
The ecological importance of *Macrocystis pyrifera* (Phaeophyta) forests towards a sustainable management and exploitation of Chilean coastal benthic co-management areas

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Abstract: The giant kelp *Macrocystis pyrifera* forms dense aggregations in rocky subtidal areas along the Chilean coast. Seasonal abundance of seaweed and invertebrate populations associated with kelp forests and control sites without forests were monitored for two years in Southern Chile. Monitoring took place in areas under co-management fisheries administration provision entitled 'Management and exploitation areas for benthic resources (MEABR)' where several species that are under commercial exploitation have to be monitored. This study provides evidence indicating the importance of giant kelp in the maintenance of exploited organisms and biodiversity in general. The results showed that kelp influences the abundance of other macroalgae and benthic invertebrates, including species exploited by the local fisheries. Kelp size and density varied seasonally, generating cyclical variation in habitat, species composition and community structure. A consequence of the exploitation and depletion of *Macrocystis* forests will be a decrease in the abundance of other economically important species and therefore the sustainable development of coastal communities may be compromised.

Keywords: biodiversity; community structure; giant kelp; *Macrocystis* forests; management and exploitation areas for benthic resources; MEABR; Southern Chile; sustainable coastal development.

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1 Introduction

The globally distributed giant kelp *Macrocystis pyrifera* is the world's largest benthic organism and acts as a foundation species (Dayton, 1972) that sustains an energy rich trophic web, including different economically important resources (Graham et al., 2007). The importance of the kelp forest structure has been shown to be highly relevant in determining the diversity and trophic structure of coastal ecosystems (e.g., Graham, 2004; Lilley and Schiel, 2006). Trophic studies including kelp forest organisms have demonstrated the importance of kelp in supplementing the detrital pathways (Kaehler et al., 2000), and energy exportation to other systems (Harrold et al., 1998; Graham, 2004). Food web dependence on temporal variability in kelp abundance is a key issue in marine ecology (Bustamante and Branch, 1996; Graham, 2004) that has not received sufficient attention (Graham et al., 2007). Therefore, there is a need to study the role of foundation species on benthic communities in particular in those areas where resources are under a high extraction pressure, such as those on the Chilean coast (Graham et al., 2007; Vásquez, 2008). This issue is relevant as different outcomes can result from the removal of key kelp species. They may have suppressive effects on understory algae, mainly through strong light reduction (Reed and Foster, 1984; Clark et al., 2004) and reduced grazing pressure (Santelices and Ojeda, 1984a; Benedetti-Cecchi and Cinelli, 1992a), or it may enhance species diversity and trophic complexity associated with an increase in habitat complexity as found by Graham (2004) or enhanced recruitment success (Duggins et al., 1990; Schroeter et al., 1996; Leonard, 1999; Bègin et al., 2004; amongst many others).

On the Chilean coast, different herbivore assemblages and benthic organisms depend on the energy flux provided by *Macrocystis pyrifera* (Vásquez et al., 1984; Castilla, 1985). The structure of the holdfasts provides a habitat for invertebrates (Ojeda and Santelices, 1984), fishes (Moreno et al., 1984; Vega et al., 2005; Villegas et al., 2008) and marine birds (Rey and Schiavini, 2000). In Southern Chile (Beagle Channel) 30 + herbivores and predators have been identified in the *Macrocystis* forests (Castilla, 1985). However, these systems have a relatively less complex community structure, with reduced species diversity and richness than the *Macrocystis* forests of the northern hemisphere (Santelices and Ojeda, 1984a; Castilla, 1985; Vásquez and Buschmann, 1997; Vásquez et al., 2006). These differences highlight the need to understand community patterns in kelp forests on a global scale (Graham et al., 2007).

Many of the organisms associated with kelp forests in Chile are subject to fisheries exploitation. These resources include the sea urchin *Loxechinus albus*, the muricid gastropod *Concholepas concholepas*, the herbivore gastropod *Tegula* spp., keyhole limpet species *Fissurella* spp., crabs *Taliepus* spp., *Cancer edwardsi* and *Homalaspis plana* (Castilla and Fernández, 1998; Castilla and Defeo, 2001; Almanza, 2007), and understory red algae such as *Callophyllis variegata*, *Sarcothalia crispata* and *Gigartina skottsbergii* (Buschmann et al., 2004). Kelp harvesting has increased in recent years along the Northern Chilean coastline, where it is used for alginate extraction and as a fresh food source for abalone (*Haliotis rufescens*) cultivation (Flores-Aguilar et al., 2007; Buschmann et al., 2008; Vásquez, 2008). This demand for seaweed has already produced local depletion of *Macrocystis* forests and, at present, regulations are being considered that will establish extraction quotas. The proposed introduction of mechanical harvesting, to replace less efficient manual collection, may increase the impact on kelp biomass (Vásquez, 2008). Therefore, the abundance of commercially important organisms, as well as the benthic community in general, may vary if kelp forests are exploited, causing unknown economic and social consequences for coastal communities that rely on these natural resources.

