Biogenic habitats as drivers of invertebrate benthic community variability in Tongoy Bay (SE Pacific coast): implications of macroalga harvesting

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Summary: Habitat biogenic complexity is thought to exert a significant positive influence on benthic communities. We examined the link between the seasonal variability of macroinvertebrate community structure (species and trophic richness, diversity and biomass) and habitats with different macroalgal assemblages. We identified macroinvertebrates and algae from 336 samples spread over four types of habitat: sand, mud, sand-gravel and seagrass meadows. Considering the whole macroalgal and macroinvertebrate assemblage, we confirmed that macroinvertebrate community variability within and among habitats can be mainly (but not only) explained by a few macroalgal structuring species. The variability of macroinvertebrate communities between habitats and seasons depended on the changes in the relative contribution of the explanatory biostructuring species in the overall algal community. Biomass, trophic behaviour and species richness remained stable in habitats with conspicuous macroalgal communities in contrast with habitats devoid of macroalgae. However, invertebrate species richness and biomass remained stable only in habitats whose dominant species did not change between seasons and not in those where dominant structuring species shifted. The seasonal change in a key structuring macroalgal species (*Condracanthus chamissoi*), probably as a result of harvesting, led to a major reduction in invertebrate community biomass and richness both in the particular habitat and in those nearby at species level. These consequences are especially important for invertebrates linked by trophic relationships and targeted by fisheries.

Keywords: benthic communities; biogenic habitat; diversity; macroalgae; fisheries.

Hábitats biogénicos como reguladores de la variabilidad de las comunidades bentónicas de invertebrados en la bahía de Tongoy (costa del Pacífico SE): implicaciones de la cosecha de macroalgas

Resumen: La complejidad biogénica del hábitat ejercería una importante influencia positiva sobre las comunidades bentónicas. Examinamos la relación entre la variabilidad estacional de la estructura de las comunidades de macroinvertebrados (riqueza, diversidad y biomasa de especies y grupos tróficos) en hábitats con diferentes ensambles de macroalgas. Identificamos macroinvertebrados y algas en 336 muestras distribuidas en cuatro tipos de hábitats: arena, lodo, arena-grava y praderas de pastos marinos. En este estudio, considerando todo el conjunto de macroalgas y macroinvertebrados, confirmamos que la variabilidad de la comunidad de macroinvertebrados dentro y entre los hábitats puede ser explicada principalmente (pero no sólo) por unas pocas especies estructurantes de macroalgas. La variabilidad de la comunidad de macroinvertebrados entre hábitats y estaciones dependió de los cambios de la contribución relativa de las especies biostructurales explicativas en la comunidad algal. La biomasa, el comportamiento trófico y la riqueza de especies permanecieron estables en los hábitats con comunidades de macroalgas conspicuas, en contraste con los hábitats desprovistos de macroalgas. Sin embargo, la riqueza de especies de invertebrados y la biomasa sólo se mantuvieron estables en los hábitats cuyas especies dominantes no cambiaron entre estaciones, pero no en aquellos en los que las especies estructurantes dominantes cambiaron. El cambio estacional de una especie de macroalga estructurante clave (*Condracanthus chamissoi*), probablemente debido a su cosecha, tuvo importantes consecuencias en la reducción de la biomasa y la riqueza de la comunidad de invertebrados, tanto en su hábitat como en los hábitats adyacentes. Estas consecuencias son especialmente relevantes para los invertebrados vinculados por relaciones tróficas y que además son recursos pesqueros

Palabras clave: comunidades bentónicas; hábitat biogénico; diversidad; macroalgas; pesquerías.

INTRODUCTION

Habitat complexity and heterogeneity have been linked to changes in organism abundance and diversity in a variety of aquatic habitats (Beck 2000, Thrush et al. 2001, Hauser et al. 2006, Smith et al. 2014). Habitat complexity is one of the most important factors structuring biotic assemblages (Kovalenko et al. 2012). It is associated with habitat heterogeneity, which exerts an important influence on ecological patterns and processes, affecting species distributions (Hewitt et al. 2008) and persistence and resilience (Pimm 1984, Kovalenko et al. 2012). Most studies of benthic communities define habitat complexity on the basis of the categorical geomorphological classifications of the substrate (Taniguchi and Tokeshi 2004, Thrush et al. 2001), but some have suggested that the characterization of heterogeneity should include physical and biological components such as substrate type, algal assemblages, currents, depth, type of recruitment and ecological relationships (Witman and Dayton 2001, Hauser et al. 2006, Hermosillo-Nuñez et al. 2015).

Biogenic substrates, three-dimensional structures formed by living species (Morrison et al. 2014) such as bivalve reefs, worm tubes, sea grass, coral and algae have been appropriately termed foundation species (Bruno and Bertness 2001) and ecosystem engineers (sensu Jones et al. 1994) and are thought to play a major role in structuring subtidal benthic marine communities (Lindsey et al. 2006). Community biomass, species richness, and density of marine fauna tend to be much greater in biogenic habitats than on adjacent bare substrate (Reise 2002). The biogenic complexity of habitats affects organisms living in their structures. Biogenic components can stabilize underlying substrates against erosion and can provide a hard substrate in an otherwise soft-sediment environment, facilitating the presence of sessile, encrusting or epifaunal organisms (Reise 2002, Lindsey et al. 2006). Furthermore, the structural complexity afforded by these habitats can allow them to become a nursery habitat and refuge for small and young organisms against predation (Almany 2004, Hereu et al. 2005), disturbance and environmental stresses (Bruno and Bertness 2001). Furthermore, the role of complexity is likely also dependent on whether species exhibit mobile or sessile life histories (McGuinness and Underwood, 1986). Finally, habitat complexity is one of the most important factors structuring biotic assemblages (Kovalenko et al. 2012, Smith et al. 2014). The characteristics of the bottom could affect the local food supply for predators and grazers, making them an important factor in bottom-up trophic control of ecosystems (Witman and Dayton 2001).

In the subtidal benthic habitats, spatial complexity is partly generated by irregularities on the bottom, such as boulders, cracks and other projections (including caves), as well as by the presence of algal communities that exert a significant influence on the abundance and diversity of benthic species (Hauser et al. 2006, Hermosillo-Nuñez et al. 2015, Attrill et al. 2000). In communities dominated by macroalgae, the habitat complexity is identified as the most powerful factor influencing the richness and abundance of organisms (Thrush et al. 2001, Almany 2004, Hauser et al. 2006, Stelling-Wood et al. 2020). The cover and morphological traits of different macroalgae species create a biogenic structure that plays an important role in defining the complexity of the studied habitats. Studies have found a positive correlation between algal and coral complexity and species abundance for echinoderm assemblages (Hermosillo-Nuñez et al. 2015), and complex algae have been found to have a higher amphipod density than structurally simpler algae (Hacker and Steneck 1990).

Though the role of structuring biogenic macroalgae in macroinvertebrate communities has been widely reported in the literature (Airoldi et al. 2008, Morrison et al. 2014), most studies have focused on the particular structuring species, ignoring the variability of the macroalgal ensembles and their potential contribution to variability of macroinvertebrates, as well as that of species with a minor presence but a large impact. As a consequence of the increasing human impacts on coastal habitats, such as that of commercial harvesting, efforts have been focused on understanding the structure and function of these systems for conservation purposes (Stagnol et al. 2013, Stelling-Wood et al. 2020). To achieve this, it is necessary to obtain biological and ecological community data to determine baseline conditions for habitats subject to exploitation (Borja and Heinrich 2005).

Community studies often consider species composition as the basic level of analysis (Hewitt et al. 2008). However, the use of functional groups such as trophic behaviour can be highly suitable for the analysis of benthic communities, because species associations can be examined through variable responses to particular habitats (Duffy 2002, Bremner et al. 2006). This approach could be used, as a complement to species diversity for evaluating the community structure, thus providing a better understanding of processes operating within habitats (Hewitt et al. 2008). The distribution and abundance of functional groups are partially linked to the

physical factors in the environment, and their trophic relationships determine the function of the community (Pearson and Rosenberg 1987, Duffy 2002). The relationship among trophic groups determine the flow of energy within the communities (McQuaid and Branch 1985), one of the central processes structuring marine ecosystems, which is related to properties such as stability and resilience of ecosystem function (Bremner et al. 2006, Hewitt et al. 2008, Kovalenko et al. 2012).

