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RESEARCH ARTICLE

Experimental evidence for the effects of the thalassinidean sandprawn *Callianassa kraussi* on macrobenthic communities

D. Pillay · G. M. Branch · A. T. Forbes

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Abstract Bioturbation by thalassinidean sandprawns is known to structure soft-bottom communities, and field observations have suggested that the sandprawn *Callianassa kraussi* is a significant force influencing macrofaunal communities. To investigate causal relationships, a field experiment was undertaken in Durban Bay, South Africa, in which experimental cages were used to exclude or include *C. kraussi* and the abundance of macrofauna in these treatments documented. Cage effects were assessed by comparing macrofauna in inclusion cages with that of unmanipulated areas containing high densities of *C. kraussi* equivalent to those in inclusion cages. Measurements were made in 3 months, in March, June and September 2005. Total abundance and species richness of macrofauna were significantly greater in exclusion cages than in inclusion treatments during all sampling seasons, while diversity differed between these treatments in June and September only. Ordinations indicated that macrofaunal assemblages in exclusion cages differed statistically from inclusion and control treatments in all three sampling seasons. In general, the surface-grazing gastropod *Nassarius kraussianus* and suspension and deposit-feeding species such as the polychaetes *Prionospio sexoculata* and *Desdemona ornata*, cumaceans, and the bivalves *Dosinia hepatica* and *Eumarcia paupercula* were significantly more abundant in prawn-exclusion plots, implying that they are negatively affected by bioturbation by *C. kraussi*, whereas burrowing infauna were not affected.

Introduction

The activities of soft-substratum macrofauna can have major effects on the physical and chemical nature of the sediments in which they live, including oxygen levels, microbial activity and the organic and inorganic content (Koike and Mukai 1983; Aller and Yingst 1985; Reise 1985; Branch and Pringle 1987). They also affect sediment geochemistry through the deposition of pellets or residual by-products from feeding (Reise 1985).

Callianassid sandprawns in particular radically alter sedimentary properties because of their activities, including burrow digging, sediment ingestion and defecation, and the expulsion of sediment from burrows to the sediment-water interface (Cadée 2001). Their bioturbation also influences pore water exchange, principally by increasing nutrient and gaseous interchange between the sediment and the water column (Aller et al. 1983; Waslenchuk et al. 1983; Murphy and Kremer 1992).

Because of these activities, callianassids have profound and varied effects on the benthic fauna and flora, including macrofauna (Berkenbusch et al. 2000; Siebert and Branch 2005), meiofauna (Branch and Pringle 1987), seagrasses (Townsend and Fonseca 1998) and bacteria (Koike and Mukai 1983; Branch and Pringle 1987). Negative effects of sandprawns have been recorded on bivalves (Murphy 1985; Berkenbusch et al. 2000), corals (Aller and Dodge 1974), macrofauna with limited mobility such as tanaids and

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D. Pillay (✉) · A. T. Forbes
School of Biological and Conservation Sciences,
University of KwaZulu-Natal,
Durban 4041, South Africa
e-mail: pillayd1@ukzn.ac.za

G. M. Branch
Marine Biology Research Institute,
Zoology Department, University of Cape Town,
PB X3, Rondebosch 7701, South Africa

spionid polychaetes (Posey 1986), and filter-feeding gastropods (Flach and Tamaki 2001). Conversely, promotive effects of sandprawns have been recorded for mobile burrowing taxa such as ostracods (Riddle 1988), bivalves, polychaetes and amphipods (Tudhope and Scoffin 1984; Posey 1986; Wynberg and Branch 1994; Riddle 1988; Siebert and Branch 2005, 2007).

The primary mechanism by which callianassids influence other species is through their destabilization of the sediment, which buries and smothers surface-dwelling species and clogs the filtration apparatus of filter feeders (Rhoads and Young 1970), but favours other burrowing organisms (Brenchley 1981, 1982; Siebert and Branch 2005, 2007). Investigations in South Africa have shown that *Callianassa kraussi* Stebbing has substantial effects on the fauna and flora of estuaries and lagoons because it turns over sediment at a prodigious rate (Branch and Pringle 1987; Siebert and Branch 2005). Work in Durban Bay on the East Coast of South Africa demonstrated that macrofaunal assemblages are radically different in areas with high versus low *C. kraussi* densities, with lower species richness, diversity and abundance in areas densely populated by the sandprawn (Pillay 2006).

