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A state-wide assessment of marine, intertidal, molluscan death assemblages for NSW

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*Report prepared for the NSW Department
of Environment and Climate Change, June 2009*

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Cover photos: Shells on Valla Beach (S. Smith); Shelly Point, Kioloa (S. Smith); Collecting at Guerilla Beach (K. James).

Executive Summary

Aggregations of dead mollusc shells (death assemblages) on rocky shores have been shown to provide a good indicator of regional biodiversity for nearshore habitats. As such, surveys of these assemblages can provide rapid and cost-effective assessment of patterns of biodiversity over broad spatial scales. This study surveyed death assemblages at 50 sites across NSW (and one site in SE Queensland) with the objectives of evaluating patterns of assemblage structure and gradients of diversity. Surveys comprised 2-hr surface searches of well-developed death assemblages during which all species found were identified and allocated an abundance rating.

While the lowest species richness was recorded at southern sites, general patterns of species richness showed no simple (monotonic) latitudinal pattern. Instead, patterns revealed a major hot spot in the northern section of the Solitary Islands Marine Park with a lesser one around Port Stephens. Rather than displaying coincidental, disjunct distributions according to nominated bioregional boundaries, species mainly showed overlapping ranges. However, distributions for some of the more common species suggested that there was some coincidence of range boundaries for a number of species in the southern Solitary Islands Marine Park, and between Port Stephens and Dudley. Sampling intensity was insufficient to provide an adequate evaluation of bioregional boundaries in the southern part of the state.

While there was evidence for broadscale biogeographic patterns at the community level, the most obvious patterns related to the relative prevalence of reef-associated and sand-associated taxa. Thus, while three primary community types were discernable over the state-wide scale (northern, mid- and southern), the site relationships within these clusters related primarily to the dominance of sand- or reef-associated taxa in the deposits. Disjunct boundaries in the dominance of these suites of species were evident at the largest scale of evaluation (sites in the Port Macquarie region) and also within broad.

Intensive sampling in northern NSW allowed for more in depth evaluation of patterns. The Clarence River was identified as an important boundary between assemblage types and this is hypothesised to be due to the influence of riverine sediment plumes and northward transport of sediments, on the composition of nearshore benthic habitats.

Overall, the study indicates that there are obvious bioregional patterns related to disjunct distributions of species but that the structure of death assemblages is strongly influenced by bio-physical processes acting at medium scales (50-150 km).

Introduction

Recent studies of molluscan death assemblages, both in Australia (Smith 2008) and overseas (Warwick & Light 2002, Warwick & Turk 2002), have indicated that they hold considerable promise for assessment of biodiversity at regional scales. Research in northern New South Wales (NSW) has demonstrated that a fully representative snapshot of mollusc diversity (prosobranch gastropods and bivalves) can readily be obtained by sampling 3 sites within an area using a standardised protocol (Smith 2008). Targeting death assemblages has some considerable advantages when conducting broadscale assessments of biogeographic patterns and biodiversity. Firstly, field time is dramatically reduced when compared to surveys of living molluscs over the same scales (Rose 2003). Secondly, as accumulations of shells in the intertidal environment represent specimens transported from a range of adjacent habitats, a more realistic estimate of regional biodiversity is contained within these deposits (Warwick & Light 2002, Smith 2008). For example, death assemblages on rocky intertidal shores in the Solitary Islands Marine Park are generally 1.5-2 times richer than living assemblages on the same shores (Rose 2003).

However, studies of death assemblages also have a number of caveats. Firstly, the composition of assemblages is likely to be biased towards: more robust species (delicate shells are more likely to broken during transportation); specimens that are readily transported onshore (shell shape may have a considerable effect of transport dynamics – pers. obs.); less “charismatic” species that are not targeted by collectors (Kidwell & Bosence 1991, Kidwell 2001, Warwick & Light 2002, Smith 2008). Secondly, the death assemblage represents a time-averaged deposit and so, in many cases, there is no way of determining how recently individual shells were deposited. For example, mineralised shells of species no longer extant in the region are sometimes found in death assemblages (e.g. *Pyrazus ebeninus* on Tasmania’s south-east coast – unpublished data) (Kidwell & Bosence 1991, Kidwell 2001). Despite these caveats, surveys of death assemblages provide rapid, broadscale descriptions of patterns of biodiversity. As such, they are a valuable, cost effective, method of obtaining preliminary data on biogeographic patterns of this dominant taxon of marine invertebrates (Beesley et al. 1998).

This study had the primary objective of sampling a range of suitable headlands along the NSW coast. Data collected over such a large area (i.e. spanning > 1000 km of coast and ~ 9 degrees of latitude) provide the opportunity to address a number of questions; specifically, this study addressed the following: Does the distribution of molluscs support the current bioregionalisation of the NSW coast? Are there obvious hot spots, or areas of low diversity? In the former case, are these sites represented within current marine protected areas (MPAs)?; and, in the latter case, what factors may be contributing to low diversity?

The current bioregionalisation model for the Australian coast was established by the Australian Government in 2006 (IMCRA Version 4.0) (Commonwealth of Australia 2006). This scheme recognises 5 meso-scale marine bioregions within NSW. From north to south, these are: Tweed-Moreton (SE Qld south to Nambucca); Manning Shelf (Nambucca to Stockton); Hawkesbury Shelf (Stockton to Shellharbour); Batemans Shelf (Shellharbour to Tathra); and Twofold Shelf (south from Tathra). The definition of bioregions is based on broadscale patterns, evident within a combination of biological and physical data. During the initial evaluation process, the primary biological data sets that were available across a large enough spatial scale were for sponges, corals, fishes and sea grasses (IMCRA 1998). While there is some evidence for the concordance of distribution patterns of unrelated taxa (e.g. grazing molluscs and their food source – unpublished data), there is nevertheless scope for non-modelled taxa to show patterns of distribution that do not align with these bioregional boundaries. Given the very high diversity and abundance of the Mollusca, representatives of this phylum should provide a robust test of the meso-scale bioregional model.

While there has been some debate about the importance placed on the identification of hot spots, especially with respect to establishing marine protected areas in these locations despite the possibility of temporal variability (e.g. under impacts of climate change) (Soto 2001), their identification is a common approach in marine conservation (Benkendorff & Davis 2002, Gladstone 2002). The generation of a state-wide data-set for mollusc death assemblages allows for the identification of patterns of species richness over a range of scales. Analysis of these patterns will facilitate, in particular, an assessment of whether or not the current system of MPAs covers the main areas of high diversity. By analyses of species-specific habitat requirements, the analysis of patterns of community structure may also provide insight into the dominant habitats adjacent to the different sites. As such, this analysis complements the current, state-wide habitat mapping program (e.g. Davies et al. 2007).

Methods

Site selection

Twenty-five headland sites had recently (since mid-2005) been surveyed in northern NSW prior to the field work for this study. The intention of additional field work was to survey a further 24 sites between Crescent Head (mid-north coast) and Eden (south coast). An initial list of suitable sites was determined following consultation with malacologists at the Australian Museum and other shell collectors. However, it was apparent from this exercise that knowledge of good, shell-retaining headlands was relatively poor over the scale required for this study. For this reason, planning included a "remote" inspection of the relevant section of the NSW coast using Google Earth.

From previous work on the NSW mid-north and north coasts, is has been possible to generalise about the topographical features that are common to sites with well-developed death assemblages. The three primary features are: sheltered aspects (mainly associated with longer headlands); rocky benches, especially in the upper intertidal, that aid the retention of shells; and relatively gentle slopes, allowing shells to wash up the shore. Generally, sites with highly dynamic sand movement, precipitous rock benches, or that face into the predominant pattern of swell (S-SE for the NSW coast), support poorly-developed or very selective death assemblages (e.g. dominated by larger, robust species in exposed conditions). From the Google Earth search, sites that looked promising were short-listed and aerial images of these were used to aid navigation in the field. While the study targeted only 24 sites, over 60 were short-listed and subsequently inspected during field work.

In addition to the 49 headland sites in NSW, an additional site was included for SE Queensland, Burleigh Heads, which has a very well-developed shell deposit. One site at offshore North Solitary Island (approx. 11 km from shore) was also included as this provides a contrast between coastal and island sites and, potentially, the influence of the East Australian Current which regular bathes the habitats associated with this island. Details of the 51 sites are shown in Fig. 1 and Table 1.

