

**Full Length Research Paper**

## Biotic Forces Shaping Benthic Communities : A Critical Review of the Role of Niche Interactions

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**Abstract**

*Ecologists have long been interested in the role of biotic forces in shaping communities. This interest has focused on the way species interact and the differences in the way they utilize resources in the same community and the consequences of such relationships for ecosystem processes and function. Detection of patterns in community organization, the identification of dominant forces that underlie these patterns, and the more universal application of theories to elucidate patterns are often major goals in the study of an ecological community. Given the complexity of most ecological systems however, the identification of causative mechanisms influencing community organization is extremely difficult. Observed community patterns may be the result of responses to spatial or temporal change in the environment, to competition, to predation, to chance events, or to the product of two or more interacting processes. Although long-term environmental fluctuations and spatial heterogeneity in substrate characteristics have been shown to influence benthic community patterns, subtle biological factors are also thought to significantly affect community organization changes. The presentations made in this review will buttress and further aid the syntheses of basic understanding of the systematic importance of niche relationship and interactions as determinants of the nature of benthic biocoenosis and processes taking place in the benthic region.*

**Keywords:** *Biotic forces, Niche interaction, benthic communities.*

**Introduction**

Not long after Grinnell (1924) introduced the concept of niche to ecology, Elton (1927) prominently featured niche as one of four principles regulating communities, defining an organism's niche as "its place in the biotic environment, its relations to food and enemies. Hutchinson's (1957) reformulation of the concept of ecological niche provides a precise definition for the description of resource partitioning. He proposed that a species' population could be characterized by its position along each of a set of a few independent dimensions, ordering environmental variables. In a more recent attempt to clarify the use of the term niche, Whittaker and Levin (1975) restricted their definition to include intracommunity variables that are both intensive and local, as well as a population response to these variables. That part of hyperspace that each species in the community utilizes, occupies, or is affected by, is the niche hypervolume (Makarewicz and Likens, 1975). Within this space occupied by a species, the species' population response to the environmental variables provides the best characterization of the niche.

There are many definitions of the term, niche, but George Evelyn Hutchinson made conceptual advances in 1957 and introduced the most widely accepted definition; "The niche is the set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes". Ecological niche is a central concept in the ecology of organisms and is sub-divided into the fundamental and the realized niche. The fundamental niche is the set of environmental conditions under which a species is able to persist. The realized niche is the set of environmental plus ecological conditions under which a species persists. In simpler terms ecological niche is the full range of ecological characteristics for a species e.g. feeding habits (what it eats), specific habitat (where it lives), reproductive strategies (when and how it reproduces), behavior and all other aspects of the species' lifestyle. How an organism interacts with other organisms is also part of its niche. Interactions among organisms strongly influence the behavior and ecology of organisms. The interactions (Fig. 1) are defined as whether they are competitive, beneficial, harmful or neutral. The niche concept has remained of fundamental importance to ecology. It establishes a link between individual-level traits and population dynamics.

A theoretical dichotomy in community ecology distinguishes between niche interactive mechanisms that stabilize species coexistence and those that cause neutral drift. Stable coexistence is predicted to occur in communities where species have niche-partitioning mechanisms that reduce interspecific competition. Neutral communities are predicted to be structured by stochastic processes that are not influenced by species niche identity, but that may be influenced by priority effects and dispersal limitation. Recent developments have suggested that neutral interactions may be more common at local scales, while niche structuring may be more common at larger scales.

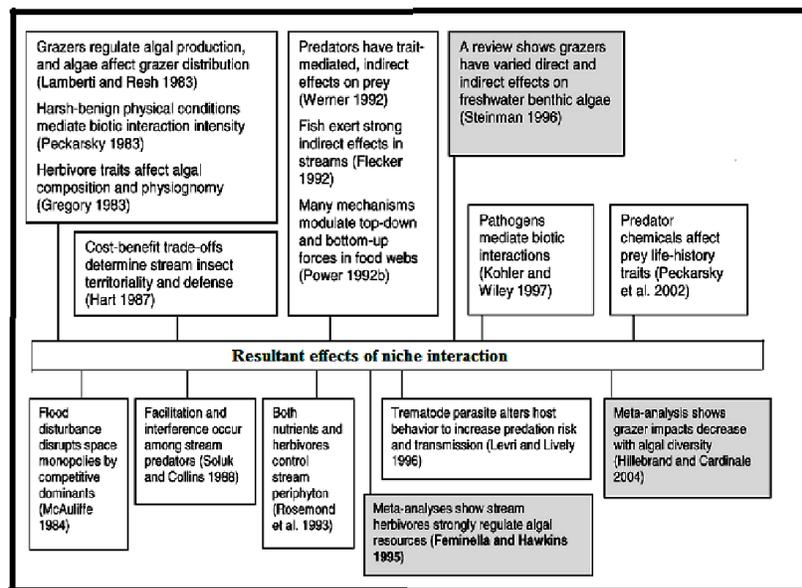


Fig 1. Biotic interactions in freshwater benthic habitats. Adapted from Joseph *et al.* (2010)

The structure and biodiversity of benthic communities vary on both small and large spatial scales in response to a myriad of factors acting independently or synergistically. For example, the structure of intertidal soft-sediment macroinvertebrate communities and the diversity of species they comprise vary among localities as a function of the abundance of primary producers, the presence of key bioturbator species (Berkenbusch *et al.* 2000), or various sediment characteristics (Ysebaert and Herman 2002; Fujii, 2007). There are many examples where biotic factors influence smaller scale distribution patterns (e.g. different habitats within a region) but not necessarily larger patterns. For example, competition may influence the vertical distribution of species on mountains. Species assemblages of damselfly larvae (*Enallagma*) in lakes differ depending on whether fish or dragonfly larvae are the top predator. Here, predation creates a mosaic of different habitats for damselflies within a region, but not a large-scale biogeographic pattern.

The niche concept is a useful framework for considering both the local distribution and ecological tolerance of a species. The fundamental niche describes the range of environments that an organism can inhabit based on physiological tolerances (Hutchinson 1959, Holt 2003). Rates of dispersal across the habitat and biotic interactions with other species may further alter the actual area occupied, termed the realized niche (Hutchinson, 1959). Species interactions often vary across environmental gradients (Louda and Rodman, 1996). As a result, interspecific interactions that decrease population growth rates, such as competition (Choler *et al.* 2001), predation (Davis *et al.* 1998), disease (Augspurger and Kelly, 1984), and herbivory (Harley, 2003), can restrict the observed distributions of local species to a subset of otherwise suitable habitats. Similarly, the presence of mutualists can allow for the expansion of species distributions to otherwise unsuitable habitats (i.e., facilitation; Bruno *et al.* 2003).