Multispecific fisheries develop thanks to subtidal communities, so both biogenic species and those dependent on them at some point of their life cycle or along the food web can be targeted by fisheries in the same area, with feedback interactions overlaying on the particular environment with poorly reported consequences so far (Wright et al. 2014, Pérez-Matus et al. 2017). Rocky subtidal habitats in eastern boundary upwelling systems, such as the Humboldt current system, are well recognized for sustaining productive benthic communities that have historically been under human exploitation (Thiel et al. 2007). Along the Chilean coast, in the last few decades, the collection of stranded kelps and other algae from the coast has been complemented by the direct diving to remove living biogenic specimens (Buschmann et al. 2008, Mac Monagail et al. 2017). In the last two decades the brown seaweed (*Lessonia spp*) has been heavily extracted (Berrios et al. 2022). Among the red algae, harvesting of *Chondracanthus chamissoi* has been variable since the beginning of its commercialization in the 1980s (www.Sernapesca.cl). This variability seems related to time and area harvested, with harvest volumes driven by demand cycles on the international markets (Vásquez and Vega 2001, Lotze et al. 2019) and heavy harvests in the last few years, especially in Tongoy Bay (González et al. 2016).

In central Chile, the productivity of benthic communities depends on periodic upwelling (Montecino and Quiroz 2000), which has enabled the development of large benthic fisheries (González et al. 2016). Exposed rocky subtidal habitats and those of protected bays sustain a variety of multispecific fisheries. While communities from exposed areas have been widely covered in the literature (Thiel et al, 2007), those of coastal bays have not. In Tongoy Bay, the main targets for exploitation are the crab *Romaleon setosus*, the snail *Xanthochorus cassidiformis*, the bivalve *Mulinia edulis,* the scallop *Argopecten purpuratus* and the red alga *C. chamissoi*. The latter, a biogenic species that adheres to sand-gravel substrates forming heterogeneous algal beds (González et al. 1997, Uribe et al. 2020), where the stability of its populations could be related to the variability of the structuring of coastal communities (Vásquez and Vega 2001), indicates that habitat-forming organisms can influence the interspecific relationships of the macroinvertebrate community in the intertidal system (Umanzor et al. 2019). Moreover, studies usually focus on very narrow coastal bands, comprising only partially the range of occupancy through which community members actually spread. In addition, the structuring role of the ecologically important *C. chamissoi* has not yet been addressed despite

the serious problems of over-exploitation that extensive commercial harvesting seems to have posed (González et al. 2016. Lotze et al. 2019). Thus, the aim of this study was to elucidate the relationship between habitats with different degrees of bio-physical complexity (associated with biogenic structure) and benthic communities, with *C. chamissoi* as a model for analysis.

MATERIALS AND METHODS

Study area

Tongoy Bay is influenced by a nearby upwelling centre ("Lengua de vaca"), which provides periodic intrusions of nutrient-rich water (Montecino and Quiroz 2000), and strong daily winds in the afternoon maintain a high degree of water circulation. The water temperature ranges from approximately 11ºC on the bottom to 19ºC on the surface in the summer. Under the summer conditions of high radiation and weak winds, a thermocline develops at a depth of approximately 10 to 15 m, which separates the warm surface water (16ºC-19ºC) from the colder bottom water (12ºC-15ºC). The deepest part of the bay reaches 90 m, and the average depth is approximately 25 m. Approximately 70% of the bay's substrate is composed of sand, but gravel bottoms, sand mixed with shell debris, and areas with stones can also be found (Wolff and Alarcón 1993).

Four different types of habitat were detected in Tongo Bay according to depth and basal substrate (Fig. 1): seagrass beds, sand-gravel, sand and mud (Jesse and Stotz 2002, Ortiz and Wolff 2002a, Ortiz et al. 2003). The seagrass beds (constituted of *Zostera chilensis*) are the shallowest, between 0 and 4 m depth. The sand habitat dominates at depths between 10 m and 14 m and is characterized by coarse sand and shells with a low organic matter content. The sand-gravel habitat is located between 4 and 10 m depth, and it is a transition zone characterized by high heterogeneity with sectors dominated by gravel, stones or rocks. The mud habitat is located in deeper waters (>14 m) with higher organic content (Ortiz and Wolff 2002a).

Sampling

Two field assessments (summer-February and winter-August 2012) were carried out in this study. Each time, 28 transects were established perpendicular to the coast throughout the bay, from the coast to 20 m depth. The single transects were about 300 m apart from one another. Each transect had four stations, one in each of the four habitats corresponding to different depth ranges (0-4 m, seagrass beds; 4-10 m, sand-gravel; 10-14 m, sand; 14-18 m, mud). Samples were taken by diving, and a single diver was responsible for the entire sample collection. For each sampling point, depth and habitat type were recorded, and three replicate samples were taken at each station. For each sample, all macroalgae and invertebrates were removed within a 0.25 m^2 quadrant, manually and with the aid of a stainless-steel spatula. This resulted in 336 samples in
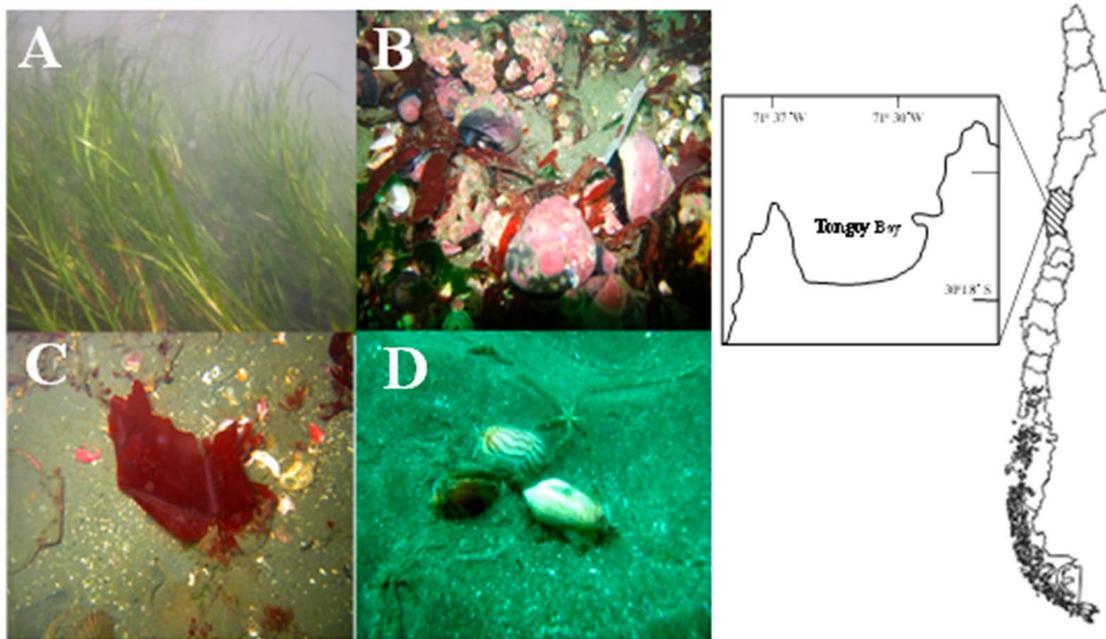
Fig.1. – Study area and habitat types with different structural complexities present in the Tongoy Bay benthic system: A, seagrass; B, sand-gravel; C, mud; and D, sand.

total for each season. The macroalgae and invertebrates sampled were retrieved from the subtidal in 0.25 mm mesh bags and brought immediately to the laboratory to be separated. Macroalgae species and biomass (g wet weight) were recorded as soon as the samples arrived at the lab, while the benthic macrofauna retained using a 0.25 mm mesh bag was preserved in 70% isopropyl alcohol for later processing in the laboratory. The macrofauna were weighed (wet weight) and identified to the lowest possible taxonomic resolution (generally to species level). The species were checked for synonymy and updated taxonomy using the WoRMS online taxon match tool (http://www.marinespecies.org/).

