

The Japanese alga *Polysiphonia morrowii* (Rhodomelaceae, Rhodophyta) on the South Atlantic Ocean: first report of an invasive macroalga inhabiting oyster reefs

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Abstract Conspicuous tufts of the filamentous algae *Polysiphonia* Greville inhabit the reefs of *Crassostrea gigas* on the Atlantic Patagonian coast. The population was recorded for the first time in 1994 and identified as *P. argentinica*. This study exhaustively investigated the morphology and reproduction of specimens and the seasonality of the population. The results revealed the identity of the specimens as the invasive Japanese macroalga *Polysiphonia morrowii* Harvey, on the basis of several striking features: the setaceous and tufted thalli, the corymbose growing apices, the endogenous axillary branches, the urceolate cystocarps and the sharply pointed branches. Sexual reproduction was evidenced; however, fertile male gametophytes were absent in the samples. The population was found almost all year round, but its abundance became higher in autumn and winter. The present study constitutes the first record of this invasive macroalga on the South Atlantic Ocean; the fourth record of an exotic macroalgal species on the Atlantic Patagonian coast; and the first record of an invasive species related to the establishment of *C. gigas* in Atlantic Patagonia.

Keywords Atlantic Patagonia · *Crassostrea gigas* · Endogenous axillary branches · Invasive macroalgae · Oyster reefs · *Polysiphonia morrowii*

Introduction

Polysiphonia Greville is a widespread genus of red macroalgae of which numerous species have been recognized (Meñez 1964; Hollenberg and Norris 1977; Womersley 1979; Kapraun and Rueness 1983; Yoon 1986). Members of this genus are characterized by filamentous and often delicate thallus that grows within intertidal and subtidal habitats, ranging from turbid estuaries to clear waters (Adams 1991). This algal group has a long nomenclatural history (e.g., Kim et al. 2000; Kim 2003). Molecular tools have helped understanding the phylogeny of related species (Choi et al. 2001; McIvor et al. 2001; Stuercke and Freshwater 2008), while morphological studies contributed to the comprehension of phenotypic variability and the relation of distant populations (Curiel et al. 2002; Kim et al. 2004; Kim and Abbot 2006; Stuercke and Freshwater 2010).

Some *Polysiphonia* species are responsible for algal epiphytism and blooms that affect the natural communities (Lobban and Baxter 1983; Kapraun and Searles 1990); therefore, many studies have been focused on ecological and physiological aspects of this genus (Fralick and Mathieson 1975; Lee and Lee 1991; Lining and Garbary 1992). There is evidence that filamentous invasive macroalgae such as *Polysiphonia* are able to produce changes in the biodiversity of native ecosystems, providing substrate for the settlement of protozoa, colonial diatoms and early stages of macroalgae, hence increasing the complexity of the ecosystems that they invade (Thomsen et al. 2006).

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Several species of *Polysiphonia* have been found in non-native habitats where introductions are supposed to be the result of aquaculture initiatives (Maggs and Stegenga 1999; Haydar and Wolff 2011; Geoffroy et al. 2012). The most invasive species include *P. morrowii* Harvey, *P. brodiei* (Dillwyn) Sprengel, *P. breviarticulata* (C. Agardh) Zanardini and *P. harveyi* J.W. Bailey (currently considered a synonym for *Neosiphonia harveyi* (J.W. Bailey) M.S. Kim, H.G. Choi, Guiry and G.W. Saunders) (Gardner 1927; Kapraun and Searles 1990; Eno 1996; McIvor et al. 2001; Sliwa et al. 2009). As noticed by several authors, the possible vectors of their introductions include ballast water, vessel fouling and transport of oysters, especially of *Crassostrea gigas* (Thunberg, 1793) (Kapraun and Searles 1990; Curiel et al. 2002; Kim et al. 2004; Geoffroy et al. 2012). Oyster transfer for commercial purposes is considered the most important vector of macroalgae introductions (Gruet 1976; Verlaque 1981; Stegenga et al. 1997; Mineur et al. 2007).

In 1994, the presence of *C. gigas* was detected at the north Patagonian Atlantic coast of Argentina, and later in 2001, a monitoring campaign of the established reefs was started (Borges et al. 2005, Borges 2006). According to the literature, these reefs comprise the only established populations of *C. gigas* currently known in Argentina, which are inhabited by conspicuous macroalgal assemblages (Borges et al. 2005; Borges 2006; Croce and Parodi 2012). The local information suggests that oysters were transplanted from Chile in 1982 for culture purposes (Orensanz et al. 2002).

Several individuals of a red seaweed were found in Anegada Bay for the first time in 1994, which were identified as *P. argentina* W.R. Taylor (currently considered a synonym of *N. harveyi*) (Borges et al. 2005). From 2001 to 2005, ecological surveys were carried out in the region, and the red seaweed was found again as part of the fouling communities on artificial substrates and also in epibiosis with *C. gigas* (Borges et al. 2005). Later on, the species was recognized as *Polysiphonia abscissa* J.D. Hooker and Harvey during an ecological survey of the macroalgal community inhabiting the reefs (Croce and Parodi 2012). Currently, this *Polysiphonia* population dominates the macroalgal community and forms almost monospecific stands in this habitat (Croce and Parodi 2012). The particular location of the population in the oyster reefs led to us to check the identity of this macroalga. The aim of the present study was to analyze the vegetative and reproductive morphology of *Polysiphonia* specimens from the oyster reefs located in Anegada Bay and to evaluate the seasonality of the population. In addition, as only a few *Polysiphonia* species from the South Atlantic Ocean have been studied and detailed descriptions are scarce (Lazo 1982; Boraso et al. 2004), our results contribute to the

understanding of distribution and morphology of *Polysiphonia* populations in this region of the world.

Methods

Sampling site

The survey was carried out in the oyster reefs located in Anegada Bay (40°25'S; 62°25'W) at the north Patagonian Atlantic coast of Argentina (Fig. 1). The coast has a semidiurnal tidal regime and is constituted by tidal flats where *Crassostrea gigas* has established large populations of approximately 127.982 m² (Spalletti 1980; Borges 2006).

Field methods

Surveying of specimens was carried out during 2009, 2010 and 2011 in the pools formed on *C. gigas* intertidal reefs. Collection of thalli for identification and morphological studies was done from March to November of consecutive years.

In order to estimate the seasonal changes in abundance of this species, biomass samples were obtained in four sampling months, representative of each season, during 1 year. A total of 72 pools (18 per season) were randomly selected along transects haphazardly located in the intertidal and orthogonal to the shoreline. *Polysiphonia* biomass was harvested inside the pools using quadrates of 0.25 m² to estimate relative biomass.

