

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Mollusks as ecosystem engineers: the role of shell production in aquatic habitats

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Mollusk shells are abundant, persistent, ubiquitous physical structures in aquatic habitats. Using an ecosystem engineering perspective, we identify general roles of mollusk shell production in aquatic ecosystems. Shells are substrata for attachment of epibionts, provide refuges from predation, physical or physiological stress, and control transport of solutes and particles in the benthic environment. Changes in availability of these resources caused by shell production have important consequences for other organisms. Colonization of shelled habitat depends on individual shell traits and spatial arrangement of shells, which determine access of organisms to resources and the degree to which biotic or abiotic forces are modulated. Shell production will increase species richness at the landscape level if shells create resources that are not otherwise available and species are present that use these resources. Changes in the availability of resources caused by shells and the resulting effects on other organisms have both positive and negative feedbacks to these engineers. Positive feedbacks appear to be most frequently mediated by changes in resource availability, whereas negative feedbacks appear to be most frequently mediated by organisms. Given the diversity of species that depend upon resources controlled by shells and rapid changes in global shell production that are occurring due to human activities, we suggest that shell producers should not be neglected as a targets of conservation, restoration and habitat management.

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Ecosystem engineering is the creation, modification and maintenance of habitats by organisms. Ecosystem engineers control the availability of resources to other species by causing physical state changes in abiotic or

biotic materials (Jones et al. 1994, 1997). Although many organisms change the environment to some extent, and most ecosystems are likely engineered to some degree, impacts of engineers on other species and

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ecosystem functioning range from trivial to highly significant (Jones et al. 1994, 1997). Engineering activities also vary in their distribution across species (Jones et al. 1997). Some activities are restricted to one or a few organisms (e.g. dam construction by beaver); others are common to whole groups of species (e.g. shade creation by trees). While the engineering role of some groups of organisms is well-recognized (e.g. soil organisms: Anderson 1995; benthic bioturbators: Levinton 1995; some herbivores: Wilby et al. 2000; also see Jones et al. 1994, 1997 for reviews), identifying common, significant engineering features of groups of species is a major challenge in ecology.

Here we review the ecosystem engineering roles of an important, widespread group – aquatic mollusks. These organisms have community and ecosystem-level impacts via several mechanisms that are restricted to particular guilds (e.g. suspension feeding: Peterson and Black 1987, 1991, Strayer et al. 1999; deposit feeding: Fenchel and Kofoed 1976, Bianchi and Levinton 1981; grazing: Hill et al. 2000, Buschbaum 2000; predation: Peterson 1982, Young 1985; biodeposition: Bertness 1984, Stewart et al. 1998; bioturbation: Flach 1996, Austen et al. 1998; boring: Highsmith 1980). However, nearly all mollusks produce shells, and it is the general engineering consequences of shell production on which we focus. We argue that shell production by mollusks is an underappreciated but important ecosystem engineering process. Under the term ‘shell’ we include empty shells, shell fragments, and shells of living mollusks. Although the diversity of shell characteristics and environments in which mollusks occur suggest overwhelming idiosyncrasy and contingency to any engineering effects, here we develop general predictions about the engineering consequences of shell production on resources and species in aquatic habitats. We review current literature on shell production and its effects in aquatic habitats to: (1) identify general engineering mechanisms of resource control, (2) illustrate how engineered habitat characteristics influence colonization by organisms, (3) show when shell production can increase the number of species in the landscape, and (4) indicate how feedback effects on the engineer may contribute to maintenance of habitat heterogeneity.

Why shell production by mollusks is an important ecosystem engineering process

Shell production is important for at least five reasons:

(1) Shells and shell aggregations introduce complexity and heterogeneity into benthic environments and are important elements of habitat structure affecting population-, community- and ecosystem-level processes (McLean 1983, Kidwell 1986, Lenihan and Peterson 1998, Crooks and Khim 1999, Gutiérrez and Iribarne 1999, Lenihan 1999; Table 1). Architectural complexity can determine the success of some organisms in coloniz-

ing or using habitats, and it is often a strong local control on species composition (Werner and Hall 1977, Crowder and Cooper 1982). In addition, habitat heterogeneity is important for maintaining high species richness, given that a landscape of different habitat types should contain more species than a homogeneous one (Sousa 1984, Pickett and White 1985).