This work was however based on field observations and correlations, leaving doubt whether the patterns observed can be attributed to *C. kraussi*. In this paper, we experimentally examined the effects of *C. kraussi* on the macrofauna by manipulating density of *C. kraussi* in cages. The majority of studies examining the effects of sandprawn bioturbation on macrofauna have been based on field correlations (e.g. Posey 1986; Berkenbusch et al. 2000), with comparatively few manipulative field experiments (e.g. Posey et al. 1991). We hypothesized a neutral or positive affect of *C. kraussi* on mobile burrowing infauna, but a negative affect on suspension feeders and surface grazers.

Materials and method

Experimental design

An exclusion/inclusion experiment was designed to experimentally test the effects of *C. kraussi* on macrofauna. The experiment was conducted in the mid-intertidal zone at a site of low *C. kraussi* density (mean = 2.7 individuals m^{-2}) in Little Lagoon, Durban Bay (29°53′00.41′′S, 31°00′34.43′′E) and a dense population existed at adjacent sandbanks 800 m away (mean = 130 individuals m^{-2}). Three treatments were employed: (1) cages including *C. kraussi*, (2) cages excluding *C. kraussi* and (3) a method control. For the latter, samples were taken from unmanipulated sediments in an area of high *C. kraussi* density and compared with samples taken from inclusion cages that contained equivalent densities of sandprawns, as advocated by Posey et al. (1991) and Reinsel (2004). The rationale behind this was that if macrobenthic assemblages from sites of naturally high *C. kraussi* densities (hereafter referred to as the ‘control’) are similar to those inside inclusion cages containing comparably high densities of *C. kraussi*, then it is likely that caging is not inducing experimental artifacts.

Square cages (length = 50 cm, width = 50 cm, depth = 30 cm) were constructed with a PVC frame with mosquito netting of 1-mm mesh diameter covering the sides and bottom. The cages were not roofed since (1) roofing is problematic because it becomes fouled and would have hindered colonization from the water column, and (2) sandprawns do not leave the sediment, so roofing was not necessary to exclude or retain them. The use of mesh rather than solid walls also ensured oxygen and chemical fluxes between sediments inside and outside the cages. Before installing the experimental cages, a four-sided square frame was pushed into the sediment, and the sediment within the frame was removed. A cage was then placed inside the frame and then filled with intertidal sediment that had previously been defaunated by sun drying for a period of 4 weeks. The frame surrounding each cage was then removed. In total, ten cages were installed in an array with systemic interspersion of inclusion and exclusion treatments (Hurlbert 1984). Two days after installing the cages, 30 sandprawns (50–60 mm total length) were introduced into each of five inclusion cages, and five exclusion cages were left free of sandprawns. Two sandprawns were added every month to each inclusion cage, to compensate for any possible mortality. The cages thus had the same densities of prawns throughout the 9 months. Once installed, each cage protruded 2–5 cm above the sediment surface. Cages were allowed to stand for 3 months before sampling commenced to allow colonization of macrofauna by larval settlement or adult immigration from the adjacent sediment. *C. kraussi* lacks a planktonic larval stage (Forbes 1973) and its juveniles and adults are too large to have been able to invade the cages from adjacent sediments, so the cages prevented entry or exit of the sandprawns.

Sampling strategy

Sampling began in March, 3 months after the cages were installed, and was repeated 3-monthly, in June and September 2005. Three cores (diameter = 10 cm, length = 20 cm) were collected from each of the five cages in the inclusion and exclusion treatments, and five groups of three cores collected for the method control. An analysis of similarity (ANOSIM) indicated that there was no significant difference in macrofaunal communities between cores collected within cages or groups of samples in any of the treatments ($P = 0.49$). The three samples from each of cage and control treatments were therefore pooled to constitute a single replicate, thus generating a balanced sample size of five for each treatment for each sampling period.

