INTRODUCTION

The bipolar-antitropically distributed *Macrocystis pyrifera* (L.) C. Agardh kelp forest is a characteristic element of the Magellan region, which in Argentina extends along the south Atlantic from Península de Valdés to Tierra del Fuego (Kühnemann, 1970).

Like other macroalgae, this species serves as substratum to a great number of organisms. Previous studies on the fauna associated with *Macrocystis pyrifera* were carried out at the Patagonian locality of Puerto Deseado (Santa Cruz) by Elías (1981), Kreiboehm and Escofet (1985), López Gappa et al. (1982) and Pallares and Hall (1974), among others.

For the Magellan region, Darwin (1889) made the first observations of the great variety of organisms that live on *Macrocystis pyrifera* of the Straits of Magellan during his trip on the "H.M.S. Beagle". Other recent investigations on the communities associated with this species were also made at the...

The main objectives of this work have been to recognize the different taxa associated with holdfasts and fronds of the macroalga *Macrocystis pyrifera* surrounding Ushuaia, at Tierra del Fuego Island in the Argentinian sector, and to detect temporal and spatial changes in its community structure.

**MATERIAL AND METHODS**

**Study area**

The material studied was collected in the forests of *Macrocystis pyrifera* within a sector of the north coast of the Beagle Channel (54°00'S, 68°20'W; Fig. 1). The studied area was divided into two zones. The western zone, which comprises Bahía Ensenada, Isla Dos Lomos and Islas Bridges, is called here “Area 1”. The eastern zone, which includes Bahía Ushuaia and a sector adjacent to Isla Casco, is named “Area 2”. Water temperature ranges between 6.0 (winter) and 8.9 °C (summer) in Bahía Ensenada and between 5.9 and 8.9 °C in Bahía Ushuaia, respectively (Quirós *et al.*, 1993).

With respect to winds, Area 1 is more exposed to westerly winds than Area 2, which is protected by the presence of the Península Ushuaia. A more detailed description of the physical characteristics of the region is provided by Derrotero Argentino (1981). In relation to nutrients, Bahía Ushuaia is characterized by a high deposition of organic matter since it is a harbour and Ushuaia’s waste outlet. Oxygen level ranges between 8.3 and 8.8 mg/l in Bahía Ensenada and between 8.6 and 9.2 in Bahía Ushuaia (Quirós *et al.*, 1993).

**Sampling design**

Surveys were conducted during 9 seasonal samplings, throughout a 1-year study between June 1995 and July 1996. A total of 43 samples were obtained randomly, at depths ranging from 2 to 10 meters, within the considered area. Field collections were made by means of three methods of sampling: SCUBA diving; hand collection from a rubber boat; or the collecting of fresh plants recently dragged by the currents onto the shores. Each sample consisted of a plant or part of it (holdfast or fronds). Following extraction, the holdfast of each plant was separated (cut off) from the fronds to avoid the mixing of the respective fauna. Immediately, each sample was placed in plastic bags in order to reduce loss of animals. In the laboratory, the different samples were weighed. Plants with holdfast and non-holdfast parts weighed between 1.8 and 3.6 kg. Plants without holdfasts weighed between 0.5 and 15.0 kg. The maximum weight of 15.3 kg corresponds to a holdfast obtained from Islas Bridges (Area 1). Specimens were maintained under laboratory conditions (aquaria) for few days. After counting, a great part of the specimens were returned alive to the sea, but some taxa were taken for closer determination and fixed in a 4% formaldehyde solution (Annelida, Nemertea) or in a 40% alcohol solution (the remaining groups) according to Boltovskoy (1981).
Identification of taxa

The fauna was identified by means of systematic catalogues (Bernasconi, 1953, 1964; Bernasconi and D'Agostino, 1977; Castellanos, 1988; Gordillo, 1995; Hernandez and Tablado, 1987; López Gappa, 1975; Ringuet, 1969) and the help of specialists on the different taxonomic groups (see acknowledgments). The different taxa were identified to the species level whenever possible. No attempt was made to identify Porifera to species.

