Hydrobiologia (2011) 673:205–214
DOI 10.1007/s10750-011-0780-7

PRIMARY RESEARCH PAPER

Latitudinal gradients in macroalgal biodiversity in the Southwest Atlantic between 36 and 55°S

María G. Liuzzi · Juan López Gappa · María L. Piriz

Received: 21 March 2011 / Revised: 17 May 2011 / Accepted: 21 May 2011 / Published online: 8 June 2011

Abstract Different groups of marine benthic organisms show contrasting latitudinal patterns of biodiversity. The widely accepted paradigm of increasing biodiversity towards the tropics does not seem to be valid for macroalgal floras of the Southern Hemisphere. We compiled a database summarizing the distributional ranges of macroalgae along the coast of Argentina to test whether biodiversity decreases towards lower latitudes, as in the Pacific coast of South America, and whether breaking points in the geographical distribution can be recognized in one or more areas of the Southwest Atlantic south of 36°S. We found a clear trend of decreasing biodiversity with decreasing latitude. The interpretation of some biodiversity declines is confounded by changes in the intensity of the sampling effort. A 51% reduction in algal species richness between 42 and 41°S coincides with the boundary between the Argentine and Magellanic Zoogeographic Provinces. This sharp breaking point is related to a thermal anomaly caused by long residence times of water masses within San Matías Gulf, suggesting an upper thermal tolerance limit for most Antarctic/sub-Antarctic seaweeds. A further reduction occurs at 38–37°S. This breaking point can be explained by the disappearance of suitable hard substrata, since rocky outcrops give place to wide extensions of sandy beaches. The impoverished algal assemblage inhabiting the northern coast of Argentina is mainly related to the reduction or disappearance of the Antarctic/sub-Antarctic floristic component. This area is characterised by a predominance of widely distributed species, Chlorophytes and opportunistic filamentous or foliose algae.

Keywords Biogeography · Species richness · Sampling effort · Algal functional groups · Breaking points · Argentina

Electronic supplementary material The online version of this article (doi:10.1007/s10750-011-0780-7) contains supplementary material, which is available to authorized users.

Handling editor: Vasilis Valavanis

M. G. Liuzzi · J. López Gappa (✉)
Museo Argentino de Ciencias Naturales, Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina
e-mail: lgappa@macn.gov.ar

M. L. Piriz
Morgan 2455, U9120AFM Puerto Madryn, Chubut, Argentina

Introduction

One of the most striking characteristics of life in terrestrial ecosystems is the gradient of increasing biodiversity from the poles to the equator (Brown & Lomolino, 1998; Gaston, 2000). In the marine environments of the Northern Hemisphere, species richness also increases from the Arctic to the tropics (e.g. Roy et al., 1998, 2000), but there does not seem to be a similar cline in the Southern Hemisphere (Clarke, 1992), as biodiversity is high in Australia (Crame, 2000; Smale et al., 2011) and also at higher latitudes (Gray, 1997). A long history of geographical isolation may account for the relatively high species richness of Antarctica (Gray, 2001). Different groups of marine benthic invertebrates show contrasting latitudinal patterns of biodiversity along the coasts of southern South America. Thus, diversity decreases with increasing latitude in groups which exhibit planktonic larval development (Astorga et al., 2003), but increases poleward in direct developers (López Gappa et al., 2006; Fernández et al., 2009).

A study on global seaweed diversity found that there is no evidence of a peak in species numbers in tropical latitudes, although polar floras are species poor (Bolton, 1994). A comparison amongst 21 Antarctic/sub-Antarctic algal floras showed that species diversity is considerably greater on the coasts of Patagonia, Tierra del Fuego and the Malvinas/Falkland islands than elsewhere in the Southern Ocean (John et al., 1994). Phytogeographical characterizations of the temperate coast of Pacific South America (Santelices, 1980; Santelices & Meneses, 2000) showed that the number of benthic seaweed species increases to the south, in sharp contrast to the widely accepted paradigm of increasing biodiversity towards the tropics. On the Southwest Atlantic, the benthic algal flora of Uruguay (Coll & Oliveira, 1999) was regarded as poor and transitional, with a majority of eurythermic and euryhaline taxa and a relatively lower representation of brown algae. A sketch of the marine vegetation along the coast of Argentina showed that a clear phytogeographical transition separates two distinct algal assemblages at 42°S (Kühnemann, 1972). Almost one hundred taxonomic articles on Argentine marine benthic macroalgae have been published during the last 38 years (Online Resource 1), and a distribution atlas is currently available online (Boraso & Zaixso, 2008). Therefore, a more complete and accurate checklist can be used for investigating whether latitudinal gradients in macroalgal biodiversity can be recognised along the coast of Argentina.

During this study, we analyse (1) whether macroalgal species richness decreases towards lower latitudes as in the Pacific coast of South America, and (2) whether breaking points or discontinuities in the geographical distribution can be recognised in one or more areas of the Southwest Atlantic south of 36°S. We also discuss the possible influence of changes in the sampling effort on the observed phytogeographical patterns.

