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Quantifying habitat structure: surface convolution and living space for species in complex environments

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Habitat complexity is often used to explain the distribution of species in environments, yet the ability to predict outcomes of structural differences between habitats remains elusive. This stems from the difficulty and lack of consistency in measuring and quantifying habitat structure, making comparison between different habitats and systems problematic. For any measure of habitat structure to be useful it needs to be applicable to a range of habitats and have relevance to their associated fauna. We measured three differently-shaped macrophyte analogues with nine indices of habitat structure to determine which would best distinguish between their shape and relate to the abundance and rarefied species richness of their associated macroinvertebrate assemblages. These indices included the physical, whole-plant attributes of surface area (SA) and plant volume (PV), the interstitial space attributes of average space size and frequency (ISI), average refuge space from predation (Sp/Pr), and total refuge space (FFV), and the degree of surface convolution at a range of scales (i.e. the fractal dimension at four spatial scales: 7.5 ×, 5 ×, 2.5 × and 1 × magnification). We found a high degree of inter-correlation between the structural indices such that they could be organised into two suites: one group describing interstitial space and surface convolution at coarse scales, the other describing whole-plant attributes and surface convolution at fine scales. Two of these indices fell into both suites: the average refuge space from predation (Sp/Pr) and the fractal dimension at 5 × magnification. These two measures were also strongly related to macroinvertebrate abundance and rarefied species richness, which points to their usefulness in quantifying habitat structure and illustrates that habitat structure depends not just on shape, but on the space associated with shape.

Habitat structure refers to the physical structures in space which support plant and animal communities and is therefore of intrinsic importance to ecologists (Bell et al. 1991). It can refer to abiotic structures such as the size and arrangement of stones on a stream bed (Flecker and Allan 1984), the crevices and pits on stones (Downes et al. 1998) and the holes and fissures found on marine rocky shores (Menge et al. 2005). It can also refer to living structures such as trees (Lawton 1986) or oyster reefs (Grabowski 2004), or any surface upon which organisms live. In vegetated aquatic systems such as lakes, lowland rivers, estuaries and marine littoral zones, habitat structure can be provided by vascular macrophytes and macroalgae (Heck and Crowder 1991). In lowland rivers in particular, macrophyte beds have been described as food web 'valves' (Power and Dietrich 2002), linking mainstream and floodplain food webs (Winemiller and Jepsen 1998) and riverine and terrestrial food webs (Dettmers et al. 2001).

Habitat structure is generally considered to influence local species abundance and diversity, and many studies have shown that assemblages are more abundant and diverse in more complex habitats (McCoy and Bell 1991). However, the ecological importance of more complex habitats is often inferred, or bestowed as a post hoc explanation of experimental results where either greater food resources or greater refuge space associated with more complex habitats are invoked as mechanisms. As a consequence, there is little capacity to make generalisations regarding the role of habitat structure in community structure, and its regulating mechanisms remain obscure (McCoy and Bell 1991, Sanson et al. 1995). One of the major reasons for this gap in our knowledge is the difficulty in quantifying habitat structure in a way that allows comparison between different habitats and is relevant to the associated fauna (Beck 2000, Downes et al. 1998).

Habitat structure comprises two components, quantitative and qualitative (Stoner and Lewis 1985), which refer to the amount or density of structures and the heterogeneity or diversity of structures, respectively. Furthermore, both these aspects of structure depend on the scale at which they are being observed and used (McCoy and Bell 1991, Taniguchi et al. 2003). Where habitat structure is provided by aquatic vegetation, density is relatively straightforward to measure, which may explain which habitat structure has so often been

quantified simply by the presence or biomass of vegetation (Cyr and Downing 1988), or by a range of vegetation densities (Hacker and Steneck 1990, Gee and Warwick 1994, Swisher et al. 1998). Quantifying vegetation structure by presence or density does not distinguish the specific, scale-dependent aspects of plant morphology to which invertebrates may be responding, and so their descriptive power is low (Lawton 1986). Numerous studies have shown different invertebrate assemblages occur in differently-shaped habitats (Humphries 1996), and more recent research shows that plant density and plant shape can indeed have separate effects on predator success (Warfe and Barmuta 2004), attesting to the fact that density is only one aspect of structure. Macroinvertebrates are more likely to be making choices between habitats at the scale of individual plants or plant parts (Davenport et al. 1996), or on the basis of refuge space associated with habitats (Sanson et al. 1995, Bartholomew et al. 2000), and therefore may not respond to coarse-scale measures such as plant presence and biomass. If the shape of a habitat is to be used as a tool describing the distribution of associated fauna, illustrating its role as a qualitative component of habitat structure, then it should be quantified at a scale relevant to the fauna utilising it as habitat, and in a way that allows comparisons to be made between habitats (McCoy and Bell 1991, Beck 1998, Downes et al. 1998).

The measures of structure which have been applied to aquatic vegetation, to relate their structure to the distribution of their associated invertebrate assemblages, can be grouped into three categories: those that measure the physical whole-plant attributes of the plant, those that measure the surface convolution or rugosity of the plant, and those that measure the interstitial space associated with the plant. Each of these categories is considered in turn.

