

## ORIGINAL ARTICLE

# Spatial heterogeneity of epibenthos on artificial reefs: fouling communities in the early stages of colonization on an East Australian shipwreck

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## Keywords

Artificial reef; colonization; fouling; sessile invertebrates.

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Accepted: 12 August 2007

doi:10.1111/j.1439-0485.2007.00193.x

## Abstract

Artificial reefs are spatially complex habitats and serve as good model systems to study patterns of community succession and the response of epibiota to environmental clines over small spatial scales. Here, we quantified spatial heterogeneity in community composition and diversity of fouling communities across a number of environmental gradients that included water depth, surface orientation of habitats, exposure to currents, and shelter. Assemblage structure was quantified by spatially replicated photo transects on a recently scuttled large navy ship off the East Australian coast, lying in 27 m of water. A rich assemblage of epifauna had colonized the wreck within a year, dominated by barnacles, sponges and bryozoans. Community structure varied significantly over small spatial scales of meters to tens of meters. Depth, surface orientation and exposure were the major environmental drivers. Assemblages were substantially less diverse and abundant on the deepest (23 m near the seafloor) part of the hull with residual antifouling paint, on sheltered surfaces inside the wreck, and on the sediment-laden horizontal surfaces. Overall, the wrecks' habitat complexity corresponds with small-scale heterogeneity in the fouling communities. This study supports the notion that wrecks enhance local diversity and biomass within the habitat mosaic of their location, and habitat complexity may be an important mechanism for this, as demonstrated by the large spatial variability in the assemblages documented here.

## Problem

Artificial reefs, including purposefully sunken vessels, are widely regarded as significant ecological assets (Pickering *et al.* 1998; Baine 2001; Svane & Petersen 2001). The ecological values of artificial reefs encompass primarily the creation of habitat and the provision of refugia from commercial fishing (Santos *et al.* 2005; Boaventura *et al.* 2006; Moura *et al.* 2006; Ramos *et al.* 2006). Epibiota dominate the benthic assemblages on most artificial reefs, providing food resources for consumers, secondary habitat for other benthic invertebrates, and increased habitat complexity including shelter for fish (Bailey-Brock 1989;

Mintz *et al.* 1994; Pickering & Whitmarsh 1997; Santos *et al.* 2005). Artificial reefs also function as coastal defense structures (Bacchiocchi & Airoidi 2003; Edwards & Smith 2005), and provide socio-economic benefits mainly as sites for recreational fishing and diving (Wilhelmsson *et al.* 1998; Airoidi *et al.* 2005; Pendleton 2005; Leeworthy *et al.* 2006).

Artificial reefs are good model systems to assess colonization of newly created, artificial substrates (Cummings 1994; Svane & Petersen 2001; Perkol-Finkel & Benayahu 2005; Boaventura *et al.* 2006). Colonization of artificial structures occurs mainly through dispersal and settlement of larvae or spores (Underwood & Fairweather 1989;

Roberts 1997), and artificial reefs can enhance recruitment when they create favourable hydrodynamic regimes and settlement cues for pelagic larvae (Baynes & Szmant 1989; Svane & Petersen 2001).

A wide range of environmental factors influence recruitment rates and colonization trajectories of artificial reefs including: water depth and light availability (Relini *et al.* 1994; Svane & Petersen 2001), orientation in relation to prevailing currents (Baynes & Szmant 1989), orientation of surfaces (Glasby 2000; Glasby & Connell 2001; Knott *et al.* 2004; Boaventura *et al.* 2006), and rates of sedimentation (Baynes & Szmant 1989). Surface orientation is an important physical attribute of a settlement surface that can influence the development of epibiotic communities (Glasby 2000; Irving & Connell 2002), and sedimentation is often higher on horizontal surfaces (Baynes & Szmant 1989; Irving & Connell 2002). Increased sediment loads can smother many plants and filter-feeding invertebrates, resulting in considerable changes of benthic assemblages between vertical and horizontal surfaces (Glasby 2000).

Habitat heterogeneity and structure are central themes in ecology (McCoy & Bell 1984), and scuttled ships form complex habitats in terms of physical architecture. The prominence of habitat complexity as a key driver for species diversity and assemblage structure is encapsulated in the 'habitat heterogeneity hypothesis' which predicts that structurally complex habitats provide greater niche and resource diversity, which translates into higher species diversity (Tews *et al.* 2004). Thus, the physical architecture of shipwrecks provides a good model system to assess how biological assemblages respond to variations in environmental attributes across a complex habitat domain. To this end we quantified spatial patterns in the assemblage structure and diversity of encrusting biota on a large, recently scuttled, ex-naval ship off the East Australian Coast. Our field assessments incorporated environmental gradients that are predicted to influence the structure of the epibiotic assemblages, such as water depth, light intensity, exposure to currents and surface orientation of settlement surfaces. Specifically, we aimed to determine: (i) the effect of depth on the structure of epifaunal assemblages, (ii) how assemblage structure responds to differences in surface orientation of the settle-

ment substrates, (iii) the effect of differential exposure to prevailing current regimes, and (iv) the degree to which shelter affects the structure of epifaunal assemblages.