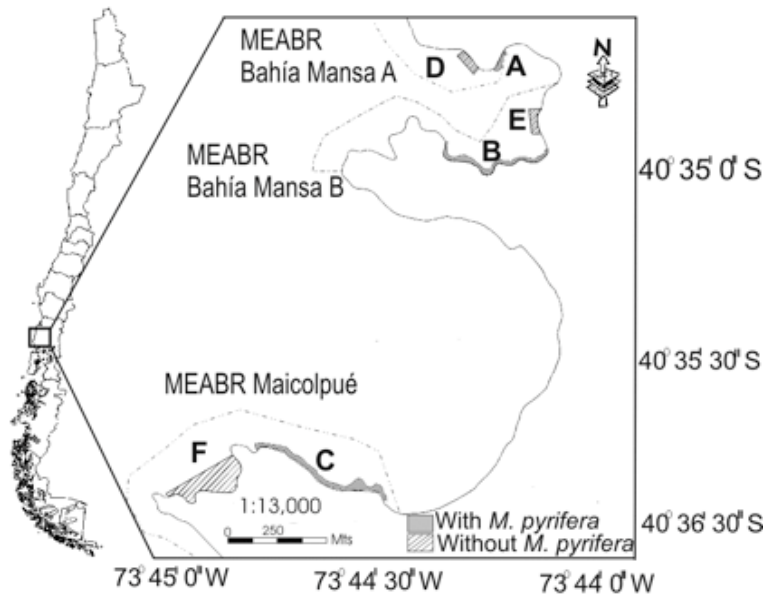
A co-management regulatory system for benthic resources has been developed in Chile to enhance the sustainability and promote the economic growth of coastal communities by artisanal fisher organisations in well-defined inshore coastal areas, known as management and exploitation areas for benthic resources (MEABRs) (Castilla and Fernández, 1998; Castilla and Defeo, 2001; Gelcich et al., 2008). A key feature of this comanagement system is the preservation of ecologically important organisms, such as kelp and provides important additional conservation effects for species that are not the focus of the management policies (Gelcich et al., 2008). Considering the ecological importance of kelp forests and the importance of benthic fisheries in Chile, we studied the relationship between *M. pyrifera* forest structure and the abundance and diversity of other seaweeds and mobile invertebrates, especially those exploited by artisanal fisheries. This natural experiment also allows us to design future key manipulative experiments to address the questions raised by the present investigation.

2 Material and methods

2.1 Study sites

This study was carried out in three MEABRs located in two different bays in Southern Chile, separated by a distance of 2.2 km: Bahía Mansa and Maicolpué (Figure 1). In each MEABR, kelp forest patches and control sites without a dense kelp populations were identified. In Bahía Mansa, the kelp forests are separated by 0.5 km of sandy bottom and open to different wind-driven water movements with one exposed to northerly and the other southerly winds (Figure 1). While a single open-forest pair of sites was located in Bahía Maicolpué (Figure 1). The three MEABRs are managed by different artisanal fishermen unions and are subject to different exploitation planning and controls. Therefore, as management strategies, environmental regimes, especially those associated with water movement, spatial discontinuities of kelp population, and hard bottom benthic resources are all distinct, and the three MEABRS and the control sites can be considered independent units.

Figure 1 Study locations showing the three MEABR in Bahía Mansa (40° 34'S, 73° 44'W) and Maicolpué (40° 35'S, 73° 44'W)



Notes: A, B and C areas with *Macrocystis pyrifera*. D, E and F areas without *M. pyrifera*.

2.2 Sampling protocol

The sampling procedure started in summer 2005 and extended over a two-year period. All field measurements were made seasonally (summer, autumn, winter and spring) by SCUBA divers. In each MEABR ($n = 3$) or study site, macroalgae and benthic invertebrate abundance were sampled. The without kelp sites ($n = 3$) chosen were areas where the kelp colonise at lower abundances or are controlled by sea urchins following Graham (2004).

The magnitude of the sampling procedure was determined based on the capacity to get the full sampling for each period during few days to avoid time differences that could bias our results. Following a strict interpretation of the experimental protocol we should have removed kelp from large areas of the kelp forests. However, for bioethical reasons it was decided that this was unacceptable, and the impact that this may have on the interpretation of our results is addressed in the discussion. Four samples were taken along three transects ($n = 12$ for each study site) running perpendicular to the coastline, placed haphazardly at the shallowest (2 m), mid and deepest depths (10 m) of the kelp forest, as well as at sites without kelp forest (Figure 1). Each sample was taken with a 1 – m² quadrat. The total number of *Macrocystis* individuals and benthic invertebrates were counted directly in each quadrat by scuba diving. The understory algal cover was registered with 0.5 m² quadrats with 100 regularly distributed points. The size of each *M. pyrifera* plant in the quadrat was obtained by measuring the diameter of the holdfast and then calculated following Buschmann et al. (2006).

2.3 Data analysis

The abundance of benthic algae and mobile invertebrates in each transect, was transformed using a rank transformation (Potvin and Roff, 1993). After establishing that no significant variations between years existed, the data for 2005 and 2006 were pooled and only the seasonal variation was analysed using three-way ANOVA in STATISTICA 6.0. Normality and homogeneity of the data were tested with Shapiro-Wilk's and Levene's tests. The factors analysed were season, locality (MEABRs) and habitats with and without *M. pyrifera* kelp forest. When significant differences were detected for seasonality and location, an a posteriori Tukey-test was performed. In the particular case of *Macrocystis* abundance and plant size, the data were analysed with a two-way ANOVA that tested for seasonality and locality.

Benthic biodiversity between habitats was measured using species richness [d Margalef: $(S - 1)/\text{Log}(N)$], Shannon-Wiener Index $H' = -\text{SUM}(P_i * \text{LOG}(P_i))$ and Pielou evenness ($J' = H'/\text{Log}(S)$), calculated with the PRIMER 6.0 software. These data were statistically analysed with a t-test using as factors with and without *M. pyrifera*. The community structure of the sites, with and without the kelp forest, were compared using conglomerate analysis and non-metric multidimensional scaling (MDS). Abundance data were fourth root transformed, and ranked matrices of similarities among habitats were constructed, using the Bray-Curtis similarity measure. Tests were performed to determine differences in community samples between habitats. The analysis of similarities ANOSIM permutation test (Clarke, 1993) was used to examine formal significance.