Analyses

Diversity

To document temporal and spatial changes in the structure of the invertebrates inhabiting the *Macrocystis pyrifera* kelps and to detect variations of the fauna associated to different sectors of a plant (holdfast and fronds), the same number of plants was considered for each treatment. On this basis we compared the taxa associated to *Macrocystis pyrifera* in order to establish the existence of: (a) environmental variations, comparing two differently exposed areas (i.e, 9 samples from Area 1 vs. 9 samples from Area 2); (b) seasonal or temporal patterns (autumn-winter period and spring-summer period; N=21) and (c) ecological differences based on the parts of the plant (frond and holdfast; N=17). Statistical analysis of diversity was performed using 3 diversity indices: the Shannon-Wiener index (Magurran, 1988); the Equitability index (Odum, 1972); and the Dominance index (Begon et al., 1987). The significance of differences in diversity measures between compared sets of data within each treatment was assessed with the Krustal-Wallis non-parametric test (Miller et al., 1992). Taking into account that the indices above do not include colonial groups (Porifera, Bryozoa and Cirripedia), another Diversity index, used previously by Martínez (1988), was considered to estimate the relative taxa richness of the fauna under study. This index is given by the equation (number of taxa in each locality / total number of taxa) * 100.

Relative abundance

The relative abundance of each group was calculated on the base of the numerical proportion of each taxon/total number of specimens. In this quantitative analysis the colonial taxa were excluded.

Trophic analysis

In addition, for trophic analysis, individual species were grouped into larger groups based on trophic characteristics. Species were classified as producers, suspension feeders, browsers, carnivores and detritus feeders. Based on our data, and previous information on the species associated with holdfasts (Ojeda and Santelices, 1984) and non-holdfasts (Castilla, 1985), a trophic web of the *Macrocystis pyrifera* community from the Beagle Channel is described.

Size frequency distribution of Gaimardia trapesina

Finally, the size-frequency distribution of the bivalve *Gaimardia trapesina* was calculated since the species was -a priori- recognized as extremely abundant as an attached form of the fronds of this kelp. Specimens of *Gaimardia trapesina* were measured in length and height with a caliper to 0.1 mm accuracy. Size frequency distribution of this bivalve was estimated by height, using arbitrarily age class groupings: Class A (< 5 mm), Class B (5 to 10 mm) and Class C (>10 to 15 mm).

RESULTS

Species richness and diversity indices

A total of 68 taxa representing 7 phyla associated with *Macrocystis pyrifera* were recorded in this study (Table 1). Mollusca was the most species-rich group (22 species) with three classes (Gastropoda, Bivalvia and Amphineura) contributing with 12, 8 and 2 species, respectively. Crustacea was the next most species-rich group (15 species), with Amphipoda (7 species) contributing the greatest number of taxa within this phylum, followed by
Isopoda (4 species), Decapoda (3 species) and Cirripedia (1 species). Polychaeta contributed with 10 species to the total taxa collected. Echinodermata contributed with 7 species, with Asteroidea (3 species), Ophiuroidea (2 species), Echinoidea (1 species) and Holothuroidea (1 species). Bryozoa also contributed with 7 species. Taxa which contributed with minor number of species were Algae (5 species) and Nemertea (2 species). Porifera were not considered here because the taxonomy of this group was not analyzed. Figure 2 shows variations in species richness according to the parts of the plant (A), to different localities (B), and to seasonal periods (C).

In relation to diversity indices, statistically significant differences were obtained when comparing the parts of the plant and two different environments (Table 2). When the parts of the plant were considered separately, diversity indices show that holdfasts exhibit a higher diversity of taxa compared to the fronds. When considering different environmental conditions, a comparison between both localities studied showed higher diversity values for Area 1. Finally, a seasonal comparison of the invertebrates based on the Shannon Index shows a higher diversity value for the autumn-winter period, but using another diversity index indicating taxa richness

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total of ind.</th>
<th>Diversity</th>
<th>Dominance</th>
<th>Equitability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parts of the plant</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fronds</td>
<td>(N=17)</td>
<td>7026</td>
<td>1.68 (*)</td>
<td>0.43 (*)</td>
</tr>
<tr>
<td>Holdfasts</td>
<td>(N=17)</td>
<td>1930</td>
<td>2.21 (*)</td>
<td>0.41 (*)</td>
</tr>
<tr>
<td>Different environments</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area 1</td>
<td>(N=9)</td>
<td>596</td>
<td>3.12 (*)</td>
<td>0.15 (*)</td>
</tr>
<tr>
<td>Area 2</td>
<td>(N=9)</td>
<td>12855</td>
<td>1.35 (*)</td>
<td>0.53 (*)</td>
</tr>
<tr>
<td>Seasonal periods</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring/Summer</td>
<td>(N=21)</td>
<td>13674</td>
<td>1.59</td>
<td>0.48</td>
</tr>
<tr>
<td>Autumn/Winter</td>
<td>(N=21)</td>
<td>794</td>
<td>2.63</td>
<td>0.27</td>
</tr>
</tbody>
</table>

