Effects of habitat complexity on benthic assemblages in a variable environment

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SUMMARY

1. Habitat complexity is thought to exert a significant influence on ecological communities, but its operation under variable natural conditions is not well understood, particularly in freshwater. To elucidate the role of habitat complexity, in particular the fractal structure of surface irregularity, in a stream system, field colonisation experiments were conducted at three times of year (summer, winter and spring) using natural substrates with different levels of fractal dimension in a small coastal mountain stream of southern Japan.

2. In the winter experiment, comparison was also made between the standard (control) treatment and the resource-preconditioning treatment whereby experimental plates were conditioned in the natural stream environment to allow the accumulation of potential food resources (algae and detritus) for 1 month prior to the experiment.

3. Species abundance patterns observed at different times of year showed little systematic variation with levels of habitat complexity but largely followed the patterns expected from, or lying in between, the Random Assortment model and the random fraction model.

4. Taxon richness and density increased with habitat complexity in all seasons except for density in spring. Different taxa showed different patterns of change with habitat complexity, which also varied with seasons. Biomass of invertebrates showed no systematic trend with an increase in habitat complexity.

5. Chlorophyll-a concentrations tended to be lower in more complex habitats, particularly in summer. In contrast, fine particulate organic matter (FPOM) tended to increase with habitat complexity. However, the relationship between these potential food resources and invertebrate assemblages remain unclear.

6. While there were no significant differences in taxon richness and biomass of invertebrates between the resource-preconditioning and the control treatment, density was higher in the former than in the latter. The abundance of relatively large, surface-dwelling animals showed more marked temporal variation over the entire period of colonisation in the resource-preconditioning treatment than in the control treatment.

7. Body size of invertebrates tended to decline with fractal complexity, indicating that crevice sizes could affect habitat use by benthic animals of different sizes. In addition, body size was larger in the resource-preconditioning treatment than in the control treatment, suggesting that body size in invertebrate assemblages was controlled by a mixture of factors. Thus, the present study demonstrates that habitat structure affects benthic invertebrate assemblages in a complex manner.

Keywords: body size, fractal dimension, habitat structure, species abundance patterns, stream invertebrates, temporal variation

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Introduction

A large body of work, both theoretical and empirical, has been undertaken to investigate how species diversity is controlled in different communities (Tokeshi, 1999). In particular, habitat structure has been thought to play an important role in determining diversity, with more physically complex habitats supporting greater species richness than simple ones (Menge & Lubchenco, 1981; Underwood & Chapman, 1989; Bell, McCoy & Mushinsky, 1991). Despite the popularity of this idea, there has been a limited number of studies in which this was tested in a rigorous manner, due partly to the technical difficulty of quantifying habitat structure and the complicated manner in which supposed habitat complexity affects biotic communities.

In stream systems, habitat complexity generated by surface irregularities such as pits, crevices, moss and other projections, has been recognised to exert a significant influence on the abundance and diversity of benthic invertebrates (Dudley & D'Antonio, 1991; Douglas & Lake, 1994; Downes, Lake & Schreiber, 1995; Robson & Barmuta, 1998). Surface features are important because they could affect food supply such as epiphytic algae (Dudley, Cooper & Hemphill, 1986) and detritus (O'Connor, 1991; Douglas & Lake, 1994), and generate 'refuges' from high flow conditions and mobile predators (Crowder & Cooper, 1982; Palmer *et al.*, 1996; Resh *et al.*, 1998; Lake, 2000). Stream habitats are also subject to temporally variable conditions such as algal growth in spring and litter fall in autumn affecting food availability (Dudley & D'Antonio, 1991; Downes *et al.*, 2000) and seasonal spates having negative impacts on invertebrate assemblages (Giller, Sangpradub & Twomey, 1991; Resh *et al.*, 1998; Lake, 2000). While these marked temporal changes provide excellent opportunities for assessing how habitat complexity influences the diversity of stream assemblages under variable conditions, there have been few studies in which experiments were conducted in more than one season (Robson, 1996).

As there is no fixed approach to quantifying habitat complexity, the majority of previous experimental studies on benthic communities relied on categorical classifications of substrate characteristics such as 'rough versus smooth' and 'gap versus no gap'. With such an 'all-or-nothing' design of habitat complexity,

the presumed 'effect' of habitat complexity may be easily detected; this, however, cannot provide accurate information on how complexity affects assemblages. On the contrary, increasing attention has been paid to the concept of fractal geometry that allows the quantification of some aspects of habitat complexity as a continuous variable and is applicable to a variety of types of habitats, (e.g. tree branches for insects – Morse *et al.*, 1985; mussel beds for marine benthos – Commito & Rusignuolo, 2000; submerged macrophytes for freshwater invertebrates – Jeffries, 1993; see Schmid's (2000) excellent review on the application of fractal concepts to benthic ecology). Despite this background, little experimental work has been undertaken involving fractal approaches in freshwater benthic research, apart from Jeffries' (1993) work.

The objective of the present study was to elucidate the effect of one component of habitat complexity, namely the fractal structure of surface irregularity, on stream invertebrate assemblages in a seasonally variable environment. To overcome some of the problematic issues described above, attempts were made to generate gradually changing levels of habitat complexity rather than adopting an 'all-or-nothing' design, using the same substrate material as found in the field. The field experiments were also repeated at different times of year under different hydrological regimes. Furthermore, the effect of resource conditioning was independently assessed by introducing a resource-preconditioning treatment in addition to the standard treatment. The combination of these experimental approaches has allowed a more rigorous examination of the effects of the some aspects of habitat complexity on stream benthic communities than have been attempted to date.