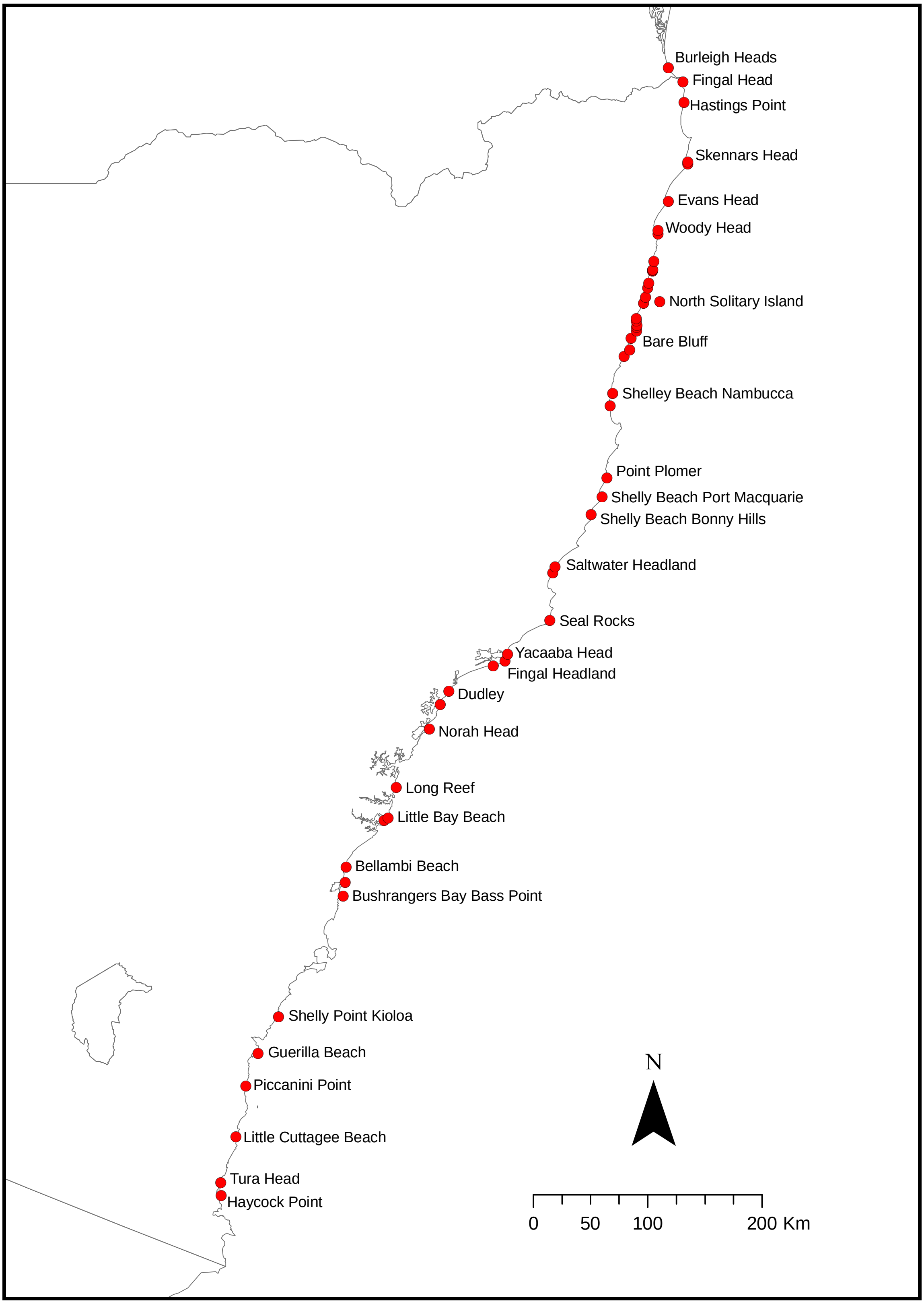

Fig. 1. Outline of the NSW coastline showing the spatial extent of sites sampled for this study (note that not all sites are labelled – for a full list see Table 1).

Table 1. List of locations (listed from north to south) at which surveys of death assemblages were conducted. S = species richness; quality = the quality rating (1-5 – Table 1); Abbrev. = abbreviation used on plots.

No.	Site name	S	Quality	Latitude	Longitude	Abbrev.
1	Burleigh Heads	132	5	28.08938	153.45559	Bu
2	Fingal Head (Tweed)	83	3	28.19906	153.57067	FiT
3	Hastings Point	146	5	28.36199	153.57949	Ha
4	Skennar's Head	127	4	28.83030	153.60711	Sk
5	Flat Rock (Ballina)	127	4	28.84370	153.60808	Bal
6	Evans Head	140	4	29.13847	153.45534	Ev
7	Woody Head	138	4	29.36515	153.37440	Wo
8	Iluka Bluffs	130	5	29.39673	153.37322	Il
9	Brooms Head	115	4	29.61063	153.34128	Br
10	Sandon 2	151	5	29.67476	153.33227	Sa2
11	Sandon 1	145	5	29.67905	153.33124	Sa1
12	Sandon 3	144	5	29.68374	153.32978	Sa3
13	Tree Point	162	5	29.77879	153.30280	Tr
14	Diggers Camp	168	4	29.81626	153.29270	Di
15	Jones Point	173	5	29.89313	153.27465	Jo
16	North Solitary Island	168	5	29.92498	153.38851	NSI
17	Pebbly Beach Headland	179	5	29.94007	153.26073	Pe
18	Arrawarra Headland	144	4	30.05847	153.20293	Ar
19	Mullaway Headland	166	5	30.07637	153.20475	Mu
20	Woolgoolga Headland	158	5	30.11269	153.21051	Wg
21	Flat Top (Woolgoolga)	174	5	30.13046	153.20700	FT
22	Bare Bluff	137	4	30.15676	153.20610	Ba
23	Green Bluff	137	3	30.21438	153.16354	Gr
24	Muttonbird Island	102	4	30.30460	153.15160	MBI
25	Boambee Headland	136	3	30.35600	153.10915	Bm
26	Shelly Beach (Nambucca)	124	5	30.64691	153.01958	Na
27	Scotts Head	97	4	30.74360	152.99700	Sc
28	Point Plomer	62	3	31.31238	152.97148	PP
29	Shelly Beach (Port Macquarie)	89	4	31.45906	152.93475	PtM
30	Shelly Beach (Bonny Hills)	105	5	31.59798	152.84696	Bo
31	Saltwater Headland	120	4	32.00702	152.56570	SW
32	Shelly Beach (Diamond Head)	119	5	32.05747	152.54738	DH
33	Seal Rocks	92	4	32.43072	152.52574	Se
34	Yacaaba Head	136	5	32.69440	152.19288	Ya
35	Fingal Headland (Pt. Stephens)	126	4	32.74859	152.17281	Fi
36	Birubi Point	132	4	32.78683	152.07862	Bi
37	Dudley	135	4	32.98763	151.72967	Du
38	Reid's Mistake Headland	124	4	33.09016	151.66456	Re
39	Norah Head	129	4	33.28226	151.57642	No
40	Long Reef	131	5	33.74219	151.31748	LR
41	Little Bay Beach	89	3	33.98029	151.25231	Li
42	Inscription Point (Kurnell)	112	5	34.00166	151.22243	In
43	Bellambi Beach	100	4	34.36739	150.92482	Bel
44	Red Point (Port Kembla)	137	5	34.48571	150.91564	RPt
45	Bushrangers Bay (Bass Point)	112	5	34.59450	150.90082	Bas
46	Shelly Point (Kioloa)	116	5	35.54326	150.39199	Ki
47	Guerilla Beach	92	4	35.82958	150.22948	Gu
48	Piccanini Point	123	5	36.08637	150.13548	Pi
49	Little Cuttagee Beach	121	4	36.48729	150.05701	LC
50	Tura Head	112	4	36.84703	149.93861	Tu
51	Haycock Point	90	3	36.94987	149.94174	Hy

Study design

Previous work in NSW indicated that 3 sites are necessary in order to ensure regional representation of molluscs (Smith 2008). For this reason, for the additional field work conducted for this study, the NSW coast between Crescent Head and Eden was divided into approximately 150-km sections and, where possible, 3 sites were sampled within each of these. For the northern part of the state, previous sampling included all suitable headland sites (all were inspected) and so more than 3 sites were available in most sections of coast. This level of sampling intensity proved to be important for determining patterns and potential causative processes at medium scales (see *Results*). As one of the objectives of the study was to determine if data from death assemblages support the current bioregionalisation of the NSW coast, wherever possible (i.e. suitable, accessible sites), sampling was concentrated around recognised boundaries (from north to south – Nambucca Heads, Newcastle, Shellharbour and Tathra).

Field methods

Sampling followed the protocol established by Smith (2008). Thus, two-hour surface searches (to a depth of approximately 150 mm) were conducted across the spatial extent of the primary shell bank at each site and all species of gastropod and bivalve ≥ 5 mm were documented and given an abundance score. Fragmented shells were only included if they could be unambiguously identified to species. The scoring system was based on a $\log_3$ scale: score 1 = 1-3 individuals; 2 = 4-10; 3 = 11-30; 4 = 31-100; 5 = 101-300; 6 > 300. Representative specimens of all species were retained in a reference collection and were initially identified using published resources (primarily Lamprell & Whitehead 1993, Wilson 1993, 1994, Lamprell & Healy 1998, Beechey 2007). Identifications were later confirmed using the collections of the Australian Museum.

In some regions, well developed death assemblages were hard to find necessitating surveys of scattered and/or poorly developed aggregations. The quality of an assemblage is highly likely to influence both its representation and overall species richness. For this reason, each deposit was qualitatively evaluated and given a rating (from 1 to 5): 1 = shells absent or thinly scattered throughout the site; 2 = small deposits with no main shell bank; 3 = shell bank present but small, poorly developed, scattered, thin or comprising fragmented older shells; 4 = good shell deposits but occurring across > 50m of the shore; 5 = very well developed deposits in large and concentrated shell bank. Only sites with a quality rating ≥3 were surveyed; all sites examined were rated in this way.

Analytical methods

Data were analysed in a number of ways to address the primary objectives of the study. Latitudinal patterns of species richness (S) were explored by plotting species richness at each site against latitude (decimal degrees). In order to reduce confounding, only sites with a quality rating of 4 or 5 were included in this exploration (6 sites excluded – see Table 1). The relationship between S and latitude was also more formally explored using regression analysis.

Changes in community structure across the entire study were evaluated using a range of multivariate methods (in PRIMER-E 6). Untransformed data (species and abundance scores) were used for the analyses as the scoring system already represents a relatively severe transformation of absolute abundance values (Smith et al. 2008). The similarity between each pair of samples was calculated using the Bray-Curtis similarity measure and community patterns were subsequently displayed in a non-metric multidimensional scaling (nMDS) ordination and a hierarchical clustering analysis. To aid pattern visualisation, appropriate similarity contours (from the cluster analysis) were superimposed on the 2-dimensional nMDS plot.

A number of different approaches were taken for subsequent analysis. Firstly, sites were labelled according to group membership (using 55% similarity contours) so that the species primarily responsible for differences at the largest spatial scale could be identified using SIMPER. Secondly, each of the main sample groups was explored separately, using nMDS, similarity contours (60 and 70%), and SIMPER, in order to discern patterns at a finer scale. Finally, the relationship between community patterns and latitude was further explored using the BEST procedure.

Results

General

A total of 505 species was found during the surveys of the 51 sites. Of these, 114 were found at only 1 site (unique species) and only 7 species were found at all sites- *Austrocochlea porcata, Cabestana spengleri, Cellana tramoserica, Montfortula rugosa, Saccostrea glomerata, Siphonaria denticulata, Thais orbita* (Table 2). Unique species were found at 37 of the 51 sites but 2 sites stood out as supporting a disproportionately high number – North Solitary Island (22), and Burleigh Heads (12) (Table 3). These sites were the only offshore site, and the most northerly site, respectively. Yacaaba Head at Port Stephens also contained a relatively high number of unique species; all of these were sand-dwelling taxa comprising mostly bivalves and one species of deep-water cone (Family Conidae) shell.

All except one of the unique species found at North Solitary Island were reef-associated taxa with tropical affinities; this is consistent with the position of the island with respect to the flow of the East Australian Current and the coral-dominated habitats surrounding the island (see *Discussion*). Indeed, 6 of these unique taxa are corallivorous species that feed exclusively on hard (F. Muricidae) or soft (F. Ovulidae) coral. At Burleigh Heads, the suite of unique species comprised sand-dwelling taxa.

Table 2. Frequency of occurrence of the 505 species across the 51 sites surveyed.

