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Seaweed biodiversity in the south-western Antarctic Peninsula: Surveying macroalgal community composition in the Adelaide Island / Marguerite Bay region over a 35-year time span

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Abstract

The diversity of seaweed species of the south-western Antarctic Peninsula region is poorly studied, contrasting with the substantial knowledge available for the northern parts of the Peninsula. However, this is a key region affected by contemporary climate change. Significant consequences of this change include sea ice recession, increased iceberg scouring, and increased inputs of glacial melt water, all of which can have major impacts on benthic communities. We present a baseline seaweed species checklist for the southern Adelaide Island and northern Marguerite Bay region, combining data obtained during a small number of surveys completed in 1973-5 and a six week intensive diving-based field campaign in 2010-2011. Overall, with a total of 41 macro-algal species recorded (7 brown, 27 red, 6 green, 1 chrysophyte), the region is species-poor compared to the north of the Antarctic Peninsula, and even more so in comparison with the sub-Antarctic. The key canopy-forming species is *Desmarestia menziesii*, which is abundant in Antarctic Peninsula waters, but lacking in the sub-Antarctic. *Himantothallus grandifolius*, which is a common species further north in the Antarctic phytobenthos, was absent in our recent collections. This paper also reports the first record of *Aplanochytrium* sp. (Labyrinthulomycetes) from this part of Antarctica and in association with *Elachista* sp..

Keywords

Aplanochytrium sp., climate change, *Desmarestia menziesii*, marine macroalgae, maritime Antarctic, ice recession

Introduction

Seaweeds, in particular brown algae, are the major primary producers in temperate and polar rocky inshore environments. They are important contributors to global biogeochemical cycles, for instance through the transfer of iodine from the marine environment to the atmosphere and the land (Küpper et al. 2011). Compared to the sub-Antarctic region, the Antarctic is generally considered depauperate in terms of seaweed species diversity (Wiencke and Clayton 2002). Pioneering studies of Antarctic seaweed biodiversity, taxonomy and biogeography were conducted over a century ago by Skottsberg (1907), with a recent synopsis provided by Wiencke and Clayton (2002). Polar seaweeds show adaptations enabling survival in temperatures around freezing, and of months of winter darkness (Wiencke et al. 2009). In clear contrast to temperate and tropical bioregions, polar regions are characterized by an intertidal almost devoid of seaweeds. This is due to the extreme environmental conditions in the intertidal zone – with temperature extremes ranging from -50 to +5ºC (Peck et al. 2006; Waller et al. 2006) and strong impacts of abrasion by sea ice (Barnes and Souster 2011; Barnes et al. 2014). Remarkably, the Antarctic phytobenthos has no representatives of the Laminariales, which are present in Arctic and all other cold and cold-temperate bioregions of the world. Instead, their ecological niche and role, as canopy providers, is largely fulfilled by members of the Desmarestiales (Moe and Silva 1977).

Climate change is altering parts of the Antarctic and Arctic faster than any other region on Earth. In the Antarctic, this applies particularly to the Antarctic Peninsula, where major changes have been observed in only the last 20-50 years (Meredith and King 2005; Turner et al. 2009, 2013; Convey et al. 2009). Changes in the physical environment are characterized by increasing temperatures, receding sea ice cover and increased iceberg scouring of the inshore seabed caused by the combination of increased calving of shelf ice and glaciers coinciding with resulting icebergs being less restrained by sea ice (Barnes and Souster 2011; Barnes et al. 2014). Population expansions of alien microbes, fungi, plants and animals have been recorded in sub-Antarctic and Antarctic areas, although most documented examples are from the terrestrial environment (Frenot et al. 2005; Greenslade et al. 2012; Molina-Montenegro et al. 2012). Southward range expansion into previously inaccessible or uninhabitable areas of the Antarctic has been documented for some penguins (Lynch et al. 2012) and has been highlighted as a likely

scenario for toxic cyanobacteria (Kleinteich et al. 2012). So far it is not clear whether, or to what extent, this also applies to sub-Antarctic and Antarctic seaweeds, but it is reasonable to hypothesize that such changes in distribution will occur in the foreseeable future.

In this study, we have revisited the south-eastern Adelaide Island area, which has been much less studied in terms of seaweed diversity than the more northern regions of the Antarctic Peninsula. While numerous phycological investigators (DeLaca and Lipps 1976; Moe and De Laca 1976; Quartino et al. 2001; Wiencke and Clayton 2002; Oliveira et al. 2009) have worked in particular around King George Island and Anvers Island since the 1960s, and the region of Adelaide Island is well studied for other marine biota (Barnes and Brockington 2003; Smale et al. 2007), little consideration has been given to the seaweeds of the latter. In this respect, the work of Moe and DeLaca (1976) stands out in its extensive coverage of the western Antarctic Peninsula over a wide latitudinal gradient, including an unsurpassed number of study sites, and its relatively long duration. However, even though this remains the most comprehensive survey of the phytobenthos of the western Antarctic Peninsula to date, this study includes 24 recorded taxa from only three dives in the Adelaide Island / Marguerite Bay area.

Here we present the results of a six week diving-based field campaign in the vicinity of Rothera Point (south-eastern Adelaide Island) in 2010-2011, integrating our data with that of Moe and DeLaca (1976). The main objective of this work was to establish an inventory for this region, where currently little knowledge about seaweed biodiversity exists. This will provide important baseline data for future biogeographical and comparative studies. Given that eukaryotic pathogens have been documented for most marine bioregions outside Antarctica (e.g. Strittmatter et al. 2009) and considering their potentially significant impact on seaweed ecology (Küpper and Müller 1999; Gachon et al. 2010), the seaweed survey presented here is complemented by the first ever such survey of filamentous brown algae for such pathogens in Antarctica.