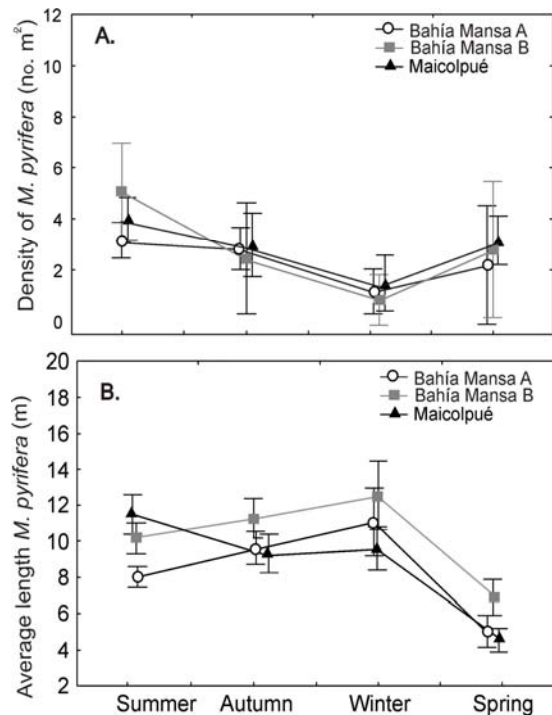
3 Results

3.1 *Macrocystis pyrifera* population structure

Macrocystis pyrifera exhibited a clear seasonal pattern, with maximum densities in summer (4.1 individuals m⁻²), and significantly (two-way ANOVA; $F_{3,53} = 14.4$; $p < 0.05$) lower densities in winter (2.0 individual m⁻²) [Figure 2(a)]. The seasonal pattern of abundance was similar for all three kelp forests studied (Two-way ANOVA;

$F_{6,53} = 0.53$; $p = 0.37$). The average length of the kelp plants was significantly lower (two-way ANOVA; $F_{3,703} = 68.4$; $p < 0.05$) during spring than in summer [Figure 2(b)], due to plant loss in winter and the presence of new recruits in spring. These data indicate a higher habitat complexity of the kelp forest during summer as compared to the winter period.

Figure 2 Seasonal changes of *Macrocystis pyrifera* at the three locations studied, (a) density (number m^{-2}) and (b) length (m) (mean ± 1 SD)



3.2 Macroalgae and invertebrate abundance in sites with and without kelp

Understory seaweed and benthic invertebrate abundance patterns varied temporally, at sites with and without kelp forests. Nine abundant algal species were found and five of them (*Ulva* spp., *Gigartina skottsbergii*, *Trematocarpus dichotomus*, *Codium dimorfum* and *Sarcothalia crispata*) increased significantly in the kelp forest, as compared to outside. *Callophyllis variegata*, calcareous encrusting algae (*Lithothamnion* spp. and *Lithophyllum* spp.), and *Lessonia trabeculata*, were significantly more abundant in habitats without the presence of a *M. pyrifera* forest (Figure 3, Table 1). Only *Desmarestia ligulata* cover did not differ significantly between habitats. In the case of *S. crispata*, the effect of kelp depends on the location (MEABR) (Table 1). Most species varied in abundance seasonally, with the exception of *L. trabeculata* and *C. dimorfum*.

Figure 3 Temporal patterns in the abundance (means \pm SD) of understory macroalgae, (a) *Ulva* spp. (b) *Gigartina skottsbergii* (c) *Trematocarpus dichotomus* (d) *Codium dimorfum* (e) *Sarcothalia crispate* (f) *Desmarestia ligulata* (g) *Callophyllis variegata* (h) *Lessonia trabeculata* (i) Calcareous encrusting algae in localities with and without *Macrocystis pyrifera*

