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Sampling patchily distributed taxa: a case study using cost–benefit analyses for sponges and ascidians in coastal lakes of New South Wales, Australia

P. B. Barnes[1,*], A. R. Davis[1], D. E. Roberts[2]

[1]Institute for Conservation Biology, School of Biological Sciences, University of Wollongong, New South Wales 2522, Australia
[2]BIO-ANALYSIS: Marine, Estuarine & Freshwater Ecology, 7 Berrys Head Road, Narara, New South Wales 2250, Australia

ABSTRACT: Estuaries worldwide are under increasing threat from human impacts. Because much of their fauna remains unstudied and in many cases undescribed, these systems present real challenges for effective management. In eastern Australia the study of estuarine fauna is often further complicated by its patchy distributions. This is particularly the case for assemblages of sessile invertebrates in coastal saline lakes. This study quantified distributions of sponges and ascidians at a hierarchy of spatial scales in the seagrass meadows of 2 coastal saline lakes in New South Wales, Australia. Nine species of sponge, many of which were undescribed, and 3 species of ascidians were found. Nested analyses of variance were used to identify spatial scales at which variation was significant. Most sponges and ascidians were very patchily distributed at a range of spatial scales from 10s of metres up to 100s of kilometres. The composition of assemblages differed greatly between the 2 lakes. In addition, unlike other published examples of cost–benefit analyses, in the present study very few taxa were widespread over the larger spatial scales. Cost–benefit analyses done to determine the optimal sampling design for future experiments revealed inclusion of patchily distributed taxa in analyses could improve the overall precision of sampling.

KEY WORDS: Sponges · Ascidians · Patchiness · Cost–Benefit analyses · Lakes

INTRODUCTION

Estuaries worldwide are under increasing threat from urbanisation and development (Kennish 2002). Threats come from a myriad of sources, including fishing (Blaber et al. 2000), loss of habitat (Alongi 2002), industrial and urban contamination (Matthiessen & Law 2002), changes to natural patterns of freshwater flows (Gillanders & Kingsford 2002) and introduced species (Ruiz et al. 1999). Threats also range in scale (Underwood & Chapman 1996a), from very large estuary-wide impacts (e.g. changes to the Nile Delta caused by the construction of the Aswan Dam; Stanley & Warne 1993) to much smaller impacts affecting smaller patches of an estuary (e.g. impacts of boat wash; Bishop 2004). Together, the variety and complexity of threats and range of scales over which impacts may occur provide serious challenges for the management of these systems.

In southeastern Australia, coastal saline lakes and lagoons are a common type of estuary (Roy et al. 2001). These systems are also under extreme pressure with an estimated 85% of the population living near the coast (Zann 1995). Just 6 of 90 New South Wales (NSW) coastal lakes and lagoons are classified as near pristine, while 12 are considered severely affected by development and a further 17 moderately affected (Healthy Rivers Commission of NSW 2002). Conservation of these lakes will require effective management, which will, in turn, require anthropogenic impacts to be identified and their effects on the ecology of these systems to be understood. While research effort has increased in recent years, the ecology of these systems and the exact nature of the impacts are poorly understood.

*Email: pbb47@uow.edu.au

The identification of ecologically important impacts and processes may, however, be a complex and difficult task, particularly against a background of natural variability. A useful starting point in identifying and understanding processes is first to identify patterns and important scales of variability in the distribution of organisms (Underwood et al. 2000). Spatial scales at which significant variation exists often then reveal the scales at which processes are operating. Thus, once appropriate scales have been identified, informed causative models can be examined to understand the relevant processes (Underwood & Chapman 1996a).

The reliable identification of patterns of distribution of organisms is therefore a key component of a research programme. The design of any study examining patterns of distribution of organisms should include adequate replication at spatial scales at which variation is significant (Morrisey et al. 1992). Inadequate replication at these spatial scales may confound results and reduce the power of statistical tests to detect differences (Underwood & Chapman 2003). Various strategies and techniques have been developed to help design experiments with appropriate replication to overcome this problem. Such strategies may involve up to 3 stages. First, most rely on having preliminary estimates of variances, which may be obtained from existing data, the literature, or pilot studies. Second, spatial scales at which variation is significant are identified. Third, replication at each spatial scale may then be optimised to obtain a statistical test with a desired level of power or to keep within an allocated budget.