All biological material was transferred to the laboratory in plastic bags, inside cold boxes.

Laboratory methods

Observations on the external appearance and morphology were made on fresh specimens with a stereoscopic microscope Wild Heerbrugg. Cross sections of thalli were examined with an inverted microscope Nikon Eclipse TE (Nikon, Tokyo, Japan), and photographs were taken with a digital camera Nikon FDX 35 (Nikon, Tokyo, Japan). Selected portions of specimens were preserved in glutaraldehyde–seawater 2.5 % at 5 °C in cacodylate buffer, mounted on slides and dehydrated for further observations with a Leo Evo 40 SEM (Cambridge, UK). Morphometric measurements were taken using a micrometric ocular and/or obtained from photographs using the UTHSCSA Image Tool version 3.00 software (developed by University of Texas Health Science Center of San Antonio, Texas, <ftp://maxrad6.uthscsa.edu>, 2011). Identification of the specimens was carried out, and their morphology was compared with other descriptions. The material identified was

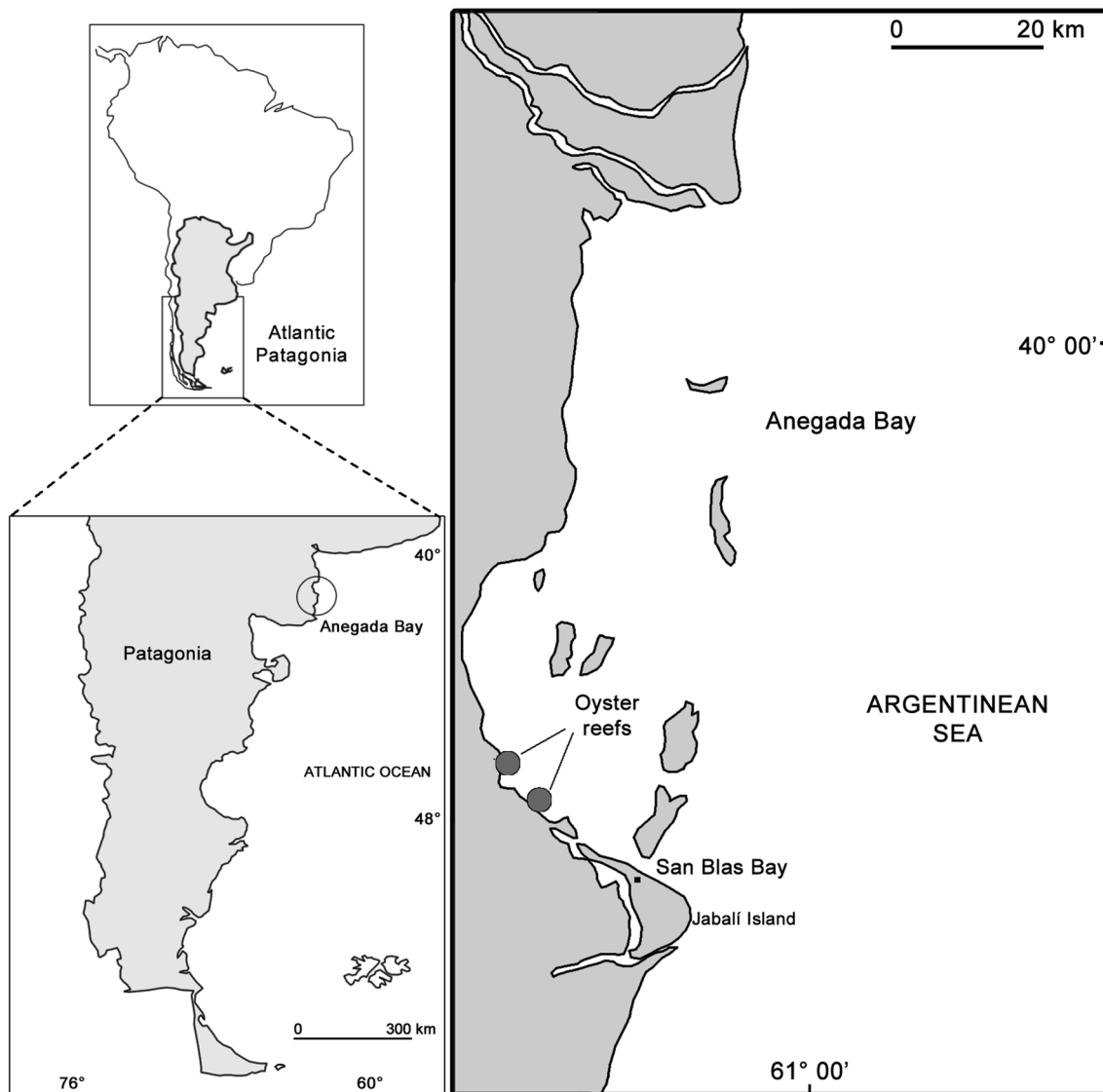


Fig. 1 Geographical location of the oyster reefs in the Southwest Atlantic coast, where *Polysiphonia* specimens were collected

deposited in the Herbarium of Universidad Nacional del Sur, Argentina: BBB (Croce 344–Croce 347) and BBB (Croce 020F–Croce 025F).

Polysiphonia biomass was rinsed with seawater, drained for 2 h on blotting paper, then weighted and dried in an oven at 60 °C. An average of relative wet weight (WW) and dry weight (DW) was obtained for each season, and the differences in abundance were tested using Kruskal-Wallis analysis and Fisher's pairwise comparisons with the R software (R Development Core Team 2012).

Results

Polysiphonia grew densely and formed extensive patches in the oyster reefs. The thalli were strongly attached to the

shells of the exotic oyster *C. gigas* and less frequently to the mussel *Brachidontes rodriguezii* d'Orbigny.

On the basis of the morphological characteristics observed, the specimens were identified as *Polysiphonia morrowii*. Thalli were long and slender, up to 26 cm, and formed dense tufts (Fig. 2a, b). The color of thalli varied; well-developed and “healthy” specimens were dark red (Fig. 2d), while epiphytized thalli were yellowish or brownish (Fig. 2c). The texture of thalli was setaceous.

