

Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants

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SUMMARY

1. The compound influence of habitat complexity and patch size on stream invertebrate assemblages associated with submerged macrophytes was investigated through field sampling of two natural macrophyte species with contrasting leaf morphologies (complex, *Ranunculus yezoensis*; simple, *Sparganium emersum*) and an experiment with two artificial plants with different levels of morphological complexity.
2. The artificial plant experiment was designed to separate the effects of habitat area (patch size) and habitat complexity, thus enabling a more rigorous assessment of complexity *per se* than in previous studies where only a single patch size was used. Simple and complex artificial plants were established with five different patch sizes corresponding to the range found in natural plants.
3. Invertebrates occurred on both complex and simple forms of natural and artificial plants at similar abundances with dipterans and ephemeropterans being predominant. Taxon richness was higher on structurally complex *Ranunculus* than on simple *Sparganium* and was similarly higher on the complex artificial plant than on the simple one, over the entire range of habitat patch sizes. Thus, architectural complexity affected the taxon richness of epiphytic invertebrates, independently of habitat scale.
4. On the natural plants there was no difference in the abundance (both number of individuals and biomass) of invertebrates between simple and complex forms, while on artificial plants more invertebrates occurred on complex than on simple forms. The amount of particulate organic matter, >225 µm (POM) and chlorophyll *a* showed mixed patterns on natural and artificial plants, suggesting that the availability of these resources is not an overriding proximate factor controlling invertebrate abundance on plants. The difficulty of extrapolating from experimental results involving use of artificial plants is discussed, especially when considering the relationship between habitat structure and the occurrence of epiphytic invertebrates on natural plants.

Keywords: abundance, architecture, diversity, habitat complexity, stream invertebrates

Introduction

Habitat structure plays an important role in determining species diversity, with more physically complex habitats containing more species (Bell *et al.*, 1991). There has been some controversy over what factors characterise complex versus simple habitats and affect the number of coexisting species (Hart & Horwitz, 1991; Tokeshi, 1999). Habitat structure encompasses both qualitative and quantitative

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aspects, the former mainly referring to the relative abundance of different structural elements and latter to the absolute abundance of elements (Bell *et al.*, 1991). A major problem in dealing with the issues of habitat structure concerns the difficulty of identifying structural heterogeneity/complexity relevant to a set of organisms under study.

In aquatic systems the heterogeneous nature of habitat generated by substrate materials, submerged plants and other objects has been known to have a significant influence upon the diversity of invertebrates communities (Bell *et al.*, 1991; O'Connor, 1991; Sebens, 1991; Douglas & Lake, 1994; Cooper *et al.*, 1997). In particular, submerged macrophytes increase the physical complexity of an aquatic environment and provide habitat for colonisation by invertebrates (Heck & Westone, 1977; Crowder & Cooper, 1982; Gregg & Rose, 1982; Tokeshi & Pinder, 1985; Lodge, 1991; Newman, 1991). Macrophyte architecture has a close bearing upon food supply through detritus trapping (Rooke, 1984) and growth of epiphytic algae (Dudley, 1988), consequently leading in some cases to distinct invertebrate communities on different types of macrophyte (Minshall, 1984; Rooke, 1986). Further, macrophytes create patches of various sizes over a streambed, thereby presenting different scales of habitat to invertebrates (Haslam, 1970). Thus, macrophytes are an ideal system to examine the relationship between habitat complexity, scale and the structure of invertebrate communities. However, there have been few experimental studies involving aquatic plants where different aspects of habitat structure were manipulated and their effects on associated invertebrate communities were examined (Jeffries, 1993; Downes *et al.*, 1998, 2000). This is partly because of the difficulty of recognising measures of habitat structure that are practical and comparable across different sets of organisms. Further, two factors, habitat scale and complexity, are often used synonymously in the ecological literature. In some studies on seagrass and associated communities, plant biomass was used as a surrogate measure of habitat complexity, although the appropriateness of such a practice is questionable (Heck & Orth, 1980; Heck & Crowder, 1991; Tolan, Holt & Onuf, 1997; Attrill *et al.*, 2000).

The present study aims to elucidate the effects of macrophyte architectural complexity and patch size on the diversity and abundance of epiphytic invertebrates. We combined field sampling of morphologi-

cally distinct plant species with a colonisation experiment using artificial plants that had different levels of structural complexity and patch sizes.

Materials

Study area

The study was conducted in a 40-m stretch of a second-order stream, the Uenae Stream, a tributary of the Yufutsu River running through the Tomakomai National Forest in northern Japan (42°43'N, 141°36'E). Temperature and discharge of this cold spring-fed stream (3.6–4.8 m wetted width, 0.3% > gradient) were relatively stable at 8–10 °C and *c.* 0.58 m³ s⁻¹, respectively. In the study reach, *c.* 60% of the streambed was covered by patches of macrophytes dominated by *Ranunculus yezoensis* Nakai and *Sparganium emersum* Rehmman.

