

Temporal development of hull-fouling assemblages associated with an Antarctic supply vessel

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ABSTRACT: Introduction of non-native species poses one of the greatest, but least understood threats to marine biodiversity. Whilst considerable research effort has focused on vectors such as ballast water, hull fouling remains poorly understood and there is a notable lack of data concerning the temporal development of fouling communities. Here we use remote video capture techniques to assess the development and change of fouling assemblages on an Antarctic supply vessel over a 2 yr period. Assemblages were dominated by cosmopolitan species, some of which are known to be invasive. We demonstrate that whilst areas surrounded by sea-ice are at low risk of introductions from this pathway, substantial fouling assemblages are routinely transported to sub-Antarctic islands where the thermal conditions may allow their establishment. Extent of fouling assemblages, and thus the threat of invasion, may be reduced by changing the dry docking regime and minimising port layover times and in-water cleaning of submerged hull surfaces.

KEY WORDS: Hull fouling · Invasion · Non-indigenous · Antarctica · Marion Island · Gough Island · Propagule pressure · ROV

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INTRODUCTION

The introduction of species to environments in which they have not evolved is one of the major threats to marine ecosystem function and biodiversity (e.g. Lubchenco et al. 1991). These introductions occur through a range of mechanisms, including shipping activities, aquaculture, the connection of waterways through canals and the activities of research facilities (Ruiz et al. 1997, Godwin 2005). However, introductions associated with shipping take primacy as the cause for marine non-indigenous species (NIS) introductions worldwide (Mills et al. 1993, Bax et al. 2001, Streftaris et al. 2005, Flagella et al. 2006, Mineur et al. 2007). Propagules are transported in ballast water (Carlton 1996, Ruiz et al. 1997, Grigorovich et al. 2003, Holeck et al. 2004) and on the hulls of ocean-going vessels (Gollasch 2002, Lewis et al. 2003, Mineur et al. 2007), and are moved around the world by a growing global network of shipping traffic (Drake & Lodge 2004).

The ecological and economic impacts of species introduced with ballast water are so extensive that

substantial legislation exists to reduce the flow of introductions via this pathway (Ruiz et al. 2000, Hewitt & Campbell 2007, Barry et al. 2008). Principally, this involves the International Convention on the Control and Management of Ship's Ballast Water and Sediments (IMO 2004). The recommendations of the Convention are focused on mid-ocean ballast water exchange (International Maritime Organization Resolution A.868[20], <http://globallast.imo.org/resolution.htm>) as a means to prevent the transfer of water (and organisms) between coastal habitats. In contrast, bio-fouling remains largely unmanaged and recent bans on the use of tri-butyl tin in anti-fouling paints are likely to result in increases in fouling until suitable alternatives are developed (Hewitt & Campbell 2007).

Marine introductions are of particular concern in Antarctica, because one of the main routes of transport of goods and people (scientists, logistics staff and tourists) to the continent is via ships. It is highly likely that these vessels also transport non-indigenous species to the region (Lewis et al. 2003, Tavares & De Melo 2004, Lee & Chown 2007). Unlike the rest of the world,

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ballast water introductions are typically of little concern in Antarctica as few vessels discharge ballast in the region, and it is prevented by the Antarctic Treaty (ATCM Resolution 3 2006). Therefore, biofouling is the greatest potential pathway for marine introductions and initial investigations have shown this potential could be realised (Hewitt & Campbell 2001, Lewis et al. 2003, Minchin & Gollasch 2003).

For economic reasons, modern commercial shipping typically has short port layover times (Lewis et al. 2003), which prevent the accumulation of large fouling assemblages (Godwin 2005). However, for Southern Ocean shipping, port layover times can be substantial during the austral winter, allowing large fouling assemblages to accumulate. Furthermore, because of the generally low travel speeds of these vessels, fouling communities are unhindered by physical disruption (e.g. shear stress) and so may survive transport over relatively long distances (Carlton & Hodder 1995, Davidson et al. 2008)