Data analysis

The optimum sampling effort was determined in quadrats using sample-based rarefaction curves based on the Chao2, Jackknife 1 and Jackknife 2 nonparametric procedures. These curves were constructed from 10000 randomizations without replacement. Two datasets were established for the benthic invertebrate biomass. The first consisted of the biomass of each species by station and season. The second consisted of the invertebrate trophic group biomass for each station and season. The functional trophic group was partitioned into seven categories: (1) suspension feeders, (2) top predators, (3) middle predators, (4) lower predators, (5) scavenger snails, (6) grazer snails and (7) deposit feeders. The allocation of the different species to each trophic group was based on the criteria and trophic levels described by Ortiz and Wolff (2002a) and González et al. (2016).

Each station was characterized by the habitat type and sampling season. The observed species richness, biomass (g m^{-2}) and Shannon diversity (H', nats) was compared among seasons and habitat types for both categories. The data were fourth-root transformed and analysed through a permutational multivariable analysis of variance (PERMANOVA) following the routines in Primer V6+ (Anderson et al. 2008). These non-restricted analyses were used because the data did not meet the parametric statistical assumptions. PERMANOVA was conducted using a Bray-Curtis similarity matrix, and the design was based on two crossed factors (season and habitat, with two and four levels, respectively), using a type I model (fixed factor). The statistical significance in PERMANOVA was tested with 10000 permutations under a reduced model and a type III sum of squares. To assess the significant difference between habitat types statistically, a post hoc pairwise test was used.

A one-way similarity percentage (SIMPER) analysis was performed to compare the contributions of the species within and between sampling habitats. SIMPER analysis is based on the Bray-Curtis index for estimating the average dissimilarity between pairs of sample groups and determining the contributions to the average similarity within each group (Clarke and Gorley 2006).

A canonical redundancy analysis (RDA) was carried out to assess the relationship between the spatial-temporal variation of the invertebrate community and trophic groups, the habitat type and the macroalgae community (Legendre et al. 2005). The response variables were one Y matrix generated from the total abundance (biomass) of each species in each habitat type and season. Predictive variables were organized into an X matrix using the biomass of 17 species of benthic macroalgae and the four habitat types and season.

The RDA ordination was performed using the CANOCO v4.5 software (terBraak and Smilauer 2002),

assuming a linear relationship between biological and environmental components. The trace statistic indicated the variation of Y explained by X. Stepwise forward selection was conducted to identify the environmental variables that best explained the variation in Y. Multicollinearity was evaluated among the environmental variables because it could modify the RDA model outputs. Only environmental factors with Pearson correlation (r) values below 0.90 were selected. The RDA outputs were obtained after running 9999 permutations.

RESULTS

A total of 175 taxa were recorded from four habitats. Taxa of the Arthropoda and Mollusca accounted for 75% of the total species richness. The sample-based rarefaction for season and habitat type curves indicated that the efficiency and representativeness of total species richness was over 85% given by the best fit of Chao 1.

Most macrophytes included in Table 1 showed a widespread distribution in the study area despite between-substrate and seasonal variability. Nevertheless, *Zostera chilensis*, the species that defined the shallower sea grass habitat, was the only species restricted to that particular habitat between 0 and 4 m depth, while *Gracilaria chilensis* was absent in the mud habitat. Invertebrate species that contributed the largest overall mean biomass were distinguished as i) those that showed a widespread distribution among habitats e.g. the grazer snail *T. cingulata*, the middle predator *Romaleon setosus* and the filter feeder *Argopecten. Purpuratus*; ii) those restricted to a particular habitat type regardless of season, such as the structuring filter feeder *Pyura chilensis* and the grazer snail *Trochita trochiformis* in the sand-gravel; and iii) those that were only absent from a particular habitat: e.g. *Heliaster helianthus* and *Luidia magallanica* never occurred in the mud habitat and *M. edulis* did not occur in the seagrass habitat.

The richness, diversity and community structure of the invertebrate species were significantly different between seasons and habitats (Table 2). The greatest species richness occurred in winter, the greatest diversity was observed in summer, and biomass was similar in the two seasons. (Fig. 2A, B, C; Table 2). The three community indices showed the greatest difference at the substrate level. Meanwhile, the richness, biomass and diversity of total macroalgae were higher in summer than in winter (Fig. 2G, H, I; Table 2). The sand-gravel and seagrass habitats showed the greatest richness and diversity of algal species, whereas the sand and seagrass habitats showed the highest biomasses. Within seagrass, the mean biomass contribution of macrophytes was about 10 times that of invertebrates (Table 1, Fig. 2) and accounted for 6 of the 10 species of greatest within-habitat biomass. Most invertebrate species listed in Table 1 showed two- to tenfold differences in mean biomass between seasons, but large standard deviations, with grazing snails tending to diminish in winter and no clear pattern for predators. The largest individual species contributors of biomass by an order of magnitude were the macrophytes

Z. chilensis (accounting for over 40% of the biomass), which were also the least variable between seasons in fractional terms. *Sarcodiotheca gaudichaudii*, by contrast, dropped tenfold in winter. The other macrophytes also dropped in winter but within narrower ranges and large standard variability. In sand-gravel, on the other hand, the contribution of macrophytes was lower than that of invertebrates, which peaked in this habitat (Fig. 2, Table 1), and also lower than that in seagrass and sand (Fig. 2). Despite the significantly larger biomass of invertebrates in sand-gravel than in sand and seagrass, sand-gravel invertebrate species and trophic richness and diversity remained statistically indistinguishable from those of seagrass. All meaningful species regarding biomass contribution to any other habitat type could also be found in sand-gravel (Table 1). On the other hand, in the seagrass habitat at least one of the dominant macrophytes was conspicuously present regardless of season, and three of the macrophytes that peaked in sand-gravel experienced several-fold increases (*C. chamissoi*) and decreases (*S. gaudichaudii* and *Rhodymenia skottsbergii*) in mean biomass in winter in comparison with summer. Dominant grazer snails and filter feeders remained within a fractional seasonal change, while middle and top predators again varied several-fold (Table 1).

In the sand habitat, macrophyte biomass was equal to that of seagrass, but with significantly lower richness and diversity. Invertebrate biomass was the lowest among the studied habitats and an order of magnitude lower than that of macrophytes. In this habitat, species and trophic invertebrate richness were the lowest, as was species diversity, while trophic diversity was lower than in the previous cases. *M. edulis* (suspension feeders) and the macrophyte *Gracilaria chilensis* showed the highest biomass in the sand habitat. *G. chilensis* had a biomass one to two orders of magnitude larger than that of any other macrophyte in the sand habitat and remained within a fractional change between seasons. In fact, this species accounted for 85% of macroalgal biomass in the sand habitat. Though it was also found in sand-gravel and seagrass habitats, its contribution there was marginal. In fact, in contrast with all other macrophytes listed in Table 1 that made an important contribution to more than a single habitat, *G. chilensis* contributed significantly only within the sand habitat, as did M. edulis among the invertebrate community. Only the middle predator *R. setosus* and the suspension feeder *Sinum cymba* contributed comparably with *M. edulis* in winter. Top predators were barely present in terms of biomass contributors. Finally, invertebrate biomass was two orders of magnitude higher than macrophyte biomass in the mud habitat, where the lowest macrophyte biomass was recorded.

Seasonal trends in the mud habitat were the opposite of those of the sand-gravel habitat for the most important macrophytes. The large invertebrate community was similar to that in the sand-gravel and seagrass habitats at species level, although trophic diversity matched that of the sand habitat. All the most important middle predators and surface filter feeders in the mud habitat in terms of biomass were present in a single

Table 1.–Species with the highest contribution in biomass (g m⁻²) for the four communities studied in summer and winter. For each community, the 10 species with the highest contribution were selected (bold). The functional trophic groups are indicated for species: grazer snails (GS), middle predators (MP), macrophytes (MA), top predator (TP), suspension feeders (SF), scavenger snails (SS).