Materials and methods

The study area encompasses the coast of Argentina from 36 to 55°S (Fig. 1). The Malvinas/Falkland Islands and the Chilean islands located south of the Beagle Channel were not included in this survey. The geographical distribution of species was obtained from various sources: (1) The main source was an online atlas of the marine macroalgae of Argentina (Boraso & Zaixso, 2008), which summarises a great amount of published and unpublished taxonomic and distributional information gathered by Alicia Boraso during many phycological surveys along the Argentine coast. (2) Since approximately one fourth of the seaweed species occurring in Argentina were not dealt with by Boraso & Zaixso (2008), distributional data of these taxa were obtained from the taxonomic literature (Online Resource 2). (3) The distribution of 27 species was extended based on unpublished information on seaweed collections made by one of the authors (MLP). (4) The distribution of other six species was also complemented by examining material deposited in the phycological herbarium of the *Museo Argentino de Ciencias Naturales* (BA). A database was compiled summarising the distributional ranges of all macroalgae occurring along the coast of Argentina (Online Resource 2). For most species, a continuous (i.e. interpolated) distribution between scattered records in Argentina has been assumed (see also Boraso & Zaixso, 2008), with the exception of a few cases of conspicuous species where a disjunct distribution was positively known. Seaweeds recorded for the study area without precise distributional data [e.g. *Cladophora lehmanniana* (Lindenberg) Kützing, *Gymnogongrus griffithsiae* (Turner) Martius, *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq, *Rhodymenia corallina* (Bory de Saint-Vincent) Greville, *Ulothrix subflaccida* Wille; see Boraso et al., 2004], and several species of microscopic green and red algae [e.g. *Coccomyxa parasitica* R. N. Stevenson & G. R. South, *Entocladia maculans* (A. D. Cotton) Papenfuss, *Porphyridium purpureum* (Bory de Saint-Vincent) K. M. Drew &

R. Ross, *Prasinocladus marinus* (Cienkowski) Waern] were not included in this study. We also ignored species of uncertain status or whose presence in Argentina was dubious, most of them described or recorded for the study area before 1930 but not dealt with in modern taxonomic articles. The validity status, generic placement and synonymy of each species were consulted in Algaebase (www.algaebase.org, accessed August 2010).

Latitudinal changes in the sampling effort were assessed by recording all the localities where the examined material was collected in 105 articles on Argentine seaweeds published between 1939 and 2008 (Online Resource 1).

The sampling units were lists of seaweed species for each of the 19 degrees of latitude. Localities of collection were allocated to the corresponding degree of latitude after truncating minutes and seconds. For instance, 47°S should be interpreted as an interval comprising all the localities between 47°00′00″ and 47°59′59″.

Following previous phytogeographical studies (Santelices, 1980; Meneses & Santelices, 2000; Santelices & Meneses, 2000), we analysed the world

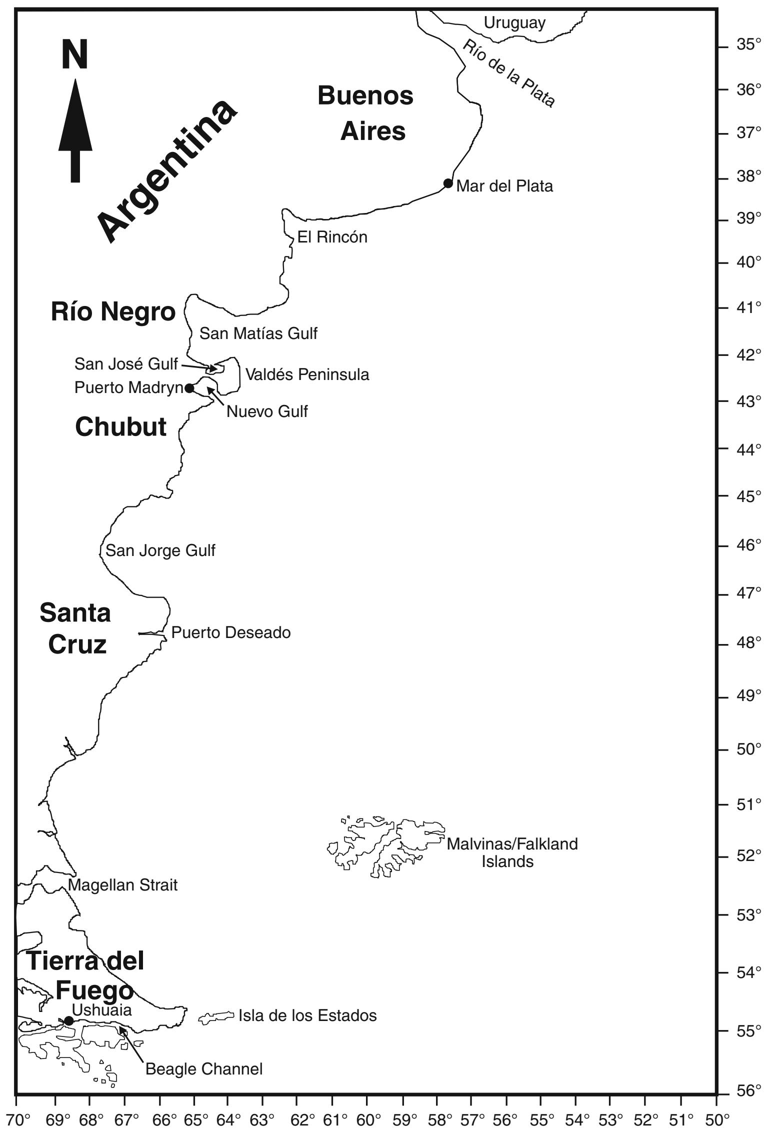

Fig. 1 Study area in the Southwest Atlantic between 36 and 55°S. Geographical references cited in the text are indicated

distribution of each species (in this study taken from Algaebase) and allocated them to one of the following floristic components: wide distribution, Antarctic/sub-Antarctic, bipolar, tropical/sub-tropical and endemic.