(2) Mollusks make large amounts of shell. Most marine mollusks produce 50–1000 g CaCO₃ m⁻² yr⁻¹, and calcium carbonate production by oysters is estimated at 90 000 g m⁻² yr⁻¹ (Beukema 1982, Powell et al. 1989). Shell production rates of freshwater mollusks may also reach 50–1000 g CaCO₃ m⁻² yr⁻¹ (Chase 1996, McMahon and Bogan 2001, Strayer et al., unpubl.). Based on calcium carbonate production of 50–1000 g m⁻² yr⁻¹, the density of calcite and aragonite, and assuming shells have a calcite/aragonite ratio of 1:1, mollusks may deposit 0.02 to 0.35 mm of CaCO₃ yr⁻¹. This is surprisingly high given that sedimentation rates in estuaries are 1–3 mm yr⁻¹ (Nichols 1989). Considering that average production of wood in temperate forests is ca 600 g m⁻² yr⁻¹ (Whittaker and Likens 1973, Jordan and Herrera 1981, O’Neill and DeAngelis 1981), persistent structure is produced by mollusks at rates comparable to trees.

(3) Shells persist over geological time when processes of mechanical breakage and chemical dissolution are negligible (Kidwell 1985, 1991, Powell et al. 1989). Molluskan remains are the major components of death assemblages (i.e. assemblages of dead organisms and parts of dead organisms; Powell et al. 1989), and these death assemblages are widespread (Kidwell 1985, Powell et al. 1989). The durability of shells and their occurrence at locally high densities in reefs and beds are characteristics that increase the likelihood of important engineering effects over large temporal and spatial scales (Kidwell and Jablonski 1983, Kidwell 1985, 1986, Gutiérrez and Iribarne 1999, Palacios et al. 2000).

(4) Molluskan shell production is ubiquitous: all marine and most freshwater habitats contain mollusks (Russell-Hunter 1983, Dillon 2000).

(5) Humans have caused large changes in mollusk density and biomass in aquatic habitats through exploitation of shellfish populations, cultivation of species, species introductions and habitat modification (Roadhouse and Roden 1987, Rothschild et al. 1994, Beukema and Cadée 1996, Carlton 1999, Strayer et al. 1999, Palacios et al. 2000). Shell extraction is also important in certain locales (La Salle and de la Cruz 1985, Beukema and Cadée 1999). All these activities alter rates of shell production. However, with a few exceptions (Ricciardi et al. 1997, Lenihan and Peterson 1998, Stewart et al. 1998, Lenihan 1999, Palacios et al. 2000), most studies dealing with community or ecosystem impacts of changes in mollusk density and biomass have not considered the engineering-mediated consequences of altered shell production.

General mechanisms of resource control by shell producers

Shell production affects the structure of benthic habitats by modifying their heterogeneity and complexity, ultimately changing the availability of resources to other organisms. Changes in resource availability can occur directly as a consequence of the habitat structure created by the engineer, or indirectly through the modulation of biotic or abiotic forces by the engineered structure (Jones et al. 1994, 1997). Here, we distinguish between the modulation of forces that act as a source of mortality or stress to other organisms and the modulation of forces that play a role in the transport of resources to other organisms. We illustrate these pathways with a simple example.

Imagine an empty gastropod shell occurring on an otherwise flat muddy bottom in an intertidal setting. The shell has added heterogeneity to the local habitat that otherwise has only mud particles as structural elements. The shell itself is a substratum for boring and sessile epibenthic organisms that cannot settle on the soft bottom and may serve as a site for oviposition. The shell also modifies the availability of resources by modulating abiotic or biotic processes. For instance, the internal shell cavity may be a microhabitat where the impact of temperature extremes, hydrodynamic forces, or predation is reduced. Consequently, organisms may exploit the cavity to reduce physiological stress, damage or removal by currents or predators. In addition, the shell may cause changes in near-bed flow and infiltration of water through the sediments, with subsequent alteration of particle and solute transport in the benthic habitat.

We can see that the addition of the shell changed the relative abundance of a variety of resources. Although this simple example represents just one particular situation, the processes revealed are very general. Shell production is known to control (1) the availability of substrata for settling by fouling organisms, (2) the availability of enemy- or stress-free space, and (3) the transport of particles and solutes in the benthic environment (Table 1). While the processes are general, the magnitude of these controls and their ecological consequences varies from one situation to another. The influence of specific shell traits and their interplay with the environment where shell production takes place is the focus of the next two sections.