Community/substrate		Mud				Sand				Sand_gravel				Seagrass				Whole area	
Species	T G	Summer	Std	Winter	Std	Summer	Std	Winter	Std	Summer	Std	Winter	Std	Summer	Std	Winter	Std	S & W	Std
Sinum cymba	(SS)	0	0	0	0	**13.4**	14.7	**18.3**	14.7	0	0	3.7	7.2	0	0	0	0	**7**	4.3
Xanthochorus spp.	(SS)	**8.1**	10.8	**3.4**	3.1	0.5	0.5	**2.2**	1.2	15.4	17.7	4.6	2.5	0	0	1	1.2	**6**	4
Priene rude	(SS)	**8.1**	6.4	**4**	2.9	1.3	1.4	0	0	2.9	1.3	5.8	3.1	0	0	0	0	**2.6**	0.8
Turritella cingulata	(GS)	**232.4**	202.3	**120.5**	80.9	**1.8**	3.5	0	0	**83.3**	52.7	**135**	51.4	2	3.8	**0.3**	0.5	**62.6**	19.4
Calliptraea trochiformis	(GS)	0	0	0	0	0.6	1.2	0	0	**29.5**	28.9	**45.4**	37.6	**4.6**	8.9	0	0	**15.2**	9.6
Tegula spp.	(GS)	**3.2**	4.3	0.1	0.1	**5**	5.4	1	1	**17.8**	11.5	11.2	7.9	1.4	1.7	0.3	0.3	**7.5**	3.3
Gracilaria chilensis	(MA)	0	0	0	0	**77.1**	71.2	**34.2**	25.6	5.4	6.7	0	0	**9.6**	18.8	**3.8**	5.9	**23.3**	14.4
Chondrocanthus chamissoi	(MA)	**13.3**	23.6	0	0	0.1	0.3	0.1	0.2	**13.5**	8.1	**93.6**	152.7	**8.8**	7.2	**5.2**	9	**20.7**	26.8
Sarcodiotheca gaudichaudii	(MA)	**9.2**	14.8	**18.1**	16.6	1.6	1.8	**9**	6.8	**41.6**	19.4	0.5	0.7	**132.4**	76	**12.7**	16.4	**19.1**	6.1
Ulva spp.	(MA)	**5.4**	6	0	0	0.2	0.3	0.1	0.1	**27**	12.3	**36.9**	17	**23.1**	14.8	**6.1**	8.3	**14.1**	4.4
Zostera chilensis	(MA)	0	0	0	0.1	0	0	0	0.1	0.1	0.3	0	0	**150.1**	59.2	**202.8**	60.7	**13.3**	4.8
Rhodymenia corallina	(MA)	**17**	16.8	**7.7**	8	0.5	0.7	**2.2**	3	**20.4**	8	**26.8**	14.6	1.1	1.7	0	0	**11.4**	3.5
Dendrimenia skottsbergii	(MA)	**0.4**	0.8	2.6	3.1	**9**	9.8	0.1	0.1	**20.5**	10.7	5.2	3.4	**9.8**	16.8	1	1.2	**8**	3.3
Romaleon setosus	(MP)	0	0	**69.1**	32.4	**14.8**	13.8	**18.9**	12.5	**16.5**	12.2	**72.9**	29	0.2	0.2	**45.4**	50.3	**30.1**	7.8
Cancer coronatus	(MP)	0	0	**7.2**	14.2	**8.6**	11.1	**3.1**	5	**26.2**	17.9	1.8	3.5	**10.2**	19.9	0	0	**9.6**	4.5
Homalaspis plana	(MP)	0	0	**2.6**	5.2	0	0	**1.6**	3.2	3.4	4.1	0.8	1.6	0	0	**9.9**	19.7	**1.9**	1.4
Argopecten purpuratus	(SF)	0	0	0	0	**6.3**	5.6	**2.3**	2.1	**23**	13.1	**38.5**	22.1	**11.5**	16	**43.6**	32.3	**27.8**	12
Mulinia edulis	(SF)	0	0	**12.9**	25.6	**78.4**	93.8	**13.8**	16	0.8	0.8	0	0	0	0	0	0	**18.4**	17.7
Pyura chilensis	(SF)	0	0	0	0	0	0	0	0	**38.6**	38.2	**29.8**	32.1	0	0	0	0	**14.3**	10.7
Heliaster helianthus	(TP)	0	0	0	0	0.4	0.8	0	0	6.1	9.1	**15.3**	15.2	**65**	127.3	0	0	6.5	5.8
Meyenaster gelatinosus	(TP)	**10.9**	21.4	0	0	0	0	0	0	5.6	7.6	**21.6**	23	0	0	**15.7**	30.8	6.2	4.7
Luidia magallanica	(TP)	0	0	0	0	0	0	**3.1**	5.2	7.1	7.5	**12.2**	13.5	0	0	0	0	4.5	3.2

Table 2. – PERMANOVA outputs of the spatial-temporal variation of community epifauna, trophic groups and macroalgae at Tongoy Bay. Bold numbers correspond to a significant statistical difference at p≤0.05. Se is Season; Ha is Habitat.

	Richness		Biomass		Diversity H'		Community structure	
Source	Pseudo-F	P(perm)	Pseudo-F	P(perm)	Pseudo-F	P(perm)	Pseudo-F	P(perm)
Community epifauna								
Season	11.91	**0.0007 ***	1.19	0.263	7.03	**0.0071***	2.22	**0.0199***
Habitat	35.14	**0.0001***	9.50	**0.0001***	10.54	**0.0001***	4.84	**0.0001***
Se*Ha	1.34	0.259	1.33	0.270	3.97	**0.0101***	1.07	0.342
Trophic behaviour								
Season	1.56	0.221	1.19	0.281	3.32	0.072	1.90	0.095
Habitat	41.99	**0.0001***	9.50	**0.0001***	11.97	**0.0001***	12.55	0.0001*
Se*Ha	1.62	0.188	1.33	0.267	0.76	0.523	2.48	**0.0027***
Macroalgae								
Season	9.90	**0.0018***	4.80	**0.0148***	5.81	**0.0018***	3.23	**0.0015***
Habitat	6.39	**0.0003***	5.19	**0.0002***	7.46	**0.0001***	8.14	**0.0001***
Se*Ha	0.51	0.685	1.07	0.365	1.28	0.258	0.82	0.695
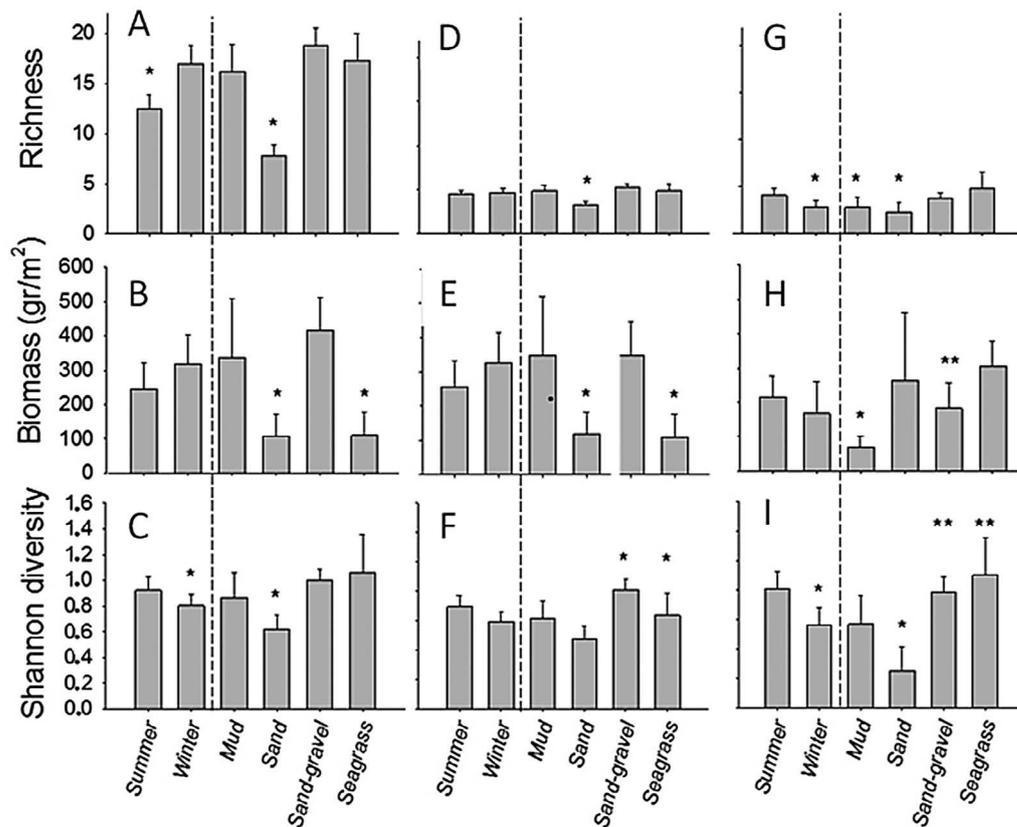
Fig. 2. – Invertebrate community richness, biomass and Shannon diversity (H') variability across seasons and habitats in Tongoy Bay. (A, B, C), index estimations calculated for groups of species based on trophic behaviour (D, E, F) and macroalgae (G, H, I) in Tongoy Bay. The statistical differences (p≤0.05) between seasons and habitats are indicated by asterisk.

season. Three middle predators present only in winter only in the mud habitat, *Cancer coronatus* in particular, showed the opposite pattern in the other habitats, diminishing overall in winter and disappearing completely from seagrass in that season. The targeted species *R. setosus* followed the same trend, increasing several-fold in sand-gravel in winter and remaining relatively stable in the other habitats, where it maintained similar levels within seasons. *C. coronatus*, on the other hand, diminished in sand-gravel in winter. The filter feeder *A. purpuratus*, one of the important target species for fisheries, appeared in the largest numbers in winter in the mud habitat, an order of magnitude higher than in the other substrates, while its lower biomass in the sand, sand-gravel and seagrass habitats also showed an increase in winter. The top predator *Megynaster gelatinosus* appeared in the mud habitat only in summer, when it decreased in sand-gravel and seagrass.