Prior to collecting each core, a grid was placed on the top of each cage, which divided the cage into nine segments. This grid system was used to record where samples were taken, to avoid re-sampling the same position on successive sampling dates. Whole cores were preserved with 4% formaldehyde solution, stained with Phloxine-B, sieved through a 500-μm mesh, and all macrofauna collected, identified and counted.

Statistical analyses

All multivariate analyses were performed using PRIMER v 5 (Plymouth Routines in Multivariate Ecological Research). Non-metric multidimensional scaling (MDS) was used to assess differences in macrofaunal assemblages between exclusion, inclusion and control treatments. ANOSIM was employed to test if assemblages differed statistically among treatments. Post-hoc pairwise tests were utilised for inter-treatment comparisons. A two-way ANOSIM was used to determine if macrofaunal communities differed between cores and between cages across the three treatments. For this analysis, each of the five groups of three cores was classed as a cage. Two-way crossed interactions between treatments and seasons were not tested, as the effect of season was not part of the primary hypothesis. Rather, one-way ANOSIM tests were run for each sampling season. MDS ordinations were constructed from similarity matrices generated from Bray-Curtis similarities, with untransformed and unstandardised abundance data. For each treatment, the DIVERSE procedure was used to calculate total abundance (N), species richness expressed as total number of species per sample (S), and Shannon-Weiner diversity (H') to the base e. SIMPER was used to determine the significance of differences in abundances of taxa among treatments. Differences in macrofaunal community parameters among treatments were determined using one-way ANOVAs separately for each sampling season. Normality and homogeneity of variance required for parametric testing were assessed using the Kolmogorov–Smirnov test and Levene's test, respectively. In instances where these assumptions were not met, data were transformed (log + 1 or arcsin) and then subjected to parametric analyses.

Results

A two-way ANOSIM of pooled data across all sampling seasons indicated that macrofaunal assemblages did not differ between cores within cages ($P = 0.47$) but significant differences between cages were detected ($P = 0.001$). MDS ordinations (Fig. 1) indicated that macrofaunal assemblages in exclusion cages (cluster 1) differed significantly from inclusion and control treatments (cluster 2) during all three sampling seasons (pairwise analyses $P < 0.05$, $n = 15$ for all seasons). Inclusion treatments never differed from control treatments ($P > 0.05$, $n = 15$ for all sampling seasons).

