

Indirect effects of bioturbation by the burrowing sandprawn *Callichirus kraussi* on a benthic foraging fish, *Liza richardsonii*

Deena Pillay^{1,*}, Chantel Williams¹, Alan K. Whitfield²

¹Marine Research Institute, Department of Zoology, University of Cape Town, Private Bag X3, Rondebosch 7701, Cape Town, South Africa

²South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa

ABSTRACT: The alteration of sediments by bioturbating organisms plays a major role in aquatic ecosystems, from both ecological and evolutionary perspectives. Several studies have highlighted the ability of bioturbators to alter sedimentary biogeochemical processes and community structure, but the potential influence of bioturbators on pelagic species is unexplored in marine ecology. In the present study, we investigated the direct effects of bioturbation by a southern African burrowing sandprawn, *Callichirus kraussi*, on primary producers (benthic microalgae) and the indirect effects on the growth of a fish (grey mullet *Liza richardsonii*) that consumes microalgae. A mesocosm experiment was undertaken in which similar-sized *L. richardsonii* at 2 densities were exposed to 3 increasing densities of *C. kraussi*. After 3 wk of exposure to the effects of *C. kraussi*, the fish were weighed and their lengths measured to calculate their physical condition and growth rates. At the termination of the experiment, the microalgal biomass and sediment turnover were measured in each mesocosm. Higher *C. kraussi* densities resulted in an increase in sediment turnover and caused reductions in microalgal biomass, which in turn led to a reduction of the biomass and lengths of *L. richardsonii*. Increasing densities of *C. kraussi* evidently enhance sediment turnover from burrows to the sediment surface, leading to the burial of microalgae and indirect reductions in food availability to *L. richardsonii*. This reduction in turn leads to metabolic losses and reductions in the growth of this fish species. These results indicate that benthic bioturbators can have strong effects on aquatic ecosystems, especially by modulating energy flow to nektonic species.

KEY WORDS: Bioturbation · Food webs · Marine benthos · Sediment turnover · Benthic-pelagic coupling

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Organisms play crucial roles in structuring communities in aquatic and terrestrial ecosystems. Competition for resources and trophic interactions, such as predation and grazing, have traditionally been the main areas of interest (Wilby et al. 2001). However, the alteration of ecosystems by organisms, commonly referred to as ecosystem engineering, has been recognised over the last few decades to be equally

important (Wright & Jones 2006). Ecosystem engineering refers to the ability of organisms to alter resource flow patterns to co-occurring species by physically altering biotic and abiotic matter. Through such actions, they 'modify, maintain and/or create habitats' (Jones et al. 1994, p. 374).

In marine soft-sediment ecosystems, bioturbation, or the alteration of the sedimentary environment through solute and particle movement by organisms, is a major form of ecosystem engineering (Meysman

*Email: deena.pillay@uct.ac.za

et al. 2006, Pillay & Branch 2011). Bioturbating organisms feature prominently in driving changes at both evolutionary and ecological scales. At the evolutionary level, burrowing species and bioturbation have been implicated in the Cambrian-substrate revolution, in which burrowers are thought to have contributed to the transition between pre- and post-Cambrian animal life in marine sediments (Meysman et al. 2006). Burrowing species, through their bioturbative activities, can also indirectly drive micro-evolutionary change that ultimately influences the evolution of novel morphology, behaviour and social interactions (Pillay 2010).

At the ecological level, bioturbation influences a number of processes and properties, including nutrient fluxes, sediment granulometry and pore-water characteristics (Suchanek 1983, Lohrer et al. 2004, Meysman et al. 2006). These modifications translate into significant effects on the associated soft-sediment communities. Bioturbators have been shown to influence the community structure, abundance and distribution of the major benthic biotic components (Suchanek 1983, Flach & Tamaki 2001, Pillay & Branch 2011).

Current perspectives on the ability of bioturbators to structure communities are restricted to sediment-dwelling biota, with little consideration of the possible effects on pelagic or nektonic organisms. Benthic bioturbators can potentially influence the structure of pelagic assemblages by modifying food availability in the benthos on which nektonic species may feed. In the present study, we explore this concept by examining the effects of bioturbation by a burrowing South African callianassid sandprawn, *Callichirus* (= *Callianassa*) *kraussi*, on primary producer (microalgal) abundance and the indirect consequences for a predominantly detritivorous/microalgivorous fish, grey mullet *Liza richardsonii*. Both species commonly occur sympatrically in South African estuaries and shallow marine systems, with field evidence from Langebaan Lagoon on the west coast indicating that the biomass and abundance of *L. richardsonii* may be significantly enhanced at sites where *C. kraussi* is known to be rare or absent (Clark 1997).

