Polar Biology (2018) 41:1923–1935
https://doi.org/10.1007/s00300-018-2332-3

ORIGINAL PAPER

Patterns in the distribution and abundance of sea anemones off Dumont d'Urville Station, Antarctica

Leslie A. Watson[1] · Jonathan S. Stark[2] · Glenn J. Johnstone[2] · Erik Wapstra[1] · Karen Miller[1,3]

Received: 18 May 2017 / Revised: 16 March 2018 / Accepted: 30 April 2018 / Published online: 24 May 2018

Abstract

Knowledge of ecological interactions is integral for informed management, especially in the rapidly changing Antarctic marine ecosystem. Nonetheless, even basic ecological relationships are unknown for most benthic species, including conspicuous predatory species such as sea anemones. The aim of this study is to understand the ecology of sea anemones in the Terre Adélie region. Using video footage collected by remote operated vehicle (ROV), we examined sea anemone distribution and abundance in relation to predator and prey abundance, presence of other taxa and habitat structure. The ROV was deployed over ten different transects with depths ranging from 32 to 251 m. A total of 332 sea anemones were observed across 6.6 km^2 of seabed surveyed. We compared sea anemone abundance with habitat type and substrate attachment. Multivariate analysis in PRIMER was used to examine community composition. Sea anemone density was not significantly associated with habitat types. However, sea anemones were associated with the biogenic substrates, ascidians and bryozoans. This association suggests a potential future vulnerability for Antarctic sea anemones if bryozoan and ascidian distributions are impacted by climate change-associated ecosystem disturbances.

Keywords Marine benthos · Actiniaria · Biodiversity · Terre Adélie · Distribution · Abundance

Introduction

Distribution, abundance, and habitat association in Southern Ocean sea anemones (Actiniaria) are poorly understood, particularly at local (hundreds of metres to tens of kilometres) and regional (tens of kilometres to hundreds of kilometres) scales. Many Southern Ocean sea anemone species are endemic to the Southern Ocean with 25% having a circumpolar distribution (Rodriguez et al. 2007). The majority of existing studies are from the Antarctic Peninsula region and have been conducted at a relatively broad scale with individual species distributions described under large generalized Antarctic sectors (Rodriguez et al. 2007; Rodriguez and Fautin 2014). The few records that do exist from regions other than the Antarctic Peninsula (Dunn 1983; Fautin 1984) are from early last century (Carlgren 1927, 1949; Carlgren and Stephenson 1929). Furthermore, these studies give few details on habitat associations and other ecological factors that may influence species distributions.

In non-polar regions, there are strong associations between anthozoan communities and the physio-chemical properties of habitats (Fautin 1988). Even slight changes, such as small changes in depth (< 5 metres) or a few degrees in temperature, can cause a shift in the distribution and dynamics of anthozoan communities (Fautin 1988). Recently, extreme warming events have increased globally and in 2015 and 2016 the longest or most intense marine heat wave was experienced by one-quarter of the ocean surface area (Oliver et al. 2017). These record temperatures caused a global-scale coral bleaching event (Hughes et al. 2017). Individual anthozoan taxa bleached to different extents with large robust corals showing little or no bleaching (Hughes et al. 2017). However, when the marine heat

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00300-018-2332-3) contains supplementary material, which is available to authorized users.

✉ Leslie A. Watson
Leslie.Watson@utas.edu.au

[1] School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, TAS 7001, Australia

[2] Australian Antarctic Division, 203 Channel Hwy, Kingston, TAS 7050, Australia

[3] Australian Institute of Marine Science, 35 Stirling Hwy, Crawley, WA 6009, Australia

waves were at the most extreme, all coral taxa showed severe bleaching (Hughes et al. 2017). Sea anemones may be similarly sensitive to changes in physical conditions, including the environmental stresses generated by human disturbance and predicted under climate change scenarios.

Regions of the Antarctic continental shelf with high influxes of nutrients carried by outflow of deep bottom water across the shelf support diverse benthic communities, structured by sponges and corals (Post et al. 2010). Strong currents and increased turbulence in submarine canyons resuspend particles enhancing food supply, which support high densities of filter feeders such as sea anemones (Post et al. 2010). Along the Antarctic Peninsula, sponge species diversity is influenced by temperature and depth with cold deep spots supporting higher sponge species numbers (Kersken et al. 2016). In shallow benthic waters, communities are strongly influenced by sea ice, sedimentation and light (Clark et al. 2017). For example, the shallow waters around Casey Station with shorter sea ice duration, more light and less sedimentation are typically dominated by algae, whereas in areas where sea ice duration is longer, with less light and higher sedimentation, invertebrates dominate (Clark et al. 2017). Changes in sea ice concentration and duration are a major concern for Southern Ocean ecosystems (Gutt et al. 2015; Clark et al. 2015, 2017). Forecast changes in Southern Ocean environments are predicted to effect benthic communities in many ways, for example, via an increase in phytodetritus in newly exposed benthic habitats after ice shelf breakout (Gutt et al. 2015), through ocean acidification effects on calcifying communities such as bryozoans (Gutt et al. 2015), increases in sedimentation around retreating glaciers (Sahade et al. 2015), and changes in coastal sea ice influencing macroalgae distribution (Clark et al. 2013). Understanding sea anemone distribution and ecology at a local and regional level can help resolve key ecological interactions in the Antarctic benthic ecosystems and allow us to infer how environmental stressors, such as climate change, might impact sea anemone distribution and benthic community structure.

Sea anemones are important members of benthic communities and play several roles including as predators, filter feeders, prey and/or epibionts. Some sea anemone species are opportunistic feeders taking advantage of a variety of readily available food (Shick 1991), feeding on diatoms, eggs, and small crustaceans in the water column [e.g. *Metridium senile* (Sebens 1981)]. Other sea anemones [e.g. *Isotealia antarctica and Urticinopsis antarctica* (Brueggeman 1998)], are active predators (Shick 1991) preying on echinoderms (starfish and sea urchins), other cnidarians, and copepods (Dayton and Robilliard 1970; Brueggeman 1998; Amsler et al. 1999; Gutt et al. 2015). Some species of sea anemone attach to gastropods or hermit crabs forming a symbiotic relationship (Mercier and Hamel 2008; Goodwill et al. 2009). In these relationships, sea anemones have been observed protecting the other organism and in return the sea anemones benefit from greater access to food and are able to escape predators (Mercier and Hamel 2008; Goodwill et al. 2009). Symbiotic relations with gastropods have been observed in both species of the Southern Ocean sea anemone genus *Isosicyonis* (Rodriguez and López-González 2008). There is very little literature on the predators of Antarctic sea anemones but nudibranchs, fish, starfish, larger worms, and pycnogonids have been observed feeding on them in regions other than the Southern Ocean (Ottaway 1977), and are likely to be predators of Southern Ocean sea anemones. Thus, with limited information on their diets and especially their predators in the Southern Ocean, we have limited understanding of the role that biological interactions have in driving sea anemone distribution, especially combined with habitat features such as suitable attachment substrate availability, or physical factors (e.g. currents and temperature).

The Southern Ocean benthic ecosystem is highly diverse with representatives from most major groups of marine plants and animals (Pearse et al. 1991). Benthic diversity is known to increase with depth in Polar regions, due to the impact of ice scouring from sea ice, icebergs, and/or anchor ice in shallow waters (Gutt 2001). These habitats are characterized by a constant low, but stable temperature (seasonal changes of ± 0.5–2.8 °C) and low fluctuations in salinity (34.6–34.9 range) (Knox 2007). A review of the Antarctic benthic ecosystem identified several different community types based on their ecological interactions (Gutt 2007). These community types comprised suspension, filter and deposit feeder communities; a predator-driven community; physically controlled assemblages; and low or zero abundances assemblages (Gutt 2007). Although recent research has seen an increase in studies of Southern Ocean ecosystems, including habitat and biological interactions (Stark 2000; Peck et al. 2005; Gutt 2007; Baird and Stark 2014; Peña Cantero 2014; Peña Cantero and Manjon-Cabeza 2014; Stark et al. 2014), most of the biological interactions in these communities remain poorly understood.