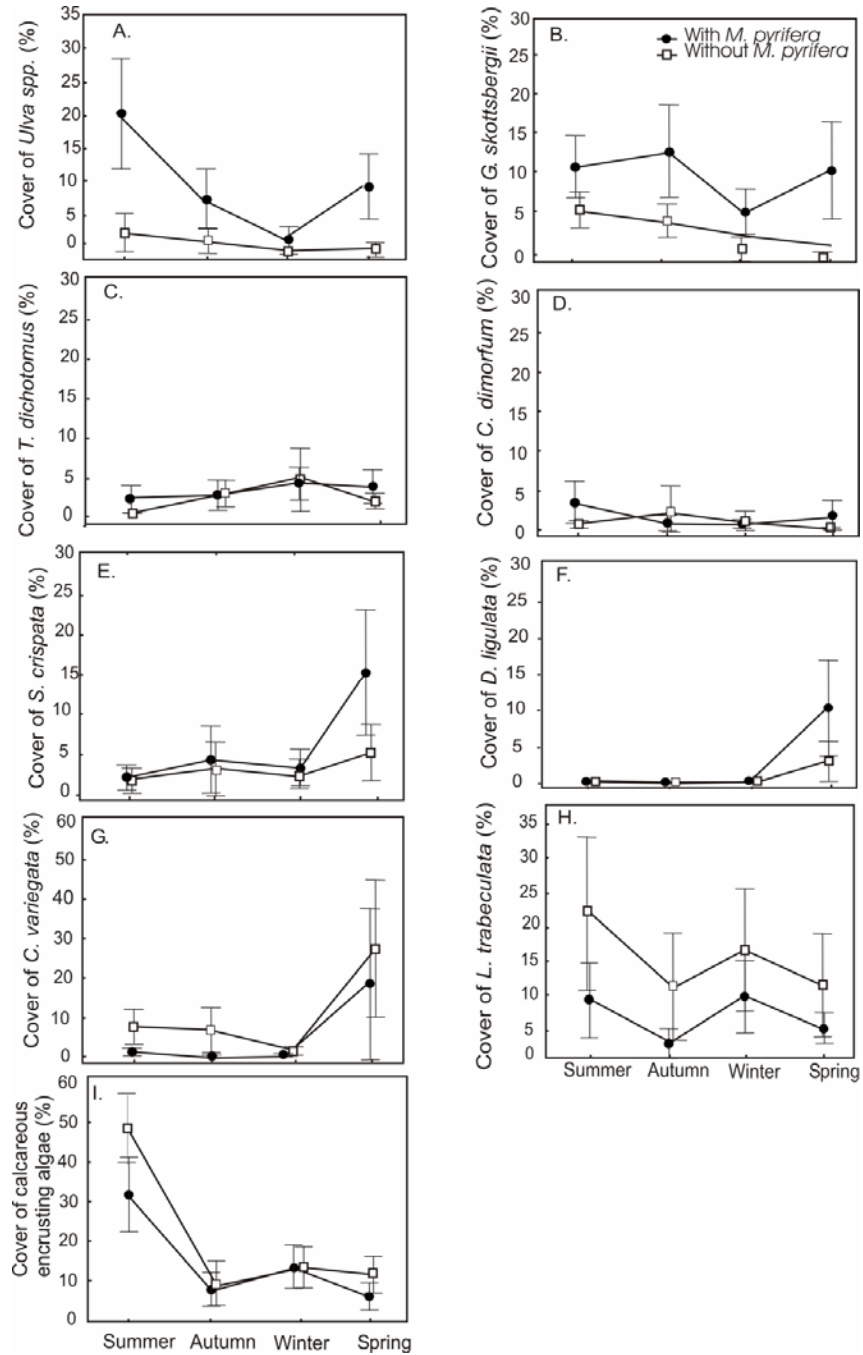


Table 1 Multifactorial analysis of variance (ANOVA) in the understory macroalgae cover with and without *M. pyrifera*, season and locality

Species	Effect	Season (S)	Locality (L)	Effect of <i>M. pyrifera</i> (E)	S * L	S * E	L * E	S * L * E
<i>Ulva</i> spp.	F	20.16	5.27	109.51	1.59	6.76	4.76	4.04
	df	3	2	1	6	3	2	6
	p-value	<0.001	<0.001	<0.001	0.155	<0.001	<0.001	<0.001
<i>Gigartina skottsbergii</i>	F	7.90	3.80	34.20	0.28	0.47	2.20	1.67
	df	3	2	1	6	3	2	6
	p-value	<0.001	<0.001	<0.001	0.945	0.703	0.115	0.133
<i>Trematocarpus dichotomus</i>	F	5.93	4.26	5.30	1.43	1.30	23.80	2.95
	df	3	2	1	6	3	2	6
	p-value	<0.001	<0.001	<0.001	0.211	0.277	<0.001	<0.001
<i>Codium dimorfum</i>	F	1.61	4.65	4.03	3.66	1.34	0.13	1.43
	df	3	2	1	6	3	2	6
	p-value	0.19	<0.001	<0.001	<0.001	0.26	0.87	0.21
<i>Sarcothalia crispata</i>	F	8.49	0.79	1.53	2.63	0.09	5.10	0.60
	df	3	2	1	6	3	2	6
	p-value	<0.001	0.46	0.22	<0.001	0.97	<0.001	0.73
<i>Desmarestia ligulata</i>	F	28.83	1.23	0.75	1.11	0.69	0.50	0.49
	df	3	2	1	6	3	2	6
	p-value	<0.001	0.30	0.39	0.36	0.56	0.61	0.81
<i>Callophyllis variegata</i>	F	4.31	6.61	35.18	2.89	3.89	7.21	2.73
	df	3	2	1	6	3	2	6
	p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
<i>Lessonia trabeculata</i>	F	1.71	4.05	21.67	1.98	1.43	23.13	1.45
	df	3	2	1	6	3	2	6
	p-value	0.16	<0.001	<0.001	0.07	0.24	<0.001	0.20
<i>Calcareous encrusting algae</i>	F	41.05	10.80	9.02	0.95	1.69	8.94	2.15
	df	3	2	1	6	3	2	6
	p-value	<0.001	<0.001	<0.001	0.459	0.171	<0.001	0.052

Figure 4 Temporal patterns in the abundance (means \pm SD) of herbivores invertebrates, (a) *egula* spp. (b) *Fissurella* spp. (c) *Loxechinus albus* (d) *Taliepus* spp. in localities with and without *Macrocystis pyrifera*