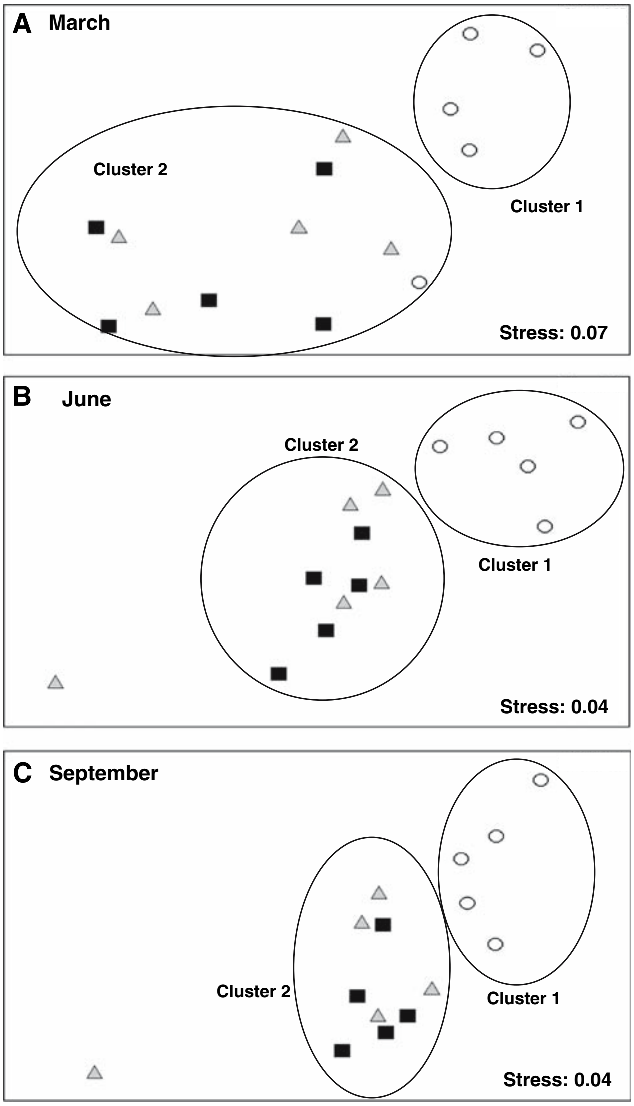

Fig. 1 MDS ordinations of macrobenthic assemblages between exclusion (*circles*), inclusion (*triangles*) and control treatments (*squares*); **a** March, **b** June, **c** September. *Solid lines* unite samples that formed discrete clusters between 55 and 60% similarity

Total abundance (Fig. 2a; $P < 0.01$ for all sampling seasons, $n = 5$, $DF = 2, 12$), and species richness (Fig. 2b; $P < 0.05$ for all sampling seasons, $n = 5$, $DF = 2, 12$) were significantly greater in exclusion cages than in inclusion treatments during all sampling seasons, but never differed between inclusion and control treatments ($P > 0.05$). Diversity did not differ among treatments in March (Fig. 2c; $P > 0.05$, $n = 5$, $DF = 2, 12$), but in June and September was greater in exclusion cages than inclusion cages

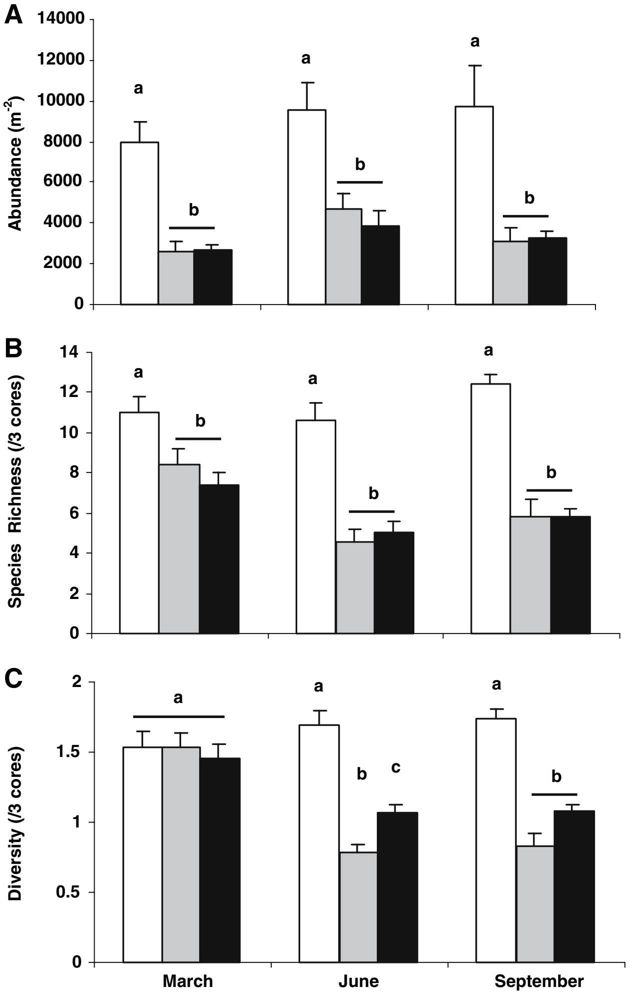

Fig. 2 Differences in abundance m^{-2} (**a**), species richness per sample (**b**) and Shannon–Wiener diversity H′ (**c**) of macrofauna between exclusion, inclusion and control treatments. Means + 1 SE are presented. *Black bars* = control, *grey* = inclusion, *unfilled bars* = exclusion treatment. *Shared letters* between treatments indicate an absence of statistical difference within any given month ($P > 0.05$)

($P < 0.0001$, $n = 5$). Diversity differed among all three treatments in June (inclusion and control; $P = 0.021$, $n = 5$), and was statistically similar between control and inclusion samples in September ($P > 0.05$, $n = 5$).

