

MARINE ENVIRONMENTAL RESEARCH

Marine Environmental Research 52 (2001) 115-125

www.elsevier.com/locate/marenvrev

Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs

S.D. Connell *

Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories A11, University of Sydney, N.S.W. 2006, Australia

Received 3 January 2000; received in revised form 15 July 2000; accepted 15 August 2000

Abstract

There remains little understanding of the relationship between the ecologies of urban habitats (pilings and pontoons) and natural habitats (rocky reef) for sessile plants and animals (epibiota) living on urbanised coasts. This study describes the structure of subtidal assemblages of epibiota among pilings, pontoons and adjacent rocky reef in Sydney Harbour, Australia. I tested the prediction that the experimental provision of substrata of the same age and composition in all three habitats would produce assemblages that: (1) differed among all three habitats; and (2) differed most on floating pontoons relative to the two fixed habitats (pilings and reef). As predicted, the results suggested that both pilings and pontoons, particularly the latter, create novel habitats for epibiotic assemblages independent of age and composition of substratum. It is not fully understood why these urban structures act as such different habitats from natural rocky reefs. The important point is that they are different and we are yet to understand the implications of this for the ecology of coastal areas subject to urbanisation. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Fouling organisms; Artificial habitats; Biodiversity; Disturbance

E-mail address: sean.connell@adelaide.edu.au

0141-1136/01/\$ - see front matter \odot 2001 Elsevier Science Ltd. All rights reserved.

PII: S0141-1136(00)00266-X

^{*} Present address: Department of Environmental Biology, University of Adelaide, Adelaide, South Australia 5005, Australia. Tel.: +61-8-8303-6125; fax: +61-8-8303-4364.

1. Introduction

More than half (67%) of the human population lives on the coast (Hammond, 1992) and within 30 years this population will probably double (Norse, 1995). A disproportionate amount of the coastal population lives around estuarine habitats because they provide valuable resources for the harvesting of food, assimilation of waste and safe anchorage for shipping (Shabman & Batie, 1980). While the effects of these activities on the degradation of habitat have been a focus of ecological research (reviews Lunden & Linden, 1993; Norse; Sebens, 1994), there remains little understanding of the role of urban structures as habitats for marine organisms (review: Glasby & Connell, 1999).

Rocky reef is the primary habitat for a diverse set of marine biota (Moore & Seed, 1986; Shepherd & Davies, 1997; Womersley, 1987), but this habitat continues to be destroyed and replaced with urban structures. Importantly, these structures provide habitats for a substantial number of subtidal plants and animals normally attached to rocky reef (e.g. Connell & Glasby, 1999; Fletcher, 1980; Karlson, 1978). Despite this apparent surrogacy, there remains a poor understanding of how the ecology of these man-made habitats relates to the ecology of their adjacent natural habitats (Glasby & Connell, 1999). This understanding is of practical importance; epibiotic organisms are sources of food and shelter for many types of organisms (e.g. Minchinton & Ross, 1999; Connell & Anderson, 1999) and are an important component of subtidal systems.

Pilings and pontoons are common to estuarine and coastal areas throughout the world because they are the primary structures used to anchor boats. Epibiotic assemblages attached to these structures differ substantially from those on adjacent natural reefs (Connell & Glasby, 1999). Understanding the causes of these differences will not only contribute to an understanding of urban structures as marine habitats, but this is a key to predicting how continued urbanisation will effect the ecology of coastal habitats. An important next step in this research, therefore, is the identification of the nature of differences in the composition and abundances of epibiota between rocky reef and pilings and pontoons.

A previous study of the effect of urban structures on local abundance and diversity of subtidal epibiota indicated that differences in age of substratum (length of time immersed in water) and composition of substratum may have a profound affect on differences in structure of assemblages among these habitats (Connell & Glasby, 1999). Age and composition of substratum are important determinants of the identity and abundances of epibiotic organisms within a habitat (e.g. Anderson & Underwood, 1994; McGuinness, 1989; Menge & Sutherland, 1976; Underwood & Anderson, 1994) and these factors differ greatly between rocky reef and urban structures. There is a need, therefore, to identify how the abundances of taxa differ among these habitats (pilings, pontoons, reef) without confounding these observations with differences in age and composition of substratum.

