumn, while during spring and early summer, highest abundance of these invertebrates coincided with generation and growth of new

kelp blades. Damage of fronds increased during periods of limited kelp growth, but no lasting damage was observed. These findings suggest that bottom-up processes shape the structure of the epifaunal community inhabiting large perennial seaweeds during spring and early summer, while top-down processes are more important during late summer and autumn.

ACKNOWLEDGMENTS

We thank Andrés Jofré, Angelika Graiff, Fabián Ramírez, Miren Altuna, Lucía Barahona, Juan Carlos González, Germán Penna, and specially David Jofré for their enthusiastic support and unconditional help during the field samplings. In addition, we thank Dr. Bernardo Broitman, the Ceaza Met (www.ceaza-met.cl), and Chango Lab team for providing water temperature data for the site and the region.

REFERENCES

- Adami M. L. & Gordillo S. (1999) Structure and dynamics of the biota associated with *Macrocystis pyrifera* (Phaeophyta) from the Beagle Channel, Tierra del Fuego. *Sci. Mar.* **63**, 183–91.
- Bravo L., Ramos M., Sobarzo M. *et al.* (2013) Barotropic and baroclinic semidiurnal tidal currents in two contrasting coastal upwelling zones of Chile. *J. Geophys. Res. Oceans* **118**, 1226–38.
- Broitman B. R., Navarrete S. A., Smith F. & Gaines S. D. (2001) Geographic variation of southeastern Pacific intertidal communities. *Mar. Ecol. Prog. Ser.* **224**, 21–34.
- Brown M. T., Nyman M. A., Keogh J. A. & Chin N. K. M. (1997) Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. *Mar. Biol.* **129**, 417–24.
- Buschmann A. H., Vázquez J., Osorio P. *et al.* (2004) The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Mar. Biol.* **145**, 849–62.
- Carvacho A. (1982) Isopódos litorales de la costa de Concepción, Chile central. *Stud. Neotrop. Fauna Environ.* **17**, 195–207.
- Cerda O., Karsten U., Rothäusler E. *et al.* (2009) Compensatory growth of the kelp *Macrocystis integrifolia* (Phaeophyceae, Laminariales) against grazing of *Peramphithoe femorata* (Amphipoda, Ampithoidae) in northern-central Chile. *J. Exp. Mar. Biol. Ecol.* **377**, 61–7.
- Cerda O., Hinojosa I. A. & Thiel M. (2010) Nest-building behavior by the amphipod *Peramphithoe femorata* (Krøyer) on the kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh from northern-central Chile. *Biol. Bull.* **218**, 248–58.
- Chess J. R. (1993) Effects of the stipe-boring amphipod *Peramphithoe stypotrurpetes* (Corophioidea: Ampithoidae) and grazing gastropods on the kelp *Laminaria setchellii*. *J. Crustac. Biol.* **13**, 638–46.
- Choat J. H. & Kingett P. D. (1982) The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. *Oecologia* **54**, 88–95.
- Christie H. & Kraufvelin P. (2004) Mechanisms regulating amphipod population density within macroalgal communities with low predator impact. *Sci. Mar.* **68**, 189–98.
- Christie H., Jørgensen N. M., Norderhaug K. M. & Waage-Nielsen E. (2003) Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian Coast. *J. Mar. Biol. Assoc. U.K.* **83**, 687–99.
- Christie H., Norderhaug K. M. & Fredriksen S. (2009) Macrophytes as habitat for fauna. *Mar. Ecol. Prog. Ser.* **396**, 221–33.
- Clarke K. R. & Gorley R. N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Coleman R. A., Underwood A. J., Benedetti-Cecchi L. *et al.* (2006) A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* **147**, 556–64.
- Coyer J. A. (1984) The invertebrate assemblage associated with the giant-kelp, *Macrocystis pyrifera*, at Santa-Catalina Island, California – a general description with emphasis on amphipods, copepods, mysids, and shrimps. *Fish. Bull.* **82**, 55–66.
- Davenport A. C. & Anderson T. W. (2007) Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. *Ecology* **88**, 1548–61.
- Dayton P. K. (1985) Ecology of kelp communities. *Annu. Rev. Ecol. Syst.* **16**, 215–45.
- Dolecal R. E. & Long J. D. (2014) Chemically mediated foraging by subtidal marine predators: a field test of tritrophic cues. *Mar. Ecol. Prog. Ser.* **498**, 161–71.
- Duggins D., Eckman J. E., Siddon C. E. & Klinger T. (2001) Interactive roles of mesograzers and current flow in survival of kelps. *Mar. Ecol. Prog. Ser.* **223**, 143–55.
- Ebeling A. W., Larson R. J., Alevizon W. S. & Bray R. N. (1980) Annual variability of reef-fish assemblages in kelp forests off Santa-Barbara, California. *Fish. Bull.* **78**, 361–77.
- Edgar G. J. (1983) The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. *J. Exp. Mar. Biol. Ecol.* **70**, 159–79.
- Geange S. W., Powell A., Clemens-Seely K. & Cárdenas C. A. (2014) Sediment load and timing of sedimentation affect spore establishment in *Macrocystis pyrifera* and *Undaria pinnatifida*. *Mar. Biol.* **161**, 1583–92.
- Graham M. H. (2002) Prolonged reproductive consequences of short-term biomass loss in seaweeds. *Mar. Biol.* **140**, 901–11.
- Graham M. H., Vasquez J. A. & Buschmann A. H. (2007) Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanogr. Mar. Biol. Annu. Rev.* **45**, 39–88.
- Graiff A., Pantoja J.F., Tala F. & Thiel M. (2016) Epibiont load causes sinking of viable kelp rafts - seasonal variation in floating persistence of giant kelp *Macrocystis pyrifera*. *Mar. Biol.* (forthcoming).
- Gutow L., Giménez L., Boos K. & Saborowski R. (2009) Rapid changes in the epifaunal community after detachment of buoyant benthic macroalgae. *J. Mar. Biol. Assoc. U.K.* **89**, 323–8.
- Gutow L., Long J. D., Cerda O. *et al.* (2012) Herbivorous amphipods inhabit protective microhabitats within thalli of giant kelp *Macrocystis pyrifera*. *Mar. Biol.* **159**, 141–9.
- Haggitt T. R. & Babcock R. C. (2003) The role of grazing by the lysianassid amphipod *Orchomenella aahu* in dieback of the kelp *Ecklonia radiata* in north-eastern New Zealand. *Mar. Biol.* **143**, 1201–11.