Some studies have quantified plant shape in a way that is specific to the system under investigation, such as the number of different plant structures (Stinson and Brown 1983) or average frond length (Kelaher and Castilla 2005). These measurements are sufficient to indicate relative differences in structural complexity but do not allow comparisons between different habitats or different systems, nor do they show how these different habitats are being used. The indices that are most often used to quantify the physical attributes of macrophyte structure are surface area and plant volume (Coull and Wells 1983, Strayer et al. 2003). Macrophytes with a more structurally complex morphology (e.g. those with a higher degree of leaf dissection) are hypothesised to have relatively more surface area, and therefore support greater species abundance and richness (Heck and Orth 1980, Parker et al. 2001). We used the indices of surface area and plant volume to test this hypothesis and to determine if surface area sufficiently distinguishes between plant shape and relates to the distribution of associated invertebrates.

Many natural objects have irregular surfaces and cannot be sufficiently described by simple geometry (Sugihara and May 1990, Halley et al. 2004). Integral calculus has been used to determine the degree of surface 'folding' (Jacobi and Langevin 1996), but we rejected this method on the basis of it requiring too many simplifying assumptions without providing any extra information. Fractal geometry, on the other hand, has been shown to offer considerable promise in quantifying ecological patterns and processes, particularly due to its multi-scale nature (Halley et al. 2004). Fractal geometry describes the measurement of an object or surface where that measurement depends on scale; if a smaller 'ruler' is used, the measurement picks up more detail at greater magnification (Schmid 2000). Thus, it is independent of the nature of the habitat and is related to the scale at which the habitat is viewed (Lawton 1986, Gee and Warwick 1994, Schmid 2000). The fractal dimension (D) of an object is a non-integer dimension estimated from measuring the object's surface. As D increases it indicates the object becomes more convoluted, departing from a two-dimensional surface and approaching a three-dimensional object. D has been shown to be a relatively good indicator of structural complexity, with more complex habitats having a higher D and supporting more animals, for both rocky substrates (Beck 1998, Schmid 2000) and plants (Shorrocks et al. 1991, McAbendroth et al. 2005, Thomaz et al. 2007). If there are differences in D at different scales, then the dimensionality depends on scale, suggesting small animals perceive the habitat differently from larger animals. We estimated the D of differently-shaped plants at four different scales to determine its effectiveness at distinguishing plant shape and how well it related to invertebrate abundance and richness.

Several researchers have noted that invertebrates respond to the interstitial space within a habitat (Hacker and Steneck 1990, Sanson et al. 1995). Hacker and Steneck (1990) compared the interstitial volumes of four macroalgal species (two of which were artificial) and found that plants with an intermediate amount of interstitial volume, relative to plant volume, provided optimal habitat for amphipods; there was enough space to accommodate amphipod body volume, yet enough substrate on which to cling. However, measuring the overall volume of interstitial space in a plant canopy gives no indication of how this space is split or partitioned among structural elements, and assumes all the interstitial space is equally available to the epifauna. Dibble et al. (1996) developed an index of interstitial space (ISI) which measures the frequency and size of interstitial spaces between structural elements along vertical and horizontal axes, such that a greater number of smaller gaps indicates a more structurally complex plant shape. Bartholomew et al. (2000) went further and addressed the potential role of vegetation structure as a prey refuge, developing a dimensionless index of structure which incorporated the size of a predator. This Sp/Pr index takes the average interstitial space size, Sp, and divides it by the predator size (the size at which predators are restricted in their ability to move through the structure), Pr, thereby estimating the relative 'refuge value' of the habitat based on the amount of interstitial space where prey are safe from predation. We used these ISI and Sp/Pr indices, together with a third index, the fish-free volume (FFV), we developed which measured the absolute amount of space unavailable to a fish predator but available to invertebrate prey. If invertebrates are tracking refuge space, and a more complex plant shape provides more refuge space, then the amount of predator-free space should relate to the distribution of macroinvertebrates between plants.

Macrophyte structure, in providing a habitat for epifaunal invertebrates, is comprised of both density and

shape. Our aim was to identify a means of quantifying macrophyte shape which would 1) indicate the degree of structural complexity of different macrophyte habitats, and 2) relate to the abundance and species richness of invertebrate assemblages inhabiting different macrophytes. We measured three macrophyte analogues, originally designed for a long-term field experiment (Warfe and Barmuta 2006), using the indices described above to evaluate their effectiveness at quantifying the qualitative aspects of habitat structure which are of relevance to the associated fauna.