Similarities amongst degrees of latitude were calculated with the Sørensen index based on species presence/absence data. A cluster analysis using arithmetic averages was then performed using the PRIMER package (Clarke & Warwick, 2001).

The *EstimateS* software (Colwell, 1997) was utilized to assess taxonomic turnover (beta diversity, Ellingsen, 2001) by calculating the number of shared species between every degree of latitude and the next.

Based on Steneck & Dethier (1994), each algal species was assigned to a functional group. Microscopic algae were not taken into account. All foliose algae, whether corticated or not, were allocated to the same group. Therefore, the functional groups dealt with in this study were as follows: (1) filamentous algae, (2) foliose algae, (3) corticated macrophytes, (4) leathery macrophytes, (5) articulated calcareous algae, and (6) crustose algae. Seaweeds composed of filamentous thalli with several rows of pericentral cells but mainly uncorticated (e.g. *Polysiphonia*) were regarded as filamentous.

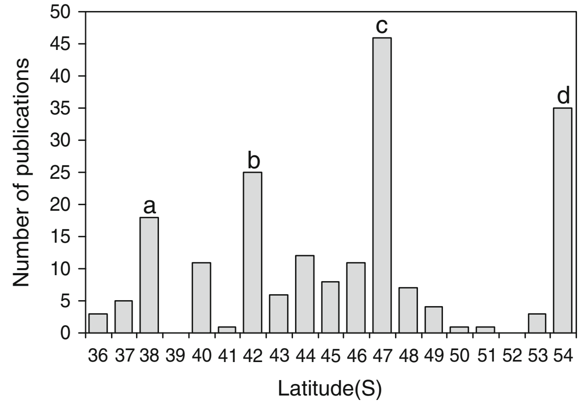

Fig. 2 Latitudinal changes in the sampling effort along the coast of Argentina based on the material examined in 105 phycological articles published between 1939 and 2008. *Letters* show the location of the most important marine research stations used as bases for collection of macroalgal material: (a) *Instituto de Biología Marina*, currently *Instituto Nacional de Investigación y Desarrollo Pesquero*, (b) *Centro Nacional Patagónico*, (c) *Centro de Investigación de Biología Marina* (CIBIMA), and (d) CIBIMA and *Centro Austral de Investigaciones Científicas*

Results

The sampling effort has been very heterogeneous. It is clearly related to the location of marine research stations along the coast of Argentina, attaining maximum intensity at four latitudes: 38, 42, 47 and 54°S (Fig. 2). By contrast, our search in the literature showed that no algal material had been published with regard to relatively remote areas located far away from the urban centres or marine stations, (e.g. 39 and 52°S, Fig. 2).

A total of 222 macroalgal species belonging to 139 genera have been recorded for Argentina (48 Chlorophycophyta, 58 Heterokontophyta and 116 Rhodophycophyta, Online Resource 2). A clear trend of decreasing biodiversity with decreasing latitude can be seen (Fig. 3), with the highest species richness in Tierra del Fuego and southern Patagonia (54–45°S), and the lowest species richness along the coasts of Río Negro and Buenos Aires provinces (41–36°S). Critical changes in the number of species take place mainly in five coastal areas: (1) between 54 and 53°S, i.e. the transition between Beagle Channel–Isla de los Estados and the Atlantic coast of Tierra del Fuego; here, 26 species (16.6%, mainly Antarctic/sub-Antarctic crustose coralline algae) reach their northern distribution limit (Online Resource 2; Fig. 3). This decline is coincident with a sharp reduction in the sampling effort, which drops from 35 to just 3 articles based on collections of Fuegian seaweeds (Fig. 2). The number of species then remains more or less constant up to 48°S. (2) A slight increase in biodiversity can be seen at 47°S (Puerto Deseado), but then another decline occurs from 47 to 46°S, i.e. between Puerto Deseado and the southern half of San Jorge Gulf. Here, 31 species disappear (19.7%, Online Resource 2), together with another reduction in the sampling effort, which drops from 46 to 11 phycological articles based on material from this area. (3) Another impoverishment is observed from 45 to 44°S, i.e. in the transition from the northern half of San Jorge Gulf to the exposed coast of Chubut Province, where 21 further species are lost (16.2%, Online Resource 2). In this case, however, there is no reduction in the sampling effort, which increases from 8 to 12 articles based on material from this region (Fig. 2). (4) The most dramatical reduction in species richness occurs from 42 to 41°S, i.e. along the transition between Valdés Peninsula and San Matías Gulf. More than half the number of species reaching this point disappear [58 (50.9%), Online Resource 2] coincidentally with a sharp decrease in the sampling effort, which falls from 25 to just 1 article based on algae from this area (Fig. 2). The Antarctic/sub-Antarctic floristic component undergoes the most severe reduction at this breaking point (Fig. 3). (5) The last decline in species richness occurs from 38 to 37°S, i.e. in the transition between the quartzitic outcrops at Mar del Plata and wide expansions of sandy beaches extending to the north of this city, where 39 algal species disappear (84.8%, Online Resource 2). The sampling effort decreases from 18 to 5 articles based on material from this area (Fig. 2). Just five to eight seaweed species per degree of latitude are known between 38 and 36°S (Mar del Plata to Río de la Plata).