This study describes the structure of subtidal assemblages of epibiota among pilings, pontoons and rocky reef on substratum of the same age and composition. I predicted that the experimental provision of substrata of the same age and

composition in all three habitats would produce assemblages that: (1) differed among all three habitats; and (2) differed most on floating pontoons relative to the two fixed habitats (pilings and reef). This hypothesis was derived from the model that pontoons are distinct habitats for subtidal epibiota because pontoons spend more time near the sea surface than subtidal surfaces of pilings and reef, and factors affected by depth (e.g. light, flow, larval supply, etc.) have considerable effects on the abundances of epibiota.

2. Materials and methods

2.1. Study area and experimental treatments

The study was done from June (winter) 1998 to January (summer) 1999 in Middle Harbour, the northern part of Sydney Harbour, Australia ($33^{\circ}48'$ S, $151^{\circ}14'$ E, Fig. 1). Rocky reefs in Middle Harbour extend about 5 m from the shore and reach a depth of \sim 4 m. Pontoons (3×4 m) are typically moored 5–10 m from the shore and \sim 5 m above the sandy bottom. Pilings are positioned at each corner of a pontoon. Experimental plates (15×15 cm) made of concrete were fastened vertically to pilings, pontoons and reef.

Experimental plates were attached to the outer edges on two sides of a pontoon $(3\times4 \text{ m})$ at a depth of ~25 cm. Plates were attached to a beam of PVC pipe that was strapped to a bottom edge of a pontoon. Experimental plates were attached to pilings and reef at a depth of approximately 1.5 m below low water spring tide. Plates were fastened to pilings with wire that was attached to a flat piece of PVC plastic glued to the back of the plates. Experimental plates on the reef were supported by beams of aluminium 90° angle (1.6 m long) bolted to the reef with stainless steel screws. PVC brackets were glued on to the backs of plates and these were bolted

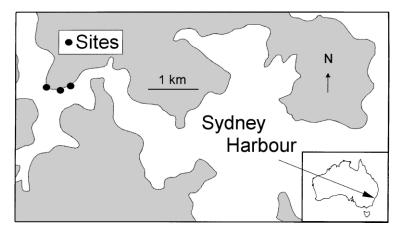


Fig. 1. Map showing location of sites of study within Sydney Harbour. Location of Sydney Harbour indicated on insert of map of Australia.

onto the PVC pipes and beams. Five replicate plates (1–5 m apart) were attached to each habitat (pilings, pontoons, reef) and this design was replicated at each of three sites \sim 200 m apart.

After 7 months, each panel was collected and taken to the laboratory for examination under a dissecting microscope in which the abundances of benthic invertebrates were estimated. Primary cover (organisms attached directly to the plate) and secondary cover (organisms attached to primary cover) were estimated for sessile organisms on the front of plates using 64 regularly spaced points within a 13×13 cm grid (i.e. a 1-cm border around each plate was not sampled to avoid "edge effects"). Taxa on the front of plates, but not under a point were assigned a cover of 0.5%.

2.2. Analytical methods

Data were standardised by converting raw data to percentages before summing the primary and secondary covers for all multivariate and univariate tests. Observations of secondary cover were rare. Multivariate analyses were done using the 37 taxa identified and bare space. Data were fourth-root transformed and the Bray-Curtis measure (Bray & Curtis, 1957) was used to calculate dissimilarities among replicates. A visual assessment of dissimilarities in the structures of assemblages was provided by a dendrogram in which replicate plates were pooled within each habitat for each site. One-way analyses of similarities (ANOSIM) were done (Clarke, 1993) using all replicates to test for differences between substrata and habitats. The significance level was adjusted for multiple pairwise comparisons (Bonferroni procedure; Rice, 1989).

Univariate analyses were done using two-way analyses of variance (ANOVAs; e.g. Underwood, 1981) in which both factors (habitat, site) were crossed, and "habitat" was treated as fixed and "site" as random. All data were arc-sine transformed and if Cochran's *C*-test detected heterogeneous variances, significance of ANOVA *F*-ratios was judged at the more conservative probability of 0.01 (Underwood).