- Henderson S. M. (2000) The swimming behavior of the marine wood borer *Limnoria quadripunctata* (Isopoda: Limnoriidae). *Crustac. Issues* **12**, 227–38.
- Himmelman J. H. & Carefoot T. H. (1975) Seasonal changes in calorific value of three Pacific coast seaweeds, and their significance to some marine invertebrate herbivores. *J. Exp. Mar. Biol. Ecol.* **18**, 139–51.
- de Juan S., Gelcich S., Ospina-Alvarez A. et al. (2015) Applying an ecosystem service approach to unravel links between ecosystems and society in the coast of central Chile. *Sci. Total Environ.* **533**, 122–32.
- Kraufvelin P., Lindholm A., Pedersen M. F., Kirkerud L. A. & Bonsdorff E. (2010) Biomass, diversity and production of rocky shore macroalgae at two nutrient enrichment and wave action levels. *Mar. Biol.* **157**, 29–47.
- Macaya E. C., Rothäusler E., Thiel M. et al. (2005) Induction of defenses and within-alga variation of palatability in two brown algae from the northern-central coast of Chile: effects of mesograzers and UV radiation. *J. Exp. Mar. Biol. Ecol.* **325**, 214–27.
- Miranda L. & Thiel M. (2008) Active and passive migration in boring isopods *Limnoria* spp. (Crustacea, Peracarida) from kelp holdfasts. *J. Sea Res.* **60**, 176–83.
- Moore P. G. (1972) Particulate matter in the sublittoral zone of an exposed coast and its ecological significance with special reference to the fauna inhabiting kelp holdfasts. *J. Exp. Mar. Biol. Ecol.* **10**, 59–80.
- Moore P. G. (1981) The life histories of the amphipods *Lembo websteri* Bate and *Corophium bonnellii* Milne Edwards in kelp holdfasts. *J. Exp. Mar. Biol. Ecol.* **49**, 1–50.
- Muñoz A. A. & Ojeda F. P. (1997) Feeding guild structure of a rocky intertidal fish assemblage in central Chile. *Environ. Biol. Fishes* **49**, 471–9.
- Myers A. A. & Moore P. G. (1983) The New Zealand and South-east Australian Species of *Aora* Krøyer (Amphipoda, Gammaridea). *Rec. Aust. Mus.* **35**, 167–80.
- Narváez D. A., Poulin E., Leiva G. et al. (2004) Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. *Cont. Shelf Res.* **24**, 279–92.
- Navarrete A. H., Lagos N. A. & Ojeda F. P. (2014) Latitudinal diversity patterns of Chilean coastal fishes: searching for causal processes. *Rev. Chil. Hist. Nat.* **87**, 2.
- Nielsen K. J. & Navarrete S. A. (2004) Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecol. Lett.* **7**, 31–41.
- Nordenstam A. (1930) Tanaidacea and marine Isopoda from Juan Fernandez. In: *The Natural History of Juan Fernandez and Easter Island*, Vol. III (ed. C. Skottsberg) pp. 525–52. Almqvist & Wiksells Boktryckeri, Uppsala.
- Ojeda F. P. & Santelices B. (1984) Invertebrate communities in holdfasts of the kelp *Macrocystis pyrifera* from southern Chile. *Mar. Ecol. Prog. Ser.* **16**, 65–73.
- Pansch C., Gómez I., Rothäusler E. et al. (2008) Species-specific defense strategies of vegetative versus reproductive blades of the Pacific kelps *Lessonia nigrescens* and *Macrocystis integrifolia*. *Mar. Biol.* **155**, 51–62.
- Pérez-Matus A. & Shima J. S. (2010) Density- and trait-mediated effects of fish predators on amphipod grazers: potential indirect benefits for the giant kelp *Macrocystis pyrifera*. *Mar. Ecol. Prog. Ser.* **417**, 151–U68.