The risks of biological invasions in the Antarctic are only now being fully appreciated (Frenot et al. 2005). Whilst the threats and consequences of terrestrial invasions have been quantified and assessed for some areas, demonstrating that invasive species can cause extinctions and the alteration of ecosystem functioning (Frenot et al. 2005, Bergstrom et al. 2006, Chown et al. 2008), the picture for marine systems in the Antarctic is less clear (Aronson et al. 2007). To date there have been few published studies which explicitly consider the threat of marine introductions into the Southern Ocean as a result of shipping traffic (Lewis et al. 2003, 2005, 2006, Tavares & De Melo 2004, Clarke et al. 2005, Barnes et al. 2006, Lee & Chown 2007). Whilst it might seem plausible that the decline in temperature associated with the Antarctic Polar Frontal Zone would pose a barrier to introductions, this is not necessarily the case. Natural variation in temperature, and increases associated with global warming (Meredith & King 2005, Turner et al. 2005, 2006, 2007, Chapman & Walsh 2007), might enable species to survive in a region generally considered too extreme for them. Indeed there have been several documented cases of species which are usually found in temperate regions surviving in Antarctic waters (Clayton et al. 1997, Thatje & Fuentes 2003, Tavares & De Melo 2004, Lee & Chown 2007).

Each year more than 60 tourist (www.iaato.org) and 69 scientific support vessels (www.comnap.aq) leave temperate ports and travel to the Antarctic. All at least have the potential to transport non-indigenous species into the region. However, the level of risk posed by these vessels has not been fully assessed. It is known that some gateway ports to the Antarctic harbour several highly invasive species. For example, Cape Town,

South Africa, is infested with the highly invasive European shore-crab *Carcinus maenas*, while areas surrounding the port are home to other high-profile invasives such as the Mediterranean mussel *Mytilus galloprovincialis* (Robinson et al. 2005). Given the provisions of the Antarctic Treaty and its associated protocols (Mansfield & Gilbert 2008), as well as the management plans for many of the Southern Ocean islands visited by scientific support vessels (de Villiers et al. 2006), which all call for prevention of biological invasions, there is a substantial need for understanding the likely risks posed by hull fouling in the region.

Understanding of hull fouling in the Antarctic is currently limited to a few snapshot studies which have examined assemblages only once or twice (Lewis et al. 2003, 2004). Whilst such studies provide basic information on the types of organisms which typically associate with ship hulls, they likely underestimate the total diversity of biota being transported, since fouling assemblages develop and change over time (Berntsson & Jonsson 2003, Bram et al. 2005). Furthermore, sampling events often take place when the hull is occupied by a climax community (Mineur et al. 2007) which, whilst showing maximum abundances of fouling biota, may represent a low diversity state (Berntsson & Jonsson 2003). To appreciate fully the range of biota transported in association with ship's hulls, it is necessary to examine all developmental stages of assemblages and to assess the temporal scale over which they develop.

As a first step to achieving this, we undertook systematic surveys of the hull of the South African National Antarctic Programme (SANAP) supply vessel, SA 'Agulhas', which almost exclusively services South Africa's scientific stations in the region, over a period of 2 yr. We tracked the development and change of fouling communities from immediately after the vessel left dry dock, through 2 complete re-supply seasons. Biota which become entrained with the hull will be highly related to the propagule source pool (Palmer 1988, although see da Fonsêca-Genevois et al. 2006), and so species level identifications will not be comparable between locations. Therefore, rather than focusing at the species level, here biota have been broadly classified into 4 functional groups: (1) biofilms and slimes, (2) fine and filamentous algae, (3) macroalgae and (4) macrofauna.

MATERIALS AND METHODS

Study vessel. The SA 'Agulhas' is a flat-bottomed, ice-strengthened cargo vessel, 115 m in length. To prevent accumulation of fouling biota, the hull and sea-chests are painted with Interspeed 340 (International Paints), a controlled depletion, self-polishing, anti-

fouling paint containing a gum resin polymer system and copper oxide and zinc oxide biocides. The vessel is based in Cape Town and its primary purpose is to resupply the SANAP research stations on Marion Island (46° 54' S, 37° 45' E), Gough Island (40° 20' S, 09° 54' W) and at Dronning Maud Land (71° 40' S, 02° 51' W, continental Antarctica) (Fig. 1). Typically these voyages occur in the austral summer: Gough Island is resupplied in September, Marion Island in April and the South African National Antarctic Expedition (SANAE) station (Dronning Maud Land) in December.