Traits of the engineered habitat and resources for potential colonizers

There is a bewildering variety of forms of mollusk shells and shell habitats. Nevertheless, this complexity can be simplified by considering: (1) individual shell traits and (2) shell spatial arrangement. By 'individual shell traits'

we mean shell-specific properties that affect resources for other organisms by determining characteristics of the shell habitat irrespective of whether shells are isolated or aggregated. Individual shell traits are relevant in two ways. First, they determine whether the resource is accessible to a given organism. Second, they determine the degree to which a given biotic or abiotic force can be modulated. The latter aspect is not relevant to the provision of substrata for attachment, because this kind of resource provisioning does not involve the modulation of forces. We address 'shell spatial arrangement' by focusing on aggregation. The degree of aggregation determines whether effects of shells remain isolated or interact with neighboring shells leading to broader-scale impacts on resources that are not a linear function of the number of shells in the aggregation. First we exemplify the role of individual shell traits and then we discuss the interactive effects of shell spatial arrangement and individual shell traits. In both situations we consider effects on substrata for attachment, enemy- or stress-free space, and particle and solute transport.

Individual shell traits and resources

Substrata for the attachment of fouling organisms

Several shell traits affect potential colonization by fouling organisms. Shell size is particularly important. Larger shells usually support more individuals of a given fouling species (Caceres-Martinez et al. 1999, Creed 2000) and a greater richness of fouling species (Beckett et al. 1996) than smaller ones. Shell size can also impose limits on the size of colonizing organisms. For instance, the brown macroalga *Hormosira banksii* occurs preferentially on larger individuals of the infaunal cockle *Katelysia* spp., as a consequence of selective spore settlement on large cockles that have a lower probability of dislodgment by waves during storms (Black and Peterson 1987). Fouling species are also often selective with respect to the textural characteristics of the shells they colonize (Schmitt et al. 1983, McKinney 1996, Olabarria 2000). The type and degree of shell ornamentation (McKinney 1996, Olabarria 2000) and the presence of shell damage (Schmitt et al. 1983) can also determine colonization success.

Refuges. The most obvious trait affecting accessibility of a shell as a refuge is whether the shell belongs to a living mollusk or is empty. For empty shells, individual traits determine the space available for shelter hence the maximum size of the sheltering organisms. Shell volume and aperture width are often key attributes in affecting shell selection by shell-dwellers (Bertness 1980, Mather 1982, Hazlett 1996, Osorno et al. 1998), but other shell traits are also influential. For example, shell weight and

Table 1. Examples of direct and indirect effects of shell production by aquatic mollusks on resources.

A. Substrata for attachment			
Habitat	Shell structure	Settling species	References
Rocky intertidal	Beds of mussel, <i>Mytilus californianus</i>	Algae, barnacles, anthozoans, sessile polychaete worms, limpets	Lohse (1993)
	Limpets, <i>Scurria boehmita</i> , <i>S. ceciliana</i> , <i>S. araucana</i>	Lichen, <i>Thelidium litorale</i>	Espoz et al. (1995)
Rocky subtidal	Sessile clam, <i>Chama pellucida</i>	Sponges, hydroids, anemones, bryozoans, entoprocts, tunicates, algae	Vance (1978)
	Beds of mussel, <i>Modiolus modiolus</i>	Kelp, <i>Laminaria digitata</i> , <i>L. saccharina</i>	Witman (1987)
	Kelp snail, <i>Norrisia norrisi</i>	Barnacle, <i>Megabalanus californicus</i>	Schmitt et al. (1983)
Soft bottom intertidal	Beds of blue mussel, <i>Mytilus edulis</i>	Barnacles, <i>Balanus crenatus</i> , <i>Semibalanus balanoides</i>	Buschbaum (2000), Buschbaum and Saier (2001)
	Infauunal cockle, <i>Katelysia</i> spp.	Brown macroalga, <i>Hormosira banksii</i>	Black and Peterson (1987)
	Beds of Holocene shells of clam, <i>Tagelus plebeius</i>	Barnacle, <i>Balanus improvisus</i> ; mussel, <i>Brachydontes rodriguezii</i> ; bryozoan, <i>Conopeum</i> sp.	Gutiérrez and Iribarne (1999)
Soft bottom (sandy) intertidal	Hydrobiid snails (various spp.)	Alga, <i>Enteromorpha</i> spp.	Schories et al. (2000)
	Oysters, <i>Crassostrea cucullata</i> ; mussels, <i>Perna viridis</i> ; windowpane oysters, <i>Placuna placenta</i> ; turritellas, <i>Turritella turritella</i>	Shell boring algae, <i>Hyella caespitosa</i> , <i>H. gigas</i> , <i>Mastigocoleus testarum</i> , <i>Plectonema terebrans</i> , <i>Phormidium</i> sp.	Raghukumar et al. (1991)
Soft bottom intertidal/shallow subtidal	Reefs of eastern oyster, <i>Crassostrea virginica</i>	Anemones, barnacles, bivalves, polychaetes	Zimmerman et al. (1989)
Soft bottom shallow subtidal	Black clam, <i>Chione fluctifraga</i>	Shell-boring worm, <i>Polydora</i> spp.	Caceres-Martinez et al. (1999)
Seagrass beds, Soft bottom shallow subtidal	Shells of snails, <i>Cerithium atratum</i> , occupied by hermit crabs (various spp.)	Oyster, <i>Ostrea puelcheana</i> ; tube-forming polychaete, <i>Hydroides plateni</i>	Creed (2000)
Exposed sandy beach	Clams, <i>Tivela mactroides</i> , <i>T. ventricosa</i>	Egg capsules of gastropod, <i>Olivancillaria vesica vesica</i>	Borzzone and Vargas (1999)
River	Unionid bivalves (various spp.)	Turbellarians, oligochaetes, larvae of caddisflies, chironomids, other insects	Beckett et al. (1996)
Freshwater lake	Shells of snails, <i>Lymnaea peregra</i>	Eggs of <i>Lymnaea peregra</i>	Piggott and Dussart (1995)