3. Results

Assemblages on plates were composed of bivalves (Mytilus edulis, Crassostrea gigas), encrusting bryozoans (Watersipora arcuata, W. subtorquata, Cryptosula pallasiana, Schizoporella errata, Beania magellanica, Fenestrulina mutabilis, Conopeum seurati, Celleporaria sp., Microporella spp.), arborescent bryozoans (Bugula neritina, B. stolonifera, Tricellaria inopinata), barnacles (Balanus variegatus and B. trigonus), calcareous tubeworms (spirorbids and serpulids), solitary ascidians (Styela plicata), colonial ascidians (Diplosoma listerianum, Didemnum sp.), five taxa of sponges, green algae (Cladophorales, Enteromorpha, Ulvales, Codium), red algae (Ceramiales, Laurencia, Hypnea, Rhodymenia), brown algae (Feldmania, Sphacelaria, Dictyotalean spp. Dictyota dichotoma), and coral (Culicia sp.). Assemblages differed among all three habitats (ANOSIM: P < 0.001), and pontoons supported the most distinct assemblages (Fig. 2). The dendrogram indicated that the structure of assemblages

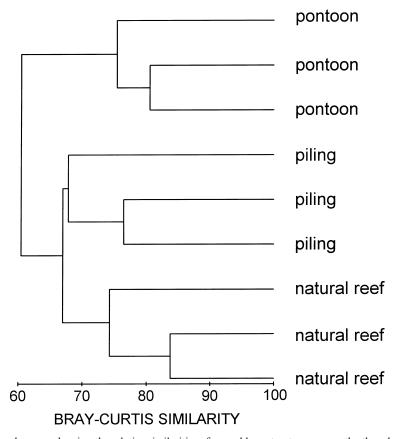


Fig. 2. Dendrogram showing the relative similarities of assemblage structure among the three habitats at each of three sites.

was most similar between pilings and rocky reef and these were most distinct from pontoons (Fig. 2). Correspondingly, multivariate differences between pontoons and reef (R = 0.933) and pontoons and pilings (R = 0.727) were large compared to the difference between reef and pilings (R = 0.474). Under the null hypothesis H₀: no differences among habitats, the test statistic R of ANOSIM tends towards 0 (Clarke, 1993). Values that tend towards 1 indicate large departures from H₀. These results support the hypotheses that: (1) the structure of assemblages would differ among all three habitats; and (2) the structure of assemblages would be most similar between fixed habitats (pilings and reef) and most different between these and floating pontoons.

Of 12 common taxa tested for differences in abundance among habitats, differences were detected for six taxa. One taxon, spirorbid polychaetes, was least abundant on pontoons (Fig. 3a, Table 1: SNK test, pontoons < pilings = reef). The abundance of most taxa, however, was greatest on pontoons and did not differ between pilings and reef. *Mytilus edulis* and solitary ascidians were more abundant

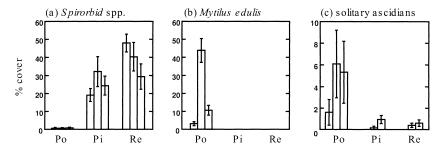


Fig. 3. Percentage cover of taxa (per 15×15 cm \pm S.E.) on pontoons (PO), pilings (PI) and reef (RE) at each of three sites (n=5). The first three bars representing each type of habitat (PO, PI, RE) represent sites 1-3 respectively.

Table 1

Analysis of variance comparing the percentage cover of selected taxa among habitats (reef, pilings, pontoons) at three sites^a

Source	d.f.	MS	F	P	MS	F	P	MS	F	P
		(a) Spirorbid polychaetes			(b) Mytilus edulis			(c) Solitary ascidians		
Habitat	2	4571.73	43.62	**	2467.63	5.41	> 0.05	233.02	8.32	b
Site	2	65.95	1.04	-	503.66	21.70	-	89.55	3.20	_
Habitat×Site	4	104.81	1.66	> 0.05	455.92	19.64	b	16.44	0.59	> 0.25
Residual	36	63.24			23.21			29.28		

^a Direct comparison of sites was not relevant for testing the hypothesis.

on pontoons than reef and pilings at all sites (Fig. 3b, c, Table 1). This pattern was also detected for barnacles and arborescent bryozoans at two of the three sites (Fig. 4a, b, Table 2a, b: SNK test on Habitat×Site interaction). Although there was a trend for green algae to be most abundant on pontoons at two sites, SNK tests could not distinguish among habitats for the significant Habitat×Site interaction (Fig. 4c, Table 2c). Encrusting bryozoans varied inconsistently among structures and sites (Fig. 4d, Table 2d). No differences were detected among surfaces for the remaining five taxa (Fig. 4, Table 2). Colonial ascidians were mainly absent from pilings and reef, but patchily distributed among pontoons (Fig. 4g).