Frequency of occurrence	No. species
Unique (1 site only)	114
2-3 sites	86
4-14 sites	131
15-26 sites	79
27-38 sites	42
39-50 sites	46
51 sites	7

Patterns of species richness

Species richness ranged from 62 at Point Plomer to 179 at Pebbly Beach (Table 1). While there was evidence of a general reduction in species richness from north to south (Fig. 2), this was by no means monotonic and was associated with high levels of variation despite the highly significant regression ($P < 0.001$). The coefficient of variation ($r^2 = 0.242$) indicated that only 24% of the variation in species richness could be explained by latitude. Indeed, the main feature of the plot is the large variation from region to region with: i) a very prominent spike in species richness in the northern section of the Solitary Islands Marine Park (SIMP) (Sandon south to Arrawarra); ii) generally depauperate assemblages between Muttonbird Island and Seal Rocks; iii) a smaller spike in richness around Port Stephens and Newcastle; and iv) a high richness at Red Point, Port Kembla.

Table 3. List of sites supporting more than 3 unique species.

Site	No. unique species
North Solitary Island	22
Burleigh Heads	12
Yacaaba Head	7
Diggers Camp	5
Fingal Head (Pt. Stephens)	4
Fingal Head (Tweed)	4
Flat Rock (Ballina)	4
Mullaway Headland	4
Tree Point	4

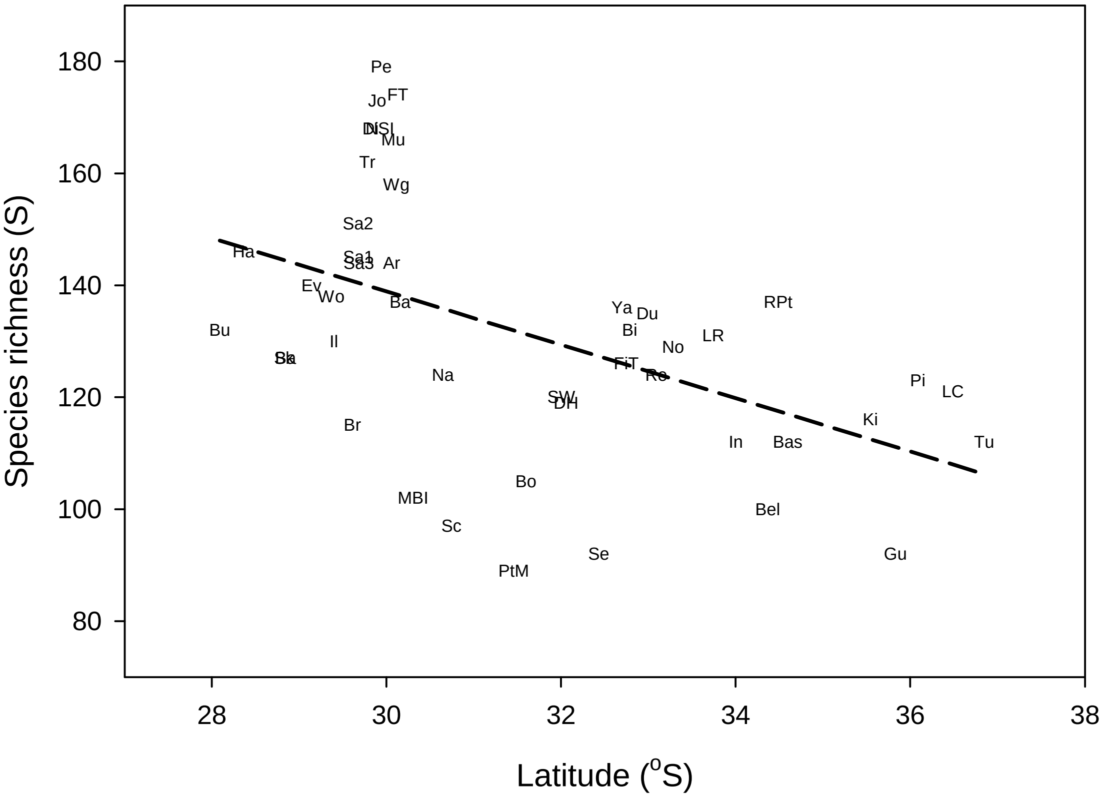

Fig. 2. Relationship between species richness and latitude across sites with a quality rating ≥4. The line-of-best-fit is shown but there is considerable variation around this ($r^2 = 0.242$). Site abbreviations appear (from Table 1) as plot symbols.

Patterns of community structure

Patterns of similarity between death assemblages at each site were explored using both nMDS (Fig. 3) and cluster analyses (Fig. 4). Although displaying the same data as the nMDS (and therefore not often presented in summaries of such analyses), the hierarchical detail in the cluster analysis in this case provides additional information not evident within the nMDS plot (especially with respect to the level of similarity at which different clusters can be defined). This is particularly useful for determining finer detail about site relationships within the main clusters (see below).

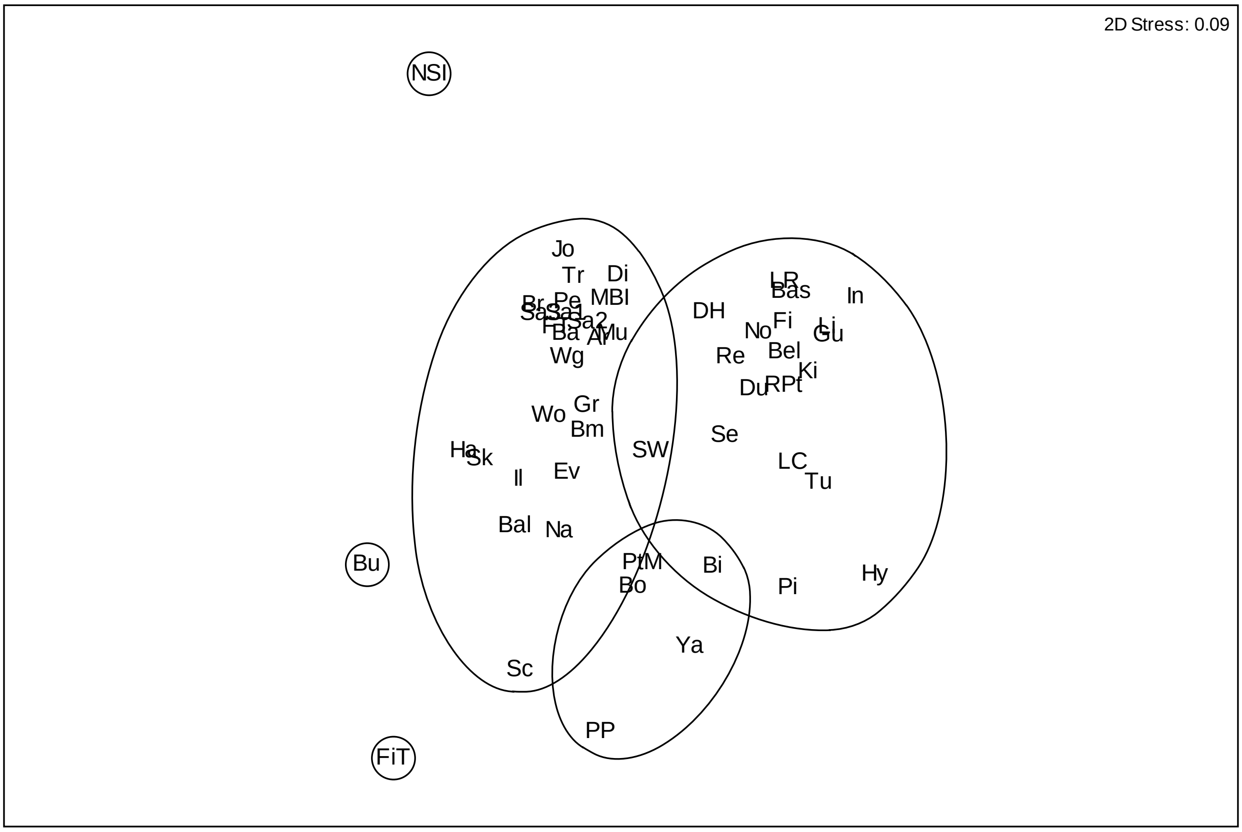

Fig. 3. Non-metric MDS of death assemblage data from 51 sites. Contours represent 55 % similarity. Site abbreviations as in Table 1.

Both analyses (Figs. 3 and 4) indicated that sites could generally be split into 3 major groupings at a similarity of 55%. Only 3 sites fell outside these 3 groups, Burleigh Heads (Bu), Fingal Head (Tweed Coast) (FiT) and North Solitary Island (NSI), each of which supported very different assemblages to any other site (separating from these at a similarity < 40% - Fig. 4). Fingal Head differed in that: i) most species occurred in low abundance (the deposit was not well-developed and had a quality rating of 3 – Table 1); ii) many reef-associated species common to most other sites were absent; iii) the common sand-dwelling species, and especially bivalves, predominated in deposits (with maximum abundance scores). North Solitary Island differed from other sites due to the presence of a wide range of tropical species that were not found elsewhere (Table 3) (especially from the families Cypraeidae, Conidae, Cerithiidae and Muricidae) and the absence, or low abundance, of a number of reef-associated species that were common at headland sites. Likewise, Burleigh Heads supported a range of species that were either rare or absent (Table 3) from other sites, some of these being in high abundances (e.g. *Callista disrupta*, *Conus cyanostoma*, *Calthaliota fragum*) and also lacked some of the common, larger grazers found to the south (especially turban shells – F. Turbinidae).