Material and methods

Study system

Artificial analogues of three macrophyte species were constructed for a field predator-exclusion experiment, which was designed to test the interacting effects of habitat structure and fish predation on macroinvertebrate and periphyton assemblages (Warfe and Barmuta 2006). The experiment was conducted in the Macquarie River (41°56′S, 147°26′E), Tasmania, Australia, which is a slow-flowing, perennial river draining 3765 km^2 over its 155 km length and has a mean daily discharge ranging from 1.5 to 20 $m^3\ s^{-1}$. The riparian vegetation is sparse, comprising woolly tea-tree *Leptospermum lanigerum*, native graminoids (*Poa labillardieri* and *Lomandra longifolia*), remnants of *Eucalyptus viminalis* and *E. amygdalina* woodland, and some introduced crack willow *Salix fragilis*. The aquatic vegetation is abundant and diverse, comprising up to 30 macrophyte species but dominated by *Myriophyllum* spp., *Vallisneria gigantea*, *Scirpus fluitans*, *Juncus* spp., *Eleocharis sphacelata* and *Triglochin procera* (Warfe unpubl., Humphries 1996). These macrophyte beds support abundant and diverse assemblages of macroinvertebrates, which in turn are prey to large populations of the southern pygmy perch, *Nannoperca australis* (Humphries 1995).

The macrophyte analogues were constructed to imitate species common to the Macquarie River but varying in shape (Fig. 1), to ensure consistent and quantifiable sampling units for the field experiment, and to prevent decay and senescence of sampling units. Pilot tests showed no significant differences in macroinvertebrate community composition between macrophyte analogues and their natural counterparts (Warfe unpubl.). The most structurally simple macrophyte analogue was constructed of 280 mm lengths of green electrical conduit (7 mm diameter) sealed with neutral silicon, to resemble stems of the spikerush *Eleocharis sphacelata*. Four stems comprised a sampling unit (or 'plant'). Eighteen lengths of green packing strap (three of each length 100, 130, 170, 200, 260 and 280 mm, all of width 12 mm) were attached together at the base with epoxy-resin in a tuft-like shape to represent the water ribbon *Triglochin procera*. Commercially produced plastic aquarium plants, each consisting of four stems (2×280 mm length and 2×250 mm length) of highly-dissected whorled leaves were designed to specifically imitate *Myriophyllum* spp. (Tetra Secondnature, Virginia, USA, pers. comm.), and were used to represent the plant of the greatest structural complexity, *Myriophyllum variifolium*. Numerous analogues of each species were constructed for the field experiment, but only four replicates of each species were measured with the structural indices presented here. Macrophyte analogues are hereafter referred to by their genus names.

Figure 1. Illustration of the macrophyte analogues (left) and their natural counterparts (right). The analogues were constructed to imitate differently-shaped species common to the Macquarie River: *Myriophyllum variifolium* (top), *Triglochin procera* (middle) and *Eleocharis sphacelata* (bottom). Each analogue was 280 mm in height.

The macrophyte analogues were attached to 500 (w) $\times$ 500 (l) $\times$ 300 (h) mm cages of plastic, 6 mm oyster-mesh, each with an upper frame of sealed PVC pipe (75 mm diameter) which acted as a float, suspending the cage in the water column to a depth of approximately 300 mm. Each cage had removable panels (300 (w) $\times$ 240 (h) mm) on two opposing sides to allow colonisation by periphyton and macroinvertebrates over the 10-week colonisation period. Cage controls were designed to control for the surrounding presence of the cage, and comprised the cage floor only, with its attached macrophyte analogues, weighted to 300 mm depth by lead sinkers. There were 72 cages constructed, which were split into four predator treatments (fish enclosure, fish exclusion, fish access and cage control), and

fully crossed with three macrophyte treatments (*Myriophyllum*, *Triglochin* and *Eleocharis*), and six blocks (sites), three of which were initiated in summer, and three in winter (Warfe and Barmuta 2006). A previous laboratory experiment showed that the feeding efficiency of fish predators, *Nannoperca australis*, was affected by macrophyte shape but not density (Warfe and Barmuta 2004), so the densities of each analogue were based on median field densities as follows: *Myriophyllum* at 45 plants $cage^{-1}$ (180 plants m^{-2}), *Triglochin* at 25 plants $cage^{-1}$ (100 plants m^{-2}) and *Eleocharis* at 220 stems $cage^{-1}$ (880 stems m^{-2}).

Individual analogues were randomly sampled from each cage and replaced with uncolonised plants, and their location in the cage recorded to prevent further sampling. Three blocks were sampled on three occasions over summer (7 Feb, 6 Mar and 3 Apr 2000), and all six blocks were sampled on two occasions over winter (24–25 Jul and 21–22 Aug 2000) (Warfe and Barmuta 2006). After sampling, each plant analogue with all attached material was preserved with 5% formalin, and on return to the laboratory was rinsed and cleaned of macroinvertebrates and periphyton over a 250 μm sieve. Macroinvertebrates were counted and identified to the lowest taxon possible, which was predominantly species so taxon richness is hereafter referred to as 'species' richness. Seventy-seven species were sampled over the course of the experiment, and comprised approximately 55% crustaceans, 26% insects, 16% soft-bodied taxa (including hydrozoans, nematodes and oligochaetes), and the remaining 3% molluscs and mites.