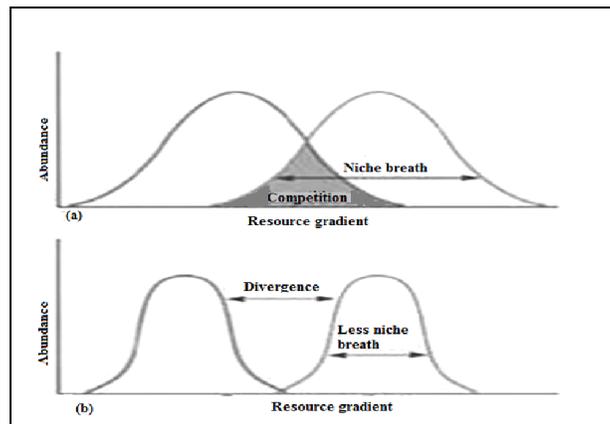
Despite the importance attached to the niche in ecology and the role it plays in community structure as demonstrated in several reports (Hutchinson, 1957; 1965; MacArthur, 1968; Whittaker and Levin, 1975; Pianka, 1983; Arthur, 1987; Begon *et al.* 1996; Case and Leibold, 2003; Meszéná *et al.* 2006), its application in benthic community studies to define its role in community structure has not attracted enough research interest. In this review, my focus is on the strength of interactions of species with their environment, where emphasis is on the biotic component of the environment, as mechanism shaping benthic communities.

#### ‘Struggle’ for resources: competition

Competition is the contest among organisms to obtain all the requirements for life, within a niche. Individuals of a species may compete with each other, especially for food, living space and mates. The individuals within species that survive are those best adapted to current conditions in the ecosystem. Species which simultaneously occupy the same habitat and whose niche in a habitat overlap (Fig. 2), are likely to compete for resources available.

Interest in competition among organisms may have originated with Malthus’ (1798) projections that food competition arises from geometrical increases in populations. Darwin (1859) argued that a struggle for existence would inevitably follow population increases, until competitors, enemies, or epidemics resumed ‘a limiting check. Smith (1935) proposed the now-familiar, self-defining terms

density-dependent and density-independent, and Elton (1949) articulated the meaning and importance of density-dependent mortality factors. It is becoming increasingly understood by population ecologists that the control of populations is brought about by density-dependent factors, either within the species or between species. The chief density-dependent factors are intraspecific competition for resources, space, or prestige, and interspecific competition, predators or parasites, with other factors affecting the exact intensity and level of operation of these processes (Joseph, *et al.* 2010). Coexistence of species is largely driven by an interacting system of disturbance and competition (Airoldi, 2000). While disturbances clear space, competitive success ultimately determines who inhabits the space.



**Fig. 2.** Resource partitioning and niche specialization caused by competition. Nilsson (2005).

#### What do benthic organisms compete for?

A variety of different limiting resources have been proposed for the benthos, especially deposit feeders. Food of a particular type is usually the resource that is cited as being in short supply for the soft-bottom benthos. Space has also been cited as a limiting factor. Woodin (1974) argued that tube-building organisms compete with burrowing organisms for access to the surface. An increased abundance of tube-building surface organisms was shown to result in a decrease in the abundance of the burrowing orbiiniid polychaete *Armandia*.

Habitat may be a key limiting resource for some deep-sea populations. Many 'passive' suspension feeders in the deep sea must settle on objects on the sea floor so that their feeding appendages protrude through the approximately 1-cm thick deep-sea diffusive sublayer. Jumars and Gallagher (1982) posited that the scarce supply of these objects, *e.g.*, pieces of wood or skeleton, could set the limit on population abundance for these populations.

Food is usually the key resource that animals compete for, but not all food are consumed. White (1979) opined that it is not the organic content of the food so much that limits populations, but the nitrogen content of the food. Soft-bottom benthic ecological studies have largely confirmed this idea. There are usually high concentrations of organic matter in shallow subtidal and intertidal marine sediments. The nitrogen content of the sediments is often low. The ingestion and growth rate of populations is often poorly correlated with the percentage of organic matter in bulk sediments (Uwadiae, *et al.* 2009; Uwadiae, 2013). It is more often more closely coupled with the amount of nitrogen or labile organic matter in the sediments (Tenore, 1977).

The clearest examples of competition for scarce resources probably involve benthic diatoms. Benthic diatoms have a high protein content, high nitrogen content and essential fatty acid composition ideal for the nutrition of marine worms. Much of the standing stock of benthic diatoms may be unavailable to deposit feeders. Either the cells are too large to be ingested, or they pass through the guts of deposit feeders intact. Benthic algae might compete for nutrients, light, and space when control by grazers or physical disturbance (*e.g.*, flooding) is unimportant (Biggs *et al.* 1998). N-, P-, and N+P colimitation occur in many benthic habitats (Borchardt, 1996; Francoeur, 2001). Competitively dominant species are typically those with extended growth forms (mucilaginous stalks, filaments) or motility enabling individuals to acquire nutrients and light supplied from the overlying water. McCormick and Stevenson (1991) showed that algal succession occurs when stalked diatoms (*Cymbella* sp., *Gomphonema olivaceum*) reduce reproductive rates of low-lying, early-successional species, by an indirect competitive mutualism (facilitation). Luxury uptake of nutrients during times of high availability might alleviate competition in variable nutrient environments (Stevenson and Stoermer, 1982). Sometimes grazing pressure supersedes nutrient limitation (Flecker *et al.* 2002). Stevenson (1997) suggested that diatoms are regulated by competition for nutrients and light only above some herbivory threshold, a resource condition in which algal accrual and grazing rates are equal.

Determining this threshold under various environmental conditions might help us better assess the role of competition in structuring benthic algae (Joseph *et al.*, 2010). The number of species sharing a limited resource that can coexist in a given community depends on the niche width of the different species and on the degree to which their niches overlap. The availability of an ecological niche for a species depends, in a great variety of ways, on interactions among the species comprising an ecological community.

Competition can be real or apparent. Real competition can occur directly through interference competition or indirectly through resource exploitation within or between species. Data often interpreted as evidence for competition include negative correlations between density and mean individual size, increased densities and growth or survival from resource supplementation, resource based emigration, territoriality, habitat-use restrictions, and niche expansion or density compensation by one species when a second is absent or experimentally reduced (Richardson, 1991; Kohler and Wiley, 1997). Just as consumer species can reciprocally reduce each other's abundance by depleting a shared resource, prey species can sometimes indirectly depress each other by increasing the abundance of a shared predator, an effect called apparent competition (Holt, 1977).