4. Discussion

An important result was that floating pontoons appear to provide very different habitats for epibiota than rocky reef and pilings that are fixed in one position relative to tidal rise and fall. This study did not attempt to assess the cause of these differences, but the identification of these patterns of similarity/dissimilarity in structure of assemblages are important to the construction of conceptual models to

^b Significance was judged at $\alpha = 0.01$ because variances were heterogeneous (Cochran's *C*-test P < 0.05). **P < 0.01.

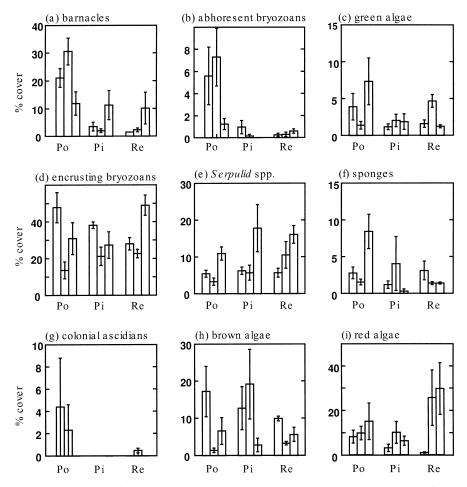


Fig. 4. Percentage cover of taxa (per 15×15 cm \pm S.E.) on pontoons (PO), pilings (PI) and reef (RE) at each of three sites (n=5). The first three bars representing each type of habitat (PO, PI, RE) represent sites 1-3 respectively.

explain them. No studies have specifically compared the development of assemblages with and without the influence of tides, but it is likely that factors associated with proximity to the sea surface (e.g. light) have some of the strongest effects on the development of subtidal assemblages of epibiota (Glasby, 1999a; Saunders & Connell, 2001). This would explain why assemblages develop most differently on pontoons (which spend all their time near the sea surface) compared to pilings and reef (which spend less time near the sea surface).

While these results may not appear surprising, they provide some of the first quantitative information on the types of taxa likely to be affected by the continued addition of pilings and pontoons into our waterways. In many cases the addition of pilings and pontoons involves the creation of additional patches of hard substratum

Table 2
Analysis of variance comparing the percentage cover of selected taxa among habitats (reef, pilings, pon-
toons) at three sites ^a

Source	d.f.	MS	F	P	MS	F	P	MS	F	P
		(a) Barna		(b) Arbo	(c) Green algae					
Habitat	2	1221.57	5.18	> 0.05	57.95	0.29	> 0.25	62.97	0.93	> 0.25
Site	2	33.22	0.62	_	631.27	8.65	_	5.32	0.25	_
Habitat×Site	4	236.00	4.43	**	198.46	2.72	*	68.02	3.15	*
Residual	36	53.28			72.99			21.62		
		(d) Encrusting bryozoans			(e) Serpu	(f) Sponges				
Habitat	2	346.29	6.35	> 0.05	65.50	2.13	> 0.05	132.82	1.55	> 0.25
Site	2	45.17	2.41	_	369.09	12.02	_	5.54	0.23	_
Habitat×Site	4	54.49	2.90	*	23.26	0.76	> 0.25	85.82	3.53	> 0.05
Residual	36	18.76			31.54			24.39		
		(g) Colonial ascidians			(h) Brow	(i) Red algae				
Habitat	2	39.94	2.37	> 0.05	37.59	0.19	> 0.25	293.56	1.28	> 0.25
Site	2	23.03	0.88	_	391.77	4.19	_	613.32	4.51	_
Habitat×Site	4	16.87	0.65	> 0.25	196.79	2.11	> 0.05	228.74	1.68	> 0.05
Residual	36	27.04			93.39			136.14		

^a Direct comparison of sites was not relevant for testing the hypothesis.

in areas lacking such habitats. This may change the dispersal of sessile organisms, allowing species that are poor dispersers (Butler & Keough, 1990) to cover greater distances by using urban structures as "stepping stones" (sensu Glasby & Connell, 1999). This may not only allow the expansion of native taxa to new areas, but also facilitate the invasion of exotic taxa that arrive in harbours as a result of international shipping. The capacity for pontoons to be relocated suggests that of the many urban structures (e.g. pilings, rock walls, tunnels, pipes), floating structures are likely to have some of the most profound implications for urban planning and wildlife and fisheries management. While shipping introduces taxa over global scales, pontoons and barges are frequently relocated on local scales and have been suspected to spread introduced species within the recipient region. Recent introductions of exotic plants and animals to Europe, North America and Australia have had profound effects on native species, and led to the collapse of fisheries (review: Carlton & Geller, 1993).