Methods

Study area

The study was conducted in a 150 m stretch of a small coastal mountain stream, the Kamitsu-Futae Stream, in the Amakusa Shimoshima Island, southern Japan (32°32′N, 130°02′E). The water temperature of this subtropical stream was relatively stable (summer, 12–15 °C; winter and spring, 8–12 °C), while rainfall fluctuated markedly during the typhoon season (June to November), a typical climatic situation in temperate-subtropical East Asia (Fig. 1).
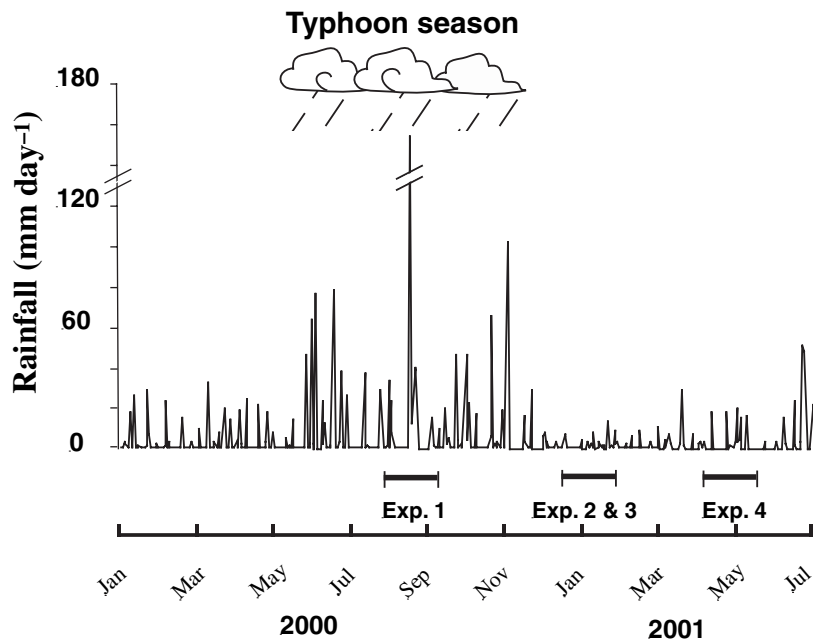
In this system, high discharge events were typically flashy and caused substantial physical disturbance to the streambed. The streambed had a rocky base (predominantly serpentinites of the Miocene or younger origin) on which stones of various sizes were scattered (dominant size: 20–30 cm in largest dimension). The riparian vegetation was character-ised by temperate-subtropical broadleaved trees with the Japanese green oak (*Quercus glauca* Thunberg) being the most dominant. The study site was heavily shaded by these trees with no growth of submerged macrophytes. No scientific work has been previously undertaken in this stream.

Experimental design

Field experiments were carried out using experimen-tal plates with a set of fractal designs in summer, winter and spring. The plates were cut out from natural serpentinite stones, which were of the same material as the streambed. Five levels of complexity were created with stone squares of different sizes (10 × 10 cm, 5 × 5 cm, 2.5 × 2.5 cm, 1 × 1 cm, all of 0.3 cm thick) attached to a basal plate (20 × 20 × 1 cm) such that the total upper surface area remained constant (400 cm^2) while increasing numbers of cav-ities with decreasing cavity sizes were formed (Fig. 2). Fractal dimension, calculated by the grid method

(Williamson & Lawton, 1991), ranged from 1.12 at level 1 (the least complex design) to 1.81 at level 5 (the most complex design). In each experiment, a total of 60 experimental plates (12 replicates for each of five complexity levels) were placed on the streambed randomly and animals on the surfaces of plates were counted *in situ* at 4-day intervals for 36 days using a viewing box. Note that these in situ counts refer to large individuals (>3 mm in overall size) only, which were recognisable by eye without removing the experimental plates in the field. For the resource-preconditioning experiment in winter, a total of 30 experimental plates (six replicates for each level of complexity) were placed on the streambed 1 month before the start of the experiment to allow the accumulation of algae and detritus. These were then recovered and all visible invertebrates were removed by hand before reintroducing the plates to the stream. The preconditioning experiment was conducted at the same time as the winter experiment [i.e. with standard (non-precondition) plates].

On the last day of the experiments, plates were retrieved and invertebrates and particulate organic matter were washed into a 125 μm mesh Surber sampler by gently rubbing the plate surface with the fingers. Remaining invertebrates, often with their tube cases and/or nets attached to plates (mainly midge and caddis larvae), were picked off using tweezers.
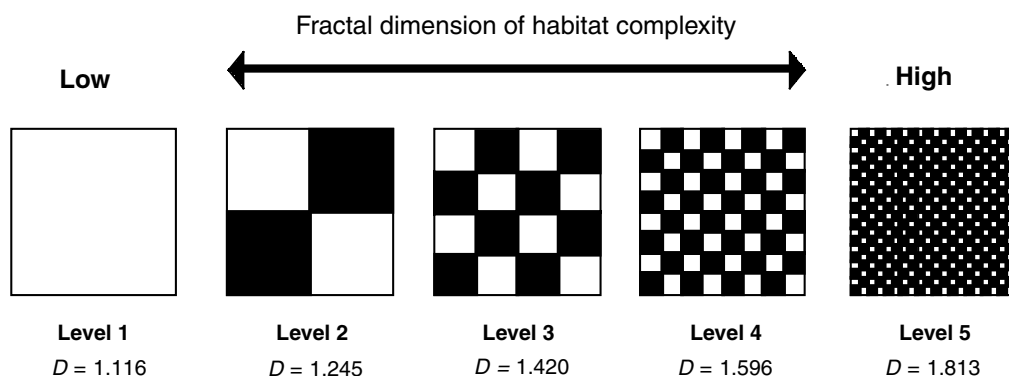
Fractal dimension of habitat complexity

Low   ⟵⟶   **High**

Level 1	Level 2	Level 3	Level 4	Level 5
$D = 1.116$	$D = 1.245$	$D = 1.420$	$D = 1.596$	$D = 1.813$

Fig. 2 Five designs of experimental plates (top view). Raised parts are shown in black. D indicates fractal dimension.

These samples were immediately preserved in 70% alcohol. Algae were removed from the top surface of each experimental plate using a toothbrush and kept in an aluminium-coated polythene bag. These were transported in a cool box (approximately 5 °C) and immediately preserved in a freezer (−15 °C) in the laboratory until analysis. During the summer experiment, a heavy spate (rainfall of 164 mm day^{-1}, the highest value recorded for this year) destroyed 11 plates and replications were reduced. No plate was lost in the winter and spring experiments.

In the laboratory, invertebrates were separated from particulate organic matter, and identified and counted under a dissecting microscope. In most cases identification was carried out to the species level with some designated as 'morphospecies' (Chironomidae in particular), while some groups with uncertain taxonomy and/or young instar 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). Particulate organic matter was divided into fine matter (<1 mm; hereafter FPOM) and coarse matter (>1 mm; hereafter CPOM) and dried at 60 °C for 24 h, weighed to the nearest 0.01 mg, combusted at 550 °C for 5 h and reweighed to obtain ash-free dry mass (AFDM). To estimate algal biomass, scraped algae samples were filtered onto Whatman GF/C filters and photosynthetic pigments were extracted in 99.5% ethanol. These solutions were measured using a spectrophotometer and algal biomass was assessed as the amount of chlorophyll-a (Unesco, 1969).

Data analysis

Variation in different community measures (taxon richness, number and biomass of individuals, chlorophyll *a*, FPOM and CPOM) in relation to habitat complexity as expressed by fractal dimensions was examined by linear regression analysis. Linear regression was adopted not because an underlying pattern of change was assumed to take a linear form but because (i) detection of a simple increasing/decreasing trend, irrespective linearity/non-linearity, can be most efficiently achieved by linear regression, and (ii) data with a total of five levels of fractal dimension are too coarse for a reliable detection of non-linearity including peaked patterns, given naturally large variability in measured values. Differences in the community measures between the resource-preconditioning and the control treatments (winter) were tested by either a *t*-test or one-way analysis of covariance (ANCOVA), the latter being applied only where regression lines were significant. Data on taxon richness and number of individuals were log transformed where necessary to satisfy the assumptions of statistical tests. Variation in body size of invertebrates in relation to habitat complexity was also examined by linear regression analysis.