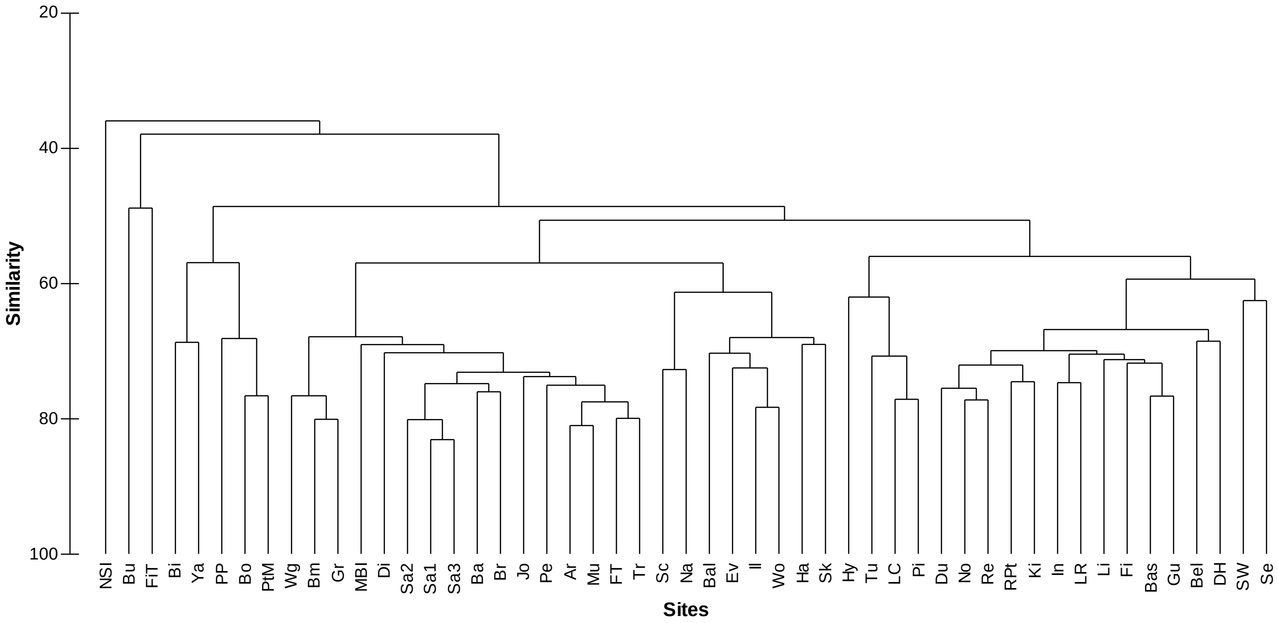

Fig. 4. Group-average clustering of death assemblage data from 51 sites. Site abbreviations as in Table 1.

A general latitudinal trend was evident across the nMDS plot with northern sites to the left and those from southern NSW to the right (Fig. 3). The importance of latitude in explaining the pattern of site similarities was confirmed using the BEST procedure in PRIMER with a Spearman Rank correlation of $\varrho = 0.551$.

While the nMDS plot shows considerable overlap between sites amongst clusters, the 3 main clusters were clearer in the hierarchical analysis (Fig. 4) allowing sites to be allocated into 3 groups at the 55% similarity level: Cluster 1 - most sites from Hastings Point south to Scotts Head; Cluster 2 – some of the sites between Point Plomer and Port Stephens; and Cluster 3 - all sites to the south, and 3 sites to the north (Shelley Beach Diamond Head [DH], Saltwater Headland [SW] and Seal Rocks [Se]), of Port Stephens.

The species primarily responsible for differences between the 3 clusters were assessed using SIMPER analyses (Tables 4-6). Differences between the northern cluster (Cluster 1) and the southern cluster (Cluster 3) were related to shifts in the abundance of a large number of taxa (74 species contributed the first 50% to the overall differences between clusters). In some cases these reflected disjunct biogeographical distributions of taxa (e.g. the absence some species from one of the 2 clusters), and in others, clear trends in the abundance of species. For example, the dove shells (F. Columbellidae) that characterise death assemblages in northern NSW (*Pyrene testudinaria* and *P. scripta*) were absent from southern sites and a number of species from the F. Trochidae were absent or rare at northern sites (e.g. *Granata imbricata, Austrocochlea concamerata*) (Table 4).

Table 4. Summary of SIMPER analyses between the left (North – Cluster 1) and right (South – Cluster 3) site groupings in Fig. 3. Average abundance scores are shown as well as species habitat preference (S = sand, R = reef) and the contribution of each species to overall differences between groups.

Species	Habitat	North	South	Contrib%	Cum.%
Pyrene testudinaria	R	4.92	0.00	1.28	1.28
Amoria zebra	S	4.12	0.26	1.04	2.32
Patelloida mufria	R	1.04	4.63	0.99	3.31
Pyrene scripta	R	3.68	0.00	0.94	4.25
Thais ambustulatus	R	4.12	0.53	0.94	5.19
Donax brazieri	S	3.68	0.37	0.93	6.12
Patelloida alticostata	R	0.00	3.53	0.93	7.05
Granata imbricata	R	0.00	3.58	0.93	7.98
Austrocochlea concamerata	R	0.28	3.58	0.93	8.91
Cronia aurantiaca	R	4.56	1.53	0.91	9.82
Turbo militaris	R	3.64	1.37	0.81	10.63
Cominella eburnea	R	4.08	1.58	0.79	11.42
Neverita incei	S	3.00	0.11	0.79	12.21
Lepsiella reticulata	R	5.48	2.84	0.77	12.98
Bankivia fasciata	S	5.16	2.74	0.77	13.75
Donax deltoides	S	3.08	1.26	0.74	14.49
Eurytrochus strangei	R	3.76	2.16	0.74	15.23
Cantharidella picturata	R	3.12	4.95	0.74	15.97
Astralium tentoriformis	R	3.00	4.89	0.73	16.70
Anadara trapezia	S	2.92	1.37	0.73	17.43
Glycymeris grayana	S	2.48	2.74	0.72	18.15
Pyrazus ebeninus	S	2.96	1.05	0.72	18.87
Hipponix australis	R	4.32	2.89	0.70	19.57
Conus coronatus	R	2.76	0.11	0.69	20.26
Cacozeliana granarium	S	1.92	3.79	0.69	20.95
Corbula coxi	S	2.80	0.63	0.68	21.63
Batillaria australis	S	3.36	1.79	0.68	22.31
Haliotis rubra	R	0.84	3.21	0.67	22.98
Limatula strangei	R	0.20	2.74	0.67	23.65
Nassarius jonasii	S	2.68	1.74	0.66	24.31

Comparisons between the northern cluster (Cluster 1) and the Port Macquarie cluster (Cluster 2) (Table 5), indicated that the Port Macquarie sites generally contained higher abundance of sand-associated species and either lacked a number of reef-associated species that were common to the north, or contained these in low abundance (Table 5).

Table 5. Summary of SIMPER analyses between the left (North – Cluster 1) and right (South – Cluster 3) site groupings in Fig. 3. Average abundance scores are shown as well as species habitat preference (S = sand, R = reef) and the contribution of each species to overall differences between groups.

Species	Habitat	North	Pt. Macq.	Contrib%	Cum.%
Pyrene testudinaria	R	4.92	0.00	1.38	1.38
Cronia aurantiaca	R	4.56	0.40	1.20	2.58
Thais ambustulatus	R	4.12	0.00	1.16	3.74
Mactra contraria	S	2.12	6.00	1.09	4.83
Turbo militaris	R	3.64	0.00	1.00	5.83
Austroginella muscaria	S	1.60	4.80	0.95	6.78
Eurytrochus strangei	R	3.76	0.60	0.95	7.73
Hipponix australis	R	4.32	1.40	0.94	8.67
Pyrene scripta	R	3.68	0.80	0.92	9.59
Bassina pachyphylla	S	0.28	3.40	0.91	10.50
Turbo torquatus	R	3.80	1.80	0.89	11.39
Cominella eburnea	R	4.08	1.20	0.87	12.26
Hemidonax dactylus	S	1.76	3.20	0.86	13.12
Pseudamycla dermestoidea	R	3.24	0.20	0.85	13.97
Nassarius nigellus	S	0.00	3.20	0.84	14.81
Anadara trapezia	S	2.92	5.60	0.82	15.63
Glycymeris grayana	S	2.48	4.80	0.80	16.43
Scutellastra chapmani	R	3.84	1.40	0.80	17.23
Tugali parmophoidea	R	3.84	1.40	0.79	18.02
Cantharidella picturata	R	3.12	1.00	0.77	18.79
Conus coronatus	R	2.76	0.00	0.76	19.55
Barbatia pistachia	R	3.08	0.40	0.76	20.31
Austrolittorina unifasciata	R	3.52	1.00	0.76	21.07
Acropsis afra	R	2.68	0.00	0.74	21.81
Donax deltoides	S	3.08	5.40	0.74	22.55
Neverita incei	S	3.00	2.00	0.73	23.28
Lepsiella reticulata	R	5.48	3.20	0.72	24.00
Donax brazieri	S	3.68	2.60	0.72	24.72
Cypraea xanthodon	R	2.72	0.20	0.71	25.43
Astralium tentoriformis	R	3.00	1.00	0.70	26.13

Differences between sites from the Port Macquarie group (Cluster 2) and the southern group (Cluster 3) showed similar trends to those between the northern group (Cluster 1) and Cluster 2. Thus, the sites from Cluster 2 generally supported higher abundances of sand-associated species and lower abundances of reef-associated species than southern sites (Table 6). While 30 of the species that contributed the most to differences between the groups were present at sites within both groups, there were some clear trends related to the biogeographic affinity of species. For example, *Austrocochlea concamerata, Granata imbricata* and *Patelloida alticostata*, were all more common in deposits at southern sites.

Further description of patterns within each of the 3 major clusters is provided below.

Table 6. Summary of SIMPER analyses between the right (South – Cluster 1) and middle (Pt. Macquarie – Cluster 2) site groupings in Fig. 3. Average abundance scores are shown as well as species habitat preference (S = sand, R = reef) and the contribution of each species to overall differences between groups.

Species	Habitat	South	Pt. Macq.	Contrib%	Cum.%
Mactra contraria	S	0.84	6.00	1.61	1.61
Anadara trapezia	S	1.37	5.60	1.34	2.96
Antisabia foliacea	R	5.53	1.20	1.34	4.30
Donax deltoides	S	1.26	5.40	1.31	5.61
Astralium tentoriformis	R	4.89	1.00	1.29	6.89
Cantharidella picturata	R	4.95	1.00	1.26	8.15
Patelloida mufria	R	4.63	0.60	1.25	9.40
Pseudamycla dermestoidea	R	3.95	0.20	1.16	10.56
Scutellastra chapmani	R	5.11	1.40	1.15	11.72
Turbo torquatus	R	5.11	1.80	1.09	12.81
Austrocochlea concamerata	R	3.58	0.20	1.08	13.88
Tylospira scutulata	S	0.89	4.40	1.07	14.96
Pyrazus ebeninus	S	1.05	4.20	1.07	16.02
Granata imbricata	R	3.58	0.20	1.05	17.07
Haliotis coccoradiata	R	3.68	0.40	1.04	18.12
Agnewia tritoniformis	R	5.47	2.60	1.04	19.16
Hemidonax dactylus	S	0.42	3.20	1.03	20.19
Austrolittorina unifasciata	R	4.26	1.00	1.02	21.21
Bankivia fasciata	S	2.74	6.00	1.01	22.22
Bassina pachyphylla	S	0.32	3.40	0.98	23.21
Patelloida alticostata	R	3.53	0.60	0.97	24.18
Austroginella muscaria	S	2.37	4.80	0.95	25.12
Glycymeris grayana	S	2.74	4.80	0.87	25.99
Cacozeliana granarium	S	3.79	2.40	0.83	26.83
Mitrella tayloriana	R	5.68	3.40	0.82	27.64
Siphonaria funiculata	R	3.79	1.60	0.81	28.45
Batillaria australis	S	1.79	3.60	0.81	29.26
Limatula strangei	R	2.74	0.20	0.79	30.05
Mesoginella turbinata	S	0.89	2.80	0.79	30.84
Conus papilliferus	R	2.95	0.60	0.77	31.61

Cluster 1

There is primary break between groups of sites (at the 60% similarity level) that separate those from north of the Clarence River, plus the two sites closest to the Nambucca River (Sc, Na), from all sites between Brooms Head (Br) and Boambee Headland (Bm) (Fig. 5). In the left-hand group, and at a similarity level of 70%, sites immediately north of the Clarence River from a discrete group and, below this, Nambucca sites from a separate group. In the right-hand group, and with the exception of Muttonbird Island (MBI) which shows clear differences to other sites, there are 2 primary site groups: i) Woolgoolga Headland (Wg), Green Bluff (Gr) and Boambee Headland (Bm); and ii) sites from the northern section of the SIMP (Bare Bluff north to Sandon) (Fig. 5).

