

Habitat complexity in aquatic systems: fractals and beyond

M. Tokeshi · S. Arakaki

Received: 29 April 2011 / Accepted: 15 July 2011 / Published online: 10 August 2011
© Springer Science+Business Media B.V. 2011

Abstract Despite the intensity with which ecological information involving habitat complexity has been amassed to date, much remains to be revealed for a comprehensive understanding of the mechanics and implications of the structural complexity of habitats and its influences on ecological communities. This review examines the multi-faceted characteristics of habitat complexity, focusing in particular on aquatic ecosystems. Habitat complexity in aquatic systems is characterised by at least five different traits of physical structure: (1) spatial scales, (2) diversity of complexity-generating physical (structural) elements, (3) spatial arrangement of elements, (4) sizes of elements, (5) abundance/density of elements. Of these five traits, the concept of fractal dimension fully encompasses only the last one; in this sense, habitat complexity is more complex than what fractal measures represent. It is therefore important to investigate exactly which traits of habitat structure are exerting influences on organisms/communities. We hypothesise that, where an entire range of possible fractal dimension D is considered, intermediate levels of

D are most likely to be associated with the highest level of biodiversity, to which the body size spectra of assemblages would have a close bearing. In most aquatic ecosystems, broadly two-dimensional structures of bottom substrate at the scale of 1–10 m mean that the addition of vertical, three dimensional structures almost always implies an increase in both the ‘diversity’ and ‘abundance’ components of structural elements, resulting in more habitats being made available to organisms of different sizes and functional designs. The conservation and management of aquatic ecosystems would be facilitated by rigorous assessments of linkages between habitat complexity and aquatic communities, for which an integrative approach to habitat complexity seems to offer a useful and versatile framework.

Keywords Diversity · Abundance · Substrates · Structural elements · Fractal dimension · Body size

Introduction

The question of how biological diversity is maintained is central to community ecology. While many aspects of biodiversity, particularly of the aquatic domain, remain unknown and require much research effort, increasingly devastating climatic and anthropogenic threats to the Earth’s environments mean that biodiversity is being lost at a pace faster than the speed at which we are gaining information and

Guest editors: K. E. Kovalenko & S. M. Thomaz / The importance of habitat complexity in waterscapes

M. Tokeshi (✉) · S. Arakaki
AMBL-Kyushu University, Reihoku-Amakusa,
Kumamoto, Japan
e-mail: tokeshi@ambl-ku.jp

knowledge from it. In this respect, the conservation of biodiversity is a priority for which efforts cannot be spared in a race against time.

As one of the aspects that closely bear upon the mechanics and maintenance of biodiversity and species coexistence, habitat complexity has long been a focus of ecological research (Bell et al., 1991; Tokeshi, 1999; Johnson et al., 2003). While studies concerning habitat complexity started more prominently on the terrestrial side with the MacArthur's landmark paper on the distribution and abundance of forest birds (MacArthur & MacArthur, 1961), aquatic ecologists have increasingly taken up research initiatives with more emphasis on analytical and experimental approaches (O'Connor 1991; Jeffries, 1993; Downes et al., 1998, 2000; Taniguchi & Tokeshi, 2004; Lingo & Szedlmayer, 2006; Moore & Hovel, 2010). Generally these studies have revealed the important role that habitat complexity appears to play in the structuring and functioning of aquatic communities, particularly in terms of increasing the abundance and diversity of organisms. Notwithstanding these, habitat complexity has varied facets which are little understood to date. Detailed patterns and mechanics of habitat complexity in the organisation of aquatic communities need to be investigated further. This would include consideration of community-wide traits such as abundance-body size relationships and relative abundance patterns in relation to the aspects of habitat complexity. In this connection it is necessary to draw some attention to the use of fractal concepts in this discipline, as there has been a continued trend of applying fractal geometry to various fields of ecology in the past quarter century (Morse et al., 1985; Sugihara & May, 1990; Frost et al., 2005).

In this work, we look into some conceptual, theoretical and empirical issues of habitat complexity which are of general importance and yet have been insufficiently dealt with in the community ecology of aquatic assemblages. The main objective here is to identify and highlight those aspects fundamental to the understanding of habitat complexity that would require more research, while placing into perspective our existing knowledge. As most of these issues are equally relevant to both freshwater and marine systems, similarities rather than differences are emphasised in discussing the problems of habitat complexity across a range of aquatic systems.

What is special about habitat complexity in aquatic habitats?

Notwithstanding an increasing body of works involving generalist terrestrial consumers (e.g. birds (Hurlbert, 2004), small mammals (August, 1983) and ants (Lassau & Hochuli, 2004)), it seems correct to say that research dealing with the concept of habitat complexity has been more vigorously pursued on aquatic organisms/communities. Are aquatic systems more ideal for studying ecological issues relating to habitat complexity? There are reasons to believe that a positive answer may be given to this somewhat philosophical question, with some qualifications, given the nature of habitat complexity as well as the ecological characteristics of biodiversity in aquatic versus terrestrial systems.

First of all, it is notable that water as a more viscous, dense medium than air exerts greater drag forces upon objects including organisms (Mann & Lazier, 1996), with a result that seeking refugia from and acquiring morphological/behavioural adaptation to currents are crucial for aquatic organisms. In this respect, the physical structures of habitat including substrate surface characteristics directly affect how effectively organisms can protect themselves in high-drag environments (Denny & Wethey, 2001). This protection implies not only against physical forces of water itself but also against predators which may possess superior mobility even in the high-drag medium. Clearly, exposure to an open-current environment is a risky and energetically costly undertaking, while an apparent benefit accrues in the form of matter transport (i.e. food resources and gas exchange). This in turn points to the overwhelming importance of three-dimensional structures in aquatic ecosystems in enhancing the diversity and coexistence of species (Tokeshi, 1999; Bruno & Bertness, 2001; Kawai & Tokeshi, 2004), e.g., macrophyte stands in lakes and rivers, sea grasses and macroalgae in shallow coastal waters, mussels in intertidal habitats, scleractinian coral assemblages in tropical/subtropical waters, and kelp forests in cold-temperate waters. These are all known to afford protected habitat space to many organisms and consequently help increase biodiversity. It is worth noting here that the diversity of forest birds in MacArthur's study (MacArthur & MacArthur, 1961) is an analogous terrestrial example that highlights the importance of

three-dimensional structures; others include arboreal arthropods (e.g., Lassau et al., 2005).

Secondly, the predominance of particle-feeding generalists (suspension-feeders, deposit feeders, grazers of microalgae, etc.) in aquatic systems makes a sharp contrast to terrestrial systems where feeding specialists predominate (e.g. majority of insect species feeding on a limited range of other insect/plant species) and particle-feeding is of minor occurrence. For many terrestrial consumers with a limited range of food resources, habitat choice is more strongly dictated by the occurrence of those foods, rather than the physical characteristics of habitat per se. In aquatic systems, the physical architectures of substrates are often crucial for the settlement and/or mobility of organisms and for the availability of particulate food materials, both dead and alive. This is particularly the case with sessile suspension feeders which occur commonly in all types of marine habitats and often form important secondary habitats for other organisms (e.g. mussel beds on rocky substrates (Sebens, 1991; Tokeshi, 1995; Tokeshi & Romero, 1995; Koivisto & Westerborn, 2010), polychaete tubes in soft sediments (Bell & Coen, 1982), vermetid reefs (Safriel & Ben-Eliahu, 1991) and scleractinian corals in tropical/subtropical waters (Nozawa et al., 2008; Tokeshi & Tanaka, 2010)). Consequently, surface structures (interface between the water and the substrate) directly affect benthic organisms in terms of colonisation, growth, food acquisition, predator avoidance and reproduction.

Therefore, environmental and evolutionary characteristics of aquatic ecosystems combine to make their inhabitants more susceptible to the physical structures of aquatic habitats and the availability of suitable structures tends to bear directly on the abundances of aquatic organisms. This implies that in aquatic systems issues relevant to habitat complexity are more clearly identifiable, with a consequence that research is likely to yield useful information on the linkage between habitat complexity and the functionality and organisation of communities. In this sense, aquatic systems seem ideal for such investigations.

What is ‘habitat complexity’?

The fact that the term ‘complexity’ has often been interchangeably used with ‘heterogeneity’ or

‘diversity’ indicates that, first and foremost, the concept of habitat complexity implies the existence of different ‘kinds’ of elements that constitute a habitat. Put into the context of shallow freshwater/marine systems, for example, these ‘different elements’ may refer to moss patches, half-submerged logs, stones and rock surfaces in a single riffle section of a stream, rocky/gravelly/sandy/muddy substrates and submerged vegetation (algae/higher plants) stands on the spatial scale of a coast, or sets of geomorphological structures such as spits, peninsular headlands and zeta-curve bays (Carter, 1988) on a local/regional scale. While easily recognisable and superficially not controversial, such a ‘qualitative’ side of habitat complexity does in fact pose a serious problem of quantitative analysis in the absence of common or universal measure. Although these different kinds of habitat elements may be analogous to different species in an ecological assemblage and hence ‘diversity’ may be calculated using one of many information-theoretic indices (e.g. Tokeshi, 1993; Magurran, 2004), the efficacy of such an approach remains unknown. We note at least that MacArthur & MacArthur (1961) successfully adopted this approach to calculate forest habitat diversity for birds.

This qualitative side of habitat complexity (i.e., complexity encompassing different structural elements) tends to be put aside while dealing with the ‘measurable’ side of habitat complexity (complexity within element) that can be more readily handled, in particular using the techniques of fractal geometry. The fractal concept has been found to be of practical value and applicable to a variety of situations (Li, 2000; Schmid, 2000; Halley et al., 2004; Frost et al., 2005), but there is still a paucity of studies that have closely examined its application to the analysis of habitat complexity in aquatic systems. Here, our focus with respect to fractal geometry will be on the conceptual/theoretical basis of its application, rather than on the practical problems of actually measuring and estimating fractal values; for a review, see Halley et al. (2004). To start, it is important to note that, in most practical applications, fractal dimension emphasises one aspect of habitat complexity only, in effect what may be described as the ‘density’ of the projected profile of solid geometry in a chosen plane/volume. Whether such a measure can suitably and sufficiently represent habitat complexity in ecological investigations needs to be carefully

assessed according to individual circumstances. In all probability habitat complexity is more subtly complex than what fractal geometry can express, as the discussions below illustrate.

We are inclined to propose, for all practical reasons, habitat ‘complexity’ be interpreted as encompassing different characteristics of structure, rather than referring solely to ‘the abundance of structural components’ as suggested by McCoy & Bell (1991). This ‘integrative’ perspective is more compatible with research in scientific disciplines other than ecology where the term ‘complexity’ is extensively used, e.g. physics of dynamical systems and evolutionary biology (Adami, 2002). We shall return to this issue in the closing section of the present work. Assuming this standpoint, we recognise at least five traits that need to be taken into account when assessing habitat complexity:

- (1) Scales of habitat complexity;
- (2) Diversity of complexity-generating elements;
- (3) Spatial arrangement of elements;
- (4) Sizes of elements;
- (5) Abundance/density of elements

These inter-related aspects will be considered in turn. Our emphasis here is on physical structures; non-structural aspects such as substrate chemistry (e.g. plant secondary metabolites adding to the complexity of plants as habitats for other organisms), though potentially very important, are not considered here.