The SIMPER results for the invertebrate community (Table 3) showed the highest dissimilarities between the seagrass and sand habitats (94%), as well as the sand-gravel and sand habitats (93%). The species that contributed to the greatest dissimilarity were the clam *A. purpuratu* and the crab *R. setosus*, both present in all the habitats with large seasonal and spatial variability, whereas *Oliva peruviana* and *Mulinia edulis* were only present in the sand habitat. The mud habitat exhibited over 86% dissimilarity to the other habitats, the species with the greatest contribution to this difference being the grazing snail *Turritela cingulata. (*Table 3*),* which in spite of its presence in all the habitats had a biomass two orders of magnitude larger in mud than in sand and seagrass.

The comparison of richness and biodiversity indices according to trophic groups showed differences between habitats, but not between seasons for the three

Table 3. – One-way SIMPER results of average dissimilarity between habitats for the invertebrate community at Tongoy Bay. % C is percentage of contribution.

Habitats	Species	% C	Habitats	Species	% C
Sand-gravel and mud	*Turritella cingulata*	14,7	Sand-Gravel and seagrass	*Romaleon setosus*	11,3
Average dissimilarity	*Romaleon setosus*	10,6	Average dissimilarity	*Argopecten purpuratus*	10,9
86%	*Argopecten purpuratus*	9,5	85%	*Turritella cingulata*	7,7
	Lagenicella variabilis	5,5		*Cancer coronatus*	4,7
	Cancer coronatus	4,5		*Lagenicella variabilis*	4,6
	Calliptraea trochiformis	3,6		*Calliptraea trochiformis*	3,9
	Priene rude	3,0		*Taliepus dentatus*	3,3
	Xanthochorus buxea	2,7		*Heliaster helianthus*	3,2
	Xanthochorus cassidiformis	2,5		*Xanthochorus cassidiformis*	3,0
	Piura chilensis	1,9		*Meyenaster gelatinosus*	2,7
Mud and seagrass	*Turritella cingulata*	15,6	Sand-Gravel and sand	*Romaleon setosus*	11,2
Average dissimilarity	*Argopecten purpuratus*	14,1	Average dissimilarity	*Argopecten purpuratus*	7,3
85%	*Romaleon setosus*	11,3	93%	*Turritella cingulata*	7,0
	Taliepus dentatus	3,6		*Oliva peruviana*	5,5
	Cancer coronatus	3,4		*Cancer coronatus*	4,7
	Lagenicella variabilis	3,2		*Lagenicella variabilis*	4,1
	Xanthochorus buxea	2,9		*Mulinia edulis*	4,0
	Homalaspis plana	2,9		*Calliptraea trochiformis*	3,6
	Heliaster helianthus	2,4		*Xanthochorus cassidiformis*	2,9
	Tegula luctuosa	2,3		*Sinum cymba*	2,8
Mud and sand	*Turritella cingulata*	15,8	Seagrass and sand	*Argopecten purpuratus*	12,7
Average dissimilarity	*Romaleon setosus*	10,7	Average dissimilarity	*Romaleon setosus*	11,3
85%	*Argopecten purpuratus*	7,8	94%	*Oliva peruviana*	8,4
	Oliva peruviana	7,5		*Mulinia edulis*	4,4
	Mulinia edulis	4,7		*Taliepus dentatus*	4,2
	Xanthochorus buxea	3,7		*Cancer coronatus*	3,2
	Cancer coronatus	3,3		*Sinum cymba*	3,1
	Sinum cymba	2,8		*Diopatra* sp.	2,8
	Lagenicella variabilis	2,6		*Heliaster helianthus*	2,7
	Tagelus dombeii	2,6		*Tegula luctuosa*	2,4

indices evaluated (Fig. 2D, E, F, Table 2). The lowest values for biomass, diversity and richness (based on trophic groups) were observed in the sand habitat, while the other three habitats showed no significant differences in richness and intermediate diversity in muds. The sand-gravel and mud habitats showed higher biomass and richness diversity at the trophic group level than the other habitats.

For the invertebrate community, the RDA ordination revealed significant spatial and temporal variation of the community with a good fit and high statistical significance (Trace=0.910, p=0.002). In the RDA biplot, sites were separated mainly along the first axis, with sand and seagrass, the lowest biomass communi-
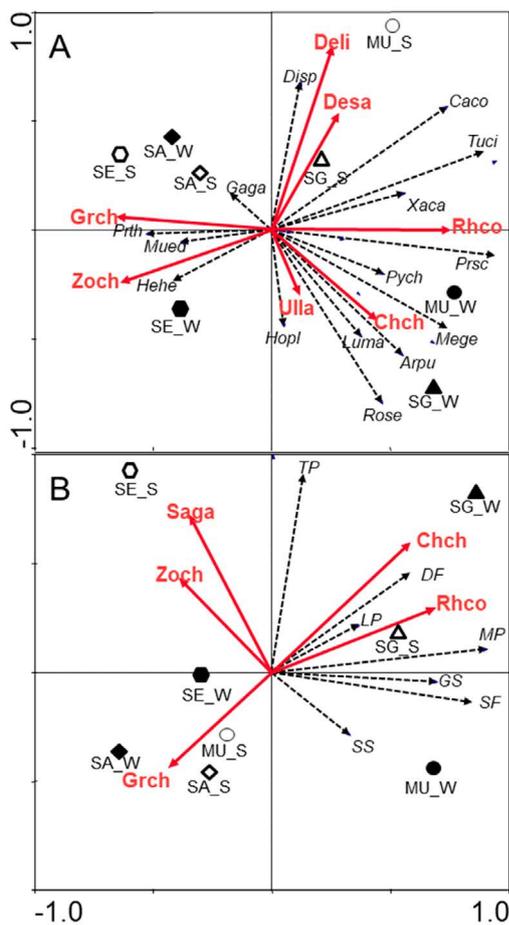
Fig. 3. – Redundancy analysis (RDA) of spatial and temporal variation of invertebrate epifauna (A) and trophic groups (B). Habitat-season distribution in the RDA biplot: SA_S=sand summer, SA_W=sand winter, MU_S=mud summer; MU_W=mud winter; SG_S=sand-gravel summer, S_GW=sand-gravel winter; SE_S=seagrass summer, and SE_W=seagrass winter. Significant macroalga species (red solid arrows): *Chondracanthus chamissoi* (Chch), *Ulva lactuca* (Ulla), *Delesseria sanguínea* (Desa), *Rhodymenia corallina* (Rhco), *Desmarestia lingulata* (Deli), *Gracilaria chilensis* (Grch), *Sarcodiotheca gaudichaudii* (Saga) and *Zostera chilensis* (Zoch). The code of invertebrates (A); Gaga (*Gaudichaudia gaudichaudi*), Disp (*Diloma sp*), Caco (*Cancer coronatus*), Tuci (*Turritella cingulata*), Xaca (*Xanthochorus sp*), Prsc (*Priene scabrum*), Pych (*Pyura chilensis*), Mege (*Meyenaster gelatinosus*), Luma (*Luidia magallánica*), Arpu (*Argopecten purpuratus*), Rose (*Romaleon setosus*), Hopla (*Homalaspis plana*), Hehe (*Heliaster helianthus*), Mued (*Mulinia edulis*) and Prth (*Prothothaca thaca*). The trophic groups (B) are listed in Table 1.

ties within negative x axis quadrants and sand-gravel and mud and sand-gravel in positive x quadrants, while the second axis indicated temporal separation between summer and winter. The differences between habitats were driven by the presence of differences species in a particular habitat (Fig. 3A). Consistent with the SIMPER analysis, some species showed a high degree of habitat specificity (e.g. the crab *Gaudichaudia gaudichaudii* and the clam *M. edulis*), while other species, such as the suspension feeder scallop *A. purpuratus* and the top predator crab *R. setosus* were present in more than one habitat. *Pyura chilensis* showed a significant role for sand-gravel habitat separation at the substrate level (first axis) but not along the seasonal dimension (second axis). Seasonal differences were mostly associated with changes in the relative contribution of species to overall biomass within substrates rather than changes in species composition.