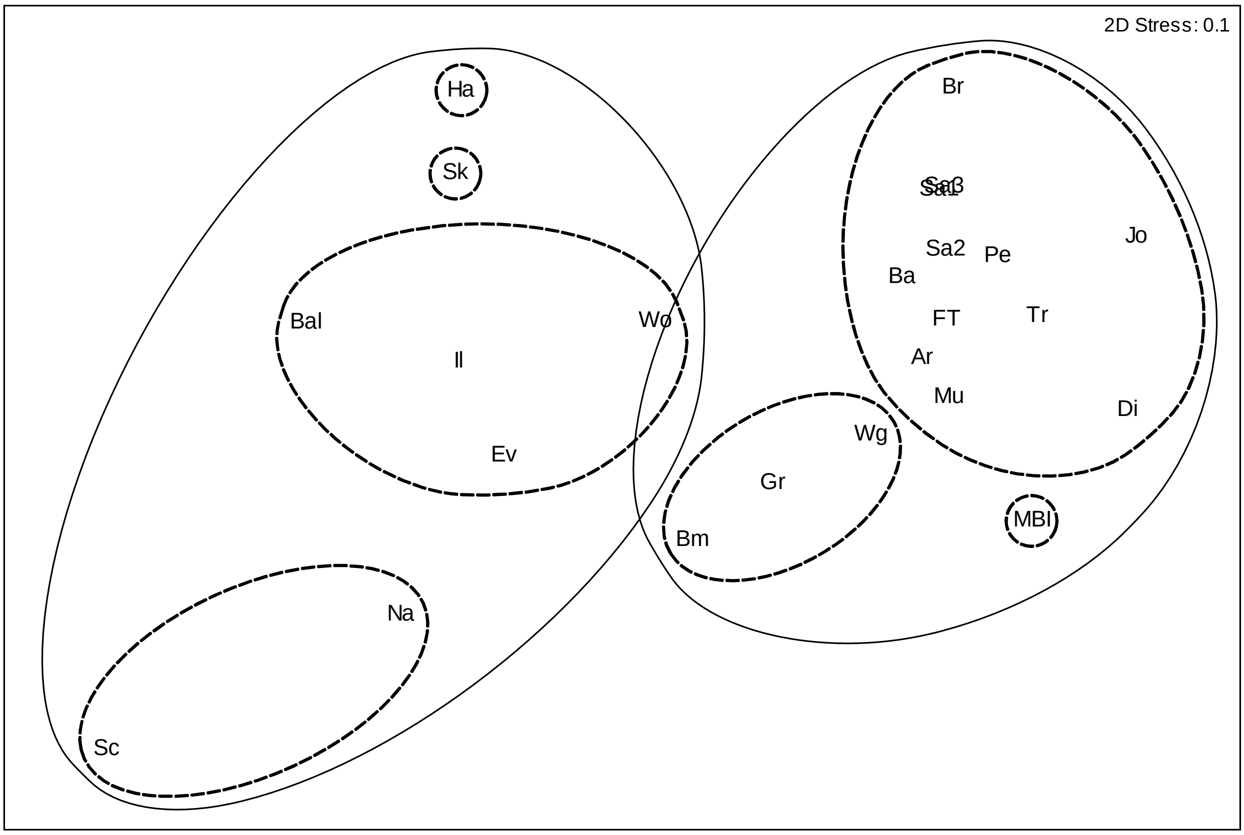

Fig. 5. Non-metric MDS of death assemblage data from sites within Cluster 1 of Fig. 3. Contours represent 60 and 70% similarity. Site abbreviations as in Table 1.

The species primarily responsible for similarities within and between the main site groupings were determined using SIMPER analyses. The most obvious difference between the 2 primary (60% similarity) groups was clearly related to the presence and relative abundance of sand-dwelling species. This is best illustrated by the fact that, of the 30 species contributing the most to similarities within groups, only 1 soft-sediment-associated species was listed for the right-hand group in comparison to 13 species for the left-hand group. The assessment of dissimilarities between groups reinforced this pattern. Thus, of the 30 species contributing the most to differences between groups, 16 were reef-associated species that had higher abundance at sites in the right-hand group, and 14 were soft-sediment-associated species with higher abundance at sites in the left-hand group (Table 7).

Table 7. Summary of SIMPER analyses between the 2 main groups of sites in Cluster 1 (Fig. 5). Average abundance scores are shown as well as species habitat preference (S = sand, R = reef) and the contribution of each species to overall differences between groups. Groupings refer to relative positions in Fig. 5.

Species	Habitat	Right group	Left group	Contrib%	Cum.%
Turbo torquatus	R	5.75	0.38	1.56	1.56
Spisula trigonella	S	0.00	4.63	1.35	2.91
Turbo militaris	R	5.31	0.75	1.33	4.24
Hipponix australis	R	5.94	1.63	1.26	5.50
Donax deltoides	S	1.56	5.88	1.26	6.76
Anadara trapezia	S	1.56	5.25	1.19	7.95
Conuber sordidus	S	0.50	4.38	1.18	9.13
Paphies elongata	S	0.19	4.13	1.17	10.30
Mactra contraria	S	0.75	4.75	1.17	11.47
Timoclea scabra	S	0.69	4.25	1.11	12.58
Astralium tentoriformis	R	4.25	0.63	1.08	13.66
Siliquaria ponderosa	R	5.13	1.50	1.05	14.72
Cantharidella picturata	R	4.31	1.13	1.03	15.75
Nassarius jonasii	S	1.50	4.75	0.99	16.74
Tylospira scutulata	S	1.50	4.50	0.93	17.67
Glycymeris grayana	S	1.56	3.88	0.92	18.59
Scutellastra chapmani	R	4.88	2.00	0.89	19.48
Clypeomorus petrosa	R	3.50	0.88	0.88	20.36
Bostrycapulus pritzkeri	R	3.50	1.00	0.88	21.24
Hemidonax dactylus	S	0.81	3.25	0.88	22.12
Donax brazieri	S	2.75	5.50	0.88	23.00
Cominella eburnea	R	5.13	2.38	0.84	23.84
Pyrene scripta	R	4.13	2.88	0.84	24.67
Nerita albicilla	R	3.25	1.50	0.83	25.50
Eurytrochus strangei	R	4.56	2.63	0.81	26.31
Bassina jacksoni	S	0.13	2.88	0.80	27.12
Pyrene testudinaria	R	5.69	3.38	0.77	27.88
Corbula coxi	S	2.00	4.00	0.75	28.64
Phasianotrochus eximius	R	5.56	3.13	0.75	29.39
Pseudamycla dermestoidea	R	4.19	1.75	0.75	30.14

Cluster 2

Cluster 2 comprises a selection of 5 sites between Point Plomer and Port Stephens and the relationship between these sites is clear in the main analyses (Figs. 3 and 4). While they form a group at the 50% similarity level, they clearly fall into 2 sets of sites at 60% similarity. Thus, the 3 sites adjacent to Port Macquarie (PP, PtM, Bo) group to the left and those from Port Stephens (Ya, Bi) to the right of the cluster (Fig. 3). Unlike in Cluster 1, the main differences between the 2 groups were not as clearly related to habitat of component species. As determined in the

SIMPER analyses between primary clusters, this group of sites is characterised by a dominance of sand-dwelling species. For this reason, it is unsurprising that there was little difference in the habitat preferences of species primarily responsible for within groups – 16 out of 30 for the right-hand group and 12 out of 30 for the left-hand group. In this case, differences were mostly related to the presence of a number of species in one group that did not occur in the other. Thus, 8 of the 30 highest-ranked discriminators between groups were only found at the Port Stephens sites (Bi, Ya) and 6 were found only at the Port Macquarie sites (Bo, PtM, PP) (Table 8).

Table 8. Summary of SIMPER analyses between the 2 groups of sites in Cluster 2 (Fig. 3). Average abundance scores are shown as well as species habitat preference (S = sand, R = reef) and the contribution of each species to overall differences between groups.