## Material and Methods

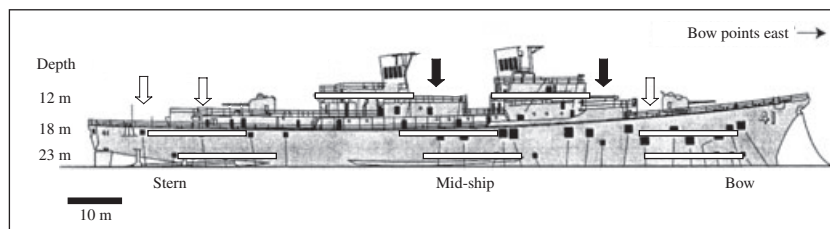
### Study site

The study was done on the ex-HMAS Brisbane, sunk in July 2005, 7.5 km NNE off the coast of Mooloolaba, Australia (26°36' S 153°10' E). The ship was a 133 m, Charles F Adams Class DDG, Guided Missile Destroyer. It was purposefully scuttled to create an artificial reef that would become a premier dive destination in the region. The ship lies upright on the sandy seafloor, with the base resting in 27 m of water and top of the stacks being 3 m below the water surface (Fig. 1).

### Field data collection

Encrusting assemblages were quantified 1 year after the ship had been scuttled, using a spatially replicated survey design that included: (i) three depth levels (12, 18 and 23 m) on both the starboard and port side of the ship; (ii) horizontal and vertical surfaces matched for depth at 12 and 18 m and, (iii) vertical surfaces on the inside of the wreck compared with vertical surfaces on the outside of the ship at the corresponding depth (Table 1, Fig. 1). Three 20 m long transects were sampled along the length of the vertical hull from the bow to the stern, at 18 and 23 m depth on both the starboard and port sides of the wreck. Three transects were also sampled along the main deck (horizontal surface) at 18 m. Vertical surfaces inside the wreck were sampled along three transects, corresponding to the position of the vertical sites outside the wreck at 18 m depth. At 12 m depth, only two vertical transects on both the starboard and port sides of the wreck and two horizontal transects could be sampled, because of a lack of available surfaces around the superstructures of the ship at this depth (Table 1, Fig. 1).

At each site, the encrusting community was documented using a photo-transect method as the sessile assemblages generally encrusted over the flat surfaces of the wreck and lacked foliose macroalgae or fauna that could have created a canopy or shading effect (Kennelly



**Fig. 1.** Diagram of the starboard side of the ex-HMAS Brisbane showing orientation on the sea floor and location of transects sampled. Transects on vertical surfaces are shown as white bands, and black and white arrows indicate where horizontal transects were sampled at 12 and 18 m respectively.

**Table 1.** Summary of the spatial survey design, incorporating three principal factors.

A – 'location'	A1 – outside		A2 – inside	
	B1 vertical	B2 horizontal		
B – 'orientation'	C1 – port		C2 – starboard	
12 m	2	2	2	–
18 m	3	3	3	3
23 m	3	3	–	–
no. of transects	8	8	5	3

A – Location (inside *versus* outside), B – Orientation (vertical *versus* horizontal surfaces) and C Aspect (starboard *versus* port side of the ship). The tabulated values are the number of replicate transects sampled with 15 photo frames per transect.

1989). Individual transects were 20 m long and included 15 replicate plots (photo quadrat frames) separated by 1 m. Each photo quadrat covered a total area of 625 cm<sup>2</sup>. Digital photos were taken by SCUBA divers with an Olympus 4MP UZ digital camera. We also collected representative voucher specimens for subsequent laboratory identification to the lowest possible taxonomic level.

#### Data analysis

In the laboratory, each photo-quadrat was analysed using the image analysis software 'Coral Point Count' (Kohler & Gill 2006). One hundred randomly distributed points were superimposed over each photo-quadrat image, and the identity of each taxon was recorded under each point.

Multivariate differences in assemblage structure were tested between *a priori* identified factors (*i.e.* depth, aspect, orientation, and location) with analysis of similarities (ANOSIM) complemented by non-metric multi-dimensional ordinations (nMDS) (Clarke 1993). Data were fourth-root transformed and all subsequent analyses were based on the Bray–Curtis resemblance measure. Principal species contributing to any separation between groups were determined using the SIMPER routine (Clarke 1993).

Spatial variation in total coverage and species richness were analysed using the following univariate statistical methods: (i) the difference between depth and aspect was examined using a two-factor ANOVA with depth (12, 18 or 23 m) and aspect (port or starboard) as fixed factors, (ii) the difference between orientations at two depths was examined with a two-factor ANOVA with orientation (vertical and horizontal) and depth (12 and 18 m) as fixed factors, and (iii) the difference between inside and outside surfaces at 18 m was examined, using a one-way ANOVA with location as the single fixed factor. Homogeneity of variance was checked with Cochran's test.

Percent coverage data were converted to proportions and arcsine transformed and species richness was  $\log_{10}(x + 1)$  transformed to meet assumptions of homogeneity of variances and normality (Underwood 1981, 1997).

Species accumulation curves were plotted in PRIMER using the species area routine with 999 random permutations. The curves were used to determine total species richness across successive quadrats grouped within the replicate transects for each of the following: (i) depth and aspect, (ii) orientation and depth, and (iii) location inside and outside the wreck.