The use of spatially nested designs followed by analyses of variance (ANOVA) has been identified as a powerful technique for identifying scales at which variation is significant (Green 1979, Andrew & Mapstone 1987, Morrisey et al. 1992, Underwood 1997). Procedures are relatively straightforward for studies examining a single taxon or variable. For studies examining assemblages (i.e. many taxa), optimising sample size is not as straightforward, because there are no procedures available for calculating the power of a multivariate statistical test. In studies comparing assemblages of organisms, it is common practice first to compare whole assemblages (i.e. multivariate sets of data) and then compare specific taxa of interest using univariate techniques (e.g. ANOVA; e.g. Bishop 2004). If preliminary estimates of variances exist, the design of such experiments may be optimised to sample abundances of a particular taxon or another univariate measure using ANOVAs and cost–benefit analyses. An experimental design would then be optimised for certain taxa. It is, of course, unlikely that cost–benefit analyses done for several taxa would all produce the same optimised experimental design (e.g. Benedetti-Cecchi et al. 1996). Compromises will need to be made in the design of experiments in terms of which taxa to sample most precisely. Ultimately, an experiment should be designed to test the hypotheses of interest. It is, however, sometimes unclear which species of an assemblage are or will be of most interest before the start of a research programme. This is particularly the case for unsurveyed habitats, where taxa may be undescribed or very patchy in their distribution. For example, a recent search of the published literature and unpublished reports found no studies directly relating to sponges, no quantitative descriptions of their distribution, nor any reliable names of species in NSW coastal lakes. It is clear in this case that it is impossible to identify particular species of interest before the start of a research programme. Under these circumstances, the first objective of a research programme will be to identify the species present and describe their basic patterns of distribution.

Detailed case studies examining variation at a hierarchy of spatial scales exist for soft-sediment macrofauna (Morrissey et al. 1992) and intertidal rocky shore assemblages (Underwood & Chapman 1998) in temperate eastern Australia. Spatial variation in sponge assemblages has been quantified in shallow (<5 m; Underwood et al. 1991) and deeper (20 to 50 m; Roberts & Davis 1996) rocky reefs on the open coast of NSW and in semi-enclosed or isolated bodies of water elsewhere in the world (e.g. on mangrove roots in Caribbean lagoons; Farnsworth & Ellison 1996; tropical estuaries; Kuenen & Debrot 1995; freshwater lakes; Rader 1984, De Santo & Fell 1996), but it is unclear whether the extrapolation of such results to the considerably different habitats of seagrasses and soft substrata of relatively shallow and sheltered temperate coastal lakes is likely to be useful.

This paper presents a pilot study examining spatial variation in the distribution of sponges and ascidians in 2 NSW coastal lakes. The aims of this study were 2-fold. First, to identify spatial scales at which variation was significant and, hence, scales at which important processes may be operating. Second, to assist in the design of further larger scale experiments to examine spatial and temporal changes among and within several NSW coastal lakes. Variation in the abundance of sponge and ascidian fauna was examined at a hierarchy of spatial scales using fully nested sampling designs. When a species was absent from some replicate levels of a spatial scale, variation was examined within the levels of the subsequently nested spatial scale(s) where the species was present. Cost–benefit analyses were used to determine the optimal numbers of locations, sites and replicate samples to be used in future work.

MATERIALS AND METHODS

Study sites and sampling methods. Individual sponges and solitary ascidians were counted in relatively shallow (0.5 to 2 m depth) seagrass meadows at a hierarchy of spatial scales in each of 2 saline coastal lakes in New South Wales, Australia, in January and February 2002. Wallis Lake and St Georges Basin (Fig. 1) were chosen as representative of relatively large lakes, moderately affected by development, with entrances that usually remain open to the ocean (Roy et al. 2001). In each lake, 6 locations (kilometres apart), each with 4 sites (100s of metres apart), each with 20 replicate 10 × 2 m transects (10s of metres apart) were sampled using SCUBA or by snorkelling depending on depth. Sites were approximately 80 m in diameter. This design allowed spatial variation to be examined at 4 spatial scales: (1) between lakes 100s of kilometres apart, (2) among locations kilometres apart, (3) among sites 100s of metres apart and (4) among transects within sites 10s of metres apart. Voucher specimens of sponges were lodged with the Queensland Museum, Brisbane, Australia.

Statistical analyses. ***Analyses of variance:*** Three sets of fully nested ANOVAs were used to identify spatial scales at which significant variation occurred. First, 3 variables (the ascidian *Styela plicata* Lesueur, total numbers of taxa and total numbers of individual sponges) were identified as widespread in both lakes, with non-zero values at most sites in most locations. Each was analysed with a 3-factor (lake, location and site) nested ANOVA, with all factors random.