RDA forward selection detected that the invertebrate community biomass variability in the sand-gravel habitat was associated with the presence of *C. chamissoi*, especially in winter (Fig. 3A). In this habitat snails (*Tegula* spp.) and sea stars (*Luidia magallanica* and *Meyenaster gelatinosus*) were associated with C. chamissoi in the winter season. Meanwhile, snails (e.g. *Priene rude* and *X. cassidiformis*) showed a strong relationship with the alga *Rhodymenia corallina*, which was also present in the mud habitat. The sand habitat was clearly associated with the alga *G. chilensis*, on which the clam *P. theca* was a characteristic species (Fig. 3 A).

The RDA analyses conducted on trophic groups also showed great spatial and temporal variability of the communities, although the variance explained was lower than the analysis based on species (Trace=0.960, p=0.001). Different trophic groups characterized the different habitats. Temporal variability of each habitat (separation along the second axis of RDA) was associated with changes in the relative contribution of the same trophic group except in the mud habitat, where there was a shift in the dominant trophic group. Scavenger snails and suspension feeders dominated in winter in the mud habitat but were almost absent in summer. Grazer snails contributed to both the mud and the sand-gravel habitat in winter, but lower and middle predators dominated exclusively the sand-gravel habitat (Fig. 3B). The biomass of the commercial alga *C. chamissoi* was positively correlated with the occurrence of these predators and deposited feeders. *C. chamissoi* showed the largest biomass in sand-gravel, especially in winter. Meanwhile, the algae *G. chilensis* and *Z. chilensis*, which were present in the sand and seagrass habitat, respectively, were not related to the presence of any trophic group category (Fig. 3B).

DISCUSSION

In this study considering the entire macroalgal and macroinvetebrate assemblage from four different habitats and two seasons, we confirmed that macroinvertebrate community variability within and between habitats can be mainly (but not only) explained by a

few macroalgal structuring species and previously neglected species. This study is one of the few that deals with macrobenthic communities in a depth range from intertidal to subtidal in four different types of habitat that share species of invertebrates and macrophytes, showing that population and community level analysis are interdependent between habitats, and seasonal changes cannot be understood in isolation from neighbouring habitats and pelagic conditions (Ortiz and Wolff 2002b). Structuring macrophyte distribution in the habitats of this protected oceanic bay also depends on substrate type, since the substrate required to hold also depend on the stability and energy of the environment, and depth.

Despite the seasonal biomass change of *Zostera chilensis and Sarcodiotheca gaudichaudii* in the intertidal sea grass habitat and of *Gracilaria chilensis* in subtidal sand, which typically dominate in summer (Santelices 1989), they remained as the dominant species in winter in their respective substrates. Macroalgae are considered "niche constructers" for themselves or other organisms or as "ecosystem engineers" (Jones et al. 1994). *G. chilensis* and *S. gaudichaudii* are coarsely-branched species and, together with the seagrass bed of *Z. chilensis*, constitute a complex seagrass habitat that seems to offer optimum conditions for other species/groups, such as microepifauna, epiphytes and infauna (Vásquez et al. 2003, Short et al. 2011). It has been widely reported that seagrass beds rank among the most productive ecosystems supporting benthic communities (Edgar and Barrett 2002), and this habitat could offer an optimum refuge (structural function) for recruits of the commercial species *Argopecten purpuratus* (Jesse and Stotz 2002) and serve as a nursery (Stotz and González 1997). However, the high productivity and ecological importance of a complex habitat is not necessarily translated into stable high in situ biomass, but rather into high richness and diversity of macroinvertebrate communities, as occurs in the sea grass in the present case. The structuring role of a diverse macrophyte habitat in sea grass throughout the year could also explain the fact that, despite seasonal changes, the macroinvertebrate community was stable between seasons. Habitat complexity supports a community structure that increases stability if food webs are organized (Duffy 2002, Duplisea and Blanchard 2005, Kovalenko et al. 2012). More complex environments contain more refuges and suitable substrates, increasing the ecological interactions (Jesse and Stotz 2002, Ortiz and Wolff 2002b, Almany 2004, Vásquez and Vega 2005). In contrast with sea grass, in the more unstable sand substrate, the habitat was formed by the filamentous *Gracilaria chilensis*, which dominated the low-diversity macroalgal community throughout the year, and the very simple macrobenthic community at species and trophic level showed little change in the trophic structure.

Both mud and sand-gravel showed structural changes in macroalgal communities between seasons. In the mud habitat, which had the lowest macroalgal biomass, the diversity and richness increased in summer, while in the sand-gravel habitat there was a change in dominance of structuring species despite a more stable large biomass. In the mud and sand-gravel habitats we found the largest macroinvertebrate variability in biomass and species richness (but not trophic richness). In the mud habitat, invertebrate community structure at trophic level was not associated with macrophyta structuring species. Small snail species (e.g. *T. cingulata* and *Priene rude*), dominated the mud habitat and can be considered "opportunistic" species because they inhabit sediment enriched with organic matter (Pearson and Rosenberg 1987). Likewise, there was a high abundance (especially in winter) of *T. cingulata*, which could stabilize the soft-sediment habitat (Gaymer and Himmelman 2008) and could be directly related to the richness and abundance of the associated infaunal species. In addition, in winter mobile species such as *A. purpuratus* and *R. setosus* were the main species responsible for the overall biomass increase of macrofauna, which could be associated with migratory responses to environmental seasonality (Ortiz and Wolf 2002b, León and Stotz 2004). *R. setosus* is a highly mobile predator of *A. purpuratus*, so environmental changes that drive *A. purpuratus* distribution would indirectly affect the predator distribution (Ortiz and Wolff 2002a, Ortiz et al. 2003).

In sand-gravel, overall macroalgal biomass did not change between summer and winter, but the macrophyte community structure did. *Chondracanthus chamissoi* increased its biomass by two orders of magnitude from summer to winter, and appeared as one of the two main structuring species. The abundance and morphological traits of *C. chamissoi* (a shrubby structure that offers surface area and internal space) increases the complexity of habitats and could play an important role in the biodiversity productivity of the habitats of Tongoy Bay, as has been reported for other algae (Vásquez and Vega 2001, Stelling-Wood et al. 2020). In winter, macroinvertebrate biomass and richness increased together with *C. chamissoi*, while trophic richness and diversity remained constant. A contribution to the stable structure at the trophic level between seasons can be associated with the high presence of the structuring filter feeder *Pyura chilensis* (Sepúlveda et al. 2003). Sand-gravel shows higher production in the Tongoy Bay benthic system (Ortiz and Wolff 2002a), where the hard, shrub-like *C. chamissoi* can offer a refuge and settlement habitat for other organisms, thus also contributing to sediment stability (Jesse and Stotz 2002). The second important species in sand-gravel was *Rhodymenia corallina*, which had a larger biomass in summer. The red alga *R. corallina* in the sand-gravel habitat was associated with herbivorous epifauna. In sand-gravel, *R. setosus* was the dominant top predator and fed mainly on the scallop *A. purpuratus*. By switching prey in response to changes in food availability (e.g. by reducing habitat complexity), top predators can modify the community structure in response to changes in prey availability (Ortiz et al. 2003). This allows for a view of dynamic communities with an integrity beyond habitat types that at different times of the year display different combinations of biomass and biodiversity, allowing the persistence of populations

that redistribute themselves and re-form bio-physical associations.