Remote video survey technique. A Videoray Explorer remotely operated vehicle (ROV) unit was used to capture continuous video footage at a rate of 15 MB s⁻¹ for each transect. A quadrat was fitted to the unit so that when it was perpendicular to the side of the vessel a 0.01 m² section was demarcated. Digital footage was stored in the form of an MPEG2 file. Images were randomly extracted from the MPEG2 files using VirtualDub 1.6.15 (Free Software Foundation). Only frames which were in focus and contained the requisite 0.01 m² area were used. Because of the difficulty in obtaining frames which met these criteria for surveys conducted in the Antarctic, it was possible only to use 10 frames from each port and starboard transect and 20 from the underside of the vessel. Coverage by abiotic and biotic variables was visually estimated. Abiotic variables were the proportions of intact and damaged paint (either by abrasion from ice or floating debris or by the ad-

dition of rubber from the fenders), and biotic variables comprised 4 groups: microalgae and slime, filamentous algae, macroalgae and macrofauna (Coutts & Taylor 2005) (see Fig. S1 in MEPS Supplementary Material at www.int-res.com/articles/suppl/m386p097_app.pdf for examples of the extracted images).

Other studies investigating hull-fouling assemblages, such as Lewis et al. (2003), have used scrapers to collect samples for later identification. This method is advantageous as it allows closer examination of organisms post-sampling and thus potentially more accurate identification. Collecting physical samples of organisms may also allow researchers to test the organisms' viability. However, in addition to the logistical difficulties associated with using SCUBA, scraping hulls to collect samples is likely to dislodge organisms that may settle onto substrata and subsequently establish (Minchin & Gollasch 2003). Whilst this is unimportant when the vessel is docked in Cape Town, it would clearly be a concern for the Antarctic region, where several of the present surveys were undertaken to understand the extent of transportation of hull-fouling assemblages to the ship's destinations.

Using a remote photographic capture device allows easy and safe access to hull surfaces but its advantages may be limited by the difficulties of classifying organisms correctly. However, previous studies (e.g. Carleton & Done 1995, Hughes & Atkinson 1997, Mayfield et al. 2000, Floerl & Inglis 2005) have successfully used similar equipment and methods to determine the composition of benthic communities. Because inaccurate classification of biota was likely to be the primary source of error in this methodology, the confidence limits of this photographic surveying method by comparison with a physical scraping method were determined.

Measurement of sampling error. The SA 'Agulhas' was put into dry dock in June 2006 for 14 d. Immediately prior to dry docking, the ROV was used to take video footage and still images were then extracted of twenty 0.01 m² areas of fouled hull. Once the vessel was in dry dock, the previously photographed areas were scraped clean. Samples were stored in 70% ethanol and later identified at the laboratory (Day 1969). Identification of these samples was the prime source of data used to construct the list of species found in each fouling class, although some macrofauna (*Ciona intestinalis* and *Obelia dichotoma*) which were not present at the time of this test were added later (Table 1). Thus, biota recorded in the images were verified by identification of samples. In addition, following Coutts & Taylor (2005), biota from the scrapings and the photographic images were classified as being fine algae or slime, filamentous algae, macroalgae or macrofauna. The composition of assemblages identi-