The Terre Adélie region of the Southern Ocean is an area where many of the biological interactions remain unknown and little is known of species distributions. The majority of research on the benthos that has been conducted around Terre Adélie was during a single marine census of the deeper benthic communities, in depths > 150 m (Causse et al. 2011). Only one study has focused on benthic communities from shallower depths and found that physical parameters such as disturbances from glaciers, iceberg scouring, light, and current regime influence the benthic diversity from depths of 20 to 110 m (Gutt 2007). The diversity of sea anemones is unknown for the shallower depths from 30 to 150 m from the Terre Adélie region around Dumont d'Urville Station. The aim of this study was to describe sea anemone distribution and abundance in the benthic habitats of the Terre Adélie region around Dumont d'Urville Station, between 30 and 250 m, based on observations made using a Remotely Operated Vehicle (ROV). It examines the relationships between sea anemone distribution and other factors including other sea anemone species, predator–prey interactions, presence of other taxa, and habitat structure.

Materials and methods

There is a short period during the austral summer when the sea ice breaks out that allows access to benthic ecosystem in the Antarctic continental shelf region. ROV videos are a useful tool in providing coverage of large areas (100 s of metres) in fine detail. Benthic research and observation by diving is not possible below 30 m. Some remote methods of sampling, such as trawl collections are non-selective and only provide community composition data but not information on ecological associations. The use of an ROV, however, allows non-destructive fine-scale examination at greater depths and the collection of more detailed information, such as sea anemone associations with substrate attachment and habitat type. An ROV, Achille M4, Comex, with a high-resolution camera (Sony HVRA1E), was deployed from the "Sea Truck" barge. Video samples were collected in Terre Adélie, near Dumont d'Urville Station, during the REVOLTA project 1124 supported by the French Polar Institut (IPEV) and the Muséum National d'Histoire Naturelle (MNHN) during the Austral summer of 2012/13.

The ROV was deployed in a single direction from designated study stations (Fig. 1). Stations were selected from a range of areas around Dumont d'Urville with average depths ranging from 32 to 251 m and transect lengths ranging from 338 to 999 m (Table 1). The depth, latitude and longitude were collected at the start, finish (Table 1) and at 10 min intervals, during the ROV deployment. From the video footage, sea anemones were identified and counted for each 10 min transect interval. The field of view from the ROV was estimated to be approximately 1 m wide, and this was used to determine total bottom area surveyed.

We concentrated on large sea anemone species, with body columns approximately 5 cm or greater because the video quality did not allow us to enlarge smaller sea anemones adequately for identification. Each sea anemone was identified (where possible) based on gross morphology according to Brueggeman (1998). *Urticinopsis antarctica* (Carlgren 1927) and *Glyphoperidium bursa* (Roule 1909) are difficult to tell apart through visual inspection on videos and were combined as "Peach Anemones" based on their large size, numerous tentacles and a yellowish peach colour (Fig. 2a, b). *Isotealia antarctica* (Carlgren 1899) was identified by its orange colour and fewer tentacles than the Peach Anemones (Fig. 2c). The morphological difference between *Artemidactis victrix* (Stephenson 1918) and *Hormathia lacunifera* (Carlgren 1927) was based on the colour of the body column whereby *Artemidactis* is smooth and white and *Hormathia* has a brownish lower column (Fig. 2d, e). *Stomphia selaginella* (Stephenson 1920) and *Hormosoma scotti* (Stephenson 1918) are also difficult to distinguish from each other through visual inspection on a video and were grouped as "Marbled Anemones" based on their marbled orange and white column (Fig. 2f).

When a sea anemone was observed on the video, a still image was captured from the video footage, and from this all other taxa present within one metre (bryozoans, ascidians, sponges, holothurians, brittle stars, sea urchins, sea stars, crinoids, fish, zooplankton, jellyfish, pycnogonids, gastropods, polychaetes, and bivalves) were recorded along with the primary attachment substrate of each sea anemone (sediment, rock, bryozoans, ascidians and other species). At the end of every 10 min transect interval, a general habitat category was assigned (sediment, bryozoan dominated, ascidian dominated or mix) for the entirety of the interval.

Total sea anemone density, densities of each taxa, and the density of other invertebrate species (density = number of individuals/m^2) were calculated per 10 min interval by dividing the total number observed by the area surveyed (distance between the latitude and longitudinal points of the 10 min interval multiplied by the 1 m transect width). When fields of ascidians or bryozoans were observed, a maximum of 50 individuals was recorded, as it was impossible to count and distinguish between every individual. All densities of individual sea anemone species and other taxa per 10 min interval were used to analyse community patterns and to examine species distributions and species associations by means of non-parametric multivariate techniques using the PRIMER-6 software package (Clarke and Gorley 2015). Averaged sea anemone densities were compared across habitat types and substrate attachment was compared across transects. Community analysis amongst sea anemones and other taxa was conducted using Bray–Curtis similarity matrices and non-metric multidimensional scaling ordinations (nMDS) and cluster analysis (using group average clustering). Only transect intervals that had sea anemones present were included. SIMPROF and SIMPER analysis (similarity percentages, PRIMER) were used to identify the key species and taxa of the assemblage that contributed the most to dissimilarity between groups and similarity within groups indentified by cluster analysis. Pearson correlations were used to examine associations between predators (i.e. gastropods and pycnogonids), prey species (i.e. ophiuroids, urchins, asteroids, medusozoans, and bivalves) and sea anemone densities.