Changes in the proportion of different floristic components along the coast of Argentina are shown in Online Resource 3. There are just 14 (6.3%) endemic species. Their proportion remains almost constant from 54 to 38°S (Beagle Channel to Mar del Plata), but they disappear north of 38°S. The tropical/sub-tropical component is represented by just seven species (3.2%). It attains its highest percentage at 37°S, where only one species represents 13% of the total, since the remaining floristic groups become very scarce. The bipolar floristic component shows an intermediate abundance (36 species, 16.3%). Its proportion remains relatively constant along almost the whole study area, disappearing at 36°S. The widely distributed species are the second most important floristic group (73 species, 33.0%). This component is represented throughout the study area. It becomes dominant north of 45°S and comprises more than 70% of the macroalgal flora between 39 and 37°S. It is the only floristic group that persists at 36°S (Fig. 3; Online Resource 3). The Antarctic/sub-Antarctic component is the main floristic group of Argentina, being represented by 91 species (41.2%). It dominates along southern Patagonia and Tierra del Fuego, from 54 to 45°S (Beagle Channel to the northern end of San Jorge Gulf). This is a characteristically cold water group, undergoing two sharp reductions from 42 to 41°S, and from 40 to 39°S, and eventually disappearing at 37°S (Fig. 3; Online Resource 3).

Some interesting patterns can be recognised when the analysis of floristic groups is performed separately for each macroalgal phylum (Online Resource 3). No endemic species occur in the Chlorophycophyta (Online Resource 3). For green algae, a clear predominance of widely distributed species can be observed throughout the study area. On the contrary, in this case the Antarctic/sub-Antarctic component is poorly represented and disappears at 41°S. No Heterokontophyta with tropical/sub-tropical distribution are present along the coast of Argentina (Online Resource 3). For brown algae, the Antarctic/sub-Antarctic floristic component is the most diversified from 54 to 45°S (i.e. Tierra del Fuego to the northern end of San Jorge Gulf), then declining and

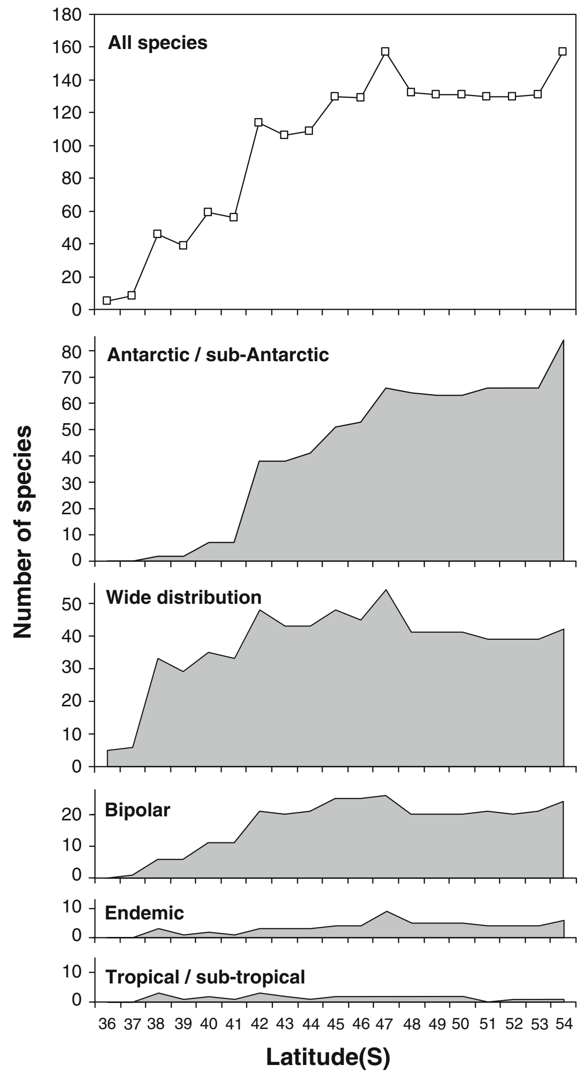

Fig. 3 Latitudinal gradient in the number of macroalgal species belonging to five floristic components along the coast of Argentina. Total number of species is shown in the *top panel*

eventually disappearing at 39°S. As the Rhodophycophyta is the most speciose macroalgal phylum (Online Resource 2), its latitudinal pattern of biodiversity is similar to that observed for the whole flora (Online Resource 3).

Latitudes were perfectly classified from north to south by cluster analysis based on species presence/absence data (Fig. 4). Three main groups were obtained at the 50% similarity level: (A) 36–37°S (sandy shores between Río de la Plata and Mar del Plata), showing the lowest algal biodiversity (mean: 6.5 species), (B) 38–41°S (Mar del Plata to San Matías Gulf), with a relatively low biodiversity (mean: 49.5 species), and (C) 42–54°S (Valdés Peninsula to Beagle Channel), with the highest number of species (mean: 129.8 species). The latter is further divided into two smaller subgroups at the 75% similarity level (Fig. 4): (C1) 42–46°S (Valdés Peninsula to the southern end of San Jorge Gulf; mean: 117.6 species), and (C2) 47–54°S (Puerto Deseado to Tierra del Fuego; mean: 137.4 species).

Taxonomic turnover, expressed as the number of species shared between each degree of latitude and the next, was maximum between 42 and 41°S, and between 38 and 37°S (Fig. 5).

The proportion of species belonging to the Chlorophycophyta (21.6%), Heterokontophyta (26.1%) and Rhodophycophyta (52.3%) showed relatively small variations along the study area except from 40 to 36°S, where the percentage of green algae increased at the expense of brown algae (Fig. 6).

There are 46 species (20.8%) whose distribution in Argentina is apparently restricted to just one degree of latitude (Online Resource 2). Most of them are Antarctic/sub-Antarctic species attaining the southern end of Tierra del Fuego (54°S).