Their high rates of expulsion of sediment from burrows to the sediment-water interface place burrowing callianassid sandprawns amongst the most dominant physical ecosystem engineers in marine systems (Cadée 2001). These burrowing crustaceans have the highest sediment turnover rates of any marine organism, which can be as high as $14 \text{ kg m}^{-2} \text{ d}^{-1}$ in the case of *Callichirus kraussi* (Branch & Pringle 1987). *C. kraussi* is a key ecosystem engineer in South

African estuaries and lagoons, where it occurs in dense aggregates (up to 200 ind. m^{-2}) spanning several kilometres. This sandprawn feeds on organic material along its burrow walls and can burrow to depths greater than 1 m (Branch & Pringle 1987). Much research has been conducted on *C. kraussi*, and the engineering effects of this sandprawn have been shown to influence the abundance and distribution of bacteria, microalgae, meiofauna, macrofauna and seagrasses (Branch & Pringle 1987, Siebert & Branch 2005a,b, 2006, Pillay et al. 2007a,b,c, 2008).

In this experiment, we predict that sediment turnover by *Callichirus kraussi* will bury microalgae on the sediment surface and indirectly reduce food availability to *Liza richardsonii*, leading to reductions in the growth of this fish. This mechanism may explain the contrast in the abundance and biomass of *L. richardsonii* between areas with and without *C. kraussi*.

MATERIALS AND METHODS

Experimental design

A mesocosm experiment was used to test the influence of ecosystem engineering by *Callichirus kraussi* on microalgal abundance and the growth of *Liza richardsonii*. Eighteen mesocosms (diameter = ~30 cm, length = 60 cm) were half-filled with intertidal sediment and linked to a continuous flow-through system in which seawater (salinity = 35, temperature = 21°C) was circulated from a reservoir to each mesocosm and then back to the reservoir. The reservoir was fitted with 2 biofilters and an aerator to remove nutrients generated from animal excretion and to oxygenate the water. Nutrient (nitrate, nitrite and ammonia) levels were monitored weekly in each mesocosm using standard aquarium test kits (Serra) and a multiprobe system (YSI MP550) used to measure salinity, dissolved oxygen levels and temperature. Of the nutrients measured, ammonia was most variable among the mesocosms, especially toward the end of the experiment. Following the termination of the experiment, single water samples were collected 10 cm above the sediment from each mesocosm using a 50 ml syringe and sent to the Council for Scientific and Industrial Research (CSIR) to determine the ammonia concentrations. The water flow to each mesocosm was standardised using controlled-flow valves.

Prior to commencing the experiment, the sediment surface of each mesocosm was inoculated with 5 μl of *Chaetoceros muelleri* (diatom culture), and micro-

algal biofilms were allowed to develop for 4 d. This culture would form the main dietary item of *Liza richardsonii*. Three density treatments of *Callichirus kraussi* were used during this experiment: a control with no *C. kraussi*, the natural mean density (7 *C. kraussi* per mesocosm) and the maximum density (13 *C. kraussi* per mesocosm). The maximum density of *C. kraussi* was based on a value of ~200 individuals m^{-2} that can be achieved in South African estuaries and lagoons (Branch & Pringle 1987). Two densities of fish were used in the experiments, namely 5 *L. richardsonii* per mesocosm (the mean natural density) and 10 *L. richardsonii* per mesocosm (the maximum natural density observed). The densities of *L. richardsonii* used in the experiment were based on estimated fish densities at the site where the fish were collected. For this purpose, we used a seine net ($n = 3$, length = 5 m, mesh size = 5 mm), and the experimental densities were determined by dividing the numbers of fish caught per haul by the area sampled. *In situ* fish densities were then scaled down in proportion to the area of each mesocosm. All treatments were replicated 3 times and randomly interspersed. *L. richardsonii* between 5 and 6 cm in length were tagged and randomly allocated to mesocosms so that the lengths, mass and growth rates of individuals could be determined.

Data collected

Data on *Liza richardsonii* growth were collected after 3 wk. The fish were weighed, the standard lengths were measured, and the condition (body mass divided by body length) and growth rates were calculated. The mortality of fish was monitored daily in each mesocosm, and new fish were added to maintain the required fish densities in proportion to the losses due to mortality. The added fish were also tagged, and data on their growth were collected after 3 wk of exposure to the ecosystem engineering effects of *Callichirus kraussi*.