The remaining taxa were patchily distributed and restricted to a single lake or some locations or sites within a lake. Preliminary examination of these data suggested that 3-factor ANOVAs (as used above) would be inappropriate because of the large numbers of zero values. These species, however, represented the majority of taxa and may presumably occur in other lakes or at subsequent times of sampling. The omission of such taxa from analyses may result in important processes operating at smaller scales and affecting patterns of distribution being overlooked. In the absence of widespread taxa, a broader understanding of spatial variation can be obtained by analysing these patchily distributed taxa in the places where they do occur. Therefore, a second set of ANOVAs was done to test for significant spatial variation among locations and sites within St Georges Basin only, for the solitary ascidian *Pyura stolonifera* Heller and the sponge *Aplysinella* cf. *rhax*. Each was analysed with a 2-factor (location and site) nested ANOVA.

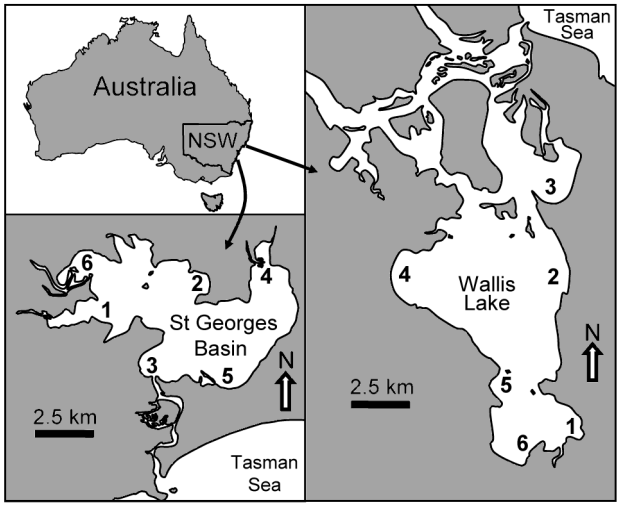

Fig. 1. Locations sampled in Wallis Lake and St Georges Basin on the coast of New South Wales, Australia

Finally, using the same logic as above, a third set of ANOVAs was done for those species found in only 1 or a few locations in Wallis Lake. Abundances of *Halichondria* spp., *Mycale* sp. and *Suberites* sp. were analysed by a 1-factor (site) ANOVA to test for significant variation among sites in the locations where they occurred. Abundances of very uncommon taxa (<10 ind. lake^{-1}) were not analysed.

The assumption of homogeneity of variances was tested using Cochran's test (Winer et al. 1991). Data were transformed to $\ln(x + 1)$ when significant. When transformations did not remove heterogeneity, analyses proceeded, because ANOVA can be robust to deviations from heterogeneity of variances, particularly with fully balanced designs with many independent estimates of variance (Underwood 1981).

In addition, the relative contribution of each spatial scale to the total variation was examined. Variance estimates were calculated for each taxon or derived variable for each spatial scale using ANOVAs of untransformed data (see standard procedures in Underwood 1997).

Cost–benefit analyses: Cost–benefit analyses were done to determine the experimental design appropriate for sampling most taxa most effectively. Analyses were done using variance estimates calculated from ANOVAs of untransformed data (see standard procedures described in Winer et al. 1991, Underwood 1997). The limiting cost was time. Given the relatively large amount of travelling and preparation time needed to get to a lake, it was inefficient for lakes to be sampled in fractions of days. Thus, it was important that a lake could be sampled within a single day. Therefore, the number of replicate locations, sites and transects were optimised to keep within a budget of 1 d lake^{-1} (i.e. 360 min on the water, excluding travelling to and from a lake). The average time to sample 1 transect was 2 min, time to manoeuvre the boat between

sites was 10 min and between locations was 20 min. Cost–benefit analyses were done only within levels of spatial scales in which taxa were present.

The number of replicate transects per site (n) was determined using:

$$n = \sqrt{\frac{S_e^2 \times C_b}{S_{B(A)}^2 \times C_n}} \quad (1)$$

The number of replicate sites per location (b) was determined using:

$$b = \sqrt{\frac{S_{B(A)}^2 \times C_a}{S_A^2 \times C_b}} \quad (2)$$

The optimal number of locations per lake (a) was then determined as:

$$a = \frac{\text{Cost of lake}}{C_a + bC_b + bnC_n} \quad (3)$$

where S_e^2 is the estimated variance among transects, $S_{B(A)}^2$ is the estimated variance among sites, S_A^2 is the estimated variance among locations, C_a is the cost per location, C_b is the cost per site and C_n is the cost per transect.

RESULTS

List of taxa

In Wallis Lake, 9 species of sponges and 3 species of ascidians were found and, in St Georges Basin, 2 species of sponges and 2 species of ascidians (Table 1). Of the 9 species of sponges collected, only 2 could be identified to species level. The remainder were either undescribed or presently unable to be assigned to a known taxa, given the plethora of taxa in the older literature the identities of which still remain a mystery (Hooper & Wiedenmayer 1994). Because it was not possible to distinguish among species of *Halichondria* in the field, all species in this genus were simply recorded as *Halichondria* spp.