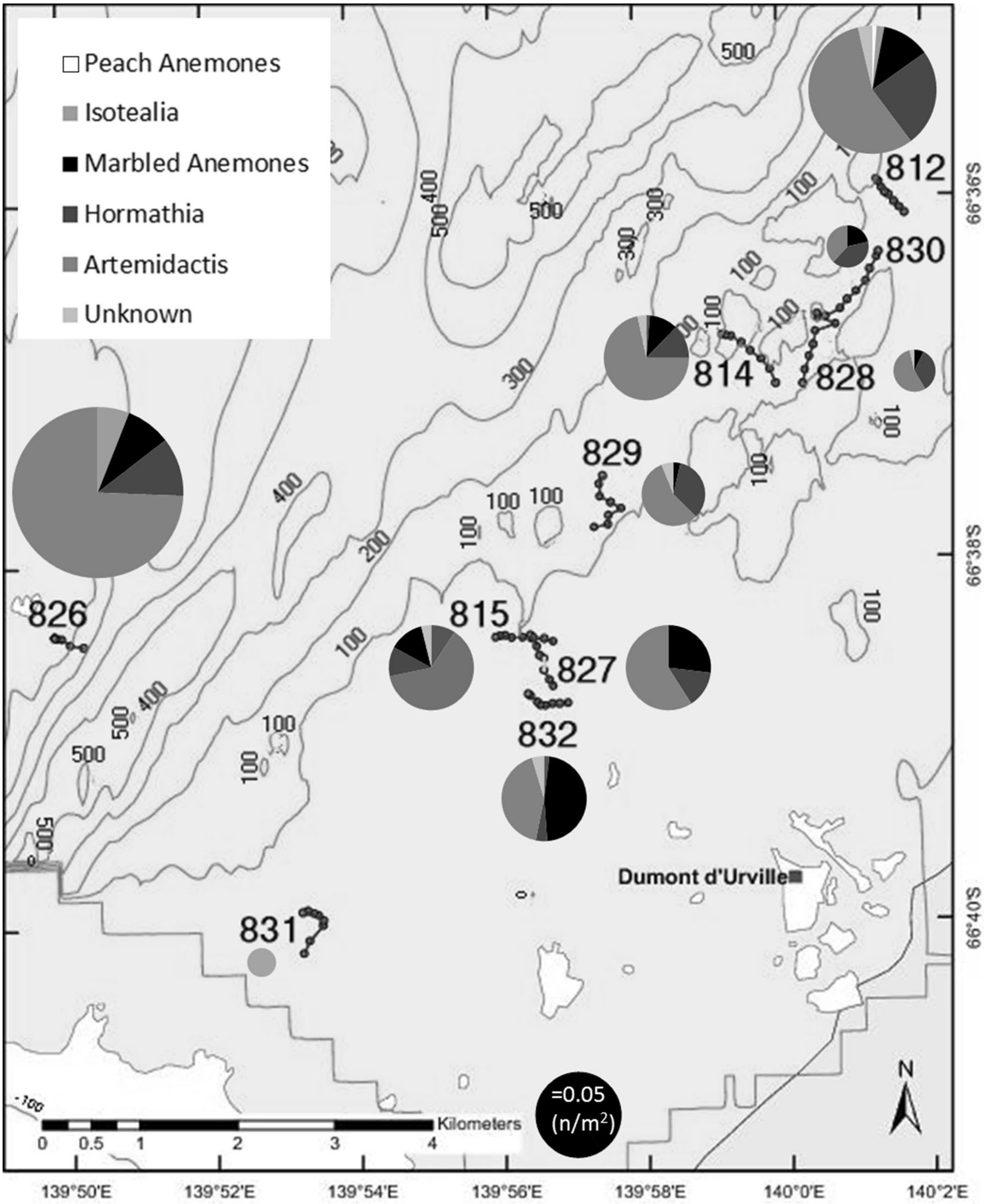

Fig. 1 Revolta campaign ROV video transects at each station from the Terre Adélie region near Dumont d'Urville (DDU) with sea anemones density (number of individuals/m^2) for each transect indicated in pie charts. Pie chart size is relative to total sea anemone density for the transect

Results

A total of 332 sea anemones were observed across the ~ 6.6 km^2 of seabed surveyed. Sea anemone diversity varied among transects and with depth; *Artemidactis*, *Hormathia* and Marbled Anemones were the most abundant sea anemones across all transects (Fig. 1). *Isotealia* was the only sea anemone identified in the shallowest transect (32 m) (Fig. 1), and it was otherwise only found on the two deepest transects. There were very few individuals of Peach Anemones or *Isotealia* (Table 1).

The majority of sea anemones were observed to be in close proximity to other sea anemones in their area, occurring in intermittent or patchy clusters along each transect.

Table 1 ROV video transect location with average depth (m) and transect length (m) for sampling of sea anemones from Terre Adélie region near Dumont d'Urville station

Station	Latitude	Longitude	Depth (m)	Length (m)	Total anemone density (n/m^2)	Peach anemone density (n/m^2)	Isotealia density (n/m)	Marbled Anemone density (n/m^2)	Hormathia density (n/m^2)	Artemidactis density (n/m^2)	Unknown anemone density (n/m^2)
831	− 66.669,083	139.887317	32	647	0.001	0.000	0.001	0.000	0.000	0.000	0.000
832	− 66.646,367	139.949583	87	461	0.078	0.002	0.000	0.036	0.003	0.033	0.004
827	− 66.6448	139.946117	98	593	0.056	0.000	0.000	0.015	0.008	0.033	0.000
814	− 66.61725	139.998733	99	783	0.076	0.001	0.000	0.008	0.010	0.054	0.003
815	− 66.640717	139.946267	99	597	0.083	0.008	0.000	0.052	0.009	0.011	0.003
828	− 66.617267	140.0051	109	999	0.026	0.000	0.000	0.002	0.009	0.014	0.001
829	− 66.630283	139.95625	110	853	0.032	0.000	0.000	0.001	0.011	0.018	0.002
830	− 66.611133	140.010617	119	886	0.025	0.000	0.000	0.005	0.010	0.010	0.000
812	− 66.601667	140.029133	128	451	0.155	0.002	0.003	0.019	0.038	0.087	0.006
826	− 66.640583	139.83745	251	338	0.27	0.000	0.016	0.023	0.030	0.201	0.000
Average					0.802	0.001	0.002	0.016	0.013	0.046	0.002

Overall average sea anemone density (number of individuals/m^2) per transect and individual sea anemone group densities per transect

An analysis of their spatial pattern of distribution using the index of dispersion (Fisher 1970) (variance/mean ratios) found that sea anemones (all species combined) were randomly distributed (Chi squared test, I $((s^2/\text{mean})/(n-1)) = 0.14$, $p > 0.05$, df = 9). Individual species were also randomly distributed along the transects. However, analysis of distribution for ascidians ($I = 2.15$, $p = 0.02$, df = 9) and bryozoans ($I = 25.6$, $p < 0.001$, df = 9) found that both showed clumping and clustering along transects. Sea anemones were found in a variety of habitats that included fields of ascidians or bryozoans, sedimentary bottoms, and mixed habitats (Fig. 3). Sea anemone density was not significantly different amongst habitats (Fig. 3); however, this may be due to the coarse resolution used for habitat classification and difficulty in identifying sediment habitats on video. A Pearson's correlation showed only weak relationships between sea anemone density and bryozoan and ascidian density (Table 2). Sea anemones were found attached to a range of different substrates including bryozoans, ascidians, tube worms and sponges; however, the majority of attachment for sea anemones was to either bryozoans or ascidians (Fig. 4). Despite sea anemone density being highest in sedimentary habitats, sea anemones in sedimentary habitats were attached to biogenic substrate. Sea anemone density varied with depth. The highest density occurred in the deepest transect, while the shallowest transect had the lowest density (Fig. 1).

An nMDS and cluster analysis, with a SIMPROF test, of community data showed the majority of transect intervals formed three main groups (Fig. 5, cluster groups C, D, and E overlaid on MDS; Table 3) and two smaller groups (cluster groups A and B) containing one and two intervals (Fig. 5; Table 3). The SIMPER analysis showed that group A was categorized by high bryozoan density, group B had low ascidian and anemone density, group C had high ascidian and sponge density, group D had medium bryozoan and ascidian density, and group E had low bryozoan and ascidian density (Fig. 5). To detect bias from depth, a second cluster analysis removing the shallowest and deepest transects (831 and 826) resulted in the same trend. Bubble plots of sea anemone, bryozoan and ascidian densities were overlayed on the MDS plot (Fig. 6) and showed that groups with a higher concentration of sea anemones also had higher concentrations of bryozoans and ascidians. Bubble plots of individual sea anemone species supported the relationship with bryozoans and ascidians (Fig. 6). Bubble plots of predator/prey species' density mirrored the sea anemone density trend and also showed a relationship with bryozoans and ascidians (Fig. 6). Densities of prey and predator species were not correlated with overall sea anemone density. There were significant positive correlations between *Hormathia* and *Artemidactis* with prey species, ophiuroids and asteroids (Table 2).