The sediment turnover and microalgal biomass were also measured at the end of the experiment. For sediment turnover, single 15 ml centrifuge tubes (aperture area = 1.77 cm^2 , length = 12 cm), with an aspect ratio of 8 (length/diameter), were buried flush with the sediment of each bucket and left for 72 h to collect the sediment turned over by *Callichirus kraussi*. The sediment contained within each tube was dried at 60°C for 24 h before being weighed. Sediment turnover was used to quantify the expulsion of burrow sediment to the surface by *C. kraussi*.

For microalgal biomass estimation, 3 cores (diameter = 10 cm, depth = 1 cm) were collected from each mesocosm and emptied into jars containing 200 ml of 90% acetone and left in darkness for extraction of chlorophyll *a*, which was used as an index of microalgal biomass. The 3 cores from each mesocosm were pooled to generate a single measure of chlorophyll *a* biomass per mesocosm. After 48 h, a 5 ml subsample of acetone was withdrawn, and the chlorophyll *a* biomass was measured using a Turner Designs Trilogy fluorometer (wavelength = $430 \mu\text{m}$; Welschmeyer 1994).

Statistical analyses

The statistical package SPSS v 19 was used for all of the analyses. The homogeneity of variance and normality of data were assessed using Kolmogorov-Smirnov and Levene's tests, respectively. Data that were not normally distributed were transformed (square root or log) and then subjected to parametric analyses. A mixed model nested analysis of variance (ANOVA) was used to determine the effects of *Callichirus kraussi* and *Liza richardsonii* densities on fish growth. The effects of *C. kraussi* and *L. richardsonii* density on sediment turnover and microalgal biomass were assessed using 2-factor ANOVA. A curve-estimation function was employed to identify models that best related the *C. kraussi* density with the sediment properties and fish responses.

RESULTS

Ammonia concentration

Ammonia concentrations did not vary significantly among *Callichirus kraussi* densities (ANOVA: $F_{2,18} = 0.29$, $p = 0.75$), *Liza richardsonii* densities (ANOVA: $F_{2,18} = 0.54$, $p = 0.47$) or their interaction (ANOVA: $F_{2,18} = 0.81$, $p = 0.46$). The ammonia concentrations varied between 17 and $183 \mu\text{g l}^{-1}$ across all of the experimental mesocosms.

Sediment properties

Sediment turnover increased exponentially with increasing *Callichirus kraussi* density for both the 5 and 10 *Liza richardsonii* treatments (Fig. 1A; regression: $F = 5.56$, $R = 0.51$, $p = 0.031$). Due to the variability in the data, the sediment turnover did not

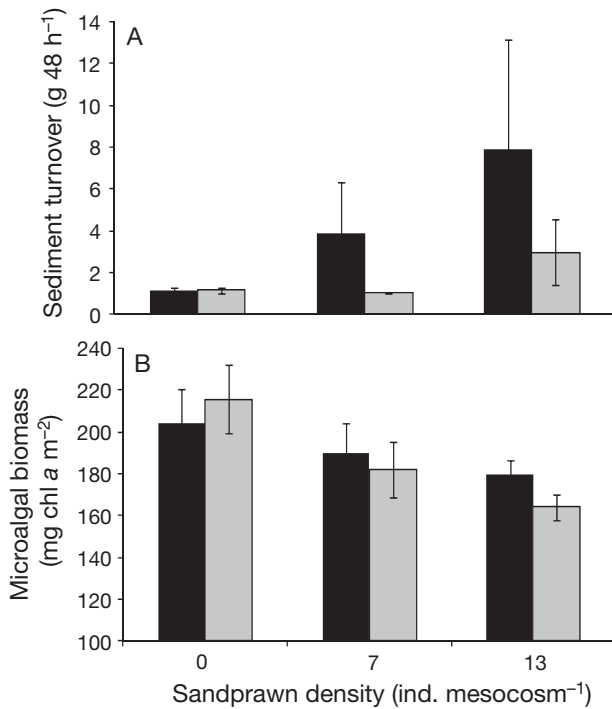


Fig. 1. (A) Sediment turnover and (B) microalgal biomass in mesocosms with differing densities of *Liza richardsonii* and *Callichirus kraussi*. ■: 5 *L. richardsonii*, □: 10 *L. richardsonii*. Means ± 1 SE

