FORUM ARTICLE

Ecosystem engineering — moving away from 'just-so' stories

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Abstract: The concept of ecosystem engineering has been proposed recently to account for key processes between organisms and their environment which are not directly trophic or competitive, and which result in the modification, maintenance and/or creation of habitats. Since the initial reporting of the idea, little work has been undertaken to apply the proposed concept to potential ecosystem engineers in the marine environment. Biological and ecological data for the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea) allowed for a formal assessment of this species as an ecosystem engineer, in direct accordance with published criteria. Despite a low population density and the short durability of its burrow structures, *Callianassa filholi* affected a number of resource flows by its large lifetime *per capita* activity. Ecosystem effects were evident in significant changes in macrofauna community composition over small spatial and temporal scales. Seasonal variation in the effects of ghost shrimp activity were associated with changes in seagrass (*Zostera novazelandica*) biomass, which revealed the probability of interactions between antagonistic ecosystem engineers. The formal assessment of *Callianassa filholi* provides the opportunity to aid discussion pertaining to the development of the ecosystem engineering concept.

Keywords: allogenic and autogenic engineers; *Callianassa filholi*; community change; ecological concept; habitat modification**;** soft-sediment environment**;** *Zostera novazelandica.*

Introduction

The notion of organisms as 'ecosystem engineers' was first developed in 1993, when ecologists at the Cary Conference at the Institute of Ecosystem Studies (U.S.A.) identified the need for an integrated understanding between population and ecosystem science (Lawton and Jones, 1993). Ecosystem engineers were defined as those organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials (Jones *et al.,* 1994). Whilst it had long been recognised that organisms alter their environment (Darwin, 1881), there has been no unifying concept that examines the relationship between the resource use of individuals, the dynamics of populations and communities, and the biogeochemical processes of ecosystems (Jones *et al.,* 1994). At the time of its initial promotion (Lawton, 1994), the concept was acclaimed as a pioneering effort to link species with ecosystems through physical consequences of biological activity. Furthermore, it was acknowledged as a potentially important advance in the endeavour to develop links between different sub-disciplines in ecology (Brown, 1995; Alper, 1998). Its application was illustrated subsequently for a number of terrestrial and aquatic habitats (chapters in Jones and Lawton, 1995).

Within a short time of the wider dissemination of the concept (Lawton and Jones, 1995), a number of studies began referring to engineering species. Following a study describing ecosystem engineering by a detritivorous fish in a tropical stream (Flecker, 1996), contention arose over whether the concept merely rephrases ecological consequences associated with habitat modification by species, and therefore, simply provides a new buzzword for ecologists (Jones *et al.,* 1997a; Power, 1997). In part, this criticism of the concept had been predicted by Jones *et al.* (1994) who highlighted the contentions that might arise from related ecological concepts.

The concept of ecosystem engineering describes aspects of the relationship between organisms and their environment that are not directly trophic or competitive (Jones *et al.,* 1994). Instead, it encompasses physical processes that are brought about by organisms

(ecosystem engineers), and which result in the modification, maintenance and/or creation of habitats. Jones *et al*. (1994) distinguished between two kinds of engineering species, 'autogenic' and 'allogenic' ecosystem engineers. Autogenic engineers impact on the habitat in which they live through their own physical structures and are an integral part of the engineered ecosystem. Allogenic engineers, on the other hand, modulate resources from one physical state to another through their behaviour and activity (Jones *et al*., 1994). Whilst the effects of ecosystem engineers on the associated community can be equally dramatic to those of keystone species (*sensu* Paine, 1966; Pimm, 1980; Krebs, 1985), critical interactions of the latter are usually regarded to be trophic. Thus, the phenomena of physical engineers and keystone species are not synonymous, even though they might be intrinsically linked (Jones *et al.,* 1994). Later, Jones *et al.* (1997b) refined the notion of ecosystem engineering by distinguishing it from trophic interactions, and by exploring probable net effects of physical ecosystem engineers on species diversity and abundances, and upon population, community and ecosystem stability. They also posed a number of open questions that would help to predict which species will be important physical engineers and which ecosystems will be most affected by them.