Scales of habitat complexity and the diversity of complexity-generating elements

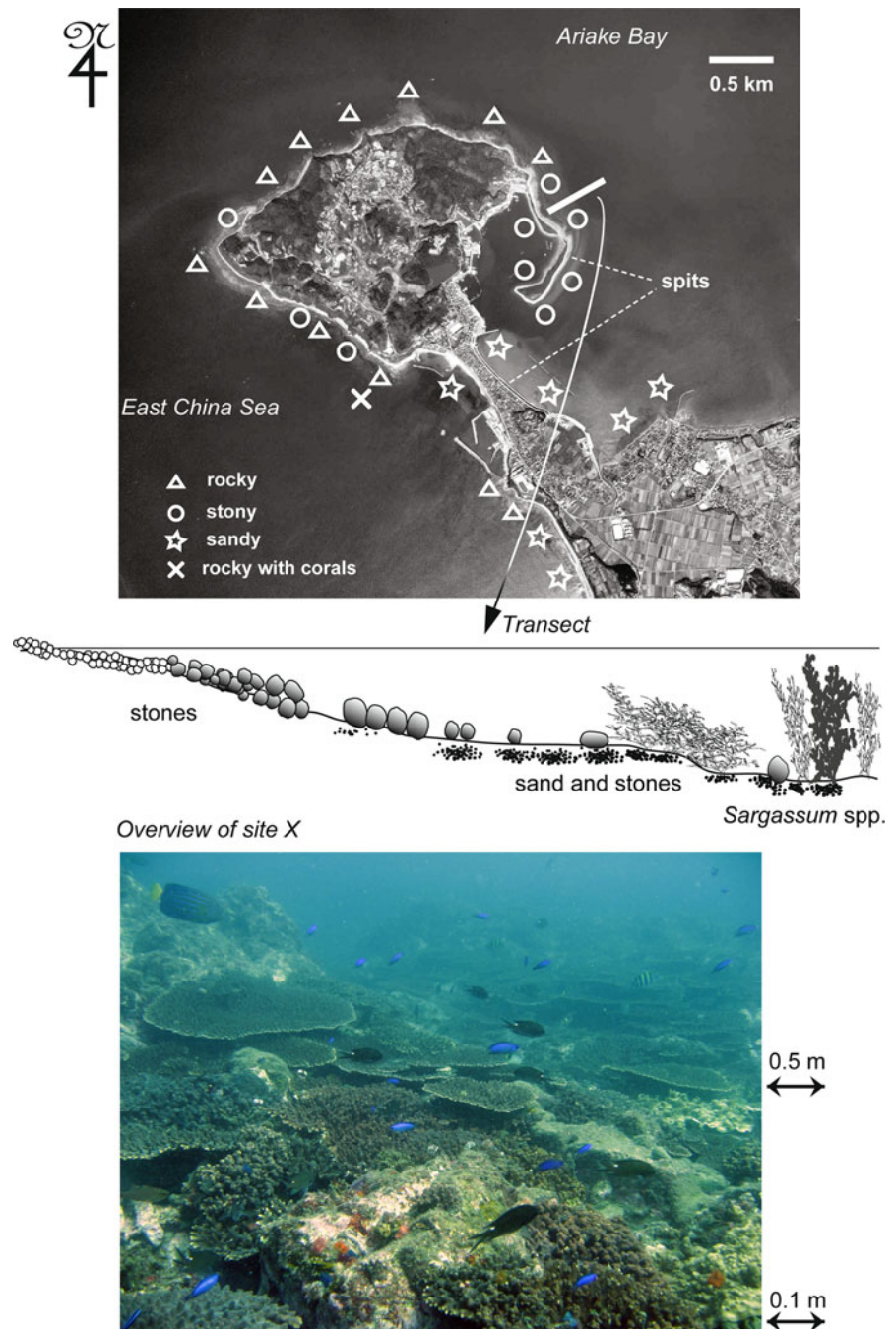
For all assemblages of organisms, habitat complexity exists at different spatial scales, i.e. global, regional, local and microhabitat scales, with concomitant variation in the nature of complexity-generating processes and structural elements. At global to regional scales, large-scale physical factors and processes predominantly dictate what structural elements of habitat occur. At local scales, small-scale physical characteristics of the habitat interact with large/medium-scale oceanographic and geographic processes to generate complexity. At smaller spatial scales, not only physical processes but also biological processes have increasingly important roles in generating and defining habitat complexity.

An example of the scale-variant nature of habitat complexity is illustrated with the shallow coastal ecosystems of Amakusa, south-western Japan, in the western Pacific (Fig. 1). At the spatial scale of kilometres, the coastline represented by the Tomioka Peninsula of the Amakusa Shimoshima Island (32°31–32′N, 130°00–02′E) is quite varied due to a sand-spit formation linking the small island to the mainland (Fig. 1, top) at the entrance to the largest estuarine water in Japan, the Ariake Bay. As a result, rocky, stony and sandy shores occur in short sequences along the coastline with different levels of exposure to currents and wind-induced disturbances, depending on positions and orientations (Kurimoto & Tokeshi, 2010 and unpublished data). Shores to the east represent less-disturbed habitats as they face the Ariake Bay, with the dominance of *Sargassum* and other algal stands in the subtidal. Shores to the north are exposed to strong currents and winter winds while the western shores experience variable currents of the open sea (East China Sea) with an increasing occurrence of coral patches towards south. Thus the physical characteristics of shores around this peninsula are more variable than what a similarly rugged coastline per se suggests as a complex geometrical entity.

On scales of ~100 m, patches of elements that constitute local habitats are recognisable. For example, along the outer shoreline of a naturally formed spit on the eastern side of the peninsula (Fig. 1, top), boulders and stones show progressive changes in size, forming qualitatively variable habitats (Ota & Tokeshi, 2000; Paruntu & Tokeshi, 2003; Londoño-Cruz & Tokeshi, 2007). Stone size increases from south to north along this spit, as currents become stronger towards the mouth of the Ariake Bay. Such a horizontal change in stone size is also reflected along the line perpendicular to the coast (Fig. 1, top), as demonstrated by a 500 m transect (Fig. 1, middle). Stone size increases from the upper intertidal to subtidal, eventually giving way to the mixed substrates of large boulders with sand. In addition to these elements of habitat, there are patches of *Sargassum* species and other algae that enhance the three-dimensional characteristics of shallow coastal waters, particularly on the eastern-northeastern coasts of the peninsula.

At smaller scales of tens of metres downwards, different types of habitat elements constituting

Fig. 1 *Top* Different types of shore habitats (at the scale of km) occurring around the Tomioka Peninsula of the Amakusa Shimoshima Island in south-western Japan. *Middle* Shore habitats at the scale of ~ 100 m. A schematic diagram showing a 500 m transect perpendicular to the shore of a spit to the west of Tomioka Peninsula; *Bottom* Small-scale (~ 1.0 m) topographical variability of a single isolated site with aggregations of acroporan and other coral colonies, accompanied by coral-associated organisms



complexity are recognisable, e.g. tidepools of various shapes/sizes (Kurimoto & Tokeshi, 2010; Arakaki & Tokeshi, 2011), rocks/stones of different sizes as well as different sides of a stone (Londoño-Cruz & Tokeshi, 2007). At small spatial scales, individuals of sessile organisms themselves also constitute habitat-forming elements. Another example of small-

scale habitat complexity concerns a single site in this locality dominated by corals on a rocky platform (Fig. 1, top and bottom). The three-dimensional structures created by different Acroporid table corals such as *Acropora japonica*, *A. glauca*, *A. hyacinthus* and *A. solitaryensis* (Tokeshi & Tanaka, 2010) add extra complexity to this habitat (Fig. 1, bottom).

Micro-topographic features of substrates, such as orientation, concavity and surface texture apparently enhance complexity, affecting the colonisation of sessile organisms, which in turn would affect organisms associated with them.

An analogous scale-related variation in structural complexity is seen even with one type of ecosystems, e.g. seagrass beds (Williams & Heck, 2001). These cases clearly show the variable nature of habitat complexity recognisable at different scales of enquiry, which cannot be overcome by a scale-independent approach of fractal measures. For example, recognition of elements constituting complexity is different among surveys involving the entire coastline, 500 m transects and 50 cm quadrats. It is therefore important to note that the nature of habitat complexity is generally different across different scales and data need to be taken from multiple spatial scales to enable a comprehensive understanding of the patterns and functionality of habitat complexity in a particular type of ecosystem. In studies involving habitat complexity, extrapolation across scales is mostly inappropriate and often quite misleading.

Diversity of elements and their spatial arrangement

We have emphasised above that different habitat elements need to be recognised at different spatial scales. This is easier said than done, as such differences are not necessarily apparent. In this connection, unsuspecting reliance on fractal geometry for assessing complexity should be guarded against, as many aspects of what should be considered as constituting complexity are not adequately covered by the fractal concept. For example, geometry does not distinguish differences among different kinds of sediments while they present similar fractal dimensions, or among different species of algae having different surface textures. In view of the fact that fractal concepts continue to be applied to the analyses of topography in aquatic systems (Commito & Rusignuolo, 2000; Frost et al., 2005), our attention is drawn to those features that tend to be overlooked or inadequately handled by fractal geometry.

Rock surfaces are important habitats for aquatic organisms in both marine and freshwater environments. As water currents directly impact on such

surfaces, seemingly small differences in surface geometry could have large influences on benthic organisms, particularly sessile ones. Consider a rock surface with concave structures or notches (cross section shown in Fig. 2A). This has exactly the same fractal dimension as a surface with convex structures or projections (Fig. 2B), but these two present qualitatively different habitat conditions to benthos. Further, a mixture of concave and convex structures (Fig. 2C) presents a yet another habitat condition with a different type of complexity. Note that the rock surface of Fig. 2C also has the same fractal dimension as the two cases above. Under these circumstances, comparison of habitat complexity cannot effectively be performed with fractal geometry. If one recognises concave (Fig. 2A) and convex (Fig. 2B) structures as qualitatively separate entities (which clearly we should as aquatic ecologists), habitat of Fig. 2C is considered more complex than either of the above two cases alone. Note also that different spatial scales in which these structures may occur would present different situations.