Material and Methods

Nine sites were surveyed in the vicinity of the British Antarctic Survey's Rothera Research Station (Adelaide Island): Anchorage Island, Biscoe Wharf, Cheshire Island, Hangar Cove, Honeybucket, Lagoon Island, Léonie Island, Shack's Crack and South Cove (Fig. 1). A total of 17 scuba dives (duration 10-52 min, maximum depth 35.6 m) were conducted at all of these sites. Destructive purposive sampling took place along the full depth profile (0 – 35m). For safety reasons due to the presence of leopard seals, snorkeling was not permitted.

Immediately following each day of diving herbarium specimens were prepared by mounting seaweed thalli on Bristol paper (Online Resource 1), or samples were fixed as permanent mounts on microscope slides, using acetocarmine (to preferentially stain for pathogens) and 50% Karo Syrup™ and subsequently sealed with nail polish once dried (Küpper and Müller 1999). They were deposited in the herbarium of the British Antarctic Survey (BAS, Cambridge, UK). Fragments of all specimens were kept in silica gel or CTAB buffer (Phillips et al. 2001), both of which conserve DNA for further molecular studies. Filamentous brown algae were surveyed for eukaryotic pathogens as described previously (Küpper and Müller 1999; Strittmatter et al. 2013).

Given the limited time and logistic constraints at these remote locations, inevitably leading to a limited coverage of the smaller representatives of the flora, collections of seaweed specimens were supplemented by collections of substratum samples in sterile tubes. Following return to Europe and based upon a protocol developed for a similar study in the Juan Fernandez Islands (Müller and Ramirez 1994), these samples were incubated in Provasoli-enriched sea water (Starr and Zeikus 1993) under light and temperature regimes corresponding to their region of origin. Over approximately 3 months, they were monitored for algal outgrowth, from which unialgal isolates were made. Isolates were characterized and identified, both morphologically using a Zeiss PrimoVert™ inverted microscope and a Zeiss Axio Imager.D2™ compound microscope (Online Resource 2), and by DNA sequencing and comparison with published data. The isolates have been deposited in the Culture Collection of Algae and Protozoa (CCAP, Oban).

DNA extractions were performed using CTAB buffer as described previously (Gachon et al. 2009). Polymerase chain reactions (PCR) were performed to amplify a fragment of nuclear ribosomal DNA containing 3'-SSU, ITS1, 5.8S, ITS2 and 5'-LSU, using the primer pair ITS-

ITSPI/KIRI, ITSP1 (5' GGAAGGAGAAGTCGTAACAAGG 3'; Tai et al. 2001) and KIR1 (5' TTCAAAGTTTTGATGATT 3'; Lane et al. 2006), was used. PCR was carried out with an initial denaturation at 94˚C for 5 min, followed by 40 cycles of amplification consisting of denaturation at 94˚C for 30 sec, annealing at 45°C for 30 sec, and elongation at 72°C for between 1 min. The 40 cycles were followed by a final extension at 72°C for 5 min. PCR amplification was performed in a total volume of 25 μL, containing 1.25 units of Taq DNA Polymerase (Promega), 1x GoTaq Buffer, 5mM $MgCl_2$, 0.5mM dNTPs, 0.3mM of each primer and 1μL of template DNA. The alignment of each DNA sequence was conducted with the BioEdit Sequence Alignment Editor™ (Hall 1999). For identifying taxa, sequences were compared to published data by means of NCBI BLAST searches (Altschul et al. 1997).

Identification of herbarium specimens and live cultures was conducted (Online Resource 3) using available keys, in particular that of Wiencke and Clayton (2002). For present-day taxonomic and nomenclatural aspects AlgaeBase (Guiry & Guiry 2013) was consulted. Taxonomic details of species recorded by Moe and DeLaca (1976) have been updated (Table 1, see also Moe and Silva 1981; Moe 1986; Hommersand et al. 2009; Lin et al. 2012).

Our study also used diversity data obtained in 1975 at three sites in the region of the 2010-2011 sampling points, also sampled by scuba diving (maximum depth 33 m) (Moe and DeLaca 1976; Online Resource 4). These were Henkes Island (off the southern tip of Adelaide Island), Horseshoe Island and Square Bay (Fig. 1).

Affinities of seaweed species composition in the three sites that were sampled by Moe and DeLaca in 1975 (Henkes Island, Horseshoe Island and Square Bay) and the seven sites of the current study (Anchorage Island, Biscoe Wharf, Cheshire Island, Hangar Cove, Honey-bucket, Shack's Crack and South Cove) were compared using the Sørensen similarity index (Sørensen 1948).

Permanent mounts of filamentous algae, prepared at Rothera were surveyed after the expedition using a ZEISS Axio imager D2™ compound microscope at magnifications of 40-1000x, in search of novel pathogens and saprotrophs and imaged using Zeiss Zen 2011™ image processing software. Upon identification of organisms of interest, cultures were subjected to morphological examination, using a Zeiss Primo Vert™ inverted microscope initially to inspect

cultures and then by creating wet slides for investigation using the aforementioned compound microscope to try to reveal the affinities of these organisms.