The taxonomic composition of macrofaunal communities (Fig. 3) was significantly different between inclusion and exclusion treatments in all three sampling seasons. In March, densities of the bivalve *Eumarcia paupercula*, the polychaete *Prionospio sexoculata* and cumaceans were significantly greater in exclusion than in inclusion treatments. In June, the difference in community composition between exclusion and inclusion treatments was more pronounced. The same three taxa remained significantly more abundant in exclusion treatments, together with four additional species: the gastropod *Nassarius kraussianus*, the bivalve *Dosinia hepatica*, cirratulid polychaetes and the polychaete *Desdemona ornata*. In September, densities of *N. kraussianus*, cirratulid polychaetes, and *D. ornata* were statistically greater in exclusion cages than inclusion cages. Although other taxa did not differ significantly among treatments, most showed the same trend, having higher numbers in exclusion than inclusion plots. The only exceptions were the polychaete *Glycera* sp. and *Scoloplos johnstonei*, both of which were more common in inclusion plots. Only one taxon, viz. *Glycera* sp., differed statistically between inclusion and control plots, and in September only.

Ordination plots and univariate analyses indicated that particular functional groups of macrofauna were especially susceptible to bioturbation by *C. kraussi*. Suspension feeders ($P = 0.002$), deposit feeders ($P < 0.0001$) and surface grazing gastropods ($P < 0.0001$) were negatively affected by the presence of *C. kraussi*. Densities of organisms belonging to these feeding modes were significantly greater in exclusion treatments as compared to inclusion and control treatments, but did not differ between inclusion and control treatments (Fig. 4). Burrowing infaunal species ($P = 0.238$) were not affected by *C. kraussi*, as their densities did not differ statistically between inclusion and exclusion plots.

Discussion

Our overall aim was to investigate the bioturbative effects of *C. kraussi* on macrobenthic invertebrates by using experiments to build on the foundations of an initial “natural experiment” approach. The argument frequently used against natural experiments is that causality can never be tested using this approach, but only inferred, since other variables may co-interact with the one of interest and confound the interpretation of results.

To overcome this criticism, we employed experimental manipulations in the form of field exclusion and inclusion experiments. However, exclusion and inclusion cages may themselves introduce artifacts into the experiment, and may change patterns that exist under natural conditions. To counter this possibility, a method control was introduced into the experimental design (Posey et al. 1991; Reinsel 2004). Macrofaunal assemblages from inclusion treatments were compared with those from unmanipulated sediments in which *C. kraussi* was present at equivalently high densities. Any differences in community composition between these two treatments would have raised the spectre of cage artifacts.

In reality, there was almost no evidence that the presence of experimental cages influenced the composition or structure of macrobenthic assemblages. Species richness and abundance of macrobenthic assemblages never differed statistically between inclusion treatments and control plots