B. Enemy- or stress-free space				
Habitat	Shell structure	Refugee species	Predator or stress	References
Cobble intertidal Rocky subtidal	Blue mussel, <i>Mytilus edulis</i> Sessile clam, <i>Chama pellucida</i>	Barnacle, <i>Semibalanus balanoides</i> Shell epibionts: Sponges, hydroids, anemones, bryozoans, entoprocts, tunicates, algae	Thermal stress Grazing/predation by sea urchin, <i>Centrostephanus coronatus</i>	Stephens and Bertness (1991) Vance (1978)
Soft bottom intertidal	Oyster shell gravel of <i>Crassostrea virginica</i> Artificial beds of oyster shells of <i>Crassostrea gigas</i> Small aggregations of oyster, <i>Crassostrea virginica</i> Beds of Holocene shells of clam, <i>Tagelus plebeius</i>	Hard clam, <i>Mercenaria mercenaria</i> Juvenile Dungeness crab, <i>Cancer magister</i> Ribbed mussel, <i>Geukensia demissa</i> Polychetes <i>Laeonereis acuta</i> , <i>Neanthes succinea</i> , <i>Heteromastus similis</i>	Predation by blue crab, <i>Callinectes sapidus</i> Adult crab cannibalism, fish predation Predation by mud crab, <i>Panopeus herbstii</i> Predation by shorebirds, current impact (?), thermal stress (?)	Arnold (1984) Fernández et al. (1993), Iribarne et al. (1995) Lee and Kneib (1994) Gutiérrez and Iribarne (1999), Gutiérrez et al. (2000)
Freshwater (laboratory experiment)	Clams <i>Rangia cuneata</i> or their shells at high densities Beds of zebra mussel, <i>Dreissena polymorpha</i>	Infaunal clams, <i>Mya arenaria</i> , <i>Macoma balthica</i> Snails, <i>Physella heterostropha</i>	Refuge from epibenthic predators Predation by redear sunfish, <i>Lepomis microlophus</i>	Skilleter (1994) Stewart et al. (1999)
C. Transport of particles and solutes				
Shell structure	Effect	References		
Mats of mussel, <i>Musculista senhousia</i> Small aggregations of blue mussel, <i>Mytilus edulis</i>	Trapping of fine-grained sediments and organic particles Enhancement in advective porewater exchange in sediments to depths of 15 cm	Crooks and Khim (1999) Huettel and Gust (1992)		
Beds of horse mussel, <i>Atrina zelandica</i> Sea scallop, <i>Placopecten magellanicus</i>	Decrease in drag coefficient acting on seabed Alteration of sediment transport patterns – presence of horseshoe-shaped trough around shell and smaller erosion-deposition features downstream	Green et al. (1998) Grant et al. (1992)		
Shells of sea scallop, <i>Placopecten magellanicus</i>	Enhancement of phytoplankton retention by sediments in areas of increased skim friction upstream and downstream of shell	Pilditch et al. (1998)		
Beds of blue mussel, <i>Mytilus edulis</i>	Enhancement of turbulent transport increases phytoplankton flux to bed	Fréchette et al. (1989)		
Beds of Holocene shells of clam, <i>Tagelus plebeius</i>	Decrease in sediment erodability	Gutiérrez and Iribarne (1999)		
Reefs of oyster, <i>Crassostrea virginica</i>	Reef height controls flow speed, rates of sediment deposition, exposure to hypoxia/anoxia	Lenihan (1999)		
Mobile disarticulated shells of cockles, <i>Cerastoderma edule</i>	Increased abrasion of cohesive clay substrate	Thompson and Amos (2002)		