Changes to the distribution and abundances of native taxa may also have wide-scale consequences to estuarine and coastal ecology. It is well known that many suspension-feeding bivalve molluscs (e.g. oysters and mussels that attach in abundance to pontoons) have key functional roles within estuarine and coastal habitats. Bivalves can influence at least two key functions viz. the flux of particles between the water and the sediment, and the recycling of nutrients (Dame & Dankers, 1988; Heip, Goosen, Herman, Kromkamp, Middelburg & Soetaert, 1995). In many bays

^{*}P < 0.05.

^{**}P < 0.01.

and estuaries, bivalves may filter the entire volume of water three or more times for every single exchange effected by tidal flushing and runoff (B.L. Bayne personal communication). Hence, change in the distribution and abundances of bivalves may result in substantial changes in the biomass of phytoplankton and larvae that are important components of coastal systems.

While there has been much discussion of the roles of fragmentation of habitat as a cause of human-generated heterogeneity (Pickett, Burch, Dalton, Foresman, Grove & Rowntree, 1997), there has been less emphasis on the capacity for temporal heterogeneity of development to do the same. The addition of urban structures has and will continue to occur haphazardly through time, hence, temporal heterogeneity will be an important source of variation in the structure of assemblages among urban structures and between urban structures and native habitat. Consequently, some of these differences may be explained by time since provision of new substrata (Underwood & Anderson, 1994) associated with the timing of recruitment, disturbance (Dean & Hurd, 1980) and stage of succession (Connell & Slatyer, 1977).

Connell and Glasby (1999) proposed that such differences in age potentially explain why assemblages directly attached to pilings were more similar to those on pontoons and not reef. Our reasoning was that relative to rocky reef, pilings and pontoons have been introduced into estuaries at very similar times and therefore have experienced the most similar history. If these temporal differences do not explain this pattern (i.e. reef\neq piling\pi pontoon), then the experimental provision of substratum of the same age (i.e. removing age as a factor affecting observations) should result in the same pattern (i.e. alternative processes cause these patterns independently of age). The results of the current study (i.e. reef\neq piling\neq pontoon) are not consistent with this hypothesis and support the model of temporal heterogeneity as an explanation for some of the observed differences in assemblages among these habitats.

An important conclusion of this study is that pilings and pontoons provide novel habitats for marine plants and animals that naturally occur on rocky reef. It is not fully understood why these urban structures are such different habitats from one another, and from natural rocky reefs, but their floating nature and proximity to the sea surface are likely to have a major impact on the physical and biological factors that affect the development of epibiota (Glasby, 1999a). Regardless of the reason for the differences among these habitats, the fact is that they are different and we are yet to understand the implications of this for the ecology of coastal areas affected by urbanisation (Glasby & Connell, 1999).

While a substantial amount of our understanding of the ecology of epibiota is based on urban structures (particularly pilings and pontoons), few of these studies have been designed to understand the consequences of man-made habitats on the ecology of coastal areas. It would be prudent to assess how our current understanding of the ecology of epibiotic assemblages on urban structures relates to rocky reef. There is mounting evidence to suggest that such assessment is urgently needed; major anomalies between these habitats have been become apparent (Butler & Connolly, 1996; Connell, 2000; Connell & Glasby, 1999; Glasby, 1999a, b; this study). A better understanding of the causes of these differences will not only

improve our understanding of the ecology of urban structures but also provide greater insight into the effects of continued addition of these structures on the ecology of coastal habitats.

Acknowledgements

This study was supported by funds from the Centre for Research on Ecological Impacts of Coastal Cities. I gratefully acknowledge assistance in the field and laboratory from T. Glasby, S. Heislers, G. Housefield, and J. People. This paper was improved by T. Glasby and benefited from discussions with B. Bayne, G. Chapman and A. Underwood.