As an attempt to assess such surface geometry, we have devised a simple, practical methodology (the ‘Minimal Angle’ method) for use under field conditions. On an exposed rocky shore of the west of Tomioka Peninsula (Fig. 1), surface topography

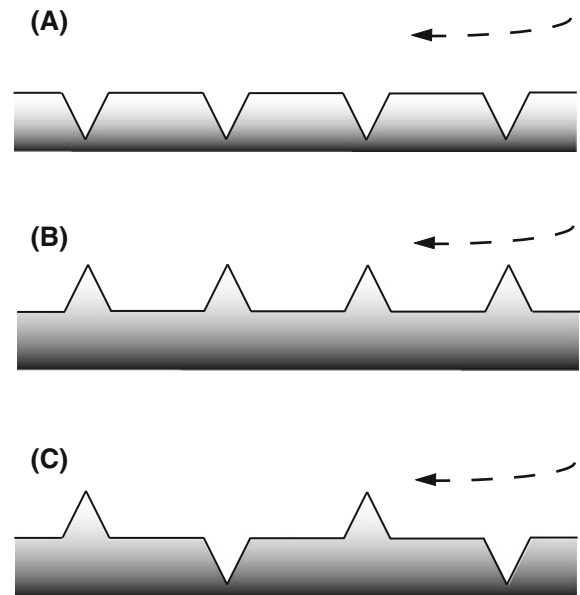


Fig. 2 Schematic diagrams showing three different types of substrate topography (concave-convex system) viewed as vertical sections

centred around each individual benthic animals was measured with a 10 cm flexible wire marked at 1 cm intervals (Fig. 3). A mid point of the wire was placed where an animal was positioned and the wire was turned around 360° to bend on a vertical (cross-sectional) plane along the surface to find the minimal angle (MA, θ) formed by the mid point and two other marked points (Fig. 3A, B). In order to characterise the available surface topography, the same methodology was applied to an area of 5×5 m of the same rock surface and measurements were taken at 5-cm mesh points. The resultant distributions of MAs clearly show differences among different benthic taxa in relation to the surface topography of this habitat (Fig. 3C). Some species, such as a barnacle *Tetraclita japonica* and a rock oyster *Saccostrea kegagi*, showed MAs not departing from the average MA values of the background substrate (i.e. nearly flat surface with MA $\sim 180^\circ$), while others demonstrate apparently low MAs (concave microhabitats, medians $< 100^\circ$). Occurrence in convex microhabitats (MA $> 180^\circ$) was demonstrated most frequently by *T. japonica*. Interestingly, only one of these species, a limpet *Siphonaria japonica*, seems to span a wide range of MAs. Clearly, ‘concavity’ and ‘convexity’ are important components of habitat complexity that need to be distinguished from flatness. In this case, an analogous situation may also occur on a larger scale if we imagine Fig. 3B as depicting a coastline (i.e. on a horizontal plane), for example. As water currents and substrate characteristics would vary with associated MAs (of course using scales larger than a wire of 10 cm), ecological assemblages (fish, macroinvertebrates, algae) would be different, probably suggesting that wider the range of MAs encountered on this particular scale, the more diverse the assemblages of taxa.

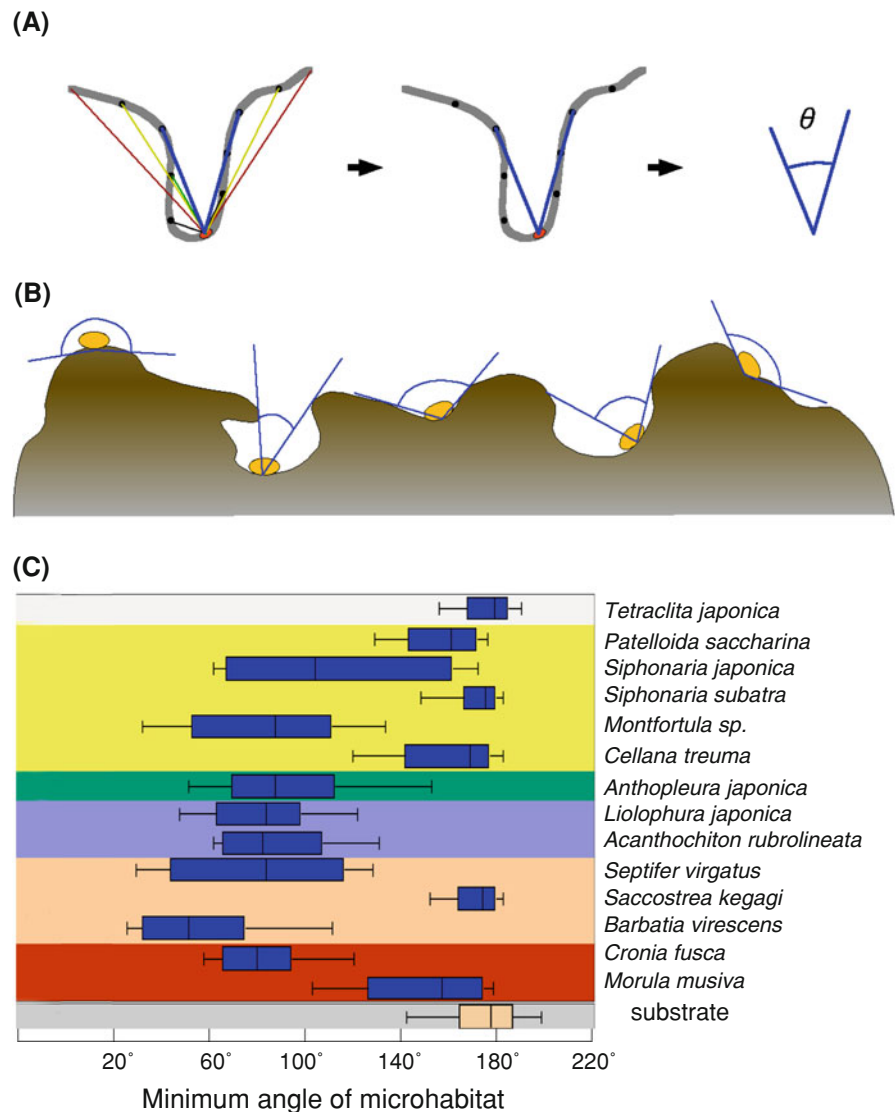
Another aspect of habitat complexity which has been inadequately handled concerns the spatial arrangement of complexity-generating elements. Let’s consider habitats with three different kinds of elements (Fig. 4A), be these crevices, rock formations, algal/moss patches, or corals of different forms. These three elements may be scattered randomly within a prescribed area (A1). Alternatively, more ‘orderly’ forms of arrangement may be observed, such as clustering of the same kind of element (A2), patches consisting of different kinds of element (A3) or zonation of elements (A4). In other words, different structural elements may not be mutually

independent, but partially related in different ways through some physical or functional processes. These again can occur at different scales and spatial patterns are most likely to vary across scales. These variable patterns of arrangement surely have different implication for habitat complexity and for the distribution and abundance of organisms. If a randomly scattered pattern (A1) is more common in nature, then an experimental design whereby different elements are closely grouped (A3) (which may be a quite common procedure to create the same numbers of replications) may produce a misleading picture, i.e. an artefact, due to interactions/influences of neighbouring elements; an opposite situation may also occur.

A simple example of the importance of varied spatial arrangement is depicted by another case of surface concavity (Fig. 4B). A substrate with a single type of concavity (B1) is replaced by habitats with two types of concavity having the same fractal dimension (B2 and B3). Geometrically, the difference between B2 and B3 concerns the relative positions of two small notches in relation to a single large notch. While fractal dimension does not distinguish cases such as these, ecological implications are bound to be different for organisms utilising these two habitats.

With respect to habitat complexity in terms of spatial arrangements of elements, we note that zonation or orderly sequence of elements (A4) is not uncommon in current-dominated systems, particularly at medium to large scales. These may occur in both vertical and horizontal planes. The phenomenon of intertidal/subtidal zonation is a typical example (Fig. 1, middle; Hughes & Barnes, 1999; Witman & Dayton, 2001). Figure 5 depicts the cases of stream and coastal systems where prevailing water currents help generate repeated habitat structures. In the upper reaches of rivers a pool-riffle sequence occurs repeatedly along the line of flow, with concomitant changes in substrate particle sizes (Fig. 5A). The current speed increases and the depth decreases from the pool to the riffle, presenting gradually changing habitat structures (Takemon, 1996; Ward & Robinson, 1999). The size of each pool-riffle sequence gradually increases downstream and the pool-riffle gradient becomes increasingly blurred, resulting in uniformly fine sediment. Thus, habitat complexity in terms of substrate variability within a fixed spatial scale is higher in upper reaches. In coastal systems, a headland-bay sequence occurs repeatedly, with

Fig. 3 Characterization of substrate topography by the minimum angle (MA) method. **A** Measurement of MA using a 10 cm wire which is bent along the cross section of substrate centred around a benthic animal. **B** Examples of variation in MA. **C** Ranges of MA (median with 95% and max/min values) for different benthic species (colour bands grouping species of similar morphological/functional characteristics) on a rocky substrate of the Tomioka Peninsula, Amakusa-Shimoshima Island



smaller substrate particles accumulating in the bays where hydrodynamics forces are reduced (Denny & Wethey, 2001). However, the sorting of particle sizes may not be as clear as in the freshwater pool-riffle system, as coastal currents are more variable, often coupled with tidal fluctuations, and consequently coasts are affected by multiple currents of different spatio-temporal scales.

Note that any orderly pattern (Fig. 4A) tends to manifest predominantly at certain scale, while it may be either non-existent or vague at other scales. This again emphasises the problem of extrapolating from one scale to another when studying habitat complexity. In sum, we note that the relative spatial

positioning or arrangement of structural elements is an important aspect of habitat complexity that would benefit from various approaches of pattern recognition (e.g. Hills et al., 1999; Fortin & Dale, 2005; Shumway et al., 2007).

Size and density of elements

An aspect of habitat complexity that has been most vigorously pursued in aquatic studies concerns the varying sizes and densities of structural elements. In this respect, one of the most conspicuous lines of investigations involved submerged aquatic plants/

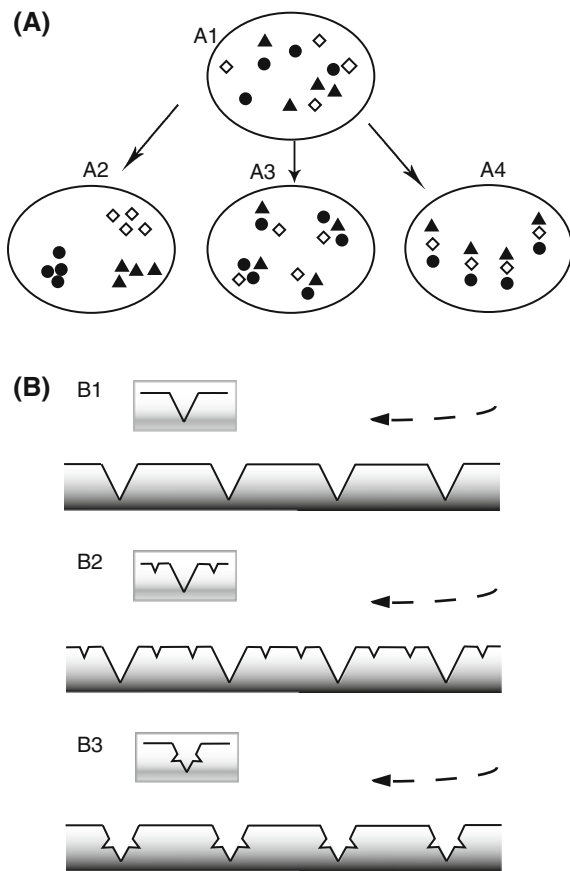


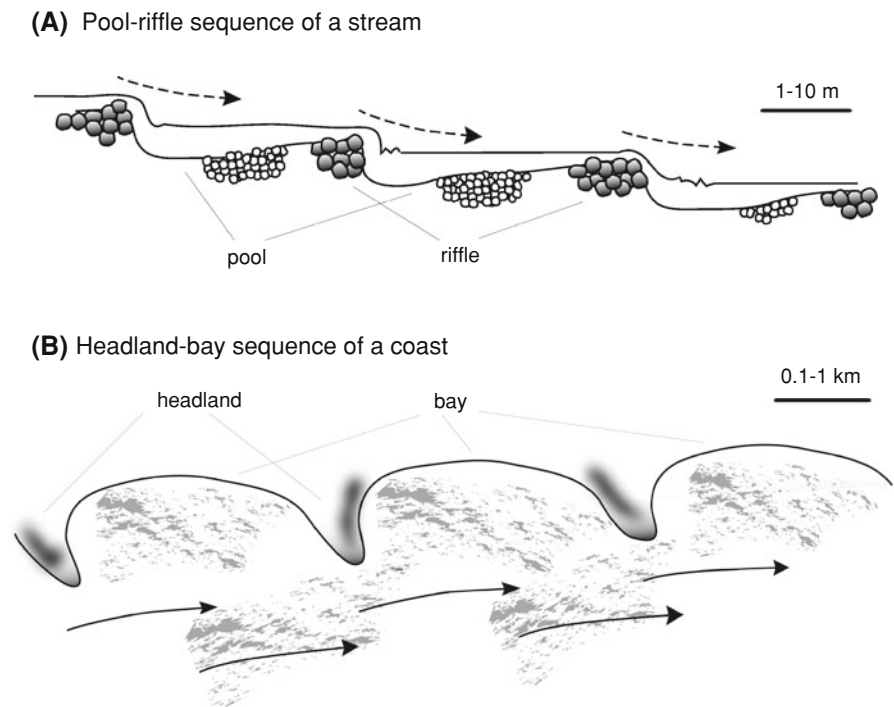
Fig. 4 **A** Spatial distribution of the structural elements of habitat. Different symbols denote different structural elements. Random occurrence (*A1*), groups of homogeneous (*A2*) and heterogeneous (*A3*) elements, and zoned arrangements (*A4*). **B** Variation in substrate topography, shown as vertical sections. Large uniform crevices (*B1*) may be modified with small crevices in different arrangements but with the same fractal dimensions (*B2* and *B3*); insets show the basic unit of each design