differ significantly among the different *C. kraussi* density treatments (ANOVA: $F_{2,18} = 2.74$, $p = 0.10$). Neither the *L. richardsonii* density (ANOVA: $F_{1,18} = 2.20$, $p = 0.163$) nor the interaction between the *L. richardsonii* and *C. kraussi* densities (ANOVA: $F_{1,18} = 0.57$, $p = 0.57$) influenced sediment turnover. Microalgal biomass was significantly affected by *C. kraussi* density (Fig. 1B; ANOVA: $F_{2,18} = 4.6$, $p = 0.032$) and decreased linearly with increasing *C. kraussi* density (regression: $F = 10.45$, $R = 0.62$, $p = 0.005$). Microalgal biomass was not affected by *L. richardsonii* density (ANOVA: $F_{1,18} = 0.23$, $p = 0.64$) or the interaction between the *L. richardsonii* and *C. kraussi* densities (ANOVA: $F_{1,18} = 0.61$, $p = 0.55$).

Fish responses

Fish mortality was significantly greater in the 10 *Liza richardsonii* treatments than in the 5 *L. richardsonii* treatments (Fig. 2; nested ANOVA: $F_{1,18} = 19.64$, $p < 0.001$). Fish mass was significantly greater in the 5 *L. richardsonii* treatments compared to the 10 *L. richardsonii* treatments (Fig. 3A; nested ANOVA: $F_{1,135} = 12.8$, $p < 0.001$) and decreased significantly with increasing *Callichirus kraussi* density

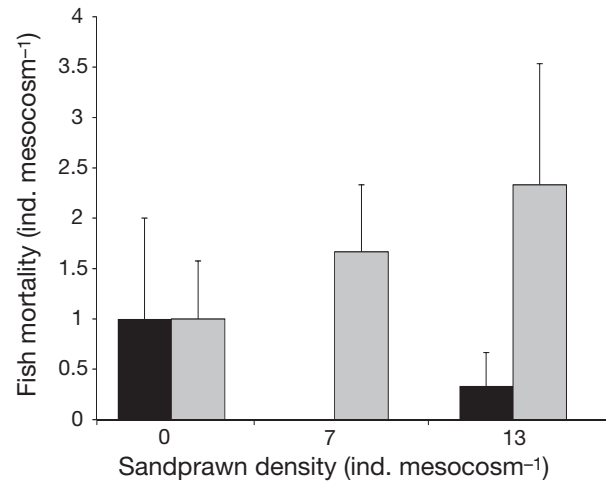


Fig. 2. *Liza richardsonii* mortality with differing densities of *L. richardsonii* and *Callichirus kraussi*. ■: 5 *L. richardsonii*, □: 10 *L. richardsonii*. Means ± 1 SE

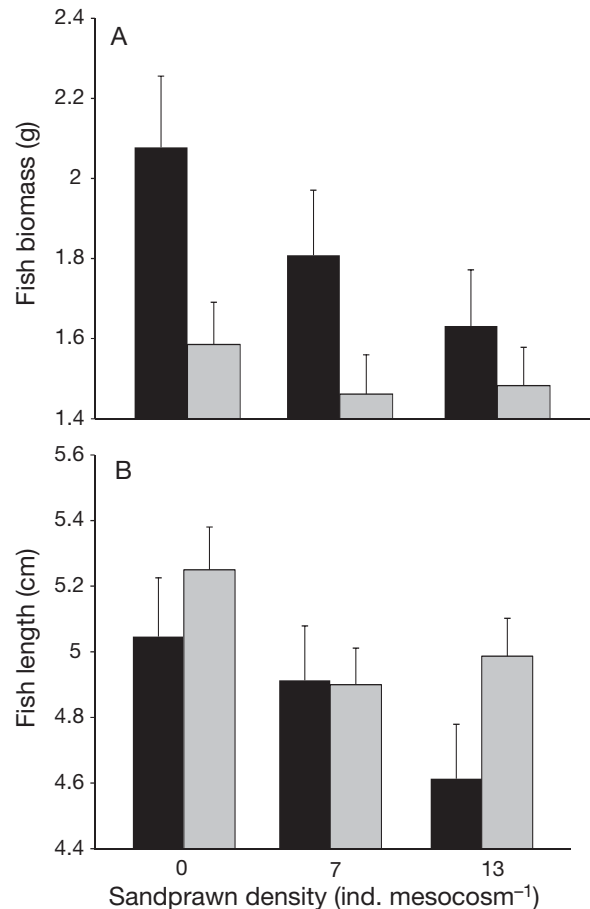


Fig. 3. *Liza richardsonii*. (A) Mass and (B) length of *L. richardsonii* in mesocosms with differing densities of *L. richardsonii* and *Callichirus kraussi*. ■: 5 *L. richardsonii*, □: 10 *L. richardsonii*. Means ± 1 SE

(nested ANOVA: $F_{2,135} = 6.83$, $p = 0.02$), this trend being most evident in the 5 *L. richardsonii* treatment. The lengths of fish also decreased significantly with increasing *C. kraussi* density (Fig. 3B; nested ANOVA: $F_{2,135} = 6.8$, $p = 0.02$).