References

- Anderson, M. J., & Underwood, A. J. (1994). Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *Journal of Experimental Marine Biology and Ecology*, 184, 217–236.
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, 27, 325–349.
- Butler, A. J., & Connolly, R. M. (1996). Development and Long term dynamics of a fouling assemblage of sessile marine invertebrates. *Biofouling*, 9, 187–209.
- Butler, A. J., & Keough, M. J. (1990). A comment on short supply-lines. *Trends in Ecology and Evolution*, 5, 97.
- Carlton, J. T., & Geller, J. B. (1993). Ecological roulette: the global transport of nonindigenous marine organisms. Science, 261, 78–82.
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18, 117–143.
- Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role on community stability and organisation. *American Naturalist*, 111, 1119–1144.
- Connell, S. D., & Anderson, M. J. (1999). Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology*, 241, 15–29.
- Connell, S. D., & Glasby, T. M. (1999). Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour. *Marine Environmental Research*, 47, 373–387.
- Connell, S. D. (2000). Floating pontoons create novel habitats for subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, 183–194.
- Dame, R. F., & Dankers, N. (1988). Uptake and release of materials by a Wadden Sea mussel bed. Journal of Experimental Marine Biology and Ecology, 118, 207–216.
- Dean, T. A., & Hurd, L. E. (1980). Development in an estuarine fouling community: the influence of early colonists on their later arrivals. *Oecologia*, 46, 295–301.
- Fletcher, R. L. (1980). The algal communities on floating structures in Portsmouth and Langstone Harbours (South coast of England). In J. H. Price, D. E. G. Irvine, & W. F. Farnham, *The shore environment: ecosystems. Vol. 2* (pp. 843–874). London: Academic Press.
- Glasby, T. M. (1999a). Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages. *Marine Ecology Progress Series*, 190, 113–124.
- Glasby, T. M. (1999b). Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. *Estuarine, Coastal and Shelf Science*, 48, 281–290.
- Glasby, T. M., & Connell, S. D. (1999). Urban structures as marine habitats. Ambio, 28, 595-598.

- Hammond, A. (1992). World resources 1992–1993: towards sustainable development. Oxford: Oxford University Press.
- Heip, C. H. R., Goosen, N. K., Herman, P. M. J., Kromkamp, J., Middelburg, J. J., & Soetaert, K. (1995). Production and consumption of biological particals in temperate tidal estuaries. *Oceanography and Marine Biology Annual Review*, 33, 1–149.
- Karlson, R. H. (1978). Predation and space utilization patterns in a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology*, 31, 225–239.
- Lunden, C. G., & Linden, O. (1993). Coastal ecosystems: attempts to manage a threatened resource. Ambio, 22, 468–473.
- McGuinness, K. A. (1989). Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama. *Journal of Experimental Marine Biology and Ecology*, 104, 97–123.
- Menge, B. A., & Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition and environmental heterogeneity. *American Naturalist*, 110, 351–369.
- Minchinton, T. E., & Ross, P. M. (1999). Oysters as habitat for limpets in a temperate mangrove forest. Austalian Journal of Ecology, 24, 157–170.
- Moore, P., & Seed, R. (1986). The ecology of rocky coasts. New York: Colombia University Press.
- Norse, E. A. (1995). Global marine biological diversity. Washington: Island press.
- Pickett, S. T. A., Burch, W. R., Dalton, S. E., Foresman, T. W., Grove, J. M., & Rowntree, R. (1997). A conceptual framework for the study of human ecosystems in urban areas. *Urban Ecosystems*, 1, 185–199.
- Rice, W. R. (1989). Analysing tables of statistical tests. *Evolution*, 43, 223–225.
- Saunders, R. J., & Connell, S. D. (2001). Interactive effects of shade and surface orientation on the recruitment of spirorbid polychaetes. *Austral Ecology* (in press).
- Sebens, K. (1994). Biodiversity of coral reefs: what are we losing and why? *American Zoologist*, 34, 115–133.
- Shabman, L. A., & Batie, S. S. (1980). Estimating the economic value of coastal wetlands: conceptual issues and research needs. In: V. S. Kennedy, *Estuarine perspectives* (pp. 3–16). New York: Academic Press.
- Shepherd, S. A., & Davies, M. (1997). Marine invertebrates of Southern Australia, Part III. Adelaide: Graphic Print Group.
- Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology Annual Review*, 19, 513–605.
- Underwood, A. J., & Anderson, M. J. (1994). Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. J. Mar. Biol. Assoc. U. K., 74, 563–584.
- Womersley, H. B. S. (1987). The marine benthic flora of Southern Australia, Part II. Adelaide: South Australian Government Printing Division.