algae as habitats for other sessile and mobile organisms both in freshwater and marine environments (Sozka, 1975; Tokeshi & Pinder, 1985; Dudley, 1988; Gee & Warwick, 1994; Attrill et al., 2000; Taniguchi et al., 2003; Boström et al., 2006; Wilkström & Kautsky, 2007; Thomaz et al., 2008; Nohren & Odelgard, 2010). It has been widely known that greater abundances of freshwater macrophytes and sea grasses lead to higher abundances of associated organisms (Heck & Wetstone, 1977; Heck & Orth, 1980; Rennie & Jackson, 2005). In freshwater works, relative ease of making and setting artificial submerged plants in the field helped formulate research into the effects of habitat structure on the diversity and

abundances of plant-associated organisms (Macan & Kitching, 1972; Rooke, 1986; Jeffries, 1993; Taniguchi et al., 2003; Hansen et al., 2010). With both macrophyte-associated and bottom substrate-associated assemblages, experimental studies generally adopted a dichotomous design where either a presence/absence or a simple/complex setup was used as treatments. With the introduction of fractal concept, it has become more common to incorporate, (i) in field studies, a series of measurements of fractal dimension for field-derived data (e.g. Johnson et al., 2003); (ii) in experimental studies, not just a pair of simple versus complex treatments but a set of more than two treatments with increasing levels of fractal dimension representing a gradient of habitat complexity (Jeffries, 1993; Taniguchi & Tokeshi, 2004). Such gradients of complexity can be generated by progressive fragmentation of a basic shape, either of bottom substrate or submerged macrophyte (Fig. 6). This is most appropriately termed a ‘fractal design’, as similarity in shape is maintained with changing scales.

In Taniguchi & Tokeshi’s (2004) study on the benthic assemblages of a coastal stream in Amakusa, sets of stone tiles (10 × 10 cm) with five different levels of surface complexity (alternately raised surfaces in lattice form, Fig. 6, top) were used for colonisation experiments. Note that in this experimental setup, the problem of variable concavity–convexity (Fig. 2) does not exist, as the design (cross-sections, Fig. 6, top) circumvents concavity/convexity distinction. These experiments were run for 1 month in Winter, Spring and Summer. In the Winter experiment, an additional treatment with tiles pre-conditioned with biofilm (i.e. resource for benthic invertebrates) was also introduced. The results show that taxonomic diversity and the density of individuals tended to be higher in treatments with higher fractal dimension (Fig. 7A, B). Further, the fact that biomass did not change across fractal dimensions (Fig. 7C) suggests that increase in density was compensated by decrease in individual body size (see the next section). Interestingly, in terms of individual density, contrasting patterns were shown by different taxa (Fig. 7D). While *Baetis* (Ephemeroptera) increased in number with increasing fractal dimension, *Simulium* (Diptera) showed an opposite trend, demonstrating that these two taxa have different responses to changes in the surface topography of habitat. It is widely known that the latter prefers

Fig. 5 Repeated arrangements of structural elements observed along the flow of water: **A** vertical (longitudinal) section of a stream system, **B** horizontal view of a coast



habitats with fast, laminar flow of water (Tokeshi & Pinder, 1985). That different groups of organisms may respond differently to changing fractal dimension will be considered in more detail below.

In order to place results from fractal-design experiments such as these into perspective, it is worth looking into the general concept of fractal geometry in relation to ecological realities. Figure 8 shows the formation of fractal habitats, according to two different schemes of form-generation. For ease of understanding, two-dimensional sequences are shown for the eventual representation of three-dimensional habitats. While these two schemes follow similar patterning as well as fractal dimension, there are noticeable differences which have important implications for organisms. In scheme A leading to what is known as the 'Menger sponge' (i.e. three-dimensional version of the Sierpinski carpet, Mandelbrot, 1982), cavities once formed are replaced by cavities of the same sizes plus smaller ones, generating a sequence of smaller cavities. In other words, cavities once formed are retained as they are. In contrast, scheme B undergoes a progressive decrease in cavity size and a faster increase in cavity number. With respect to a two-dimensional plane, the number of cavities at the i th stage of fractioning, n_i , is

$$\text{Scheme A : } n_i = 9n_{i-1} - 8n_{i-2}$$

$$\text{Scheme B : } n_i = 9n_{i-1}$$

In consequence, scheme B leads to a more finely fragmented structure than scheme A, with fractal dimension approaching 3, i.e. the inside of a cube is infinitely packed with fragmented surfaces, leading to surface \sim volume. In contrast, the fractal dimension of the Menger sponge is ~ 2.7268 . As most organisms are primarily associated with surfaces, the simplest approach here is to consider total surfaces available per unit volume. Thus, fractal geometry envisages that the eventual form of scheme B habitat is more complex in terms of fractal dimension than that of scheme A (note that due to graphical constraints, Fig. 8 cannot effectively depict such an eventual entity which, in the case of scheme B, is a solid and a void at the same time!).

It is now apparent that a fractal design of Fig. 6, as a close analogue of scheme B fractal formation, can eventually achieve the highest level of fractal complexity (in a plane, the total length of lattice boundaries approaches the tile area). Thus, high fractal dimension is synonymous with the occurrence of numerous, smaller and smaller, structural elements. An important implication to note here is that,

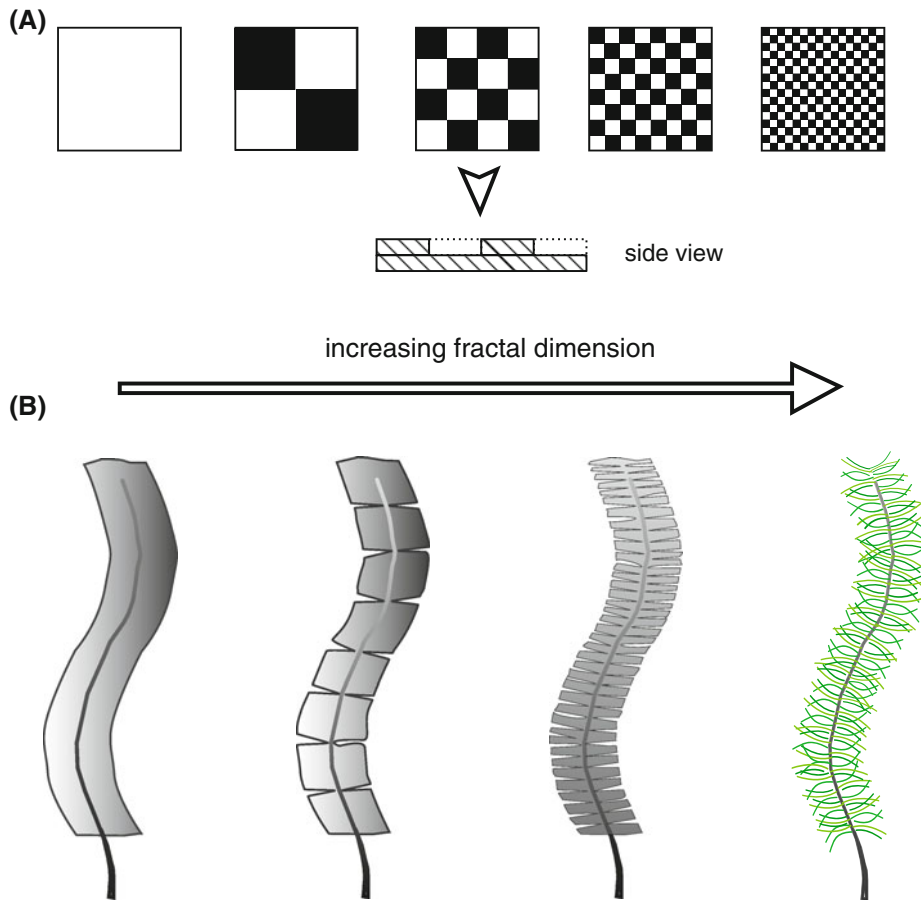


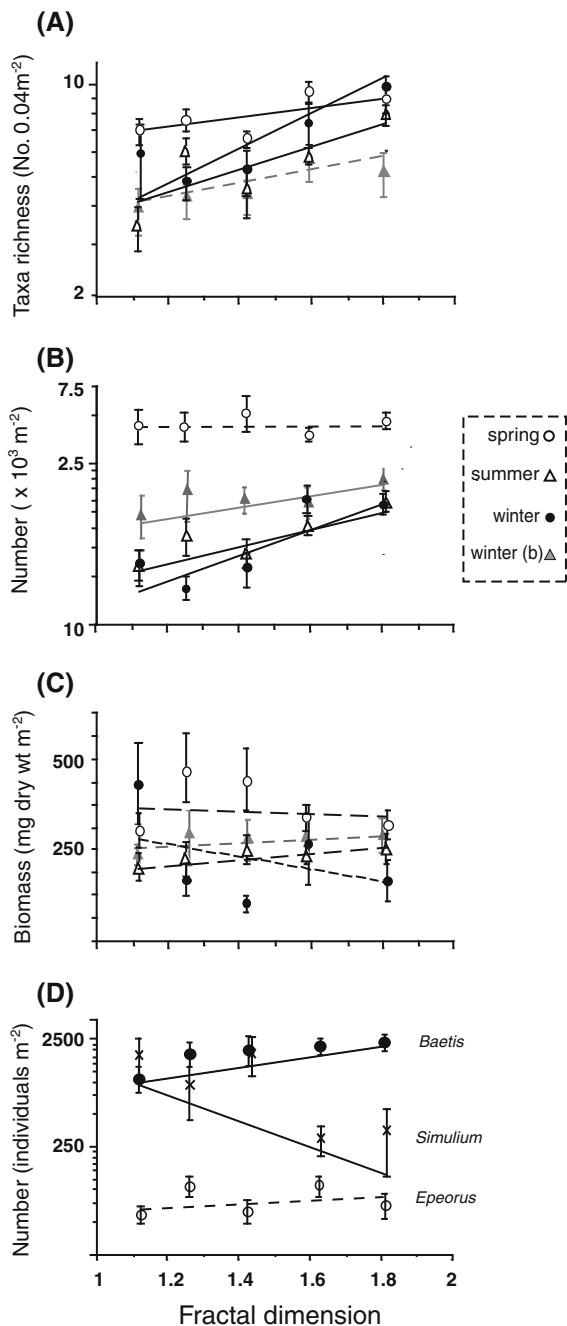
Fig. 6 Examples of fractal substrate designs for colonisation experiments in aquatic systems. **A** Tiles with high-low lattice formation used in Taniguchi & Tokeshi (2004). **B** Artificial macrophytes (simpler designs used in Taniguchi et al., 2003)

as fractal dimension increases towards more extreme cases of fractal shape, structural elements of habitat are bound to become too small to be useful for organisms of any size. In other words, fractal measure does not always represent the aspect of habitat structure that is meaningful for organisms, towards higher ends of its values. Of course, natural objects do not follow endless patterns of fragmentation, but it is important to realise that such boundaries cannot always be clear.