#### Results

A diverse assemblage of encrusting invertebrates occupied a large proportion of the surface of the wreck. Thirty-one epifaunal taxa were identified across the 315 photo quadrats. Bryozoans were the most speciose group with eight taxa, followed by sponges (seven taxa), ascidians (six taxa), bivalves (five taxa), polychaetes (three taxa) and barnacles (two taxa; Table 2). Barnacles dominated the assemblage on vertical surfaces at all depths, occupying more than 32% of the available space on the wreck (Table 3). Bivalves were the second most abundant group (8%), followed by bryozoans (5%), sponges (3%), polychaetes (2%) and ascidians (<1%). The barnacle *Balanus* sp. 1, the bivalve *Pictata maculata* and the bryozoan *Schizoporella* sp. 1 were the most abundant species of the fouling assemblages (Table 2).

Spatial heterogeneity in the structure of these fouling assemblages was pronounced (Fig. 2a). The composition of each assemblage, and the coverage and diversity of individual species varied significantly with depth, surface orientation, and location (Figs 2–4).

#### Effect of depth and aspect

The composition of epifaunal assemblages differed substantially with depth (Fig. 2b). Assemblage structure differed significantly between the two shallowest depths sampled, even though these strata were only separated by 6 m (*i.e.* 12 m *versus* 18 m depth; ANOSIM,  $R = 0.409$ ,  $P = 0.019$ ). Aspect (*i.e.* port *versus* starboard) had less of an influence on assemblage structure (ANOSIM,  $R = 0.152$ ,  $P = 0.001$ ). Assemblages at the shallowest and intermediate depth were both highly disjunct from the deepest layer near the seafloor at 23 m (Fig. 2b; ANOSIM,  $R = 0.985$ ,  $P = 0.002$ ). Assemblages at this depth were exposed to residual antifouling paint on the hull that can retard the settlement of fouling species (Chambers *et al.* 2006), and thus potentially confound a pure depth effect on assemblage structure. Therefore, further analyses on the effects of depth and aspect were

group	species	orientation depth (m), outside					orientation depth (m), inside	
		vertical			horizontal			
		12	18	23	12	18		
Cirripedia	<i>Balanus</i> sp. 1	*****	*****	****	**	***	****	
	<i>Megabalanus tintinnabulum</i>	—	*	—	—	—	—	
Bivalvia	<i>Pictada maculata</i>	***	*	—	****	***	*	
	<i>Dendostrea folium</i>	**	*	—	*	*	**	
	<i>Pteria coturnix</i>	*	*	—	*	*	—	
	<i>Pteria penguin</i>	*	—	—	—	—	—	
	<i>Scaechlamys livida</i>	*	—	—	—	*	—	
Bryozoa	<i>Biflustra</i> sp. 1	*	*	—	—	—	—	
	<i>Celleporaria</i> sp. 1	*	*	—	—	—	—	
	<i>Schizoporella</i> sp. 1	**	***	**	*	—	****	
	<i>Reteporella graeffei</i>	—	*	—	—	—	—	
	<i>Membranipora savertii</i>	—	*	—	—	—	—	
	Bryozoa sp. 1	—	—	—	—	—	*	
	Bryozoa sp. 2	*	—	—	—	—	—	
	Bryozoa sp. 3	*	—	—	—	—	—	
	Porifera	<i>Chondropsis</i> sp. 1	*	*	—	—	—	*
		<i>Mycale (Mycale)</i> sp. 1	—	*	*	—	—	—
<i>Cliona</i> sp. 1		*	*	*	—	—	****	
<i>Cliona</i> sp. 2		*	**	*	—	—	**	
<i>Haliclona</i> sp. 1		*	*	—	—	—	—	
<i>Aplysilla</i> sp. 1		*	—	—	—	—	—	
<i>Haliclona (Haliclona)</i> sp. 1		*	*	—	—	—	—	
Polychaeta	<i>Spirorbis</i> sp. 1	—	—	*	—	—	**	
	<i>Filograna implexa</i>	*	*	—	—	—	****	
	Sabellidae sp. 1	*	*	*	—	*	****	
Asciacea	<i>Cnemidocarpa stolonifera</i>	*	*	—	—	—	—	
	<i>Phallusia julinea</i>	*	*	—	—	—	—	
	<i>Didemnum</i> sp. 1	—	*	—	—	—	—	
	<i>Botryllus</i> sp. 1	*	—	—	—	—	—	
	<i>Microcosmus exasperatus</i>	*	*	—	—	—	—	
	<i>Polycarpa ovata</i>	—	—	—	—	—	*	
Total algae		****	***	**	****	*	**	
Total bare space		***	***	*****	****	***	*****	
Total sand		—	—	—	****	*****	—	

— = 0%, \* = <2%, \*\* = 2–8%, \*\*\* = 8–16%, \*\*\*\* = 16–32%, \*\*\*\*\* = 32–64%, \*\*\*\*\* = >64%.

restricted to comparisons between the 12 and 18 m depth strata.

The three species, *Pictada maculata*, *Schizoporella* sp. 1 and *Dendostrea folium* contributed to 45% of the difference between the uppermost and middle depth strata (Table 4). *Pictada maculata* declined in coverage substantially with increasing depth on both the port and starboard sides of the wreck (Table 4). However, the coverage of this species was higher on the port side of the wreck especially at the shallowest depth. The abundance of *Dendostrea folium* also declined with depth but was similar on both sides of the ship. Conversely, coverage of the bryozoan *Schizoporella* sp. 1 increased with depth and

**Table 2.** List of taxonomic groups showing species present and matrix of relative abundance using log-2 (octave) cover classes.

this species was more abundant on the starboard side of the wreck at both depths (Table 4). Despite these differences between depth and aspect for individual species, the total cover of epibiota was similar on both sides of the ship, but species richness was significantly higher on the starboard side of the wreck (Fig. 3).