Sampling of natural macrophytes

Sampling of natural macrophyte beds was conducted in summer 1998. Leaf morphology of these macrophytes differed considerably; *Ranunculus* had a branching stem with subdivided fine-leaves, whereas *Sparganium* had no stem but elongated undivided leaves (Fig. 1). Water velocity was measured at nine equidistant points within a macrophyte stand (three depths at each point, i.e. upper, middle and lower), using a portable current meter (Model CR-7WP, Cosmo-Riken Inc., Kashiwara, Japan). Mean current velocity was greater in *Sparganium* beds than in *Ranunculus* (*t*-test: *t* = 7.16, *P* < 0.001), while the coefficient of variation of current velocity was not significantly different between the two beds (*t*-test: *t* = 1.93, Bonferroni-corrected probability: *P* > 0.05).

A total of 40 (20 each of *Ranunculus* and *Sparganium*) small natural macrophyte stands, ranging in streambed area between 100 and 1250 cm², were sampled together with associated invertebrates. Plants were cut off approximately 3 cm above the streambed and immediately placed in a 225-µm mesh Surber sampler. For the measurement of epiphytic algae, five shoots were selected randomly from each stand after invertebrates were removed and kept in a bucket covered by a black plastic sheet to hinder photosynthesis. The remaining plants and invertebrates were immediately preserved in 5% buffered formalin solution.

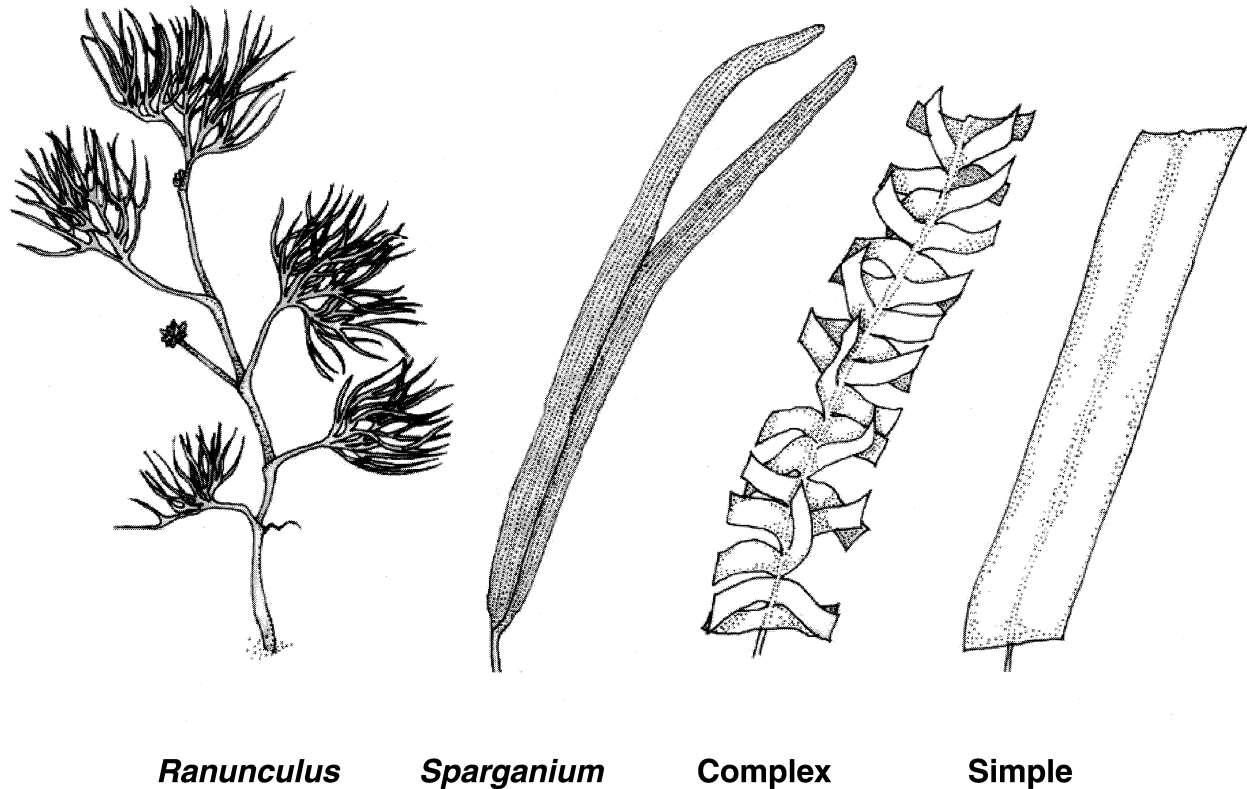


Fig. 1 Two species of natural macrophytes and two types of artificial macrophytes used in the study.