Measures of plant shape

Four replicates of each macrophyte analogue were measured by each index of plant shape. Both surface area (SA) and plant volume (PV) were measured geometrically using vernier calipers. The surface area of four *Eleocharis* stems were added to provide the total surface area of a 'plant' sampling unit, and the surface area of the individual leaf straps of each *Triglochin* analogue was calculated and summed to provide total surface area per 'plant'. For the *Myriophyllum* analogues, the length and width of each leaflet was measured, summed over the total number of leaflets per plant, and combined with the surface area of the mainstems to provide the total surface area. Plant volume was corroborated by determining the volume of water each analogue displaced. The detergent method of Harrod and Hall (1962) was initially used, but a relatively high standard error in the final weights (up to 33% of the mean) led us to abandon this method.

The fractal dimension was estimated at each of four scales based on methods used by Jeffries (1993) and Thomaz et al. (2008). Each macrophyte analogue was suspended upside-down so its stems resembled their position as if they were suspended in water. A camera was mounted in front of each plant so that the middle section of the plant was in frame, and the base and tips of the plant were excluded from the frame. Four photographs, each with a shallow depth of field (approximately 5 mm), were taken of each macrophyte analogue. The first was taken focussing on the analogue parts closest to the camera, and each successive photograph was taken focussing back 'through' the analogue at approximate 5 mm intervals. Beyond this point, proximate analogue parts were blurry and obscured other parts of the analogue. This method is recommended over other methods that 'force' plants onto a two-dimensional plane (Hacker and Steneck 1990) because it retains the three-dimensional shape of the plant (Sugihara and May 1990). The procedure was repeated at four different scales of magnification: scale 1 had the finest resolution at 7.5 × magnification, scale 2 at 5 × magnification, scale 3 at 2.5 × magnification, and scale 4 was the coarsest scale and unmagnified (1 × magnification). We used an Olympus OM-1 SLR camera with a Sigma 50 mm macro lens and the f-stop set at 1.4 for our photography, with Hoya +1, +2 and +4 macro filters and black and white Agfa APX 100 film. This method yielded four two-dimensional photographs, or 'slices', of each macrophyte analogue at each scale. As in Jeffries (1993) and Thomaz et al. (2007), grid squares of 100 mm, partitioned into 2^n squares (where n was 2, 4, 6, 8 or 10 and the square size was therefore 50, 25, 12.5, 6.25, 3.125 mm respectively), were progressively placed over each photograph, and the number of squares (per grid) in which the plant was sharply defined and in focus was counted. The log of this number was plotted against the log of the total number of squares along the respective grid edge, and the slope of the resulting regression line was D, the fractal dimension. D was calculated separately for each scale.

We used the photographs (described above for measuring D) for calculating the interstitial space indices, using the four photos at 1 × magnification from each analogue. Three horizontal and three vertical axes were drawn at least 30 mm apart on each photo. The total number of gaps along each axis was counted, and the length of each gap along the axis (its width or height depending whether it was on a horizontal and vertical axis, respectively), was also measured (to the nearest mm). These measurements provided the mean frequency of gaps along the horizontal axes (f_h), the mean length (height) of those gaps (l_h), the mean frequency of gaps along the vertical axes (f_v), and the mean length (width) of those gaps (l_v). These values were then used to calculate the ISI using the formula $I_{hv} = (f_h/l_h + (f_v/l_v))$ (Dibble et al. 1996). A higher value of I_{hv} results from a greater frequency of smaller gaps, and indicates the space is more frequently 'split' by structural elements. Using the data obtained for the ISI, the gaps between structural elements was averaged across both vertical and horizontal axes to determine the average space size of each macrophyte analogue for the Sp/Pr index (Bartholomew et al. 2000). This was then divided by the average predator size, which was measured as the minimum gape width (5 mm from operculum to operculum) of pygmy perch used in the field experiment (Warfe and Barmuta 2006). An Sp/Pr value below 1.0 indicated the fish predator could not access the average gap size.

The FFV was estimated geometrically and assumed pygmy perch could only access spaces larger than their minimum gape width, therefore any space under 5 mm wide was considered to be FFV. *Eleocharis* had no FFV, and this was confirmed by direct observations of pygmy perch under laboratory conditions (Warfe and Barmuta 2004). The FFV in *Triglochin* comprised the wedge-shaped spaces between leaves at the base of the tuft, each of which was

measured geometrically using the formula lwd/2 which measured the length (l), width (w) and depth (d) of the wedge-space as if was oblong, and then divided by 2 to obtain the wedge volume. The volume of all the spaces under 5 mm were summed for each replicate *Triglochin* analogue to provide an average total FFV volume for *Triglochin*. The four stems, including the whorled leaves, comprising each *Myriophyllum* analogue were treated as cylinders; the space 'inside' the leaves was unaccessible by pygmy perch (Warfe and Barmuta 2004) and therefore FFV. The volume of each 'cylinder' was calculated with the formula $\pi r^2 h$, where r denoted the radius of the cylinder (the stem and the leaves) and h the height, and added to provide the overall volume. The PV was then subtracted from this value to give the FFV for *Myriophyllum*.