#### Vertical versus horizontal surfaces

Horizontal surfaces supported significantly fewer species at substantially reduced cover, resulting in strong shifts in the composition of the assemblage between different surface orientations at both depths (Figs 2c and 3b;

**Table 3.** Summary of ANOVA results comparing coverage and species richness among: (a) depth (12, 18, and 23 m) and aspect (port and starboard); (b) Orientation (horizontal and vertical) and depth (12 and 18 m); (c) location (inside and outside) at 18 m depth.

factor	df	sessile coverage		sessile species richness	
		MS	F-value	MS	F-value
<b>(a)</b>					
depth	2	12.60	<b>183.58***</b>	211.66	<b>141.63***</b>
aspect	1	0.11	1.59	48.59	<b>32.51***</b>
depth × aspect	2	0.02	0.34	16.02	<b>10.71***</b>
error	234	0.07		1.49	
<b>(b)</b>					
orientation	1	12.58	<b>456.12***</b>	14.61	<b>179.70***</b>
depth	1	0.00	0.05	0.23	2.86
orientation × depth	1	0.84	<b>30.62***</b>	0.36	<b>4.48*</b>
error	221	0.03		0.08	
<b>(c)</b>					
location	1	6.20	<b>148.14***</b>	50.64	<b>20.91***</b>
error	133	0.04		2.42	

Coverage data were arcsine transformed for each comparison and species density was  $\text{Log}_{10}$  transformed for the orientation × depth comparison to correct for heterogeneous variance (Cochran's test  $P < 0.05$ ). Significant results are bold (\* $P < 0.05$ , \*\*\* $P < 0.001$ ).

ANOSIM: 12 m  $R = 0.315$ ,  $P = 0.001$ ; 18 m  $R = 0.772$ ,  $P = 0.001$ ). Total cover on horizontal surfaces was halved at 12 m, and reduced to a third at 18 m compared with vertical habitats. Horizontal surfaces contained a maximum of six species compared to 18 to 19 species found on the vertical surfaces at 18 and 12 m, respectively (Fig. 4b). Sediment covered >60% of the horizontal surfaces, while vertical surfaces were free of sediment (Table 2).

Coverage of the barnacle *Balanus* sp. 1 decreased most strongly on horizontal surfaces, being three times less than on vertical surfaces (Table 5). In contrast, the bivalve *P. maculata* was significantly more abundant on horizontal surfaces by a factor of two to eight times (Table 5). Other taxa were either extremely sparse or absent from the horizontal surfaces (Table 5). Turfing algae covered more area on horizontal surfaces at 12 m, but the pattern was reversed at 18 m where algae covered more surface area on the vertical sides of the ship.

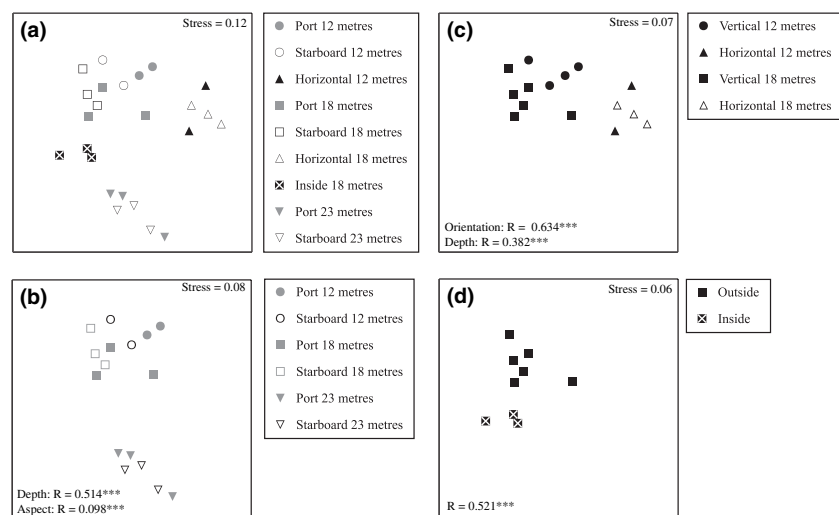
#### Inside versus outside areas of the wreck