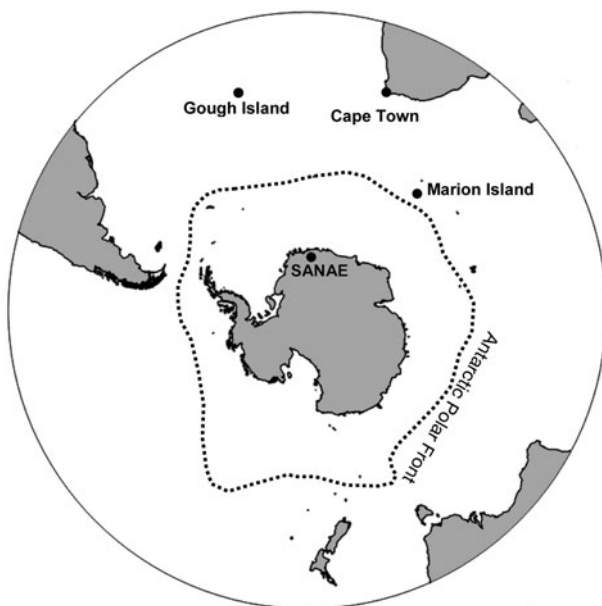


Fig. 1. Locations visited by the SA 'Agulhas' and relative position of the Antarctic Polar Front. SANAE: South African National Antarctic Expedition station

Table 1. Description of fouling classes (adapted from Coutts & Taylor 2005) with taxa identified from the hull of the SA 'Agulhas' (this study)

Class	Taxa
Biofilms	Slime Fine algae
Filamentous algae	<i>Ceramium</i> sp. (Rhodophyta) <i>Ectocarpus siliculosus</i> (Phaeophyta)
Macroalgae	<i>Ulva</i> sp. (Chlorophyta) <i>Enteromorpha intestinalis</i> (Chlorophyta) <i>Grateloupia filicina</i> (Rhodophyta)
Macrofauna	<i>Ciona intestinalis</i> (Ascidiacea) <i>Obelia dichotoma</i> (Hydrozoa) <i>Lepas</i> sp. (Cirripedia)

fied with the 2 methods was then compared using a 1-way analysis of similarity (ANOSIM) based on Bray-Curtis similarities (Primer 5.1.2, Plymouth Marine Laboratory).

Hull surveys. Between August 2006 and May 2008, 12 surveys of the hull were carried out. For the first part of the sampling period, until April 2007, when not at sea, the vessel was docked at Quay 500 in Cape Town Harbour. After this time, the vessel moved its permanent berth to the Victoria and Alfred Waterfront, approximately 1 km away. Both sites are commercial docks which are protected by a harbour wall and are likely to have a similar propagule source pool.

Surveys of the hull were carried out in Cape Town Harbour immediately before departure for Marion Island, Gough Island and the Dronning Maud Land

coast and then again as soon as possible after arrival at the islands or in Antarctica. The underside of the ship was classified as a single zone due to homogeneous abiotic conditions and the difficulty in identifying transect boundaries, whereas the port and starboard hull surfaces were divided into ten 2 m wide transects separated by 4 m (see Fig. 2). Operational constraints, such as the presence of thrusters, the main screw and discharge ports, meant that it was not possible to survey the rear 40 m of the ship's hull. In addition, the first 5 m of the hull was not included in surveys as this region slopes steeply; thus a 2 m transect would cover a smaller area than a 2 m transect conducted on the vertical hull surface towards the centre of the vessel. Although these areas have been highlighted as niche areas where fouling biota may develop because of abrasion of anti-fouling coatings (Lewis et al. 2003, Piola & Johnston 2008), their omission in sampling area selection should not affect the overall pattern of temporal development of assemblages in this particular case, as biota in these niche areas are likely to develop at the same rate as in other areas of hull equivalently damaged by ice scour which are included in the sampling methodology.

The influence of location on the ship's hull on the abundance of fouling cover was analysed using a generalized linear model (GLZ) in R 2.3.1 (R Development Core Team 2006) assuming a binomial error distribution and using a logit-link function. A second GLZ was used to compare fouling cover before and after voyages. Total fouling cover (from all groups) and voyage stage were included as parameters in the model.