The originators of the concept suggested that it would probably be a decade before the shape of the models, and ultimately the theory, would be known. To date, there has been little effort to formally assess the engineering potential of individual organisms (van Breemen, 1995) or to explore aspects of the concept of ecosystem engineering itself (e.g. parasites as ecosystem engineers, Thomas *et al.,* 1998, 1999). Instead, there have been an increasing number of studies merely providing examples of engineering species in various habitats (lugworms, Riisgard and Banta, 1998; blackflies, Wotton *et al.,* 1998; prairie dogs, Ceballos *et al.,* 1999; crayfish, Statzner *et al.,* 2000), in what Jones *et al.* (1994) described as "just-so" stories. That is, publications that fail to address issues raised by the conceptual framework, and that ignore the scaling system proposed by Jones *et al.* (1994) which allows for a formal evaluation of the impact of engineering species. As a consequence, it is currently unresolved whether the ecosystem engineering concept can explain the effects of species on an associated ecosystem through physical interactions with resource flows, and whether the concept provides the basis for productive theoretical and empirical research (Brown, 1995).

In the present communication, we attempt to advance the concept of ecosystem engineering by presenting for the first time a formal assessment of a marine species as an allogenic engineer and by addressing some of the questions posed by Jones *et al.* (1994).

Scaling organisms as ecosystem engineers

Jones *et al.* (1994) provided six criteria according to which the most significant engineering species can be assessed formally: 1) lifetime *per capita* activity of individual organisms; 2) population density; 3) spatial distribution of the population, both locally and regionally; 4) length of time a population has been present at a site; 5) durability of constructs, artifacts, and impacts in the absence of the original engineer; and 6) number and types of resource flows that are modulated by the constructs and artifacts, and the number of other species dependent on these flows.

Callianassid shrimps belong to a group of ubiquitous burrowing decapods that have long been recognised as significant bioturbators of intertidal and shallow subtidal soft sediments (Cadée, 2001). Bioturbators have been identified as classic examples of ecosystem engineers (Levinton, 1995), and are highly likely to be present in soft sediments, which provide an "abiotic substrate amenable to biogeomorphic action" where "many abiotic resources are integrated" (Jones *et al.,* 1997b, p.1953, 1954). Callianassids have not been included explicitly in the concept of ecosystem engineering to date. However, a number of recent studies on the biology and ecology of the endemic New Zealand species *Callianassa filholi* allow an assessment of the impact of the species as an ecosystem engineer, with respect to the six scaling criteria.

1. Lifetime *per capita* activity of a population in Otago Harbour was high given the considerable sediment turnover by the shrimp (Berkenbusch and Rowden, 1999). The mean amount of sediment expelled by individual *Callianassa filholi* throughout the year was 17.48 g (dry weight) d^{-1}. Sediment turnover activity was dependent on seawater temperature, position of the burrow on the shore, time, and size of the shrimp. Accounting for these variables and population density resulted in an estimate of annual sediment turnover of 96 kg (dry weight) m^{-2} y^{-1} for the *Callianassa filholi* population in Otago Harbour. This is at least six times higher than comparable sediment turnover estimates (that also account for population variables including population size structure and density, see also below) of callianassid bioturbation (Stamhuis *et al.,* 1997; Rowden *et al.,* 1998).

2. The population density of *Callianassa filholi* was 16 individuals m^{-2} across the intertidal sandflat. Density varied little over time, and both mortality and recruitment rates were low (Berkenbusch and Rowden, 1998). Callianassids frequently exhibit such low population densities in intertidal regions, although the densities of some species may be an order of magnitude

higher (Koike and Mukai, 1983; Posey, 1986).