The physical condition of the fish was significantly affected by the density of *Liza richardsonii*, being reduced 2- to 3-fold in the 10 *L. richardsonii* density treatments relative to the 5 *L. richardsonii* density treatment (Fig. 4A; nested ANOVA: $F_{1,135} = 17.346$, $p < 0.0001$). The interaction between *Callichirus kraussi* and *L. richardsonii* also had a significant effect on *L. richardsonii* condition (ANOVA: $F_{2,135} = 7.29$, $p = 0.002$), with *L. richardsonii* condition decreasing with increasing densities of *C. kraussi*. The 5 *L. richardsonii* density treatment showed a decrease in the fish growth rate with increasing *C. kraussi* density, with the largest decrease occurring in the 13 *C. kraussi* treatment (Fig. 4B). Neither the fish nor sandprawn density was statistically shown to influence the fish growth rate (nested

ANOVA: $p > 0.1$), even though there was graphical evidence of a decrease in the fish growth rate with increasing *C. kraussi* density (Fig 4B).

DISCUSSION

The prediction that ecosystem engineering by *Callichirus kraussi* in the form of sediment turnover would directly decrease microalgal abundance and indirectly reduce the growth of *Liza richardsonii* was largely upheld in this experiment. This mechanism could explain the greater biomass and abundance of *L. richardsonii* under field conditions at sites where *C. kraussi* is scarce, although other habitat differences might also play a role (Clark 1997). It is likely that reductions in food availability on the sediment surface may cause the migration of *L. richardsonii* away from sites dominated by *C. kraussi*, or conversely, *L. richardsonii* might be attracted to those littoral sites where *C. kraussi* is scarce or absent. These results indicate that the direct and indirect consequences of ecosystem engineering by *C. kraussi* might be influential in structuring food webs in shallow marine and estuarine ecosystems by altering energy flows and possibly the spatial distribution of consumers.

The negative effect of *Callichirus kraussi* on microalgal abundance observed in this experiment is most likely linked to sediment turnover and not consumption by this sandprawn because *C. kraussi* does not feed on surface microalgae. Sediment turnover by *C. kraussi* most likely buries microalgae, thus, starving them of light and nutrients required for photosynthesis (Branch & Pringle 1987, Pillay et al. 2007a). Alternatively, sediment turnover may prevent the development of microbial biofilms that bind sediments, thereby enhancing sediment erodability (Patterson & Hagerthey 2001) and resulting in microalgae that were attached to the sediment being washed into the water column (Pillay et al. 2007c). Under natural and experimental conditions, sediment erodability is 2- to 3-fold greater in areas with dense beds of *C. kraussi* relative to sediments lacking this sandprawn (Pillay et al. 2007a).

The negative effects of *Callichirus kraussi* on microalgal biomass observed in this experiment are in agreement with previous field and laboratory experiments (Pillay et al. 2007a). Under natural conditions, sediments lacking *C. kraussi* usually have microalgal biomasses 2- to 4-fold greater than those in areas occupied by this sandprawn, while experimental manipulations of *C. kraussi* densities resulted