In the laboratory, invertebrates were sorted under a dissecting microscope, identified and counted. In most cases identification was carried out to the species level with some designated as 'morphospecies', while some groups with uncertain taxonomy and/or juvenile larvae could be identified to genus only. Body size of each individual was measured to the nearest 0.05 mm using an ocular micrometer and biomass was estimated using a length-dry weight relationship established for each taxon (H. Miyasaka, Y. Miyake & H. Taniguchi, unpublished data). Detrital material was dried at 60 °C for 24 h, weighed to the nearest 0.01 mg, combusted at 550 °C for 3 h and re weighed to obtain ash-free dry mass (AFDM). Algal biomass was assessed as quantity of chlorophyll *a*, after epiphytic algae were mechanically removed from plants using a toothbrush and by 60-s treatment in a sonic automatic washer. The majority of algae were removed by this process and sonication did not break algal cells. Photosynthetic pigments were extracted in 99.5% ethanol and the solution was measured using a spectrophotometer. The data were converted into the amount of chlorophyll *a* (Unesco, 1969).

Surface areas of natural macrophytes were calculated from their dry weight. Twenty shoots (3–30 cm length) of each species were photocopied after specimens were pressed onto a piece of paper, digitised with an image scanner and the surface area was analysed. Dry weight was obtained after these plant specimens were dried at 60 °C for 24 h. Following Harrod & Hall, 1962), a linear relationship was used to relate surface area to dry weight for *Ranunculus* [A (cm²) = 6.98 + 0.81 W (mg); $r^2 = 0.50$, $F = 18.87$, $P < 0.001$] and *Sparganium* ($A = 18.03 + 1.59 W$; $r^2 = 0.57$, $F = 21.32$, $P < 0.001$).

Experiment with artificial macrophytes

Colonisation experiments were carried out using artificial macrophytes with two levels of structural complexity, simple and complex, having the same surface area (Fig. 1). Both plants were made of two pieces of green plastic tape (0.02 mm thick, 3.6 cm wide, 20 cm length, 144 cm² area) tied by galvanised iron wire. The simple plants were made with intact tapes, whereas the complex ones had cuts of 2 cm

deep at 1 cm intervals along the edge. For both simple and complex plants, nine stands were made with different numbers of leaves (1, 2, 3, 5, 7, 11, 13, 15 and 19 leaves) attached to a wire mesh base of approximately 25 cm in diameter, resulting in different total surface areas. Thus, 18 patterns (two levels of complexity and nine levels of surface area) with five replicates each (i.e. a total of 90) were used in the experiment. In July 1998 all the stands were placed randomly across the study reach and left for 3 weeks. Mean current velocity in the simple patches was not significantly different from that in the complex patches (t -test: $t = -0.60$, $P = 0.552$), while CV of current velocity in the latter was greater than that in the former ($t = 3.77$, $P < 0.001$). Our preliminary study indicated that an experimental period of 3 weeks was long enough for invertebrates to colonise artificial macrophytes (cf. Sozka, 1975). After sampling, artificial plants were processed in the same manner as natural plants in the laboratory.

Data analyses

Data on natural and artificial macrophytes were analysed separately. In this study 'patch' or 'patch size' refer to the total surface area of plants constituting a stand (estimated from dry weight). Six large stands of *Sparganium* which lay outside the size range of *Ranunculus* stands were excluded from analysis. Difference in the amount of algae and detritus available, taxon richness and abundance of invertebrates between the simple and complex type of natural/artificial macrophytes were tested by either a t -test or one-way analysis of covariance (ANCOVA), depending on the nature of relationships between these variables and patch size (surface area) of macrophytes. ANCOVA was applied only where the homogeneity of residual variances and of regression slopes were confirmed. Probabilities for significance judgement were adjusted by Bonferroni corrections with reference to substrate types (natural/artificial and simple/complex) and the nature of variables (resource quantity and animal abundance measures) to attain values corresponding to $P = 0.05$ in a single test: consequently, for differences in resource quantity (detritus and algae on each substrate) and in animal abundance, respectively, $P = 0.025$ and 0.0166 were used as a critical level of significance, while non-significant values were simply indicated as $P > 0.05$

(in the Results) to avoid confusion. Data were log transformed where necessary to satisfy the assumptions of t -test and one-way ANCOVA. Data on species abundance patterns were analysed with reference to two niche-apportionment models, the Random Fraction and the MacArthur Fraction model (*sensu* Tokeshi, 1990, 1993). The Random Fraction model represents a sequentially random allocation of abundances among taxa and has been found to fit freshwater chironomid assemblages (Tokeshi, 1990; Fesl, 2002), while the MacArthur Fraction model represents another sequential process that generates the same result as the simultaneous breakage (Broken Stick) model, leading to a more equitable distribution of abundances [for general reviews of niche-apportionment models, see Tokeshi (1993, 1999)].