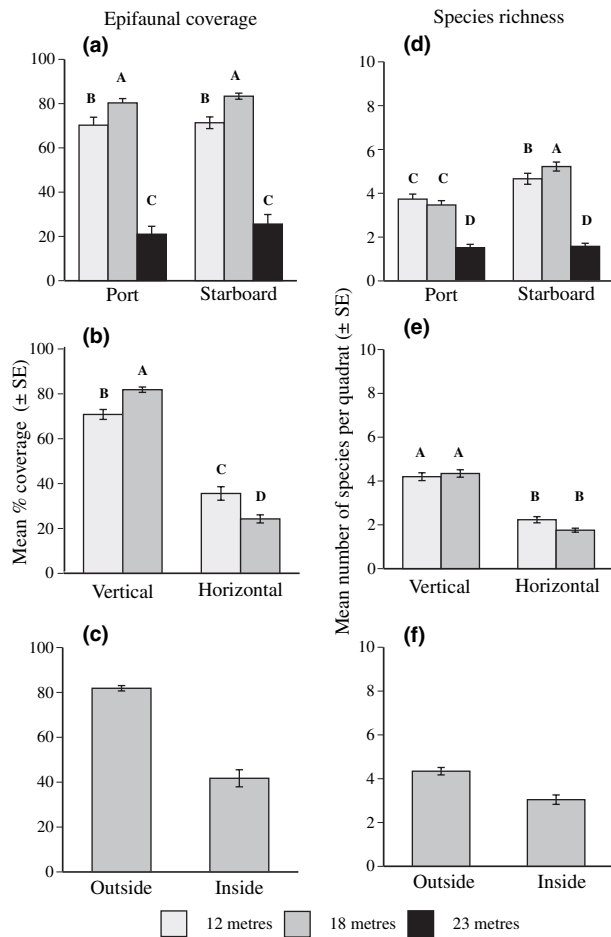
Fouling assemblages inside the wreck comprised significantly fewer species, and epifauna covered less surface area than on the outside, resulting in marked shifts in assemblage structure (Fig. 2d; ANOSIM:  $R = 0.617$ ,  $P = 0.01$ ). Total cover of sessile biota was halved on the inside surfaces and these assemblages had 30% fewer species (Fig. 4c). For example, *Balanus* sp. 1 and *Schizoporella* sp. 1 decreased substantially from the outside to inside vertical surfaces and contributed to 34% of the difference between the two locations (Table 6). Polychaetes were the exception, with coverage increasing from 1% on the outside to 15% on the inside of the wreck (Table 6), where the dominant polychaete species was *Filograna implexa*. The tube dwelling polychaetes contributed to 26% of the difference between the inside and outside of the wreck.

#### Discussion

Spatial heterogeneity is a key trait of artificial reefs (Svane & Petersen 2001). Artificial reefs and shipwrecks provide a complex mosaic of habitats for the establishment of

**Fig. 2.** Ordinations (non-metric multidimensional scaling) contrasting the structure of epifaunal assemblages at multiple spatial scales: (a) across all 24 transects sampled showing depth, aspect, orientation and location, (b) between the three depth bands (12, 18 and 23 m), (c) between vertical and horizontal surface orientations at 12 and 18 m, and (d) between locations inside and outside of the wreck at 18 m depth.





**Fig. 3.** Comparison of coverage (left panels) and the number of species per sample (right panels) among: (a,d) depth (12, 18 and 23 m) and aspect (port and starboard), (b,e) orientation (vertical and horizontal) at 12 and 18 m, and (c,f) location and degree of exposure (inside and outside) at 18 m.

both fouling and fish assemblages. A diverse assemblage of sessile invertebrates and algae had colonized the wreck after being submerged for only 1 year. Fouling organisms may enhance food availability for fishes in the local area, increasing the resource availability and enhancing fish abundance and diversity around the wreck (Relini *et al.* 1994; Svane & Petersen 2001).

#### Spatial heterogeneity and epifaunal assemblages

We predicted that the epifaunal assemblages would display small-scale spatial heterogeneity in response to increasing depth, aspect and surface orientation. There was a substantial decrease in the species richness and cover of epifauna at 23 m depth because of residual anti-fouling paint on the hull of the wreck, which can retard the settlement of fouling species (Chambers *et al.* 2006).

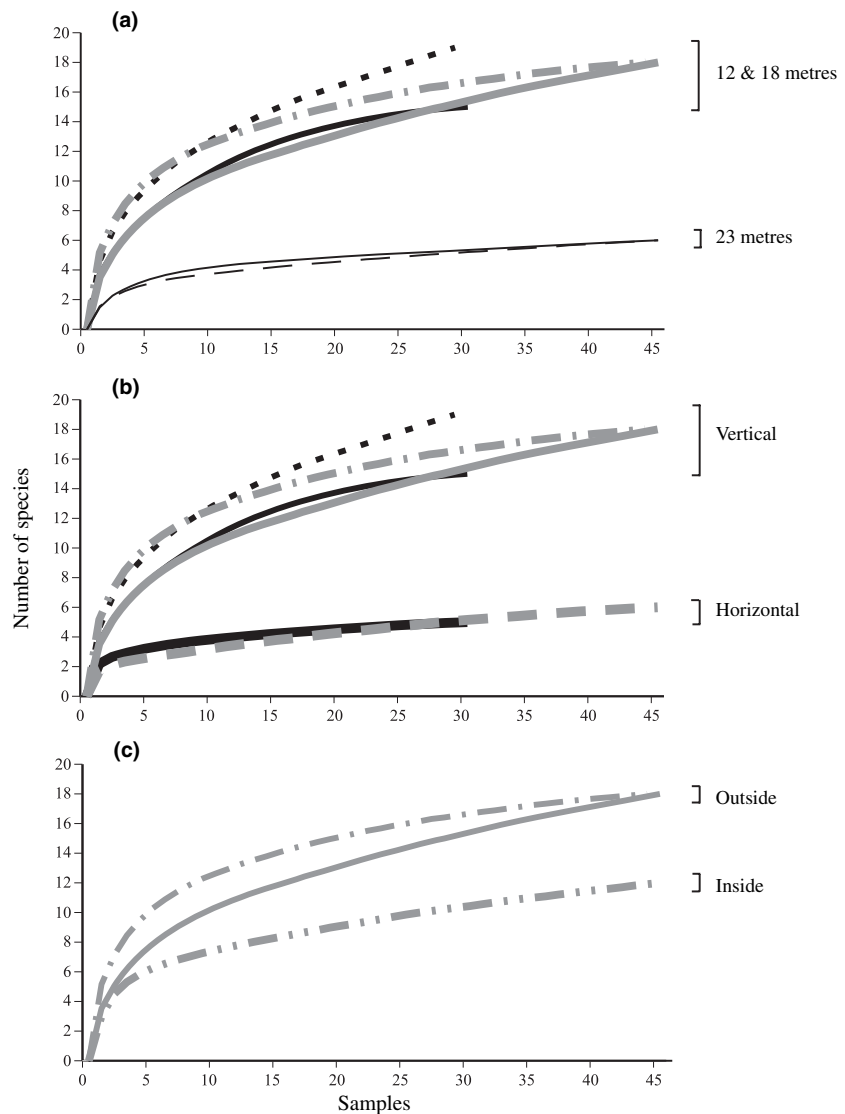
The presence of antifouling paint confounded a pure depth effect, so our interpretation on the effect of depth and aspect on the epifaunal assemblages was restricted to comparisons between the uppermost and middle depth strata, where antifouling paint was not present.