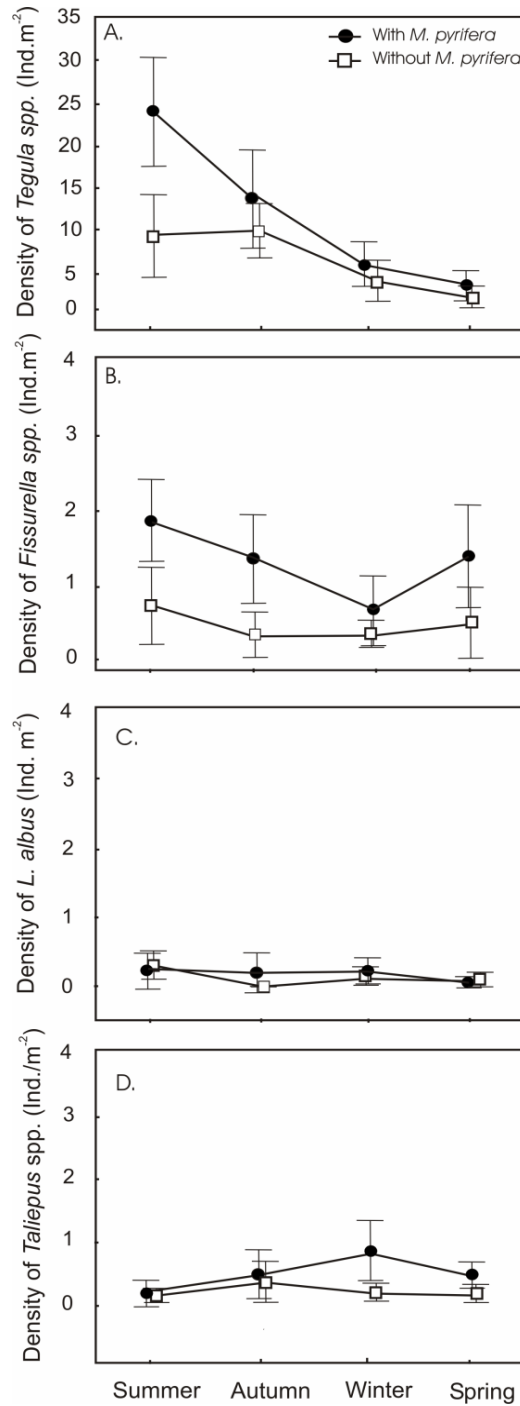


Table 2 Multifactorial ANOVA in the herbivores invertebrates density with and without *M. pyrifera* kelp, season and locality

Species	Effect	Season (S)	Locality (L)	Effect of <i>M. pyrifera</i> (E)	S * L	S * E	L * E	S * L * E
<i>Tegula</i> spp.	F	26.35	5.09	17.97	4.60	2.65	6.59	0.72
	df	3	2	1	6	3	2	6
<i>Fissurella</i> spp.	p-value	<0.001	<0.001	<0.001	<0.001	0.05	<0.001	0.63
	F	3.81	2.91	32.87	1.91	2.48	3.18	1.49
	df	3	2	1	6	3	2	6
	p-value	<0.001	0.05	<0.001	0.08	0.06	<0.001	0.19
<i>Talitopus</i> spp.	F	3.20	0.52	7.59	1.63	2.33	2.27	1.44
	df	3	2	1	6	3	2	6
	p-value	<0.001	0.60	<0.001	0.14	0.08	0.11	0.21
<i>Loxechinus albus</i>	F	1.78	1.26	0.001	3.55	2.17	1.93	0.91
	df	3	2	1	6	3	2	6
	p-value	0.15	0.29	0.99	<0.001	0.09	0.15	0.49

The most abundant herbivores were the snail *Tegula* spp. (*Tegula atra* and *T. tridentata*), three species of keyhole limpets (*Fissurella picta*, *F. latimarginata*, and *F. crassa*), the sea urchin *Loxechinus albus*, and the crab *Taliepus* spp. (*T. dentatus* and *T. marginatus*) (Figure 4, Table 2). The snails, keyhole limpets and crabs were significantly more abundant inside the kelp forests, and varied seasonally (Table 2). Only the abundance of the sea urchin *L. albus* did not vary between habitats.

The carnivores *Concholepas concholepas*, *Homalaspis plana*, *Meyenaster gelatinosus* and *Stichaster striatus* were significantly more abundant in the kelp forest (Figure 5). Only *Cancer edwardsii* did not exhibit significant differences between habitats (Table 3). In the case of *S. striatus*, the effects differed between study sites and seasons, as indicated by a significant interaction between habitat, season and locality (Table 3).

Figure 5 Temporal patterns of the density (means \pm 1 SD) of carnivorous invertebrates, (a) *Concholepas concholepas* (b) *Homalaspis plana* (c) *Meyenaster gelatinosus* (d) *Stichaster striatus* (e) *Cancer edwardsii* in localities with and without *Macrocystis pyrifera*