(*) significant differences between comparisons within the considered treatment (Kruskal-Wallis test).
Table 3. – Martínez (1988) diversity index (colonial taxa included).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Diversity index</th>
<th>Number of taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holdfasts</td>
<td>78.26</td>
<td>54</td>
</tr>
<tr>
<td>Fronds</td>
<td>52.17</td>
<td>36</td>
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<tr>
<td>Area 1</td>
<td>91.30</td>
<td>63</td>
</tr>
<tr>
<td>Area 2</td>
<td>56.52</td>
<td>39</td>
</tr>
<tr>
<td>Spring/Summer</td>
<td>88.40</td>
<td>61</td>
</tr>
<tr>
<td>Autumn/Winter</td>
<td>53.62</td>
<td>37</td>
</tr>
</tbody>
</table>

When considering the fauna associated with different parts of the plant, results show that the fronds (N=22) were dominated by Mollusca (46.0%) with 14 species. The numerically dominant species comprised Gaimardia trapesina (16.2%); Mytilus edulis chilensis (6.6%); Margarella violacea (5.3%); Nacella mytelina (5.0%) and Laevilitorina caliginosa (4.6%). Amphipoda occupies the second place in abundance (41.33%) with Paramphitoe femorata as the main taxa. Groups absent on the fronds were Nemertea, Ophiuroidea and Holothuroidea. Holdfasts (N= 17) were dominated by Polychaeta (33.4%), followed by Mollusca (25.4%; 21 spp.) with Trophon geversianus (6.1%) as the main taxon. Other major groups were Isopoda (19.0%) and Echi-noidea (6.4%) with one species, Pseudochinus mag-ellanicus. Continuing with Mollusca, the bivalve Zygochlamys patagonica appeared only on the fronds. Gaimardia trapesina is well known as a typical species of the fronds, but appeared in very low proportion within the holdfasts (0.9%). Some taxa exclusively on the holdfasts were Trophon geversianus, Calyptacta pileolus, Crepitapetla dilatata, Nacella deaurlata, Nacella magellanica, Tawera gayi, Brachidontes purpuratus, Limatula pygmaea and Plaxiphora sp.

A temporal comparison of the invertebrates showed that Mollusca (41.26%, 13 spp.) and Amphipoda (36.0%) dominate during the autumn-winter period (N=9), but a more varied fauna consisting of Mollusca (30.5%; 28 spp.), Amphipoda (25.4%), Polychaeta (18.0%) and Isopoda (16.8%) characterize the spring-summer period (N=21). Some absent major groups in the autumn-winter period were Holothuroidea, Isopoda and Nemertea. Finally, when comparing Area 1 (Ensenada) with Area 2 (Ushuaia), data show that in Area 1 (N=21) Mollusca was the dominant group, with 21 species, constituting 30.5% of the total. Amphipoda, and then Polychaeta were the next most abundant groups, contributing 23.6% and 21.1%, respectively. In Area 2 (N=9), Amphipoda (40.2%) is the most abundant group, followed by Mollusca (35.5%; 12 spp.), Isopoda (15.8%) and Polychaeta (4.9%). Entire groups like Holothuroidea, Ophiuroidea, Nemertea and Algae are absent in this area. The index of presence always showed Mollusca as the best represented group. Excluding Mollusca, when the parts of the plants are considered, fronds are best represented by Amphipoda (3 in the scale) and holdfasts (2 in the scale) by Nemertea, Spirobridae, Isopoda, Amphipoda and the sea-urchin Pseudochinus magellanicas. Considering the two areas, Area 1 is best represented by Spirobridae, Amphipoda and Pseudochinus magellanicas. In Area 2, Amphipoda exhibits the highest value (3 in the scale) followed by Isopoda (2 in the scale).

Fig. 2. – Species richness (percent share) of major groups. Comparison between holdfasts and fronds (A); between Bahía Ushuaia and Bahía Ensenada (B); and between spring/summer and autumn/ winter period (C).