The distribution and abundance of the alga *C. chamissoi* and the filter feeder *Pyura chilensis* associated with the sand-gravel habitat generates high spatial heterogeneity. The higher sand-gravel habitat complexity could also reflect the interactions of algae with grazers and of preys with predators (filter feeders and top and middle carnivores), as reported by Kovalenko et al. (2012) and observed in the benthic community of the Tongoy Bay in the present study and in Jesse and Stotz (2002) and Ortiz et al. (2003). Our results therefore coincide with Stelling-Wood et al. (2020), who conclude from a literature review that the availability of more microhabitats can lead to an increase in the number of organisms or species that can reside in a given habitat through more available substrate and the fact that biogenic structures also articulate trophic interactions .

The commercial resources such as the crab *R. setosus*, the snail *X. cassidiformis*, the bivalve *A. purpuratus*, the red alga *C. chamissoi* and the filter feeder *P. chilensis* are trophically linked in the four habitats. The presence of *C. chamissoi* and *P. chilensis* could be increasing the habitat complexity and may decouple trophic interaction with a subsequent increase in ecosystem stability, as suggested by Kovalenko et al. (2012) for predator-prey relationships. *C. chamissoi* has a natural annual cycle regarding standing stock with maximums in spring-summer (González et al. 1997, Vásquez and Vega 2001). This contrasted with our results, but González et al. (2016) reported that 37 t of *C. chamissoi* was harvested from Tongoy Bay in the summer of 2012, and our summer sampling was carried out post-harvest. Macroalgal harvesting often disturbs both the seabed and the organisms living within or on it, directly affecting the community attributes of the benthic system and indirectly changing the properties of the habitat structure (Blanchard et al. 2004). The same type of disturbance of spatial heterogeneity and diversity could be expected from the removal of *P. chilensis*, a filter feeder harvested along the Chilean coast in large amounts, but it was not harvested in the Tongoy Bay during our study period. Therefore, the increase in the richness and biomass of the macrobenthic community observed in winter in sand-gravel was related to the increase in the commercial alga *C. chamissoi*. An intensive harvest of *C. chamissoi* could be regulating the overall dynamics of the benthic community, as is suggested by this study. The loss of such biogenic structures would have concomitant impacts on marine communities, because the loss of habitat structure generally leads to lower abundances and often declines in species richness, as has been found in other studies (Airoldi et al. 2008, Stagnol et al. 2013). Therefore, it is necessary to include habitat heterogeneity explicitly within studies trying to predict the effect of fisheries on ecosystems. This is important to fisheries management. Habitats that are less damaged are suggested to contribute more recruits to fisheries, and to contain greater diversity than disturbed habitats (Thrush et al. 2001, Ortiz and Wolf 2002b).

Invertebrate community attributes cannot be directly inferred from single habitat seaweed diversity or biomass. Changes in seaweed biodiversity are likely to have implications for invertebrate epifauna only under specific scenarios or algal change (Bates and De Wreede 2007, Kelaher and Castilla 2005). According to our results, the consequences of macroalgal/sea grass community variability on invertebrate communities will depend on the dominance of structuring species within each algal assemblage and habitat. As pointed out, the association of benthic communities and their particular habitats (physical and biogenic) could be used as an indicator of ecological variability in coastal ecosystems and has important implications for marine conservation and resource management (Airoldi et al. 2008). The impact of fisheries activities on seafloor habitats and associated assemblages has only recently become the focus of research (Morrison et al. 2014). Identifying and monitoring biogenic habitats of high conservation value has the potential to improve the efficacy of resource management (Handley et al. 2014, Lotze et al. 2019).

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REFERENCES

Airoldi L., Balata D., Beck M.W. 2008. The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. J. Exp. Mar. Biol. Ecol. 366(1): 8-15.
https: //doi.org/10.1016/j.jembe.2008.07.034

Almany G.R. 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106: 275-284.
https: //doi.org/10.1111/j.0030-1299.2004.13193.x

Anderson M.J., Gorely R.N., Clarke K.R. 2008. PERMANOVA + Primer: Guide to software and statistical methods. PRIMER-E Limited.

Attrill M.J., Strong J.A., Rowden A.A. 2000. Are macroinvertebrate communities influenced by structural complexity? Ecography 23: 114-121.
https: //doi.org/10.1111/j.1600-0587.2000.tb00266.x

Bates C.R., DeWreede R.E. 2007. Do changes in seaweed biodiversity influence associated invertebrate epifauna? J. Exp. Mar. Biol. Ecol. 344: 206-214.
https: //doi.org/10.1016/j.jembe.2007.01.002

Beck M.W. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. J. Exp. Mar. Biol. Ecol. 249: 29-49.
https: //doi.org/10.1016/S0022-0981(00)00171-4

Blanchard F., Le Loc'h F., Hily C., Boucher J. 2004. Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. Mar. Ecol. Prog. Ser. 280: 249-260.
https: //doi.org/10.3354/meps280249

Borja A., Heinrich H. 2005. Implementing the European Water Framework Directive: the debate continues. Mar. Pollut. Bull. 5: 486-488.
https: //doi.org/10.1016/j.marpolbul.2005.01.002

Bremner J., Rogers S.I., Frid C.L.J. 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indic. 6: 609-622.
https://doi.org/10.1016/j.ecolind.2005.08.026

Bruno J.F., Bertness M.D. 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness, M.D. (ed) Marine Community Ecology. Sinauer Associates Inc., Sunderland, MA, pp. 201-218.

Buschmann A.H., Hernandez-González M.D.C., Varela D. 2008. Seaweed future cultivation in Chile: perspectives and challenges. Int. J. Environ. Pollut, 33: 432-456.
https://doi.org/10.1504/IJEP.2008.020571

Clarke, K.R, Gorley R.N. 2006. Primer v6: user manual/tutorial. Primer-E Ltd, Plymouth, UK. 260 pp.

Duffy J. E. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99: 201-219.
https://doi.org/10.1034/j.1600-0706.2002.990201.x

Duplisea D.E., Blanchard F. 2005. Relating species and community dynamics in an heavily exploited marine fish community. Ecosystems 8: 899-910.
https://doi.org/10.1007/s10021-005-0011-z

Edgar G. J., Barrett N. S. 2002. Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. J. Exp. Mar. Biol. Ecol. 270: 1-24.
https://doi.org/10.1016/S0022-0981(02)00014-X

Gaymer C. F., Himmelman, J. H. 2008. A keystone predatory sea star in the intertidal zone is controlled by a higher-order predatory sea star in the subtidal zone. Mar. Ecol. Prog.Ser, 370: 143-153.
https://doi.org/10.3354/meps07663

González J., Meneses I., Vásquez J. 1997. Field studies in *Chondracanthus chamissoi* (C. Agardh) Kützing. Seasonal and spatial variations in life cycle phases. Biología Pesquera (Chile) 26: 3-12.

González J., Ortiz M., Rodríguez-Zaragoza F., Ulanowicz R.E. 2016. Assessment of long-term changes of ecosystem indexes in Tongoy Bay (SE Pacific coast): Based on trophic network analysis. Ecol. Indic. 69: 390-399.
https://doi.org/10.1016/j.ecolind.2016.04.019

Handley S.J., Willis T.J., Cole R.G., et al. 2014. The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems. J. Sea Res. 86: 58-68.
https://doi.org/10.1016/j.seares.2013.11.005

Hacker S.D., Steneck R.S. 1990. Habitat architecture and the abundance and body size dependent habitat selection of a phytal amphipod. Ecol. 71: 2269-2285.
https://doi.org/10.2307/1938638

Hauser A. M., Attrill J., Cotton P. A. 2006. Effects of habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts. Mar. Ecol. Prog. Ser. 325: 93-100.
https://doi.org/10.3354/meps325093

Hereu B., Zabala M., Linares C., Sala E. 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. Mar.Biol. 146: 293-299.
https://doi.org/10.1007/s00227-004-1439-y

Hermosillo-Nuñez B., Rodríguez-Zaragoza F., Ortiz M., Galván-Villa M. C., et al. 2015. Effect of habitat structure on the most frequent echinoderm species inhabiting coral reef communities at Isla Isabel National Park (Mexico). Community Ecol. 16: 125-134.
https://doi.org/10.1556/168.2015.16.1.14

Hewitt J. E., Thrush S. F., Dayton P.D. 2008. Habitat variation, species diversity and ecological functioning in a marine system. J. Exp. Mar. Bio. Ecol. 366: 116-122.
https://doi.org/10.1016/j.jembe.2008.07.016