Results

Ranunculus harboured a larger number of invertebrate taxa (54) than *Sparganium* (45), with the numerical dominance of Diptera (61 and 82% on *Ranunculus* and *Sparganium*, respectively) and Ephemeroptera (18 and 11%). The assemblage on *Ranunculus* showed a slightly more equitable pattern of relative abundance than that on *Sparganium* in terms of both the number of individuals and biomass (Fig. 2 left). On artificial macrophytes comparable total numbers of taxa occurred on complex and simple plants (55 and 53, respectively), with similar patterns of relative abundance (Fig. 2 right). In common with natural plants, the associated fauna were numerically dominated by Diptera (58 and 49% on complex and simple plants, respectively) and Ephemeroptera (19 and 30%). Thus, when all samples were combined and patches differences were ignored, species abundance patterns of invertebrates were quite similar on complex and simple artificial plants and approximated by Random Fraction model, while the difference in pattern was apparent on the two natural plants and each curve showed a distinct pattern approximated by neither MacArthur Fraction model nor Random Fraction model.

Taxon richness, number of individuals and biomass of invertebrates scaled positively with patch size on artificial plants ($P < 0.001$), but not on natural plants (all $P > 0.05$) (Fig. 3). Number of taxa was significantly higher on *Ranunculus* than on *Sparganium* ($t = 4.53$, $P < 0.001$), while there were no significant differences in terms of the number of individuals and