Data on relative abundance patterns were analysed with reference to two niche-apportionment models, the random fraction and random assortment models (*sensu* Tokeshi, 1990, 1993). These two models were chosen as they often appeared to fit abundance patterns of stream invertebrate assemblages which are under the strong influences of supposedly stochastic factors such as immigration and disturbance (Tokeshi, 1990, 1999; Schmid, 1997; Fesl, 2002). The

random fraction model represents random allocation of abundances among taxa, while the random assortment model represents no or little interaction among existing species, due mainly to unfilled total niche space [for general reviews of niche-apportionment models, see Tokeshi (1993, 1999 and Magurran (2003)]. In the present analysis, the models were used simply as a benchmark for general comparison rather than for a model-fitting exercise, as the abundance data were usable only as an unreplicated, amalgamated data set for each experimental trial. For model calculations, see Tokeshi (1990) and Magurran (2003).

Results

Faunal composition and relative abundance patterns

A total of 44 taxa and 15 813 individuals were recorded from the samples collected at the end of each experimental trial; faunal composition is shown in the Appendix. Taxon richness was higher in summer (29) and spring (27) than in winter (control plates, 22; resource-preconditioning plates, 19), while number of individuals and biomass were higher in spring than in summer and winter. Ephemeropterans were dominant (in terms of both number and biomass) in all experimental trials. Marked seasonal variation in abundance was apparent in some taxa, including *Paraleptophlebia westoni* Imanishi, *Goerodes* sp. and *Simulium* spp.

Relative abundance patterns demonstrated some seasonal variation, but largely lay within the patterns expected of the random assortment model and the random fraction model (Fig. 3). In summer, assemblages at all (except the highest) levels of complexity had similar patterns of relative abundance, mostly following the random assortment model. The assemblage associated with the highest level of complexity showed a more equitable pattern approaching the random fraction. Patterns in winter seemed to depart more from the random assortment, while the assemblages in the resource-preconditioning treatment showed different patterns, with less difference among complexity levels and largely following the random assortment. The spring data also demonstrated indistinct differences among different levels of complexity and appeared to approach the random fraction (particularly assemblages at the two high levels of complexity).

Colonisation patterns

Temporal patterns of colonisation of large invertebrates varied greatly among habitat complexity levels within a season and across the three seasons (Fig. 4). In summer the colonisation process was disrupted by a particularly strong spate on day 20 that set assemblages at all five levels of complexity to near zero. Interestingly, basically the same pattern of colonisation emerged before and after the spate, with visible invertebrate densities closely scaling with the levels of habitat complexity. Differences among complexity levels were most pronounced before the spate with the greatest density being achieved at the highest complexity level.

The pattern in winter was similar to summer in that invertebrate density was highest on the most complex plates, while differences in density were less clear among lower levels of complexity. Comparing this with the resource-preconditioning treatment, the latter had a more marked temporal variation and larger differences among different complexity levels.

The spring pattern was similar to winter but slightly more variable; again density was largely related to complexity levels, with the highest and lowest density coinciding with the highest and lowest level of complexity, respectively.

Invertebrate assemblages, resources and habitat complexity

Three community measures, taxon richness, density and biomass of individuals, showed varied patterns in relation to habitat complexity (Fig. 5). Taxon richness increased with fractal dimension in all three seasons, while the trend was insignificant in the winter resource-preconditioning treatment. Density was markedly higher in spring than in other seasons; it showed an increasing trend with habitat complexity in summer and winter but not in spring. In contrast, biomass showed no systematic variation with complexity levels in any of the experiments, including the resource-preconditioning treatment. Comparing the resource-preconditioning with the control treatment in winter, invertebrate density was significantly higher (ANCOVA, y-intercept, $F_{1,83} = 2.89$, $P < 0.05$) in the former than in the latter while taxon richness and biomass were not significantly different.
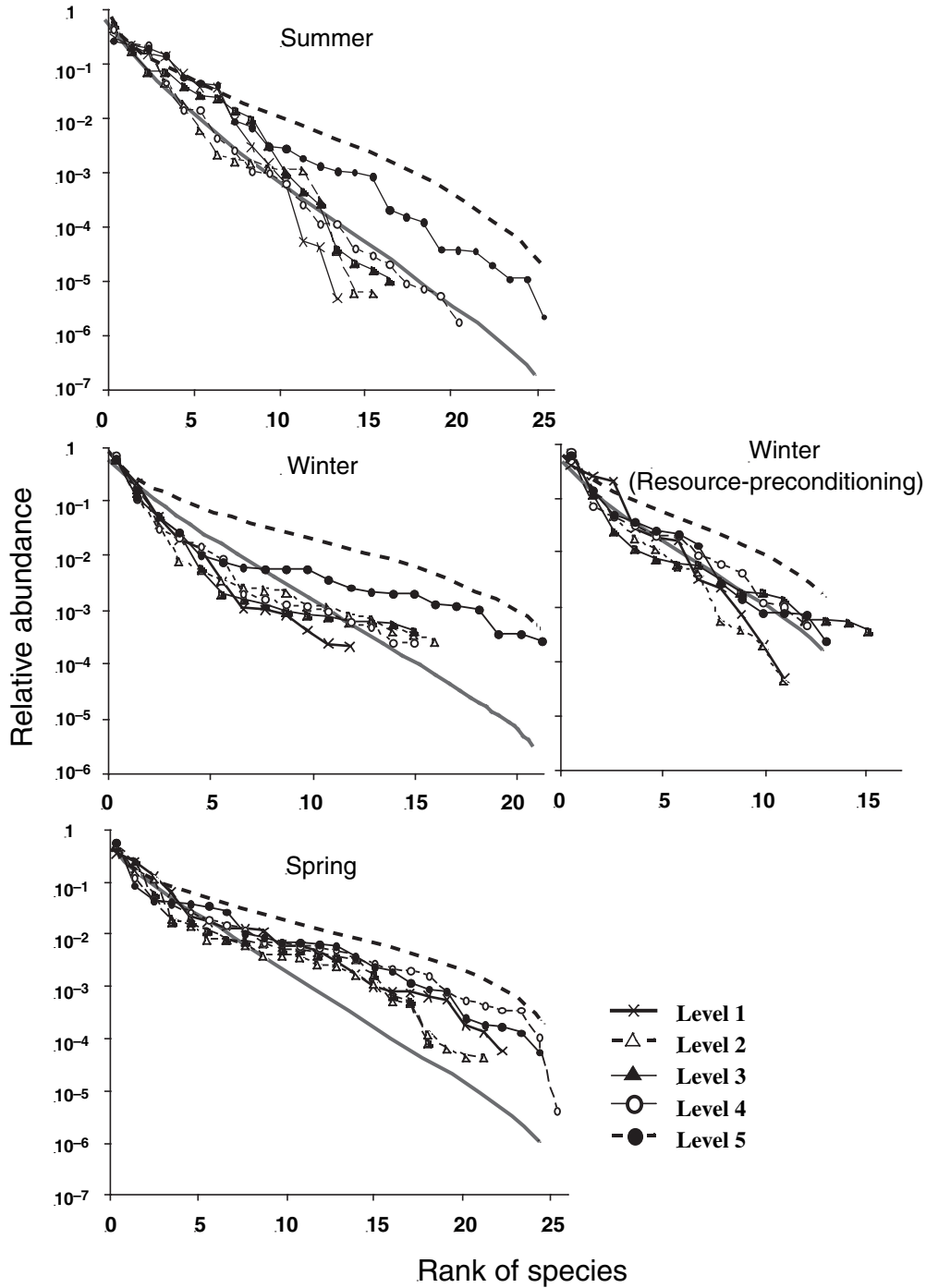
Fig. 3 Relative abundance patterns of benthic assemblages at five different levels of habitat complexity. Fitted lines represents the random fraction model (broken lines) and the random assortment model (continuous lines).