center of gravity are important in shell selection by hermit crabs, where carrying a heavy shell or uneven load may be energetically costly or not possible (Hazlett 1996, Osorno et al. 1998).

Shell traits also influence the degree to which biotic or abiotic forces are modulated. For example, several hermit crab species select for shell characteristics that diminish predation risk, such as high strength (Wilber 1990, Brown 1992), absence of shell damage (McClin-tock 1985, Brown 1992) or cryptic shell coloration (Partridge 1980). Characteristics of the shell such as a low aperture/shell axis ratio (Bertness 1981) and absence of shell damage (Wilber 1990, Brown 1992) are also important in preventing physiological stress from desiccation. Hermit crabs also select heavier shells in areas of higher water turbulence and wave action (Partridge 1980, Hahn 1998).

Transport of particles and solutes. Predictions about the role of individual shell traits in modulation of water flow are mostly based on shell size. Shells usually protrude from the sediment surface, altering boundary layer characteristics. Most of the quantitative research on flow characteristics around objects protruding from the sediment is based on the analysis of flume flows around simple shapes such as hemispheres or erect cylinders (Nowell and Jumars 1984). For an isolated, rigid object protruding from a sediment bed, shear stress increases in the bed area immediately surrounding the object, leading to erosion features such as scour pits (Eckman and Nowell 1984). Given a level of boundary shear stress imposed by the flow, the magnitude of the flow perturbation caused by a protruding structure is positively correlated to the diameter of the structure and its height (Eckman and Nowell 1984). For example, the size of erosion and deposition features formed by sediment transport around isolated scallop shells was positively related to shell size (Grant et al. 1992), with large shells perturbing flow more than small ones and exerting greater control on the nearbed transport of particles and solutes. The magnitude of the effect of shells on nearbed transport of particles and solutes is also affected by shell shape. Shape-related properties such as convexity, elongation, asymmetry or surface roughness affect the magnitude of the drag and lift forces acting on shells (Way et al. 1993, Olivera and Wood 1997, Denny and Blanchette 2000), with concomitant variation in fluid transport around them.

Predicting how individual shell traits affect accessibility of a resource whose provision depends on the characteristics of fluid transport is more difficult than predicting the consequences of shell traits on fluid transport itself. However, the fact that the degree of hydrodynamic disturbance is positively related to shell size suggests that the spatial scales at which resources transported by the flow are affected also depend on shell size. The sensitivity of an organism to the heterogeneity

of a particular resource depends on the scale at which the heterogeneity occurs (Morris 1987). For instance, patches rich in organic matter occurring at a centimeter-scale around isolated shells arising from flow disturbance are expected to affect the distribution of microorganisms and small infauna (Pilditch et al. 1998). However, we should not expect much of an effect on larger organisms, because they may not perceive heterogeneity at that scale. Unfortunately, so little is known about the mechanisms determining access of organisms to flow-mediated resources that we cannot say more than these general statements.

Spatial arrangement of shells and interaction with individual shell traits

Shells can be solitary, but are often grouped in beds, reefs, middens and windrows, having effects that are the result of interactions among shells. The magnitude of resource effects of aggregations is obviously greater than that of isolated shells.