3. The spatial distribution of this burrowing ghost shrimp extends throughout the latitudinal range of New Zealand (*c.* 1300 km) and it has also been recorded around offshore islands including the subantarctic Auckland Islands (Luckens, 1991; Berkenbusch and Rowden, 2000a). Populations of *Callianassa filholi* are found in soft-sediment environments from the intertidal (tidal flats and sandy beaches) to water depths in excess of 60 m (muddy sands) (see Berkenbusch and Rowden, 1998; 2000a). Species of callianassid can have relatively restricted spatial distributions. Of the 15 species found in Australia, 6 are recorded from one site only, and the others have latitudinal distributions that range from approximately 700–2000 km (see Poore and Griffin, 1979). However, at least one callianassid species has a latitudinal range extending into both hemispheres (*c.* 6000 km, Dworschak, 2000).

4. The length of time the population has been present at a site is difficult to establish. Callianassid shrimps reside in deep burrows (~10s of centimetres depth) and frequently are not sampled or are under-sampled by typical benthic surveys. However, since the first recorded observation of *Callianassa filholi* in New Zealand (Milne-Edwards, 1878), periodic studies in Otago Harbour have documented the species' persistence at one location since the early 1950s (Ralph and Yaldwyn, 1956; Devine, 1966; Rainer, 1981). Physiological adaptations to severe environmental conditions, such as extreme hypoxia and toxic sulphide levels (Powilleit and Graf 1996; Johns *et al.*, 1997), demonstrate the ability of callianassid shrimp populations to persist under adverse conditions. However, it is possible that extreme events of hypoxia may cause mass mortality (Legovic *et al.*, 1991). Whilst callianassid populations inhabiting shallow subtidal sand have been shown to be relatively unaffected by dramatic abiotic disturbances, such as a tropical cyclone (Riddle, 1988), in areas of more stable muddy substrate, it is possible that the bottom-reaching effects of severe storms may be responsible for mass population losses. As no record of mass mortality for *Callianassa filholi* exists to date, it is likely that ghost shrimp populations have persisted at individual sites for at least the past hundred years, and probably longer.

5. Durability of constructs, artifacts, and impacts in the absence of the original engineer are associated with the dynamics of *Callianassa filholi* burrows. Observed short-term seasonal variation in burrow morphology was shown to be related to seawater temperature and sediment organic content (Berkenbusch and Rowden, 2000b). It has been documented for a number of species that burrows are stabilised by mucus-lined walls (Dworschak and Ott, 1993; Dworschak 1998). Such lining is necessitated by an unstable environment (Manning and Felder, 1986), and resin casts of *Callianassa filholi* burrows are consistent with partial or complete mucus lining of the burrow system. Due to the necessity for burrow stabilisation and maintenance, the long-term durability of these constructs (i.e. physical structures) in the absence of shrimps is unlikely (Dworschak, 1983; Stamhuis *et al.,* 1997).

6. The number and types of resource flows that are modulated by the constructs and artifacts, and the number of other species dependent on these flows can be inferred from previous studies as well as our own. Burrows constructed by callianassids affect resource flows in the substrate by virtue of their microbial and biogeochemical properties. Oxygenation and burrowing activities of inhabiting shrimps result in increased levels of bacteria and chlorophyll in the burrows (Branch and Pringle, 1987; Dobbs and Guckert, 1988) and by doing so, influence resource flows to associated organisms, such as meiofauna species, by providing a rich microbial and microalgal food source (Dittmann, 1996). Furthermore, burrow walls are enriched in organic carbon (Vaugelas and Buscail, 1990) and trace metals (Abu-Hilal *et al.,* 1988), features indicative of further resource flow effects within the soft sediment ecosystem. Burrow maintenance by shrimps is linked intrinsically to their sediment turnover activity, estimates of which provide indirect measures of resource flows. The latter include physical changes to the substrate (Tudhope and Scoffin, 1984), resuspension of particulate matter and organic carbon (Roberts *et al.,* 1981), nutrient cycling (Waslenchuk *et al.,* 1983) and organic decomposition (Ziebis *et al.,* 1996). The measured effects of bioturbation by *Callianassa filholi* were significant changes in macrofauna community composition between areas of high and low ghost shrimp density, evident over small spatial and temporal scales (10s of metres and months). In particular, abundances of a corophiid amphipod and a cyamiid bivalve were adversely affected by sediment disturbance attributable to the shrimp (Berkenbusch *et al.,* 2000).