Cultures which revealed pathogenic / saprotrophic organisms were also investigated molecularly with the SSU rRNA of existing DNA extractions being amplified using the primer pair ALG1 & ALG8 (Moro et al. 2003). The resulting amplicon was then ligated into the pJet™ cloning vector following the protocol of the CloneJet™ PCR cloning kit (ThermoScientific) and transformed into competent *Escherichia coli* cells (ActivMotif™) using the supplied protocol, through heat shock utilizing a water bath. These cells were then plated onto LB media$^{+Ampicillin}$ and left at 37°C overnight according to the manufacturer's instructions. Single colonies were picked and placed into a colony PCR using the pJet Forward™ and pJet Reverse™ sequencing primers. The PCR reaction was made up of 1x PCR buffer, 1.5 mM $MgCl_2$, 8 mM dNTPs, 0.2 mM primers and half a unit of GoTaq™ (Promega) in a 20 µl reaction, ran for 30 cycles (95°C-30s, 60°C-30s, 72°C-60s) with an initial 95°C denaturation step for 3 minutes. No final extension step was employed. A 5 µl aliquot was then run on a 1% (w/v) agarose gel and a single reaction was purified using the GeneJet™ PCR purification kit and sent for sequencing using the Eurofins Value Read sequencing service, with primers ALG1 and ALG8, to obtain the brown algal SSU rRNA sequence. Following the tentative identification of *Aplanochytrium* sp., this sequence was placed in an alignment with Labyrinthulomycete sequences and restriction enzyme sites were located and assessed for conservations with the members of the labyrinthulomycetes. *PleI* (New England Biolabs) was then used to digest 5µl of the colony PCR product following the manufacturers guidelines (37°C 1hr) and representatives of each restriction pattern were sent for sequencing using the primers ALG1, ALG8 and internal sequencing primers F706 (5'-TGTTGTCTCCAGCCATCC -3') and R796 (5'- ATTTTTGGTCTCCAACGAGG -3'). Acquired ABI files were checked for quality, trimmed and aligned with one another using Bioedit (Hall 1999). A consensus sequence was then produced and the sequence was imported into an alignment, in MEGA 6.0, containing several members of the Labyrinthulomycetye class, specifically *Aplanochytrium* sp., *Oblongichytrium* sp. and *Thraustochytrium* sp., the accession numbers of sequences contained within the alignment can be found on the resulting cladogram (Fig. 2). *Aplanochytrium minuta* is listed in the NCBI database *Labyrinthuloides minuta* (L27634; Leander et al. 2004), the species name label was therefore changed in the alignment.

The cladogram was produced by firstly using the ClustalW alignment tool available in MEGA 6.0 (Tamura et al. 2013) and manually checking the alignment to ensure parsimony. The alignment was then tested with a Tamura-Nei Maximum Likelihood model, with a Nearest Neighbour Interchange heuristic model. Gaps/missing data with a site coverage above 95% were treated as partial deletions and 1000 bootstraps were used as a test of phylogeny.

Results

All data on species encountered are provided in Table 1. A total of 110 macroalgal samples were collected, augmented by 3 live isolates from substratum samples. Among the 24 species recorded in the vicinity of Rothera Point during the 2010-2011 field season (Table 1), six were Phaeophyceae (brown algae), 12 Rhodophyta (red algae), five Chlorophyta (green algae) and one Chrysophyceae (golden algae). Two taxa of Chlorophyta were only identified among the three live isolates obtained from substratum samples (confirmed by both morphological and molecular approaches), and constitute new records for this region.

Sørensen's Similarity Index (Table 3) showed very low overlap in species composition of the communities sampled in the current study and those sampled in 1975. The highest similarity that was recorded between the two campaigns was at Henkes Island (1975) and South Cove (2010-2011) with 3 shared species, *Desmarestia menziesii*, *Plocamium cartilagineum* and *Trematocarpus antarcticus*, and a similarity index value of 0.18. In contrast, the highest similarity between the sampled areas in this study (2010-2011) was observed between Honeybucket and South Cove with 9 shared species and a similarity index value of 0.69, but also between Cheshire Island and South Cove with 9 shared species and a similarity index of 0.6.

A microscopic survey of filamentous brown algae (226 x *Pylaiella* sp., 58 x *Geminocarpus* sp., 1 x *Elachista antarctica*) did not reveal any unambiguous symptoms of eukaryotic pathogens, even though in several instances structures reminiscent of early-stage infections of *Eurychasma dicksonii* or *Anisolpidium* sp. were observed. Observations of permanent mounts of *E. antarctica* revealed single cells, not of algal origin, attached to the surface of algal filaments. Dimensions of the cells are approximately 35 µm in diameter. This, together with other morphological features comparable to previous reports of the labyrinthulomycete class (Moro et al. 2003; Damare and Raghukumar 2006) such as the presence

of an ectoplasmic net (Fig. 2 B, arrowed), which does not enrobe the cell (i.e. *Labyrinthula* sp.; Leander et al. 2004), led to the tentative identification of the organism as an *Aplanochytrium*. and is seen to attach the cells to the brown algal filament. Evidence for the association of this cell with the brown algal filament includes the observation that the cell was not washed away during the creation of permanent mounts, something that occurs to small organic matter that is not attached to the main body of the filament during permanent mount preparation. Due to the nature of the observations (i.e. within a permanent mount) the investigation of cellular movement along the ectoplasmic net and spore generation was not possible. Whether the processing of this material to permanent mounts has any effect upon the dimensions of the *Aplanochytrium* cell/ectoplasmic net is unknown. A 1635 base pair SSU rRNA sequences was successfully obtained from the organism under study here, which is shown to branch within the *Aplanochytrium* clade (94/100). The specimen appears to be a basal species of this genus, sitting on a long branch at an equal distance from all other *Aplanochytrium* sp. (97/100) (Fig. 3). The cladogram has been coded to allow easy interpretation of linkage between species. From this it can be noted that the substrate of the *Aplanochytrium* specimen can be a good indicator of its relations with other species, yet this new specimen, does not appear to have any close affinities to *A Aplanochytrium stocchinoi* previously isolated from Antarctica or *Aplanochytrium* sp. PR1-1 (*A. minuta*) previously isolated from brown algae.

Discussion

Seaweed biodiversity. The Antarctic is generally known for its low diversity of marine algae, attributed to the presence of sea ice and icebergs for much of the year. Comparison of the records from 2010-2011 with the previous 1975 study (Moe and DeLaca 1976) reveals a number of new records for this part of the Antarctic Peninsula, both at species and genus level (18 species and 14 genera; Table 1). The new records include four brown, eight red, five green and one golden algae. Seven species were observed in both sampling campaigns, separated by 35 years, while 18 species were only observed in 1975 and 18 species were only observed in 2010-2011.