Substrata for the attachment of fouling organisms. The provision of substrata for the attachment of sessile organisms increases with the number of shells. However, the total shell surface area available for colonization is not just the sum of the areas of the shells in the aggregation. Commito and Rusignuolo (2000) investigated the fractal geometry of surface topography in mussel beds at scales from 1.44–200 mm, proposing that the fractal dimension (D) – an indicator of the total surface area exposed to colonization – is higher at intermediate levels of mussel cover and density (Snover and Commito 1998). Of course, D values are also affected by individual shell traits such as their size. Commito and Rusignuolo (2000) also proposed that an intermediate percentage cover of mussels of different sizes would have a highly irregular surface and a large D value, while similar-sized, densely packed mussels at 100% cover might have a relatively smooth surface and a small D .

Refuges. The provision of refuges by shell aggregations is also not necessarily a linear function of the number of shells in the aggregation. First, although refuges in shell aggregations are found in shell cavities, they also occur in the interstices between shells. Second, interstices among shells that can be used as refuges by small, mobile organisms are also likely to be related to D . As with the provision of substrata for attachment, the degree of shell packing and the size of the shells in the aggregation therefore influence refuge availability. The size–frequency distribution of the organisms living in a habitat is often related to fractal dimension properties (Morse et al. 1985). For example, Kostylev et al. (1997)

found a positive relationship between the average sizes of the snail *Littorina saxatilis* and fractal dimension values of a rocky surface covered by mussels and barnacles.

Transport of particles and solutes. The degree of shell aggregation affects characteristics of hydraulic flow over the bed. When rigid objects protruding from the bed are sparsely distributed, their effects on flows are essentially isolated, and, as in the case of the provision of substrata for attachment and refuge by shells, the flow disturbance caused by the group is equivalent to the sum of individual flow disturbances (Nowell and Jumars 1984). However, if these rigid objects are similar in height, and if the aggregation is sufficiently extensive to allow the boundary layer to attain equilibrium, then turbulence levels in the fluid among the objects will be higher than that observed away from the structures. This effect occurs up to a threshold density of objects. Above this density fluid flows over rather than through the structures (i.e. skimming flow) and flow velocities and turbulence levels among the objects decrease (Nowell and Church 1979, Nowell and Jumars 1984). It is important to note that skimming flow only occurs when aggregations of objects are similar in height.

As mentioned earlier, flow perturbation is positively correlated to the height and diameter of the protruding object (Eckman and Nowell 1984), which has important implications for shell aggregations. Despite the fact that isolated larger shells are expected to have a greater effect on flow than smaller shells, it should be recognized that many shells, typically living bivalves such as mussels and oysters, often occur in densely packed beds or reefs. Thus, apart from the effect on flow caused by each single shell and the characteristics of flow among the shells, broader scale flow perturbation is caused by the aggregation itself (Lenihan 1999).

Positive effects of shell production on landscape-level species richness

As Jones et al. (1997) point out, if we consider just the local area where engineering occurs, there can be a positive, a negative, or no effect of an engineer on species richness, and no a priori basis for predicting the direction of the effect. Nevertheless, if the scale of analysis encompasses both engineered habitat and un-engineered habitat (i.e. not modified by the shelled mollusk of interest), the net increase in habitat diversity suggests that engineering effects on species richness will generally be positive (Jones et al. 1997, Wright et al. 2002, Lill and Marquis, in press).

Positive effects of shell production on landscape-level species richness may occur as a consequence of any of the three general mechanisms of resource control by shell producers identified above (i.e. via provision of

substrata for attachment, refuges, or resources transported by hydraulic flow). However, the relative importance of each mechanism will vary depending on where the engineering takes place. This point is well illustrated by comparing the consequences of mussel bed establishment in rocky versus soft-bottomed environments. In both cases, mussel beds have positive effects on landscape-level species richness, but for different reasons. Mussels in soft-bottomed environments provide substrata for the attachment of invertebrates and algae that are usually unable to attach to bare mud (Albrecht and Reise 1994, Buschbaum 2000). However, the provision of these substrata has little effect on species richness on rocky shores, because most species that attach to mussel shells also attach to rocks (Lohse 1993, Tokeshi and Romero 1995). On the other hand, mussel beds on rocky shores allow colonization by infaunal organisms in the sediment trapped in the interstices among shells – organisms which otherwise cannot live in rocky habitats (Tokeshi and Romero 1995). In contrast, mussel beds in soft-bottomed environments do not add much to the richness of infaunal species, because these organisms already occur in the surrounding sediments (Ragnarsson and Raffaelli 1999).