The taxa identified differed markedly between the 2 lakes, with 2 of the 3 ascidians, *Styela plicata* and *Pyura stolonifera*, but only 1 sponge, *Halichondria* spp., found in both lakes (Table 1). In addition, patterns of presence/absence of individual taxa within lakes differed greatly between the 2 lakes. While *Aplysinella* cf. *rhax*, *Halichondria* spp., *P. stolonifera* and *S. plicata* were widespread throughout St Georges Basin, most taxa in Wallis Lake were found in 1 or a limited number of locations, with the exception of the introduced *S. plicata*.

Table 1. Taxa found in each location (1 to 6) in St Georges Basin and/or Wallis Lake. +: species present; –: not present

Taxon	St Georges Basin						Wallis Lake					
	1	2	3	4	5	6	1	2	3	4	5	6
Porifera												
Aplysilla cf. *sulphurea*	–	–	–	–	–	–	+	–	–	–	–	–
Aplysinella cf. *rhax*	+	+	–	+	+	+	–	–	–	–	–	–
Halichondria spp.	+	–	+	+	+	+	–	–	+	–	–	–
Haliclona sp. 1	–	–	–	–	–	–	–	–	+	–	–	–
Haliclona sp. 2	–	–	–	–	–	–	–	–	–	+	–	–
Dysidea sp.	–	–	–	–	–	–	+	–	–	–	–	–
Mycale sp.	–	–	–	–	–	–	+	–	–	–	+	–
Raspailia sp.	–	–	–	–	–	–	–	–	–	–	+	–
Suberites sp.	–	–	–	–	–	–	+	+	–	–	–	+
Ascidiacea												
Microcosmus sp.	–	–	–	–	–	–	+	–	+	–	–	–
Pyura stolonifera	+	+	+	+	+	+	–	–	+	+	–	–
Styela plicata	+	+	–	+	+	+	+	+	+	+	+	+

Spatial scales of variation

At the scale of lake (100s of kilometres apart), there was no significant variation in mean numbers of taxa, total numbers of individual sponges, nor abundances of *Styela plicata* per transect (Table 2, Fig. 2). In contrast, there was significant variation of these variables at the smaller scales of location (kilometres apart) and site (100s of metres apart) within lakes (Table 2, Fig. 2). Similarly, in St Georges Basin, there was significant variation in the abundances of *Aplysinella* cf. *rhax* and *Pyura stolonifera* at the scales of location and site (Table 3, Fig. 2).

In Wallis Lake, preliminary examination of raw data for each taxon showed obvious patchiness at the scale of location (kilometres apart) (Table 1, Fig. 2). ANOVAs were therefore done only within locations where specific taxa occurred and where abundances were large enough for ANOVA to be appropriate. Variation among sites was not significant for *Halichondria* spp. (Location 3), *Mycale* sp. (Location 5), or *Suberites* sp. (Location 1). In contrast, there was significant variation among sites for *Mycale* sp. at Location 1 (Table 4, Fig. 2).

Estimates of variance components for each variable are shown in Table 5. Caution should be used in the interpretation of variance components across taxa because the size of the residual variance will affect the contribution of each spatial scale to the total variance (Morrisey et al. 1992, Underwood &

Table 2. ANOVAs to examine variation for selected variables between and within St Georges Basin and Wallis Lake. ns: not significant; ***p < 0.001; Lo: location; La: lake

Source of variation	df	Total no. of taxa			Total no. of individual sponges			No. of *Styela plicata*		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
Lake	1	7.32	0.59	ns	32.53	1.20	ns	104.46	1.06	ns
Location (La)	10	12.35	8.79	***	27.00	5.04	***	98.66	10.78	***
Site (Lo(La))	36	1.40	12.29	***	5.36	11.76	***	9.16	29.86	***
Residual	912	0.11			0.46			0.31		
Transformation		Ln(x + 1)			Ln(x + 1)			Ln(x + 1)		