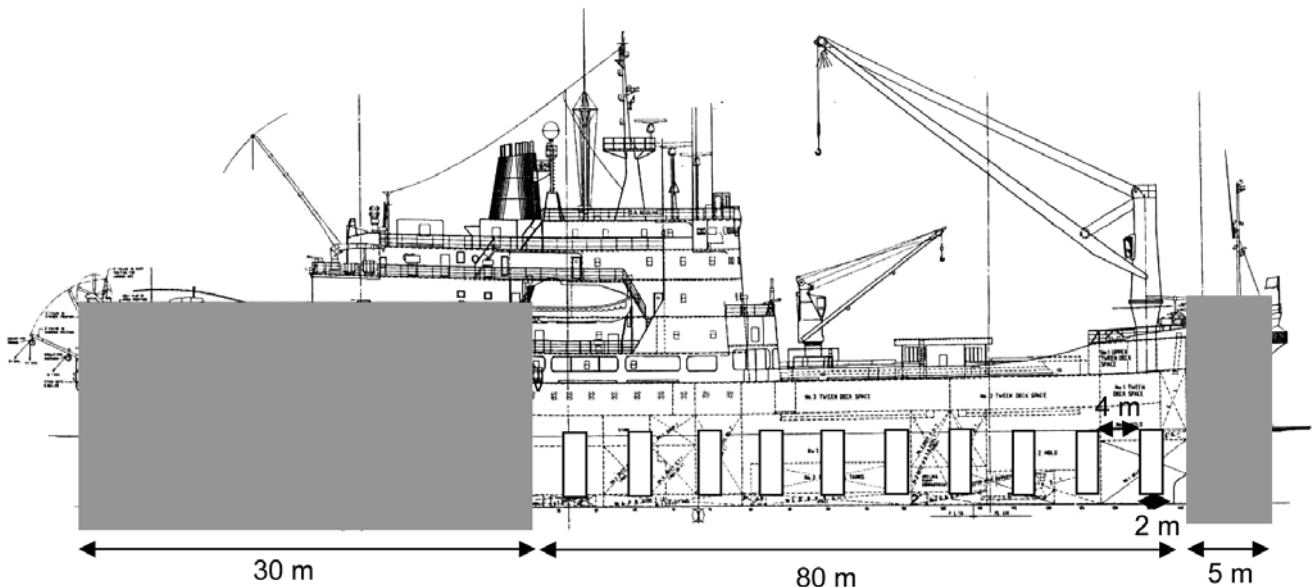


Fig. 2. No sampling zones for the SA 'Agulhas' indicated by grey boxes to fore and aft of vessel. From the foremost edge of the aft no sampling zone, ten 2 m sampling zones were demarked every 4 m along the length of the ship spanning a total of 80 m, in each of these 2 m sampling zones 10 still images of the 0.01 m² quadrat were randomly extracted from the video footage from each sampling event

RESULTS

Measurement of sampling error

The taxonomic composition of samples collected by taking physical samples and samples collected using the ROV survey method were highly similar (ANOSIM global test, $R = 0.021$, $p = 0.99$; when R is 1, samples within sampling methods are more similar to each other than samples from other sampling methods, when R is 0, similarities within and between sampling methods are the same). Thus the ROV survey method was judged an acceptable means by which to assess the taxonomic composition of fouling assemblages.

Hull surveys

Assemblages found on the SA 'Agulhas' were characterised by a low diversity. In total, only 8 species were identified (in comparison with 56 identified by Lewis et al. 2003) (Table 1), although it is possible that some cryptic species were not detected. These are all species with cosmopolitan distributions (OBIS 2008) known to occur within the Table Bay area (Robinson et al. 2005). However, the distribution of these organisms over the surface of the hull was not even: across all voyages, the starboard and underside of the vessel had significantly less fouling than the port side ($\chi^2_{2,866} = 703.28$, $p < 0.001$). The starboard side lies against the harbour wall when the vessel is in port and is in constant contact with fenders, indicating that light, supply of settling larval spores from current flow and low disturbance are important for the development of fouling assemblages. The low amount of fouling cover on the underside of the vessel may also in part be explained by the low light conditions and the fact that this area of the hull escapes significant abrasion and subsequent damage to anti-fouling paint when the vessel travels through sea-ice.