From this example we can see that for positive effects of an engineer on landscape-level species richness two conditions must be met. First, the engineered habitat must provide a resource that is not available in the unengineered environment. Second, there must be species in the regional pool capable of taking advantage of the resource(s) that exclusively occur in the engineered habitat (Wright et al. 2002). How often will these conditions be met? Given high rates of dispersal of many aquatic organisms, we might expect that the direct provision of any resource by shells will lead to positive effects on landscape-level species richness provided that the given resource does not occur in the unengineered habitat. However, in the case of resources whose occurrence depends on the modulation of forces (i.e. refuges, flow-related resources), any increase in the number of species in the landscape will also depend on the strength of the forces that are being modulated. For example, an increase in richness because shells act as refuges will depend on whether there are non-shell structures in the unengineered habitat that can serve the same function as shells, and on whether mortality sources in the landscape are strong or weak. If mortality sources are weak or negligible, then the potential enemy-free space created by shells will have no effect on landscape-level species richness.

Although there are several realistic scenarios in which shells or shell aggregations provide resources that are not available elsewhere, whether or not these resources are available in the unengineered habitat also depends on the degree of resource specialization of the responding organisms. For instance, because both gastropod

shells and cobblestones are substrata for attachment for several fouling invertebrates and algae, we should not expect a strong positive effect of shells on the richness of these species in a cobblestone habitat. The opposite situation may occur with organisms like hermit crabs that use gastropod shells as domiciles, but do not use cobblestones. In this case, an increase in the richness of species that use shells as refuges would contribute to an overall increase in species richness.

Feedback effects on the engineer and the maintenance of landscape heterogeneity

How might the engineering activities affect shell production? Feedbacks to engineering species (Jones et al. 1997) can be either positive or negative. They may occur as a consequence of changes in resource availability caused by the engineering activity (hereafter 'resource-mediated feedbacks'), or as a consequence of the facilitation or inhibition of other organisms that have responded to changes in the availability of resources caused by the engineer ('organism-mediated feedbacks').

Examples of feedbacks to the engineer

Positive resource-mediated feedbacks. Mechanisms enhancing species richness in shell habitats may facilitate the engineer. In shell habitats dominated by living mollusks, recruitment and mortality are often influenced by the structural complexity conferred by conspecific neighbors. Adult mussels create substrata for the attachment of settling conspecifics (Bayne 1964, Petersen 1984, Bertness and Grosholz 1985). Mussel predators such as starfish, forage less efficiently as mussel bed structural complexity increases (Dolmer 1998). Sources of mortality such as predation or physical disturbance are stronger at the edge of mussel aggregations, where the protection given by conspecifics is less than in the center (Bertness and Grosholz 1985, Okamura 1986, Lin 1991, Stiven and Gardner 1992). Positive effects of neighbors are not restricted to mussels. For example, seastar predation on cockles, *Katylsia* spp., decreases at high prey densities because conspecifics create a structural barrier (Peterson and Black 1993).

Positive resource-mediated feedbacks can also favor the persistence of shell habitats made up of shell remains via an increase in local shell production. Oyster, *Crassostrea virginica*, reefs, for example, develop after the larvae settle on oyster shells to which they are attracted by chemical cues (Turner et al. 1994). Although oyster settlement may occur at a similar density in reefs of oyster shells and reefs of surfclam shells, *Spisula solidissima*, post-settlement survival was higher

in oyster shells, because they provided a better refuge from predation (O'Beirn et al. 2000).

Positive organism-mediated feedbacks. Organisms that take advantage of the resources provided by the shells of living mollusks may also benefit these same mollusk species. For instance, epibionts on sessile clams, *Chama pellucida*, prevent clam predation by the starfish, *Pisaster giganteus*, because detection and/or attack of *C. pellucida* by starfish is less successful if they are covered by epibionts (Vance 1978). Other organisms can even increase the persistence of shell habitats made up of empty shells. For example, the use of gastropod shells by hermit crabs impedes shell burial by sediments (Creed 2000), a process that can be attributed to the epibenthic habits of hermit crabs plus shell turnover as crabs abandon and re-occupy shells.