Data analyses

The field experiment was a partially nested design, where the main factors of macrophyte analogue (three levels) and predator treatment (four levels) were fully crossed and replicated at six sites. Site was used as a blocking factor and nested in time-of-start (two levels: summer and winter), and the summer-start cages were sampled on five occasions while the winter-start cages were sampled concurrently on the final two occasions (Warfe and Barmuta 2006). This resulted in a potential total of 252 samples collected, but disturbance by cattle led to the removal of three samples. As we were only interested in the distribution of macroinvertebrates between different macrophyte analogues, we did not include the predator treatment or season factors into the macroinvertebrate data analyses here, but retained the six sites as a randomised-block factor. Therefore, single-factor analysis of variance (ANOVA) was conducted on the dependent variables of macroinvertebrate abundance, species density and rarefied species richness to determine if either variable differed with macrophyte shape, and planned pairwise comparisons were also conducted between levels of the macrophyte factor: *Myriophyllum* vs *Triglochin* and *Triglochin* vs *Eleocharis*. Species density in this paper refers to the number of taxa per sample unit and is inevitably correlated with abundance (Magurran 2004). Formal comparison of species richness (sensu Gotelli and Colewell 2001) was conducted via rarefaction to a constant number of individuals per sample unit using Hurlbert's (1971) formulation as implemented in the R statistical package 'vegan' (Oksanen et al. 2007, R Development Core Team 2008). The patterns for species density followed those found for rarefied species richness, so only the results for rarefied species richness are presented.

The indices of habitat structure were potentially highly correlated, so we conducted a principal components analysis (PCA) which extracts new orthogonal variables as a linear combination of the original variables, allowing us to identify any redundancy between the indices. The loadings were orthogonally rotated to maximise the high correlations and minimise the low correlations of each index with the principal components (Tabachnick and Fidell 2001).

If the macroinvertebrate assemblage is affected by differences in habitat structure, there should be significant correlations between the structural indices and macroinvertebrate abundance and richness. Furthermore, the structural index with the most significant correlations should be the best descriptor of macroinvertebrate distribution (Beck 1998). Correlations were conducted between each structural index and the dependent variables of macroinvertebrate abundance and rarefied species richness. Site was treated as independent for this analysis, so there were six correlations between each structural index and the dependent variables (after Beck 1998). As there were three sites initiated in summer and sampled on five occasions, and three sites initiated in winter and sampled concurrently on the final two occasions (Warfe and Barmuta 2006), correlations were based on 60 replicates from each summer site, and on 24 replicates from each winter site. Due to the large number of tests performed, the level of significance was reduced to $p < 0.01$ to reduce the likelihood of type I errors. Data were log-transformed where necessary, to meet assumptions of normality, and analyses were performed using SYSTAT ver. 9 (Wilkinson 1999).

Results

The abundance of macroinvertebrates significantly varied according to macrophyte analogue ($F_{2,246} = 49.73$, $p < 0.001$; Fig. 2a). *Myriophyllum* analogues supported 48% more macroinvertebrates than *Triglochin* ($F_{1,246} = 30.06$, $p < 0.001$), which supported 38% more than *Eleocharis* ($F_{1,246} = 19.59$, $p < 0.001$). Likewise, rarefied species richness was also significantly affected by macrophyte shape ($F_{2,246} = 35.14$, $p < 0.001$; Fig. 2b). There were 3.5% more species on *Myriophyllum* analogues than *Triglochin* ($F_{1,246} = 4.93$, $p < 0.001$), and 28% more species on *Triglochin* than *Eleocharis* analogues ($F_{1,246} = 8.33$, $p < 0.001$).

Each structural index gave a different value for each macrophyte analogue, except D_3, the fractal dimension at scale 3, which was the same for *Eleocharis* and *Triglochin* (Table 1). This indicates that, on the whole, each index was capable of measuring differences in structure between the differently-shaped macrophyte analogues. Surface area was very similar on *Myriophyllum* and *Triglochin* but lowest on *Eleocharis*, and this pattern was reversed for plant volume. The ISI was greatest on *Myriophyllum*, indicating many small interstitial spaces and therefore many structural elements. An Sp/Pr value under 1.0 for *Myriophyllum* suggested the structural elements of this analogue impeded access by pygmy perch; this was also reflected in the FFV being orders of magnitude greater on *Myriophyllum* than either of the other two analogues. The fractal dimension did not increase linearly with scale, as it was lowest at D_2 on each analogue, and *Myriophyllum* had the greatest D regardless of scale.