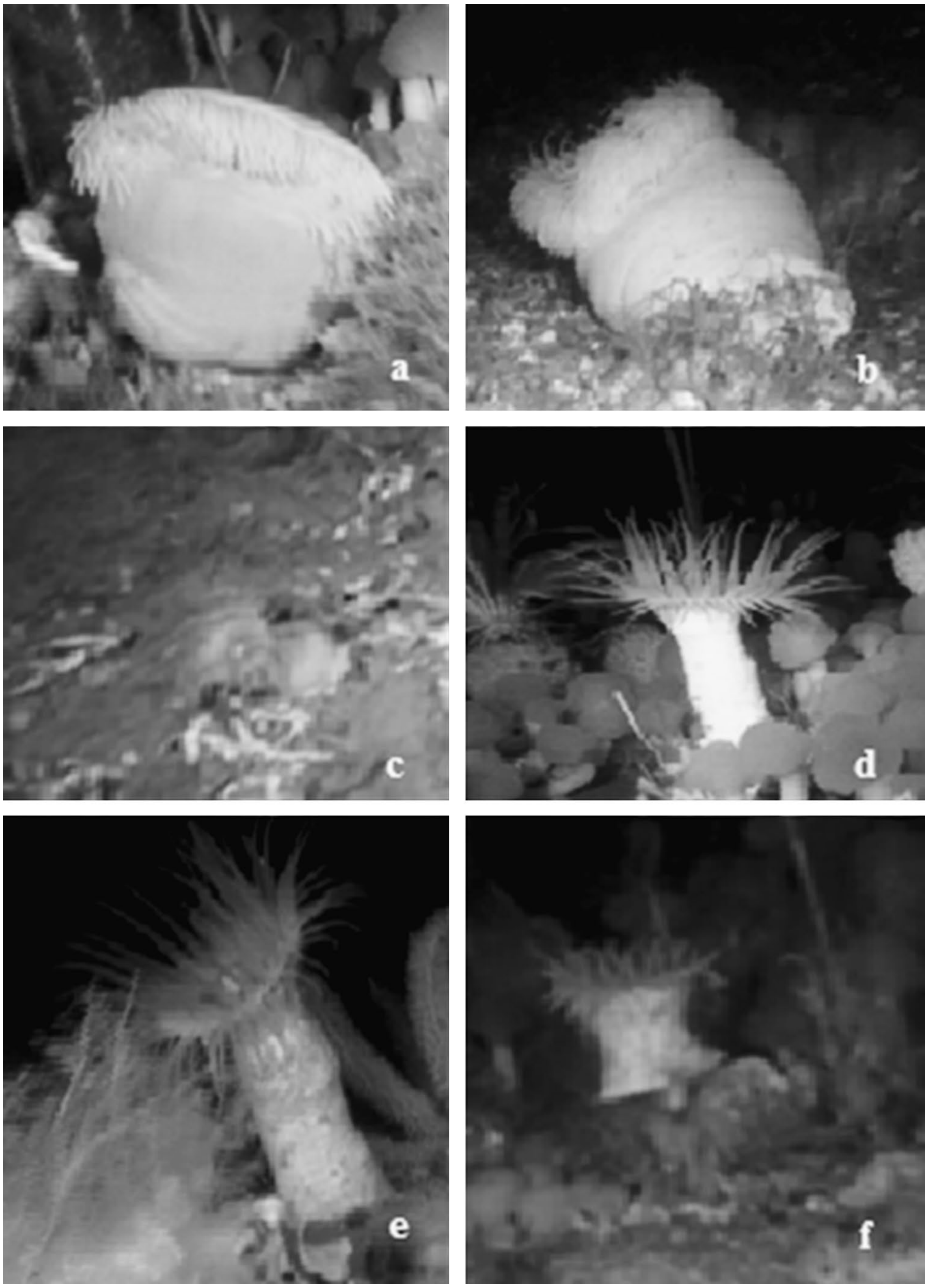

Fig. 2 Sea Anemone identification from Terre Adélie, near Dumont d'Urville station from ROV video transects: **a**, **b** Peach Anemones (includes *Urticinopsis antarctica* and *Glyphoperidium bursa*), **c** *Isotealia antarctica*, **d** *Artemidactis victrix*, **e** *Hormathia lacunifera*, **f** Marbled Anemones (includes *Stomphia selaginella* and *Hormasoma scotti*). Colour images in Online Resource 1

Discussion

Sea anemones were found in all areas surveyed around the coast of Terre Adélie, near Dumont d'Urville station in the depths ranging from 30 to 250 m. We identified sea anemones from all of the transects to species or morpho-group, based on their external morphology. Sea anemones more often relied on biogenic substrate for attachment, such as communities of ascidians and bryozoans, when compared with non-biogenic substrate, such as sediment and rocks, suggesting that biogenic habitat composition plays an important role in determining their distribution.

Species that control directly or indirectly the availability of resources to other species and thus affect the distribution and abundance of the other species have been termed ecological engineers (Gutt et al. 2015; Rimondino et al. 2015). Two important ecological engineers found in Southern Ocean benthic ecosystems are bryozoans and ascidians (Wood et al. 2012; Rimondino et al. 2015). Ascidians and bryozoans along with other ecological engineers (e.g.

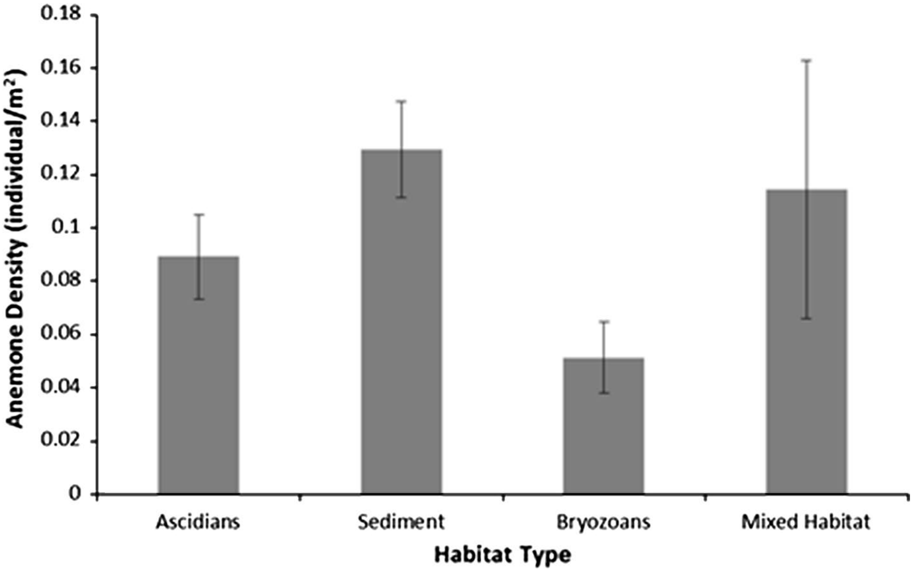

Fig. 3 Sea anemone density ± SE per habitat type with standard error from ROV video transects near Terre Adélie, near Dumont d'Urville station. PERMANOVA analysis showed no significant difference between habitat types (*p* = 0.39)

hydrocorals, gorgonians, sponges) can reach high densities in the Southern Ocean benthic ecosystems creating Antarctic marine animal forests (Gutt et al. 2015). Our study showed a clear association between the presence of bryozoans, ascidians and sea anemones in the Dumont d'Urville Sea (Figs. 5, 6, and Table 2) suggesting these taxa are important ecosystem engineers in the coastal regions of Antarctica.