Relative abundance

When considering the fauna associated with different parts of the plant, results show that the fronds (N=22) were dominated by Mollusca (46.0%) with 14 species. The numerically dominant species comprised Gaimardia trapesina (16.2%); Mytilus edulis chilensis (6.6%); Margarella violacea (5.3%); Nacella mytelina (5.0%) and Laevilitorina caliginosa (4.6%). Amphipoda occupies the second place in abundance (41.33%) with Paramphitoe femorata as the main taxa. Groups absent on the fronds were Nemertea, Ophiuroidea and Holothuroidea. Holdfasts (N= 17) were dominated by Polychaeta (33.4%), followed by Mollusca (25.4%; 21 spp.) with Trophon geversianus (6.1%) as the main taxon. Other major groups were Isopoda (19.0%) and Echi-noidea (6.4%) with one species, Pseudochinus mag-
Finally, a seasonal comparison using the Index of presence showed that Amphipoda exhibit the highest value of 3 in the two periods compared.

**Trophic relationships**

Figure 3 shows a generalized trophic web that includes 20 taxa and taxonomic groups of invertebrates. Carnivores were best represented by asteroids (Cosmasterias lurida (Philippi, 1858), Anasterias spp.) and gastropods. (Trophon spp.); herbivores included echinoids (Pseudochinus magellanicus), amphipods, chitons (Plaxiphora spp.) and several species of gastropods (Fissurella orients, Nacella mytelina, Creippatella dilatata, Margareella violacea). Suspension feeders belonged to diverse taxonomic groups (Porifera, Spirorbidae, Bivalvia, Cirripedia). Finally, detritus feeders involved isopods (Exosphaeroma spp.), decapods (Halicarcinus planatus), gastropods (Pareuthria plumbea), ophiuroid (Ophiophragmus chilensis), polychaetes and nemertines.

**Size-frequency distribution of Gaimardia trapesina**

Among a total of 500 specimens of Gaimardia trapesina counted on the fronds of one single plant of 1.9 kg, Class C with large specimens was the most abundant (N=200-250), followed by Class B with individuals of intermediate size (N=200-150) and Class A represented by juvenile specimens.
CONCLUSIONS AND DISCUSSION

The fauna associated to *Macrocystis pyrifera* from the Beagle Channel showed variations in faunal composition associated with holdfasts and fronds, and variations due to different environmental conditions and seasonal variations in its community structure.

Based on the above results, Mollusca are the best represented taxonomic group, followed by the Crustacea, Polychaeta, Echinodermata and Bryozoa, besides other minor groups.

According to the parts of the plants the major diversity of taxa was observed in the holdfasts with dominance of Polychaeta, Mollusca, Isopoda and Nemertea. Ojeda and Santelices (1984) mention that the general roles played by holdfasts of kelp-like Phaeophyta with respect to the fauna which inhabits them include those of mechanical shelter (wave impact), refuge from predators and nursery grounds. Besides Porifera, three groups -Nemertea, Ophiuroidea and Holothuroidea- were found exclusively associated with holdfasts. Within Isopoda, *Cassidinopsis emarginata* and *Cymodocella eatoni* appeared only on the fronds, but *Iais* sp. and *Exospheroma* sp. were found exclusively within the holdfasts. Taking into account the trophic groups, the holdfast was characterized by the presence of different functional groups, with detritivorous and carnivorous taxa well represented, while filter species such as the bivalve *Gaimardia trapesina* and browsers such as the amphipod *Paramphitoe femorata* found shelter on the fronds. A reason for this differential distribution could be the fact that fronds give a great surface of adherence for *Gaimardia trapesina*, and consequently, a major availability of food; while for the amphipods the fronds offer a great surface to browse.