Densities of the invasive dragonfly *Cordulegaster boltonii* increase at the expense of decreasing densities of its noncompeting caddisfly and stonefly prey (Woodward and Hildrew, 2001). Baxter *et al.* (2004) suggested that apparent competition between aquatic and terrestrial invertebrates occurs in Japanese streams when introduced rainbow trout usurp both benthic and terrestrial prey that would have been used by native charr (*Salvelinus malma*). In lakes, feeding by omnivorous fishes in pelagic and benthic habitats can increase fish production and cause apparent competition between pelagic and benthic invertebrate prey (Vander Zanden and Vadeboncoeur, 2002). Similarly, feeding by piscivores on benthic-feeding roach (*Rutilus rutilus*) and zooplanktivorous perch (*Perca fluviatilis*) can cause apparent competition between these noncompeting fish (Persson, 1997). If shared resources do become limited when predator abundance is high, then real competitors might be even more disadvantaged because they would experience the double jeopardy of high predation risk and high resource competition.

Bulldozing is an example of interference competition, many sessile benthic organisms were virtually eliminated by the appearance of burrowing deposit feeders. These bulldozer species, by moving the sediment may have led to the local extinction of a number of sessile deposit and suspension feeding groups.

#### **At what scale do Competitions occur in benthic communities?**

The effect of real competition on abundance patterns of benthic communities varies among developmental stages, taxa, and guilds. Among macroinvertebrates, herbivorous snails and larval caddisflies can exert especially strong exploitative effects. Consequences of periphytic food depletion by freshwater pleurocerid snails (*Elimia*, *Juga*) include reductions in individual growth of competitors (Hill *et al.* 1995; Lamberti *et al.* 1995), decreases in competitor abundance (e.g., nontanypodine chironomids, Harvey and Hill, 1991; caddisflies, Lamberti *et al.* 1995), or changes in overall consumer diversity (Hawkins and Furnish, 1987; Rosemond *et al.* 1993). Herbivory by the hydrobiid New Zealand mudsnail *Potamopyrgus antipodarum* slows prepupation rates of Pycnocentroides caddisflies and emergence rates of subimago *Deleatidium* mayflies, but mud snail growth and foraging appear unaffected by these potential competitors (Holomuzki and Biggs, 2006). Invasive populations of *Potamopyrgus* (300,000 snails/m<sup>2</sup>) appear to exert similar amensalistic effects on lotic grazers in the western US (Kerans *et al.* 2005). Dominance of *Potamopyrgus* over native and nonnative grazers might result from their ability to feed either on surface periphyton or subsurface heterotrophic biofilms (Rounick and Winterbourn, 1983), from potential facilitation by other grazers (Riley *et al.* 2008), or from their high bioenergetic efficiencies (Broekhuizen *et al.* 2002). Conversion efficiency of food into tissue growth might be as important as resource uptake or exploitative ability in determining competitive outcomes, but is rarely examined (Ricciardi and Whoriskey, 2004).

Density-dependent grazing by larval *Helicopsyche* caddisflies can depress periphyton abundance, which subsequently decreases grazer growth, pupation rates, pupal size, and net rate of population recruitment (Lamberti *et al.* 1987; Feminella and Resh, 1990). Glossosomatid caddisflies can exclude benthic competitors exploitatively (Kohler, 1992), as evidenced by marked increases in abundance of periphyton and most grazers and filter feeders after catastrophic declines of *Glossosoma* by microsporidian infection (Kohler and Wiley, 1997). Sublethal parasite/pathogen infections may alter competitive hierarchies and allow persistence of inferior competitors. Net- or tube-building larval insects restricted to swift-flowing sections of streams aggressively defend high-current-velocity patches with high-resource profitability, e.g., blackflies and psychomyiids, Hart (1987), hydroptilids, Englund (1991), hydroptilids, Hart and Robinson (1990). Contests over space can occur within or between trophic guilds and are usually settled by size and ownership status. For example, among filter-feeders, Hydropsyche caddisflies can restrict distributions of Simulium blackflies, except in winter when flood-induced mortality mediates competition (Hemphill, 1991). Interference competition ("nipping") by *Simulium virgatum* causes significant decreases in foraging and ingestion rates by the grazing midge *Blepharicera micheneri*, resulting in decreased growth and increased mortality and time to pupation (Dudley *et al.* 1990). Similarly, tubebound deposit feeders compete aggressively for food, space, and tube-building materials, and this competition can lead to density-dependent mortality (Ball and Baker, 1995) and emigration (Wiley and Warren, 1992). However, dispersion of resource patches can de-aggregate individuals to mitigate competition (Silver *et al.* 2000). Few studies show food or habitat limitation for shredding detritivores (Richardson, 1991;

Dobson and Hildrew, 1992), perhaps because of plentiful food subsidies from terrestrial habitats (Webster *et al.* 1995), synchrony of life and resource cycles (Feminella and Stewart, 1986), rapid switches to available secondary resources (Costantini and Rossi, 1998), and the avoidance of resource patches with heterospecific competitors (Abo's *et al.* 2006).

### **How does competition affect the structure of benthic communities?**

Many benthic species appear to experience competition occasionally, and this may affect long-term demographic structure or assemblage patterns and “carry-over effects” of sublethal competition among adults reduce offspring quality or fitness (Feminella and Resh, 1990). Moreover, effects of competition on demographic assemblage structure seem restricted to local scales for both fishes (Jackson *et al.* 2001) and macroinvertebrates (Peckarsky *et al.* 1997). However, the spatial and ecological importance of competition might hinge on resource-mediating factors, such as regional climate change, land use change, or the appearance of competitively superior invasive species.

Specific environmental conditions can determine the competitive outcomes of closely matched species. For example, water temperature can determine competitive superiority by affecting individual aggressiveness, food intake, and growth (Taniguchi and Nakano, 2000). Macrophyte abundance, which mediates environment-specific feeding efficiencies, can determine survival differences and, thus, local distributions of competing species (Briers and Warren, 1999). Both intra- and interguild predation can greatly affect competition intensity. Size-specific cannibalism on smaller individuals might decrease exploitative competition among odonate larvae, notonectids, planaria, and crayfish (Polis *et al.* 1989). Cannibalism among same-sized detritivorous larval caddisflies is necessary for completion of development in food-poor, seasonal wetlands (Wissinger *et al.* 1996). Asymmetric intraguild predation can alleviate competition between young bass and bluegill for invertebrate prey when bass grow to a size-piscivory threshold and eat bluegill (Olson *et al.* 1995). Interguild predation by fish can alleviate food or space competition between snails (Hershey, 1990), net-spinning caddisflies (Lancaster *et al.* 1988), and crayfish (Garvey *et al.* 1994). Particularly strong lethal effects can result in change competition intensity on noncontiguous trophic levels (Joseph *et al.*, 2010). Insectivorous stream fishes release tuft-weaving chironomids from predation by consuming small predators, such as aeshnid odonates, and allow midges to suppress algae and create the prerequisite food limitation necessary for competition among grazers (Power, 1992a). Predators also can nonlethally modify competitive interactions (Joseph *et al.*, 2010). However, when *Cottus nozawae* sculpins are present, *Baetis* decreases surface grazing, which significantly reduces mayfly growth, whereas growth and behavioral responses of armored glossosomatids to sculpins are negligible (Kuhara *et al.* 1999).