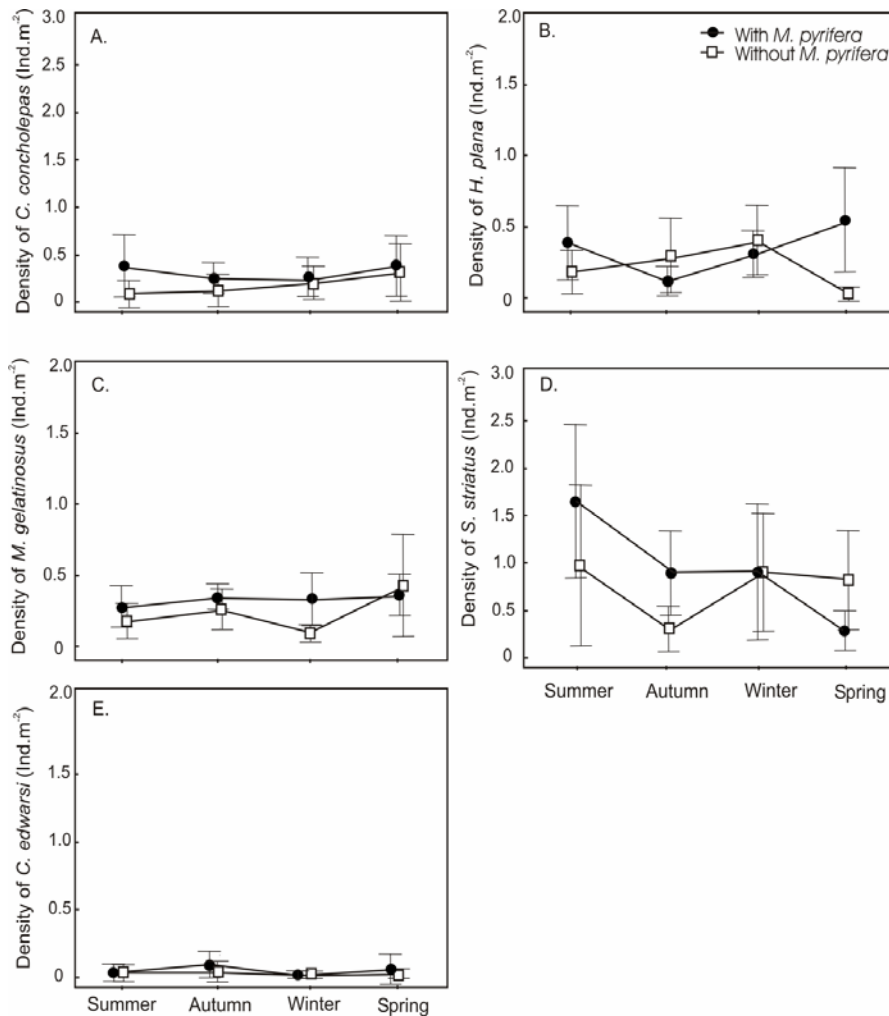


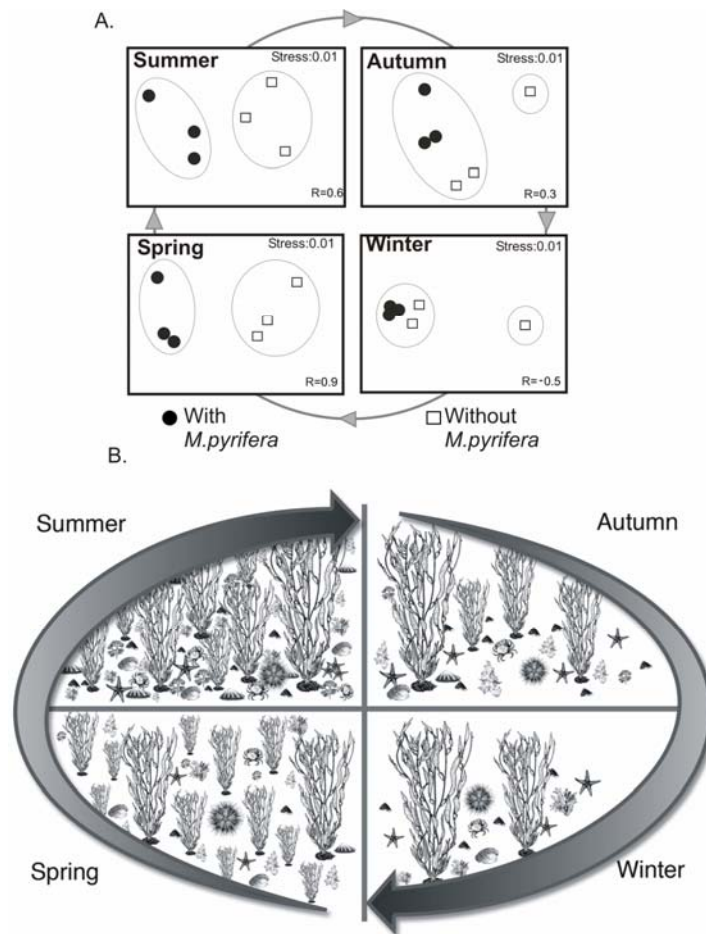
Table 3 Multifactorial ANOVA in the carnivorous invertebrates density with and without *M. pyrifera* kelp, season and locality

Species	Effect	Season (S)	Locality (L)	Effect of <i>M. pyrifera</i> (E)	S * L	S * E	L * E	S * L * E
<i>Concholepas concholepas</i>	F	1.03	0.58	8.55	1.16	0.80	4.25	1.96
	df	3	2	1	6	3	2	6
	p-value	0.38	0.56	<0.001	0.33	0.49	<0.001	0.08
<i>Homalaspis plana</i>	F	1.56	7.53	4.49	3.44	4.91	0.02	0.81
	df	3	2	1	6	3	2	6
	p-value	0.20	<0.001	<0.001	<0.001	<0.001	0.97	0.56
<i>Meyenaster gelatinosus</i>	F	3.17	0.33	9.44	1.97	0.36	1.41	0.41
	df	3	2	1	6	3	2	6
	p-value	<0.001	0.72	<0.001	0.07	0.78	0.25	0.87
<i>Sticaster striatus</i>	F	0.50	4.60	3.82	2.92	5.35	7.68	3.51
	df	3	2	1	6	3	2	6
	p-value	0.68	<0.001	0.05	<0.001	<0.001	<0.001	<0.001
<i>Cancer edwardsi</i>	F	1.98	6.97	0.40	1.70	0.89	0.62	1.12
	df	3	2	1	6	3	2	6
	p-value	0.12	<0.001	0.53	0.13	0.45	0.54	0.36