- Pérez-Matus A., Ferry-Graham L. A., Cea A. & Vásquez J. A. (2007) Community structure of temperate reef fishes in kelp-dominated subtidal habitats of northern Chile. *Mar. Freshw. Res.* **58**, 1069–85.
- Pérez-Matus A., Pledger S., Díaz F. J. et al. (2012) Plasticity in feeding selectivity and trophic structure of kelp forest associated fishes from northern Chile. *Rev. Chil. Hist. Nat.* **85**, 29–48.
- Poore A. G. B., Campbell A. H. & Steinberg P. D. (2009) Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed. *J. Ecol.* **97**, 164–75.
- Poore A. G. B., Gutow L., Pantoja J. F. et al. (2014) Major consequences of minor damage: impacts of small grazers on fast-growing kelps. *Oecologia* **174**, 789–801.
- R Development Core Team (2010) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. [Cited 11 November 2015.] Available from URL: <http://www.R-project.org>
- Reed D. C., Rassweiler A., Carr M. H. et al. (2011) Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology* **92**, 2108–16.
- Ríos C., Arntz W. E., Gerdes D. et al. (2007) Spatial and temporal variability of the benthic assemblages associated to the holdfasts of the kelp *Macrocystis pyrifera* in the Straits of Magellan, Chile. *Polar Biol.* **31**, 89–100.
- Rivadeneira M. M., Thiel M., González E. R. & Haye P. A. (2011) An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: out of the deep south. *Glob. Ecol. Biogeogr.* **20**, 437–48.
- Sala E. & Dayton P. K. (2011) Predicting strong community impacts using experimental estimates of per capita interaction strength: benthic herbivores and giant kelp recruitment. *Mar. Ecol.* **32**, 300–12.
- Schiel D. R. & Foster M. S. (2015) *The Biology and Ecology of Giant Kelp Forests*, 416 pp. University of California Press, Oakland.
- Sepúlveda R., Cancino J. M. & Thiel M. (2003) The peracarid epifauna associated with the ascidian *Pyura chilensis* (Molina, 1782) (Ascidacea: Pyuridae). *J. Nat. Hist.* **37**, 1555–69.
- Seymour R. J., Tegner M. J., Dayton P. K. & Parnell P. E. (1989) Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar. Coast. Shelf Sci.* **28**, 277–92.
- Sotka E. E. & Giddens H. (2009) Seawater temperature alters feeding discrimination by cold-temperate but not subtropical individuals of an ectothermic herbivore. *Biol. Bull.* **216**, 75–84.
- Steneck R. S., Graham M. H., Bourque B. J. et al. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* **29**, 436–59.
- Tala F. & Edding M. (2005) Growth and loss of distal tissue in blades of *Lessonia nigrescens* and *Lessonia trabeculata* (Laminariales). *Aquat. Bot.* **82**, 39–54.
- Tapia F. J., Largier J. L., Castillo M. et al. (2014) Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. *PLoS One* **9**, e110841.
- Taylor R. B. (1998) Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. *Hydrobiologia* **361**, 25–35.
- Taylor R. B. & Brown P. J. (2006) Herbivory in the gammarid amphipod *Aora typica*: relationships between consumption rates, performance and abundance across ten seaweed species. *Mar. Biol.* **149**, 455–63.