Competition for space is a major structuring force in marine benthic communities (Bertness and Leonard, 1997). Substrate competition by encrusting marine organisms usually occurs by direct overgrowth at their contact zones (Sebens, 1986). These competitive border interactions are commonly evaluated with species being ranked as winners or losers based on their abilities to overgrow the competing taxa. Although losers of interactions are overgrown by winners, this does not always result in death of the overgrown organism (Jompa and McCook, 2002). Coralline algae, in particular, can survive while they are overgrown and sometimes even continue to grow (Sebens 1986; Dethier and Steneck, 2001). While the outcome of border interactions can vary depending on species, depth, timing, and location, some taxa are typically competitively dominant over others (Nandakumar, 1996; Airolidi, 2000; Barnes and Dick, 2000; Barnes, 2002). In temperate and polar waters, ascideans, sponges, and bryozoans have been shown to be strong space competitors (Maughan and Barnes, 2000; Barnes and Kuklinski, 2004).

### **Negative interactions**

Benthic organisms occupying niches where their activities and life styles result in harmful effects on other organisms occupying other niches are said to interact negatively with other members of the community. The role of such interactions in structuring benthic communities is discussed with emphasis on predation, parasitism and herbivory.

### **The structuring roles of Predators and predation**

Predators can limit prey abundances, alter prey size or age structure, behavior or other traits, and exert indirect effects that cascade through food webs and ecosystems. Predator effects depend on prey and predator traits and the environmental context of the interaction, and clearly increase with predator densities and per capita killing rates (Joseph *et al.* 2010). The impact of benthic predator on prey have been detected at the scale of microhabitat patches (Kershner and Lodge, 1995, Fairchild and Holomuzki, 2005), macrohabitats (stream reaches, Peckarsky *et al.* 2002; stream pools, Power *et al.* 1985, Wiseman *et al.* 1993), and entire systems (small ponds or lakes, Carlisle and Hawkins, 1998, Venturelli and Tonn, 2005). However, evaluations of predator impacts often must be done in enclosures, which can impose scale dependent artifacts related to dispersal rates of organisms into and out of enclosures (Carpenter, 1996; Englund and Cooper, 2003). Furthermore, predator impacts might vary among spatial scales depending on natural transitions in predator and prey types along gradients of hydrologic permanence and habitat size (lentic systems: small ephemeral pools to large lakes; lotic systems: intermittent tributaries to large rivers (Wellborn *et al.* 1996; Creed, 2006). For example, predator impacts might be undetectable where prey adaptations allow coexistence with certain predators, but quite strong when prey move from

one size/permanence habitat to another (e.g., small tributary to perennial river) where they have not coevolved with resident predators (Fraser and Gilliam, 1992; Fraser *et al.* 1995, Creed, 2006).

Predator impacts can be short- or long-term. On behavioral time scales, predators can trigger reductions in movement or drift reactions by invertebrate prey (Holomuzki and Hoyle, 1990, Scrimgeour *et al.* 1994). In California and New Zealand streams, effects of predatory fish were strong enough to cascade down food chains to influence algal biomass several months after scouring floods (Power, 1990b; Biggs *et al.* 2000). Over generations, predation can influence evolution of traits, such as morphological shifts that confer faster size-specific swimming speed on damselflies invading lakes with dragonfly predators (McPeck *et al.* 1996). Shifts in the biotic environment, such as availability of food for prey, also affect predator impacts. For example, when *Epiptera* dragonflies are confined with sunfish in large enclosures, their life histories change from univoltine to semivoltine because of reduced foraging and intensified competition with small predators (Martin *et al.* 1991). However, in subsequent similar experiments, sunfish predation on dragonfly nymphs released survivors from density dependent competition and allowed higher per capita feeding rates that promoted the univoltine life history (Johnson *et al.* 1995). The authors hypothesized that the contrasting outcomes in the later experiment occurred during periods of higher chironomid and ostracod prey availability for dragonflies. The impact of sunfish predation on dragonfly life history has large fitness consequences because semivoltine dragonflies must postpone reproduction and endure aquatic predation for twice as long as univoltine conspecifics (Johnson *et al.* 1995).

The impact of predation differs, depending on the type of environment. In rocky intertidal communities, intense competition for space leads to the exclusion of inferior competitors (Connell, 1970; Dayton, 1971). Predation may reduce the intensity of competition for space by keeping competing species at low densities; therefore, diversity may be higher when predators are present (Connell, 1970; Dayton, 1971; Paine, 1974). In soft-bottom communities, on the other hand, the opportunity to burrow into the substrate makes it possible for interacting species to increase their spatial segregation, and space is not normally a limiting factor (Peterson and Andre, 1980). Experiments have shown that soft-bottom communities from which epibenthic predators have been excluded usually support both an increased total density and increased species richness.

Indirectly, benthic predators influence benthic algal or plant biomass indirectly through chains in food webs in experimental tanks (Hill and Lodge, 1995), lakes (Martin *et al.* 1992), ponds (Broˆnmark 1994), and rivers (Power *et al.* 1985, Power, 1990c). By limiting dispersal or foraging by prey in certain habitats, predators can create spatial refugia for their prey's prey, e.g., exclusion of fish by fishing birds creates shallow-water refugia for snails or algae (Matthews *et al.* 1986; Steinmetz *et al.* 2003). Predation also can modify ecosystem functions provided by prey. Litter processing in experimental channels (Hamish and McIntosh, 2006) and in natural streams (Malmqvist, 1993) decreases in the presence of trout and stonefly predators, respectively, because of lethal and nonlethal predator effects on invertebrate shredders. On larger scales, benthic predators feeding in one habitat but defecating or dying in another transfer nutrients, energy, or pollutants across habitat boundaries (Nakano and Murakami, 2001; Sanzone *et al.* 2003, Baxter *et al.* 2005; Lamberti *et al.* 2010). Studies are needed that examine how these transfers affect general ecosystem processes, such as primary production, community composition, and system stability (Joseph *et al.*, 2010).

### **The structuring roles of parasites and parasitism**

Parasites have been suggested to be important constituents of benthic ecosystems. Parasitism is an important ecological factor for benthic populations and communities. Through differential effects on survival, reproduction, growth and behaviour of hosts, parasites can affect host populations and communities. Parasitism has been recognized as a major force in ecosystems (Minchella and Scott, 1991; Combes, 1996; Thomas *et al.* 2005). A virulent parasite can reduce the abundance of its host, with cascading effects on the rest of the community. In addition to such direct effects, a parasite can also modify the behaviour of an ecosystem engineer species, and thus indirectly change its impact on the physical nature of the environment (Jones *et al.* 1997). Parasitism can therefore act via trait-mediated effects (Werner and Peacor, 2003), i.e. by altering the phenotypic characteristics of the host and consequently its functional role in the system, and not necessarily through direct effects on host density.