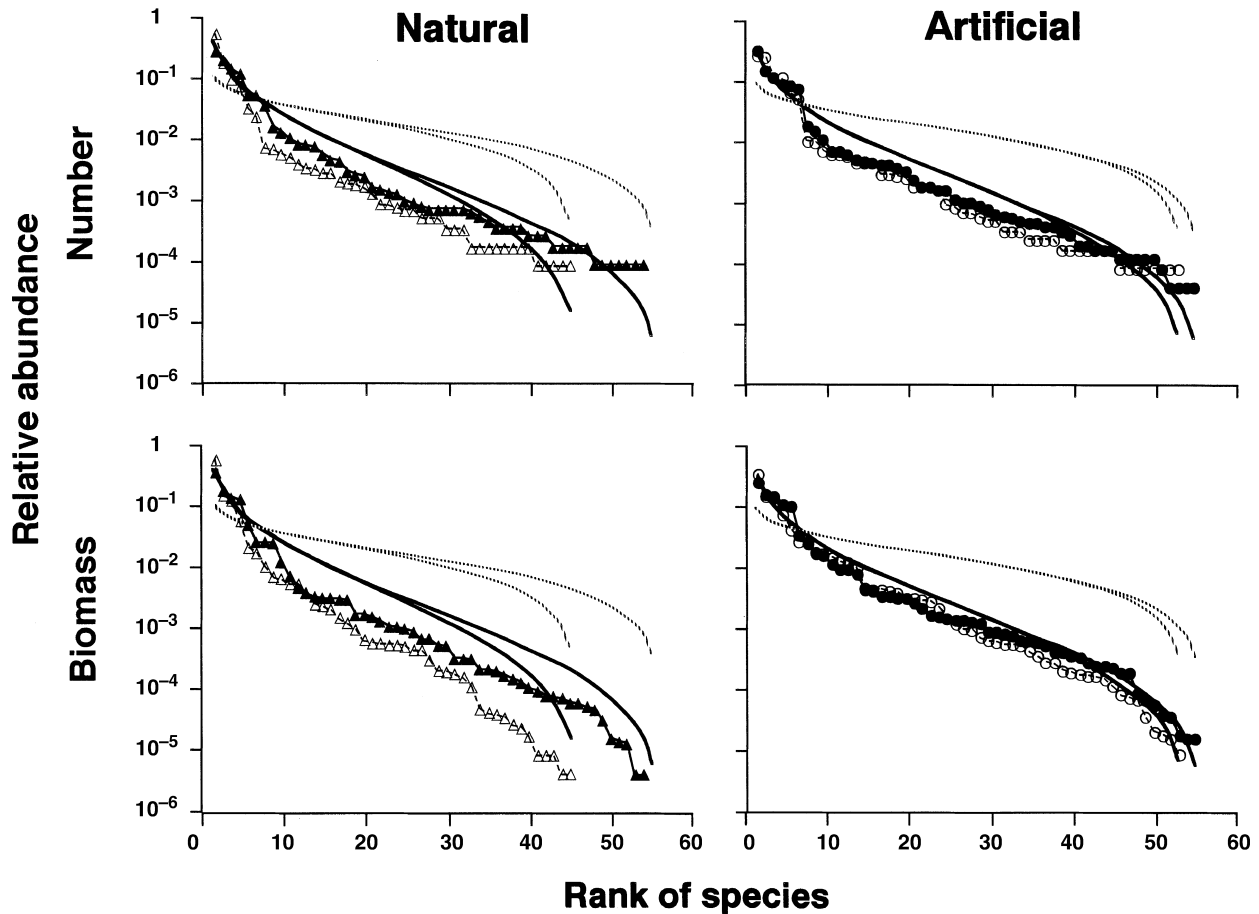


Fig. 2 Patterns of relative abundance of benthic invertebrates on natural plants (▲, *Ranunculus*; △, *Sparganium*) and artificial plants (●, complex; ○, simple). Upper diagrams are for number of individuals and lower ones for biomass. Fitted lines represent the MacArthur Fraction Model (broken lines: the upper one for *Ranunculus*/complex plants and the lower for *Sparganium*/simple plants) and the Random Fraction Model (continuous lines: the upper for *Ranunculus*/complex plants and the lower for *Sparganium*/simple plants).

biomass (number of individuals; $t = 1.08$, $P = 0.29$; biomass, $t = -0.03$, $P = 0.96$). On artificial plants, ANCOVA revealed that y -intercepts were greater in complex plants than in simple ones with respect to all three measures of invertebrate abundance (taxon richness, $F_{1,87} = 81.46$, $P < 0.001$; number of individuals, $F_{1,87} = 37.18$, $P < 0.001$; biomass, $F_{1,87} = 21.68$, $P = 0.001$), while there was no significant difference in the slope of the regressions (all $P > 0.05$).

Taxon richness expressed as per unit number of individuals was not significantly different between *Ranunculus* and *Sparganium* ($t = 0.09$, $P = 0.93$), but on artificial plants the value was higher on complex plants than on simple ones ($t = 3.46$, $P = 0.01$) (Fig. 4).

The amount of potential food resources for invertebrates, POM and chlorophyll *a*, showed variable

patterns on natural and artificial plants (Fig. 5). The amounts of POM and chlorophyll *a* were not significantly different between *Ranunculus* and *Sparganium* (POM, $t = -1.56$, $P = 0.13$; chlorophyll *a*, $t = 0.29$, $P = 0.78$). On *Ranunculus* POM was positively related to patch size, while on *Sparganium* chlorophyll *a* did so ($P < 0.0125$). On artificial plants, the amounts of both POM and chlorophyll *a* scaled positively with patch size ($P < 0.001$) with slopes for complex and simple plants not showing a significant difference ($P > 0.05$ for both POM and chlorophyll *a*). The amount of POM was significantly greater on complex plants than on simple ones (ANCOVA; $F_{1,87} = 14.93$, $P = 0.001$), while the opposite was true for the amount of chlorophyll *a* ($F_{1,88} = 33.85$, $P < 0.001$).