Thalli were composed of a basal portion of prostrate axes, highly entangled and strongly attached to the substratum from which erect axes arose. The erect part of the thallus was more developed than the prostrate part. The basal parts of erect axes were scarcely branched and had short determinate branches, sometimes recurved, while the middle and distal parts were profusely branched forming

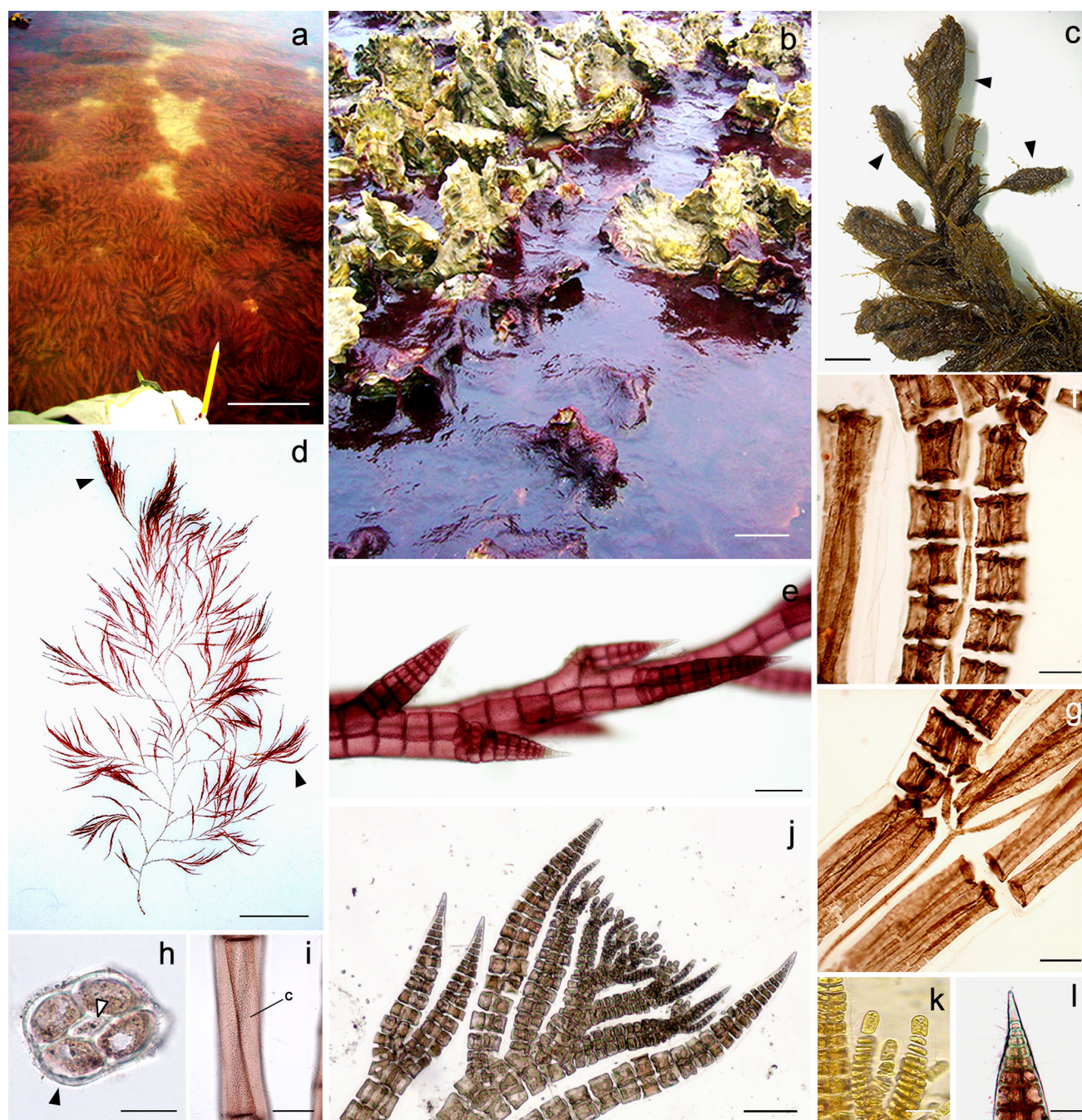


Fig. 2 *Polysiphonia morrowii*. Habitat and vegetative morphology. **a** General view of an intertidal population; **b** specimens inhabiting the intertidal pools between *Crassostrea gigas* individuals; **c** general aspect of an epiphytized thallus; *arrowheads* denote clumps of sediment; **d** branching pattern; *arrowheads* denote fascicles; **e** detail of branching, denoting the spiral pattern and the frequency of branches; **f** prostrate axes showing central and pericentral cells; **g** erect axes showing central and pericentral cells; **h** cross section of

erect axes showing the central cell (*white arrowhead*) surrounded by four pericentral cells (*black arrowhead*); **i** detail of a segment presenting the spiral arrangement of pericentral cells, *C* chloroplasts; **j** corymbose growing apices; **k** detail of rounded apical cells at growing apices; **l** detail of a spinose apical cell at determinate branches. *Scale bars* **a** = 30 cm; **b** = 4 cm; **c** and **d** = 1 cm; **e** = 125 μ m; **f**, **g** and **i** = 100 μ m; **h** and **j** = 50 μ m; **k** and **l** = 25 μ m

conspicuous fascicles (Fig. 2d). Branching was alternate in a spiral pattern every 2–6 segments (Fig. 2e).

Prostrate and erect axes were composed of a central cell surrounded by four pericentral cells without cortication

(Fig. 2f–h). The chloroplasts were small disks, densely packed and form a network (Fig. 2i).

The thickness of axes was 52–118 μ m and 46–223 μ m in prostrate and erect axes, respectively. The length/width