The PCA reduced the structural indices to two components which explained 100% of the variation (Table 2) and indicated a high degree of collinearity, or redundancy, between the indices. We acknowledge this is an unusual result, but note that these results were derived from measures of identical replicates of artificial analogues, so the only variability was between the three shapes. Principal component 1 was most strongly correlated with indices of interstitial space (ISI, Sp/Pr and FFV) and the fractal

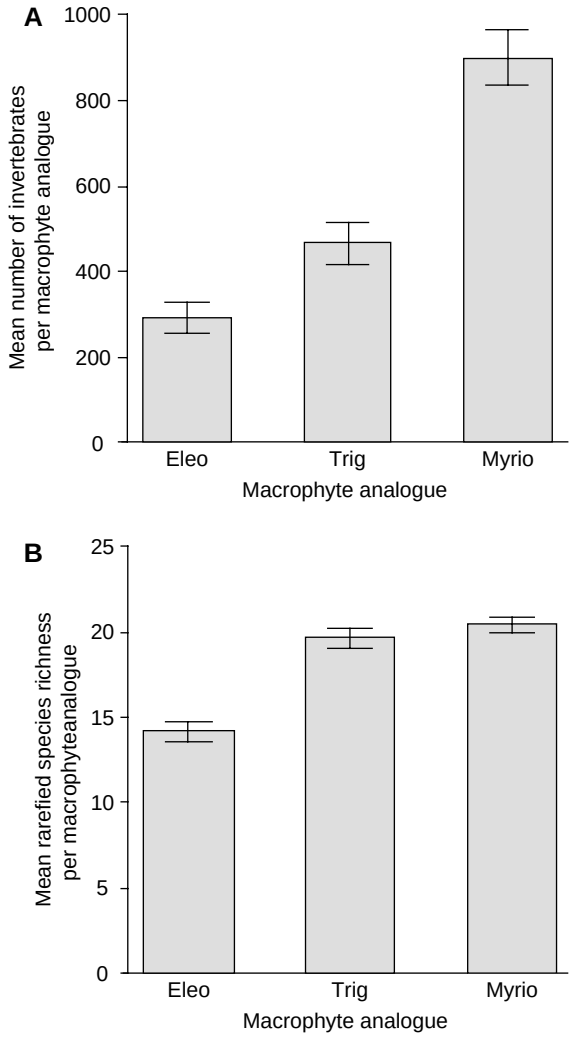

Figure 2. The effect of different macrophyte analogues *Eleocharis*, *Triglochin* and *Myriophyllum*, on (A) the mean abundance of macroinvertebrates, and (B) the mean number of macroinvertebrate taxa ($\pm$ one SE).

dimension at coarser scales (D_3 and D_4), whereas PC2 was highly correlated with indices of whole-plant attributes (SA and PV) and the fractal dimension at fine scales (D_1 and D_2). Plotting the macrophyte analogues in principal component space (Fig. 3) shows that the *Myriophyllum* analogue loads highly on PC1 and low on PC2, indicating its shape is better described by measures of interstitial space and surface convolution at coarse scales, i.e. it has more protrusions into three-dimensional space at these scales. The combination of these indices describes what can be intuitively called a more complex structure. In contrast, the *Eleocharis* analogue loads high on PC2 and low on PC1, indicating it affords little refuge from pygmy perch predation, and is best described by the whole-plant attributes of surface area and plant volume, as well as the surface convolution at fine scales (it is smoother at these scales). Again, this corresponds to an intuitive perception of *Eleocharis'* simple structure. The *Triglochin* analogue lies between *Myriopyllum* and *Eleocharis* in PC space, suggesting it is best described by both components.

The structural indices D_2 and Sp/Pr had the highest number of significant correlations with macroinvertebrate abundance (Table 3). The fractal dimension at $5\times$ magnification (D_2) also had six significant correlations with rarefied species richness, as did the whole-plant attributes of SA and PV, but the Sp/Pr index had slightly fewer (four) significant correlations with species richness.

Discussion

Both the abundance and rarefied species richness of macroinvertebrates increased with macrophyte analogue complexity and were greatest on the *Myriophyllum* analogues. The Sp/Pr and D_2 indices measured the attributes of structure that best related to macroinvertebrate abundance, and species richness was also related to the SA and PV indices and slightly less so to Sp/Pr. This indicates that macroinvertebrates respond not just to the complexity of a surface, but also to the space associated with that surface.

The greater abundance and species richness of macroinvertebrates on *Myriophyllum* than *Triglochin* and *Eleocharis* supports the many studies showing freshwater macroinvertebrates, marine epifauna and terrestrial arthropods are more abundant and diverse in more structurally complex habitats (Heck and Crowder 1991, Jeffries 1993, Jacobi and Langevin 1996, Raizer and Amaral 2001). This pattern is often attributed to the greater surface area of structurally complex plants (Heck and Orth 1980, Stoner and Lewis 1985, Parker et al. 2001), but the similar amount of surface area on *Myriophyllum* and *Triglochin* analogues supports other research which shows that apparently

Table 1. Results of structural indices used to measure each macrophyte analogue.

Structural index	*Eleocharis*	*Triglochin*	*Myriophyllum*
Surface area (cm^2; SA)	246	821	862
Plant volume (cm^3; PV)	43	20	17
Fish-free volume (cm^3; FFV)	0	10	396
Interstitial space index (ISI)	0.50	0.47	18.27
Interstitial space size/predator size (Sp/Pr)	2.59	1.83	0.42
Fractal dimension (D)			
D_1 (7.5 $\times$ magnification)	0.94	1.10	1.17
D_2 (5 $\times$ magnification)	0.86	0.94	1.02
D_3 (2.5 $\times$ magnification)	1.10	1.10	1.32
D_4 (1 $\times$magnification)	1.27	1.09	1.58

Table 2. Loadings of each structural index onto principal components 1 and 2 (after rotation). Higher correlations indicate stronger a stronger association between the index and the component.