The application of scaling criteria proposed by Jones *et al.* (1994) demonstrates that despite low population density and short durability of its burrow structures, the ghost shrimp *Callianassa filholi* affects a number of resource flows by its large lifetime *per capita* activity. We argue that the latter clearly distinguishes this callianassid as an ecosystem engineer, and that all six scaling criteria do not need to be fulfilled in their entirety to identify important engineering organisms. Instead, significant ecosystem effects can arise from various combinations of fulfilled criteria. Nevertheless, the scaling system provided a structural framework that enabled us to determine how *Callianassa filholi* has an impact on its environment,

and will allow future comparisons with the engineering effects of other species in other ecosystems.

Addressing open questions associated with ecosystem engineering

In addition to suggesting a scaling system to assess the impact of engineering species, Jones *et al.* (1994) posed a number of open questions that aid in the appreciation of the last, and most important, scaling factor. With the acknowledgment that *Callianassa filholi* is an ecosystem engineer, some of these questions can now be addressed.

1. How many species (or what proportion of species) in various communities have clearly defined and measurable impacts as engineers? Investigation of the effect of *Callianassa filholi* bioturbation on an intertidal sandflat indicated that at least this one engineering species, which represented 1.7% of the total macrofaunal species sampled at the site, had a measurable impact on community composition (Berkenbusch *et al*., 2000).

2. What happens to species richness if we remove or add engineers? Studying naturally occurring differences in shrimp densities, rather than adding or removing the engineering species, allowed for an assessment of how bioturbation influenced species richness. Whereas Jones *et al.* (1994) suggested an experimental approach to address this question, our natural experiment was successful in detecting small yet significant differences in the number of associated species; our data showed lower values at sites of high ghost shrimp density (Berkenbusch *et al.,* 2000).

3. How does the persistence of the products or effects of engineering influence population, community and ecosystem processes? Differences in community composition at a *Callianassa filholi* study site persisted even during winter when sediment turnover rates were low, but the presence of seagrass (*Zostera novazelandica*) moderated the effect during times of higher above-ground plant growth (i.e. shoots and leaves) (Berkenbusch *et al.,* 2000). Seagrass beds generally support more species and individuals than unvegetated areas (Bostroem and Bonsdorff, 1997) because seagrass plants provide living space for other fauna via their own physical structure (i.e. *Zostera* species are autogenic engineers). Thus, an increase in above-ground growth of *Zostera novazelandica* during summer may have promoted the observed increase in these two community measures (number of species and of individuals) at sites of both low and high ghost shrimp density, despite high bioturbation rates. This indicates that *Zostera novazelandica* compensates for the negative effects of high sediment turnover activity by *Callianassa filholi* in warmer months.

4. How do engineering and trophic relations interact? Because *Callianassa filholi* is a deposit-feeder (Devine, 1966), feeding, burrowing and sediment turnover activity are interconnected and reflect physical processes, which are linked by engineering and trophic interactions. However, the nature of the interaction might be complicated by suggestions that callianassids can 'garden' microbial food (Witbaard and Duineveld, 1989) and switch to suspension-feeding under certain environmental conditions (Nickell and Atkinson, 1995).

Conclusion

A lack of studies that formally scale the impact of marine engineering species, and address the 'open questions', has impeded an evaluation of the wider validity of the ecosystem engineering concept. Data from our studies made it possible to assess the importance of *Callianassa filholi* as an ecosystem engineer and attempt to elucidate the mechanisms by which it expresses its influence. These findings can be summarised in the form of a conceptual model (Figure 1), in accordance with the format originally proposed by Jones et al. (1994). The model also allows those aspects of the ecosystem engineering system that are poorly understood to be identified, and thus serves as a basis for further investigations. In this context, the apparent synergy between *Callianassa filholi* and *Zostera novazelandica*, plus the likely interaction between these engineers and trophic dynamics, warrant further attention. Habitats that contain both callianassids and seagrass promise to be useful test systems for further investigations of the concept of ecosystem engineering. Such systems provide opportunities to explore what Jones *et al*. (1997b) term 'coupled engineering and trophic cascades' and 'multiple engineers and coupled and uncoupled interactions' and to parameterize the models of ecosystem engineering proposed by Gurney and Lawton (1996). Indeed, an earlier study (Suchanek, 1983) hinted at the likelihood that callianassids and seagrass would provide a pertinent case study.