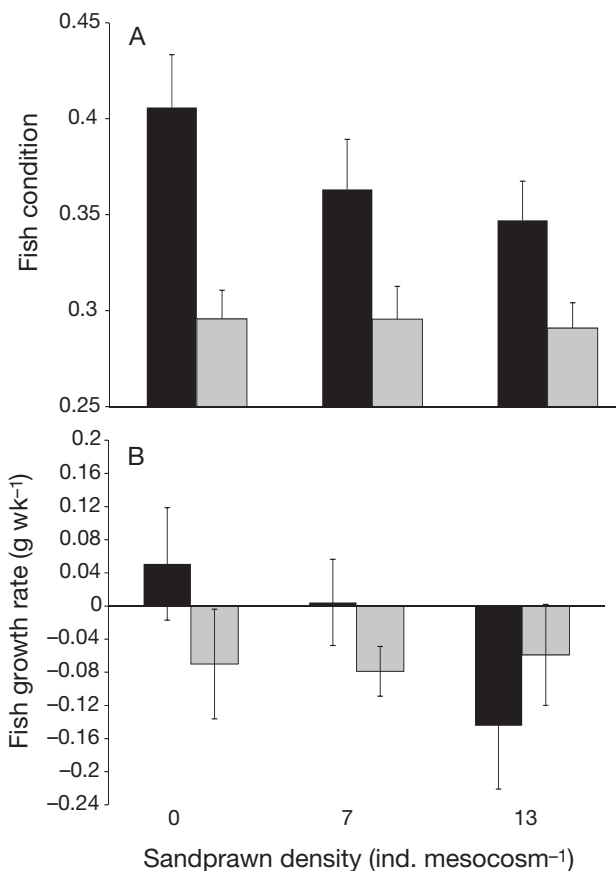


Fig. 4. *Liza richardsonii*. (A) Physical condition and (B) growth rate of *L. richardsonii* in mesocosms with differing densities of *L. richardsonii* and *Callichirus kraussi*. ■: 5 *L. richardsonii*, □: 10 *L. richardsonii*. Means \pm 1 SE

in 2- to 3-fold reductions in microalgal biomass in the presence of *C. kraussi* (Pillay et al. 2007c). Ecosystem engineering in the form of sediment turnover by other burrowing marine shrimps and prawns also reduce the microalgal biomass of surface sediments (Contessa & Bird 2004, Webb & Eyre 2004).

Our results indicate that by reducing microalgal biomass, *Callichirus kraussi* can also indirectly affect the growth of *Liza richardsonii*, leading to reductions in both fish biomass and length. By burying microalgae or increasing microalgal erodability and dispersion, *C. kraussi* limits the availability of energetic resources to such consumers. Because most mugilids have a microalgal diet almost identical to that of *L. richardsonii* (Blaber 1977), it is probable that other species of this family in South African estuaries would be equally affected by the bioturbation activities of *C. kraussi*. Mugilids are one of the most diverse and dominant fish families in South African estuaries (Blaber 1987), and therefore, the consequences of such an activity on ecosystem functioning are therefore very relevant.

The ecosystem engineering effects of *Callichirus kraussi* and the consequences for energy flow to *Liza richardsonii* observed in this experiment are similar to those observed in experiments testing the effects of the same sandprawn on the gastropod *Nassarius kraussianus* and bivalve *Eumarcia paupercula*. *N. kraussianus* is a grazer that feeds on microalgae on the sediment surface, and *E. paupercula* is a suspension feeder that feeds on phytoplankton in the water column (Pillay et al. 2007a). In the field, the densities of both species are reduced by 3- to 4-fold in habitats occupied by *C. kraussi*, and experimental removal of *C. kraussi* has been shown to elevate densities of both species by 2- to 3-fold (Pillay et al. 2007b). Further experiments showed that sediment turnover by *C. kraussi* restricts energy flow to both species, as gut chlorophyll *a* content, which is an indicator of microalgal ingestion, can be reduced up to 3-fold (Pillay et al. 2007a).

In developing the 'trophic amensalism hypothesis', Rhoads & Young (1970) demonstrated that ecosystem engineering in the form of sediment reworking by the burrowing deposit-feeding bivalves *Nucula proxima*, *Yoldia limulata* and *Macoma tenta* significantly reduced the growth rate of the filter-feeding bivalve *Mercenaria mercenaria* because the reworked sediment clogged its filtration apparatus, thereby limiting phytoplankton consumption. This effect of sediment reworking by deposit feeders on suspension feeders was used to explain the consistent spatial separation of these groups in the natural environ-

ment (Rhoads & Young 1970). Their study and the findings of the current *Callichirus kraussi* experiment indicate that ecosystem engineering by burrowers can affect the growth of other species by restricting energy flows either directly, by influencing the abundance of primary producers, or indirectly, by impinging on the feeding success of co-occurring species.