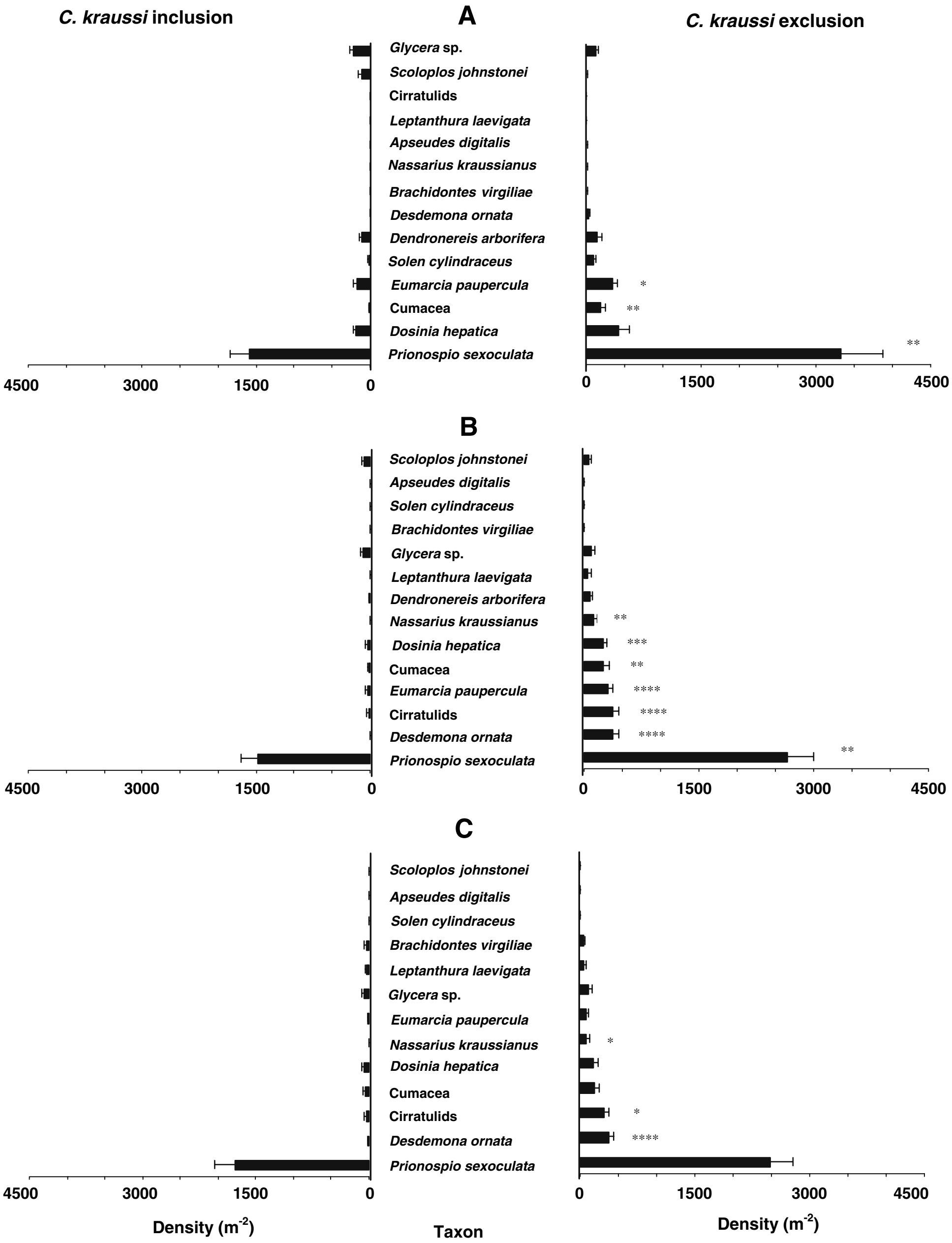

Fig. 3 Differences in densities of macrobenthic organisms (mean +1 SE) between inclusion and exclusion treatments; **a** March data, **b** June data, **c** September data. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; $****P < 0.0001$

during any sampling season, and diversity values only differed between inclusion and control treatments during one of the three sampling seasons. In addition, ordinations indicated that macrofaunal assemblages associated with inclusion cages could not be statistically differentiated from control plots. Finally, only one macrobenthic taxon, viz. *Glycera* sp., differed numerically between inclusion treatments and control plots, and this difference was recorded during one sampling season only. Densities of the other taxa never differed between inclusion and control treatments during any sampling season. All these lines of evidence indicate that cage artifacts were absent or negligible, and we are confident that the patterns in macrofaunal assemblages observed in the experiment are related to presence or absence of *C. kraussi* and not to experimental artifacts.