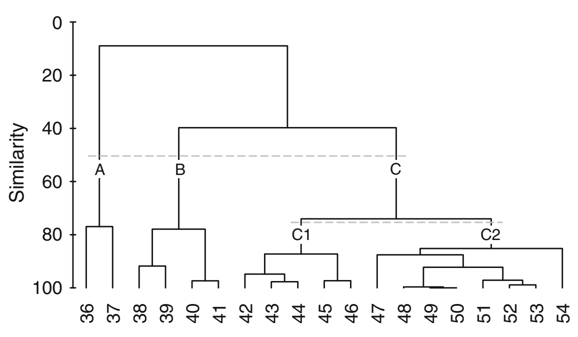

Fig. 4 Cluster analysis showing similarity amongst latitudes based on species presence/absence data. *Dashed lines* indicate similarity levels of 50 and 75%

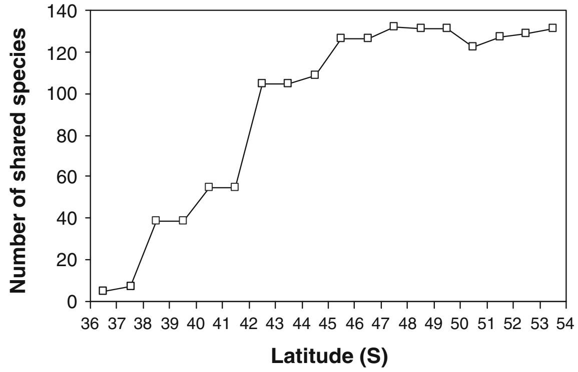

Fig. 5 Number of algal species shared between each degree of latitude and the next (taxonomic turnover)

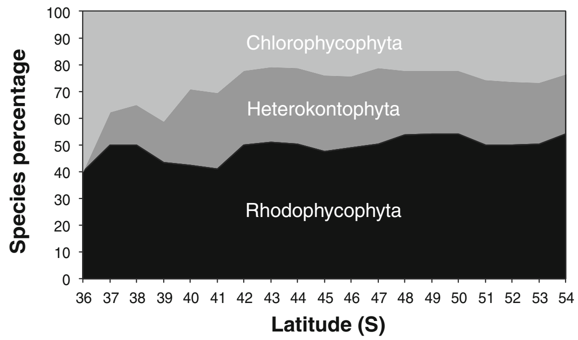

Fig. 6 Latitudinal changes in the percentage of Rhodophycophyta, Heterokontophyta and Chlorophycophyta along the coast of Argentina

Latitudinal changes in the proportion of functional groups along the study area are shown in Fig. 7. Filamentous algae (37%) are the best represented, reaching a maximum at 37°S due to the demise of other groups. Foliose algae are the second most important functional group (28%), also reaching its highest percentage along sandy beaches north of 38°S. Corticated macrophytes, the third most important group (19%), disappear north of 38°S. In spite of their ecological importance, the giant leathery macrophytes (kelps) belonging to the genera *Macrocystis*, *Lessonia*, *Durvillaea* and *Undaria* comprise just 2% of the species. The distribution of these species is probably controlled by temperature, as they are characteristically restricted to cold Patagonian waters, disappearing completely north of 42°S. With just 2% of the species, articulated calcareous algae achieve their maximum percentage in the impoverished algal assemblage found at 36°S, where they are represented just by *Jania rubens* (Linnaeus) J. V. Lamouroux. Crustose algae (12%) reach its maximum percentage at the southern end of the study area (54°S), also disappearing north of 38°S (Mar del Plata).

Discussion

The main conclusion from this study is the remarkable impoverishment of benthic macroalgal biodiversity from southern to northern latitudes along the coast of Argentina. A way to recognise to which extent a biodiversity decrease is real or it is caused by differences in the sampling effort, is to restrict the comparisons just to those latitudes where the sampling intensity has been high (54, 47, 42 and 38°S; Fig. 2). This exercise shows that algal species richness remains constant between 54 and 47°S. By contrast, 27% of the species are lost between 47 and 42°S, and almost 60% further species disappear between 42 and 38°S (Fig. 3). Therefore, it can be concluded that not only the Uruguayan macroalgal assemblages (Coll & Oliveira, 1999), but also those of Río Negro and Buenos Aires provinces should be regarded as impoverished. This pattern broadly agrees with the gradient seen on the Pacific coast of South America (Santelices & Marquet, 1998; Santelices & Meneses, 2000), where an increase in biodiversity was observed at 55–56°S due to a high number of Antarctic/sub-Antarctic taxa reaching their northern distribution limit at the Chilean archipelagos near Cape Horn. A similar trend occurs on the Atlantic coast, where several species inhabiting Antarctic or sub-Antarctic regions are present just up to 54°S. Data compiled in the present study, however, do not allow us to conclude to which extent this decrease has been overemphasised by the unequal distribution of the sampling effort. Most of the species disappearing north of 54°S are encrusting corallines, a group of red algae thoroughly studied by María Laura Mendoza, whose collections were abundant at 54°S but rarely reached 53°S (Online Resource 1). Further studies encompassing the whole Fuegian archipelago will be necessary to elucidate this issue.