3.3 Structure of the benthic community

The Shannon-Wiener diversity indexes ($H' = 1.02$ and $H' = 0.89$ with and without *M. pyrifera*, respectively) and Margalef diversity indexes ($d = 5.51$ and $d = 5.49$ with and without *M. pyrifera*) exhibited a slight tendency to increase under the kelp canopy. Uniformity of species was similar with ($J' = 0.76$) and without ($J' = 0.66$) *M. pyrifera* forest. The t-test results indicated that diversity did not differ significantly (t-test; $t_5 = 2.44$; $p > 0.05$) between habitats. However, MDS analyses revealed differences in the community structure with and without the kelp forests ($R_{(Global)} = 0.6$; $p < 0.10$). MDS analysis, separated by season, indicating that differences occur primarily during spring ($R = 0.90$; $p < 0.10$) and summer ($R = 0.60$; $p < 0.10$), while during autumn ($R = 0.30$; $p < 0.10$) and winter ($R = 0.20$; $p < 0.10$), they tend to disappear for two MEABRs (Bahía Mansa A and Bahía Mansa B) of the three studied (Figure 6).

Figure 6 (a) Non-metric MDS of the community associated to localities with and without *Macrocystis pyrifera*, during annual cycle and value of ANOSIM statistic (R) for global test for differences between seasons (b) Schematic representation of the density, size and recruitment of *M. pyrifera* associated with seasonal variations of the benthic community structure



4 Discussion

The three-dimensional structure of *Macrocystis pyrifera* forests constitute a physical barrier that alters water current velocity (Jackson and Winant, 1983; Jackson, 1998), reducing water flow, and increasing the retention of particles that are deposited under the canopy (Eckman et al., 1989). Furthermore, it protects benthic macroalgal species against wave action and influences photosynthesis by determining the light regimes within its borders (Clark et al., 2004). The giant kelp forest (abundance and size of individuals), varied temporally in complexity, generating a cyclical habitat availability that affected algae and invertebrate population abundances under the canopy.

Temporal variation in *M. pyrifera* abundance has been previously documented in Southern Chile (Moreno and Sutherland, 1982; Santelices and Ojeda, 1984b; Buschmann et al., 2006), and the North Pacific (e.g., Dayton et al., 1984, 1999; Graham, 1997; Reed et al., 2006). During this study period we did not observe kelp harvesting, and therefore temporal variation in kelp abundance patterns seems to be driven by biotic and abiotic environmental factors and not by human activities. Our results showed that these temporal variations have consequences for benthic organisms. During spring and summer, the presence of *M. pyrifera* generated differences in community composition associated with the presence or absence of the kelp, but during the winter the communities were similar. The physical disturbances in winter caused the removal of *M. pyrifera*, producing a habitat closer to that without the kelp. The following season a process of succession was observed whereby species invaded, occupied and colonised the habitat made available by disturbance during the winter (Dayton et al., 1984). This produces a rapid recovery of the community structure (Dayton et al., 1999), differentiating communities again during the spring. Colonisation of new kelp patches and the recovery of the community structure have also been documented previously California (Dayton et al., 1984, 1999). As a result, the ecological function and relevance of this foundation species changes in importance seasonally.

Numerous studies have shown that *M. pyrifera* regulates the abundance and structure of benthic macroalgae assemblages that live under its canopy (e.g., Moreno and Sutherland, 1982; Santelices and Ojeda, 1984b; Reed and Foster, 1984; Clark et al., 2004) as well as for several other kelp species (e.g., Dayton, 1975; Hawkins and Harkin, 1985). In general these models show that light limitation is one of the most relevant mechanism controlling the abundance of subcanopy organism. *M. pyrifera* removal experiments in Puerto Toro (Southern Chile) led to the disappearance of some species of macroalgae and a reduction in the seasonal variation in the biomass and distribution of benthic macroalgae (Santelices and Ojeda, 1984b). The effects of removing *Ecklonia radiata* in southern Australia has also demonstrated that canopies maintain and facilitate the growth of encrusting coralline algae and reduced the cover of articulated coralline algae (Melville and Connell, 2001). On the other hand, removal of *Undaria pinnatifida* canopy produced less change in biotic assemblages on eastern Tasmanian reefs, with the magnitude of change for fish and invertebrate taxa lower than the variation between sites and comparable to the variation between months (Edgar et al., 2004). The absence of *M. pyrifera* canopy could be generating significant changes in the abundance of algal populations studied. In addition, the most abundant herbivore found was *Tegula* spp. and it is accepted that they can regulate ephemeral seaweeds under the *M. pyrifera* canopy (Moreno and Sutherland, 1982). Our results indicated that the seasonal abundance of these grazers coincides with increasing *Ulva* spp., *G. skottsbergii* and *C. dimorfum*

abundance and *M. pyrifera* recruitment. The interaction of *Tegula* spp. and understory seaweeds requires experimental research to understand the direct and indirect effects of kelp as a foundation species.