The potential for burrowing species to indirectly affect other nektonic or pelagic species by restricting energy flow has been raised in previous work on callianassid sandprawns from Durban Bay, South Africa (Pillay et al. 2008). The research in question utilized a long-term data set to track changes in the benthic invertebrates and ichthyofauna of a littoral sandflat over an 8 yr period when *Callichirus kraussi* was initially rare and later developed high densities. Whilst *C. kraussi* was rare, burrowing bivalves (predominantly *Eumarcia paupercula*) dominated the benthos, bottom-feeding fish dominated the ichthyofauna, and bivalve siphons were the main food item found in fish stomachs (contributing up to 60% of the fish diets). When *C. kraussi* became more established, the fish community shifted to dominance by zooplanktivorous species, and bivalve siphons were no longer recorded in any of the stomachs of the previously numerically dominant demersal fish species (Pillay et al. 2008). Experimental evidence linking sediment turnover by *C. kraussi* to reductions in microalgal consumption, physical condition and survival of the bivalve *E. paupercula* points to the possible role of *C. kraussi* in driving these changes and strongly indicates the indirect consequences of ecosystem engineering by *C. kraussi* on energy flow and food web structure (Pillay et al. 2007a).

Sediment turnover by other burrowing shrimps and prawns have been implicated in population crashes of benthic invertebrates (Tamaki 1994, Flach & Tamaki 2001, Amaro et al. 2007, van Nes et al. 2007). In Ariake Sound, Japan, a 10-fold increase in the density of the ghost-shrimp *Nihonotrypaea harmandi* between 1979 and 1998 was linked to the extinction of the grazing gastropod *Umbonium moniliferum* (Tamaki 1994). In the North Sea, a 5-fold increase in the density of the burrowing shrimp *Callianassa subterranea* between 1982 and 1992 led to a 90% decline in the abundance of the brittle-star *Amphiura filiformis* (van Nes et al. 2007). The consequences of these changes on higher trophic levels, such as fish, have not been quantified.

The results of this experiment may have important implications for aquatic ecology. Aquatic ecosystems

are composed of benthic and pelagic compartments that are linked by the flow of inorganic and organic materials, often referred to as benthic-pelagic coupling (Raffaelli et al. 2003). This connectivity is crucial to the functioning of aquatic systems and is, in turn, governed by a number of biotic and abiotic processes. Of the biotic processes, bioturbation is known to be important in coupling benthic and pelagic compartments, but most studies in this area have focused on the ability of bioturbators to alter fluxes of nutrients from the benthos into the water column (e.g. Ziebis et al. 1996, Lohrer et al. 2004, D'Andrea & DeWitt 2009). This experiment, however, shows that benthic bioturbators that are strong ecosystem engineers can also influence benthic-pelagic coupling by modulating energy flow from benthic primary producers (microalgae in this case) to consumers in the pelagic environment (fish in this case). This is especially pertinent given that benthic microalgae are an important component of the diets of many nektonic species in shallow coastal ecosystems (Perissinotto et al. 2003). Also important to aquatic ecology is the finding that the ability of bioturbators to structure communities is not restricted to the benthos, as is assumed in the current paradigm. To our knowledge, the present study is the first direct evidence indicating that benthic bioturbators can influence pelagic assemblages through impacts on the food sources of nektonic consumers.

Acknowledgements. Financial support for the present study was provided by the National Research Foundation (NRF) of South Africa, Andrew Mellon Foundation and Carnegie Foundation.