Marine benthic communities dominated by large sessile suspension feeders, such as bryozoans and ascidians, create three-dimensional complex structure and provide habitat, shelter and food for other species (Wood et al. 2012; Gutt et al. 2015). They can encompass a broad range of habitats, for example, ascidians can recruit to soft sediment substrate and subsequently provide the structure for other benthic organisms such as anemones to attach (Rimondino et al. 2015). Elevation gained by attaching to ascidians may enable sea anemones to access food higher in the water column and provide stability against currents. Communities that are rich in suspension feeders are often in areas of strong currents (Gutt and Starmans 1998; Gutt et al. 2015), which provide horizontal movement of food particles across the seafloor (Jansen et al. 2018). Furthermore, the sea anemones *Metridium senile* and *Anthoe albocincta* have been observed feeding on ascidian tadpole larvae suggesting that the ascidians are potentially providing a food source for sea anemones (Nelson and Craig 2011Atalah et al. 2013). Bryozoans also form marine animal forests, providing structures for other organisms in the benthic environment, creating increased macroinvertebrate diversity (Wood et al. 2012). In Antarctica, habitat-forming bryozoan communities can extend for more than 1000 km creating a habitat for diverse benthic communities (Wood et al. 2012). Cnidarians have been recorded living directly on bryozoans (Wood et al. 2012) and sea anemones could also potentially be using the eggs and larvae from the bryozoans as a food source.

The observed patchy distribution of sea anemone species may also reflect the effects of reproductive mode on sea anemone recruitment and dispersal. Sea anemones have a wide array of reproductive strategies, with the majority using both sexual and asexual reproduction (Shick 1991; Bocharova and Kozevich 2011). Sea anemones can form clonal aggregations through fission and the release of brooded young (generated either sexually or asexually) that settle rapidly near the parent. This could explain low dispersal and patchiness observed on the transects compared with wider dispersal that might be expected through broadcast spawning of gametes and subsequent planktonic development of larvae (Ayre and Grosberg 1995). Other brooding benthic invertebrate species, for example, *Abatus cordatus* (sea urchin), have extremely low dispersal rates at a regional level due to a non-planktonic reproductive strategy (Poulin and Feral 1995; Ledoux et al. 2012). In contrast, broadcast spawners such as *Nacella concinna* (gastropod), have a high larval dispersal rate as evident by genetic connectivity (Hoffman et al. 2011). The reproductive mode of Antarctic sea anemones has scarcely been studied (Rodriguez et al. 2013), and it is unknown whether reproductive mode has influenced their patchy distribution in this study. The conspecific clustering of individuals observed along the transects, however, strongly suggests localised recruitment, which could alternatively be explained by habitat selection at the time of settlement and recruitment. This could be tested by examining the genetic structure of sea anemone populations. Brooding developmental modes can also lead to genetic differentiation among populations of Antarctic benthic invertebrates (Baird et al. 2012).

Table 2 Pearson correlations between sea anemone species, prey and predators from ROV video transects near Terre Adélie, near Dumont d'Urville Station

	Anemone Density	Peach Anemones	Isotealia	Marbled Anemones	Hormathia	Artemidactis	Unknown Anemone	Ascidian	Ophiuroids	Asteroids	Urchins	Other Anemones	Bryozoans	Medusozoa	Pycnogonid	Gastropod	Bivalve
Anemone density		–	**	**	**	**	**	**	**	**	**	**	**	–	*	**	–
Peach Anemones	0.198		–	–	–	–	*	–	–	–	–	–	–	–	**	–	–
Isotealia	0.431	− 0.087		–	–	**	–	*	–	–	–	–	**	**	–	**	–
Marbled Anemones	0.471	0.258	0.031		–	–	–	–	–	–	–	–	**	–	–	*	–
Hormathia	0.664	− 0.019	0.262	0.051		**	–	**	**	**	**	**	**	–	–	–	–
Artemidactis	0.882	0.078	0.406	0.113	0.584		**	**	**	**	**	**	**	–	–	*	–
Unknown Anemone	0.482	0.375	0.115	0.188	0.168	0.433		**	**	**	**	**	–	–	**	–	–
Ascidian	0.512	0.132	− 0.085	0.131	0.476	0.441	0.534		**	**	**	*	–	–	*	–	–
Ophiuroids	0.652	0.160	0.307	0.146	0.512	0.630	0.629	0.722		**	**	**	–	*	*	–	–
Asteroids	0.649	0.259	0.231	0.207	0.518	0.592	0.392	0.581	0.686		**	**	**	–	*	–	–
Urchins	0.405	− 0.070	− 0.045	0.040	0.432	0.410	0.372	0.665	0.657	0.383		–	–	–	–	–	–
Other anemones	0.860	0.226	0.494	0.210	0.564	0.826	0.478	0.338	0.595	0.583	0.243		**	–	*	**	–
Bryozoans	0.748	0.253	0.446	0.621	0.371	0.562	0.169	0.032	0.267	0.456	0.019	0.609		–	–	**	–
Medusozoa	0.183	− 0.087	0.574	0.113	− 0.017	0.146	0.114	0.185	0.285	0.222	0.116	0.080	0.085		–	*	–
Pycnogonid	0.344	0.647	− 0.078	0.207	0.008	0.277	0.606	0.356	0.345	0.294	0.154	0.352	0.193	− 0.078		–	–
Gastropod	0.422	− 0.123	0.630	0.281	0.277	0.318	0.063	0.031	0.234	0.204	− 0.056	0.449	0.483	0.320	− 0.048		–
Bivalve	0.010	− 0.043	− 0.040	− 0.026	0.162	0.006	− 0.055	0.111	− 0.008	0.032	0.229	− 0.077	− 0.021	− 0.040	0.275	0.144	

*Significant at $p = 0.05$; **significant at $p = 0.001$; – not significant

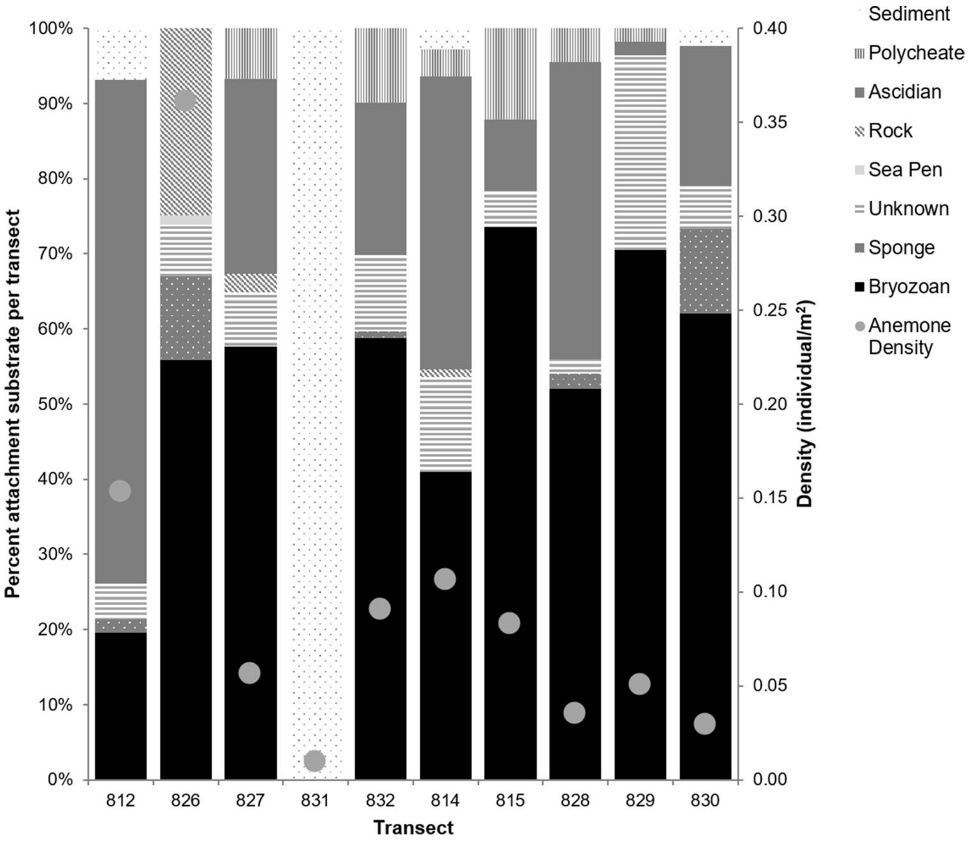

Fig. 4 Percent substrate attachment by ROV video transect with sea anemone density (black dot on bars) from Terre Adélie, near Dumont d'Urville station