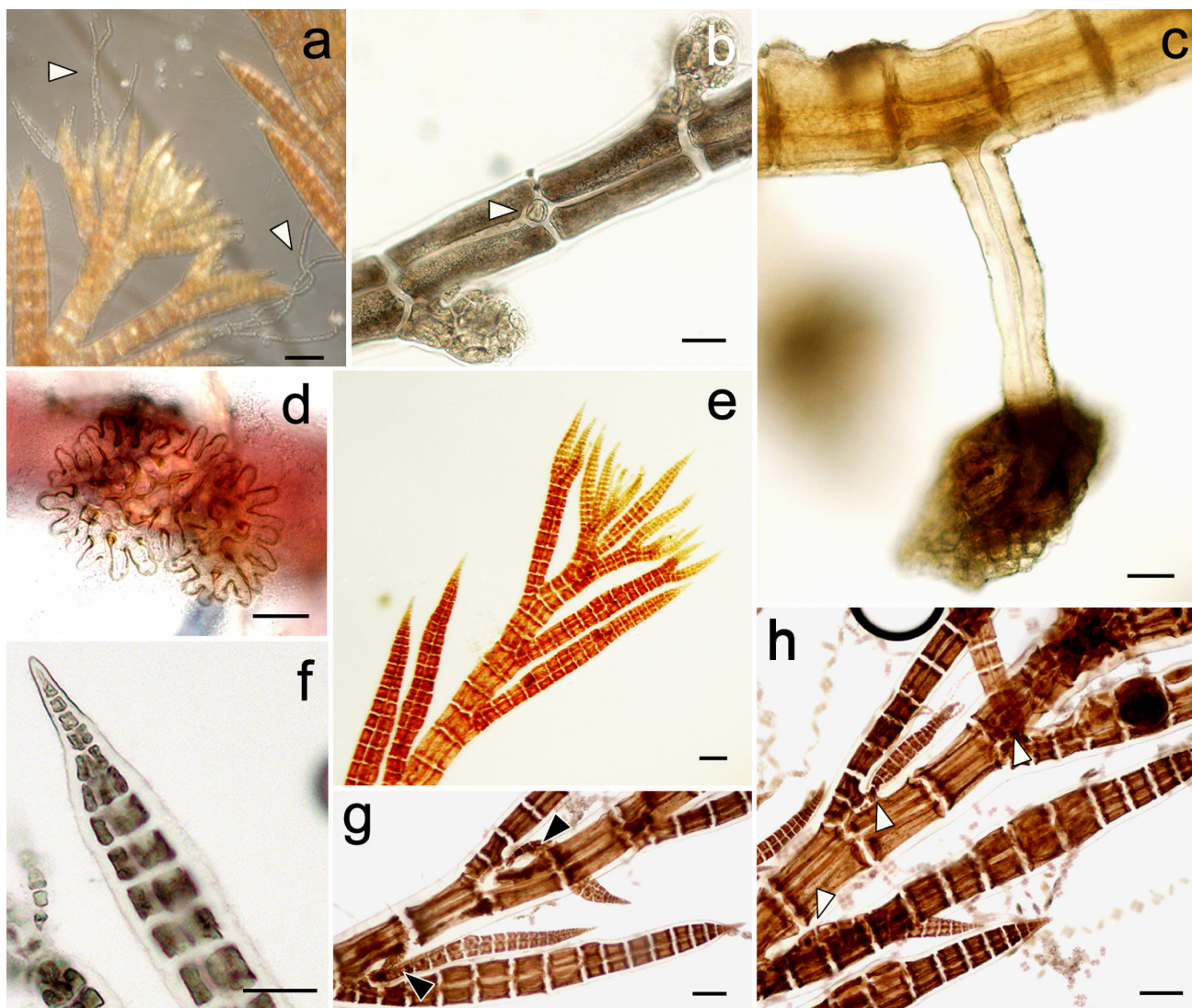


Fig. 3 *Polysiphonia morrowii*. Vegetative morphology. **a** Trichoblast presenting several furcations (arrowheads); **b** conspicuous scar cell (arrowhead); **c** rhizoid in open connection with the pericentral cell; **d** detail of highly digitated attachment disk of rhizoids; **e** sharply

pointed shape of ultimate branches; **f** detail of sharply pointed branches; **g, h** endogenous axillary branches (arrowheads). Scale bars 50 μm

(L/W) ratio of segments was between 0.8 and 11. The diameter of the central cell varied from 19 to 38 μm . Pericentral cells were longer and wider in erect axes than in prostrate axes. Pericentral cells from prostrate axes measured 21.53–96.25 μm in length and 16.76–63.27 μm in width. In erect axes, pericentral cells measured 45.15–947.05 μm in length and 23.49–103.57 μm in width.

Growing apices displayed a corymbose pattern (Fig. 2j). Apical cells were conspicuous and rounded in the growing apices (Fig. 2k), while spinose in determinate branches (Fig. 2l). Apical division was slightly oblique.

Trichoblasts were scarce, but were located near the apices of erect axes, when present. They were colorless, up to three times furcated and deciduous (Fig. 3a). Scar cells

were scarce, but were conspicuous with no evident arrangement, when present (Fig. 3b). Branches were not related to trichoblasts.

Prostrate axes were attached to the substratum by several unicellular rhizoids. Rhizoids were little-pigmented and originated from the center or the proximal end of a pericentral cell remaining in open connection with them (Fig. 3c). The shape of rhizoids was variable, some were short with a highly digitated attachment disk (Fig. 3d), and others were long and narrow, ending in a rounded tip. The length of rhizoids varied from 170 to 1,000 μm and width varied from 14 to 86 μm .

The shape of ultimate branches was sharply pointed (Fig. 3e, f). A few specimens presented lateral adventitious