Structural Index	PC1	PC2
D_4 (1 × magnification)	1.000	0.030
D_3 (2.5 × magnification)	0.913	0.408
Interstitial space index (ISI)	0.913	0.408
Fish-free volume (cm^3; FFV)	0.904	0.428
Interstitial space size/predator size (Sp/Pr)	0.717	0.698
D_2 (5 × magnification)	0.588	0.809
D_1 (7.5 × magnification)	0.397	0.918
Plant volume (cm^3; PV)	0.212	0.977
Surface area (cm^2; SA)	0.167	0.986
Eigenvalues	4.571	4.429
% variance explained	50.791	49.209

complex plants do not necessarily have a greater surface area (Sher-Kaul et al. 1995) and that faunal abundance is related to different aspects of structure (Brown et al. 1988, Jeffries 1993).

Surface area was, however, strongly related to rarefied species richness, along with plant volume, the fractal dimension at 5 × magnification (D_2), and to a lesser degree, Sp/Pr. This suggests that despite the positive relationship often observed between surface area and species richness (Dean and Connell 1987), macroinvertebrate species richness is influenced by other attributes of surface structure as well. If two habitats have similar surface areas but one has greater structural complexity, thereby creating a greater variety of resources, then that habitat tends to support greater species richness (Douglas and Lake 1994, Schmid 2000). However, given the highly inter-correlated nature of these indices, and to avoid having to use too many different indices when quantifying structural complexity, it would be logical to use the two indices, Sp/Pr and D_2, which are also the most strongly related to macroinvertebrate abundance. It should be noted that the Sp/Pr and D_2 indices which were found to be most strongly related to the distribution of macroinvertebrates in this system may not be the best for describing the abundance of other fauna in different systems. Other indices used here (e.g. plant volume), should not necessarily be discounted and may prove more useful descriptors of faunal distributions in other systems (e.g. boring insects), illustrating the need to understand the biology and ecology of the organisms under investigation.

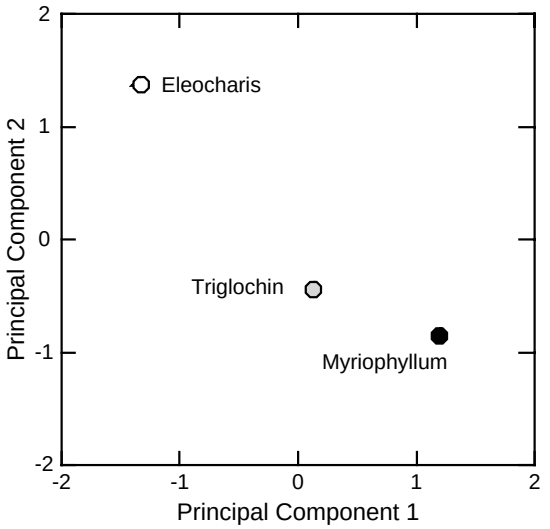

Figure 3. Loading of each macrophyte analogue onto principal components 1 and 2.

The fractal dimension at scale 2 (5 × magnification) was strongly related to both the abundance and rarefied species richness of macroinvertebrates, suggesting that the degree of surface convolution rather than the area is more relevant to how macroinvertebrates use a surface. Fractal dimension has been shown to be a good indicator of habitat structural complexity, with more complex structures having a higher D and supporting more animals (Shorrocks et al. 1991, Jeffries 1993, Beck 1998, Schmid 2000, McAbendroth et al. 2005, Thomaz et al. 2007). The fractal dimension is generally seen as an effective method of describing habitat structure because it is independent of the nature of the habitat and is related to the scale at which the habitat is viewed (Lawton 1986, Gee and Warwick 1994, Schmid 2000). This is illustrated by there being only one of the four scales measured which was strongly related to both the abundance and rarefied species richness of macroinvertebrates among macrophyte analogues, and why D_4 (1 × magnification) was by far the poorest descriptor of structural complexity in relation to macroinvertebrate distribution: it is at a scale too coarse to be relevant to macrophyte-associated macroinvertebrates. If macroinvertebrates are responding to their immediate vicinity then they are unlikely to perceive structural complexity at larger plant or mesohabitat scales (Davenport et al. 1996).

The Sp/Pr was the other index most highly correlated with macroinvertebrate abundance, and was also significantly correlated with rarefied species richness, suggesting that macroinvertebrates respond not just to a complex surface, but the refuge space associated with that surface. Hacker and Steneck (1990) measured the distribution of amphipods on marine macroalgae and also found that the interstitial space associated with plant morphology was as important as the structure itself. These results support the hypothesis that more complex structures have a greater amount of refuge from predation and/or physical disturbance (Heck and Crowder 1991, Dodds and Biggs 2002). Sanson et al. (1995) developed a method to describe the surface structure of stone substrates which modelled the amount of refuge space available to prey at risk from predators of various sizes, illustrating that refuge availability can be more accurately determined by scaling space to the relevant predator size. By scaling the average interstitial gap size to the predator of interest, in this case pygmy perch, the Sp/Pr specifically incorporates information about how the structure is used (Bartholomew et al. 2000). The refuge role of interstitial space associated with complex structures also explains why rarefied species richness was greatest on the *Myriophyllum* analogue. Despite being strongly related to the PC2 indices which best described *Eleocharis*, the *Eleocharis* analogues did not have the refuge space available compared to *Myriophyllum*.