- Thiel M. & Vásquez J. A. (2000) Are kelp holdfasts islands on the ocean floor? – indication for temporarily closed aggregations of peracarid crustaceans. *Hydrobiologia* **440**, 45–54.
- Thiel M., Macaya E. C., Acuna E. *et al.* (2007) The Humboldt current system of northern-central Chile oceanographic processes, ecological interactions and socio-economic feedback. *Oceanogr. Mar. Biol. Annu. Rev.* **45**, 195–344.
- Tuya F., Larsen K. & Platt V. (2011) Patterns of abundance and assemblage structure of epifauna inhabiting two morphologically different kelp holdfasts. *Hydrobiologia* **658**, 373–82.
- Vásquez J. A. & Buschmann A. H. (1997) Herbivore-kelp interactions in Chilean subtidal communities: a review. *Rev. Chil. Hist. Nat.* **70**, 41–52.
- Vásquez J. A., Vega J. M. A. & Buschmann A. H. (2006) Long term studies on El Niño-La Niña in northern Chile: effects on the structure and organization of subtidal kelp assemblages. *J. Appl. Phycol.* **18**, 505–19.
- Viejo R. M. & Åberg P. (2003) Temporal and spatial variation in the density of mobile epifauna and grazing damage on the seaweed *Ascophyllum nodosum*. *Mar. Biol.* **142**, 1229–41.
- Villegas M. J., Laudien J., Sielfeld W. & Arntz W. E. (2008) *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales; Phaeophyceae) kelp habitat structures and associated macrobenthic community off northern Chile. *Helgol. Mar. Res.* **62**, 33–43.
- Wieters E. A. (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Mar. Ecol. Prog. Ser.* **301**, 43–54.
- Winkler H. (1992) On two magellanic Munnidae; a new species of *Munna* and *Uromunna nana* (Nordenstam, 1933) (Crustacea: Isopoda: Asellota). *J. Nat. Hist.* **26**, 311–26.
- Winkler H. (1994) Paramunnidae (Crustacea: Isopoda: Asellota) from the Magellan Strait. *Zool. J. Linn. Soc.* **110**, 243–96.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Two-way ANOVA analyses of epifaunal abundance.

Table S2. Regression analysis of total community abundance of *Macrocystis pyrifera* holdfasts and fronds.

Table S3. PERMANOVA analyses of community abundance of *Macrocystis pyrifera* holdfasts and fronds.

Table S4. SIMPER analysis of (dis)similarity between sampling months in holdfast community.

Table S5. SIMPER analysis of (dis)similarity between sampling months in frond community.

Table S6. ANOVA analyses for effect of month on three taxa abundances on holdfasts.

Table S7. ANOVA analyses for effect of month on two taxa abundances on fronds.

Table S8. Effects of month on blade damage.

Figure S1. Regional temperature anomalies for the period 2009–2015.

Figure S2. Non-metric nMDS plots for epifaunal communities on holdfasts and fronds.