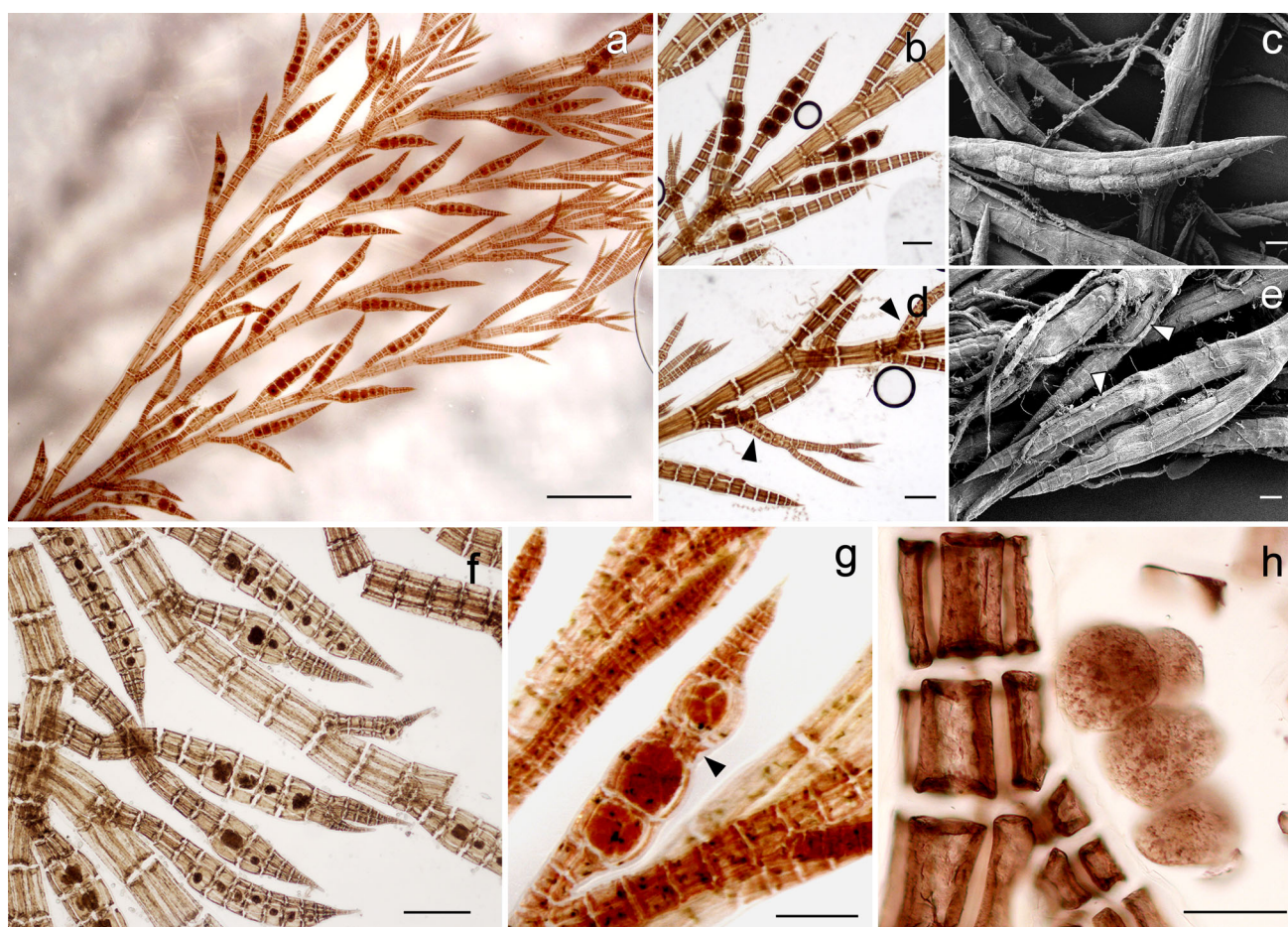


Fig. 4 *Polysiphonia morrowii*. Reproductive morphology of tetrasporophytes. **a** Aspect of the thallus; **b** determinate tetrasporangial branches; **c** detail of a determinate tetrasporangial branch in SEM; **d** endogenous axillary tetrasporangial branches bearing tetrasporangia (black arrowheads). Note the branching tip (white arrowhead).

e detail of a tetrasporangial branch showing sharply pointed apices; white arrowheads denote trichoblasts; **f** tetrasporangial series of different lengths; **g** arrangement of mature tetrasporangia; arrowhead denotes a non-fertile segment; **h** shape of released tetraspores. Scale bars **a** = 0.5 mm; **b**, **d**, **f**, **g** and **h** = 100 μ m; **c** and **e** = 30 μ m

branches, while others presented endogenous axillary branches that had tetrasporangia when fertile (Fig. 3g, h).

Fertile tetrasporophytes were found in every month. Tetrasporangia were mostly located in determinate short branches that were distributed throughout the thalli but were more abundant near the apices (Fig. 4a–c). Some specimens presented one to three endogenous axillary branches bearing tetrasporangia (Fig. 4d). Endogenous axillary branches were observed in September and October only in tetrasporic thalli. Some tetrasporangial branches were determinate, while others were branched at the tip. They had sharply pointed apices and pyramidal apical cells (Fig. 4e, f). Tetrasporangia were arranged in straight series with 1–9 fertile segments and were sometimes interspersed with non-fertile segments (Fig. 4f). One tetrasporangium developed per segment. Fertile segments became enlarged when tetrasporangia were mature and expanded laterally. Tetrasporangial segmentation was tetrahedral. Tetraspores

measured from 90 to 110 μ m in width (Fig. 4g) and were discoid (Fig. 4h).

Fertile female gametophytes were found in different stages of maturation (Fig. 5a–c). Young specimens presented procarps with a developed trichogyne protruding from them (Fig. 5d). Young cystocarps were surmounted by a slender forked trichoblast (Fig. 5e). Mature cystocarps were located laterally on erect axes and branches, supported by one cell stalk (Fig. 5f). Mature cystocarps were markedly urceolate (Fig. 5g, h), with a narrow neck and a wide ostiole (Fig. 5i) and measured 270–655 μ m in length and 200–590 μ m in width. Carpospores were clavate, measuring from 104 to 107 μ m in length (Fig. 5j).

Tetrasporophytes were more frequent than carposporophytes, whereas fertile male gametophytes were not recognized during the sampling period. The specimens were highly developed during the colder months and declined