As regards seasons, the maximum values of abundance and diversity (when colonial and non-colonial taxa are included) occurred in the spring-summer period, while in the autumn-winter period entire groups such as Nemertea, Polyplacophora, Isopoda, Cirripedia, Asteroidea and Holothuroidea disappeared. A temporal comparison of the invertebrate biomass values made by Ojeda and Santelices (1984) showed that in spring the abundance of invertebrates in holdfasts of *Macrocystis pyrifera* was significantly greater than in other seasons. These authors relate the phenomenon of seasonal migration of dominant taxa such as the sea-urchin *Pseudechinus magallanicus*, the crabs *Pagurus forcepts* H. Milne Edwards, 1836 and *Halicarcinus planatus* and the asteroid *Anasterias antarctica* to the reproductive behaviour of these taxa in the sense that holdfasts can offer refuge for spawning, reproduction or shelter for oviparous females and their embryos. Following these authors, lower values of abundance were found in summer and intermediate values occurred in autumn and winter. In that sense, a direct comparison with our data is not possible since we discriminate between spring-summer season and the autumn-winter period, with higher values during the spring-summer period. But, taking into account species richness and diversity, highest diversity values were found in the autumn-winter period. These results are quite different when colonial taxa are included, with highest taxa richness values for the spring-summer period. If only the Mollusca are considered, since they are the best rep-
resented group in abundance and diversity of species, we observed that—with the exception of Gaimardia trapesina living on the fronds— the spring-summer period was characterized by the dominance of juvenile specimens, specially associated with the holdfasts. Thus, we postulate that seasonal changes are in part related with seasonal changes of the fauna associated with the holdfasts. Besides a refuge related to reproductive behaviour of some taxa and groups, holdfasts may also represent juvenile recruitment areas for different species of molluscs that use other substrata existing outside the holdfast during the growth period (e.g. Mytilus edulis chilensis).

According to the localities, detritivorous organisms are well represented at Bahía Ushuaia (Area 2) which is characterized by a great deposition of nutrients; while at Bahía Ensenada (Area 1), the filtering taxonomic groups predominate. These differences could be related with the presence of Península Ushuaia, which protects Bahía Ushuaia from western winds; for that reason the water mass is less turbulent and relatively quieter. In addition, this bay is a harbour and Ushuaia’s waste outlet. On the other hand, Bahía Ensenada is more exposed to the western winds, and therefore it is characterized by turbulent waters, resulting in lesser sediment deposition and an increased food availability, which benefits filtering species.

Trophic analysis showed that different major taxonomic groups (at least 8 phyla) interact conforming different functional trophic groups in a complex food web associated to Macrocystis pyrifera. Asteroids such as Cosmasterias lurida and other sea stars (Anasterias spp.) were the most notable consumers in the second trophic level. Similar to observations made by Castilla (1985) in Puerto Toro, Navarino (Beagle Channel), herbivore first-level consumers were diverse in Macrocystis pyrifera kelp surrounding Ushuaia. The main herbivores were the sea urchin Pseudechinus magellanicus, amphipods and several species of gastropods (i.e. Fissurella oriens, Nacella mytelina, Crepipatella dilatata, Margarella violacea) and chitons (Plaxiphora sp.). In that sense Castilla (1985) mentioned another species of sea urchin, Loxechinus albus (Molina, 1782), but this species was not recorded in our study. The asteroid Cosmasterias lurida also preys on a group of second-trophic level carnivore snails (Trophon spp.), as was previously mentioned by Castilla (1985); however, these snails are main predators of mussels, as was observed by divers in the field and under laboratory conditions. Trophon spp. and related genera also prey, among others, on the mussels Aulacomya atra and the barnacle Chthamalus sp, such as different other bivalves including Hiattella solid and Mytilus edulis chilensis. Gaimardia trapesina appears to be a potential prey of the sea stars (Castilla, 1985), but it was also observed in Bahía Ushuaia consumed by sea gulls (Larus dominicanus Licht, 1823). The trophic web also contains a number of filter-feeding species belonging to different taxonomic groups (Porifera, Spirorbidae, Bivalvia, Cirripedia). Detritus feeders, such as the isopod Exosphaeroma sp., the crab Halicarcinus planatus, the gastropod Pareuthria plumbea, the ophiuroid Ophiofragmus chilensis, Polychaeta and Nemertea, among other groups, represent another important group.

Finally, our results show that the fronds of Macrocystis pyrifera constitute a main substrate for the population of the bivalve Gaimardia trapesina for which at least three size-classes that represent different ages are recognized. Following Aracena et al. (1997), individuals belonging to Class A are juvenile specimens. Very little published information is available with regard to the biology of this species, but it is known that Gaimardia trapesina broods its young and has no-free living larval stage (Helmuth et al., 1994). In relation to geographic distribution patterns, this Subantarctic bivalve is able to disperse over long distances by means of rafting on Macrocystis pyrifera (Figueiras, 1963; Helmuth et al., 1994).

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BIOTA ASSOCIATED WITH MACROCYSTIS PYRIFERA 191