Species	Habitat	Bi, Ya	Bo, PtM, PP	Contrib%	Cum.%
Hemidonax dactylus	S	0.00	5.33	2.09	2.09
Calthaliota fragum	S	4.50	0.33	1.63	3.72
Glycymeris holsericus	S	4.00	0.00	1.58	5.30
Nassarius nigellus	S	5.50	1.67	1.55	6.85
Mesoginella turbinata	S	5.00	1.33	1.45	8.30
Corbula coxi	S	0.00	3.67	1.42	9.72
Numella adamsi	S	3.50	0.00	1.35	11.07
Hemidonax pictus	S	3.50	0.00	1.34	12.41
Neverita incei	S	4.00	0.67	1.31	13.71
Austroginella johnstoni	S	0.00	3.33	1.30	15.02
Agnewia tritoniformis	R	4.50	1.33	1.29	16.30
Batillaria australis	S	5.50	2.33	1.25	17.56
Pecten fumatus	S	3.50	0.33	1.25	18.81
Amoria undulata	S	4.00	1.00	1.22	20.03
Cancellaria undulata	S	3.50	0.33	1.21	21.24
Amoria zebra	S	0.00	3.00	1.18	22.42
Crassostrea gigas	R	3.00	0.00	1.17	23.59
Mesoginella translucida	S	3.00	0.00	1.17	24.75
Cacozeliana granarium	R	4.00	1.33	1.16	25.92
Trimusculus conica	R	0.00	3.00	1.16	27.07
Monilea callifera	S	3.00	0.00	1.15	28.22
Conus aplustre	S	3.50	0.67	1.14	29.36
Turbo torquatus	R	3.50	0.67	1.12	30.49
Mitrella tayloriana	R	5.00	2.33	1.11	31.60
Nassarius particeps	R	3.00	0.33	1.08	32.68
Chama fibula	R	0.50	3.33	1.08	33.76
Lima lima vulgaris	R	2.50	0.00	1.01	34.77
Bulla vernicosa	R	3.50	1.00	1.01	35.79
Leiopyrga lineolaris	R	2.50	0.00	0.96	36.74
Hipponix australis	R	0.00	2.33	0.92	37.66

Cluster 3

Further analysis of Cluster 3 revealed 3 clear grouping at the 60% similarity level (Fig. 6). The left-hand group contained samples from Newcastle south to Guerilla Beach but also included Fingal Head, Port Stephens (Fi). Seal Rocks (Se) and Saltwater Headland (SW) form a discrete group at the bottom of the plot and the 4 sites south of Guerilla Beach form the final group. Two subgroups of sites can be discerned within the left-hand cluster (at the 70% similarity level) which are not obviously related to latitude. Thus, the left-hand subgroup contains samples from Fingal Head to Guerilla Beach and the right-hand group samples from Dudley to Kioloa.

As for comparisons within other clusters, the primary driver of differences appears to be the relative abundance of reef and sand-associated taxa. Thus, south of Guerilla Beach, deposits are dominated by sand-associated species while those from the right-hand group are dominated by reef-associated species (Table 9). Thus all of the 16 sand-associated species listed in the 30 most discriminatory species were more abundant in the right-hand group and 12 of the reef-associated species were more abundant in the left-hand group. Of the remaining 2 species, *Cominella lineolata* is reef-associated but was more abundant at the southern sites as most of the northern sites are beyond its distribution range.

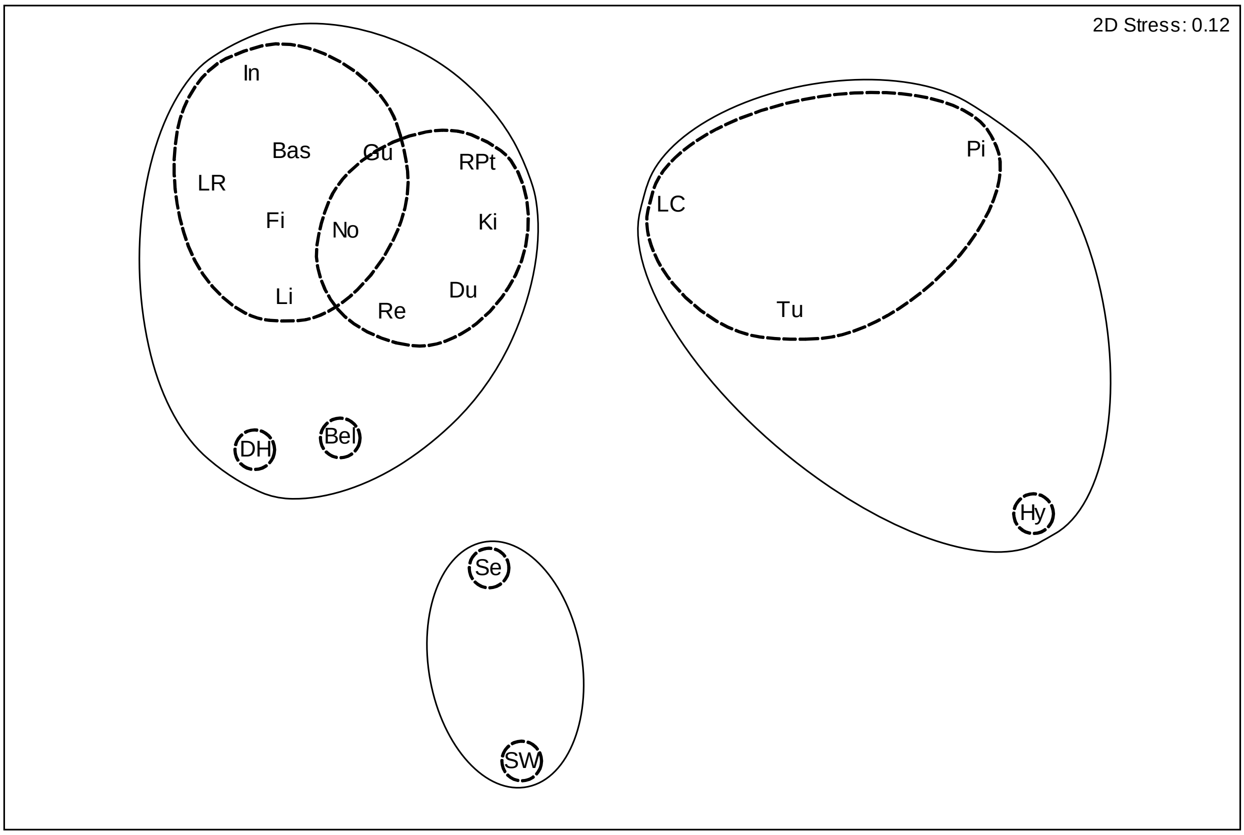

Fig. 6. Non-metric MDS of death assemblage data from sites within Cluster 3 of Fig. 3. Contours represent 60 and 70% similarity. Site abbreviations as in Table 1.

Table 9. Summary of SIMPER analyses between the 2 largest clusters in Fig. 6. Average abundance scores are shown as well as species habitat preference (S = sand, R = reef) and the contribution of each species to overall differences between groups.

Species	Habitat	Left	Right	Contrib%	Cum.%
Tawera gallinula	S	0.31	5.50	1.70	1.70
Austroginella muscaria	S	0.85	6.00	1.69	3.39
Bankivia fasciata	S	1.46	6.00	1.49	4.88
Gazameda gunnii	S	0.00	4.50	1.46	6.34
Glycymeris grayana	S	1.69	5.75	1.37	7.71
Phasianotrochus eximius	R	4.92	1.00	1.36	9.07
Nassarius nigellus	S	1.23	5.25	1.29	10.36
Austroginella johnstoni	S	0.46	4.25	1.23	11.59
Bostrycapulus pritzkeri	R	3.69	0.00	1.20	12.79
Nassarius jonasii	S	0.85	4.25	1.19	13.98
Astralium tentoriformis	R	5.69	2.25	1.18	15.16
Batillaria australis	S	1.00	4.25	1.17	16.33
Mesoginella turbinata	S	0.23	3.50	1.05	17.39
Conuber sordidus	S	0.15	3.25	0.98	18.37
Pyrazus ebeninus	S	0.23	3.25	0.97	19.33
Patelloida latistrigata	R	4.00	2.75	0.95	20.28
Amoria undulata	S	0.00	2.75	0.92	21.21
Conus aplustre	R	3.23	0.50	0.92	22.13
Cardita excavata	R	4.31	1.50	0.92	23.04
Patelloida mufria	R	5.38	3.25	0.90	23.94
Leiopyrga lineolaris	R	1.31	2.75	0.88	24.82
Donax deltoides	S	0.46	3.00	0.88	25.70
Mytilus edulis planulatus	R	0.38	3.00	0.85	26.56
Spisula trigonella	S	0.46	2.75	0.85	27.40
Eurytrochus strangei	R	2.85	0.50	0.85	28.25
Conuber conicum	S	1.46	3.75	0.81	29.05
Granata imbricata	R	4.46	2.50	0.77	29.83
Siphonaria funiculata	R	4.62	2.50	0.76	30.59
Limatula strangei	R	3.38	2.00	0.76	31.36
Cominella lineolata	R	0.38	2.25	0.76	32.11

Distribution ranges of individual species

Patterns revealed by multivariate analyses are influenced by small shifts in abundance or presence/absence of a large number of species. In this respect, while they are useful to show discrete community patterns, supplementary examination of the data is necessary to reveal geographic ranges of the different species and any evidence for disjunct biogeographical boundaries. The approach that was taken was to examine the distribution range for species that were found at between 4-38 sites (see Table 2) and determine if there were sites or clusters of sites at which range boundaries were concentrated; such a pattern would be an indication of a clear biogeographic boundary. Note that this evaluation referred only to the data collected during this study (the implications of this are covered in the *Discussion*). Species were evaluated if: i) they were common enough to unambiguously evaluate distribution range (i.e. species that occurred in low abundance and those that showed sporadic occurrence across the state, were omitted); and ii) they had a published distribution boundary within NSW.

An examination of the southern and northern limits of distribution for eligible species (Fig. 7) does not readily support the idea of disjunct boundaries, at least not coinciding with the 4 primary bioregions within the sampling area (north to south – Tweed-Moreton, Manning Shelf, Hawkesbury Shelf and Batemans Shelf – see Fig. 7). Thus, the southern distributional limits for 93 species were spread across the state with only one obvious concentration of species around Coffs Harbour and the Solitary Islands Marine Park. Within this cluster of sites, Bare Bluff was the southernmost limit for the greatest number of species (8) although most sites between Flat Top Point and Scotts Head yielded at least 1 species that did not occur further south. Smaller concentration of sites, hosting the southernmost records for different species, occurred around Saltwater and Diamond Head (central Manning) and Port Stephens, (southern Manning). Most sites in the Hawkesbury Shelf bioregion supported at least 1 species that was not found further south. The southern distribution limit for 8 species occurred at Long Reef, Sydney, although this site is in the central section of the Hawkesbury Shelf bioregion.

Patterns of northern distributional limits were more difficult to interpret as there were fewer species within this category (35) and they were spread widely across the study area. However, the northern limit of distribution for 12 species occurred in the northern part of the state (between Skennars Head and Sandon and in the middle of the Tweed-Moreton bioregion). A further 14 species had their northern distributional boundaries within the Manning Shelf bioregion, with Saltwater and Diamond Head supporting 5 of these. There was a small concentration of sites supporting at least one northernmost record in the Port Stephens area.

The distribution records for a sample of 42 species, including abundance scores, are shown in Appendix 1.