Evidences have shown that parasites, especially trematodes, in fact may play important roles in structuring both soft-sediment and rocky intertidal communities (Sousa 1991; Wood *et al.* 2007; Mouritsen and Haun, 2008), but to date their influence on spatial variation in community metrics has been ignored (Joseph *et al.* 2010). The cockle *Austrovenus stutchburyi* (Grey) not only dominates New Zealand soft-sediment intertidal communities in terms of both biomass and its impact on sympatric invertebrate species (Stewart and Creese, 2002), but it is also a major host for trematode parasites. Echinostome trematodes (genera *Curtuteria* and *Acanthoparyphium*) use cockles as second intermediate hosts in their life cycle. After multiplying asexually inside the first intermediate snail host, infective larvae of these trematodes penetrate cockles through the inhalant siphon and encyst as metacercariae in the foot tissue of cockles, awaiting predation of the cockle host by oystercatchers or other suitable avian definitive hosts. The different echinostome species involved are essentially equivalent in terms of their impact on cockles and transmission mode (Babirat *et al.* 2004), and are hereafter referred to only as echinostomes. By concentrating in the foot of their cockle hosts, these parasites

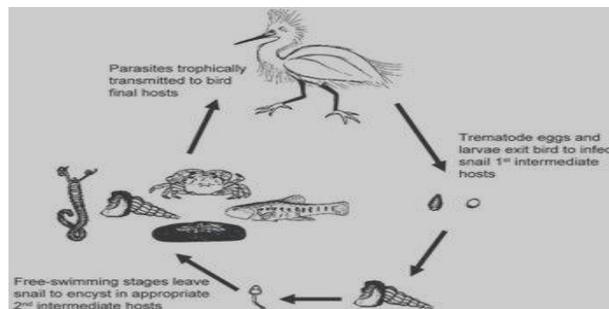
impair the bivalve’s ability to both burrow and move through the sediment; heavily infected cockles are less mobile than the uninfected and accumulate on the sediment surface where they incur greater predation by birds (Mouritsen, 2002; 2004).

This manipulation of host burrowing ability benefits the parasite by improving its transmission success to avian definitive hosts, but the modification of this key functional trait can also indirectly impact the whole benthic community. The presence of cockles stranded on the sediment surface, for which echinostome parasites are exclusively responsible, creates a greater diversity of substrates for organisms living attached to cockle shells, possibly facilitating their coexistence (Thomas *et al.* 1998). In addition to generating increased surface structures, parasite-induced impairment of cockle burrowing can also affect sediment bioturbation, seabed hydrodynamics and particle deposition (Mouritsen and Poulin, 2005a) aside from reducing the structural complexity within the substrate. Even if infected cockles are buried, their reduced activity within the substrate (bioturbation) may also impact the infaunal community (Mouritsen and Poulin, 2005a).

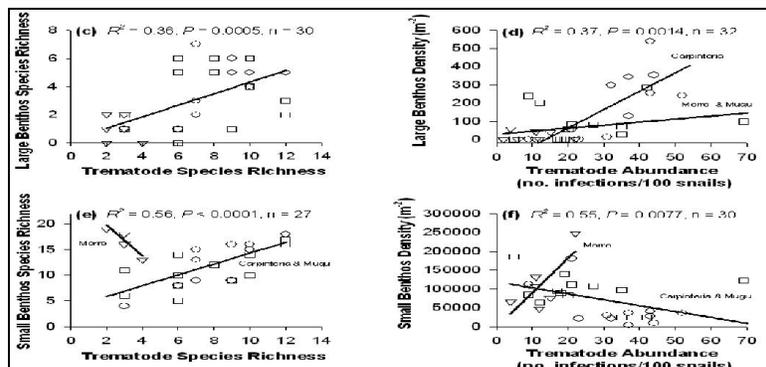
The abundance of trematodes can vary considerably between sites, on different spatial scales (Fredensborg *et al.* 2006; Byers *et al.* 2008). According to Mouritsen and Poulin, 2003a, the density of cockles found stranded on the sediment surface of intertidal flats was strongly and positively related to the mean infection level by echinostomes in the local population. Spatial variation in the intensity of parasites is a necessary condition for any role of cockle parasitism as a determinant of spatial variation in community structure.

Evidence suggesting the existence of associations between free-living benthic communities and the communities of trematode parasites in snails (Figs. 3 and 4) was reported in (Joseph *et al.* 2010). This is important because it demonstrates that trematode parasites in snails may not only serve as indicators of bird populations, but also benthic fauna, such as crabs, clams, and polychaete worms. These parasites use several types of hosts, as well as predator-prey interactions, to complete their life cycles; so they are intimately and necessarily connected to the abundance, diversity, and the food web interactions of the ecosystem.

Nematomorph parasites manipulate crickets to enter streams where the parasites reproduce. These manipulated crickets become a substantial food subsidy for stream fishes. A field experiment was used to investigate how this subsidy affects the stream community and ecosystem function (Joseph *et al.* 2010) and it was discovered that, when crickets were available, predatory fish ate fewer benthic invertebrates. The resulting release of the benthic invertebrate community from fish predation indirectly decreased the biomass of benthic algae and slightly increased leaf break-down rate. This experimental demonstration revealed that host manipulation by a parasite can reorganise a community and alter ecosystem function. Nematomorphs are common, and many other parasites have dramatic effects on host phenotypes, suggesting that similar effects of parasites on ecosystems might be widespread.



**Fig 3.** The complex life cycle of trematode parasites. The various trematode species are intimately connected to several types of benthic animals throughout their life cycles. Kevin *et al.* (2005).



**Fig. 4.** Relationships between trematodes in snails and the benthos. Data are represented as circles for Carpinteria Salt Marsh, squares for Mugu Lagoon, and triangles for Morro Bay. Kevin *et al.* (2005)

### **How does host–parasite Interactions influence benthic community structure?**

Like predators, parasites consume prey resources (host tissues), but unlike predators, typically do not kill their host (Jokela *et al.* 1999). Some parasites cause relatively little harm to their host, e.g., freshwater mussel glochidia temporarily infesting fish (Watters 2006). However, many hosts incur sizable costs when infested by macro- or microparasites. For example, attack and parasitic feeding by adult *Petromyzon* lampreys on lake and riverine fishes causes considerable tissue and fluid loss, which might lead indirectly to chronic stress, secondary infection of wounds, and even death (Bergstedt *et al.* 2001).