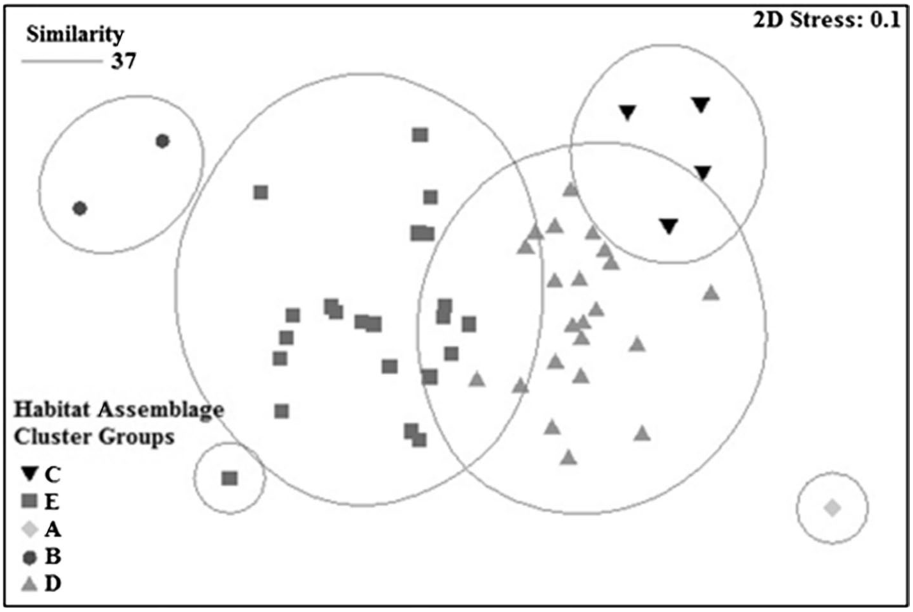

Fig. 5 nMDS ordination illustrating groups of species assemblages (identified from cluster analysis) from ROV video transect sections from Terre Adélie, near Dumont d'Urville station. Groups shown are significantly different based on SIMPROF analysis

Low dispersal and observed patchy distribution can also be linked to predator–prey relationships. We found significant positive correlations between sea anemone density and prey/predator species. Sea anemone distribution could reflect the availability of prey species (ophiuroids and asteroids). The presence of predators [gastropods and pycnogonids, 'facultative micropredators' (Braby et al. 2009)] may also reflect the availability of prey. Another explanation for the significant positive correlations with sea anemones and the predator and prey species may be that they too depend on ecological engineers to create habitat and substrate attachment, which could explain increased diversity in these

Table 3 SIMPER results showing within-group similarities for each major taxa

Species	Average Density	Av.Sim	Sim/SD	Contrib %	Cum. %
Group D—average similarity: 58.01					
Bryozoans	3.26	30.69	2.29	52.90	52.90
Ascidians	2.60	18.60	1.10	32.06	84.96
Polychaetes	0.77	2.93	0.99	5.06	90.01
Group C—average similarity: 66.45					
Ascidians	11.42	51.38	9.50	77.32	77.32
Sponges	2.14	4.27	0.91	6.43	83.75
Bryozoans	1.30	2.48	0.70	3.74	87.49
Polychaetes	0.38	1.52	1.72	2.29	89.78
Sea Anemones	0.28	1.22	4.63	1.84	91.62
Group E—average similarity: 52.10					
Bryozoans	0.73	28.38	1.59	54.48	54.48
Ascidians	0.56	17.38	1.19	33.36	87.84
Polychaetes	0.09	2.01	0.81	3.85	91.69
Group A					
Less than 2 samples in group					
Group B—average similarity: 40.60					
Ascidians	0.07	23.84	2.43	58.72	58.72
Holothurians	0.10	6.70	0.68	16.51	75.23
Sea anemones	0.01	3.35	0.34	8.26	83.49
Artemidactis victrix	0.01	3.35	0.34	8.26	91.74

Av. abund average abundance, *Av.sim* average similarity, Sim, *SD* ratio of the average similarity contribution divided by the standard deviation (SD), *Contrib %* % contribution, *Cum.%* cumulative % contribution

marine animal forests. To further understand links between predators and anemone distributions, it would be valuable to undertake further studies that assess diet of sea anemones and their predators.

Areas of the Southern Ocean have already been shown to be undergoing rapid climate change (Meredith and King 2005; Turner et al. 2013). Small changes in Southern Ocean environments have already been shown to have effects on the species within them (Meredith and King 2005; Griffiths et al. 2008; Constable et al. 2014; Gutt et al. 2015). For example, warming temperatures occurring in the Antarctic Peninsula have increased the retreat of the Fourcade glacier surrounding Potter Cove on the Antarctic Peninsula. The glacial retreat has increased the amount of suspended particles causing an alteration to the benthic community structure and ascidian species composition and abundance at Potter Cove (Rimondino et al. 2015). Warming sea temperatures combined with increased ocean acidification are affecting the growth of bryozoans (Wood et al. 2012). In extreme cases, a combination of high concentrations of CO_2 and high temperatures can result in the death of the bryozoan colonies, as seen in transplant experiments in the Mediterranean Sea (Wood et al. 2012). Predictions about the shoaling (shallowing) of calcium carbonate saturation horizons also indicate potentially serious consequences for bryozoans, whereby assemblages in deep water may begin experience conditions of undersaturation, leading to permanently undersaturated environments (McNeil and Matear 2008). What effects this may have on calcifying ecosystem engineers such as bryozoans is unknown.

Given the clear association between sea anemones, ascidians and bryozoans shown here for the Antarctic coastal ecosystem, it is likely that any changes in the ecological engineer communities in Antarctica has the potential to greatly effect a range of species including Antarctic sea anemones. Sea anemone density and diversity can be driven by different aspects of their life history, ecology and/or food availability, and this study shows there are associations between sea anemone distribution and the presence of ecological engineers in the coastal Antarctic marine ecosystem. As climate change effects are predicted to have effects on benthic communities (Gutt et al. 2015), it is vital to understand key ecological relationships, such as connections between macrobenthic organisms and biogenic substrate. This will contribute information to aid in the management and conservation of the Southern Ocean benthic environment.

Acknowledgements We thank the research programme led by Guillaume Lecointre, REVOLTA 1124 (2009-2013) supported by the French polar institute "Institut Paul-Émile Victor" (IPEV) and the Muséum national d'Histoire naturelle (MNHN). We would also like to thank the Département du Finistére for providing the ROV and to Océanopolis for the camera. We thank also the ROV pilot Alain Pottier.