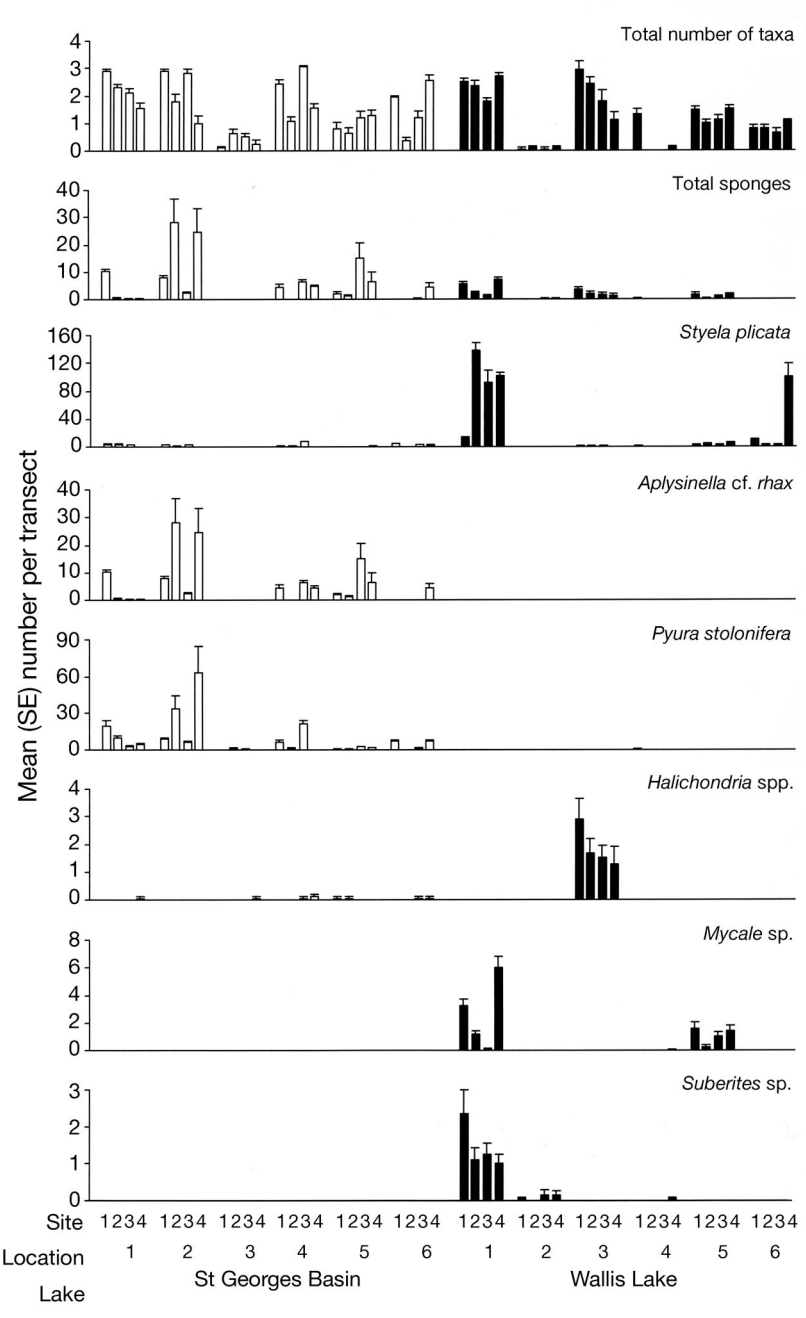

Fig. 2. Mean (SE) numbers per transect (n = 20) at each site

Petraitis 1993). When the proportion of the residual variance differs among taxa, proportions of other spatial scales should not be compared across taxa. The size of residual variance, however, will not affect the ratio among other variance components within a taxon (Underwood & Petraitis 1993). Therefore, ratios of variance estimates can be compared. In the present study, there was considerable residual variance (i.e. among transects within sites) for all taxa examined. The proportion of residual variance ranged from 27 to 73% for variables examined in both lakes, 74 to 76% for *Aplysinella* cf. *rhax* and *Pyura stolonifera* in St Georges Basin and 43 to 98% for *Suberites* sp., *Mycale* sp. and *Halichondria* spp. in Wallis Lake. These relatively large contributions suggest that there was also considerable patchiness at small spatial scales of 10s of metres within sites.

In addition, variance components confirm that there was little variation between lakes for number of taxa, total number of sponges and *Styela plicata*, but most variation was at the smaller spatial scales of locations, sites and transects.

Optimising replication (cost–benefit analyses)

Appropriate replication was determined in 3 stages. First, cost–benefit analyses were done to determine the optimal replication for comparisons among lakes. Analyses were done for numbers of taxa, total numbers of sponges and for *Styela plicata* using data from both lakes and for *Aplysinella* cf.