The composition of the epifaunal assemblages differed between the 12 and 18 m depths and between the different aspects (Fig. 2b, ANOSIM), with species richness increasing from the port to the starboard side of the wreck (Figs 3d and 4b; Table 3). This could have been caused by a number of factors that include larval stratification within the water column (Grosberg 1982), increased larval supply (Baynes & Szmant 1989; Cummings 1994; Svane & Petersen 2001) and food availability (Lesser *et al.* 1994) caused by the predominant direction of water currents that impinge mostly on the starboard side. However, explicit tests are required to examine experimentally the physical and biological factors that structure communities in this situation.

Many algae and sessile invertebrates are susceptible to smothering by sediment (Baynes & Szmant 1989; Irving & Connell 2002). Consequently, the observed differences in sessile invertebrate and algal coverage between horizontal and vertical surfaces may be due to smothering by sediment on the horizontal surfaces (Baynes & Szmant 1989; Badalamenti *et al.* 2002; Irving & Connell 2002). Bivalves were the only taxon to be more abundant on the horizontal surfaces. Epifauna that can grow above the layer of sediment may avoid detrimental effects experienced by less robust or encrusting invertebrates (Irving & Connell 2002). Bivalve molluscs such as *P. maculata* also have a hard outer shell and attach strongly to the substrate, which could also increase their resistance to disturbance from wave action or predators.

Altered water current regimes inside the ship are likely to modify larval supply, food availability, and reduce the intensity and frequency of physical disturbance (Baynes & Szmant 1989). Cryptic habitats inside artificial reefs may also provide shelter from predators (Mintz *et al.* 1994). Previous work that examined colonization on the inside and outside of small artificial blocks has shown no difference in total coverage of epifauna with both surfaces being dominated by barnacles (Boaventura *et al.* 2006). Conversely, our data show that the structure of assemblages differs substantially between locations when an artificial structure is large enough to influence the strength and direction of water flow. The availability of space was not a limiting factor, as assemblages only covered 40% of the available space on the inside of the wreck.

Assemblages inside the wreck were dominated by serpulid polychaetes such as *Filograna implexa*. Sheltered conditions inside the wreck may allow the delicate



**Fig. 4.** Species accumulation curves contrasting: (a) depth bands (12, 18 and 23 m) at both port and starboard sides of the ship, (b) surface orientations (vertical and horizontal) at 12 and 18 m depth, and (c) inside and outside areas of the ship.

polychaete colonies to grow and occupy more than 30% of the available space in some areas of the wreck (Table 2). Similar to barnacles, polychaetes can dominate the space on artificial reefs in the early stages of colonization (Hatcher 1998).

#### Time trajectories of colonizing assemblages

Pioneer species such as barnacles, polychaetes, bivalves, hydroids and bryozoans can initially occupy a large proportion of available space on newly created artificial reefs

(Ardizzone *et al.* 1989; Bailey-Brock 1989; Relini *et al.* 1994; Hatcher 1998; Boaventura *et al.* 2006; Moura *et al.* 2006). Our results show that barnacles occupied much of the available space on most surfaces of the wreck after 1 year, which concurs with other artificial reef studies (Hatcher 1998; Boaventura *et al.* 2006).

Over time, we expect that the cover of barnacles will decrease because of colonization of more competitive species such as poriferans (Butler 1991; Hatcher 1998; Thanner *et al.* 2006). Sponges are generally slow to recruit to new habitats. They can be slow growing, long-lived