In comparing schemes A and B, one point that is patently missed by fractal measure is the ‘variability’ or ‘diversity’ of element (cavity) sizes. This goes back to our earlier section on the diversity of complexity-generating elements, where reference was made to the weakness of fractal concept in handling different kinds of structural elements contributing to habitat complexity. Here, cavities of

different sizes need to be recognised as qualitatively different elements (e.g. Figs. 4B, 8). Clearly, caution must be exercised in interpreting values of fractal dimension in individual cases.

In this connection, it is worth considering the possible relationships between the diversity and abundance of organisms and variation in fractal dimension (D) under different schemes (Fig. 9). Scheme A habitat is expected to have greater taxa diversity or richness than scheme B habitat due to the occurrence of different-sized taxa in the former (Fig. 9, left graph). Taxa diversity in habitat A would also increase monotonically with D , as progressively smaller elements are cumulatively added, providing microhabitats to smaller organisms. In contrast, assuming that a sufficiently large range of D is sampled, taxa diversity is likely to take a peaked pattern in habitat B, as an increase in diversity with



D comes to a halt when more taxa are lost due to too small element sizes and a stunned increase in the number of yet smaller-sized taxa. In terms of the number of individuals (Fig. 9, right graph), habitat B is likely to show a faster increase in number with D , as larger taxa/individuals are replaced by more numerous smaller individuals. However, a peak is likely to be reached more quickly in habitat B than in

◀ **Fig. 7** Variation in taxa richness, abundance (total density), biomass, and the density of particular species (in Spring) with fractal dimensions of substrate (data modified from Taniguchi & Tokeshi (2004). Winter (b) indicates the treatment with biofilm-preconditioned tiles. Continuous lines, $P < 0.05$ for slope; broken lines, $P > 0.05$. Taxa 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 (b), $y = 0.43 + 0.21x$, $r^2 = 0.09$, $P = 0.10$; Abundance: 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 (b), $y = 1.00 + 0.47x$, $r^2 = 0.15$, $P = 0.03$; 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 (b), $y = 5.12 + 2.27x$, $r^2 = 0.01$, $P = 0.56$. Density of *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*, $y = 2.67 - 1.02x$, $r^2 = 0.15$, $P = 0.004$

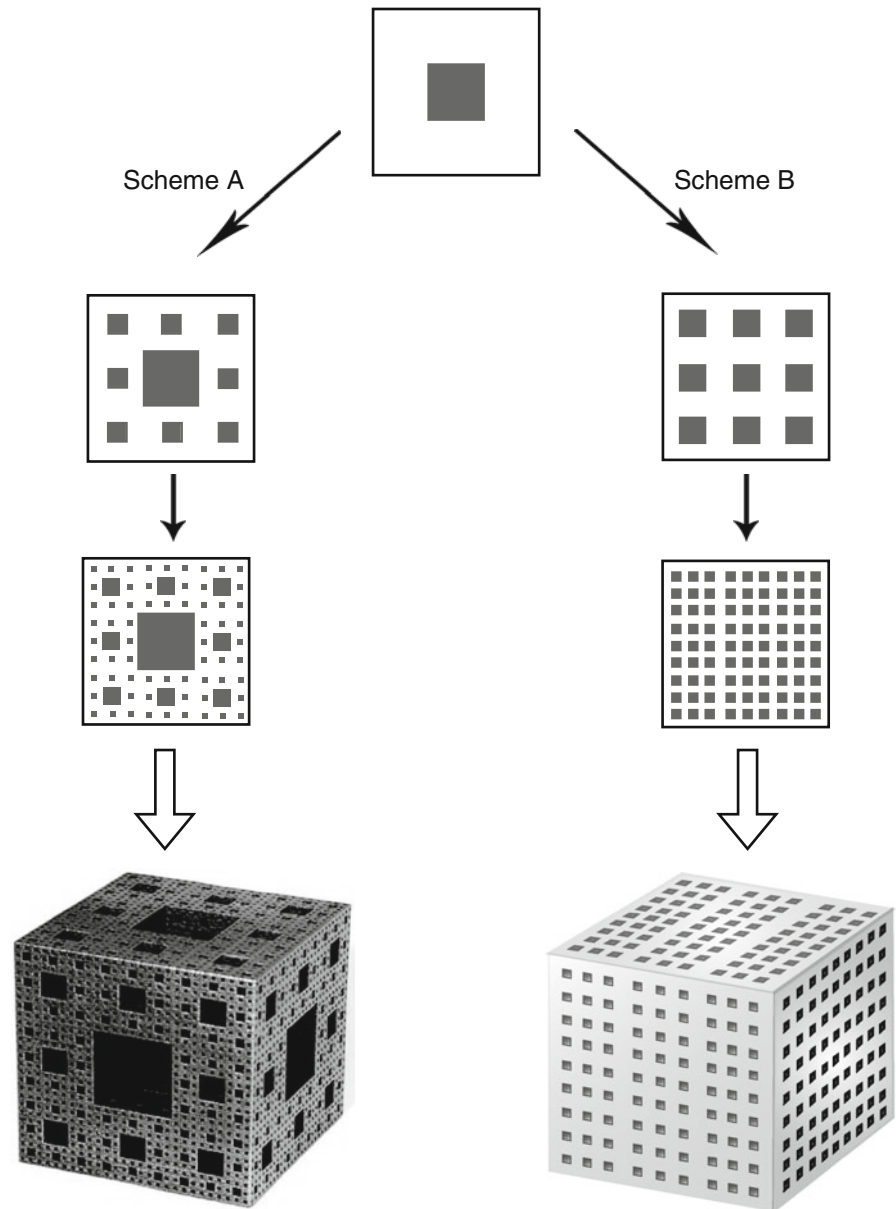
A, as the single size of habitat elements available at any one level of D may eventually constrain the rate of increase.

The patterns of taxa richness and individual numbers observed for coastal stream assemblages (Fig. 7) may correspond to the rising parts of habitat B curves to the left of a peak (Fig. 9), as it is unlikely that the range of D covered in the experiments extended to the high side where diversity/abundance of organisms on the whole are negatively affected (save some taxa such as *Simulium*). On the other hand, it is interesting to note that taxa richness was somewhat lower in the highest D treatment than in the second highest D treatment in Spring and Winter (biofilm), which might suggest that peaks in diversity had already been reached in these cases. These possibilities would need to be tested further with higher resolution data than those currently available.

Body size and the nature of habitat complexity

The previous section drew attention to an important point that high values of fractal dimension do not necessarily indicate situations compatible with what would generally be perceived as high habitat complexity. On a purely theoretical basis, the way to increase fractal dimension can be likened to an attempt to pack a continuous, convoluted line into a prescribed area so that its total length is maximised (i.e. 'line length' approaches 'area', length \sim area), or pack as many small particles as possible into a

Fig. 8 Two different schemes of fractal formation



prescribed volume to maximise the total surface area of those particles (i.e. $\text{area} \sim \text{volume}$). This can be viewed as contrasting physical settings in aquatic habitats, both above-sediment surface and below-sediment surface situations (Fig. 10, top and middle). Empirical measurements of substrate fractal dimension are known to increase with higher proportions of sand (Jia et al., 2009). Here, increased fractal dimension implies decreased mean particle size and increased total surface area of particles, which may in turn lead to higher species richness (e.g. McLachlan,

1996). In many aquatic environments, however, decreased particle sizes generally mean unstable substrates that may harbour a reduced abundance of benthos (Donohue & Irvine, 2003; Rae, 2004), particularly under current/wave-impacted conditions. It is well known, for example, that fish tend to be attracted to three-dimensional structures generated by stable artificial reefs where unstable substrates predominate (Bohnsack, 1991; Gratwicke & Speight, 2005). Clearly, the (potential) importance of the fractal dimension of habitat may vary with the

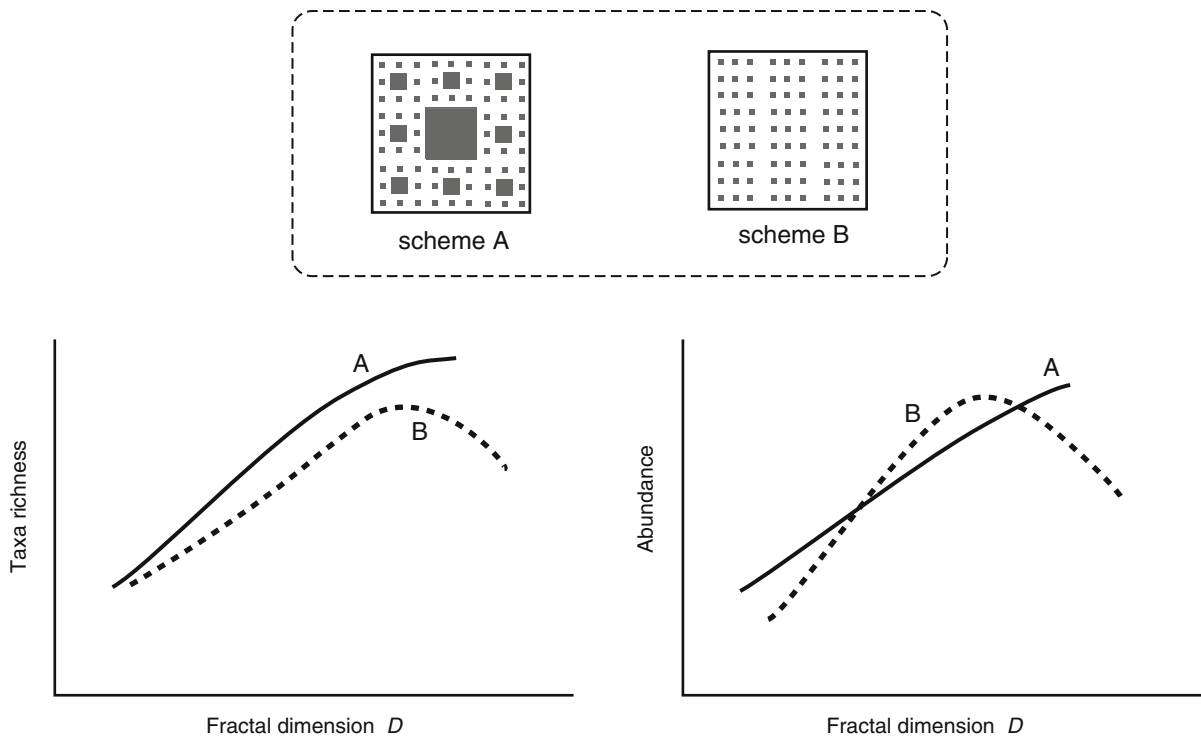


Fig. 9 Hypothetical relationship between fractal dimension and (*left*) taxa richness and (*right*) abundance of organisms for two different types of fractal habitats