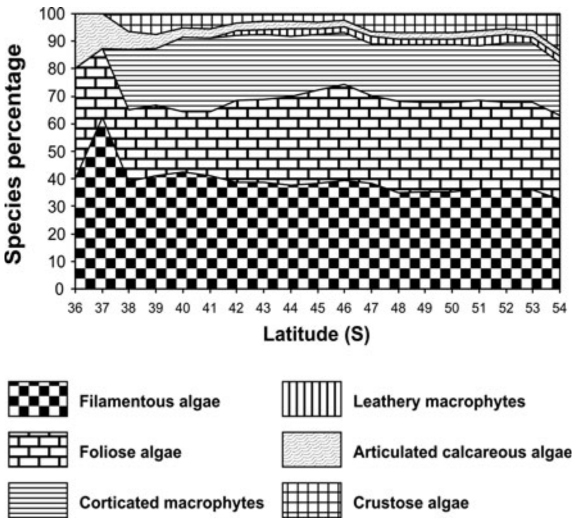

Fig. 7 Latitudinal changes in the percentage of macroalgal species belonging to different functional groups along the study area

The breaking point between 42 and 41°S is clearly evidenced by a remarkable decrease in algal biodiversity (Fig. 3), by the low number of taxa shared between adjacent degrees of latitude (Fig. 5) and also because these stretches of coast were classified in different clusters (Fig. 4). This discontinuity agrees with the boundary between the Argentine and Magellanic Provinces of marine zoologists (e.g. Boschi, 2000). Kühnemann (1972) was the first to show that a clear phytogeographical limit exists at 42°S, where he found the northernmost forest of the kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh in Argentina. He also noted that the number of macroalgal species was higher south than north of this latitude, but made no further analysis about this fact. *M. pyrifera* is an ecosystem engineer of utmost ecological importance, its giant forests providing refuge and substratum for a great variety of marine organisms (e.g. Moreno & Jara, 1984). Although the number of the published articles based on material from 41°S is low in comparison with that of 42°S, San Matías Gulf has been relatively well studied at 40°S (Fig. 2). Algae collected at 40°S (Piriz, unpubl. results) do not attain the species richness observed at 42°S (Fig. 3). In the same vein, a study of the subtidal macroalgal assemblages of San José Gulf (Boraso de Zaixso et al., 1999) showed that several common species along the coast of southern Patagonia do not reach this warm-temperate gulf (Boraso de Zaixso, 2007). An important breaking point in species composition at 42°S has also been found in the Pacific coast of South America (Meneses & Santelices, 2000).

The biodiversity reduction between 45 and 44°S is comparatively less noticeable than those observed elsewhere, but in this case, it cannot be confused by sampling bias, as the disappearance of 21 algal species (Online Resource 2) occurs simultaneously with a slight increase in the sampling effort (Fig. 2).

As has been discussed by some other authors (Parma et al., 1987; Boraso de Zaixso, 2007), the remarkable decrease in algal biodiversity that occurs from 38 to 37°S can be explained by the presence of quartzitic rocky outcrops at Mar del Plata (38°S) and the absence of suitable substrata for algal growth and persistence along a wide extension of sandy beaches between that resort and the southern margin of Río de la Plata (36–37°S). In this case, we believe that the low number of phycological articles based on material collected at 36–37°S is not due to sampling bias but to a real impoverishment of the algal assemblage, since the area is easily accessible and is not far away from marine research laboratories.

According to data compiled in this study, macroalgal diversity in Argentina is lower than in Chile (380 taxa, Santelices & Meneses, 2000), but higher than in Uruguay (72 taxa, Coll & Oliveira, 1999). No sound conclusions can be gained from this comparison, however, as this pattern is coincident with the degree of taxonomic knowledge of the marine algae in these countries. The percentage of species shared between Argentina and the impoverished Uruguayan flora (Coll & Oliveira, 1999) seems to be too low (30/72 taxa after controlling for synonyms, 41.7%). This small percentage may be real, although it also could be influenced, at least in part, by the fact that these floras were studied by different taxonomists (see e.g. Underwood & Fairweather, 1986).

In spite of its relative isolation from the main routes of maritime transport, the Southwest Atlantic Ocean has not escaped from the pervasive phenomenon of alien species invasions (Orensanz et al., 2002). With regard to benthic macroalgae, the best-studied case in the area is the appearance of *Undaria pinnatifida* (Harvey) Suringar in Nuevo Gulf (Casas & Piriz, 1996). This edible Asian kelp is progressively extending its southern distribution limit in Argentina (Martin & Cuevas, 2006), causing a dramatic decrease in species richness and diversity of native seaweeds (Casas et al., 2004). Furthermore, the sudden occurrence of unusually large amounts of *Anotrichium furcellatum* (J. Agardh) Baldock in stranded algal wrack (Boraso de Zaixso & Akselman, 2005) and the first notice of cast ashore thalli of *Sporochnus pedunculatus* (Hudson) C. Agardh in Río Negro Province (Boraso de Zaixso & Negri, 1996) suggest that more invasions of alien algae are to be expected in the future.

Different theories have been proposed to explain the latitudinal gradient in species richness (Pianka, 1966). We would like to discuss the inverse latitudinal pattern found in this study under three approaches: (1) tectonic history of southern South America and Antarctica, (2) availability of hard substrata, and (3) oceanographical processes and distribution of water masses along the coast of Argentina.