Table 3. ANOVAs to examine variation among locations and sites for abundances of *Aplysinella* cf. *rhax* and *Pyura stolonifera* in St Georges Basin. ***p < 0.001; **p < 0.01; *p < 0.05; Lo: location

Source of variation	df	*A.* cf. *rhax* MS	*F*	p	*P. stolonifera* MS	*F*	p
Location	5	30.63	3.39	*	41.92	4.35	**
Site (Lo)	18	9.04	13.68	***	9.64	11.87	***
Residual	456	0.66			0.81		
Transformation		Ln(x + 1)			Ln(x + 1)		

rhax and *Pyura stolonifera* using data from St Georges Basin. Because fractions of replicates cannot be sampled, numbers of replicates were rounded to whole numbers keeping near to the budget of 360 min lake^{-1}. These analyses produced 3 different designs: (1) 10 locations, 1 site and 3 transects for numbers of taxa; (2) 6 locations, 2 sites and 5 transects for total numbers of sponges, *A. rhax* and *P. stolonifera*; and (3) 11 locations, 1 site and 2 transects for *S. plicata* (Table 6). Because *S. plicata* is an introduced species and the primary aim of the research programme was to examine native species, Option 3 was not considered further.

Next, to determine which design would be the best compromise for sampling most taxa, cost–benefit analyses were done for *Suberites* sp., *Mycale* sp. and *Halichondria* spp. within locations in Wallis Lake (Table 6). The limiting cost in these analyses was the time available to sample 1 location (including 20 min of travelling time between locations). Analyses were done using: (1) 10 locations lake^{-1} (i.e. 36 min location^{-1}) and (2) 6 locations lake^{-1} (i.e. 60 min location^{-1}). For Option 1 (10 locations lake^{-1}), although there were originally differences among species in the numbers of sites (0.4 to 1.2) and transects (2.0 to 15.4), when the numbers were rounded to stay within the time budget, the design became the same for all species (1 site and 3 transects location^{-1}; Table 6). For Option 2 (6 locations lake^{-1}), the design varied from 1 to 3 sites location^{-1} and 15 to 2 transects site^{-1} (Table 6).

Finally, to determine the best compromise in replication, the precision of estimating the means of each design was compared among the different variables. Precision was calculated as the estimated standard error of the mean (SEM, number per sample) and expressed as a percentage. The estimated SEM was calculated as the square root of the estimated variance of the means, V, where:

$$V = \frac{\left(S_e^2 + n \times S_{B(A)}^2 + n \times b \times S_A^2\right)}{n \times b \times a} \quad (4)$$

for calculating SEM per lake and:

$$V = \frac{\left(S_e^2 + n \times S_{B(A)}^2\right)}{n \times b} \quad (5)$$

for calculating SEM per location.

At the scale of location, the precision of sampling patchily distributed taxa (*Suberites* sp., *Mycale* sp. and *Halichondria* spp.) was greatly improved by using 2 sites and 5 transects compared to 1 site and 3 transects

Table 4. ANOVAs to examine variation among sites within specified locations in Wallis Lake for each of *Halichondria* spp., *Mycale* sp. and *Suberites* sp. Locations are indicated in parentheses. ns: not significant; ***p < 0.001

Source of variation	df	*Halichondria* spp. (L3) MS	*F*	p	*Mycale* sp. (L1) MS	*F*	p	*Mycale* sp. (L5) MS	*F*	p	*Suberites* sp. (L1) MS	*F*	p
Site	3	10.82	1.42	ns	11.54	38.19	***	6.77	2.48	ns	0.44	1.04	ns
Residual	76	7.59			0.30			2.73			0.42		
Transformation		None			Ln(x + 1)			None			Ln(x + 1)		

Table 5. Variance estimates derived from ANOVA for selected variables calculated from untransformed data. Locations are indicated in parentheses. –: variances were not calculated at that spatial scale; Lo: location; La: lake

Source of variation	Total no. of taxa	Total no. of sponges	*Styela plicata*	*Aplysinella* cf. *rhax*	*Pyura stolonifera*	*Suberites* sp. (L1)	*Mycale* sp. (L1)	*Mycale* sp. (L5)	*Halichondria* spp. (L3)
Lake	0.03	4	68	–	–	–	–	–	–
Location (La)	0.53	12	478	22	67	–	–	–	–
Site (Lo(La))	0.28	16	405	31	119	0.23	6.53	0.20	0.16
Residual	0.50	86	344	169	537	3.24	5.00	2.73	7.60

Table 6. Replication at each spatial scale derived from cost–benefit analyses for sampling sponges and ascidians. Values in parentheses have not been rounded. Numbers in bold have been rounded to whole units of sampling. In cases where there was a choice between rounding up or down, the replication that produced the more precise estimate of the mean is given. S: site; L: location