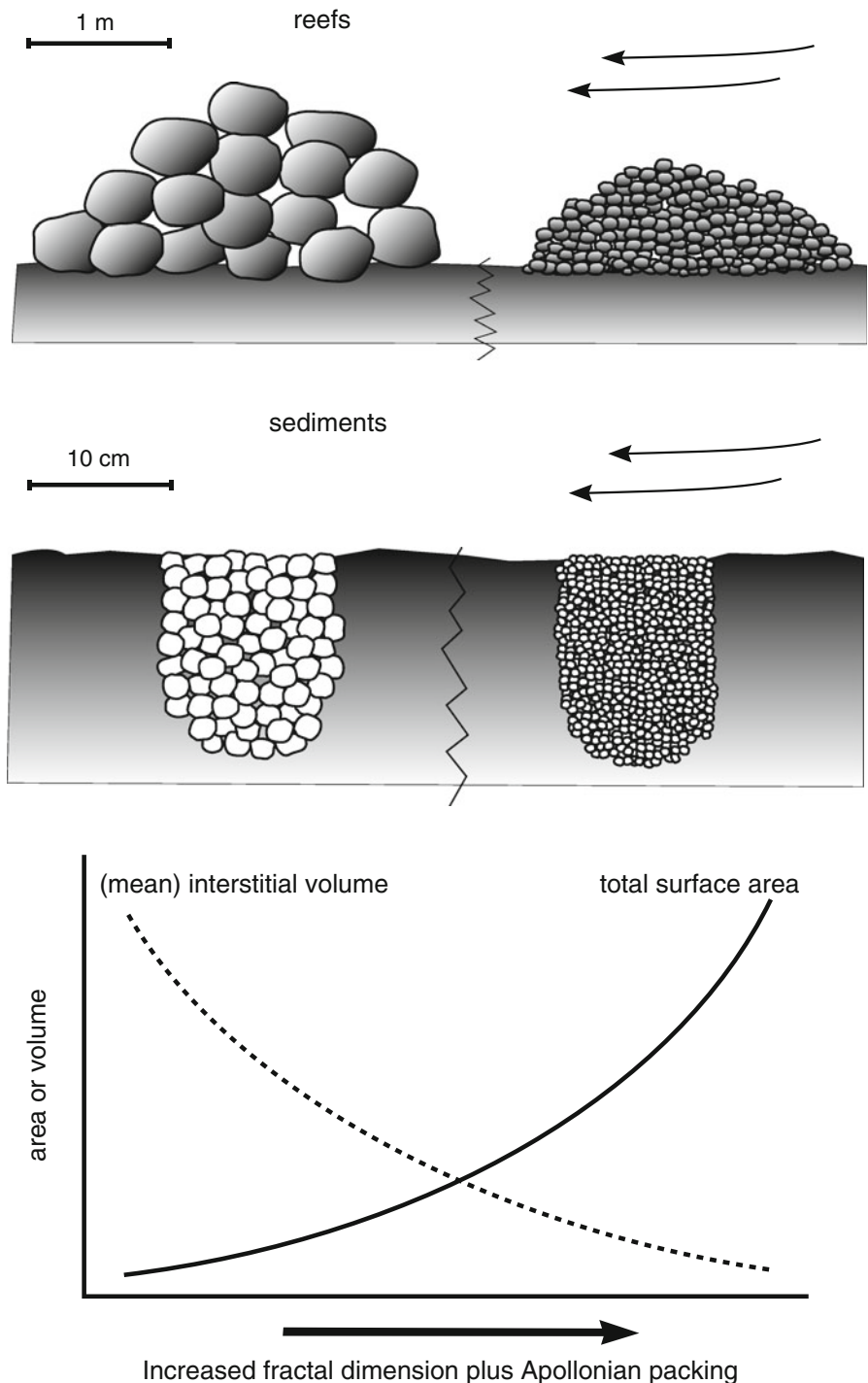
identity as well as relative body size of organisms. Further, benthic organisms often show preferences for substrates of certain particle sizes (e.g. lotic larval chironomids—Rae, 2004; benthic gobiids—Arakaki & Tokeshi, 2005). Because substrate particles are used not only as habitat but also as food by many benthic organisms, the implications of variable sediment particle sizes can be complex. In general, higher species diversity tends to be associated with a greater diversity of particle sizes (Etter & Grassle, 1992).

While increased total absolute surface area accrues to smaller particle sizes, inhabitable, stable interstitial space is reduced (Fig. 10). This is particularly the case, as small particles of different shapes and sizes are more likely to form tighter, quasi-Apollonian type packing (i.e. filling-up of space by progressively small particles, Mandelbrot, 1982) with resultant loss of interstitial space. Added to this, small particle sizes would also imply a greater tendency of particle agglomeration and coagulation depending on physico-chemical properties of different particles, which means loss of usable surface

areas as well as interstitial space. In all, less habitable space may be available despite high fractal dimensions of substrate particles (or, effectively leading to ‘reduced’ fractal dimension) with very small particle sizes.

This problem of reduced habitable space for organisms in highly fragmented, high D habitats is in fact a manifestation of the fundamental characteristics of benthic existence: an organism possesses a definite size hence it requires space (volume) to exist, while its resource intake is predominantly a surface-dependent activity. Thus, both the two-dimensional surface and the three-dimensional volume are required at the same time by these organisms. Quite importantly, however, theory dictates that these two traits of a habitat cannot be increased at the same time; a trade-off tends to occur between changes in surface area and volume (interstitial space) (Fig. 10, *bottom*). Corollary to this is that an intermediate level of fractal dimension (or ‘intermediate-high’ rather than ‘high-high’ level) is more likely to represent the state of maximum habitat complexity which would provide more habitable space, overall, to an

Fig. 10 Contrasting situations of substrate packing with different particle sizes: *top* above-substrate and *middle* below-substrate cases illustrated. The graph (*bottom*) shows hypothetical relationships between increasing fractal dimension (*horizontal axis*) and interstitial volume (*dotted line*) and particle surface area (*continuous line*)



assemblage of organisms (e.g. scheme A habitat > scheme B habitat, with respect to void or shaded area in Fig. 8), leading to highest diversity/abundances of species/individuals. Situations analogous to this have been reported from both empirical

(juvenile cod inhabiting *Zostera* meadows (Thistle et al., 2010)) and theoretical (coexistence of species in a model landscape, Palmer (1992)) studies.

Where high fractal dimension involves uniformly decreasing element size such as in Fig. 6 and scheme B,

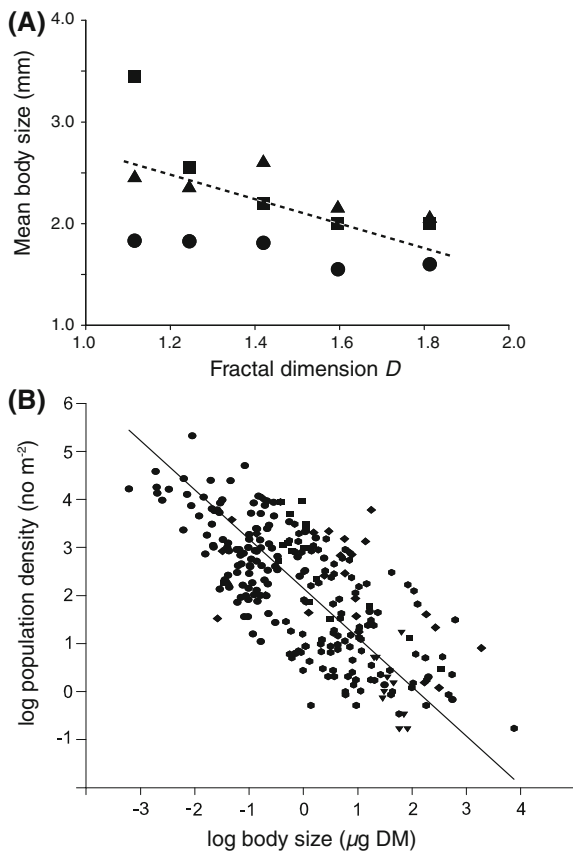


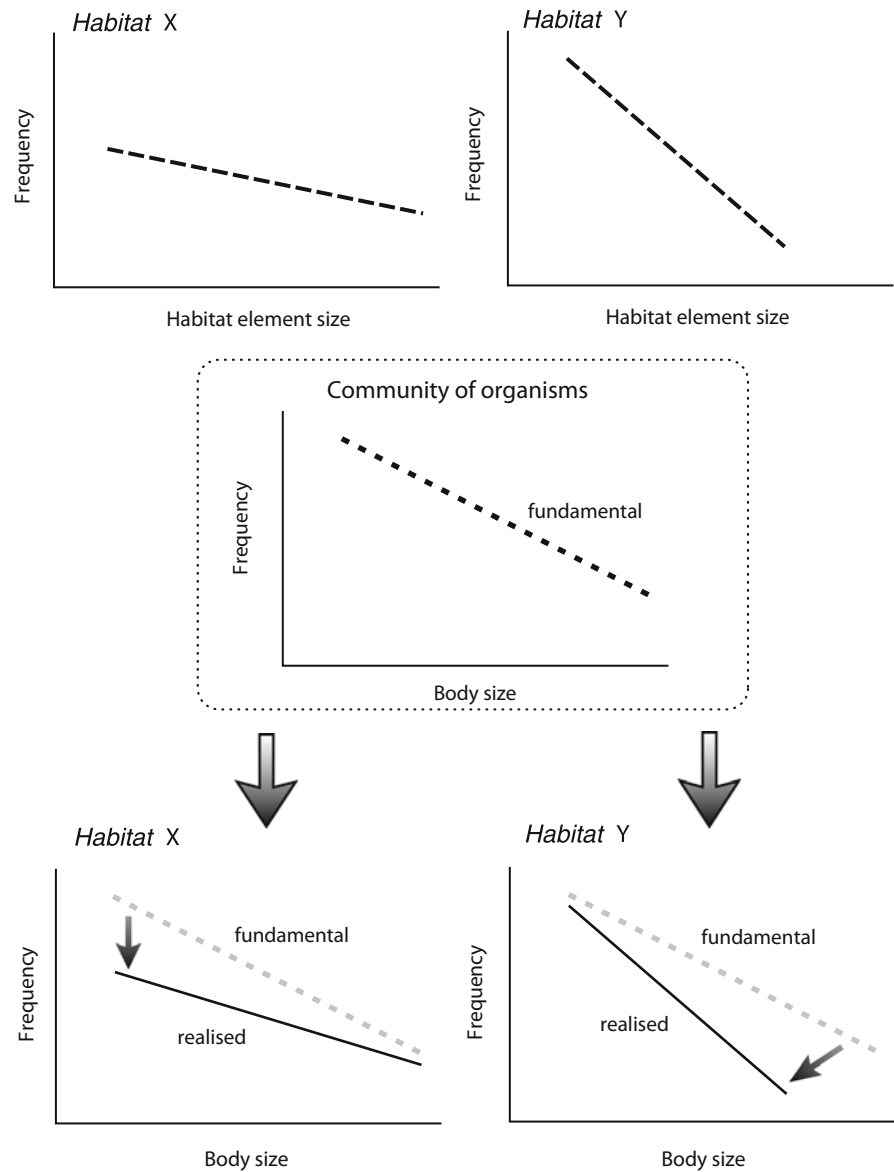
Fig. 11 **a** Variation in benthos body size with habitat fractal dimension (data modified from Taniguchi & Tokeshi, 2004). Filled square Summer; filled triangle Winter; filled circle Spring. Regression equation is: $y = 3.55 - 0.963x$, $r^2 = 0.265$, $P < 0.05$. **b** Relationship between population density and mean body size of stream benthic taxa from Mynach, North Wales (data from Schmid et al., 2000). Regression equation (bisector regression) is: $y = 2.15 - 1.03x$, $r^2 = 0.511$, $P < 0.001$

