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Lack of significant change in epiphyte biomass with increasing extent of measurement within seagrass meadows

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Abstract

A significant consideration in defining patterns of ecological interest is determining at what spatial scales these patterns are apparent. We performed a mensurative experiment to determine the effect of how changing the extent of sampling, using a fixed grain (panning up), changed our measurements of seagrass epiphyte biomass at a variety of hierarchical spatial scales, ranging from approximately 0.1 m to 2.5×10^5 m. The experiment was performed twice at two sets of nested locations, also capturing an element of seasonality within the spatial extents. While the two regions and their nested locations differed in terms of epiphyte biomass, and values did change over time, mean epiphyte values were invariant at the local scale. This indicates that at the local scale ($\leq$100 m extent), we expect seagrass epiphyte biomass to be relatively homogenous. Contrary to theoretical predictions, we did not detect predictable changes in mean values of epiphyte biomass as sampling extent increased. The results of this study highlight the importance of recognizing the spatial dependence of patterns in heterogeneous environments.

Keywords: extent; grain; hierarchical; scale invariance; panning; patchiness; variability; Australia

1. Introduction

A significant consideration in determining patterns of ecological relevance is at what spatial scales any such patterns are apparent (Legendre and Fortin, 1989). Understanding of the spatial and temporal characteristics of any ecological pattern is required before it is possible to investigate the relative importance of likely causative processes (Underwood et al., 2000). Natural sampling units (e.g. a single seagrass leaf or bundle of leaves within a sheath, Dungan et al., 2002) sampled in isolation are often not useful for making inferences regarding landscape-scale issues. Hence, researchers often investigate arbitrarily-defined spatial scales of measurement to attempt to discern patterns or generalities relevant to broader spatial extents.

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Grain and extent are important elements of studies interested in detecting pattern or changes in variability of communities or populations (Wiens, 1989; Levin and Hay, 2002), especially over broad spatial scales. Grain describes the smallest scale of resolution in a study, or window through which we view the world (Wiens, 1989; Schneider, 1994). This can be represented as, say, a replicate quadrat of 1 m^2. Extent describes the greatest distance between the two most separate grain units, or the total area of investigation (Wiens, 1989; Schneider, 1994). Sampling theory makes several predictions regarding how measures of ecological variables will respond to variations in both grain and extent. When the grain of investigation is fixed but extent is increased (referred to as "panning"; Schneider, 1994), variation around mean values is expected to increase (Wiens, 1989). This is because a greater range of patch types or landscape elements will be incorporated; essentially, more habitat heterogeneity will be encountered, seen as between-grain variability. Increasing extent should lead to increasing variability around mean values (a "red-shift"). Conversely, increasing grain size within a fixed extent ("zooming"; Schneider, 1994) should lead to a "blue-shift" in the data, with reducing variation around mean values as grain size increases. Such an outcome would be expected if ever-increasing grain captured more of the system- or landscape-level heterogeneity within the grain units.

Epiphyte biomass (total mass of epiphytes per unit of seagrass or area of benthos) has been suggested as an important measure of "ecosystem health" in seagrass meadows (Wood and Lavery, 2000), with elevated epiphyte loads eventually causing seagrass death through obstruction of light and nutrient flow to the leaves (Sand-Jensen, 1977; Neckles et al., 1993; Brush and Nixon, 2002). Increased epiphytes on seagrasses has often been correlated with eutrophication induced by human modification to coastal ecosystems (Wear et al., 1999). Epiphyte biomass or standing crop is a potentially useful metric for ecosystem health because of the potential sensitivity of the metric to changed environmental conditions (Saunders et al., 2003). However, to be a useful indicator, there is a fundamental need to understand how epiphyte load is distributed throughout natural seagrass landscapes. To date, there has only a limited amount of experimental investigation into the spatial distribution of epiphyte biomass over a hierarchy of scales.