(1) Studies on the evolution of Cenozoic seaways in the circum-Antarctic region (Lawver & Gahagan, 2003) support the hypothesis that the Magellan biota entered the Southwest Atlantic during the Tertiary period after the Drake Passage opened to deep water circulation during the Eocene–Oligocene boundary ($\sim$31–32 Ma). A biogeographical analysis of the Miocene molluscan faunas of Argentina and Uruguay (Martínez & del Río, 2002) concluded that the Argentine Biogeographical Province (i.e. southern Brazil, Uruguay and the Argentine coast north of 42°S) should be regarded as a transitional assemblage between the Magellanic and Brazilian Biogeographical Provinces. According to that study, after the development of the cold Malvinas/Falkland Current, the dominant Caribbean elements became extinct or moved northwards. Thus, at the geological time scale, the Antarctic/sub-Antarctic component, which makes up the bulk of the macroalgal flora between 55 and 45°S, should be viewed as a relatively recent arrival to the southernmost sector of the Southwest Atlantic.

(2) Some authors (e.g. Kühnemann, 1972; Boraso de Zaixso, 2007) argued that substratum hardness, i.e. the distribution of igneous and sedimentary rocks, plays a major role in the reduction of algal biodiversity observed in Patagonia. As discussed above, we agree that the disappearance of suitable substrata is a critical factor explaining the impoverished algal assemblage north of 38°S, but in this case a

relatively sharp transition occurs between intertidal/subtidal rocky outcrops and sandy beaches. Distributional data compiled in this study do not support a key role of the substratum in the decrease of algal biodiversity along Patagonian shores. We found a major breaking point between 42 and 41°S, and a less important one between 45 and 44°S, a latitudinal range where hard substrata are relatively uniform, mainly consisting of sedimentary rock.

(3) The most likely hypothesis for the major breaking point between 42 and 41°S seems to be that this latitude represents an upper thermal tolerance limit for many Antarctic/sub-Antarctic algal species. This floristic component almost disappears along the transition between Valdés Peninsula and San Matías Gulf (Fig. 3; Online Resource 3), leaving an impoverished algal assemblage mainly composed of widely distributed or bipolar species. Coastal oceanographical studies off Argentina (reviewed in Guerrero & Piola, 1997) showed the occurrence of a thermal anomaly caused by long residence times of water masses within San Matías Gulf. Relative temperature and salinity maxima have also been recorded at El Rincón, a neighbouring coastal area off the southern sector of Buenos Aires Province (Guerrero & Piola, 1997).

The biodiversity decrease from southern to northern latitudes does not occur with the same intensity across algal phyla, floristic components or functional groups. The impoverished algal assemblage of the northern coast of Argentina is mainly related to the decrease or disappearance of the Antarctic/sub-Antarctic floristic component. On the contrary, this region is characterised by a predominance of widely distributed species, Chlorophytes and opportunistic filamentous or foliose algae.

Although we supplemented the literature data with unpublished records based on macroalgal collections and herbarium specimens, the checklist analysed in this study (Online Resource 2) should not be regarded as complete. Existing knowledge of Argentine macroalgae is fragmentary, and additional studies throughout the Southwest Atlantic coast south of 36°S are necessary to update the available information. New records for the study area are to be expected in the future, except perhaps for a few thoroughly sampled localities. Two phytogeographical characterizations of the Chilean coast separated by an interval of 20 years (Santelices, 1980; Santelices & Meneses, 2000) arrived at similar conclusions, although many floristic studies published between these dates had added a significant number of new findings for the Southeast Pacific. Therefore, we are reasonably confident that the patterns shown in this study may prove to be sufficiently robust to the addition of new distributional records.

Acknowledgements The authors thank Andrea Coradeghini and Liliana Quartino who allowed us the access to the BA algal herbarium and to the phycological literature, respectively. The authors are also grateful to Alicia Boraso who shared with us her knowledge on taxonomy and distribution of Patagonian macroalgae. One anonymous reviewer is thanked for valuable comments on an earlier version of this manuscript. The authors are grateful to Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for providing the financial support during this study (PIP No. 0291 to JLG).

References

Astorga, A., M. Fernández, E. E. Boschi & N. Lagos, 2003. Two oceans, two taxa and one mode of development: latitudinal diversity patterns of South American crabs and test for possible causal processes. Ecology Letters 6: 420–427.

Bolton, J. J., 1994. Global seaweed diversity: patterns and anomalies. Botanica Marina 37: 241–245.

Boraso, A. & J. M. Zaixso, 2008. Algas Marinas Bentónicas. In Boltovskoy, D. (ed.), Atlas de Sensibilidad Ambiental de la Costa y el Mar Argentino [available on internet at http://atlas.ambiente.gov.ar, accessed August, 2010].

Boraso, A. L., A. E. Rico, S. Perales, L. Pérez & H. Zalazar, 2004. Algas Marinas de la Patagonia. Una Guía Ilustrada. Vázquez Mazzini, Buenos Aires.

Boraso de Zaixso, A., 2007. Macroalgas marinas. In Carreto, J. I. & C. Bremec (eds), El Mar Argentino y sus Recursos Pesqueros 5. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata: 71–90.

Boraso de Zaixso, A. L. & R. Akselman, 2005. *Anotrichium furcellatum* (Ceramiaceae, Rhodophyta) en Argentina. Una posible especie invasora. Boletín de la Sociedad Argentina de Botánica 40: 207–213.

Boraso de Zaixso, A. L. & R. Negri, 1996. Presencia de *Sporochnus pedunculatus* (Sporochnales, Phaeophycophyta) en la costa argentina. Physis A 54: 23–24.

Boraso de Zaixso, A. L., H. E. Zaixso & G. N. Casas, 1999. Asociaciones de algas bentónicas submareales del Golfo San José (Chubut, Argentina). Physis A 57: 17–27.

Boschi, E. E., 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. Revista de Investigación y Desarrollo Pesquero 13: 7–136.