To promote debate on the ecosystem engineering concept we pose a number of questions:

1. How do the effects on community composition of sympatric allogenic and autogenic engineers change at different spatial scales?

2. What mechanisms are responsible for any observed changes?

3. Do systems that possess putatively antagonistic engineers exhibit stability over short temporal scales?

We hope that comparative and experimental studies, designed to address these questions, will provide data suitable for developmental models. Such integration of empirical and predictive research has been called for by both proponents and critics of the concept of ecosystem engineering.

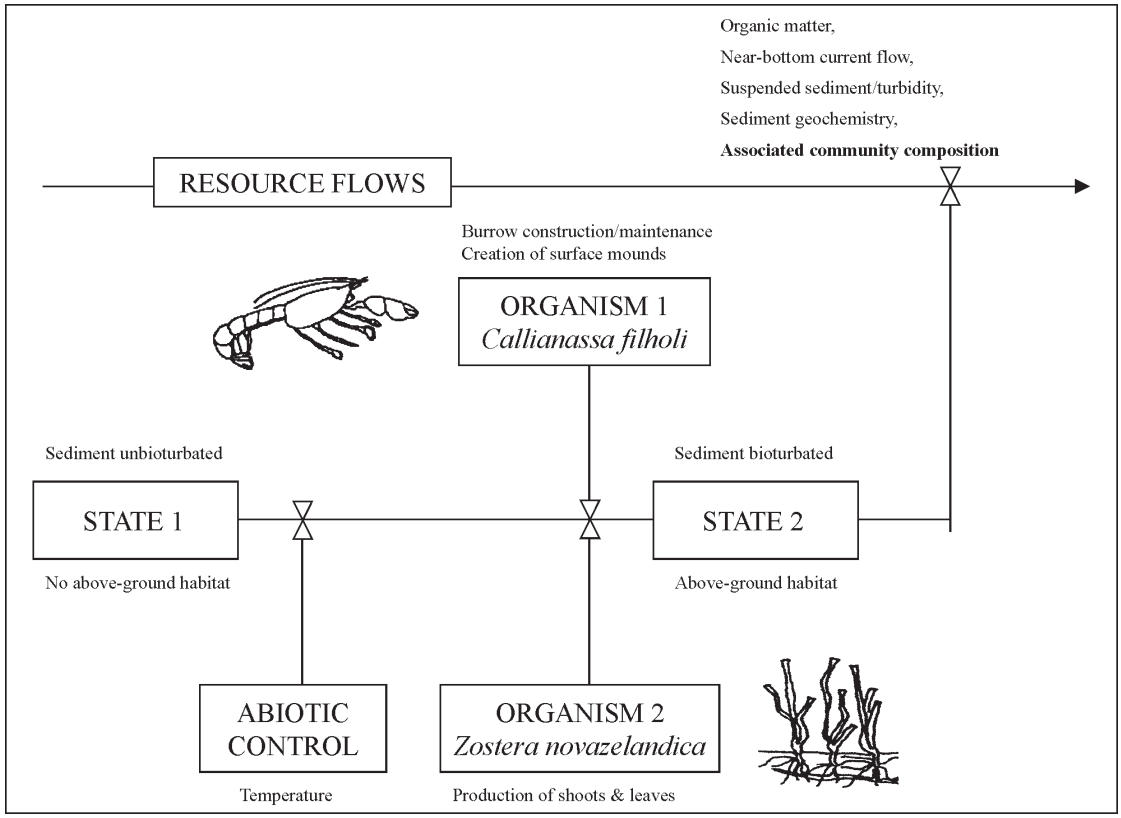

Figure 1. Conceptual model of ecosystem engineering by the burrowing ghost shrimp *Callianassa filholi* and the seagrass *Zostera novazelandica* on a tidal flat in New Zealand.

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