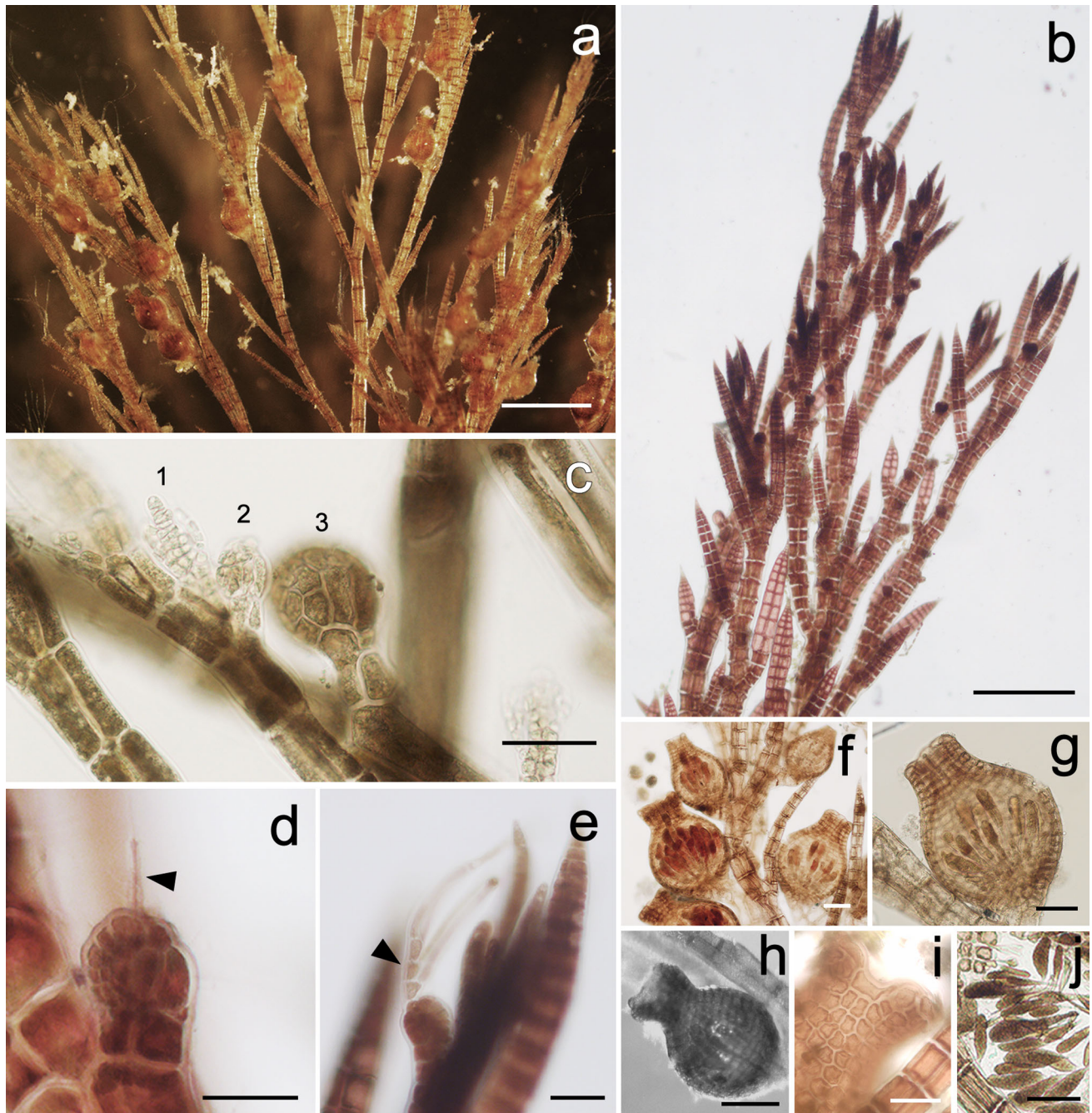


Fig. 5 *Polysiphonia morrowii*. Reproductive morphology of carposporophytes. **a** Aspect of a mature thallus; **b** aspect of an immature thallus; **c** progressive stages of maturation of cystocarps from 1 to 3; **d** detail of a trichogyne protruding from an immature cystocarp (arrowhead); **e** detail of a cystocarp surmounted by a forked hair

(arrowhead); **f** mature cystocarps; **g** urceolate shape of a mature cystocarp; **h** surface view of a mature cystocarp; **i** detail of the narrow neck and wide ostiole of a mature cystocarp; **j** shape of released carpospores. Scale bars **a** = 1 mm; **b** = 250 μ m; **c**, **f**, **g**, **i** and **j** = 100 μ m; **d** and **e** = 50 μ m; **h** = 200 μ m

toward the warmer season, when they became epiphytized by diatoms and the filaments entangled with the sediment.

The population was present throughout the year, except from December to February when macroscopic thalli were not found. There were significant differences in the seasonal biomass ($p \ll 0.01$; $F = 6.9$; $df = 71$) (Fig. 6). Maximum

DW was found in winter, and minimum DW was found in spring. No significant differences were found between autumn and winter biomass ($p = 0.48$; $t = 0.03$; $df = 17$), neither between spring and summer biomass ($p = 0.07$; $t = -1.6$; $df = 17$). The WW/DW ratio was significantly higher in summer than in spring ($p \ll 0.01$; $t = -3.32$; $df = 17$).

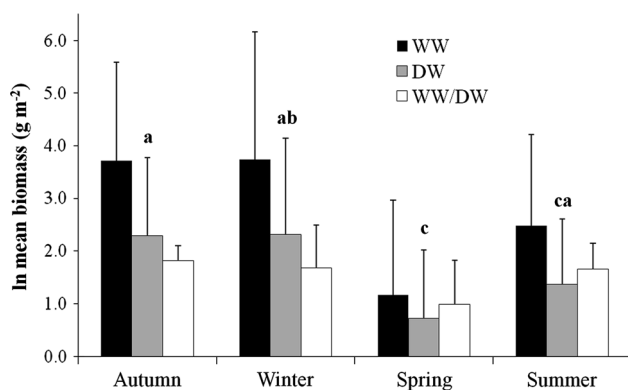


Fig. 6 Seasonal biomass of *Polysiphonia morrowii*. Letters above the bars indicate results of Fisher's pairwise comparisons. Biomass data were (ln+1) transformed. WW wet weight, DW dried weight

Discussion

Polysiphonia morrowii was first described by Harvey (1857) from specimens collected in Japan, as densely tufted thalli with setaceous texture, measuring up to 25 cm long and having subcorymbose apices. There were subsequent descriptions of specimens collected in Korea and Japan (Yoon 1986; Kudo and Masuda 1992; Kim et al. 1994), and further of specimens introduced in Italy, Chile, Turkey, France and New Zealand (Curiel et al. 2002; Kim et al. 2004; Erdügan et al. 2009; D'Archino et al. 2012; Geoffroy et al. 2012). The present study provides previously unpublished information on the vegetative and reproductive characters of *P. morrowii* from the South Atlantic Ocean.

There is some discrepancy about the morphological features used to diagnose *P. morrowii*. Kudo and Masuda (1981) mentioned the following diagnostic features: (a) the presence of primary axes and many secondary axes with indeterminate branches and stolons; (b) ecortication and 4 pericentral cells; (c) thickness of upright axes and setaceous texture; (d) ultimate branches sharply pointed; (e) endogenous axillary branches; (f) scarcity of trichoblasts; (g) straight lines of tetrasporangia on ultimate branches and on axillary branches; (h) axillary tetrasporangial branches in tufts of 7 or 8; (i) spermatangia replacing trichoblasts; and (j) urceolate cystocarps. All the characteristics observed in the present study were consistent with the majority of the descriptions of *P. morrowii*, but the most conspicuous features included the sharply pointed apices of branches and the presence of endogenous axillary branches bearing tetrasporangia in fertile thalli. Table 1 compares specimens of *P. morrowii* from the native habitat with specimens introduced in other locations, including the specimens found in the South Atlantic Ocean.