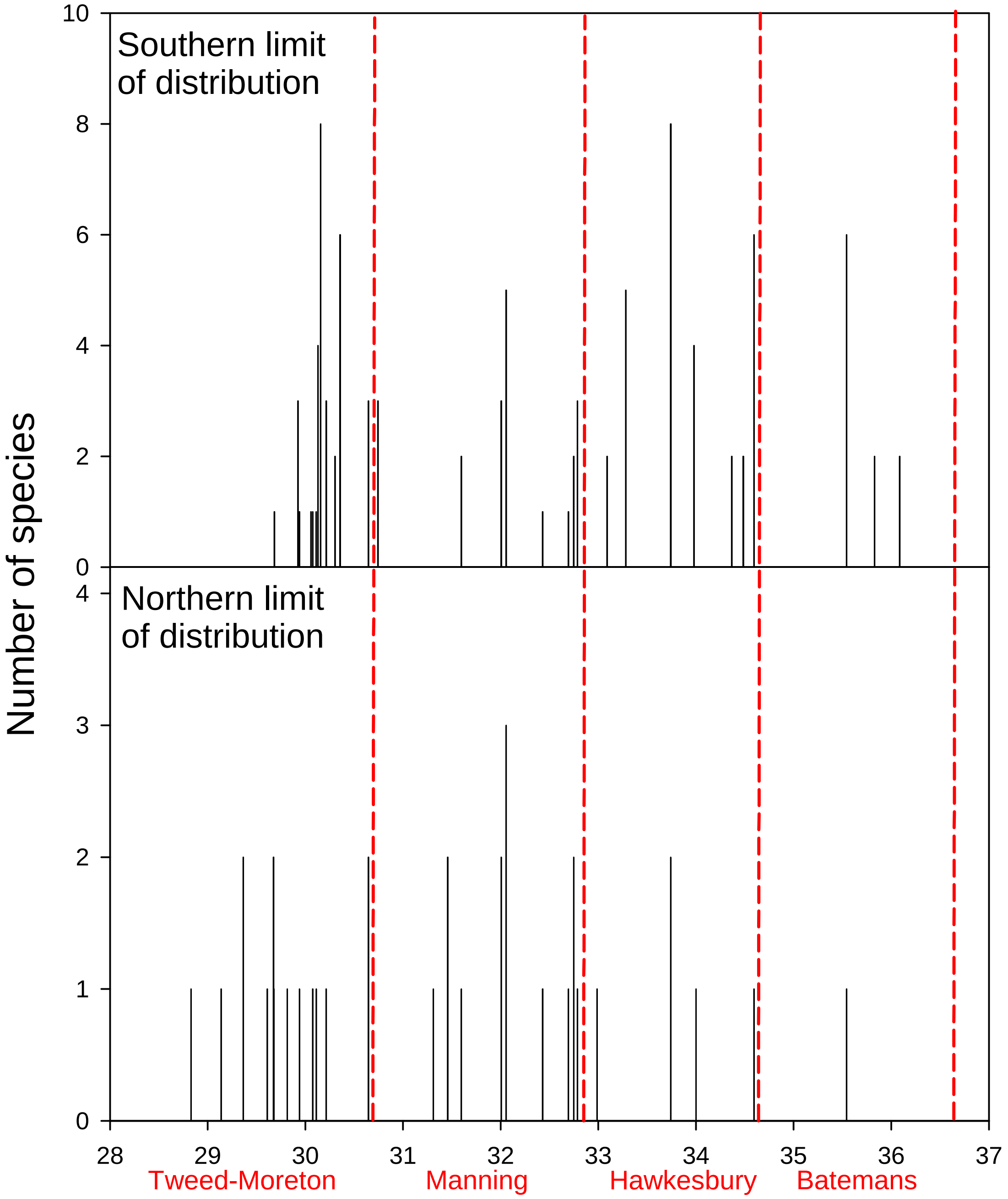

Fig. 7. Plot of the number of species occurring at each site that were found no further south (upper plot) or north (lower plot) during surveys of 51 sites (x-axis shows latitude). Approximate positions of the bioregional boundaries are shown as dashed lines.

Discussion

There are clearly a number of important limitations in using a one-off collection of data from 51 sites to make generalisations about biological and biogeographic patterns across the NSW coast. Nevertheless, the results of this study reveal some interesting patterns of distribution for gastropod and bivalve taxa and some insight into the wider application of death assemblage data for rapid assessment of ecological patterns. Underlying much of this discussion are the premises that shore-based molluscan death assemblages comprise species from a range of intertidal and shallow subtidal habitats (Warwick & Light 2002, Rose 2003) and that a sample of 3 sites within an area is sufficient to provide a representative sample of the regional, nearshore species(Smith 2008).

Patterns of species richness

While there is a general trend for species richness to decline with increasing latitude (Fig. 2), the most interesting aspects of the patterns of species richness are: i) the hotspot in the northern section of the Solitary Islands Marine Park (SIMP); and ii) the low species richness at sites at the northern end of the Manning Shelf bioregion. Interpreting the hotspot is relatively straightforward as sites within this region lie within a well-documented area of strong overlap between tropical, temperate and endemic communities. Thus, nearshore communities, from which many species contribute to shore-based molluscan death assemblages (Rose 2003, Smith 2008), comprise a large range of habitat types including reefs that are alternately dominated by kelp forests, coral communities and mixed invertebrate assemblages (Smith & Simpson 1991, Harriott et al. 1994, Smith et al. 2008), and extensive areas of soft sediment (Smith & Rowland 1999). Habitat diversity and complexity is known to be correlated with species richness across a range of habitat types and for a number of taxa (Charbonnel et al. 2002, Chemello & Milazzo 2002, Gratwicke & Speight 2005). As many molluscs show high levels of habitat specificity, this will also lead to increased species richness in areas with high habitat diversity (Wilson 1993, 1994, Smith 2005).

There is little doubt that the influence of the East Australian Current is also a key contributor to the high species richness in the SIMP (Harriott et al. 1994, Malcolm et al. In press). While this effect is manifest through the provision of habitat diversity as mentioned above (especially with respect to coral habitats), periodic transport of larvae of tropical species to north-coast waters leads to higher cumulative diversity over time (Harriott et al. 1994). The cumulative aspect of this is particularly pertinent for mollusc death assemblages as they are time averaged and thus, as long as shells are robust enough to survive sometimes harsh taphonomic processes, are likely to represent more than just the current range of species living within their effective sampling area (Kidwell 2002). The fact that 23 species recorded during this study had their southern limit of distribution in the area between Sandon and Green Bluff illustrates the potential importance of tropical species to this pattern. This is further reinforced by the results from North Solitary Island which supported 22 unique species (mostly tropical species) as well as 3 "common" species that were not found further south (Table 3, Fig. 7).

Another important aspect potentially influencing the composition of molluscan death assemblages is the broad type and areal extent of shallow nearshore habitats. Thus, reefs generally support greater diversity than soft sediments (pers. obs.) and larger areas of reef, by virtue of the species-area relationship, are likely to support more species. For this reason, it could be predicted that areas with extensive nearshore reefs are likely to support higher diversity than those with less reef. While information on the composition of nearshore habitats is lacking for many areas of the state, the northern SIMP is known to contain a particularly high cover of nearshore, reefal habitat (Rule et al. 2007). In combination with the extensive intertidal rock platforms, many of which support high diversities of molluscs (e.g. Smith 2005), this is likely to contribute to the high species richness recorded within this study.

The converse of this argument is hypothesised to be the primary reason for the low species richness in the Port Macquarie region. Death assemblages in this region were dominated by sand-dwelling species, many of which were present in very high abundances. This not only led to very different community composition as determined in the multivariate statistical analyses, but also low species richness as many of the reef-associated species were absent from deposits.

Patterns of community structure

There were clear patterns of shifting community structure across the state (Fig. 3). However, general trends related to biogeographic distributions of different species, while apparent, were largely overridden by habitat-related patterns. Thus, within Fig. 3, there is a tendency for sites to spread, left to right, from the north to the south and this is reflected in the moderate strength of correlation between latitude and biotic patterns. However, within each of the 2 primary groups of sites (north and south), further grouping was mainly related to the dominance of reef- or sand-associated species within deposits. The third group (Port Macquarie region) was formed from sites that were dominated by high abundances of sediment-associated taxa.

For the northern group of sites, those within the SIMP are clearly different to those from further north and south and this primarily reflects the dominance of shell deposits by reef-associated species. Sites north of the Clarence, and from the Nambucca region, while containing reef-associated species within their death assemblages, were dominated by sand-associated species. The sites comprising the southern cluster, again, are primarily differentiated on the basis of supporting dominant sand- or reef-associated taxa. The group to the right, which comprises sites south of Guerilla Beach, supported assemblages dominated by sand-dwelling species, the group to the left, by reef-dwelling species, with samples from Seal Rocks and Saltwater having a balance of the two sites of species.

The relative intensity of sampling in the northern section of the state allows for a more detailed examination of patterns. Differences north and south of the Clarence River were particularly noticeable and initially suggested the river as a strong sub-boundary within the Tweed-Moreton bioregion. However, the identity of species comprising deposits north and south of the Clarence were similar (i.e. species distributions were not disjunct) and the major difference was related to strong shifts in the relative abundance of some species. To illustrate this, the following shows the abundance scores for some of the more common, sand-associated bivalves (b) and gastropods (g) at Iluka (site immediately north of the Clarence) and Brooms Head (closest site to the south of the Clarence), respectively (Iluka, Brooms Head): *Amoria zebra* (g) (6, 1); *Anadara trapezia* (b) (6, 3); *Conuber sordidus* (g) (6, 0); *Corbula coxi* (b) (6, 1); *Donax deltoides* (b) (6, 1); *Donax brazieri* (b) (6, 0); *Hemidonax dactylus* (5, 0); *Mactra contraria* (b) (6, 0); *Paphies elongata* (b) (6, 0); *Terebra nebulosa* (g) (6, 0); *Tylospira scutulata* (6, 0) (note that all of these species were found in low abundance at other sites south of the Clarence). What this suggests is that nearshore habitats shift to soft-sediment dominated facies north of the river; this is likely to be due to the deposition of estuarine sediments in shallow nearshore habitats which is then transported northward through longshore processes (Davies et al. 2007). Deposits north of the river also contained a greater representation of some estuarine species (e.g. *Conuber sordidus*). Thus, these patterns in the composition of death assemblages seem to reflect medium-scale differences in ecological and bio-physical processes rather than a biogeographic boundary *per se*.