Generally, each index of structural complexity we used to measure the macrophyte analogues was capable of separating between their shapes. For example, the analogue which could intuitively be considered the most structurally

Table 3. Correlations between indices of structure and macroinvertebrate abundance, and species richness (rarefied). The range of correlation coefficient values (across six sites) and the number of significant correlations ($p < 0.01$) with each structural index are provided for both dependent variables.

Structural Index	Macroinvertebrate abundance		Species richness (rarefied)	
	Range of correlation coefficients	No. significant correlations	Range of correlation coefficients	No. significant correlations
Surface area	0.315–0.664	3	0.379–0.786	6
Plant volume	−0.321–−0.685	3	−0.796–−0.379	6
Fish-free volume	0.313–0.761	4	0.097–0.667	3
Interstitial space index	0.311–0.755	4	0.081–0.657	3
Space size/predator size	−0.348–−0.811	5	−0.767–−0.307	4
Fractal dimension				
D_1 (7.5 × magnification)	0.344–0.756	4	−0.183–0.503	2
D_2 (5 × magnification)	0.352–0.802	5	0.351–0.804	6
D_3 (2.5 × magnification)	0.310–0.754	4	0.082–0.658	3
D_4 (1 × magnification)	0.221–0.585	1	−0.177–0.453	0

complex, *Myriophyllum*, consistently had the greatest D at each scale, indicating a higher degree of surface convolution compared to the other analogues, regardless of scale. The fractal dimension did not increase linearly with scale, but was greatest at the coarse scales of D_3 and D_4 (except for *Triglochin*), suggesting that larger animals are likely to perceive the *Myiophyllum* and *Eleocharis* analogues as more complex than smaller animals. The exception was the *Triglochin* analogue which had a similar D at every scale, suggesting a degree of self-similarity over the scales measured and that both large and small animals perceive this surface in a similar manner. Given the flat, blade-like structure of leaves on this shape, it is reasonable to conclude that larger animals perceive this shape as having a less convoluted surface than either of the other two analogues. The whole-plant attributes of SA and PV were also different for each analogue, but they gave relatively similar values for both *Myriophyllum* and *Triglochin*, providing further evidence that a dissected morphology does not necessarily afford more surface area and less volume, and that these measures are insufficient for quantifying structural complexity (Jeffries 1993, Sher-Kaul et al. 1995, Taniguchi et al. 2003). The interstitial space measures indicated that *Myriophyllum* has considerably more refuge space compared to the *Triglochin* and *Eleocharis* analogues. The arrangement of structural elements in the *Myriophyllum* analogue 'split' the interstitial space into numerous small spaces which were more likely to prevent access by the predatory pygmy perch.

While each index was generally capable of separating between the macrophyte analogues, the high degree of correlation between these indices illustrated that not all need to be used to quantify structural complexity. The indices used here were reduced to two components, one component measuring the interstitial space and surface convolution at coarser spatial scales, the other measuring whole-plant attributes (SA and PV) and surface convolution at finer scales. The fact that both components effectively separated the three macrophyte analogues better than either on its own, suggests that as few as two indices could be used to describe differences in macrophyte structural complexity. While Beck (1998) did not assess the collinearity between four indices of structural complexity on a rocky shore, he also concluded that multiple indices should be used to incorporate the many correlated features of habitat structural complexity. Given that the Sp/Pr index and the fractal dimension at 5 × magnification (D_2) load onto both components and can therefore distinguish between the different analogue shapes, we suggest they are a good choice of indices to quantify structural complexity in this system, although the utility of the other indices for other systems should not be discounted.

This research is the first to compare different indices of macrophyte structural complexity and we found no single index effectively described both the shape of the macrophytes and the distribution of the associated macroinvertebrate fauna. Rather, we found the structural indices we tested had considerable redundancy between them such that they could be reduced to two indices (Sp/Pr and D_2) which sufficiently measured surface and space attributes to effectively separate between different macrophyte analogue shapes. These two indices also related to the distribution of the macroinvertebrate fauna, indicating that macroinvertebrates respond to not just surface convolution, but to the refuge space associated with that surface. We point out that while the relationships observed here are correlative, this research provides some direction for future work where elements of habitat structure may be isolated and experimentally manipulated to investigate the effects on community structure and trophic interactions. We suggest the Sp/Pr and D_2 indices are good candidates to be used for quantifying and potentially manipulating habitat structural complexity: they are dimensionless and allow comparison between different habitats, they can be scaled to have relevance to how fauna use their habitat, and they measure both surface and space, both of which contribute to habitat structure.

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