Between August and December 2006, the anti-fouling paint on the hull remained intact and provided comprehensive protection against the settlement of fouling biota. During this period, no macroalgae or macrofauna were found, with only biofilms and fine algae attached to the hull surface (Fig. 3). In December 2006 and again in December 2007, the vessel travelled to the Dronning Maud Land coast and en route passed through substantial amounts of sea-ice. In December 2006 ca. 30% of the antifouling coating was removed from the hull due to ice scour. It is likely than an equiv-

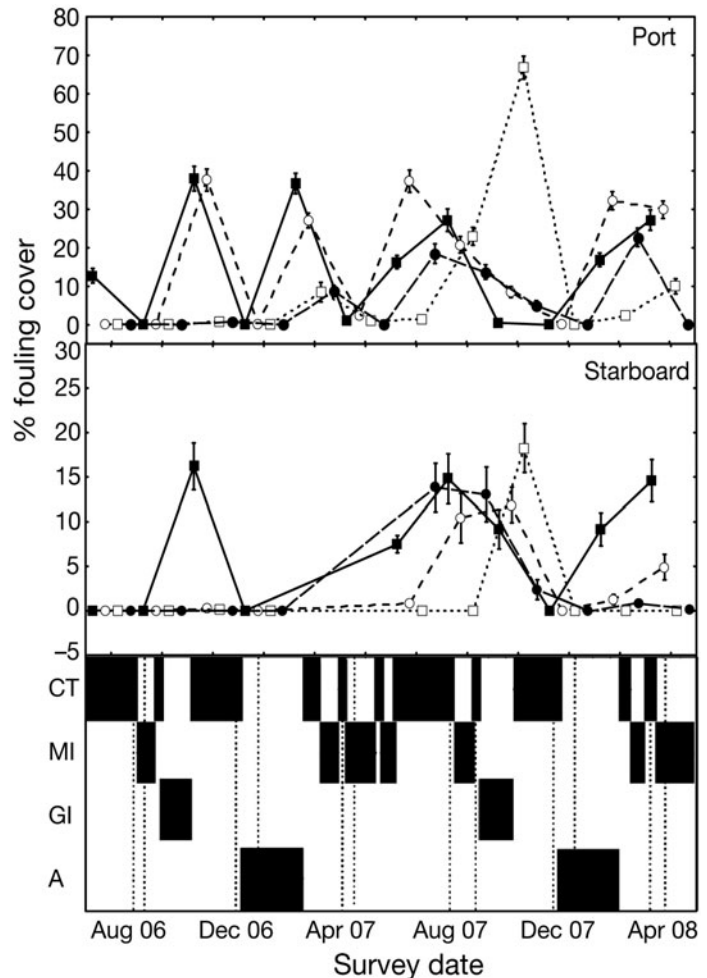


Fig. 3. Mean (\pm SE) percentage surface of the ship's hull that was covered by biota from each of the fouling 4 classes: biofilms (\blacksquare —), filamentous algae ($-\circ-$), macroalgae ($\cdots\square\cdots$) and macrofauna ($-\bullet-$), on the port (top panel) and starboard (middle panel) sides of the vessel. Note that the y-axis scales for port and starboard are different. The bottom of the ship is not displayed as no fouling cover was observed. Voyage schedule and sampling intervals (\cdots) are indicated in the bottom panel; CT = Cape Town, MI = Marion Island, GI = Gough Island, A = Antarctica

alent amount of antifouling coating was removed when the vessel passed through the ice in December 2007, but because of the extensive fouling assemblages which were present on the pre-voyage survey, it was not possible to evaluate the state of the underlying substrate to make a before and after comparison. Upon returning to Cape Town, paint-free areas were rapidly recolonised by macroalgae and macrofauna, groups that were previously not present (Fig. 3), indicating that ice scour plays a pivotal role in determining the formation and extent of fouling assemblages.