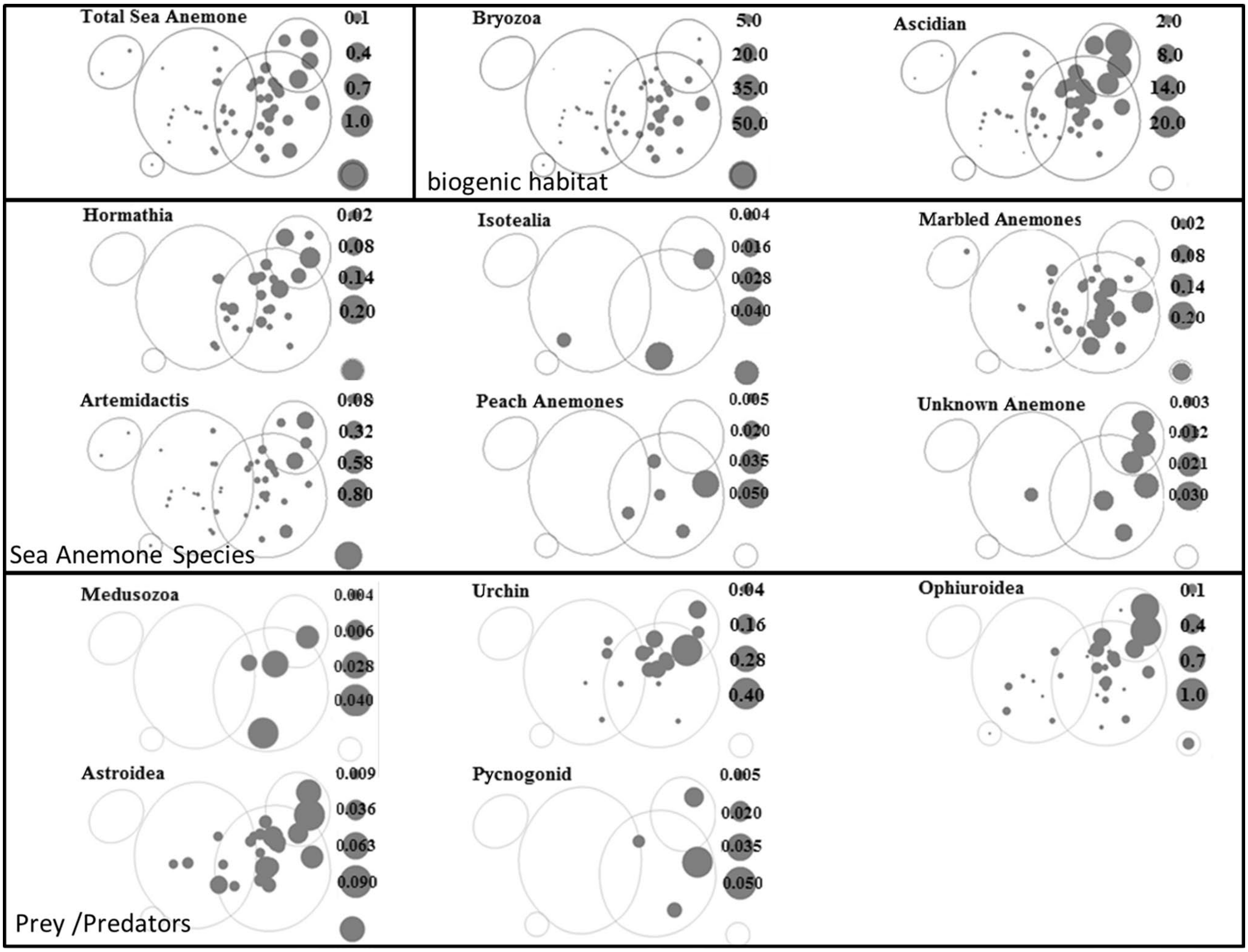

Fig. 6 Bubble plots overlaid onto the MDS ordination with groups from cluster analysis, with bubbles representing total sea anemone density, individual sea anemone species' density, bryozoan density, ascidian density, and predator/prey species' density (predator: pycnogonids; prey: urchin, asteroids, medusozoans, ophiuroids) from ROV video transects near Terre Adélie, near Dumont d'Urville station. Density = number of individuals/m^2

Compliance with ethical standards

Conflict of interest There are no conflicts of interests.

References

Amsler CD, McClintock JB, Baker BJ (1999) An Antarctic feeding triangle: defensive interactions between macroalgae, sea urchins, and sea anemones. Mar Ecol Prog Ser 183:105–114

Atalah J, Bennett H, Hopkins GA, Forrest BM (2013) Evaluation of the sea anemone *anthothoe albocincta* as an augmentative biocontrol agent for biofouling on artificial structures. Biofouling 29:559–571

Ayre DJ, Grosberg RK (1995) Aggression, habituation, and clonal coexistence in the sea-anemone *Anthopleura elegantissima*. Am Nat 146:427–453

Baird HP, Stark JS (2014) Spatial and temporal heterogeneity in the distribution of an Antarctic amphipod and relationship with the sediment. Mar Ecol Prog Ser 502:169–183

Baird HP, Miller KJ, Stark JS (2012) Genetic population structure in the Antarctic benthos: insights from the widespread amphipod, *Orchomenella franklini*. PLoS ONE 7:1–10

Bennett JR, Shaw JD, Terauds A, Smol JP, Aerts R, Bergstrom DM, Blais JM, Cheung WWL, Chown SL, Lea MA, Nielsen UN, Pauly D, Reimer KJ, Riddle MJ, Snape I, Stark JS, Tulloch VJ, Possingham HP (2015) Polar lessons learned: long-term management based on shared threats in Arctic and Antarctic environments. Front Ecol Environ 13:316–324

Bocharova ES, Kozevich IA (2011) Modes of reproduction in sea anemones (Cnidaria: Anthozoa). Biol Bull 38:849–860

Braby CE, Pearse VB, Vrijenhoek RC, Bain BA (2009) Pycnogonid-cnidarian interactions in the deep Monterey Submarine Canyon. Integr Comp Biol 49:E203

Brueggeman P (1998) Cnidaria—Anthozoa: Anemones, soft coral: Underwater field guide to Ross Island and McMurdo Sound. Antarctica, The National Science Foundation

Carlgren O (1899) Zoantharien. Hamburger Magalaensische Sammelreise 4:1–48

Carlgren O (1927) Actiniaria and Zoantharia. In: Further zoological results of the Swedish Antarctic expedition 1901–1903, vol 2. Kungl. Boktryckeriet. P. A. Norstedt and Söner, Stockholm

Carlgren O (1949) A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria, volume 1, no.1. In: Svenska vetenskapsakademien, Stockholm handlingar; 4, ser. Almqvist and Wiksells Boktryckeri AB, Stockholm

Carlgren O, Stephenson T (1929) Actiniaria: volume 9, pt. 2, zoology and botany. Australasian Antarctic expedition, 1 scientific reports: Series C. Government Printer, Sydney

Causse R, Ozouf-Costaz C, Koubbi P, Lamy D, Eleaume M, Dettai A, Duhamel G, Busson F, Pruvost P, Post A, Beaman RJ, Riddle MJ (2011) Demersal ichthyofaunal shelf communities from the Dumont d'Urville Sea (East Antarctica). Polar Sci 5:272–285

Clark GF, Stark JS, Johnston EL, Runcie JW, Goldsworthy PM, Raymond B, Riddle MJ (2013) Light driven tipping points in polar ecosystems. Glob Chang Biol 19:3749–3761

Clark GF, Raymond B, Riddle MJ, Stark JS, Johnston EL (2015) Vulnerability of Antarctic shallow invertebrate-dominated ecosystems. Austral Ecol 40:482–491

Clark GF, Stark JS, Palmer AS, Riddle MJ, Johnston EL (2017) The roles of sea-ice, light and sedimentation in structuring shallow Antarctic benthic communities. PLoS ONE 12:1