Similarly, leech infestations on fish can cause chronic anemia and might lead to secondary bacterial and fungal infections at attachment sites (Davies and Govedich, 2001). Naidid oligochaetes parasitizing invading populations of dreissenid mussels feed on the mantle, gill epithelia, and ovarian oocytes and tissues (Conn *et al.* 1995), whereas parasitic larval mites and trematodes infecting unionid mussels might reduce mussel glycogen stores and reproductive output (Gangloff *et al.* 2008). Gravid female *Asellus aquaticus* isopods exposed to the acanthocephalan parasite, *Acanthocephalus lucii*, are at higher risk of mortality and bear smaller offspring than do non-parasitized females (Hasu *et al.* 2006). However, even in non-parasitized, resistant females, offspring size is reduced by parasite exposure, a result suggesting that resistant females have fewer resources directed toward parental investment after their immune systems have been compromised by parasites (Hasu *et al.* 2006).

### **Community-scale effects of parasites**

Studies have shown that parasites can have population-scale consequences on their hosts (Joseph *et al.* 2010). Lethal effects of lampreys have devastated commercial fishes (e.g., lake trout) in the Laurentian Great Lakes (Schneider *et al.* 1996). Furthermore, sublethal infections of metacercarial trematodes slow the growth of European minnows (*Phoxinus phoxinus*), an effect that indirectly alters host population dynamics by allowing large shoaling fishes to outcompete smaller infected fishes for food (Pitcher and Hart, 1982; Müller, 1995). Microsporidian infection (*Pleistophora mulleri*) significantly reduces aggressiveness of the amphipod *Gammarus duebeni*, making it more vulnerable to intraguild predation by the invasive *Gammarus pulex* (Fielding *et al.* 2005).

*Pleistophora* also indirectly regulates its host abundance through asymmetric cannibalism, with parasitized individuals being much more likely to be cannibalized than unparasitized individuals (MacNeil *et al.* 2003). Predatory effects on *G. duebeni* might have community-wide consequences because these amphipods can function as keystone species in lentic systems (Kelly *et al.* 2003). Declines in *Astacus* crayfish follow immune system failure after infections by the parasite *Psorospermium haeckeli* (Soederhaug II and Cerenius, 1992). These population losses might have large scale effects because crayfish can act as ecosystem engineers (Creed and Reed, 2004). Depending on environmental context, chytrid fungus infection either can increase or decrease diatom proliferation, thereby affecting outcomes of interspecific competition and algal community succession (Ibelings *et al.* 2004). Bacterial infection can alter diatom species composition and abundance, and hence primary production and presumably grazer abundance (Peterson *et al.* 1993).

### **The role of herbivores and herbivory**

Herbivory is commonly defined as the consumption of living plant tissue by animals, and herbivores are considered as all those animals adapted to live solely consuming plant tissue. Thus, herbivory is related to the consumptive effects that animals can cause on populations or communities of plants, and is considered one of the most important ecological processes in marine as well as in terrestrial ecosystems around the world (Schmitz, 2008). In marine systems, herbivores can determine temporal and spatial distribution of algae in both intertidal and subtidal habitats (Hawkins and Hartnoll, 1983). Through consumption of matured algae and spores, different intertidal and subtidal herbivores can affect successional pathways, determining algae species composition and abundance (Hawkins and Hartnoll, 1983). Almost every dimension of algal life history and performance can be influenced by marine herbivores (e.g., succession, Sousa, 1979; chemical defences, Duffy and Hay, 1994). But although many species can cause negative effects on algae, positive direct and indirect effects are also important mechanisms recently considered as relevant factors in the structure of intertidal communities (Plaganyi and Branch, 2000). As herbivores are also consumed by high-level carnivores, including humans, they also have a central importance in food web dynamics and ecosystem function (Schmitz, 2008). Herbivory is a key process in all ecosystems as it results in the transfer of primary production to higher trophic levels and affects the physical structure and productivity of vegetated habitats. Critical to understanding the role of consumer control in ecosystems is quantifying the strength of herbivore impacts on primary producers and relating these impacts to mechanisms and traits that can explain variation in interaction strengths (Aguilera, 2010). These include rates of primary and secondary production (which vary on global scales), producer nutritional quality, producer resistance and tolerance to grazing, herbivore feeding behaviour and the stoichiometric match between producer and herbivore tissues (Joseph *et al.* 2010). From the grazer perspective, differences in abundance, feeding efficiency, size, taxonomy, mobility, metabolism and predator regulation of herbivore populations can all contribute to variation in the rate at which primary production is removed by herbivores.

Grazers wholly or partially eat multiple live producers, such as photosynthetic bacteria, algae, or plants, over their lifetimes. A revealing meta-analysis by Feminella and Hawkins (1995) concluded that grazers strongly regulate producer biomass and assemblage

in streams and contradicted a widely held view that herbivory was unimportant in lotic systems. A review by Steinman (1996) of herbivore impacts in freshwater lotic and lentic systems added that producer responses to grazing depended largely on producer traits and grazer type. Effects of freshwater grazers can ramify through food webs, depending on the environmental context of the herbivore–producer interaction. The effect of herbivory on primary producer diversity has been considered as beneficial and detrimental (Olf and Ritchie, 1998). High grazing pressure seems to reduce plant diversity while moderate grazing pressure seems to increase it (McNaughton, 1985; Milchunas *et al.* 1988). However, there is also circumstantial evidence that spatial heterogeneity of the grazing pressure might be more important for the maintenance of plant diversity than the mean intensity of grazing, as indicated by a comparison between the grazing impacts of digging rodents and ungulates (Olf and Ritchie 1998). However, the difference between the spatial effects of rodents and ungulates might have been confounded by other differences, e.g. in feeding selectivity.

The isopod *Idothea chelipes* (Schaffelke *et al.* 1995) and the gastropod *Littorina littorea* (Steneck and Watling, 1982) feed on benthic macroalgae and on microalgae growing on solid substrates (periphyton). They feed rather unselectively on a wide variety of microalgal species. Gelatinous coverage of algae and tight attachment to the substratum offer a relative protection (25–50% reduction of mortality) against both grazers (Sommer, 1999). The similarity in feeding selectivity is contrasted by pronounced differences in the spatial distribution of grazing pressure (Sommer, 1999c). According to Joseph *et al.* (2010), biofilms grazed by *Idothea* look quite homogenous macroscopically without visible bite marks (“lawn-mower” type of herbivory) while *Littorina* moves slowly over the biofilm producing a macroscopically visible feeding track (“bulldozer” type of herbivory). After some days, there is a diverse mosaic of fresh grazing tracks, old grazing tracks in different stages of recolonization, and untouched biofilm. Both herbivores produced a periphyton diversity optimum at intermediate grazer densities but the optimum was more pronounced in the *Littorina* (Sommer, 1999).