(i) depth	species	mean % coverage		average dissimilarity	diss./SD	cumulative %
		12 meters	18 meters			
	<i>Pictada maculata</i>	<b>11.22</b>	0.64	8.90	1.48	17.95
	<i>Schizoporella</i> sp. 1	2.15	<b>11.27</b>	8.22	1.41	34.53
	<i>Dendostrea folium</i>	<b>2.37</b>	0.46	5.68	1.25	45.99
	<i>Cliona</i> sp. 2	0.85	<b>3.98</b>	5.61	1.08	57.31
	<i>Filograna implexa</i>	0.46	<b>1.07</b>	3.60	0.87	64.57
	<i>Cliona</i> sp. 1	0.76	<b>1.22</b>	3.47	0.80	71.56
	<i>Chondropsis</i> sp. 1	1.02	<b>1.38</b>	2.24	0.51	76.07
	<i>Balanus</i> sp. 1	48.98	<b>58.57</b>	2.10	0.76	80.31
	<i>Pteria coturnix</i>	<b>0.42</b>	0.09	1.54	0.47	83.41
	Sabellidae sp. 1	<b>0.17</b>	0.08	1.26	0.43	85.95
	<i>Celleporaria</i> sp. 1	0.10	<b>0.83</b>	1.14	0.37	88.24
	<i>Biflustra</i> sp. 1	<b>0.56</b>	0.09	0.78	0.26	89.82
	<i>Haliclona (Haliclona)</i> sp. 1	<b>0.37</b>	0.26	0.76	0.28	91.35
(ii) Aspect		Port	Starboard			
	12 m					
	<i>Pictada maculata</i>	<b>15.07</b>	7.24	6.40	1.03	16.31
	<i>Schizoporella</i> sp. 1	0.87	<b>3.48</b>	5.83	1.13	31.17
	<i>Dendostrea folium</i>	<b>2.30</b>	2.45	4.91	1.05	43.69
	<i>Cliona</i> sp. 1	0.27	<b>1.28</b>	3.08	0.72	51.53
	<i>Filograna implexa</i>	0.40	<b>0.52</b>	2.86	0.72	58.83
	<i>Pteria coturnix</i>	0.23	<b>0.62</b>	2.35	0.61	64.81
	<i>Balanus</i> sp. 1	47.67	<b>50.34</b>	2.19	0.71	70.41
	Sabellidae sp. 1	<b>0.20</b>	0.14	1.60	0.50	74.49
	<i>Cliona</i> sp. 2	0.03	<b>1.69</b>	1.59	0.41	78.55
	<i>Chondropsis</i> sp. 1	0.00	<b>2.07</b>	1.58	0.36	82.57
	<i>Haliclona (Haliclona)</i> sp. 1	0.00	<b>0.76</b>	1.31	0.39	85.90
	<i>Biflustra</i> sp. 1	<b>0.97</b>	0.14	1.15	0.31	88.84
	<i>Aplysilla</i> sp. 1	<b>1.77</b>	0.00	0.91	0.26	91.17
	18 m					
	<i>Cliona</i> sp. 2	1.47	<b>6.55</b>	6.91	1.37	17.15
	<i>Schizoporella</i> sp. 1	8.20	<b>14.41</b>	5.53	1.03	30.87
	<i>Filograna implexa</i>	0.58	<b>1.57</b>	4.26	1.04	41.44
	<i>Cliona</i> sp. 1	0.64	<b>1.82</b>	4.08	0.90	51.56
	<i>Chondropsis</i> sp. 1	0.13	<b>2.66</b>	3.35	0.67	59.87
	<i>Pictada maculata</i>	<b>0.73</b>	0.55	3.11	0.80	67.57
	<i>Dendostrea folium</i>	<b>0.53</b>	0.39	2.68	0.75	74.21
	<i>Celleporaria</i> sp. 1	0.00	<b>1.68</b>	2.17	0.53	79.60
	<i>Balanus</i> sp. 1	<b>66.6</b>	50.36	1.73	1.15	83.89
	<i>Mycale (Mycale)</i> sp. 1	<b>0.24</b>	0.14	0.93	0.33	86.21
	Sabellidae sp. 1	0.07	<b>0.09</b>	0.88	0.37	88.39
	<i>Reteporella graeffei</i>	0.07	<b>0.18</b>	0.67	0.30	90.06

Showing the species that contributed to 90% of the dissimilarity between groups (average dissimilarity for (i) depth = 49.57; (ii) aspects at 12 m = 39.22; 18 m = 40.31). The largest group in each comparison is in bold font.

species, that appear at greater frequency during the later stages of community succession (Bailey-Brock 1989; Boaventura *et al.* 2006; Roberts *et al.* 2006). However, once established (after at least 5 years), sponges can dominate both artificial (Thanner *et al.* 2006) and natural reefs (Roberts *et al.* 2006).

Natural reefs in the vicinity of this wreck harbor rich epibenthic communities dominated by turfing algae, corals and sponges (Banks & Harriott 1995; Hooper &

**Table 4.** SIMPER results for comparisons of epifaunal assemblages between vertical surfaces (i) at 12 and 18 m depth (ii) between different aspects (port and starboard) at 12 and 18 m depth.

Kennedy 2002). The communities established on the wreck differ markedly in their dominance of solitary species such as barnacles and bivalves, which is similar to studies of epifaunal community composition on pier pilings from cold temperate waters (Butler & Connelly 1996; Butler & Connelly 1999). A more comprehensive study of the epifaunal assemblages on both the natural and artificial reefs is required to assess whether the assemblages on this reef become more similar to those on the

**Table 5.** SIMPER results for comparisons of epifaunal assemblages between vertical and horizontal surfaces of the wreck at (i) 12 m depth and (ii) 18 m depth, listing species that contributed to 90% of the dissimilarity between groups (average dissimilarity 12 m = 46.32; 18 m = 60.96).