Negative resource-mediated feedbacks. Although conspecific neighbors can provide a substrate for attachment and a structural barrier against predation, aggregation also has negative effects on shell production. Individual growth is frequently higher at the edges of mussel patches than in the interior (Okamura 1986, Lin 1991, Stiven and Gardner 1992, Svane and Ompi 1993). This pattern could be a consequence of a reduction in food availability from the filtering activity of the mussels as water passes from the edge to the center of an aggregation (Svane and Ompi 1993). However, observations and experiments not only show slower growth, but also distortion, thickening and twisting of the shells of individuals living in dense aggregations (Harger 1972, Bertness and Grosholz 1985). Mussel growth exerts physical pressure on neighbors (Okamura 1986) and the higher number of mussels with neighbors in the interior of aggregations may also account for their lower growth rates.

Negative organism-mediated feedbacks. Organisms that take advantage of the resources provided by shells can also have a negative effect on the persistence of the shell habitat. Epibiosis on mussels by large macroalgae increases the drag forces acting on the individuals, which then increases the probability of mussel dislodgement and mortality (Witman and Suchanek 1984, Witman 1987). Algal epibiosis on mussels can also reduce the energy of water flow, enhancing sediment deposition within mussel beds, leading to mussel burial and mortality (Albrecht and Reise 1994). Epibionts can also negatively affect shell production by diminishing the growth rates of their mollusk hosts. For example, epibionts on snails, *Littorina littorea*, increase drag on the host individuals and reduce their growth when exposed to moderate, steady flow, presumably because fouled snails invest more energy in anchorage and movement (Wahl 1996). Negative organism-mediated feedbacks are not just caused by spe-

cies that use shells for attachment. Organisms that shelter in shell habitats can be important predators on shell-producing species. Oyster, *Crassostrea virginica*, are preyed on by mud crabs, *Panopeus herbstii*, that shelter in oyster reefs on the U. S. Atlantic coast (Abbe and Breitburg 1992, Dittel et al. 1996, Micheli 1997). Predator-mediated negative feedbacks are also plausible explanations for shell habitats that are mostly full of empty shells. Low recruitment of the soft-shell clam, *Mya arenaria*, in shell deposits of the Grays Harbor estuary (Washington, USA), is attributed to predation by juvenile Dungeness crab, *Cancer magister*, whose densities are orders of magnitude higher in shell beds than in adjacent flats (Palacios et al. 2000).

Generalizations about feedbacks to the engineer

Three tentative generalizations emerge from the above examples. First, species that occur in aggregations seem particularly prone to resource-mediated feedbacks. Second, positive feedbacks appear to be more frequently mediated by resources than by organisms, whereas negative feedbacks seem to be more frequently mediated by organisms than by resources. Third, while negative resource-mediated feedbacks apparently affect shell production primarily via a decrease in individual growth rates, positive resource-mediated feedbacks seem to affect shell production mostly via increased recruitment. With gregarious shell producers, recruitment and individual growth is usually higher when individuals occur at moderate rather than high densities or when aggregations are small rather than large (Stiven and Kuenzler 1979, Okamura 1986, Lin 1989, Stiven and Gardner 1992, Svane and Ompi 1993). Overall then, we might expect that positive resource-mediated feedbacks that lead to increases in the number of individuals and the size of aggregations in turn initiate negative organism- or resource-mediated feedbacks that constrain density and aggregation size.

Prospects

Although ecosystem engineering is ubiquitous, identifying the general engineering characteristics and consequences of groups of species amidst a plethora of organismal and ecosystem idiosyncrasies is a major challenge in ecology. By focusing on the physical structures common to an entire group – the shells of mollusks – important ecological generalizations and testable general hypotheses emerge about these abundant, persistent, ubiquitous, yet under-appreciated structures and their effects on aquatic communities and ecosystems. Such an approach may be of value for understanding the effects of other groups of taxonomically-related organisms that create similar structures

(e.g. trees) as well as taxonomically dissimilar organisms that make similar types of structures (e.g. burrows of different animals, soil mounds built by animals and plants).

The generality of the engineering effects of shelled organisms on other species suggests that widespread human-induced changes in shell production via over-exploitation, shell removal, shell cultivation, habitat destruction, and exotic species introduction could have large, unintended consequences for other species. As has recently been pointed out by others (Coleman and Williams 2002), human influences on the abundance and distribution of engineers have knock-on consequences that can go well beyond the engineering species itself. Given the numerous resources controlled by shells and the variety of organisms that depend upon them, the engineering effects of mollusks that are mediated through shell production should receive serious consideration in conservation initiatives, restoration and habitat management.

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