	Both lakes			St Georges Basin		Wallis Lake			
	No. of taxa	Sponges	*Styela plicata*	*Aplysinella* cf. *rhax*	*Pyura stolonifera*	*Suberites* sp. (L1)	*Mycale* sp. (L1)	*Mycale* sp. (L5)	*Halichondria* spp. (L3)
Locations	**10** (10.0)	**6** (6.0)	**11** (10.6)	**6** (6.7)	**6** (6.0)	**Option 1: 10 locations lake^{-1}**			
Sites (L)	**1** (1.0)	**2** (1.6)	**1** (1.3)	**2** (1.7)	**2** (1.9)	**1** (0.6)	**1** (1.2)	**1** (0.6)	**1** (0.4)
Transects (S(L))	**3** (3.0)	**5** (5.2)	**2** (2.1)	**5** (5.3)	**5** (4.8)	**3** (8.4)	**3** (2.0)	**3** (8.2)	**3** (15.4)
Locations						**Option 2: 6 locations lake^{-1}**			
Sites (L)						**2** (1.5)	**3** (2.9)	**2** (1.5)	**1** (1.0)
Transects (S(L))						**5** (8.4)	**2** (2.0)	**5** (8.2)	**15** (15.4)

(Table 7). In comparison, there was only a relatively small loss in precision of the mean at the scale of lake when sampling number of taxa and *Styela plicata* with 6 locations, 2 sites and 5 transects compared to 10 locations and 3 transects. Therefore, it was concluded that the best allocation of resources would be to use 6 locations, 2 sites and 5 transects lake^{-1}.

DISCUSSION

Two key patterns of distribution of sponges and ascidians in coastal lakes are highlighted by this study. First, most of the sponges and ascidians were clearly very patchily distributed at a range of spatial scales from 10s of metres up to 100s of kilometres, which appears common for many species of sponges and ascidians in other habitats (Roberts & Davis 1996, Ferdeghini et al. 2000, Hooper & Kennedy 2002, Hooper et al. 2002). Second, few taxa were widespread over the larger spatial scales. While similar patterns have been found in other enclosed bodies of water (e.g. Kuenen & Debrot 1995), the organisation of assemblages in these lakes appears fundamentally different to those on the open coast, where assemblages of sponges and ascidians usually consist of several patchy but widespread species and numerous very uncommon taxa (e.g. Wilkinson & Evans 1989, Farnsworth & Ellison 1996, Roberts & Davis 1996, Rutzler et al. 2000).

Such variability suggests there may be many different processes operating and influencing these patterns at a range of scales from a few metres to an entire lake (Underwood & Chapman 1996b). In addition, patterns were complex and not consistent between lakes, suggesting different processes may be operating in different lakes. Numerous mechanisms, including predation (Wulff 2000), availability of substrata to settle on (Keough 1984), water quality (Burns & Bingham 2002), hydrodynamics (Guichard & Bourget 1998), competition, dispersal and recruitment (Farnsworth & Ellison 1996) have been proposed and examined to explain these distributions.

At the largest spatial scale of lakes (100s of kilometres apart), while the mean number of taxa and mean abundance of sponges per transect did not differ, the composition of assemblages differed greatly between the 2 lakes. Only 1 of 9 genera of sponges was found in both lakes, and these (*Halichondria* spp.) may be different species. Differences between lakes point to processes operating at large spatial scales of the entire lake and/or region. Although little is known of many of the taxa found in this study, it is logical to suggest different species may have different tolerances to the physiological stresses imposed by these environments and hence different distributions. For example, water quality can vary greatly among NSW lakes (Pollard 1994a, West & Jones 2000). Large-scale floods can dramatically change physical variables such as salinity, temperature, turbidity and pH and affect entire estuaries and assemblages of animals (Moverley et al. 1986). Further, the magnitude and duration of changes after input of freshwater may vary greatly among different NSW coastal

Table 7. Precision (%) of estimating means measured as the standard error of the mean for selected variables at the scales of lake and location, using different numbers of locations, sites and transects

Numbers of locations, sites, transects	Precision at the scale of lake		Precision at the scale of location			
	No. of taxa	*Styela plicata*	*Suberites* sp. (L1)	*Mycale* sp. (L1)	*Mycale* sp. (L5)	*Halichondria* spp. (L3)
10, 1, 3	24.6	92.9	80.3	108.0	100.4	89.9
6, 2, 5	27.2	101.5	46.5	73.2	58.2	50.2

lakes (e.g. Pollard 1994a). Similarly, the regime of opening and closing of entrances of NSW lakes is known to affect water quality, which can be correlated with the distribution of some organisms (Dye & Barros 2005). Differences in species composition may also be due to limited dispersal between lakes. Dispersal may be limited because: (1) coastal lakes in NSW are separated by 10s to 100s of kilometres of open coast, (2) it appears that the distributions of many of these sponges are not continuous along the coast and may be restricted to lakes or estuaries (P. B. Barnes unpubl. data) and (3) many sponges have short dispersal distances (Zea 1993, Farnsworth & Ellison 1996, Maldonado & Young 1996, but see Davis et al. 1996).