the size of organisms inhabiting would decline with D (e.g. Fig. 11A). An important issue related to this is the size distribution of organisms in aquatic assemblages (Marquet et al., 1990; Schmid et al., 2000). Schmid et al.'s (2000) comprehensive data on stream communities demonstrated a clearly declining population density of benthic invertebrates with body size (Fig. 11B). In parallel with this, the number of taxa also scaled negatively with body size. Here, we can combine these body size-related community characteristics with the information on the relative abundances of habitat elements (e.g. crevices) of different sizes that affect the occurrence of invertebrates. For example, size-frequency distributions of habitat elements would vary

from an extreme case of just single-size elements (scheme B) to more variable cases such as in scheme A where the numbers of different-sized elements vary in a geometrical manner (the number of the i th largest element is $X_i = 8X_{i-1} = 8^{i-1}$). In Fig. 12, two habitats X and Y are assumed to have different patterns of relative abundances of structural elements, with pronounced predominance of small elements in habitat Y compared with habitat X. If the size frequency distribution of organisms in this system on the whole is as depicted by the top graph of Fig. 12, structural differences between habitats X and Y would lead to differences in observed or realised patterns of body size. Habitat X describes the situation where small structural elements are relatively more scarce than the relative abundance of organisms of corresponding body size (shallower 'habitat' slope than 'organism' slope), leading to a stronger depression or reduction in realised abundance of small-sized organisms (Fig. 12, bottom left). An opposite situation pertains to habitat Y where the scarcity of large structural elements is more pronounced compared with the relative abundance of large-sized organisms. Consequently, the abundance of large-sized organisms is more strongly depressed in the realised assemblage (Fig. 12, bottom right). This would correspond to the experimental result illustrated in Fig. 11A where average body size declined with increasing fractal dimension D . In a similar vein, steepening of the slope of number-body size relations with D was observed for rocky shore macro-invertebrates (Kostylev et al., 2005).

This consideration of size-related aspects has a potentially important implication for the issues of biodiversity conservation in relation to habitat complexity. If a regional aquatic assemblage presents an abundance-body size relationship such as in Fig. 12, the optimal habitat structure for retaining the highest biodiversity should encompass the pattern of element size distribution matching that of organismal body size distribution. A mismatch between the element size distribution and the body size distribution is most likely to result in a significant loss of some parts of the wider, background community of organisms. In this respect, the balance in availability among habitat elements of different sizes is considered most important, as the abundances of large organisms tend to depend on those of smaller ones. Thus, we can hypothesise that habitats containing different kinds of structural elements, including structures of different sizes, in proportions

Fig. 12 Possible linkage between body size frequencies of community members and habitat structure. Fundamental (regional/larger scale) and realised (local/smaller scale) patterns of body size frequency distributions (*lower graphs*) are shown for two habitats X and Y with contrasting size-frequency distributions of structural elements of habitat (*top graphs, broken lines*) (see text for explanations)



more or less corresponding to the size distributions of (groups of) organisms, would contribute most to enhancing and preserving biodiversity.

Towards an integrative understanding of the relationships between habitat complexity and community structure

Earlier we have pointed out that habitat complexity should be interpreted as an integrative term covering different aspects that contribute to the overall

structural complexity. This is more in line with the use of the term ‘complexity’ in other areas of research, in particular evolutionary biology and dynamical systems theory. In both of these, the conceptual basis of ‘complexity’ is in essence the totality of information, i.e., all the information combined that is involved in the realisation of a particular system under consideration (Bonner, 1988; Gell-Mann & Lloyd, 1996; McShea, 1996, 2000; Adami & Cerf, 2000; Adami, 2004). The difficulty is to identify what information is relevant and what is not for such realisation. However, this practical difficulty should

not be taken as a valid reason to avoid the integrative interpretation of complexity in favour of a more restrictive one. The bottom line here is that both logical necessity and empirical knowledge dictate that variation in ‘complexity’ cannot be equated with variation in the quantity of elements alone, be it a physical or a biological system. At the very least, the use of the term habitat ‘complexity’ embodies a desire on the part of ecologists to quantify ‘that thing about habitat’ that help maintain the diversity of organisms occurring in given space. This inevitably makes habitat complexity a multi-factorial, multi-faceted entity, as organisms respond to multiple facets of habitat even in terms of physical structures alone. In evolutionary biology, the complexity of organisms (Bonner, 1988) is considered to be mirrored in nucleic acid sequences from which all organisms derive; as such, not only the quantity of nucleic acids but their arrangements are vitally important (Adami et al., 2000). In analogy, habitat complexity cannot be ascribed to the abundance of structural elements alone.

Following this perspective, the present review has emphasised the combined importance of (i) scale, (ii) diversity, (iii) spatial arrangement, (iv) size and (v) abundance of structural elements in generating the habitat complexity of aquatic systems. While not exhaustive, these may be considered a minimum set of traits that combine to characterise what is intuitively perceived as the structural complexity of habitats, as has been demonstrated in the preceding sections. Of these five traits, the concept of fractal dimension fully encompasses only the last one, the abundance/density of structural elements, while size (not variation in size) is only indirectly covered as a negative correlate of abundance (e.g. Fig. 6). By definition, scale is irrelevant for fractal dimension (i.e. scale-invariance), while the diversity and spatial arrangement of elements are completely outside its scope. Thus, fractal measures represent only a partial characterisation of habitat complexity. It is therefore important to examine, alongside the observation of fractal measures, exactly which traits of habitat structure are exerting influences on organisms/communities. In this sense, habitat complexity is clearly more complex than what fractal measures represent.

The above argument suggests that the structural complexity of habitat, ω , may be represented as a scale-dependent function,

$$\omega_m \sim aH_E + bH_S + cH_{E,S} + \sum^{ES} d_{ij}N_{ij} + Q(N_{i,j})$$

where ω_m is habitat complexity at spatial scale m , H_E is the diversity of structural elements (E) recognised at scale m , H_S is the diversity of the sizes of elements (S), $H_{E,S}$ is part of diversity due to the interaction between element kind and size ($c = 0$ if there is no interaction), N_{ij} is the abundance/density of element i of size j , Q is a sub-function representing the effect of spatial distribution of elements, and a , b , c , $d_{i,j}$ are parameters. For example, the value of a H_E would be greater for the case of Fig. 2C than for Fig. 2A or B, and bH_S is greater for scheme A of Fig. 8 than for scheme B. Note that the combination of $a = b = c = Q = 0$ and $d_{i,j} = 1$ would make ω_m conceptually akin to fractal measures. Clearly, the form of function Q needs to be investigated, alongside the values of $aH_E + bH_S + cH_{E,S}$, for an integrative understanding of habitat complexity.

In most aquatic ecosystems, broadly two-dimensional structures of bottom substrate at the scale of 1–10 m mean that the addition of vertical, three-dimensional structures (e.g. artificial reefs) almost always implies an increased availability of usable microhabitats and thus would help increase the abundance and diversity of organisms. Under these circumstances, both the ‘diversity’ ($aH_E + bH_S + cH_{E,S}$) and ‘abundance’ ($\sum^{ES} d_{ij}N_{ij}$) components of structural elements are increased, resulting in more habitats being made available to organisms of different sizes and functional designs. Conversely, loss of such structures leads to a significant decline in benthic diversity (Thrush et al., 2001).

Whether or not a concept such as habitat complexity is of value would depend upon to what extent it can contribute to facilitating and focusing research. To date it has at least succeeded in drawing the collective attention of both marine and freshwater ecologists to the mechanics of diversity in aquatic systems. Given the importance of habitats for organisms, the conservation and management of aquatic ecosystems would be facilitated by more critical assessments of the linkages between habitat complexity and aquatic communities (e.g. Zajac, 2008). In this respect, from both theoretical and empirical points of view, an integrative approach to habitat complexity seems to offer a useful and versatile framework.

Acknowledgments Thanks are due to Drs Nojima, Yoko-o, Kurimoto and other (past) members of the AMBL-Kyushu University for various forms of assistance. This work was financially supported by the Kyushu University P & P program, the GCOE program (Centre of excellence for Asian conservation ecology as a basis of human-nature mutualism) of the Ministry of Education, Culture, Sports, Science and Technology and the scientific research grants from the Japan Society for the Promotion of Science.

References

- Adami, C., 2002. What is complexity? *BioEssays* 24: 1085–1094.
- Adami, C., 2004. Information theory in molecular biology. *Physics of Life Reviews* 1: 3–22.
- Adami, C. & N. J. Cerf, 2000. Physical complexity of symbolic sequences. *Physica D* 137: 62–69.
- Adami, C., C. Ofria & T. C. Collier, 2000. Evolution of biological complexity. *Proceedings of the National Academy of Sciences USA* 97: 4463–4468.
- Arakaki, S. & M. Tokeshi, 2005. Microhabitat selection in intertidal gobiid fishes: species and size-associated interaction. *Marine Biology Research* 1: 39–47.
- Arakaki, S. & M. Tokeshi, 2011. Analysis of spatial niche structure in coexisting tidepool fishes: null models based on multi-scale experiments. *Journal of Animal Ecology* 80: 137–147.
- Attrill, M. J., J. A. Strong & A. A. Rowden, 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23: 114–121.
- August, P. V., 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64: 1495–1507.
- Bell, S. S. & L. D. Coen, 1982. Investigations on epibenthic meiofauna I. Abundances on and repopulation of the tubecaps of *Diopatra cuprea* (Polychaeta: Onuphidae) in a subtropical system. *Marine Biology* 67: 303–309.
- Bell, S. S., E. D. McCoy & H. R. Mushinsky, 1991. *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London.
- Bohnsack, J. A., 1991. Habitat structure and the design of artificial reefs. In Bell, S. S., E. D. McCoy & H. R. Mushinsky (eds), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London: 412–426.
- Bonner, J. T., 1988. *The Evolution of Complexity*. Princeton University Press, Princeton.
- Boström, C., E. L. Jackson & C. A. Simenstad, 2006. Seagrass landscapes and their effects on associated fauna: a review. *Estuarine, Coastal and Shelf Science* 68: 383–403.
- Bruno, J. F. & M. D. Bertness, 2001. Habitat modification and facilitation in benthic marine communities. In Bertness, M. D., S. D. Gaines & M. E. Hay (eds), *Marine Community Ecology*. Sinauer, Sunderland, MA: 201–218.
- Carter, R. W. G., 1988. *Coastal Environments*. Academic Press, London.
- Commuto, J. A. & B. R. Rusignuolo, 2000. Structural complexity in mussel beds: the fractal geometry of surface topography. *Journal of Experimental Biology and Ecology* 255: 133–152.
- Denny, M. & D. Wethey, 2001. Physical processes that generate patterns in marine communities. In Bertness, M. D., S. D. Gaines & M. E. Hay (eds), *Marine Community Ecology*. Sinauer, Sunderland, MA: 3–37.
- Donohue, I. & K. Irvine, 2003. Effects of sediment particle size composition on survivorship of benthic invertebrates from Lake Tanganyika, Africa. *Archiv für Hydrobiologie* 157: 131–144.
- Downes, B. J., P. S. Lake, E. S. G. Schreiber & A. Glaister, 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs* 68: 237–257.
- Downes, B. J., P. S. Lake, E. S. G. Schreiber & A. Glaister, 2000. Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia* 123: 569–581.
- Dudley, T. L., 1988. The role of plant complexity and epiphyton in colonization of macrophytes by stream insects. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 23: 1153–1158.
- Etter, R. J. & J. F. Grassle, 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* 360: 576–578.
- Fortin, M.-J. & M. Dale, 2005. *Spatial Analysis*. Cambridge University Press, Cambridge.
- Frost, N. J., M. T. Burrows, M. P. Johnson, M. E. Hanley & S. J. Hawkins, 2005. Measuring surface complexity in ecological studies. *Limnology and Oceanography: Methods* 3: 203–210.
- Gee, J. M. & R. M. Warwick, 1994. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Marine Ecology Progress Series* 103: 141–150.
- Gell-Mann, M. & S. Lloyd, 1996. Information measures, effective complexity, and total information. *Complexity* 2: 44–52.
- Gratwicke, B. & M. R. Speight, 2005. Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series* 292: 301–310.
- Halley, J. M., S. Hartley, A. S. Kallimanis, W. E. Kunin, J. J. Lennon & S. P. Sgardelis, 2004. Uses and abuses of fractal methodology in ecology. *Ecology Letters* 7: 254–271.
- Hansen, J. P., J. Sagerman & S. A. Wilkström, 2010. Effects of plant morphology on small-scale distribution of invertebrates. *Marine Biology* 157: 2143–2155.
- Heck, K. L. & R. J. Orth, 1980. Seagrass habitats: the roles of habitat complexity, competition, and predation in structuring associated fish and motile macroinvertebrate assemblages. In Kennedy, V. S. (ed.), *Estuarine Perspectives*. Academic Press, New York: 449–464.
- Heck, K. L. Jr., & G. S. Wetstone, 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4: 135–142.
- Hills, J. M., J. C. Thomason & J. Muhl, 1999. Settlement of barnacle larvae is governed by Euclidean and not fractal surface characteristics. *Functional Ecology* 13: 868–875.
- Hughes, R. N. & R. S. K. Barnes, 1999. *An Introduction to Marine Ecology*. Wiley-Blackwell, Oxford.