Only three species in total grew in the incubated substratum samples in which common Antarctic species, particularly gametophytes of *Desmarestia*, were missing. It is possible that the

248 latter and other particularly temperature-sensitive Antarctic endemics (Wiencke and Tom Dieck
249 1989, 1990; Wiencke et al. 1994) did not survive the conditions during transport to the European
250 laboratory. The fact that two Chlorophyte taxa were not seen macroscopically *in situ* but
251 emerged from incubated substratum samples underlines the value of isolation / culturing work to
252 underpin macroalgal biodiversity surveys especially in remote regions and demonstrates that the
253 taxa were present at least as propagules if not as full-grown thalli. For one of these isolates, the
254 most similar available ITS1 sequence (*Ulvella leptochaete*) had only 82% similarity, and future
255 studies on the variability of ITS1 in these microscopic taxa may show whether it rather belongs
256 to a related species. The second green alga and the brown alga were clearly identified to species
257 level, as their ITS1 sequences were highly similar to previously sequenced specimens (Table 2).
258 Confidence in molecular identification of these samples is high since all taxa had been collected
259 and sequenced before from localities outside Antarctica. These sequences identities were then
260 strongly correlated with morphological characters, ensuring that no doubt remains over the
261 identities subscribed here.
262 The datasets available at the current time are clearly not sufficiently robust to support
263 speculation on whether the largely non-overlapping data obtained in the two surveys are
264 representative of genuine differences in diversity between the sampled areas or of any response
265 to environmental changes in the general region. It has to be highlighted that due to logistical
266 reasons, the sampling sites in 2010-2011 were not the same as those surveyed in the region in
267 1975, and there is also a lack of detailed information on habitat conditions at any of these
268 locations. As potential explanations we propose the following hypotheses: (1) limited range and
269 number of surveys (especially in 1975, when only 3 dives were conducted in this region); (2)
270 large variation between sites; (3) local loss of species observed in 1975, and replacement by the
271 species found in the current study. Lack of both baseline and repeat survey data are increasingly
272 recognized as a fundamental impediment to Antarctic biodiversity and biogeographical research
273 (Convey 2011; Convey et al. 2012). In this context, the combined records of both campaigns
274 presented here represent a useful dataset and checklist for future comparative studies aimed at
275 assessing the impact of climate or other changes on benthic communities. For most regions of the
276 world, there are few historic datasets of seaweed biodiversity (e.g. Asensi and Küpper 2012). In

277 this context, the value of records such as those of Lamb and Zimmerman (1977) and Moe and
278 DeLaca (1976) for the Antarctic Peninsula cannot be overestimated.
279 ***Pathogenic and saprotrophic organisms on Antarctic seaweeds.*** The question as to
280 whether eukaryotic pathogens occur in Antarctica in epidemic outbreaks similar to those reported
281 from temperate latitudes (Küpper and Müller 1999; Strittmatter et al. 2013) cannot be
282 conclusively answered as no pathogens were observed – however, it is well known that such
283 outbreaks are sporadic (Küpper and Müller 1999) and the period of the survey may have been
284 too short. Instead further sampling at other sites and during other seasons should be seen as an
285 important step to unveiling the potential role that algal pathogens play in Antarctic seaweed
286 ecology.
287 Significant to this study is the finding of a presumed saprotrophic *Aplanochytrium*
288 species upon *E. antarctica*. This genus diagnosis is completed by the morphological
289 characteristics presented here, with the presence of an ectoplasmic net (Fig. 2), not encasing the
290 spore, being the defining feature of this genus from other members of the labyrinthulomycte
291 class (Leander and Porter 2001, Leander et al. 2004). Though members of the genus
292 *Aplanochytrium* have been previously recorded from Antarctica (Moro et al. 2003) and upon a
293 brown alga (Leander et al. 2004), respectively, this finding is still of significant interest because
294 the specimen under investigation here appears to fall on a long branch an equal distance away
295 from the previously surveyed species (Fig.2). Given that all 8 previously described species have
296 yet to be molecularly characterized, it is conceivable that it does fall within one of these,
297 however as only the previously surveyed *A. minuta* has been described in association with brown
298 algae (Leander et al. 2004), it does seem possible that the organism observed in this study may
299 constitute a new species. Unfortunately isolation attempts of this organism were not successful
300 so far and only a single permanent mount is currently available for morphological
301 characterization, it is not suitable here to attempt to attribute a species name. The specimen here
302 is presumed saprotrophic, as the majority of previously reported interactions between
303 *Aplanochytium* and algae/seagrasses are (Tsui et al. 2009), however given the
304 pathogenic/predator-prey/commensalist relationship *Aplanochytrium* species have with
305 zooplankton (Damare and Ragkhumar 2010, Damare et al. 2013), it is possible that the specimen
306 investigated here has other affinities with the algal substrate. Indeed this would be a suitable line

of enquiry, should this species, or a similar species of the same lineage, be successfully isolated in the future.

Climate change. Antarctic seaweeds display plasticity and adaptability in response to extreme environmental conditions such as low temperatures and limited light availability (Wiencke and Amsler 2012). It is important to examine how environmental alterations, such as those caused by climate change, are going to affect algal seasonality, depth zonation and biogeography. As sea ice extent reduces along the Antarctic Peninsula (Turner et al. 2013), sub-Antarctic seaweeds can be expected to migrate to more southerly regions. When assessing the further consequences of these developments, the role of algal communities in structuring food webs - especially of the zoobenthos – must be considered (Wiencke 1996). In the Antarctic, shallow water benthic macroalgal communities are strongly affected by the grazing pressure of amphipods. Filamentous algae can therefore be found mostly in the intertidal zone where amphipods are rare (Amsler et al. 2011). The disappearance of sea ice, leading to increased light availability but also to increased habitat instability and damage through ice scouring, is therefore likely to alter the distribution and depth zonation of filamentous macroalgae, with knock-on or reciprocal effects on amphipod population density.