Successional processes were complex, but essentially followed a cyclical pattern. Initially the most abundant types of biota were fine and filamentous

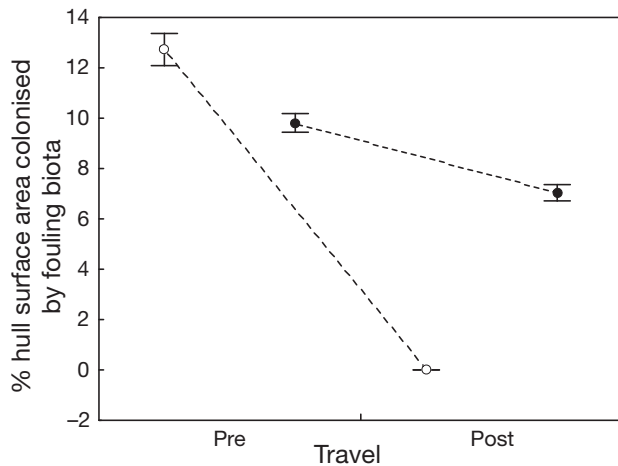


Fig. 4. Mean (\pm SE) fouling cover before and after travel through sea-ice (○) and travel not involving sea-ice (●)

algae, which are typical of early successional phases. In December 2006, the vessel first passed through sea-ice; when the vessel returned to port and the hull surface was recolonised, fine and filamentous algae declined in abundance and macroalgae and macrofauna became dominant. When the ship passed through sea-ice in December 2007, this late successional community was removed and once again biota from early successional stages dominated assemblages. However, probably because a greater amount of the hull surface was free from anti-fouling paint, after a second passage through the ice, this process appeared to occur more rapidly.

Ice scour removes all biota attached to the external surfaces of the hull, thus leading to a significant reduction in the extent of fouling recorded on surveys before and after sea-ice travel ($\chi^2_{1,3440} = 742.1$, $p < 0.001$) (Fig. 4). When travelling to Marion and Gough Islands, the vessel did not encounter sea-ice, and although there was a significant reduction in the area of hull which is covered by fouling assemblages ($\chi^2_{1,5348} = 54.3$, $p < 0.001$), a substantial proportion of assemblages remained intact, thus presenting a potential biosecurity threat (Fig. 4).

DISCUSSION

Threat of marine introductions in the Antarctic

The SA 'Agulhas' has the potential to transport substantial numbers, if not a substantial diversity, of sessile marine biota into the Antarctic region as a hull-fouling assemblage. If other vessels travelling to the region are transporting similar propagule loads, and there is every indication they do (see Lewis et al. 2003), shipping traffic must be thought of as a considerable

biosecurity concern. However, because the abundance of fouling organisms changes over time and with voyage characteristics, not all regions of the Antarctic face the same risk. Any location visited after a vessel has travelled through ice but before it has returned to a temperate port is at low risk from invasions. Whereas any locations which are not surrounded by sea-ice and are visited after a period of port layover where fouling assemblages have accumulated are at a heightened risk of invasion.

At present, even in the summer months, large stretches of the Antarctic are surrounded by pack ice (Simmonds & Jacka 1995, Yuan & Martinson 2000) and whilst this is the case, the continent remains relatively protected. However, due to recent reductions in the extent of sea-ice (de la Mare 1997, Eicken & Lemke 2001), in some years it is possible to access parts of the Antarctic, especially the northern Antarctic Peninsula, without passing through any sea-ice, potentially exposing marine communities in these areas to an increased risk of invasion. This problem is compounded as 21 of the 65 stations in Antarctica are located on the peninsula (www.conmap.aq), making it a focal point for shipping traffic. No sea-ice is encountered on voyages to sub-Antarctic islands, placing them at particular risk.

However, it is not known is whether fouling biota would be able to overcome subsequent barriers to invasion and establish in the Antarctic region. For some species there are indications that both the establishment and reproductive barrier could be surmounted (see Richardson et al. 2000 for description of barriers). For example, *Ciona intestinalis*, a common invader of mussel beds that can depress local species richness through competitive exclusion (Blum et al. 2007, Lambert 2007), is known from the Russian port of Murmansk (68° 58' N, 33° 5' E), where its critical thermal minima was recorded as 0°C (Dybern 1965). The thermal limit to reproduction for this species is somewhat higher than the limit to survival, with zygotes developing only above 8°C and larvae above 4°C (Dybern 1965). These temperatures are within the sea surface temperature range experienced at Gough and Marion Islands. Therefore it seems highly probable that if suitable habitat were available, this species would be able to establish in some regions of the Antarctic.