Jesse S., Stotz W. 2002. Spatio-temporal distribution patterns of the crab assemblage in the shallow subtidal of the north Chilean Pacific coast. Crustaceana, 75: 1161-1200.
https://doi.org/10.1163/156854002321518135

Jones C.G., Lawton J.H., Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.
https://doi.org/10.2307/3545850

Kelaher B.P., Castilla J.C. 2005. Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of northern Chile. Estuar. Coast. Shelf Sci. 63, 155-165
https://doi.org/10.1016/j.ecss.2004.10.017

Kovalenko K. E., Thomaz S. M., Warfe D. M. 2012. Habitat complexity: approaches and future directions. Hydrobiologia, 685: 1-17.
https://doi.org/10.1007/s10750-011-0974-z

Legendre P., Borcard D., Peres-Neto P. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecol. Monogr. 75: 435-450.
https://doi.org/10.1890/05-0549

Lindsey E.L., Altier A.H., Witman J.D. 2006. Influence of biogenic habitat on the recruitment and distribution of a subtidal xanthid crab. Mar. Ecol. Prog. Ser. 306: 223-231.
https://doi.org/10.3354/meps306223

León R.I., Stotz W. 2004. Diet and prey selection dynamics of *Cancer polyodon* in three different habitat typesin Tongoy Bay, Chile. J. Mar. Biolog. Assoc.84: 751-756.
https://doi.org/10.1017/S0025315404009865h

Lotze H.K., Milewski I., Fast J., et al. 2019. Ecosystem-based management of seaweed harvesting. Bot. Mar. 62: 395-409.
https://doi.org/10.1515/bot-2019-0027

McGuinness K.A., Underwood A.J. 1986. Habitat structure and the nature of communities on intertidal boulders. J. Exp. Mar. Biol. 104: 97-123.
https://doi.org/10.1016/0022-0981(86)90099-7

McQuaid C.D., Branch G.M. 1985. Trophic structure of rocky intertidal communities: Response to wave action and implications for energy flow. Mar. Ecol. Prog. Ser. 22: 153-161.
https://doi.org/10.3354/meps022153

Mac Monagail M., Cornish L., Morrison L., et al. 2017. Sustainable harvesting of wild seaweed resources. Eur. J. Phycol. 52: 371-390.
https://doi.org/10.1080/09670262.2017.1365273

Montecino V., Quiroz D. 2000. Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30º S). Aquat. Sci. 62: 364-380.
https://doi.org/10.1007/PL00001341

Morrison M., Jones E.G., Consalvey M., Berkenbusch K. 2014. Linking marine fisheries species to biogenic habitats in New Zealand: a review and synthesis of knowledge. Ministry for Primary Industries.

Ortiz M., Wolff M. 2002a. Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and assessment of management strategies. J. Exp. Mar. Biol. Ecol. 268: 205-235.
https://doi.org/10.1016/S0022-0981(01)00385-9

Ortiz M., Wolff M. 2002b. Spatially explicit trophic modelling of a harvested benthic ecosystem in Tongoy Bay (central northern Chile). Aquat. Conserv.: Mar. Freshw. Ecosyst. 12, 601-618.
https://doi.org/10.1002/aqc.512

Ortiz M., Jesse S., Stotz W., Wolff M. 2003. Feeding behaviour of the asteroid *Meyenaster gelatinosus* in response to changes in abundance of the scallop *Argopecten purpuratus* in northern Chile. Arch. Hydrobiol. 157: 213-225.
https://doi.org/10.1127/0003-9136/2003/0157-0213

Pearson T.H., Rosenberg R. 1987. Feast and famine: structuring factors in marine benthic communities. In Symposium of the British Ecological Society.

Pérez-Matus A., Carrasco S. A., Gelcich S., et al. 2017. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. Ecosphere, 8(5), e01808.
https://doi.org/10.1002/ecs2.1808

Pimm S.L. 1984. The complexity and stability of ecosystems. Nature, 307: 321-326.
https://doi.org/10.1038/307321a0

Reise K. 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48: 127-141.
https://doi.org/10.1016/S1385-1101(02)00150-8

Santelices B. 1989. Algas marinas de Chile: distribución, ecología, utilización, diversidad. Santiago. Ediciones Universidad Católica de Chile. 399 pp.

Sepúlveda R., Cancino J.M., Thiel M. 2003. The peracarid epifauna associated with the ascidian Pyura chilensis (Molina, 1782) (Ascidiacea: Pyuridae). J. Nat. Hist. 37: 1555-1569.
https://doi.org/10.1080/00222930110099615

Short F.T., Polidoro B., Livingstone S.R., et al. 2011. Extinction risk assessment of the world's seagrass species. Biol. Conserv. 144: 1961-1971.
https://doi.org/10.1016/j.biocon.2011.04.010

Smith R.S., Johnston E.L., Clark G.F. 2014. The role of habitat complexity in community development is mediated by resource availability. PloS ONE 9: e102920.
https://doi.org/10.1371/journal.pone.0102920

Stagnol D., Renaud M., Davoult D. 2013. Effects of commercial harvesting of intertidal macroalgae on ecosystem biodiver-

sity and functioning. Estuar. Coast. Shelf Sci. 130: 99-110.
https://doi.org/10.1016/j.ecss.2013.02.015

Stelling-Wood T.P., Gribben P.E., Poore A.G. 2020. Habitat variability in an underwater forest: Using a trait-based approach to predict associated communities. Funct. Ecol. 34: 888-898.
https://doi.org/10.1111/1365-2435.13523

Stotz W., González S.A. 1997. Abundance, growth, and production of the sea scallop *Argopecten purpuratus* (Lamarck 1819): bases for sustainable exploitation of natural scallop beds in north-central Chile. Fish. Res. 32: 173-183.
https://doi.org/10.1016/S0165-7836(97)00010-6

Taniguchi H., Tokeshi M. 2004. Effects of habitat complexity on benthic assemblages in a variable environment. Freshwater Biol. 49: 1164-1178.
https://doi.org/10.1111/j.1365-2427.2004.01257.x

terBraak C.J.F., Smilauer P. 2002. CANOCO Reference Manual and Cano Draw for Windows User's Guide: Software for Canonical Community Ordination, version 4.5. Microcomputer Power, Ithaca, NY.

Thiel M., Castilla J. C., Fernández Bergia M. E., Navarrete S. 2007. The Humboldt current system of northern and central Chile.

Thrush S.F., Hewitt J.E., Funnell G.A., et al. 2001. Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. Mar. Ecol. Prog. Ser. 223: 277-286.
https://doi.org/10.3354/meps223277

Umanzor S., Ladah L., Calderon-Aguilera L.E., Zertuche-González J.A. 2019. Testing the relative importance of intertidal seaweeds as ecosystem engineers across tidal heights. J. Exp. Mar. Biol. 511: 100-107
https://doi.org/10.1016/j.jembe.2018.11.008

Vásquez J.A., Vega J.A. 2001. *Chondracanthus chamissoi* (Rhodophyta, Gigartinales) in northern Chile: ecological aspects for management of wild populations. J. Appl. Phycol. 13: 267-277.

Vásquez J.A., Vega J.M.A. 2005. Macro invertebrados asociados a discos de adhesión de algas pardas: biodiversidad de comunidades discretas como indicadora de perturbaciones locales y de gran escala. In: E. Figueroa (ed) Biodiversidad Marina: Valoración, Uso y Perspectivas. ¿Hacia dónde va Chile? Santiago, Chile: Ediciones Universitaria, 429-450

Vásquez N., Guerra García J.M., Thiel M., Lancellotti D.A. 2003. The distribution of littoral caprellids (Crustacea: Amphipoda: Caprellidea) along the Pacific coast of continental Chile. Rev. Chil. Hist. Nat. 76: 297-311.
https://doi.org/10.4067/S0716-078X2003000200014

Witman J.D., Dayton P.K. 2001. Rocky subtidal communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates Inc, Sunderland. 339 - 366.

Wolff M., Alarcón E. 1993. Structure of a scallop *Argopecten purpuratus* (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in northern Chile. J. SheIIfish Res. 12: 295-304.

Wright J.T., Byers J.E., DeVore J. L., Sotka E.E. 2014. Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology, 95: 2699-2706.
https://doi.org/10.1890/14-0127.1