Grazing on marine benthic microalgae has received much less attention than has grazing on phytoplankton. Most studies have concentrated on bulk effects on biomass, but not on selectivity, between algal species. Most selectivity studies in marine benthic herbivory have concentrated on selectivity between macrophytes and microalgae (Peduzzi, 1987), cleaning of macrophytes from their microalgal epiphytes (Neckles *et al.* 1993), or selectivity between macrophytes (Schaffelke *et al.* 1995). Despite its omnivory, *Idothea baltica* is quite selective within food categories. Among macroalgae there is a clear preference for *Fucus vesiculosus* over *Fucus evanescens* (Schaffelke *et al.* 1995); within filamentous algae, germlings of the green alga *Enteromorpha* spp. are preferred over germlings of the brown alga *Pilayella littoralis* while adult *P. littoralis* are preferred over adult *Enteromorpha* (Schramm *et al.* 1996). The importance of benthic microalgae as primary producers in estuarine and other shallow ecosystems has been known (MacIntyre *et al.* 1996). In coastal waters clear enough to allow sufficient light penetration to the sediment surface, microalgae in the sediments can be expected to influence the exchange of nutrients at the sediment/water interface (Sundback *et al.* 1991).

Indirectly, effects of herbivores on producers can ramify through interaction chains (Joseph *et al.* 2010). Algal and detrital-feeding fishes can have strong indirect effects on benthic invertebrate community structure and distributions (Flecker, 1992). Macrograzers can significantly depress algal biomass and, in so doing, decrease abundance and alter community composition of epilithic meiofauna (Peters *et al.* 2007). Grazers also can indirectly determine algal dominance. Large Orconectes crayfish can exclude *Cladophora* from deep habitats and open space for colonizing diatoms and sessile grazing insects that eat diatoms (Creed, 1994). Reduction of stream diatom turfs by grazing minnows facilitates dominance of cyanobacteria (Power *et al.* 1988a). Invasive *Marisa cornuarietis* (giant rams-horn snail) can effectively mow entire macrophyte beds in Texas lakes and rivers (Horne *et al.* 1992), which can decrease faunal habitat suitability and increase nutrient and turbidity levels (Carr *et al.* 2003).

Herbivory sometimes can have an indirect stimulatory effect on grazed periphytic residues by increasing space availability, and light and nutrient penetration (McCormick, 1994, Flecker *et al.* 2002). Grazers change the movement of chemical elements for autotrophic uptake and alter producer stoichiometric ratios (Frost *et al.* 2002, Hillebrand *et al.* 2004), which might affect producer growth form (i.e., fast- vs slow growing) in the post-grazing assemblage (Liess and Hillebrand, 2006). In addition, nutrients from grazer excretions can produce patchy stimulatory effects and reduce C:N:P in algal communities (Hillebrand and Kahlert, 2001). At larger scales, reductions of periphyton biomass by grazers affect hydraulic characteristics and can increase transient storage and internal nutrient cycling in streams (Power *et al.* 1988a, Mulholland *et al.* 1994). Knowledge of the factors influencing the interaction between herbivory and contrasting abiotic factors (e.g., light, nutrient, flow disturbance) when determining producer species composition, diversity, and assemblage structure will help us understand the spatiotemporal dynamics of top-down and bottom-up forces in freshwater benthic habitats (Joseph *et al.* 2010).

### **Community structural effects of herbivore**

Herbivore effects on producers have been detected at fine (individuals, Power *et al.* 1988a), intermediate (habitat units, Feminella *et al.* 1989; stream reaches, Taylor *et al.* 2002), and large (lakes, Caraco *et al.* 1997) spatial scales. Even within scales, grazer effects on algal biomass often are patchy (Villanueva and Modenutti, 2004). Finlay *et al.* (1999) used  $\delta^{13}\text{C}$  analyses to show that most algivores rely on local production and that the importance of algal derived C to river food webs is greatly underestimated. Experiments have

generally shown that grazers can significantly reduce algal biomass over short time scales (Rosemond *et al.* 2000; Taylor *et al.* 2002), although there may be exceptions (Vaughn *et al.* 1993; Holomuzki and Biggs, 2006a). Low grazer bioenergetics and ambient light and nutrient conditions, availability of alternative food sources, and algal recruitment can delay or nullify grazer effects (Feminella *et al.* 1989; Hill *et al.* 1992). Grazer effects on algae are highly variable and differ with spatial heterogeneity in substrate, nutrient, or hydrodynamic conditions (Peters *et al.* 2007). Predators typically have strong effects on herbivores, but the magnitude of impacts can vary (Joseph *et al.* 2010). Direct lethal effects of predators can mediate herbivore impacts on benthic producers in streams (McIntosh and Townsend, 1996; Huryn, 1998), lakes (Broˆnmark, 1989), and wetlands (Batzer and Resh, 1991). However, indirect effects of predators on periphyton biomass might be weakened when grazers are armored (Ruetz *et al.* 2004) or have access to spatial refugia (Rosenfeld, 2000). Trophic cascades in freshwater systems typically are attenuated at the herbivore-producer interface (Shurin *et al.* 2002).

### Positive interactions

Interaction between organisms occupying different niches which result in beneficial effects to both organisms and the niches they occupy can be termed positive niche interaction. Positive interactions have received far less attention from ecologists than negative interactions (Kareiva and Bertness, 1997, Stachowicz, 2001). Some aspects of positive niche interactions in the benthos are discussed here.

### Species symbioses

In freshwater benthic systems, relatively few obligate species-specific mutualisms are known, but several fascinating examples have been documented. Coccoid, endosymbiotic cyanobacteria living within diatoms (*Epithemia* spp., *Rhopalodia* spp.) of the family Rhopalodiaceae (Floener and Bothe, 1980) can fix N<sub>2</sub>, which subsequently helps these diatoms become dominant in N-limited environments (e.g., Mulholland *et al.* 1991, Peterson and Grimm 1992, Marks and Power, 2001). In another benthic endosymbiosis, the cyanobacterium acts as the host. The cyanobacteria

*Nostoc parmelioides* (Dodds and Marra, 1989) and *Nostoc verrucosum* (Sabater and Munoz, 2000) are colonized by larval midges (*Cricotopus* sp.), which graze the colony from the inside. Food and protection provided by the cyanobacterium are reciprocated by the midge resculpting *N. parmelioides* from a spherical to an ear-like form, which enhances per biomass exposure to photon and nutrient flux (Brock, 1960, Ward *et al.* 1985). In addition, the midge resecures detached *Nostoc* to substrates, potentially decreasing export of colonies during scouring floods (Brock, 1960). A common, cosmopolitan freshwater sponge, *Spongilla lacustris*, hosts zoochlorellae when it occurs on sunlit substrates. Photosynthetic products from these endosymbionts supplement sponge growth, which is otherwise supported solely by filtering particles (Sand-Jensen and Pedersen, 1994). Brown *et al.* (2002) demonstrated faster growth and lower mortality for crayfish when ectocommensal branchiobdellids were present to clean debris and epibionts from crayfish gills.