Biogeographic boundaries

The data from these 51 sites proved to be insufficient to adequately test the current bioregionalisation of the NSW coast. Many of the species that were recorded only occurred at one or a few sites even though their published distribution ranges spanned a larger section of the coast (i.e. they were absent from sites within their known range). Thus, evaluations of biogeographic patterns need to take these limitations in the sampling method, and biases within deposits themselves (i.e. favouring more robust taxa), into consideration. While death assemblages are time-averaged, potentially accumulating species over lengthy time periods, repeated surveys generally add more species to the list for the site. For example, over 40 surveys of death assemblages have been conducted at Mullaway Headland since 2003 and the continuing program is still adding species to the cumulative list. While the average species richness per survey is approximately 165, the cumulative species count for the site is more than twice this figure (333 as at 18th April 2009 – unpublished data).

By far the most obvious shift in distribution patterns for species occurs in the southern section of the SIMP south to Nambucca. Most of these range boundaries represent southern limits. While this more or less coincides with the Tweed-Moreton and Manning Shelf boundary, the southern SIMP would appear to be the place at which the greatest change occurs (as for community structure). As outlined above, it is difficult to unambiguously evaluate biogeographic patterns further south due to the relatively low intensity of sampling. However, sites in the Port Stephens to Newcastle region supported a number of species that were at the northern and southern ends of their distribution range: this is coincident with the bioregional boundary for the Manning and Hawkesbury shelves. These results are encouraging with respect to current placement of marine parks along the NSW coast as both of the main areas of interest (in terms of species richness, unique species and apparent biogeographic boundaries) have gazetted marine parks in place (Solitary Islands Marine Park and Port Stephens Great Lakes Marine Park).

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Appendix 1

Distribution and abundance scores for species that occurred at 4-38 sites and had published range boundaries within the survey area of the NSW coast.

Site number	Label	Longitude	Latitude	*Clypeomorus petrosa*	*Fusinus nicobaricus*	*Pyrene testudinaria*	*Nodopelagia brazieri*	*Duplicaria vallesia*	*Terebra ballina*	*Amoria zebra*	*Maculotriton serriale*	*Neverita incei*	*Pyrene scripta*	*Conus coronatus*	*Cymbiola magnifica*	*Thais ambustulatus*	*Acropsis afra*	*Morula nodulifera*	*Nerita albicilla*	*Cypraea felina*	*Cypraea annulus*	*Cypraea xanthodon*	*Turbo militaris*	*Cypraea clandestina*
1	Bu	153.45559	-28.0894		3	5		4	1	6		3	3	1	4	3			2	1	2	2		
2	FiT	153.57067	-28.1991		2	1		1	1	3					1	2	1						2	
3	Ha	153.57949	-28.3620	1	1	6		1	2	4	3	2	4	2	1	3	1	1	6	1	2	1		1
4	Sk	153.60711	-28.8303	1	1	6	4		2	5	2	5	6	3	2	3		2	1	2	1	1		1
5	Bal	153.60808	-28.8437			3		1	2	4		4	2	2	1	4	1					1	2	
6	Ev	153.45534	-29.1385		2	2		1		5		4	1		2	3	3		1			2		
7	Wo	153.37440	-29.3652	2		6	2	2		6	1	1	6	2		4	4	1	2	1	1	2	2	1
8	Il	153.37322	-29.3967	3	2	4	1	2	3	6		5	4	2	1	3	3		1	1	2	2	1	
9	Br	153.34128	-29.6106	4		6	5		1	1	2	3	6	4		5	3	3	6	1	1	2	6	
10	Sa2	153.33227	-29.6748	5		6	3	2	1	3		3	6	3		5	3	2	6	3	3	3	3	1
11	Sa1	153.33124	-29.6791	6	1	6	4	1	1	3	1	3	6	3	1	5	2	2	6	4	3	2	3	1
12	Sa3	153.32978	-29.6837	6	1	6	3	3	2	5	1	2	6	5	2	4	3	2	6	4	4	3	6	1
13	Tr	153.30280	-29.7788	6	1	6	3	5	3	4	2		6	6	1	6	4	3	1	3	2	4	6	3
14	Di	153.29270	-29.8163	3		6	3	2		2	2		5	2	1	4	3	2	3	2	1	3	5	
15	Jo	153.27465	-29.8931	6	1	6	4			4	2		5	6	2	5	3	2	4	4	3	4	6	3
16	NSI	153.38851	-29.9250		1	6	2				3		5	4		3	1	3	4	4	3		6	5
17	Pe	153.26073	-29.9401	4	2	6	1	3	2	3	2	3	6	5	2	3	2	3	5	3	4	2	6	1
18	Ar	153.20293	-30.0585	4	1	6	4	4	3	2	1	4	6	4		5	3	2	2		1	3	5	1
19	Mu	153.20475	-30.0764	3	1	6	5	3	3	4	1	1	3	3	1	4	4	1		2		3	6	1
20	Wg	153.21051	-30.1127		1	6		5	3	6	1	5	4	4	2	6	5	2	4	2	1	4	6	2
21	FT	153.20700	-30.1305	6	1	6	2	3	4	5	2	2	6	4	1	4	5	2	5	4	2	4	6	2
22	Ba	153.20610	-30.1568	3		6		2	2	4	2	4	1	5	1	5	3	3	4	3	2	4	6	2
23	Gr	153.16354	-30.2144			4		5	2	6		5			2	5	3			1	2	4	6	1
24	MBI	153.15160	-30.3046			6	3	1		2	1	1		3	1	6	3			2	1	4	6	
25	Bm	153.10915	-30.3560		1	3	1	3	3	5		5			2	4	3			1		5	3	
26	Na	153.01958	-30.6469					3	3	5		5				3	3		1			2	1	
27	Sc	152.99700	-30.7436							3		5			1	1						1		
28	PP	152.97148	-31.3124							3					1				1					
29	PtM	152.93475	-31.4591							3														
30	Bo	152.84696	-31.5980						2	3		2			2									
31	SW	152.56570	-32.0070							5	1	2		1		2	1		1	1	1	3		1
32	DH	152.54738	-32.0575													3	3		1		1		3	1
33	Se	152.52574	-32.4307												1	1	1	1					2	
34	Ya	152.19288	-32.6944									6	2		1							1		
35	Fi	152.17281	-32.7486													1	1	1				1	5	
36	Bi	152.07862	-32.7868									2	2		2									1
37	Du	151.72967	-32.9876													1	2					1		
38	Re	151.66456	-33.0902											1	2	1		1		1	1	2	5	
39	No	151.57642	-33.2823												1	1	2	1				2	2	
40	LR	151.31748	-33.7422														3	1	1	1	2	2		2
41	Li	151.25231	-33.9803																1	1			3	
42	In	151.22243	-34.0017																				2	
43	Bel	150.92482	-34.3674																		1			2
44	RPt	150.91564	-34.4857																			1		1
45	Bas	150.90082	-34.5945																				4	2
46	Ki	150.39199	-35.5433																					
47	Gu	150.22948	-35.8296																					
48	Pi	150.13548	-36.0864																					
49	LC	150.05701	-36.4873																					
50	Tu	149.93861	-36.8470																					
51	Hy	149.94174	-36.9499																					

Site number	Label	*Cypraea caputserpentis*	*Cypraea gracilis*	*Cypraea erosa*	*Engina australis*	*Cronia aurantiaca*	*Chicoreus denudatus*	*Limatula strangei*	*Mitra carbonaria*	*Haliotis rubra*	*Austrocochlea concamerata*	*Nassarius nigellus*	*Philippia lutea*	*Patelloida alticostata*	*Granata imbricata*	*Clanculus brunneus*	*Clanculus floridus*	*Mitra glabra*	*Phasianella ventricosa*	*Mytilus edulis planulatus*	*Tawera gallinula*
1	Bu		1	3		4	2														
2	FiT	1					1	1													
3	Ha		2	2	3	8	1														
4	Sk	2	1	2	2	6	3														
5	Bal	2	1	1		4	2														
6	Ev	2	1	3		4	3	1	1												
7	Wo	2	3	3	2	6	3			1											
8	Il	1	2	3		5	3														
9	Br	3	2	2	2	6	2														
10	Sa2	3	4	3	3	5	2			3											
11	Sa1	4	3	3	3	6	1			3											
12	Sa3	3	4	3	3	5	2			3											
13	Tr	2	5	3	4	6	3			1											
14	Di	3	3	3	3	3	2	1													
15	Jo	4	4	6	3	5	2			2											
16	NSI	6	2	4	3	5	1			1											
17	Pe	4	4	3	2	6	2														
18	Ar	3	4	3	3	5				2											
19	Mu	2	3	2	4	5	4	1		2	1										
20	Wg	4	5	4	3	4	3	1	1												
21	FT	4	4	3	4	5	4														
22	Ba	3	4	3	2	6				1											
23	Gr	2	3	3	3		3														
24	MBI	4	4	4	3	6	2			2											
25	Bm	1	2	3	3	1	3	1	1	1											
26	Na	3	2	2		3	3				6										
27	Sc	3		1			2		1												
28	PP			1						1											
29	PtM	1				1	1					2									
30	Bo	1		1			1			1		3	1								
31	SW	2	2	1	3		3			1	4	3									
32	DH	1	2		2	3		1	1	5	5			1	1						
33	Se			1		2			1	1		2	1	4		1					
34	Ya		2	1		1		1	1	1		6	1	2							
35	Fi	1	1	1	1		1	4	3	1	5	2	2	5	4	1	3				
36	Bi		1						3	1	1	5	2	1	1	1		3			
37	Du	1				4		1		1		4	3	3	3	1	2	1	2		
38	Re	2		2		6		1	3	4	5	2	1	4	5	1	1	1	1		
39	No	2	2	1	1	3		3	3	3	5		2	5	6	1	2	2	1		
40	LR	2		1		3		5	2	2	3		2	4	5	1	2		1		
41	Li				1	1		4	1	3	6			4	4	1	3				
42	In	1		1		1		5	1	3	6		2	4	5	3	3			2	
43	Bel	2		1		1	1		1	3	3	3		4	5	2	2		4		
44	RPt	1	2	1	2			6	3	4	3	3		5	5	3	3	2	3		
45	Bas	1	1	1		3		5	3	4	3		3	4	5	2	1				1
46	Ki			1	1	2	1	4	4	6	3	2	4		5	2	2	2	5	1	3
47	Gu							5	6	5			3	5	5	5	4	1	1	2	
48	Pi						1	3	3	4	2	6	3	4	3	3	3	3		3	6
49	LC							4	3	4	4	6	3	5	4	4	3	2	1	2	5
50	Tu							1	4	3	6	5	3	4	3	3	2	3		4	5
51	Hy								1	4	5	4	1	2				1		3	6

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