It should also be highlighted that species numbers from limited collections alone cannot be considered as a reliable proxy to estimate changes in algal communities impacted by climate change over a time span of several decades. In this context, local processes such as retreating glaciers with subsequent changes in bottom and water column characteristics (e.g. turbidity) can cause changes in local biodiversity (Quartino et al. 2013). Further analyses of present-day patterns of composition and distribution along environmental gradients (e.g. depth) or spatial scales could enable detection of differences with previous surveys.

The decline in sea ice cover off the Western Antarctic Peninsula, along with increasing atmospheric temperatures, has consequences for populations of marine biota, including several keystone species (Meredith and King 2005). The large brown algae *Himantothallus grandifolius* and *Ascoseira mirabilis* are major structuring elements of seaweed communities in the northern part of the Antarctic Peninsula. They are not widely established in the Adelaide Island area (there is only a single record of *H. grandifolius* from Henkes Islands in 1975, and none from the area in

2010-2011) but, as canopy-forming species, their arrival and more widespread occurrence would mark a major change in the phytobenthos. At present, the only dominant, large canopy-forming species around Adelaide Island is *Desmarestia menziesii*. Even though reported by Moe and DeLaca (1976), this species is thought anecdotally to have increased in abundance in the last 10 years (unpublished observations by divers of the British Antarctic Survey at Rothera).

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533

534 **Table 1.** Taxa recorded in1975 and 2010-2011 around the Southwest Antarctic Peninsula (Adelaide Island / Margaret Bay).
535 Taxa in bold: **New records of seaweed taxa for the Adelaide Island / Marguerite Bay region in 2010-2011.** Third column (ML/now/both): This indicates whether a taxon was only recorded by Moe
536 & De Laca 1975 ("ML"), only by the investigators of this study ("now") or by both surveys ("both").

Taxa	Phylum / Class		Locations 1975			Locations 2010-2011						
Taxa	Phylum / Class	ML/now/both	Henkes Island	Horseshoe Island	Square Bay	Anchorage Island	Biscoe Wharf	Cheshire Island	Hangar Cove	Honey-bucket	Shack's Crack	South Cove
***Adenocystis utricularis* (Bory de Saint-Vincent) Skottsberg**	Phaeophyceae	now				X				X		X
***Antarctosaccion applanatum* (Gain) Delépine**	Chrysophyceae	now				X		X				
Ballia callitricha (C.Agardh) Kützing	Rhodophyta	ML	X									
Callophyllis sp. Kützing	Rhodophyta	ML	X		X							
***Capsosiphon groenlandicus* (J.Agardh) K.L.Vinogradova #**	Chlorophyta	now										X
Clathromorphum sp. Foslie	Rhodophyta	ML	X									
Codiolum sp. A.Braun	Chlorophyta	ML	X									
Curdiea racovitzae Hariot	Rhodophyta	ML	X									
Desmarestia menziesii J.Agardh	Phaeophyceae	both	X				X	X		X		X
***Elachista antarctica* Skottsberg #**	Phaeophyceae	now						X				X
***Geminocarpus austrogeorgiae* Skottsberg $**	Phaeophyceae	now					X	X		X		X
Geminocarpus geminatus (J.D.Hooker & Harvey) Skottsberg	Phaeophyceae	ML	X									
Himantothallus grandifolius (A.Gepp & E.S.Gepp) Zinova*	Phaeophyceae	ML	X									
Hymenocladia sp. J.Agardh	Rhodophyta	ML	X									
***Hymenocladiopsis crustigena* R.L.Moe**	Rhodophyta	now				X	X	X			X	X
***Iridaea cordata* (Turner) Bory de Saint-Vincent**	Rhodophyta	now				X	X	X		X	X	X
Lithoderma antarcticum Skottsberg	Phaeophyceae	both		X		X		X		X	X	X
Lithophyllum antarcticum (J.D.Hooker & Harvey) Rosanoff	Rhodophyta	ML	X									
Mesophyllum sp. Me.Lemoine	Rhodophyta	ML	X	X								
***Monostroma hariotii* Gain**	Chlorophyta	now							X			
Myriogramme manginii (Gain) Skottsberg	Rhodophyta	ML	X									
Myriogramme smithii (J.D.Hooker & Harvey) Kylin	Rhodophyta	ML	X									
Notophycus fimbriatus R.L.Moe**	Rhodophyta	ML	X									
***Palmaria decipiens* (Reinsch) R.W.Ricker**	Rhodophyta	now				X				X		X
***Pantoneura plocamioides* Kylin**	Rhodophyta	now					X					X
Paraglossum salicifolium (Reinsch) S.-M.Lin, Fredericq & Hommersand***	Rhodophyta	both	X					X				
Phycodrys antarctica (Skottsberg) Skottsberg	Rhodophyta	ML			X							
***Phycodrys austrogeorgica* Skottsberg**	Rhodophyta	now				X					X	
Phyllophora abyssalis Skottsberg	Rhodophyta	ML			X							
Phyllophora antarctica A.Gepp & E.S.Gepp	Rhodophyta	ML		X	X							
Plocamium cartilagineum (Linnaeus) P.S.Dixon	Rhodophyta	both	X					X				X
Plocamium hookeri Harvey in J.D. Hooker & Harvey	Rhodophyta	both		X				X				
***Plocamium secundatum* (Kützing) Kützing**	Rhodophyta	now										X
***Porphyra plocamiestris* R.W.Ricker**	Rhodophyta	now								X		X