Scaling with habitat complexity was apparently variable among taxa and seasons (Fig. 6). In summer, densities of two abundant ephemeropterans, *Ecdyonurus tobiironis* Takahashi and *Baetis yoshinoensis* Gose, had positive relationships with fractal dimension with

the latter showing a more marked variation. In winter, another ephemeropteran with a similar mode of life to ecdyonurids, *Epeorus uenoi* Matsumura, had a similar positive relationship, while *B. yoshinoensis* demonstrated an insignificant pattern. The stonefly *Nemoura* sp.
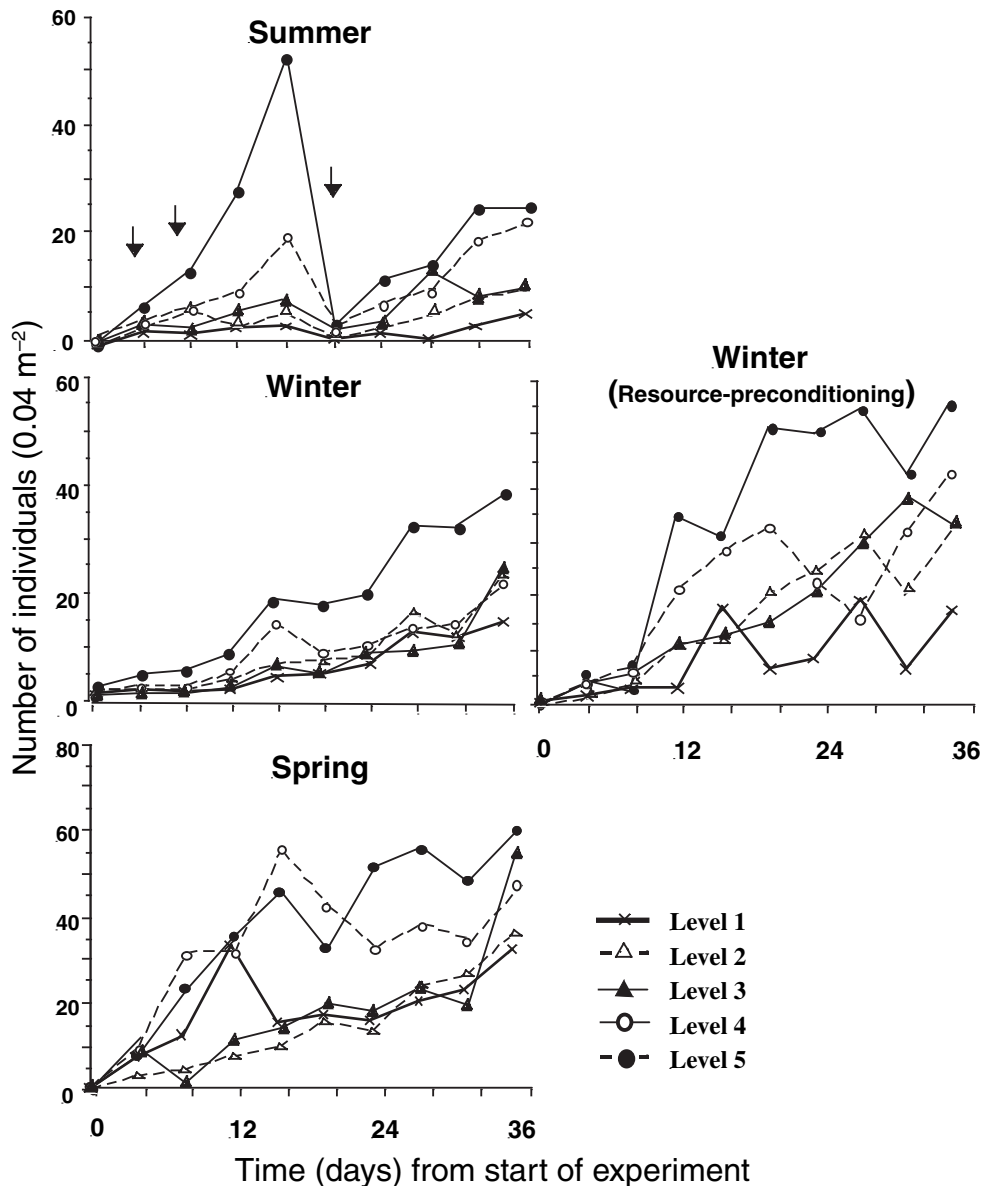
Fig. 4 Variation in the density of large invertebrates occurring on the plates (*in situ* visual counts) at five different levels of habitat complexity. In summer, arrows show spate events.

also had an insignificant increase in density with fractal dimension. The significant trend in *E. uenoi*, however, disappeared in resource-preconditioning treatment and neither *B. yoshinoensis* nor *Nemoura* sp. showed a significant trend. In spring, contrasting patterns were shown by *B. yoshinoensis* and *Simulium* spp. with the former demonstrating an increase in density with complexity levels and the latter showing a negative trend. As these two abundant taxa had opposite trends, the resultant pattern for total fauna was neutral (i.e. no significant increase in density with

increasing complexity levels). Further, *E. uenoi* mayflies that had a significantly increasing trend in winter showed a non-significant trend in spring.