Brown, J. H. & M. V. Lomolino, 1998. Biogeography, 2nd ed. Sinauer, Sunderland.

Casas, G. N. & M. L. Piriz, 1996. Surveys of *Undaria pinnatifida* (Laminariales, Phaeophyta) in Golfo Nuevo, Argentina. Hydrobiologia 326/327: 213–215.

Casas, G., R. Scrosati & M. L. Piriz, 2004. The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biological Invasions 6: 411–416.

Clarke, A., 1992. Is there a latitudinal diversity cline in the sea? Trends in Ecology & Evolution 7: 286–287.

Clarke, K. R. & R. M. Warwick, 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. PRIMER-E Ltd, Plymouth.

Coll, J. & E. C. Oliveira, 1999. The benthic marine algae of Uruguay. Botanica Marina 42: 129–135.

Colwell, R. K., 1997. EstimateS: Statistical Estimation of Species Richness and Shared Species, from Samples, Version 5. User's Guide and Application. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs [available on internet at http://viceroy.eeb.uconn.edu/estimates].

Crame, J. A., 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas. Paleobiology 26: 188–214.

Ellingsen, K. E., 2001. Biodiversity of a continental shelf softsediment macrobenthos community. Marine Ecology Progress Series 218: 1–15.

Fernández, M., A. Astorga, S. A. Navarrete, C. Valdovinos & P. A. Marquet, 2009. Deconstructing latitudinal species richness patterns in the ocean: does larval development hold the clue? Ecology Letters 12: 601–611.

Gaston, K. J., 2000. Global patterns in biodiversity. Nature 405: 220–227.

Gray, J. S., 1997. Marine biodiversity: patterns, threats and conservation needs. Biodiversity and Conservation 6: 153–175.

Gray, J. S., 2001. Marine diversity: the paradigms in patterns of species richness examined. Scientia Marina 65(Suppl.): 41–56.

Guerrero, R. A. & A. R. Piola, 1997. Masas de agua en la plataforma continental. In Boschi, E. E. (ed.), El Mar Argentino y sus Recursos Pesqueros 1. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata: 107–118.

John, D. M., I. Tittley, G. W. Lawson & P. J. A. Pugh, 1994. Distribution of seaweed floras in the Southern Ocean. Botanica Marina 37: 235–239.

Kühnemann, O., 1972. Bosquejo fitogeográfico de la vegetación marina del litoral argentino. Physis 31: 117–142, 295–325.

Lawver, L. A. & L. M. Gahagan, 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeography, Palaeoclimatology, Palaeoecology 198: 11–37.

López Gappa, J., G. M. Alonso & N. A. Landoni, 2006. Biodiversity of benthic Amphipoda (Crustacea: Peracarida) in the Southwest Atlantic between 35°S and 56°S. Zootaxa 1342: 1–66.

Martin, J. P. & J. M. Cuevas, 2006. First record of *Undaria pinnatifida* (Laminariales, Phaeophyta) in Southern Patagonia, Argentina. Biological Invasions 8: 1399–1402.

Martínez, S. & C. J. del Río, 2002. Late Miocene mollusks from the southwestern Atlantic Ocean (Argentina and Uruguay): a palaeobiogeographic analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 188: 167–187.

Meneses, I. & B. Santelices, 2000. Patterns and breaking points in the distribution of benthic algae along the temperate Pacific coast of South America. Revista Chilena de Historia Natural 73: 615–623.

Moreno, C. A. & H. F. Jara, 1984. Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fuegian Islands, Chile. Marine Ecology Progress Series 15: 99–107.

Orensanz, J. M., E. Schwindt, G. Pastorino, A. Bortolus, G. Casas, G. Darrigran, R. Elías, J. López Gappa, S. Obenat, M. Pascual, P. Penchaszadeh, M. L. Piriz, F. Scarabino, E. D. Spivak & E. A. Vallarino, 2002. No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. Biological Invasions 4: 115–143.

Parma, A., M. Pascual & E. Sar, 1987. Clave para el reconocimiento de los géneros de algas macrofitas del intermareal rocoso bonaerense. Serie Técnica y Didáctica, Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo 15: 1–29.

Pianka, E. R., 1966. Latitudinal gradients in species diversity: a review of concepts. The American Naturalist 100: 33–46.

Roy, K., D. Jablonski, J. W. Valentine & G. Rosemberg, 1998. Marine latitudinal diversity gradients: test of causal hypotheses. Proceedings of the National Academy of Sciences of the United States of America 95: 3699–3702.

Roy, K., D. Jablonski & J. W. Valentine, 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. Proceedings of the Royal Society of London B 267: 293–299.

Santelices, B., 1980. Phytogeographic characterization of the temperate coast of Pacific South America. Phycologia 19: 1–12.

Santelices, B. & P. A. Marquet, 1998. Seaweeds, latitudinal diversity patterns, and Rapoport's Rule. Diversity and Distributions 4: 71–75.

Santelices, B. & I. Meneses, 2000. A reassessment of the phytogeographic characterization of temperate Pacific South America. Revista Chilena de Historia Natural 73: 605–614.

Smale, D. A., G. A. Kendrick & T. Wernberg, 2011. Subtidal macroalgal richness, diversity and turnover, at multiple spatial scales, along the southwestern Australian coastline. Estuarine, Coastal and Shelf Science 91: 224–231.

Steneck, R. S. & M. N. Dethier, 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69: 476–498.

Underwood, A. J. & P. G. Fairweather, 1986. Intertidal communities: do they have different ecologies of different ecologists? Proceedings of the Ecological Society of Australia 14: 7–16.