Porphyra sp. C.Agardh	Rhodophyta	ML		X								
***Pylaiella sp.* Bory de Saint-Vincent**	Phaeophyceae	now				X	X	X		X	X	X
***Rhodymenia subantarctica* R.W.Ricker**	Rhodophyta	now						X				X
Sarcodia sp. J.Agardh	Rhodophyta	ML		X								
Trematocarpus antarcticus (Hariot) Fredericq & R.L.Moe****	Rhodophyta	both	X									X
Ulva sp.* Linnaeus **	Chlorophyta	now								X		X
Ulvella leptochaete (Huber) R.Nielsen #	Chlorophyta	now				X						
***Urospora penicilliformis* (Roth) Areschoug**	Chlorophyta	now				X		X				

These records are based upon live isolates. Both *Elachista antarctica* CCAP 1308/1 (sample # 150111-5 / ANT10.3) and *Capsosiphon groenlandicus* CCAP 6004/1 (sample # 150111-5 / ANT10.1) were isolated in community from epiphytic *Pylaiella* sp . on *Desmarestia menziesii*; *Ulvella leptochaete* CCAP 6000/1 was also isolated from substratum sample # 200111-2 / ANT6. - Molecular data are available.
$ *G. austrogeorgiae* was always epiphytic on *D. menziesii*.
* *Phyllogigas grandifolius* is currently regarded as a taxonomic synonym of *Himantothallus grandifolius* (Moe and Silva, 1981).
** *Notophycus fimbriatus*, a newly described genus and species of marine Rhodophyceae, was recorded as *Iridaea undulosa* back in 1976 (Moe, 1986).
*** *Delesseria stephanocarpa* is currently regarded as a taxonomic synonym of *Paraglossum salicifolium* (Lin et al., 2012).
**** *Sarcodia montagneana* records from 1976 are referable to *Trematocarpus antarcticus* (Hommersand *et al.*, 2009).
***** Tubular / *Enteromorpha* morphology

537

538 **Table 2.** Live isolates of three algal taxa included in the present study.

539

Isolate number	**Species name**	**Date of collection**	**Locality**	**% identity to closest relative with publicly available sequences**	**Query cover**	**e value**	**EBI accession numbers for new sequences** (each containing 3'-18S rRNA gene, ITS1, 5.8S rRNA gene, ITS2 and 5'-28S rRNA gene)
CCAP 6000/1 (ANT6)	*Ulvella leptochaete* (Huber) R.Nielsen	20/01/2011	Anchorage Island	82%	81%	2.00E-52	HG931702
CCAP 6004/1 (ANT10.1)	*Capsosiphon groenlandicus* (J.Agardh) K.L.Vinogradova	15/01/2011	South Cove	98%	99%	3.00E-156	HG931701
CCAP 1308/1 (ANT10.3)	*Elachista antarctica* Skottsberg	15/01/2011	South Cove	99%	91%	0	HG931703

540

541 **Table 3.** Similarity (measured by Sørensen Similarity Index) between the assemblages at each pair of sites.
542

	Sørensen Similarity Index									
Shared species		**He**	**Ho**	**Sb**	**Ai**	**Bw**	**Ci**	**Hc**	**Hb**	**Sc**	**Co**
	He		0.09	0.10	0	0.09	0.2	0	0.08	0	0.18
	Ho	1		0.2	0.13	0	0.21	0	0.13	0.18	0.09
	Sb	1	1		0	0	0	0	0	0	0.10
	Ai	0	1	0		0.38	0.52	0	0.53	0.67	0.44
	Bw	1	0	0	3		0.53	0	0.53	0.55	0.52
	Ci	3	2	0	6	5		0	0.46	0.44	0.6
	Hc	0	0	0	0	0	0		0	0	0
	Hb	1	1	0	5	4	5	0		0.43	0.69
	Sc	0	1	0	5	3	4	0	3		0.36
	Co	3	1	0	6	6	9	0	9	4	

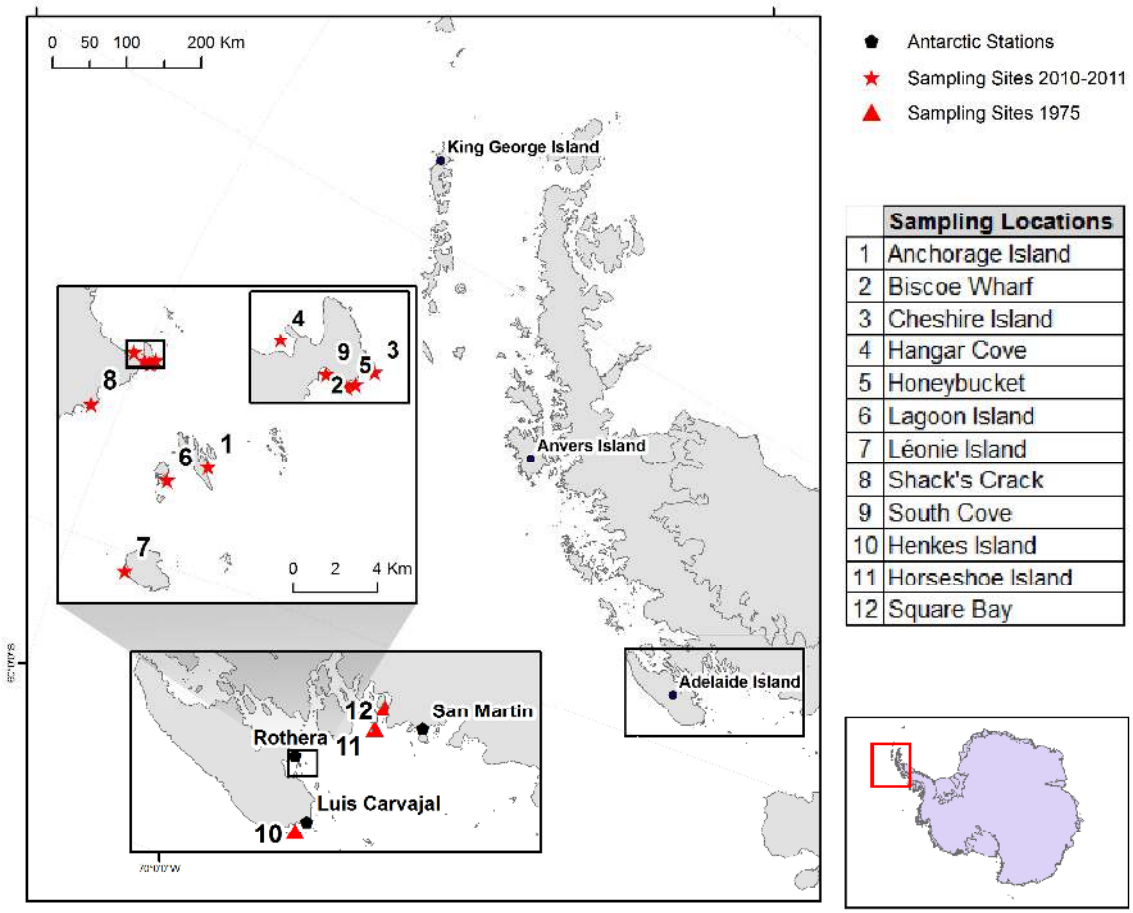
He: Henkes Island - 1975 (Moe & DeLaca 1976)
Ho: Horseshoe Island - 1975 (Moe & DeLaca 1976)
Sb: Square Bay - 1975 (Moe & DeLaca 1976)
Ai: Anchorage Island - 2010-2011
Bw: Biscoe Wharf - 2010-2011
Ci: Cheshire Island - 2010-2011
Hc: Hangar Cove - 2010-2011
Hb: Honey-bucket - 2010-2011
Sc: Shack's Crack - 2010-2011
Co: South Cove - 2010-2011