Three potential food resources also showed varied patterns with habitat complexity (Fig. 7). Chlorophyll *a* had a weakly declining pattern with increasing complexity, although the trend was significant ($P < 0.01$) in summer only. In contrast, FPOM showed an increasing pattern with increasing levels of complexity, being significant in summer and winter ($P < 0.01$). CPOM showed no systematic variation
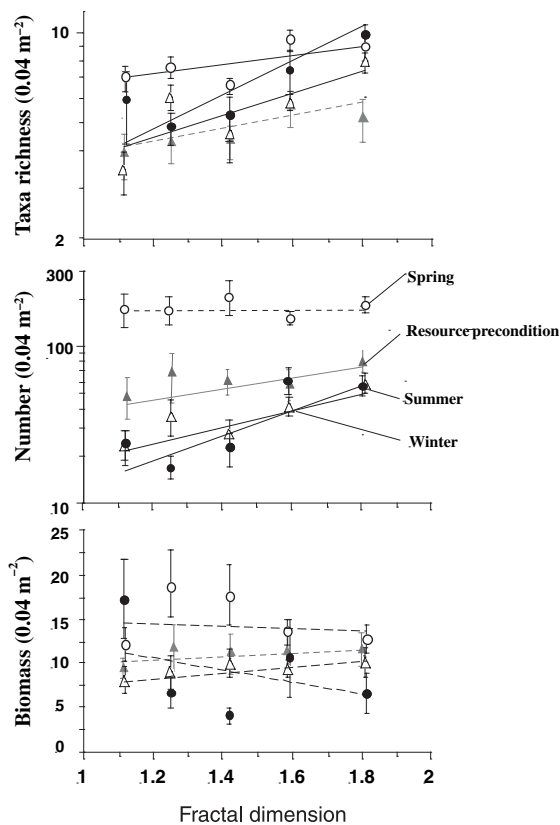
Fig. 5 Relationship between fractal dimension of habitat complexity and taxon richness (top), density (middle), biomass (bottom) of invertebrates in different trials (●, summer; △, winter; ▲, winter resource-preconditioning; ○, spring). Continuous lines indicate significant regressions and broken lines non-significant ones. Taxon richness: summer, $y = 0.06 + 0.47x$, $r^2 = 0.23$, $P = 0.001$; winter, $y = 0.26 + 0.37x$, $r^2 = 0.24$, $P < 0.001$; spring, $y = 0.64 + 0.17x$, $r^2 = 0.09$, $P = 0.02$; winter resource-preconditioning, $y = 0.43 + 0.21x$, $r^2 = 0.09$, $P = 0.10$; Density: summer, $y = 0.07 + 0.92x$, $r^2 = 0.34$, $P < 0.001$; winter, $y = 0.88 + 0.47x$, $r^2 = 0.14$, $P = 0.005$; spring, $y = 1.78 + 0.23x$, $r^2 = 0.03$, $P = 0.19$; winter resource-preconditioning, $y = 1.00 + 0.47x$, $r^2 = 0.15$, $P = 0.03$; Biomass: summer, $y = 15.99 - 5.39x$, $r^2 = 0.02$, $P = 0.34$; winter, $y = 2.39 + 4.34x$, $r^2 = 0.04$, $P = 0.12$; spring, $y = 19.16 - 2.88x$, $r^2 = 0.01$, $P = 0.56$; winter resource-preconditioning, $y = 5.12 + 2.27x$, $r^2 = 0.01$, $P = 0.56$.
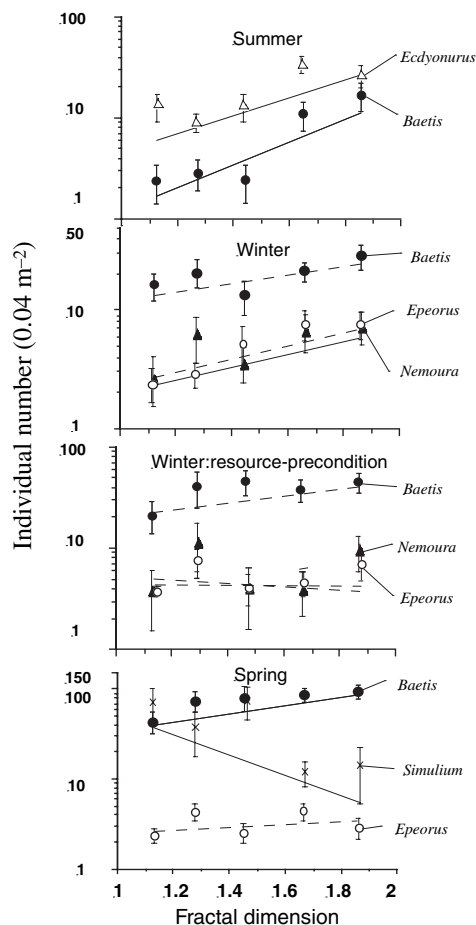

Fig. 6 Relationship between fractal levels of habitat complexity and density of different taxa (△, *Ecdyonurus*; ○, *Epeorus*; ●, *Baetis*; ▲, *Nemoura*; ×, *Simulium*). Continuous lines indicate significant regressions and broken lines non-significant ones. Summer: *Ecdyonurus*, $y = -0.15 + 0.82x$, $r^2 = 0.23$, $P < 0.007$; *Baetis*, $y = -0.89 + 1.04x$, $r^2 = 0.28$, $P < 0.001$; Winter: *Epeorus*, $y = -0.16 + 0.50x$, $r^2 = 0.09$, $P = 0.04$; *Baetis*, $y = 0.75 + 0.34x$, $r^2 = 0.04$, $P = 0.14$; *Nemoura*, $y = -0.12 + 0.55x$, $r^2 = 0.78$, $P = 0.07$; Winter resource-preconditioning: *Epeorus*, $y = 0.61 + 0.04x$, $r^2 = 0.01$, $P = 0.88$; *Baetis*, $y = 1.06 + 0.30x$, $r^2 = 0.05$, $P = 0.26$; *Nemoura*, $y = 0.74 - 0.05x$, $r^2 = 0.001$, $P = 0.92$; Spring: *Epeorus*, $y = 0.17 + 0.22x$, $r^2 = 0.03$, $P = 0.22$; *Baetis*, $y = 1.14 + 0.44x$, $r^2 = 0.11$, $P = 0.009$; *Simulium*, $y = 2.67 - 1.02x$, $r^2 = 0.15$, $P = 0.004$.

with complexity levels. Comparisons between the resource-preconditioning and control treatments showed no significant differences in any resource measurements.