Length of thalli was similar to all descriptions of *P. morrowii* except those from the Mediterranean Sea and

Table 1 Comparison between *Polysiphonia morrowii* specimens collected in Anegada Bay and specimens from native and non-native habitats

Reference	Texture	Length (cm)	N segments between branches	Rhizoids		Segments' width (µm)		L/W	Tetrasporangia (µm)	Endogenous axillary branches	Sharply pointed apices	Country
				Length (µm)	Width (µm)	Prostrate axes	Erect axes					
Yoon (1986)	-	3-25	3-8	100-1,000	50-70	150-250	80-300	0.2-13	70-80	Yes	Yes	Korea
Kudo and Masuda (1992)	Setaceous	Up to 35	-	-	-	260-550	-	1.2-11.7	-	Yes	Yes	Japan
Curiel et al. (2002)	-	Up to 50	3-7	1,600	25-90	65-115	100-300	0.4-20	-	Yes	Yes	Italy
Kim et al. (2004)	-	-	-	-	20-40	50-160	-	-	50-60	No	Yes	Chile
Erdügan et al. (2009)	Delicate	3-25	3-8	100-1,000	50-70	150-250	-	0.2-13	-	-	-	Turkey
D'Archino et al. (2012)	-	3-9	-	-	-	-	-	-	-	-	Yes	New Zealand
Geoffroy et al. (2012)	-	15-30	-	-	-	-	-	-	-	-	Yes	France
This study	Setaceous	4-26	2-6	170-1,000	14-86	52-118	46-223	0.8-11	90-110	Yes	Yes	Argentina

New Zealand (Curiel et al. 2002; D'Archino et al. 2012). Specimens described by Curiel et al. (2002) from the Mediterranean Sea were considerably larger than Japanese and Korean ones; however, some authors have emphasized on the monthly variability of thalli length (Lee and Lee 1991; Kim et al. 1994).

Polysiphonia morrowii thalli have been recently found in Punta Arenas, southern Chile, and their morphology was similar to that of specimens from Korea and Japan, except for the absence of axillary tetrasporangial branches, attributed to an early stage in the development of the thalli (Kim et al. 2004). This feature was present in the specimens collected in Anegada Bay; therefore, they represent the first record for South America of a *Polysiphonia* species bearing both endogenous axillary branches and axillary tetrasporangial branches. Kim et al. (2004) denoted a difference between Chilean and Korean/Japanese specimens in being more delicate, soft and abundantly branched. These features were also observed in the specimens collected in Anegada Bay; however, thalli were not delicate but had a setaceous texture as described by Kudo and Masuda (1992) for the Japanese ones.

Eleven species of *Polysiphonia* have been recorded for the Atlantic Patagonian coasts: *P. abscissa*, *P. anisogona* J.D. Hooker and Harvey, *Neosiphonia harveyi* (J.W. Bailey) M.S. Kim, H.G. Choi, Guiry and G.W. Saunders (as *P. argentinica* W.R. Taylor), *P. nigra* (Hudson) Batters (as *P. atrorubescens* Dillwyn (Greville)), *P. brodiei*, *P. cancellata* Harvey, *P. corymbifera* (C. Agardh) Endlicher, *P. fuscobrunnea* J.D. Hooker and Harvey, *P. hassleri* W.R. Taylor, *P. tenuistriata* J.D. Hooker and Harvey and *P. urceolata* (Pujals 1963). Only a few of these species have been studied, and descriptions are scarce (Lazo 1982; Boraso et al. 2004).

On the basis of vegetative features, *P. morrowii* groups with other Atlantic and Pacific species such as *P. stricta*, *P. atlántica*, *P. pacifica*, *P. pungens*, *P. scopulorum*, *P. senticulosa*, *P. subtilissima*, *N. harveyi* and *P. abscissa*. Given some similarities between *P. morrowii* and the last two species (four pericentral cells, presence of trichoblasts, conspicuous scar cells, urceolate cystocarps) and according to earlier records of these two species along the Patagonian coast, previous specimens collected in Anegada Bay were misidentified and recorded as *P. argentinica* (currently considered a synonym of *N. harveyi*) and *P. abscissa* (Borges et al. 2005; Croce and Parodi 2012). However, the specimens studied differed in several features from *P. abscissa* such as the thickness of thalli, which is thicker in *P. morrowii*; the L/W ratio, which is higher in *P. morrowii*; the branching pattern, which is subalternate in *P. abscissa* and alternate in *P. morrowii*; the number of segments between branches, which is higher in *P. abscissa*; the cystocarp shape, which is ovate in *P. abscissa* and

urceolate in *P. morrowii*; and the apical cells, which are rounded in *P. abscissa*, while they are acute and spinose in *P. morrowii* (Yoon 1986). In addition, the specimens analyzed by us were clearly different from *N. harveyi* (= *P. argentinica*) in several features such as cortication, which is present in *N. harveyi* and absent in *P. morrowii*; the arrangement of tetrasporangia, which is spiral in *N. harveyi* and straight in *P. morrowii*; the connection between the rhizoid and the pericentral cell, which is open in *P. morrowii* and cut off in *N. harveyi*; and the presence of trichoblasts, which are abundant in *N. harveyi* while scarce in *P. morrowii*.

Phenological studies of *P. morrowii* mention higher occurrence of vegetative and tetrasporic thalli than fertile male and female thalli (Kim et al. 1994; Curiel et al. 2002; Geoffroy et al. 2012), and only a few studies have recorded all life history stages (Yoon 1986; Kudo and Masuda 1992; Kim et al. 1994; Curiel et al. 2002; Erduğan et al. 2009). Others even mention the absence of fertile gametophytes (Kim et al. 2004; Geoffroy et al. 2012). Kim et al. (1994) found that all reproductive stages of *P. morrowii* from Korea are present in the same period of time and that the life cycle is complete after 4 months. That was not the case in Anegada Bay, where almost all specimens observed in the present study were tetrasporophytes, and fertile female gametophytes were occasionally found, whereas male thalli were not registered. According to other studies, male thalli of *P. morrowii* are less frequent than tetrasporic and cystocarpic ones, appearing only in 1 month along the year (Kim et al. 1994). The presence of carposporophytes in Anegada Bay proves that sexual reproduction occurred, and thus, spermatangia were likely rapidly deciduous. The same trend has been often observed in many populations of *P. morrowii* located in different locations all over the world, as well as other species of red algae (Guiry and Womersley 1992; Kim et al. 1994; Curiel et al. 2002; Prathep et al. 2009; D'Archino et al. 2012). Unlike other studies of *P. morrowii*, mix-phases and simultaneous occurrence of different life history stages (Lawson and Russell 1967; Lee and Lee 1991; Curiel et al. 2002; Aguilar-Rosas et al. 2006) were not observed in the specimens collected in Anegada Bay. Several authors have denoted the ability of *P. morrowii* to colonize a variety of substrata and its rapid growth and vegetative propagation (Kudo and Masuda 1992; Kim et al. 1994, 2004).