The comparisons between inclusion and exclusion plots highlight the dominant influence that bioturbation by *C. kraussi* exerts in structuring macrobenthic communities. Ordination plots indicated that there were two distinct macrobenthic communities associated with the exclusion and inclusion treatments (Fig. 1), which were statistically separable. In

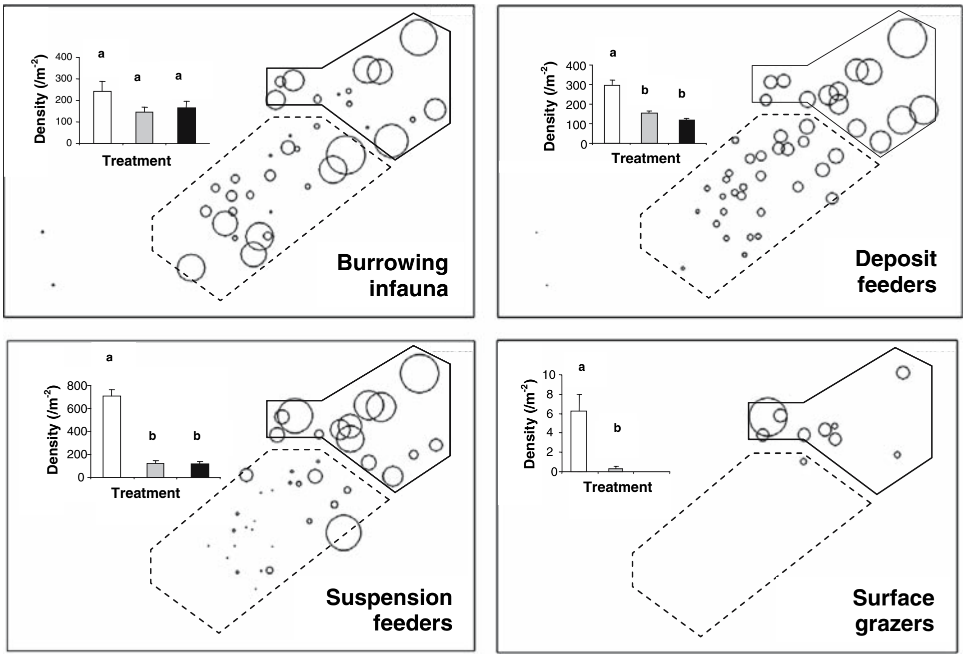

Fig. 4 Ordination plots showing differences in densities of functional groups between exclusion treatments (*solid line*) and inclusion and control treatments (*broken line*) based on data pooled across all sampling seasons. The diameters of circles are proportional to the densities of organisms within each functional group. Stress = 0.09 for all ordinations. *Insets*: Differences in densities (means + 1 SE) of organisms belonging to each functional group between control (*black bars*), inclusion (*grey*) and exclusion treatments (*white*) are indicated by *different letters* above the bars

addition, the abundance of macrofauna, species richness and (in most cases) diversity were significantly and negatively influenced by the bioturbative activities of *C. kraussi* (Fig. 2).

It was also apparent that particular functional groups of organisms were more susceptible to bioturbation by *C. kraussi* than others (Fig. 3). In treatments excluding *C. kraussi*, the macrobenthic assemblage comprised surface suspension feeders (principally *Desdemona ornata*), suspension and deposit feeding bivalves (*Eumarcia paupercula* and *Dosinia hepatica*), grazing gastropods (*Nassarius kraussianus*), subsurface deposit feeders (*Prionospio sexoculata* and cirratulid polychaetes), surface organisms that switch between filter and deposit feeding (cumaceans) and burrowing infauna (*Glycera* sp.) The community associated with treatments that included *C. kraussi* had statistically lower densities of deposit feeders, suspension feeders and grazing gastropods. Conversely, burrowing infauna, such as *S. johnstonei* and *Glycera* sp. appeared to be unaffected by bioturbation by *C. kraussi* as similar densities of organisms belonging to this functional group were recorded between inclusion and exclusion treatments.

Bioturbation by *C. kraussi* thus reduced the abundance of organisms that are surface-dwelling or dependent on the sediment surface for feeding (e.g. suspension and deposit-feeding bivalves, and surface-grazing gastropods), but had no effect on burrowing infauna. The critical questions that need to be addressed are therefore: (1) why organisms associated with the sediment surface are excluded by *C. kraussi* and (2), why burrowing deposit-feeding organisms are unaffected by it.