Body size comparisons

Body size of invertebrates tended to decline with habitat complexity in all seasons ($P < 0.01$, Fig. 8),

although the ranges of sizes varied between seasons. The resource-preconditioning treatment led to larger body size than in the control at all levels of habitat complexity (Fig. 9, Kolmogorov–Smirnov test, all $P < 0.001$); this was the case not only for the total invertebrate fauna but also for *Baetis*, *Ecdyonurus*, *Epeorus* and *Simulium* separately.
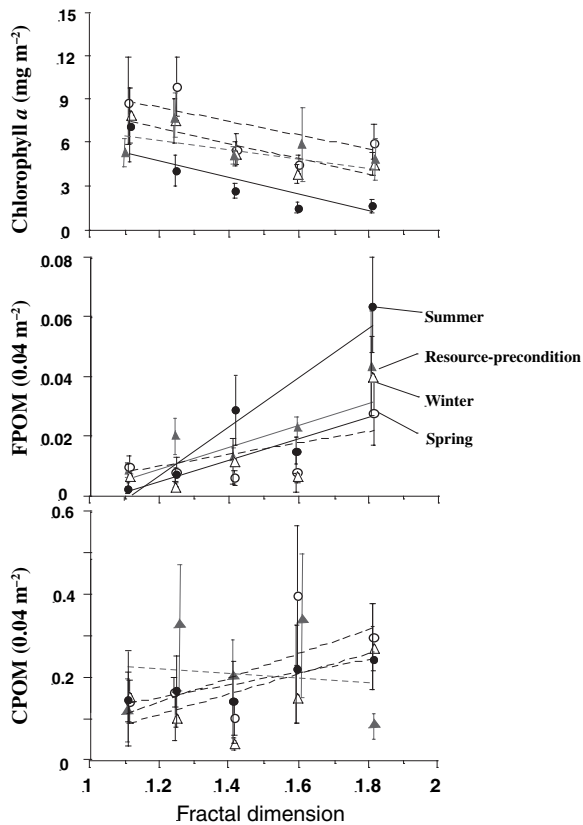
Fig. 7 Relationship between fractal dimension of habitat complexity and chlorophyll *a* (top), fine particulate organic matter (middle) and coarse particulate organic matter (bottom) abundance in different trials (●, summer; △, winter; ▲, winter resource-preconditioning; ○, spring). Continuous lines indicate significant regressions and broken lines non-significant ones. Chlorophyll-a: summer, $y = 12.91 - 6.65x$, $r^2 = 0.25$, $P < 0.01$; winter, $y = 13.33 - 5.27x$, $r^2 = 0.10$, $P = 0.06$; winter resource-preconditioning, $y = 8.61 - 1.90x$, $r^2 = 0.01$, $P = 0.53$; spring, $y = 15.66 - 5.97x$, $r^2 = 0.06$, $P = 0.07$; FPOM: summer, $y = -0.09 + 0.08x$, $r^2 = 0.30$, $P < 0.001$; winter, $y = -0.05 + 0.04x$, $r^2 = 0.17$, $P = 0.002$; spring, $y = -0.02 + 0.02x$, $r^2 = 0.06$, $P = 0.05$; winter resource-preconditioning, $y = -0.04 + 0.05x$, $r^2 = 0.23$, $P = 0.007$; CPOM: summer, $y = -0.03 + 0.15x$, $r^2 = 0.02$, $P = 0.39$; winter, $y = -0.12 + 0.19x$, $r^2 = 0.05$, $P = 0.13$; winter resource-preconditioning, $y = 0.30 - 0.06x$, $r^2 = 0.003$, $P = 0.79$; spring, $y = -0.23 + 0.32x$, $r^2 = 0.06$, $P = 0.07$.

Discussion

Habitat complexity and invertebrate assemblages

The present study has demonstrated that one aspect of habitat complexity, i.e. the fractal structure of surface irregularity, has varied effects on the diversity and abundance of benthic invertebrates. Taxon richness and total density of individuals scaled positively
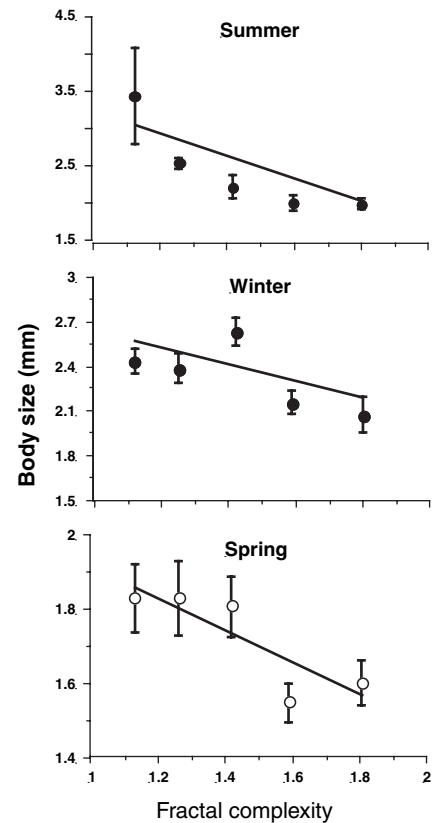
Fig. 8 Relationship between fractal dimensions and mean body size of invertebrates in summer (top), winter (middle) and spring (bottom). Summer, $y = 4.75 - 1.62x$, $r^2 = 0.30$, $P < 0.001$; winter, $y = 3.15 - 0.57x$, $r^2 = 0.15$, $P = 0.003$; spring, $y = 2.33 - 0.42x$, $r^2 = 0.07$, $P = 0.005$.

with fractal levels of complexity and the density of some taxa also showed a positive relationship with habitat complexity in some seasons, demonstrating species-specific responses. Similar results have been obtained for assemblages of intertidal gastropods (Beck, 1998, 2000) and freshwater invertebrates inhabiting submerged plants (Jeffries, 1993). The present study also agrees with our previous work, in which the architectural complexity of submerged macrophyte habitats was shown to affect invertebrate taxon richness independently of variation in habitat area (Taniguchi, Nakano & Tokeshi, 2003).

Variability in the effect of habitat complexity on freshwater invertebrate assemblages has not explicitly been demonstrated in previous studies on freshwater benthic systems. In summer, high discharge conditions accentuated the effect of habitat complexity on the temporal patterns of colonisation by surface-dwelling macroinvertebrates, probably because
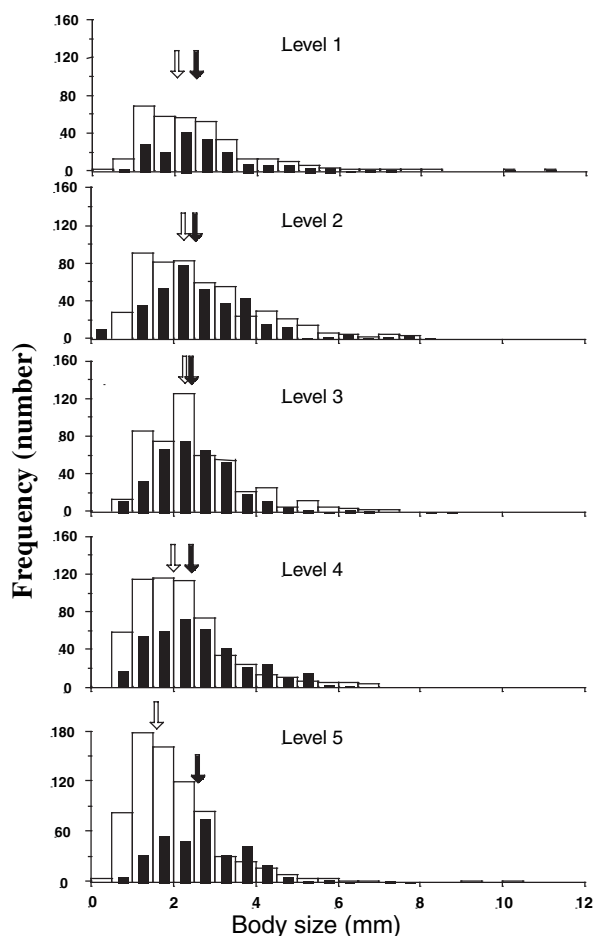
Fig. 9 Size-frequency distribution of invertebrates in winter control treatment (open bars) and resource-preconditioning treatments (filled bars) at five different levels of habitat complexity (L1–L5, see Fig. 2). Arrows indicate median values.