Figure 1. Study sites around Rothera Point, Adelaide Island, Antarctica.

Figure 2. *Aplanochytrium* cell associated with *Elachista antarctica* (ANT10.3) at 100x magnification (scale bars = 20µm). The *Aplanochytrium* cell can be seen to be rounded, around 35 µm in diameter. Internally no zoospores can be seen, thus it is assumed that this is a somatic cell. The ectoplasmic net (arrowed) is seen to attach the cell to the brown algal filament and measures approximately 34-35 µm in length and 1-3 µm in width. The ectoplasmic net does not encase the cell and migration of the cell along the ectoplasmic net was not observable due to the nature of the mount.

Figure 3. Maximum likelihood test of phylogeny of the 1635bp SSU rRNA sequence obtained from the *Aplanochytrium* sp. under investigation in this study. The sequence obtained shows strong support that this specimen falls within the *Aplanochytrium* clade (94/100) and that it is at an equal distance from all other *Aplanochytrium* sequences surveyed here (97/100). The key to the right indicates firstly the geographic location and secondly the substrate association of each sequenced tested. A trend can clearly be seen that substrate is a good predictor of branching affiliations within the genus. All sequences obtained associated with zooplankton, from three separate studies, form a monophylectic clade, while those obtained from sea grasses/algae, from six separate studies, with the exception of this novel basal sequence, form a paraphyletic clade. Within this second clade are two sequences labelled as being associated to unknown/unrecorded substrates: The first of these (*Aplanochytrium* sp. S1a) was found in salt marshes in Taiwan, the second (*Aplanochytrium kerguelense*) was taken from a culture collection and was originally described from sub-Antarctic waters.

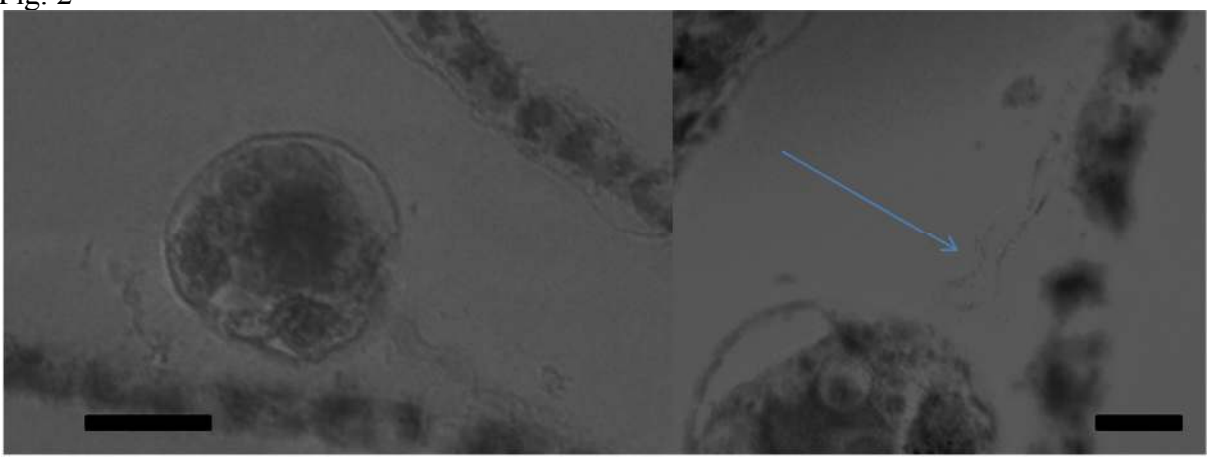
568 Fig. 1



	Sampling Locations
1	Anchorage Island
2	Biscoe Wharf
3	Cheshire Island
4	Hangar Cove
5	Honeybucket
6	Lagoon Island
7	Léonie Island
8	Shack's Crack
9	South Cove
10	Henkes Island
11	Horseshoe Island
12	Square Bay