Previous studies of epiphytic distribution are somewhat discordant in terms of their findings. While some works have suggested that epiphytes are patchy at 1–10's of m (Kendrick and Burt, 1997; Jernakoff and Neilsen, 1998) and >kilometre scales, (Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002), other studies have indicated that epiphytes may be uniform at relatively small spatial scales (e.g. 0.1 m Vanderklift and Lavery, 2000; <10 m, Saunders et al., 2003; Piazzi et al., 2004). Further studies have shown that patchiness in epiphytes as well as in seagrass morphology (Balestri et al., 2003; Balestri, 2004) is significant over a range of scales (typically cm to km). Vanderklift and Lavery (2000) theorized that patchiness of epiphytes could be detected in other measures such as biomass and productivity as well as community structure. There is little consensus between these previous studies as to what scales any patchiness of epiphytes in seagrass meadows exists, other than on the broad scale of kilometres between meadows.

This study was designed to investigate how mean values of epiphyte biomass and variability around means changed over a series of hierarchical spatial scales in seagrass meadows at various locations and also through time. We hypothesized that the differences between mean epiphyte load measured would increase with extent of sampling. We also theorized that there would be a red-shift, i.e. the data would show an increase in variation around mean values with increasing spatial scales (i.e. extent) of observation. Our expectation was based on the concept that greater spatial separation of samples should capture more occurrences and hence a greater range of the different processes influencing the abundance and distribution of epiphytes. The mensurative experiment we performed tested several null hypotheses, specifically that: there would be no effect of increasing extent of investigation on epiphyte biomass, and there would be no change in epiphyte biomass between regions and locations within each region; epiphyte biomass would not change between visits to each location; and there would be no interaction between the extent over which measures were made, and the effects of regions, locations or visits.

2. Materials and methods

2.1. Study region

In temperate southern Australia, up to 12 species of seagrasses have been identified from 5 genera (*Amphibolis, Halophila, Heterozostera, Posidonia* and *Zostera*, Westphalen et al., 2004). Gulf St Vincent and Spencer Gulf are shallow marine basins or inverse estuaries that are both connected to the Great Australian Bight by deep passages (Fig. 1). The gulfs are separated by the land mass of Yorke Peninsula, which restricts water flow between the two water bodies. Spencer Gulf is as an oligotrophic inverse estuary. Gulf St Vincent is also typically defined as oligotrophic (Westphalen et al., 2004) although the large population centre of Adelaide on the eastern shore of Gulf St Vincent means that it is subject to some anthropogenic modification. The tidal regime in the entire study area is micro-tidal, with tidal movement typically less than 2 m, and sites have low wave energy.

In each of the gulfs, two regions were selected. In Gulf St Vincent, the region was based around Adelaide, and in Spencer Gulf, the region was based around Port Lincoln. The regions are separated by approximately 250 km. Nested within each of the regions, two locations were selected. The locations within each gulf were separated by approximately 50 km of coastline. All locations were selected on the basis of having similar water depths (ranging from 1.8–6 m), similar expected

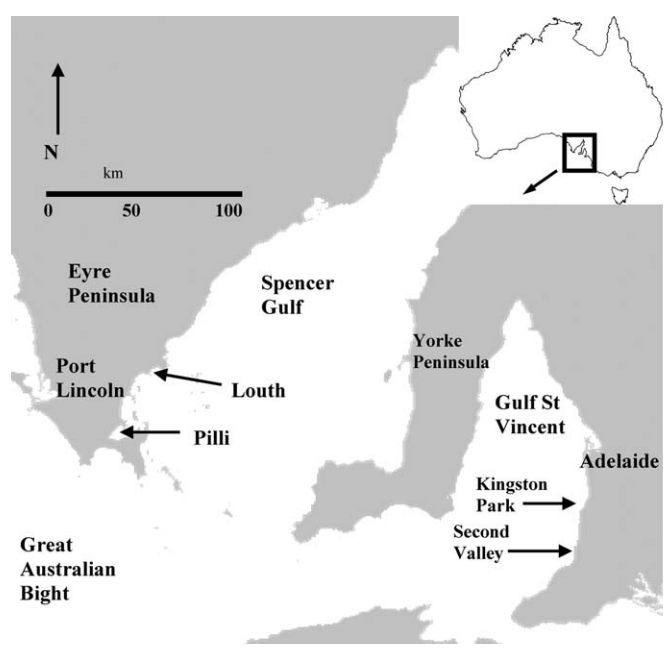

Fig. 1. Map of Gulfs of South Australia, indicating sampling regions & locations, with continental Australia as the insert.