which suggests unfilled niche space and weak or no interaction among taxa (Tokeshi, 1990, 1993). Indeed, in the summer circumstances, more vacant niches must have been available on the plates with low to intermediate levels of complexity, as competitively inferior taxa and small-size individuals were likely to have been dislodged from less complex substrates by high flow conditions. Conversely, an increased retention of invertebrates in the most complex habitat seems to have resulted in a more equitable pattern of abundance. While the present analysis only allowed a visual inspection of species abundance patterns in comparison with the two models, the indication is that the patterns in these assemblages largely lay in between what were expected from the random assortment model and the random fraction model. This suggests that these assemblages tended to be influenced by some stochastic processes, which is in agreement with previous studies where the random assortment and the random fraction models were found to be of adequate fit to observed data from lotic invertebrate communities (Tokeshi, 1990; Schmid, 1997; Fesl, 2002).

In spring, two dominant taxa, *Simulium* and *Baetis*, showed the opposite trends of density in relation to increasing levels of habitat complexity, a decrease in the former and an increase in the latter. Suspension-feeding blackfly larvae are well known for their reliance upon high-flow conditions for feeding, thus preferring relatively smooth, unobstructed surfaces, which allow a constant laminar flow (Hart & Clark, 1996).

The present study also demonstrated that habitat complexity interacted in a complex manner with resource conditions in affecting invertebrate assemblages. Indeed, it is difficult to associate habitat complexity with resource abundance, as chlorophyll *a* and FPOM showed opposite trends with habitat complexity. Lower chlorophyll *a* concentrations on more complex substrates may have been related to grazer abundance, particularly in summer. While grazers may reduce algal abundance or standing crop in some habitats, high grazing pressure can induce increased growth rates of algae (Cebrian & Duarte, 1994), which may in turn sustain a high abundance of invertebrate herbivores. Thus, a higher density of invertebrates may be supported by increased growth of algae on complex habitats, whilst algal biomass is kept at reduced levels. However, it has also been

topographic irregularities modified fine flow patterns and created refugia for animals. It has been demonstrated experimentally that benthic invertebrates tend to gather in low flow, refuge areas, particularly under high flow regimes (Lancaster, 1999, 2000). In a similar vein, Palmer *et al.* (1996) suggested that structural complexity in the form of woody and leafy debris provided invertebrates such as chironomids and copepods with effective refugia under flood conditions.

While species abundance patterns apparently changed from one season to another, differences in the levels of habitat complexity resulted in little systematic variation in relative abundance patterns of invertebrate assemblages. In summer the patterns at levels 1–4 were close to the random assortment model,

suggested that a high density of invertebrates may inhibit their food consumption rates because of competition and interference (Robson, 1996). Another possible explanation for higher algal biomass in structurally simpler habitats may relate to the dominance of filamentous algae (Downes *et al.*, 1998) that tend to be less palatable than other algal groups (Dudley, 1992). This points to the difficulty of assessing resource availability for invertebrate herbivores based on chlorophyll measurements alone and of linking resource abundance with 'niche' creation (Dean & Connell, 1987).

The fact that there were no significant differences in the amount of potential resources between the resource-preconditioning and the control treatments was unexpected before the experiment, but it may be explained by the period of experiment (=36 days) being sufficiently long to obliterate initial differences that must have existed at the beginning. In fact, a similar result was obtained in a separate study where significant differences in algal abundance that existed between the algal removal and the control treatments at the start of 32-day experiment disappeared on later days (N. Kuhara and others, unpublished data). Thus, the relationship between invertebrate abundance and potential food abundance requires further investigation.

Body size and habitat complexity

It is notable in the present study that the fractal levels of habitat complexity have affected not only diversity and abundance but also body size distributions of invertebrates. Mean body size of invertebrates tended to decrease in habitats with higher fractal dimensions, which agrees with some terrestrial studies where arthropod body size was found to be negatively related to the fractal dimension of vegetation (Morse *et al.*, 1985; Shorrocks *et al.*, 1991). In general, complex habitats contain small habitat units which can give shelter to small and/or young individuals, but simple habitats in aquatic systems may not constitute effective refugia as the scouring effects of flow could affect the inside of a cavity. For example, small crevices in rocky intertidal habitats contained small individuals of *Littorina* snails while large crevices contained both large and small individuals (Raffaelli & Hughes, 1978). Similarly, diatoms of small sizes tend to accumulate in cavities of complex habitats (Bergey,

1999). Essentially, cavities may serve as 'refugia' only if their sizes match the sizes of organisms.

Mean body size of invertebrates showed a negative relationship with habitat complexity, but the reasons varied slightly between seasons. In summer and winter, higher proportions of small-sized individuals of major taxa occurred in more complex habitats, resulting in a decline in body size with habitat complexity. In the case of the spring data, the assemblage consisted mainly of two taxa, with larger-sized *Simulium* larvae occurring in simpler habitats and smaller-sized *Baetis* occurring in mid to high complexity habitats. Overall, body size declined with habitat complexity. In a similar vein, Downes *et al.* (1998) found that a higher proportion of small-sized invertebrates occurred in rough-surface substrates with small crevices than in smooth-surface substrates. Small crevices are considered to give better protection to small invertebrates from the risks of physical disturbance and predation (Tokeshi, 1994). In the study site, while large invertebrates including predators were not directly observed on the experimental plates, predatory benthic organisms such as stoneflies and fish including freshwater gobies of the genus *Rhinogobius* occurred commonly in the stream and these must have had some influence on the occurrence of invertebrates on the experimental plates.

In the winter experiment, it was notable that more invertebrates of larger sizes were associated with the resource-preconditioning treatment over the entire range of fractal dimension, suggesting that resource conditions can affect body size distributions of stream invertebrates. This concurs with Bourassa & Morin's (1995) study in which larger benthic animals were found to be more abundant in resource-rich habitats while the abundance of small-size animals was not affected by habitat resource conditions.