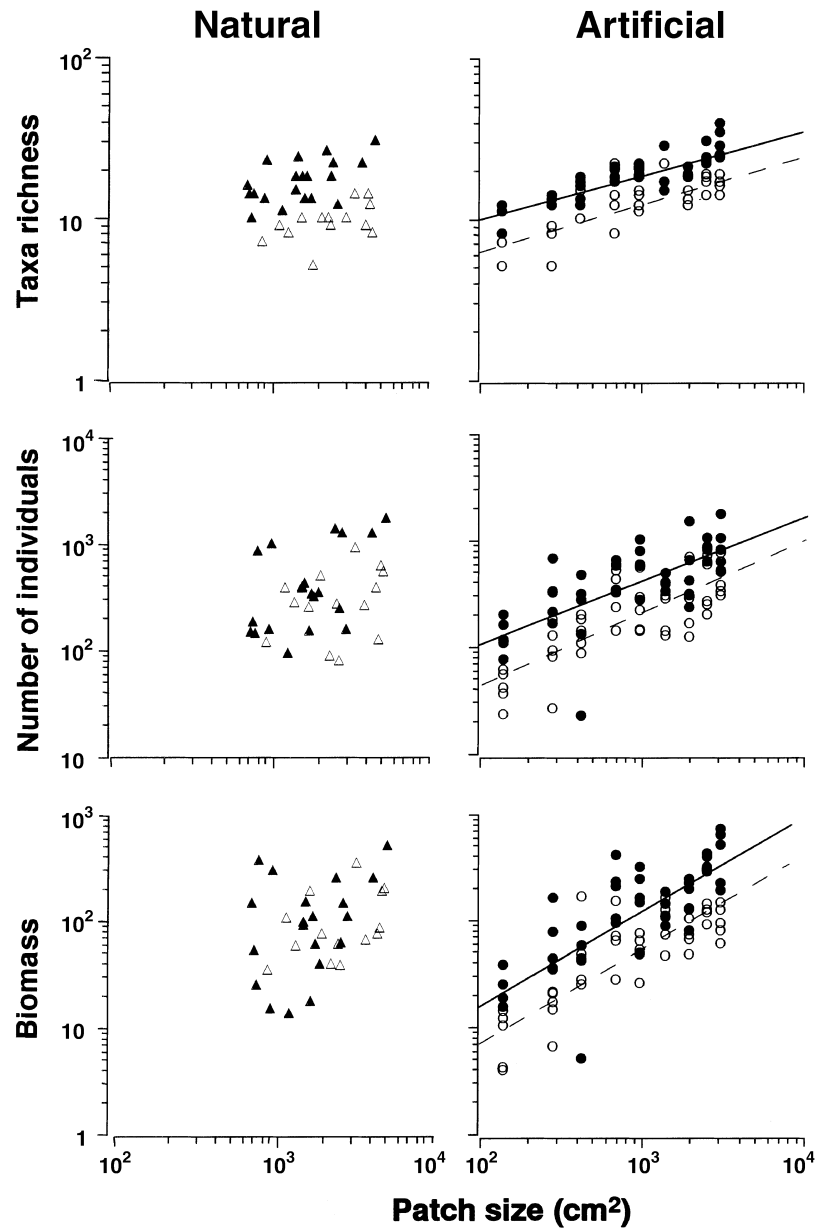


Fig. 3 Relationship between habitat patch size (plant surface area, horizontal axis) and taxa richness (top), number of individuals (middle) and biomass (bottom) in epiphytic communities on natural (▲, *Ranunculus*; △, *Sparganium*) and artificial (●, complex; ○, simple) plants. Regression lines were drawn where significant. Taxa richness: complex, $y = 0.45 + 0.27x$, $r^2 = 0.74$; simple, $y = 0.22 + 0.30x$, $r^2 = 0.67$. Number of individuals: complex, $y = 0.31 + 0.67x$, $r^2 = 0.60$; simple, $y = 0.91 + 0.57x$, $r^2 = 0.48$. Biomass: complex, $y = -1.02 + 1.95x$, $r^2 = 0.62$; simple, $y = -1.74 + 1.92x$, $r^2 = 0.67$.

Discussion

Previous studies on the relationship between habitat complexity and animal assemblages have included the increased surface area of physical structures as part of 'complexity' (Krecker, 1939; Rosine, 1955; Heck & Westone, 1977). The problem of not explicitly separating the effect of area from complexity is that the latter tends to lose its independent existence; there will be less sense in using the ambiguous term 'complexity' if a large part of it is definable/replaceable

as area. Under such circumstances the study of complexity-animal abundance/richness relationships would essentially converge on that of classical species-area relationships (see Hart & Horwitz, 1991; Rosenzweig, 1995) and consequently make it difficult to gain new insights into the effects of complexity *per se*. In the present study, habitat complexity is interpreted to refer different morphologies and numbers of physical structures of a habitat. As such, habitat complexity does not include area and is also distinct from habitat 'heterogeneity' (see Tokeshi, 1999), as the

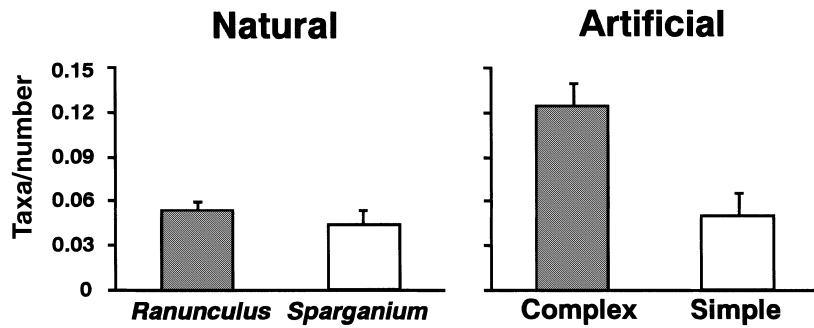


Fig. 4 Taxa density (number of taxa per individual) on natural and artificial plants.