species	mean % coverage		average dissimilarity	diss/SD	cumulative % contribution
	vertical	horizontal			
(i) 12 m					
<i>Balanus</i> sp. 1	<b>48.98</b>	7.77	11.23	1.58	24.23
<i>Pictada maculata</i>	11.22	<b>26.43</b>	8.79	0.96	43.22
<i>Dendostrea folium</i>	<b>2.37</b>	0.90	7.35	1.21	59.08
<i>Schizoporella</i> sp. 1	<b>2.15</b>	0.30	5.10	0.81	70.10
<i>Pteria coturnix</i>	<b>0.42</b>	0.20	2.25	0.51	74.96
<i>Filograna implexa</i>	<b>0.46</b>	0.00	2.14	0.51	79.58
<i>Cliona</i> sp. 1	<b>0.76</b>	0.00	2.09	0.49	84.10
Sabellidae sp. 1	<b>0.17</b>	0.00	1.16	0.36	86.60
<i>Cliona</i> sp. 2	<b>0.85</b>	0.00	0.98	0.29	88.71
<i>Chondropsis</i> sp. 1	<b>1.02</b>	0.00	0.93	0.25	90.71
(ii) 18 m					
<i>Schizoporella</i> sp. 1	<b>11.27</b>	0.00	14.48	2.05	23.76
<i>Pictada maculata</i>	0.64	<b>9.49</b>	10.22	1.18	40.52
<i>Balanus</i> sp. 1	<b>58.57</b>	14.49	9.48	1.56	56.07
<i>Cliona</i> sp. 2	<b>3.98</b>	0.00	7.40	1.07	68.22
<i>Filograna implexa</i>	<b>1.07</b>	0.00	4.08	0.75	74.91
<i>Cliona</i> sp. 1	<b>1.22</b>	0.00	3.58	0.65	80.78
<i>Dendostrea folium</i>	<b>0.46</b>	0.11	2.70	0.57	85.20
<i>Chondropsis</i> sp. 1	<b>1.38</b>	0.00	2.23	0.45	88.86
<i>Celleporaria</i> sp. 1	<b>0.83</b>	0.00	1.33	0.35	91.04

The largest group in each comparison is in bold.

**Table 6.** SIMPER results for comparisons between epifaunal assemblages on vertical surfaces outside and inside of the wreck, listing species that contributed to 90% of the dissimilarity between groups (average dissimilarity = 61.52).

species	mean % coverage		average dissimilarity	diss/SD	cumulative % contribution
	outside	inside			
<i>Balanus</i> sp. 1	<b>58.57</b>	17.04	10.67	1.07	17.35
<i>Schizoporella</i> sp. 1	<b>11.27</b>	6.27	10.28	1.40	34.06
Sabellidae sp. 1	0.08	<b>4.64</b>	8.04	1.18	47.13
<i>Filograna implexa</i>	1.07	<b>10.31</b>	7.92	1.08	60.00
<i>Cliona</i> sp. 2	<b>3.98</b>	0.53	6.46	1.06	70.50
<i>Cliona</i> sp. 1	1.22	<b>1.89</b>	4.92	0.93	78.49
<i>Pictada maculata</i>	<b>0.64</b>	0.04	2.47	0.57	82.52
<i>Dendostrea folium</i>	<b>0.46</b>	0.18	2.33	0.57	86.30
<i>Chondropsis</i> sp. 1	<b>1.38</b>	0.27	2.11	0.47	89.72
<i>Spirorbis</i> sp. 1	0.00	<b>0.31</b>	1.41	0.37	92.02

The largest group in each comparison is in bold.

surrounding natural reefs over time and to determine whether colonial species dominate over solitary species in the future.

The trajectories of species arrival and succession on the wreck are also currently not documented. Similarly, a focus of future work should be to assess how biotic factors, such as inter-specific competition and the timing of larval supply influence the epifaunal composition of this

and other artificial reefs. Also, to which extent changes in epifaunal communities propagate to mobile invertebrate and fish assemblages remains poorly understood in the local situation.

#### Artificial reefs as 'invasive' habitats

Conventional wisdom holds that artificial reefs complement natural habitats and become focal points of locally enhanced biomass and diversity (Relini *et al.* 2007). However, we know little about how the addition of a spatially complex and large structure influences the existing communities in soft-sediment habitats (Danovaro *et al.* 2002; Fabi *et al.* 2002). For example, the placement of artificial reefs may have negative effects on the composition and density of soft-sediment communities surrounding the reef (Danovaro *et al.* 2002). The scuttling of a large ship is certainly a classic type of pulse disturbance for the soft-sediment benthos, but the duration or spatial scale over which this disturbance operates remains unresolved. In the best case, it is a short-lived and localized impact, but significant changes to the hydrodynamics around a wreck can create longer-term effects of a low intensity press disturbance.

Artificial reefs have been found to enhance benthic and pelagic diversity primarily on local scales closely associated with the structures themselves (Bombace *et al.* 1994; Relini *et al.* 1994; Moura *et al.* 2006).

Connectivity between habitats is an important criterion in the management and restoration of degraded habitats (Steneck 2006). Artificial reefs may provide an important connection within an existing mosaic of habitats by creating new habitat, or supplementing degraded habitat. It is, however, not known to which extent artificial reefs become a source of new recruits which can re-colonize natural habitats following disturbances. Similarly, the spatial ambit over which artificial reefs influence population and community dynamics remains to be quantified.

### Acknowledgements

Funding for this work was provided by the Environmental Protection Agency, QLD. Geoff Johnson, John Hooper, Merrick Ekins, Peter Davie & Darryl Potter of the Queensland Museum are thanked for their logistical support and assistance with taxonomy. We also thank Lauren Thorburn and two anonymous reviewers for comments that improved the manuscript significantly.

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