Even when the absolute thermal tolerances of biota are not known, simple examination of differences in sea surface temperature between known and potential ranges provides an indication that many fouling biota would be able to survive. In the case of the SA 'Agulhas', the mean annual temperature difference between its home port of Cape Town and Marion Island is ca. 8.5°C, between Cape Town and SANAE is 17.1°C and

there is no mean annual difference sea surface temperature between Cape Town and Gough Island (Mélise et al. 2003). Similar temperature gradients are likely to also occur for other Antarctic gateway ports (such as Hobart, Ushuaia and Punta Arenas) and the destinations which they serve. If the full biosecurity threat of this pathway is to be comprehended, a pressing need exists to establish the environmental tolerances of fouling biota and their likely competitive interactions with indigenous biota, given that competition is a significant process structuring marine benthic and intertidal systems (Dayton 1971, Barnes & Kuklinski 2004, Guichard 2004).

At least for SANAP, and for vessels from other Antarctic operations using the port as a gateway to Antarctica, in part this task is simplified by the low diversity of biota found on the SA 'Agulhas'. There are several possible reasons for this low diversity including differences among fouling species in tolerance to the copper antifoulants in the hull coating (Yebra et al. 2006, Dafforn et al. 2008, Piola & Johnston 2008), insufficient time in the layover port for the hull to adequately sample the species pool and match/mismatch between the availability of the ship hull and the availability of settling larvae and spores. One more intriguing possibility for this could be the presence of an invasive species, *Carcinus maenas*, in Cape Town Harbour (Robinson et al. 2005). This crab is a voracious predator (Floyd & Williams 2004, Miron et al. 2005, but see Breen & Metaxas 2008) and the high densities found in the harbour may have eliminated many other species (Le Roux et al. 1990, Robinson et al. 2005) and prevented extensive assemblages from developing. Although no comfort for the conservation of species indigenous to the shores of South Africa (but see Hampton & Griffiths 2007), *C. maenas* may inadvertently be reducing the risk of invasion of the Antarctic region by species that might otherwise have been common in the harbour. However, whether this benefit might be outweighed by the fact that the hull-fouling assemblages are dominated by widespread, tolerant species, capable of establishing in many regions, is not yet clear. Moreover, *C. maenas* might itself pose a risk through its introduction to Antarctic regions served by vessels entering the area via the port of Cape Town. This species has not been found in the sea chests of the SA 'Agulhas' (Lee & Chown 2007), nor was it detected in the present study, but it could potentially survive either in ballast water as larvae or in sea chests as an adult.

One important limitation to the present study is the poor knowledge of the diversity of the near-shore environment in many Antarctic locations relative to the size of the region (but see Grindley 1978, Barnes 2006, Lutjeharms & Ansorge 2008). Because of this, it is un-

known whether any potential invasive species have been introduced (but see Thatje & Fuentes 2003, Tavares & De Melo 2004, Aronson et al. 2007), and whether the species transported on ships hulls are being moved outside their previous distributional ranges and therefore can be considered alien (Richardson et al. 2000) or are simply being moved around within their ranges. Even if the latter is the case, host and recipient regions may contain populations with different genetic characteristics, thus resulting in genetic homogenization (Olden 2006). If this question is to be answered, there is urgent need to identify and characterise native and introduced biota at the molecular level (Booth et al. 2007).

Mitigation

Until such time as a full biosecurity assessment can be made, the risk of introducing non-native species could be minimised by having more frequent dry dockings and changing the time of dry docking to immediately after a vessel returns from Antarctica. In so doing, the period when hull surface with damaged anti-fouling paint is available for settlement is minimised. As a result, the habitats most at risk from marine introduction (in the SA 'Agulhas' case Marion and Gough Islands) would not be exposed to such great propagule pressure. Although this would mean finding additional charters for some vessels during the austral winter, reducing port layover so that large fouling assemblages cannot accumulate would be an effective strategy and is consistent with the need for economic efficiency which dictates that ships should spend most of their lifetime at sea. Alternatively, in-water cleaning prior to departure to localities most at risk from introduction could also be a cost-effective strategy to reduce the biosecurity threat.

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