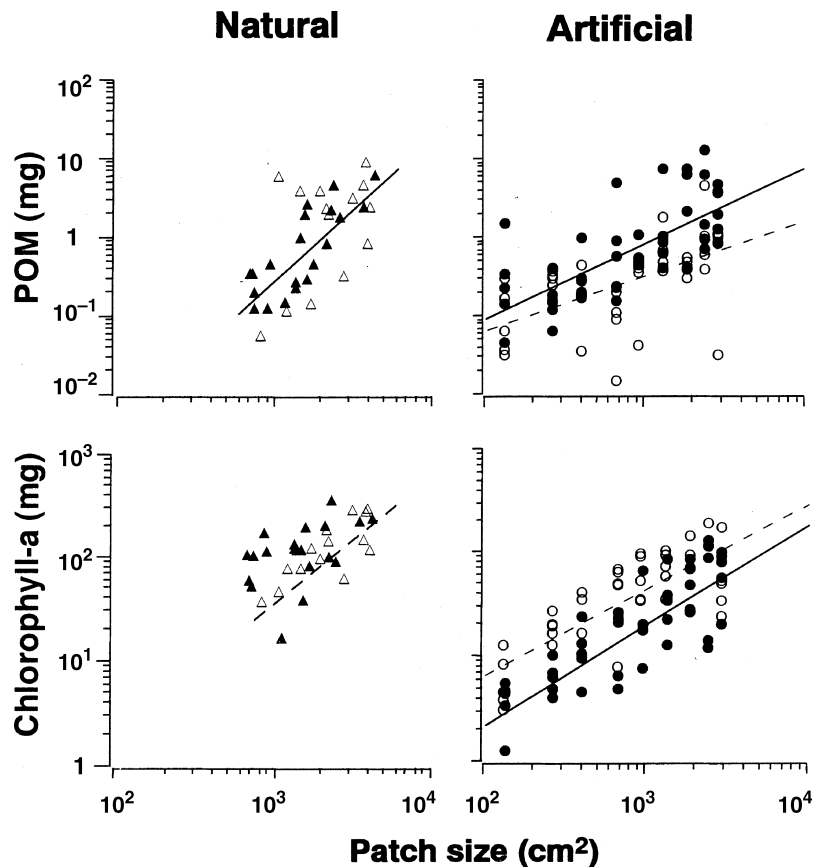


Fig. 5 Relationship between habitat patch size and amount of POM and algal biomass (chlorophyll *a*) on natural plants (\blacktriangle , *Ranunculus*; \triangle , *Sparganium*) and artificial plants (\bullet , complex; \circ , simple). Regression lines were drawn where significant. POM: *Ranunculus*, $y = -2.36 + 0.817x$, $r^2 = 0.63$; complex, $y = -1.69 + 1.17x$, $r^2 = 0.56$; simple, $y = -1.23 + 1.00x$, $r^2 = 0.44$. Chlorophyll *a*: *Sparganium*, $y = 1.19 + 0.83x$, $r^2 = 0.77$; complex, $y = 0.44 + 0.96x$, $r^2 = 0.67$; simple, $y = 1.18 + 0.82x$, $r^2 = 0.65$.

latter is only concerned with the number of different kinds of structures while the former encompasses both number and morphological characteristics.

While there may always remain uncertainty over what constitutes habitat complexity in a particular ecosystem, researchers working on benthic invertebrate assemblages often used the surface architecture of hard substrate as a medium with which to generate or modify levels of complexity. This included, for example, marking grooves on logs or

stones/bricks (O'Connor, 1991; Douglas & Lake, 1994) and making cuttings in artificial plant sheets (Jeffries, 1993), implying that an increased proportion of edges against area/volume of substrate was taken as increased habitat complexity in these systems. Further, some researchers regarded an increased amount of algal growth on hard substrates as increased habitat complexity (Kohler, 1992; Downes, Lake & Schreiber, 1995). Complexity being thus interpreted, these studies generally found that a

higher number of invertebrate taxa occurred in more complex habitats (Dean & Connell, 1987; Douglas & Lake, 1994; Downes *et al.*, 1998). In contrast, Attrill *et al.* (2000) showed that for invertebrates associated with seagrass beds, species richness was not correlated with a complexity measure which was derived from a combination of morphological characteristics of *Zostera* beds.

The present study has demonstrated that greater architectural complexity of habitat led to a higher number of macroinvertebrate taxa on both natural and artificial macrophytes, while habitat patch size varied (Fig. 3, top). In previous studies where habitat complexity was experimentally manipulated, analyses were based on a single patch size [e.g. artificial plants in Jeffries (1993) and grooved logs in O'Connor (1991)]. In this respect the present study adds an extra dimension to this line of investigation by explicitly incorporating variable patch sizes. Thus, the observation that a larger number of invertebrate taxa occurred on complex artificial plants than on simple ones was scale-independent, at least over the range of patch sizes examined here. At the same time these results also demonstrate the existence of a relationship superficially akin to species-area relationship in macrophyte-associated assemblages. The scaling of taxa number versus area was apparent in the two kinds of artificial plants. A similar observation was made with invertebrates associated with seagrasses: the number of taxa was positively related to the amount (biomass) of *Zostera* plants (Attrill *et al.*, 2000). There is, however, a notable difference between these (small-scale) cases and biogeographic species-area relationships in that the former include only one type of habitat over a limited range of spatial scale. Nevertheless, the conceptual similarity of the present analysis to a general theory of species-area relationship makes it worthwhile to discuss related issues.

In explaining variation in species-area relationships, Wright (1983) suggested that different levels of productivity (which is dependent on energy availability) per unit area in different regions may be responsible for generating such variability. From this point of view, regression lines with different intercepts as observed for a comparison of simple/complex plants in the present study may be interpreted to represent distinct groups of assemblages based on different levels of energy supply. In aquatic benthic studies,

'energy availability' is often equated with primary productivity of algae and/or variation in benthos diversity, and abundance has been related to algal abundance. This raises a question as to what exactly are the mechanisms that generate the observed differences in invertebrate taxon richness and abundance between simple and complex habitats.