Clarke KR, Gorley RN (2015) Primer v6: user manual/tutorial. PRIMER-E, Plymouth

Constable AJ et al (2014) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. Glob Chang Biol 20:3004–3025

Dayton PK, Robilliard GA (1970) Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica, vol 1. Academic Press, London

Dunn DF (1983) Some Antarctic and Sub-Antarctic sea anemones (Coelenterata–Ptychodactiaria and Actiniaria) vol 39, paper 1 Biology of the Antarctic seas; Antarctic research series. American Geophysical Union, Washington, DC

Fautin DG (1984) More Antarctic and Sub-Antarctic sea anemones (Coelenterata: Corallimorpharia and Actiniaria) vol 41, paper 1 Biology of the Antarctic seas; Antarctic research series. American Geophysical Union, Washington, DC

Fautin DG (1988) Anthozoan dominated benthic environments. Proc 6th Int Coral Reef Symp 3:231–236

Fisher RA (1970) Statistical methods for research workers. Oliver and Boyd 1954, Edinburgh

Goodwill R, Roger H, Fautin DG, Furey J, Daly M (2009) A sea anemone symbiotic with gastropods of eight species in the Mariana Islands. Micronesica 41:117–130

Griffiths HJ, Linse K, Barnes DKA (2008) Distribution of macrobenthic taxa across the Scotia Arc, Southern Ocean. Antarct Sci 20:213–226

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biol 24:553–564

Gutt J (2007) Antarctic macro-zoobenthic communities: a review and an ecological classification. Antarct Sci 19:165–182

Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. Polar Biol 20:229–247

Gutt J, Cummings V, Dayton P, Isla E, Jentsch A, Schiaparelli S (2015) Antarctic marine animal forests: three-dimensional communities in Southern Ocean ecosystems. In: Rossi S, Bramanti L, Gori A, del Valle COS (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 1–30

Hoffman JI, Clarke A, Linse K, Peck LS (2011) Effects of brooding and broadcasting reproductive modes on the population genetic structure of two Antarctic gastropod molluscs. Mar Biol 158:287–296

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? Trends Ecol Evol 15:56–61

Hughes TP et al (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377

Jansen J, Hill NA, Dunstan PK, McKinlay J, Summer MD, Post AL, Eleaume MP, Armand LK, Warnock JP, Galton-Fenzi BK, Johnson CR (2018) Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. Nat Ecol Evol 2:71–80

Kersken D, Feldmeyer B, Janussen D (2016) Sponge communities of the Antarctic Peninsula: influence of environmental variables on species composition and richness. Polar Biol 39:851–862

Knox GA (2007) Biology of the Southern Ocean. CRC, Hoboken

Ledoux JB, Tarnowska K, Gerald K, Lhuillier E, Jacquemin B, Weydmann A, Feral JP, Chenuil A (2012) Fine-scale spatial genetic structure in the brooding sea urchin *Abatus cordatus* suggests vulnerability of the Southern Ocean marine invertebrates facing global change. Polar Biol 35:611–623

McNeil BI, Matear RJ (2008) Southern Ocean acidification: a tipping point at 450-ppm atmospheric CO2. P Natl Acad Sci USA 105:18860–18864

Mercier A, Hamel J-F (2008) Nature and role of newly described symbiotic associations between a sea anemone and gastropods at bathyal depths in the NW Atlantic. J Exp Mar Biol Ecol 358:57–69

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:1–5

Nelson ML, Craig SF (2011) Role of the sea anemone *Metridium senile* in structuring a developing subtidal fouling community. Mar Ecol Prog Ser 421:139–149

Oliver ECJ, Benthuysen JA, Bindoff NL, Hobday AJ, Holbrook NJ, Mundy CN, Perkins-Kirkpatrick SE (2017) The unprecedented 2015/16 Tasman Sea marine heatwave. Nat Commun 8:16101

Ottaway J (1977) Predators of sea anemones. Tuatara 22:213

Pearse JS, McClintock JB, Bosch I (1991) Reproduction of Antarctic benthic marine-invertebrates, tempos, modes and timing. Am Zool 31:65–80

Peck LS, Barnes DKA, Willmott J (2005) Responses to extreme seasonality in food supply: diet plasticity in Antarctic brachiopods. Mar Biol 147:453–463

Peña Cantero AL (2014) Benthic hydroids (Cnidaria, Hydrozoa) from the continental shelf and slope off Queen Mary Coast (East Antarctica). Polar Biol 37:1711–1731

Peña Cantero AL, Manjon-Cabeza ME (2014) Hydroid assemblages from the Bellingshausen Sea (Antarctica): environmental factors behind their spatial distribution. Polar Biol 37:1733–1740

Post AL, O'Brien PE, Beaman RJ, Riddle MJ, De Santis L (2010) Physical controls on deep water coral communities on the George V Land slope, East Antarctica. Antarct Sci 22:371–378

Poulin E, Feral JP (1995) Pattern of spatial-distribution of a brood-protecting schizasterid echinoid, *Abatus cordatus*, endemic to the Kerguelen Islands. Mar Ecol Prog Ser 118:179–186

Rimondino C, Torre L, Sahade R, Tatian M (2015) Sessile macro-epibiotic community of solitary ascidians, ecosystem engineers in soft substrates of Potter Cove, Antarctica. Polar Res 34:9

Rodriguez E, Fautin DG (2014) Chapter 5.8. Antarctic hexacorals (Cnidaria, Anthozoa, Hexacorallia). In: De Broyer C et al (eds) Biogeographic atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 113–116

Rodriguez E, López-González P (2008) The gastropod-symbiotic sea anemone genus *Isosicyonis* Carlgren, 1927 (Actiniaria:

Actiniidae): a new species from the Weddell Sea (Antarctica) that clarifies the taxonomic position of the genus. Sci Mar 72:73–86

Rodriguez E, Lopez-Gonzalez PJ, Gilib JM (2007) Biogeography of Antarctic sea anemones (Anthozoa, Actiniaria): what do they tell us about the origin of the Antarctic benthic fauna? Deep-Sea Res PTII 54:1876–1904

Rodriguez E, Orejas C, Lopez-Gonzalez PJ, Gili JM (2013) Reproduction in the externally brooding sea anemone *Epiactis georgiana* in the Antarctic Peninsula and the Weddell Sea. Mar Biol 160:67–80

Roule L (1909) Hexactinides Expedition. Antarctique Française 1903–1905:1–19

Sahade R et al (2015) Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. Sci Adv 1:10

Sebens KP (1981) The allometry of feeding, energetics, and body size in 3 sea-anemone species. Biol Bull 161:152–171

Shick JM (1991) A functional biology of sea anemones. In: Calow P (ed) Functional biology series. Chapman & Hall, Melbourne

Stark JS (2000) The distribution and abundance of soft-sediment macrobenthos around Casey Station, East Antarctica. Polar Biol 23:840–850

Stark JS, Kim SL, Oliver JS (2014) Anthropogenic disturbance and biodiversity of marine benthic communities in Antarctica: a regional comparison. PLoS ONE 9:1–24

Stephenson T (1910) 1918), Coelenterata: part I—Actiniaria. Natural history reports on British Antarctic (“Terra Nova”. Expedition 5:1–68

Stephenson T (1920) On the classification of Actiniaria: part I. Q J Microsc Sci 64:425–574

Turner J et al (2013) Antarctic climate change and the environment: an update. Polar Rec 50:237–259

Urban MC (2015) Accelerating extinction risk from climate change. Science 348:571–573

Wood ACL, Probert PK, Rowden AA, Smith AM (2012) Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. Aquat Conserv 22:547–563