- Hurlbert, A. H., 2004. Species–energy relationships and habitat complexity in bird communities. *Ecology Letters* 7: 714–720.
- Jeffries, M., 1993. Invertebrate colonization of artificial pondweeds of differing fractal dimension. *Oikos* 67: 142–148.
- Jia, X. H., X. R. Li, J. G. Zhang & Z. S. Zhang, 2009. Analysis of spatial variability of the fractal dimension of soil particle size in *Ammopiptanthus mongolicus*’ desert habitat. *Environmental Geology* 58: 953–962.
- Johnson, M. P., N. J. Frost, M. W. J. Mosley, M. F. Roberts & S. J. Hawkins, 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. *Ecology Letters* 6: 126–132.
- Kawai, T. & M. Tokeshi, 2004. Variable modes of facilitation in the upper intertidal: goose barnacles and mussels. *Marine Ecology Progress Series* 272: 203–213.
- Koivisto, M. E. & M. Westerbom, 2010. Habitat structure and complexity as determinants of biodiversity in blue mussel beds on sublittoral rocky shores. *Marine Biology* 157: 1463–1474.
- Kostylev, V. E., J. Erlandsson, Y. M. Mak & G. A. Williams, 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: fractal application on rocky shores. *Ecological Complexity* 2: 272–286.
- Kurimoto, M. & M. Tokeshi, 2010. Variation on a theme of herbivory: *Corallina*-hermit crab relationship on a temperate-subtropical rocky shore. *Oikos* 119: 1401–1408.
- Lassau, S. A. & D. F. Hochuli, 2004. Effects of habitat complexity on ant assemblages. *Ecography* 27: 157–164.
- Lassau, S. A., G. Cassis, P. K. J. Flemons, L. Wilkie & D. F. Hochuli, 2005. Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns? *Ecography* 28: 495–504.
- Li, B. L., 2000. Fractal geometry applications in description and analysis of patch patterns and patch dynamics. *Ecological Modelling* 132: 33–50.
- Lingo, M. E. & S. T. Szedlmayer, 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. *Environmental Biology of Fishes* 76: 71–80.
- Londoño-Cruz, E. & M. Tokeshi, 2007. Testing scale-variance in species-area and abundance-area relationships in a local assemblage: an example from a subtropical boulder shore. *Population Ecology* 49: 275–285.
- Macan, T. T. & A. Kitching, 1972. Some experiments with artificial substrata. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 18: 213–220.
- MacArthur, R. H. & J. W. MacArthur, 1961. On bird species diversity. *Ecology* 42: 594–598.
- Magurran, A. E., 2004. *Measuring Biological Diversity*. Wiley-Blackwell, Oxford.
- Mandelbrot, B. B., 1982. *The Fractal Geometry of Nature*. W. H. Freeman, San Francisco.
- Mann, K. H. & J. R. N. Lazier, 1996. *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans*. Blackwell Science, Cambridge, MA.
- Marquet, P. A., S. A. Navarette & J. C. Castilla, 1990. Scaling population density to body size in rocky intertidal communities. *Science* 250: 1125–1127.
- McCoy, E. D. & S. S. Bell, 1991. Habitat structure: the evolution and diversification of a complex topic. In Bell, S. S., E. D. McCoy & H. R. Mushinsky (eds), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London: 3–27.
- McLachlan, A., 1996. Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series* 131: 205–217.
- McShea, D. W., 1996. Metazoan complexity and evolution: is there a trend? *Evolution* 50: 477–492.
- McShea, D. W., 2000. Functional complexity in organisms: parts as proxies. *Biology and Philosophy* 15: 641–668.
- Moore, E. C. & K. A. Hovel, 2010. Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. *Oikos* 119: 1299–1311.
- Morse, D. R., J. H. Lawton, M. M. Dodson & M. H. Williamson, 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314: 731–733.
- Nohren, E. & E. Odelgard, 2010. Response of epibenthic faunal assemblages to varying vegetation structures and habitat patch size. *Aquatic Biology* 2: 139–148.
- Nozawa, Y., M. Tokeshi & S. Nojima, 2008. Structure and dynamics of a high-latitude scleractinian coral community in Amakusa, southwestern Japan. *Marine Ecology Progress Series* 358: 151–160.
- O’Connor, N. A., 1991. The effects of habitat complexity on the macroinvertebrate colonizing wood substrates in lowland stream. *Oecologia* 75: 132–140.
- Ota, N. & M. Tokeshi, 2000. A comparative study of feeding and growth in two coexisting species of carnivorous gastropods. *Marine Biology* 136: 101–114.
- Palmer, M. W., 1992. The coexistence of species in fractal landscapes. *American Naturalist* 139: 375–397.
- Paruntu, C. P. & M. Tokeshi, 2003. Variability in the reproductive characteristics of local populations of an intertidal gastropod, *Nerita japonica* (Dunker). *Benthos Research* 58: 7–14.
- Rae, J. G., 2004. The colonization response of lotic chironomid larvae to substrate size and heterogeneity. *Hydrobiologia* 524: 115–124.
- Rennie, M. D. & L. J. Jackson, 2005. The influence of habitat complexity on littoral invertebrate distributions: patterns differ in shallow prairie lakes with and without fish. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2088–2099.
- Rooke, J. B., 1986. Macroinvertebrates associated with macrophytes and plastic imitations in the Erasoma River, Ontario, Canada. *Archiv für Hydrobiologie* 106: 307–325.
- Safriel, U. N. & M. N. Ben-Eliahu, 1991. Habitat structure: the evolution and diversification of a complex topic. In Bell, S. S., E. D. McCoy & H. R. Mushinsky (eds), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London: 349–369.
- Schmid, P. E., 2000. Fractal properties of habitat and patch structure in benthic ecosystems. *Advances in Ecological Research* 30: 339–401.

- Schmid, P. E., M. Tokeshi & J. M. Schmid-Araya, 2000. Relationship between population density and body size in stream communities. *Science* 289: 1157–1160.
- Sebens, K. P., 1991. Habitat structure and community dynamics in marine benthic systems. In Bell, S. S., E. D. McCoy & H. R. Mushinsky (eds), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London: 211–234.
- Shumway, C. A., H. A. Hofmann & A. P. Dobberfuhl, 2007. Quantifying habitat complexity in aquatic ecosystems. *Freshwater Biology* 52: 1065–1076.
- Sozka, G. J., 1975. Ecological relations between invertebrates and submerged macrophytes in the lake littoral. *Ekologia polska* 23: 393–415.
- Sugihara, G. & R. M. May, 1990. Applications of fractals in ecology. *Trends in Ecology & Evolution* 5: 79–86.
- Takemon, Y., 1996. Management of biodiversity in aquatic ecosystems: dynamic aspects of habitat complexity in stream ecosystems. In Abe, T., S. Levin & M. Higashi (eds), *Ecological Perspective of Biodiversity*. Springer-Verlag, New York: 259–275.
- Taniguchi, H. & M. Tokeshi, 2004. Effects of habitat complexity on benthic assemblages in a variable environment. *Freshwater Biology* 49: 1164–1178.
- Taniguchi, H., S. Nakano & M. Tokeshi, 2003. Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshwater Biology* 48: 718–728.
- Thistle, M. E., D. S. Schneider, R. S. Gregory & N. J. Wells, 2010. Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity. *Marine Ecology Progress Series* 405: 39–56.
- Thomaz, S. M., E. D. Dibble, L. R. Evangelista, J. Higuti & L. M. Bini, 2008. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. *Freshwater Biology* 53: 358–367.
- Thrush, S. F., J. E. Hewitt, G. A. Funnell, V. J. Cummings, J. Ellis, D. Schultz, D. Talley & A. Norkko, 2001. Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. *Marine Ecology Progress Series* 223: 277–286.
- Tokeshi, M., 1993. Species abundance patterns and community structure. *Advances in Ecological Research* 24: 111–186.
- Tokeshi, M., 1995. Polychaete abundance and dispersion patterns: a non-trivial ‘infaunal’ assemblage on the Pacific South American rocky shore. *Marine Ecology Progress Series* 125: 137–147.
- Tokeshi, M., 1999. *Species Coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.
- Tokeshi, M. & L. C. V. Pinder, 1985. Microhabitats of stream invertebrates on two submersed macrophytes with contrasting leaf morphology. *Holarctic Ecology* 8: 313–319.
- Tokeshi, M. & L. Romero, 1995. Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Marine Ecology Progress Series* 119: 167–176.
- Tokeshi, M. & K. Tanaka, 2010. Dominance of tabular Acroporid species and the abundance of echinoid grazers in high-latitude coral assemblages of Amakusa, southwestern Japan. *Galaxea* 12: 87.
- Ward, R. & M. Robinson, 1999. *Principles of Hydrology*. McGraw-Hill, Maidenhead.
- Wilkström, S. A. & L. Kautsky, 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science* 72: 168–176.
- Williams, S. L. & K. L. Heck Jr., 2001. Seagrass community ecology. In Bertness, M. D., S. D. Gaines & M. E. Hay (eds), *Marine Community Ecology*. Sinauer, Sunderland: 317–337.
- Witman, J. D. & P. K. Dayton, 2001. Rocky subtidal communities. In Bertness, M. D., S. D. Gaines & M. E. Hay (eds), *Marine Community Ecology*. Sinauer, Sunderland: 339–366.
- Zajac, R. N., 2008. Macrobenthic biodiversity and sea floor landscape structure. *Journal of Experimental Biology and Ecology* 366: 198–203.