The fact that there was no significant difference in the amount of detritus (POM) or algae (chlorophyll *a*) between *Sparganium* and *Ranunculus* (Fig. 5) indicates that the availability of these (potential) resources was not the cause for the observed difference in the number of invertebrate taxa between the two natural plants. This suggests that either (i) the energy-area theory is not an appropriate explanation for the patterns shown by invertebrates of natural macrophytes, or (ii) energy or resources cannot adequately be represented by detritus/algae attached onto the plants. Even if the latter statement is true, however, as there is no other apparent factor representing 'energy' in the system under study, the energy-area theory cannot be invoked with confidence in the present study. On the other hand, there is an indication that the amount of chlorophyll *a* may partly explain the variation in invertebrate taxon richness among different-sized patches of *Ranunculus*.

Interestingly, in the case of artificial plants, there was a conflicting picture where POM and chlorophyll *a* showed opposite trends: the former was more abundant on complex than on simple plants while the latter was more abundant on simple plants (Fig. 5, Artificial). This may suggest that detritus was the main factor contributing to the difference in taxon richness between simple and complex artificial plants; this would pose a further question as to why the same does not apply to the comparison between simple and complex natural plants. Thus, the mixed results presented here caution against a general, simplified interpretation of habitat complexity–invertebrate relationships.

It may be suggested that in the case of essentially simple, identical habitat/substrates such as logs, bricks and plastic plants, an addition of 'extra surface/edge structures' in the form of grooves and cuttings would greatly increase the heterogeneity of habitat (from the very low level of 'bare structure'), thereby rendering the habitat exploitable by more invertebrate taxa. In the case of natural plants, however, apart from leaf morphologies, there are

many other factors which are different among plant species (e.g. surface texture, posture and pattern of undulatory movement in water currents, the rates of leaf growth and senescence, release of allelopathic and other chemical substances) and could affect the abundance of associated invertebrate taxa. This is considered the main reason why experiments with artificial rather than natural substrates tend to demonstrate a clear pattern of difference between simple and complex structures. It is also notable that species abundance patterns were similar on simple and complex artificial plants, while different patterns were demonstrated on natural plants. These observations together suggest that architectural complexity of habitat can only partially explain differences in the taxon richness of invertebrate assemblages associated with different plant species. Nevertheless, it is considered important to recognise that 'edgy structures' are often preferably used by many benthic invertebrates associated with solid substrata such as rocks, stones and submerged plants, presumably because those structures tend to provide a better anchor to attaching invertebrates and/or protect them from being swept away by turbulent currents and from potential predators.

The present study has also demonstrated a tendency that the number of taxa per individual ('taxa density') is higher on complex than on simple substrates, particularly artificial plants. This indicates that the elevated taxon richness on complex plants is not simply attributable to a 'sampling effect' (a larger number of individuals being sampled leading to a larger number of taxa (Dean & Connell, 1987), implying no qualitative difference in (the effects of) habitat structure); it should be noted here that such a sampling effect must also have occurred in the present case, as a larger number of invertebrate individuals occurred on artificial plants with more complex structures. However, if a sampling effect was predominant, no difference in the number of taxa per individual would have been expected between simple and complex habitats. Therefore, the present result adds further to the argument that complex habitats contain more structural heterogeneity (=qualitative differences) which different invertebrate taxa could exploit. Thus, it is not the increased quantity of habitable space or food resources that has contributed to a higher taxon richness in more complex habitats but the diversity or heterogeneity of habitable space

that is considered most important for epiphytic invertebrate assemblages. On the other hand, it is notable that this pattern was only discernible in artificial plants, while natural plants presented a more complex picture. Within the range of patch sizes examined, neither taxon richness nor number of individuals scaled with patch size on natural plants, but a higher taxon richness was registered on *Ranunculus* than on *Sparganium*. Although there was no statistically significant difference in the number of invertebrate individuals on the two plants, there was a tendency that some *Ranunculus* patches harboured a higher number of individuals, suggesting that equitable taxa density on the two plants has probably resulted from coupling of individual abundance and taxon richness on some *Ranunculus* stands. Incidentally, this also seems to indicate that complexity in natural plants is variable and subtly affect invertebrate abundances.

In conclusion, the present study on benthic invertebrates associated with submerged plants has demonstrated that architectural complexity of habitat affects invertebrate taxon richness, independently of variation in habitat area and that this cannot adequately be explained by either the sampling effect alone or by the availability of potential food resources. This points to the importance of the physical complexity of habitat *per se* for colonising invertebrates, the details of which remain to be investigated further.

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