LITERATURE CITED

- Amaro TPF, Duineveld GCA, Bergman MJN, Witbaard R, Scheffer M (2007) The consequences of changes in abundance of *Callianassa subterranea* and *Amphiura filiformis* on sediment erosion at the Frisian Front (southeastern North Sea). *Hydrobiologia* 589:273–285
- Blaber SJM (1977) The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. *Biol J Linn Soc* 9:259–275
- Blaber SJM (1987) Factors affecting recruitment and survival of mugilids in estuaries and coastal waters of southern Africa. *Am Fish Soc Symp* 1:507–518
- Branch GM, Pringle A (1987) The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna, and benthic microflora. *J Exp Mar Biol Ecol* 107:219–235
- Cadée GC (2001) Sediment dynamics by bioturbating organisms. In: Reise K (ed) *Ecological comparisons of sedimentary shores*. Ecological studies, Vol 151. Springer-Verlag, Berlin, p 127–148
- Clark BM (1997) Variation in surf-zone fish community structure across a wave-exposure gradient. *Estuar Coast Shelf Sci* 44:659–674
- Contessa L, Bird FL (2004) The impact of bait-pumping on populations of the ghost shrimp *Trypaea australiensis* Dana (Decapoda: Callinassidae) and the sediment environment. *J Exp Mar Biol Ecol* 304:75–97
- D'Andrea AF, DeWitt TH (2009) Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: density-dependent effects on organic matter remineralization and nutrient cycling. *Limnol Oceanogr* 54:1911–1932
- Flach E, Tamaki A (2001) Competitive bioturbators on intertidal sand flats in the European Wadden Sea and Ariake Sound in Japan. In: Reise K (ed) *Ecological comparisons of sedimentary shores*. Ecological studies, Vol 151. Springer-Verlag, Berlin, p 276–293
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431:1092–1095
- Meysman FJR, Middelburg JJ, Heip CHR (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends Ecol Evol* 21:688–695
- Paterson DM, Hagerthey SE (2001) Microphytobenthos in contrasting coastal ecosystems: biology and dynamics. In: Reise K (ed) *Ecological comparisons of sedimentary shores*. Ecological studies, Vol 151. Springer-Verlag, Berlin, p 105–125
- Perissinotto R, Nozais C, Kibirige I, Anandraj A (2003) Planktonic food webs and benthic-pelagic coupling in three South African temporarily-open estuaries. *Acta Oecol* 24:S307–S316
- Pillay D (2010) Expanding the envelope: linking invertebrate bioturbators with micro-evolutionary change. *Mar Ecol Prog Ser* 409:301–303
- Pillay D, Branch GM (2011) Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. *Oceanogr Mar Biol Annu Rev* 49:137–192
- Pillay D, Branch GM, Forbes AT (2007a) The influence of bioturbation by the sandprawn *Callianassa kraussi* on feeding and survival of the bivalve *Eumarcia paupercula* and the gastropod *Nassarius kraussianus*. *J Exp Mar Biol Ecol* 344:1–9
- Pillay D, Branch GM, Forbes AT (2007b) Experimental evidence for the effects of the thalassinidean sandprawn *Callianassa kraussi* on macrobenthic communities. *Mar Biol* 152:611–618
- Pillay D, Branch GM, Forbes AT (2007c) Effects of *Callianassa kraussi* on microbial biofilms and recruitment of macrofauna: a novel hypothesis for adult–juvenile interactions. *Mar Ecol Prog Ser* 347:1–14
- Pillay D, Branch GM, Forbes AT (2008) Habitat change in an estuarine embayment: anthropogenic influences and a regime shift in biotic interactions. *Mar Ecol Prog Ser* 370:19–31
- Raffaelli D, Bell E, Weithoff G, Matsumoto A and others (2003) The ups and downs of benthic ecology: consideration of scale, heterogeneity and surveillance for benthic-pelagic coupling. *J Exp Mar Biol Ecol* 285–286:191–203
- Rhoads DC, Young DK (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J Mar Res* 28:150–178

- Siebert T, Branch GM (2005a) Interactions between *Zostera capensis*, *Callianassa kraussi* and *Upogebia Africana*: deductions from field surveys in Langebaan Lagoon, South Africa. *Afr J Mar Sci* 27:345–356
- Siebert T, Branch GM (2005b) Interactions between *Zostera capensis* and *Callianassa kraussi*: influences on community composition of eelgrass beds and sandflats. *Afr J Mar Sci* 27:357–373
- Siebert T, Branch GM (2006) Ecosystem engineers: interactions between eelgrass *Zostera capensis* and the sandprawn *Callianassa kraussi* and their indirect effects on the mudprawn *Upogebia africana*. *J Exp Mar Biol Ecol* 338:253–270
- Suchanek TH (1983) Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *J Mar Res* 41:281–298
- Tamaki A (1994) Extinction of the trochid gastropod, *Umboonium (Suchium) moniliferum* (Lamarck), and associated species on an intertidal sandflat. *Res Pop Ecol* 36: 225–236
- van Nes EH, Amaro T, Scheffer M, Duineveld GCA (2007) Possible mechanisms for a marine benthic regime shift in the North Sea. *Mar Ecol Prog Ser* 330:39–47
- Webb AP, Eyre BD (2004) Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Mar Ecol Prog Ser* 268:205–220
- Welschmeyer NA (1994) Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnol Oceanogr* 39:1985–1992
- Wilby A, Shachak M, Boeken B (2001) Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* 92:436–444
- Wright JP, Jones CG (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations and challenges. *Bioscience* 56:203–209
- Ziebis W, Forster S, Huettel M, Jørgensen BB (1996) Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. *Nature* 382: 619–622

*Editorial responsibility: Kenneth Heck Jr.,
Dauphin Island, Alabama, USA*

*Submitted: October 25, 2011; Accepted: January 27, 2012
Proofs received from author(s): April 20, 2012*