Sea urchins have been shown to affect *Macrocystis* abundance in many regions (e.g., Dayton, 1985a; Harrold and Reed, 1985; Graham, 2004; Graham et al., 2007). In Chile, various studies suggest that the urchin *Loxechinus albus* does not affect *M. pyrifera* abundance (Castilla and Moreno, 1982; Santelices and Ojeda, 1984b; Castilla, 1985; Vásquez and Buschmann, 1997). However, Dayton (1985b) indicated that *L. albus* can regulate giant kelp populations in Southern Chile and Buschmann et al. (2004) demonstrated that *L. albus* can control *M. pyrifera* recruitment. *L. albus* densities were significantly lower in *M. pyrifera* kelp forests as compared to areas without kelp, thus their ecological role requires further investigation. Dense aggregations of sea urchins occur in rocky areas dominated by calcareous algae called barren grounds that exhibit reduced diversity and species richness (Dayton, 1985a; Schiel and Foster, 1986; Graham et al., 2007). Top-down cascading effects can regulate the structure and organisation of these coastal communities (Estes and Palmisano, 1974; Estes and Duggins, 1995; Pinnegar et al., 2000; Shears and Babcock, 2003; Estes et al., 2004). However, our non-kelp study areas were not typical barren grounds exhibiting higher diversities. Whether this result is a consequence of the high sea urchin fisheries pressure that *L. albus* currently faces (Kino and Agatsuma, 2007) or is the natural condition in Chile requires further investigation.

In northern hemisphere kelp forests, key carnivores have significant top down effects (e.g., Estes and Palmisano, 1974; Duggins, 1980; Watanabe and Harrold, 1991; Estes and Duggins, 1995). The diets of fishes in the kelp forest on the Northern Chilean coast may set adaptations (feeding preference and partition the benthic resources) allowing their coexistence in a dynamic environment such as kelp forest (Pérez-Matus et al., 2007). In the benthic communities of Southern Chile, a guild of carnivores (fish and starfish) provides the equivalent top predators (sensu Paine, 1966) (Vásquez and Buschmann, 1997; Vega et al., 2005). The starfish *Stichaster striatus* was the most abundant predator, both within and outside the kelp forests. These predators roam between habitats in search of food and consume several species of invertebrates (Dayton et al., 1997). However, in this study we did not find an enhanced abundance inside the kelp forest and which may explain the increased abundance of the herbivores were food availability is also higher.

Our results indicated that seasonal variations in the forest cycle influenced macroalgae and invertebrate populations, constituting an important regulatory process in these ecosystems. Although the loss of *M. pyrifera* individuals occurs naturally during the winter, their elimination due to human intervention (see Vásquez, 2008) could result in the reduced abundance of several species of macroalgae and benthic invertebrates, generating significant changes in the community structure. As several important ecological differences exist between northern and southern hemisphere, the conservation of coastal subtidal areas under commercial exploitation in Southern Chile requires further study. It has been shown that annual kelp populations like *Nereocystis luteana* have weaker effects on the community after removal than do perennial kelp species (Schiel and Foster, 1986). In the case of perennial kelp stands like *M. pyrifera*, it has been shown that cleared canopy stands increased the recruitment of the giant kelp (Santelices and Ojeda, 1984a), but their ecological relevance varies in time.

In Chile, kelp species have been described in a variety of regions that sustain fisheries activities linked to alginate extraction and an increasing demand for food for abalone (Flores-Aguilar et al., 2007; Vásquez, 2008). During the last 25 years, brown algae landings have increased from 40,000 and 280,000 ton yr⁻¹ (Vásquez, 2008). Forty four percent of the most abundant species inside *M. pyrifera* kelp forests in this study are considered economically important in artisanal fisheries nationally (*C. concholepas*, *H. plana*, *Tegula* spp., *Fissurella* spp., *Taliepus* spp., *S. crispata* and *G. skottsbergii*), indicating that *M. pyrifera* systems in Southern Chile sustain benthic artisanal fisheries in areas under the fisheries management via MEABRs. To date, no records are available documenting the impact of direct *Macrocystis* exploitation on the associated community. The data obtained in this study strongly suggests that it is imperative to conduct experimental kelp removals (e.g., Dayton, 1975; Hawkins and Harkin, 1985; Melville and Connell, 2001; Lilley and Schiel, 2006) to test the effects on the associated algae and invertebrates. This first requires the establishment of the minimal area of kelp removal required to experimentally test these hypothesis over appropriate time scales.

An analysis of the abundance of *Macrocystis* forests in Southern Chile must also consider the different population dynamics that the kelps utilise (perennial vs. annual population dynamics) (Buschmann et al., 2006). The removal of annual kelp populations like *Nereocystis luteana* seems to have less ecological consequences than the removal of perennial kelps (Schiel and Foster, 1986).

In other species of brown algae like *Lessonia nigrescens* or *L. trabeculata*, it has been observed that the impact of their harvest (in whole or in part) modifies the distribution and abundance of associated flora and fauna, causing major disruptions in associated stocks (Vásquez, 1999, 2008). However, *Lessonia* like other kelp-like species affects species abundance and richness by reducing grazing pressure through a frond whiplash effect that impact on herbivores (Santelices and Ojeda, 1984c; Benedetti-Cecchi and Cinelli, 1992b; Vásquez, 1992; Johnson and Brawley, 1998). Therefore, the ecological consequence of the removal of *M. pyrifera* is not comparable. This would suggest that the exploitation of *M. pyrifera* could affect the community associated with the kelp on a local scale. Accordingly, the loss of *M. pyrifera* populations may have an impact on the presence and abundance of species, those that are economically significant, which could have implications for the sustainability of several benthic fisheries. This concern is important, as no other canopy forming algae exist at this latitude on the Chilean coast that could assume the ecological role of giant kelp. This situation seems equivalent to that found in other studies where the ecological role of canopy-forming seaweed species can not be replaced by other (Lilley and Schiel, 2006).

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