### Niche interaction in food web fragments

Processing chains of consumers that eat each other's byproducts (fecal pellets or comminuted crumbs from feeding; Heard, 1994) have been reported for various benthic invertebrates (Wallace and Webster, 1996). After being colonized by bacteria, chironomid fecal pellets are relatively high in food value, but too large for midges to reingest (McLachlan *et al.* 1979). However, when pellets are gnawed by cladocerans, particles small enough for midges to ingest are produced. This trophic facilitation supports an organic matter-based food web that otherwise would be highly refractory (Joseph *et al.* 2010). Similar microbe- or size-mediated reciprocal trophic benefits involving fecal pellets also occur between oligochaetes (Milbrink, 1993). At larger scales, shredding shrimp in upstream pools increase fine particle export (and dissolved C and N) to downstream filter-feeding shrimp by consuming leaf detritus introduced by hurricane-level storms (Crowl *et al.* 2001).

Organisms can benefit indirectly from substrate clearing by grazers. For example, the snail *Radix* bulldozes epilithon from mesocosm substrates and facilitates settlement of filter-feeding simuliids (Ledger *et al.* 2006). By removing silt or epiphytic overgrowth, benthic grazers can release understory epilithic algae (Power, 1990c) or epiphytized macroalgae (Dudley, 1992) from light or nutrient limitation. Grazing of over story diatoms by fishes in streams can uncover underlying N-fixing cyanobacteria (*Calothrix*) that might enhance N loading (Flecker and Taylor, 2004). Removal of the filamentous macroalga *Cladophora* by grazing *Gumaga* caddisflies enhances the supply of understory epilithic diatoms preferred by another grazing caddis, *Helicopsyche* (Feminella and Resh, 1991).

### Habitat amelioration at various scales

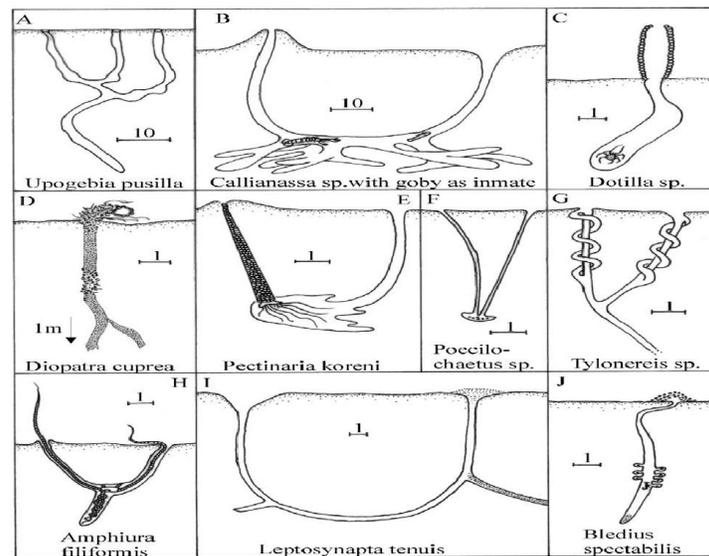
Benthic organisms might facilitate each other by ameliorating stressful physical conditions, such as fluid shear stress, bed scour, desiccation, and anoxia. Caddisfly pupal cases roughen substrates, and facilitate colonization and local persistence by other benthic species (Nakano *et al.* 2007). However, the scale of such effects is not always small. Caddisfly dominated mounds that are 9 m high and 40 m in diameter have been excavated from Eocene lakeshores in Wyoming, where caddisfly cases on mudflats provided

nucleation (phase transition) sites for microbial mats (Leggitt and Cushman, 2001). As the complex grew as a carbonate-containing stromatolite-like structure, it apparently added benthic stability and topographic heterogeneity to a soft bottomed lakeshore.

Similarly, aquatic macrophytes such as *Justicia* aid unionid mussels by stabilizing the streambed and enhancing local influx of fine organic particles (Fritz *et al.* 2004). Sedge tussocks (*Carex nudata*) growing in and along the active channel shield guest plants growing within tussocks from scour and export during winter floods and from herbivory during summer low flows (Levine, 2000). In slow-flowing lentic or wetland environments where hypoxia can stress infauna or rooted plants, aerenchymous plants can facilitate neighbors by oxygenating sediments (Callaway and King, 1996). Floating mats of algae or macrophytic vegetation provide food-rich, warm incubators that enhance development, survival, and emergence of aquatic insects (Power, 1990a), and hide juvenile fish from predators (Sazima and Zamprogno, 1985).

At ecosystem scales, certain freshwater fishes and benthic invertebrates benefit from the added habitat heterogeneity generated by ecosystem-engineering beavers (Naiman *et al.* 1988, Wright *et al.* 2002). In addition, the importance of forest cover to stream habitat structure and to retentiveness, temperature, and wood and sediment loading regimes that favor salmonids is widely recognized (Harvey 1998, Welty *et al.* 2002). Hydraulic lift by large trees that access deep ground water and leak some of it into shallow soils (Callaway 1990) might play a crucial, but overlooked, role in maintaining stream runoff during drought (Jung-Eun Lee *et al.* 2005).

Except where strong physical disturbance, stagnant anoxic water or pollution prevail, abundant large burrowers of a sessile or discretely motile life penetrate the marine coastal sediments with their tubes and burrows (Cade'e, 2001). These infaunal dwellings constitute a conspicuous habitat structure, in a way like an inverted analogue to the upright terrestrial vegetation. Some tubes or burrows are simple blind ends but many are basically Y or U shaped, often with branches and chambers, and occasionally there are interconnected communal burrows (Fig. 5). Tubes have solid polysaccharid linings which act as molecular sieves, while burrows are enveloped with mucus and often have an outer layer of fine grained sediment particles. Tubes and burrows more than double the area of the sediment water interface. Like veins and arteries, they serve to transport particles, dissolved metabolites and oxygen through the sediment, with passive and active ventilation. Collected or trapped organic detritus is stowed away in blind chambers for further microbial decomposition to serve later as digestible food. Projecting tube caps, chimneys and faecal mounds deflect the lateral flow of water and cause upwelling as well as washout of pore water solutes exceeding by far the molecular diffusion across the sediment-water interface.



**Fig. 5.** Burrows and tubes of (A, B) Thalassinidean shrimps, (C) An ocipodid crab, (D–G) Polychaetes, (H) An ophiuroid, (I) An apodous holothurian and (J) A staphylinid beetle. Sediment surface layer is shaded; scale bars in cm. A: Widening are turning chambers; C: Chimney out of pellets to trap air when the tide comes in; F: Spionid burrow with fecal chamber at the basement; G: secondary ducts spiralling around vertical shafts; I: A previous feeding pit and an old shaft filled with fecal castings; J: Burrow with lateral egg chambers and faecal pellets at the basement. Karsten (2004)

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