In conclusion, the effect of habitat complexity on stream invertebrates varied with seasonal and resource conditions. This points to the importance of considering habitat complexity in conjunction with temporal and spatial variation in other environmental factors. While increased habitat complexity may confer more refugia to stream invertebrates, the efficiency of such refugia is variable under different conditions. Further investigation is necessary to unravel the complex relationship between habitat structure and benthic assemblages.

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Appendix

Abundance of different taxa recorded in each experimental trial

Taxon	Experimental trial [MS (%)]							
	summer		winter		spring		winter resource preconditioning	
	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass
Ephemeroptera								
Baetis yoshinoensis Gose	325 (20.4)	74.8 (19.2)	1268 (55.5)	366.8 (73.3)	4866 (48.1)	516.1 (56.5)	1172 (65.4)	180.0 (67.8)
Ecdyonurus tobiironis Takahashi	645 (43.1)	121.7 (36.8)						
Epeorus uenoi Matsumura	23 (2.7)	2.9 (1.0)	287 (11.9)	84.2 (17.5)	203 (2.1)	115.2 (12.7)	182 (10.2)	41.0 (16.7)
Paraleptophlebia westoni Imanishi.			250 (11.5)	14.8 (2.8)	55 (0.6)	8.1 (0.9)	32 (1.7)	3.6 (1.2)
Trichoptera								
Apatania sp.	58 (2.8)	2.1 (0.4)	57 (2.0)	8.4 (1.5)	10 (0.1)	2.4 (0.3)	11 (0.6)	2.8 (1.0)
Chimarra sp. CA	6 (0.4)	4.9 (1.7)					7 (0.3)	3.0 (1.0)
Micrasema quadriloba Martynov	11 (0.8)	4.1 (0.9)	5 (0.2)	2.6 (0.6)	11 (0.1)	11.2 (1.3)		
Goerodes complicatus (Kobayashi)	221 (17.4)	111.0 (25.2)	63 (2.7)	5.9 (1.2)	21 (0.2)	21.9 (2.7)	7 (0.3)	3.6 (1.2)
Dolophilodes sp.	1 (0.04)	0.01 (<0.01)						
Goera curvispina Martynov	3 (0.4)	3.5 (0.9)	3 (0.2)	4.9 (1.2)	1 (0.01)	8.3 (1.0)		
Macrostemum radiatum McLachlan	12 (1.2)	13.7 (3.2)			5 (0.05)	6.3 (0.7)		
Helicopsyche yamadai Iwata	1 (0.04)	0.3 (0.1)						
Hydroptila sp.			2 (0.1)	0.5 (0.1)	4 (0.04)	0.9 (0.1)		
Glossosoma sp.					5 (0.05)	5.1 (0.5)		
Stenopsyche marmorata Navas					3 (0.03)	2.9 (0.3)		
Apsilochorema sutshanum (Martynov)					6 (0.1)	2.4 (0.3)		
Plecoptera								
Nemoura sp.	17 (1.4)	0.8 (0.2)	86 (2.5)	0.7 (0.1)	19 (0.2)	0.7 (0.1)	186 (10.2)	7.8 (3.0)
Perlodes frisonana Kohno	6 (0.7)	12.4 (2.8)	3 (0.1)	2.9 (0.5)	21 (0.2)	2.0 (0.3)	2 (0.1)	0.1 (0.04)

Appendix (*Continued*)

Taxon	Experimental trial [MS (%)]							
	summer		winter		spring		winter resource preconditioning	
	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass
Odonata								
Mnais pruinosa Selys	9 (0.7)	3.6 (1.2)	1 (0.04)	0.04 (0.01)				
Epiophlebia superstes Selys					1 (0.01)	0.5 (0.1)		
Polycathagina melanictera Selys	1 (0.04)	5.4 (1.6)						
Coleoptera								
Elminae sp.	7 (0.5)	0.01 (<0.01)	41 (1.5)	1.0 (0.2)	18 (0.2)	0.9 (0.1)	2 (0.1)	0.1 (0.02)
Nipponhydrus flavomaculatus (Kamiya)	1 (0.1)	0.1 (0.02)						
Ectopria sp.			1 (0.03)	0.2 (0.05)				
unknown							1 (0.1)	0.2 (0.1)
Diptera								
Ceratopogonidae	17 (1.0)	0.04 (0.01)			5 (0.05)	0.7 (0.1)		
Simulium spp.	13 (1.0)	0.05 (0.01)	11 (0.5)	1.2 (0.2)	2713 (25.8)	147.8 (15.8)	33 (2.2)	11.1 (5.4)
Chironominae	12 (1.0)	0.04 (0.02)	2 (0.1)	0.2 (0.05)	246 (2.5)	17.5 (2.1)	59 (2.9)	4.4 (1.6)
Tanypodinae sp.1	8 (0.3)	0.7 (0.2)	23 (1.0)	0.2 (0.1)	43 (0.4)	3.1 (0.4)	4 (0.2)	0.2 (0.1)
Tanypodinae sp.2			9 (0.3)	0.3 (0.1)	6 (0.1)	0.3 (0.04)		
Orthocladiinae sp.1	26 (1.6)	0.01 (<0.01)	48 (1.9)	0.5 (0.1)	330 (3.3)	4.7 (0.6)	15 (0.9)	0.2 (0.1)
Orthocladiinae sp.2	8 (0.3)	<0.01 (<0.01)						
Orthocladiinae sp.3	9 (0.6)	<0.01 (<0.01)			712 (7.1)	11.6 (1.2)	12 (0.6)	0.2 (0.1)
Orthocladiinae sp.4	1 (0.04)	<0.01 (<0.01)						
Orthocladiinae sp.5	19 (1.2)	<0.01 (<0.01)			736 (7.3)	14.0 (1.8)		
Orthocladiinae sp.6			67 (2.7)	0.7 (0.1)	103 (1.0)	2.1 (0.2)	81 (3.7)	1.4 (0.5)
Orthocladiinae sp.7			3 (0.1)	0.03 (0.01)			3 (0.2)	0.3 (0.1)
Orthocladiinae sp.8			114 (5.0)	1.6 (0.3)				
Orthocladiinae sp.9								
Orthocladiinae sp.10					38 (0.4)	0.5 (0.1)		
Antocha sp.	3 (0.3)	7.0 (3.7)			7 (0.1)	0.04 (<0.01)	1 (0.1)	0.01 (<0.01)
Dicranota sp.							4 (0.2)	0.3 (0.1)
Lepidoptera								
Parapoynx sp.	1 (0.04)	0.01 (<0.01)						
Amphipoda								
Gammarus sp.	1 (0.04)	2.6 (0.8)	1 (0.04)	0.1 (0.01)				
Total	1465	371.86	2345	498	10188	907.1	1814	260.27