In oyster reefs at Patagonia, the biomass of macroscopic thalli of *P. morrowii* increases in autumn and winter. The same trend has been registered in the Mediterranean Sea, Korea and France, where macroscopic thalli appear in early autumn, become covered by epiphytic algae in spring and decay in summer (Curiel et al. 2002; Geoffroy et al. 2012; Kim et al. 1994). The fact that macroscopic thalli were not found during a few months in Anegada Bay does not mean

that the species is absent, and on the contrary, it is likely that prostrate axes remain attached to the substrate, from which new growth may occur each year.

The low abundance in spring is unexpected compared to the worldwide pattern of macroalgal seasonality; however, after 3 years of surveying the population, it was evident that the population decays as the water temperature increases in late spring and summer. An increase in biomass during the months of lower water temperature was expected, given that *P. morrowii* is characteristic of cold/temperate waters (Kudo and Masuda 1992; Kim et al. 1994; Curiel et al. 2002). *Polysiphonia morrowii* is native to the North Pacific and survives temperatures between 6 and 25 °C (Curiel et al. 2002; D'Archino et al. 2012). The temperature range in Anegada Bay goes from 5.6 to 24.8 °C; therefore, the species should be adapted to this particular habitat.

The WW/DW ratio was almost constant in autumn, winter and summer, but it was lower in spring. In spring, the thalli appeared epiphytized by diatoms in long and dense mucous colonies which were sometimes virtually impossible to eliminate; therefore, spring DW is somehow overestimated, which explains the lower WW/DW ratio.

This study confirms the broad distribution of this invasive *Polysiphonia* species and facilitates the comparison of distant populations. Several *Polysiphonia* species have been frequently recorded in oyster reefs or associated with oyster ponds and mainly to the Pacific oyster *C. gigas* (Connor 1980; Hoagland 1982; Kamara 1982; Maggs and Stegenga 1999; Mineur et al. 2007). Exotic *Polysiphonia* species, such as *P. setacea* (currently regarded as a taxonomic synonym of *Womersleyella setacea*) have been also recorded in monospecific stands (Rindi et al. 1999). The specific dense occurrence of *P. morrowii* in the pools at Anegada Bay also resulted from *C. gigas* establishment, in addition to the fact that there are no other records of this species along the Atlantic Patagonian coast (Pujals 1963; Mendoza and Nizovoy 2000). This could suggest a simultaneous introduction of both Pacific species. If that was the case, Anegada Bay would probably be the first point of introduction of the species in Argentina, because the oysters were initially transplanted to this coast; however, it is likely to spread into other locations as a result of hatchery trials (Orensanz et al. 2002). It is important to notice that floristic studies are currently carried out by our research team in several locations along the Atlantic Patagonian coast from 38°S to 45°S, and to date, *P. morrowii* has not been registered outside the bay.

Economic activities in the Anegada Bay region are scarce and include oyster exploitation and sport fishing carried out in small boats. Oyster aquaculture is no longer practiced in the region; however, the reefs are exploited by the local people as an economic resource as well as a

management practice. Although fouling is considered as one of the most important sources of the introduction of exotic macroalgae (Haydar and Wolff 2011), it is unlikely that this vector is the source of *P. morrowii* introduction into Anegada Bay: the oceanographic conditions are unfavorable for industrial fishing vessels to enter the bay, and therefore, there is no harbor (Cuadrado and Gomez 2010).

Only three non-native macroalgal species have been previously recorded for the Atlantic Patagonian coast: *Undaria pinnatifida* (Harvey) Suringar, native to the Northwest Pacific Ocean (Casas and Piriz 1996; Casas et al. 2004; Martin and Cuevas 2006; Meretta et al. 2012), *Sporochnus pedunculatus* (Boraso and Negri 1997) and *Anotrichium furcellatum* (J. Agardh) Baldock (Boraso de Zaixso and Akselman 2005). The present study constitutes the fourth record of a non-native macroalgal species for the Atlantic Patagonian coast and the first record of an invasive *Polysiphonia* species. Kim et al. (2004) have suggested *U. pinnatifida* as a possible vector of *P. morrowii* in Chilean coasts, although *U. pinnatifida* has not been found in Chilean waters. On the contrary, *U. pinnatifida* has been introduced in Argentina, and there are known established populations. However, *U. pinnatifida* has never been recorded in Anegada Bay to date. Red algae are the largest taxonomic group introduced by oyster vectors, and 45% of the associated introductions originate from the Northwest Pacific (Haydar and Wolff 2011); hence, it is reasonable to consider the Pacific oyster as a vector for the introduction of *P. morrowii* into the Atlantic Patagonian coasts. Although *P. morrowii* has been registered in Punta Arenas, Chile, we consider it very unlikely that the Chilean population could be the source of the Argentinean population, since the two coasts are located in different oceans about 1,800 km distant and separated by large latitude range. Even if that was the case, there are no clues to suggest a possible vector because vessel traffic between both coasts is not known; neither oyster transfers have been confirmed. In this context, it is more parsimonious to hypothesize a simultaneous introduction “oyster–algae.”

As denoted by D'Archino et al. (2012), *P. morrowii* has been short listed as one of the 100 worst invasive species in the Mediterranean, and it is supposed to cause changes in biodiversity and problems in fisheries by clogging fishing nets (Streftaris and Zanetos 2006). The same phenomenon has been observed in Anegada Bay (Molina J.M., 2012, Universidad Nacional del Sur, pers. comm.) and denotes the imperative need for management since fishing is the primary economic activity in this region.

Given the recent establishment of *C. gigas* reefs in Anegada Bay, little is known about its interaction with the native benthic organisms (Escapa et al. 2004) and no associated exotic species have been reported to date. This

study represents the first record of an alien species that is possibly related to the introduction of the Pacific oyster, to be found in Anegada Bay.

Negative interactions between exotic macroalgae and the native organisms have already been reported in Patagonia (Casas et al. 2004); hence, the impact of the invasive macroalga *P. morrowii* on this native ecosystem needs to be considered and evaluated. Further evaluation of the phylogenetic relationship between these specimens and those introduced in other localities would be of great relevance in order to determine the origin of the introduction and the relationship with other populations.

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