Patchiness was also clear at smaller spatial scales from 10s and 100s of metres to kilometres apart within lakes. This was most evident in Wallis Lake where only 2 of the 8 species of sponge were found in >1 location. Nevertheless, some species were relatively abundant at some places. Similarly, the abundances of those more widespread taxa were significantly variable within the spatial scales in which they occurred. Again, numerous processes have been proposed to explain smaller-scale patterns. For example, abiotic factors which may affect sponges such as sedimentation rates (Burns & Bingham 2002) and turbidity (Bell & Barnes 2000) are known to differ among areas within lakes kilometres apart (Roberts 2001, Sloss et al. 2004). Larval recruitment and small dispersal distances have been proposed as important in explaining aggregated patterns of distribution of epibionts (including sponges and ascidians) over relatively small scales of metres to 100s of metres (Farnsworth & Ellison 1996). Predation by fish has been found to play a key role in structuring assemblages of sponges in some habitats (Pawlik 1998, Wulff 2000), and abundances of fishes are often patchy and differ among habitats within and among NSW lakes (Pollard 1994b).

The shallow areas sampled in these lakes are often a mosaic of patches of different species of seagrasses and macroalgae and patches of bare sediment (West et al. 1985, Cummins et al. 2004b), which vary over scales of metres to kilometres. Such patchiness in habitat may have a number of consequences for the distribution of sponges and ascidians. For example, sponges and ascidians were found attached to a variety of surfaces, including seagrasses, macroalgae and fragments of shells, and unattached on top of patches of sediment. Small-scale patchiness in the distribution of sponges and ascidians may therefore be related to the availability of suitable substratum on which to settle (Keough 1984). In addition, assemblages of potential predators may differ among types of vegetation and, therefore, affect distributions of sponges and ascidians. Overall, it is likely that many processes are interacting to influence patterns of distribution.

Greater understanding of the ecology of sponges and ascidians in coastal lakes and, hence, long-term conservation will best be achieved by experimental examination of the processes causing small- and large-scale patterns of variation. Also, because patterns of distribution varied greatly among species, further experiments should include examination of specific species (Cummins et al. 2004a). However, because assemblages of sponges and ascidians in these habitats are virtually unknown, it would be beneficial first to test the generality or otherwise of these patterns through time and among different lakes. The findings of this study have several important implications for the design of such research programmes.

At the scale of lake, although there were no significant differences in the mean number of taxa, individual sponges, or *Styela plicata* per transect, there were obvious differences in the composition of assemblages between lakes. Two-thirds of the taxa were exclusively found in one or the other lake. Wallis Lake had more taxa (11) compared to St Georges Basin (4) and taxa were widespread throughout St Georges Basin, but in Wallis Lake most were restricted to 1 or a few locations. Such obvious differences emphasise the need to include adequate replication at the scale of lake for studies examining differences in composition of assemblages among large spatial scales (e.g. regions of coast) or types of lake (e.g. urbanised versus relatively pristine, open versus intermittently open or closed to the sea). For such comparisons, inclusion of sampling at a hierarchy of spatial scales will further improve the power of tests for differences (Morrisey et al. 1992). Further, adequate replication at the smaller scales of 10s and 100s metres and kilometres will be needed to ensure differences between lakes are not masked by significant small-scale variation. Very patchy distributions at the scale of locations kilometres apart (as in Wallis Lake) also have important consequences for finding sponges in a lake. The number of locations sampled will determine the probability of a particular species being found. For example, *Mycale* sp. was widespread in only 2 of the 6 locations in Wallis Lake. Logically, the probability of sampling at least 1 location with *Mycale* sp. will increase with the number of locations sampled (for theory on sampling rare species see Kovalak et al. 1986, Green & Young 1993).

In the present study, unlike other published examples of spatial variation and cost–benefit analyses (Kennelly & Underwood 1985, Morrisey et al. 1992, Benedetti-Cecchi et al. 1996, Bartsch et al. 1998), there were very few taxa widespread over all spatial scales. Such studies quite appropriately chose to analyse taxa that were 'consistently present' (Morrisey et al. 1992), because they presumably represented a large proportion of and were therefore representative of the assem-

blage. In contrast, this study found that it was often the patchily distributed taxa that represented the largest proportion of the assemblage. In this case, it was important to optimise sampling designs for those taxa. It should not be assumed that derived variables such as total number of taxa are appropriate surrogates for designing experiments to sample individual species. Rather, if the aim of the sampling programme is to sample many taxa as precisely as possible, designs can be improved by including patchily distributed taxa in cost–benefit analyses. In this study, it was found that the selection of a sampling design that led to relatively large increases in precision of sampling patchily distributed taxa, resulted in only relatively small compromises in the precision of sampling widespread variables.

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