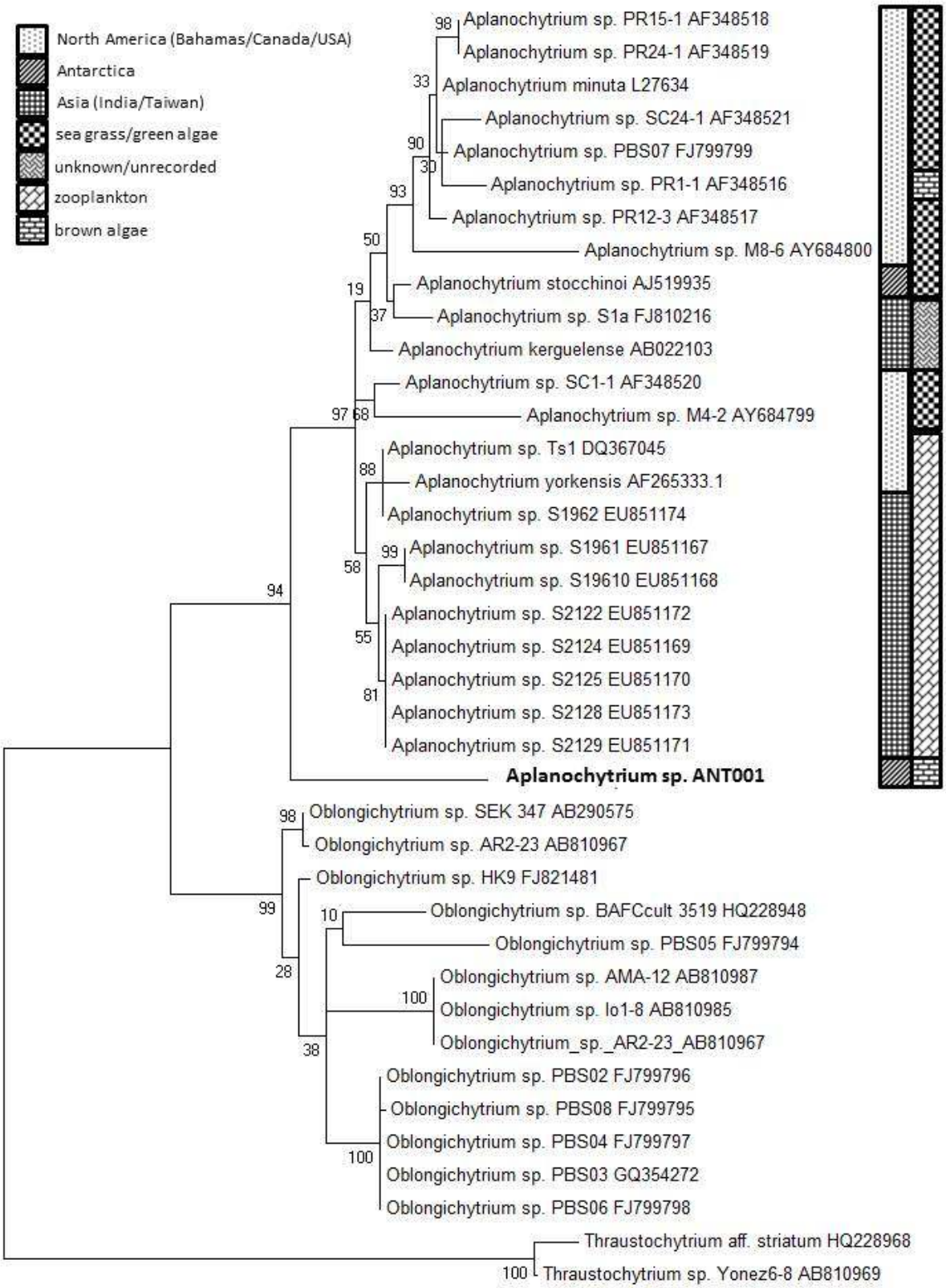
569

570 Fig. 2



571
572
573

574 Fig. 3


North America (Bahamas/Canada/USA)
Antarctica
Asia (India/Taiwan)
sea grass/green algae
unknown/unrecorded
zooplankton
brown algae
Aplanochytrium sp. PR15-1 AF348518
Aplanochytrium sp. PR24-1 AF348519
Aplanochytrium minuta L27634
Aplanochytrium sp. SC24-1 AF348521
Aplanochytrium sp. PBS07 FJ799799
Aplanochytrium sp. PR1-1 AF348516
Aplanochytrium sp. PR12-3 AF348517
Aplanochytrium sp. M8-6 AY684800
Aplanochytrium stocchinoi AJ519935
Aplanochytrium sp. S1a FJ810216
Aplanochytrium kerguelense AB022103
Aplanochytrium sp. SC1-1 AF348520
Aplanochytrium sp. M4-2 AY684799
Aplanochytrium sp. Ts1 DQ367045
Aplanochytrium yorkensis AF265333.1
Aplanochytrium sp. S1962 EU851174
Aplanochytrium sp. S1961 EU851167
Aplanochytrium sp. S19610 EU851168
Aplanochytrium sp. S2122 EU851172
Aplanochytrium sp. S2124 EU851169
Aplanochytrium sp. S2125 EU851170
Aplanochytrium sp. S2128 EU851173
Aplanochytrium sp. S2129 EU851171
Aplanochytrium sp. ANT001
Oblongichytrium sp. SEK 347 AB290575
Oblongichytrium sp. AR2-23 AB810967
Oblongichytrium sp. HK9 FJ821481
Oblongichytrium sp. BAFCcult 3519 HQ228948
Oblongichytrium sp. PBS05 FJ799794
Oblongichytrium sp. AMA-12 AB810987
Oblongichytrium sp. Io1-8 AB810985
Oblongichytrium_sp._AR2-23_AB810967
Oblongichytrium sp. PBS02 FJ799796
Oblongichytrium sp. PBS08 FJ799795
Oblongichytrium sp. PBS04 FJ799797
Oblongichytrium sp. PBS03 GQ354272
Oblongichytrium sp. PBS06 FJ799798
Thraustochytrium aff. striatum HQ228968
Thraustochytrium sp. Yonez6-8 AB810969

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