Most of the effects of *Callianassa* spp. on macrofauna arise because their bioturbation deposits residual sediment from burrows at the sediment-water interface. In the specific case of *C. kraussi*, burrows extend to a depth of 1 m and a turnover rate of 12 kg m^{-2} day^{-1} has been measured (Branch and Pringle 1987). Related to this bioturbation, three possible scenarios arise (Fig. 5). Firstly, the deposition of sediment at the surface may bury surface and subsurface fauna, directly leading to mortalities or causing metabolic losses due to loss of feeding time or to time and energy devoted to countering burial. Tube-dwelling subsurface fauna may be killed by smothering or inhibited by greater demands to keep burrows open. Adversely affected organisms may also emigrate from heavily bioturbated habitats, potentially increasing their susceptibility to predation in the process.

For example, Flach (1993) demonstrated that the lugworm *Arenicola marina* had no direct affect on the survival of the amphipods *Corophium volutator* and *C. arenarium* in aquaria, but that it did interfere with their tubes, leading to emigration of the amphipods to lugworm-free sections of tanks. In the process, the amphipods experienced significantly greater predation from the crab *Carcinus maenas* and the shrimp *Crangon crangon*.

A second potential effect of sediment deposition by *C. kraussi* at the sediment water interface is its negative influence on biofilm development on the sediment surface. Pillay (2006) has highlighted the dominant effect *C. kraussi* has in retarding growth of microalgae, bacteria, and diminishing levels of extracellular polymeric substances produced by the microbiota (EPSs), and Branch and Pringle (1987) documented a similar effect on microalgae and bacteria. Consequently, organisms such as grazing gastropods and sub-surface deposit feeders that feed directly off the

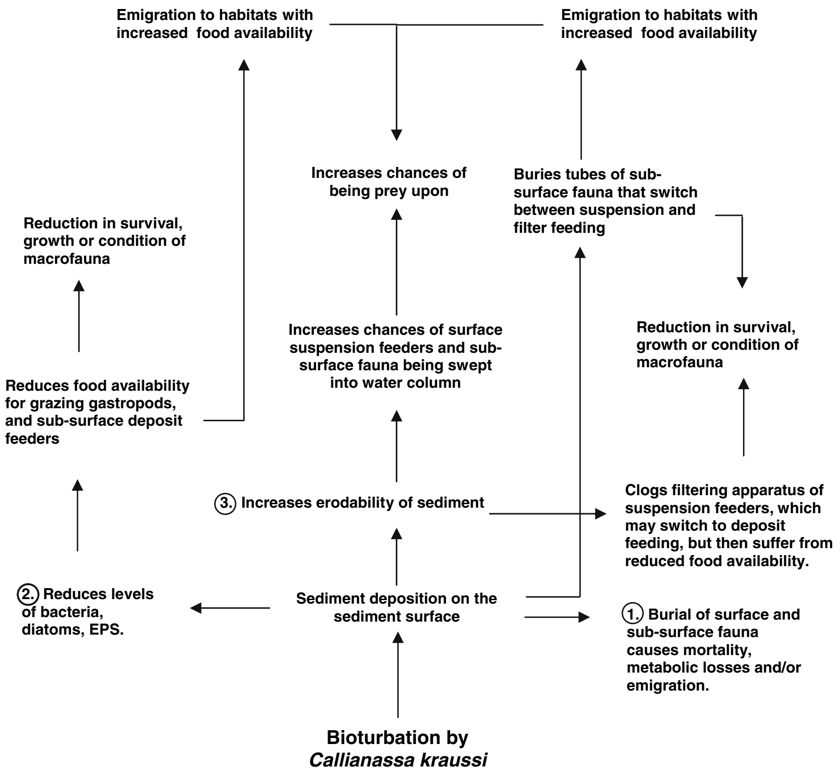

Fig. 5 Potential mechanisms by which bioturbation by *C. kraussi* influences macrofaunal assemblages

sediment surface may face a depleted food supply in habitats heavily bioturbated by *C. kraussi*, with resultant metabolic losses reducing survival and condition (Ellis et al. 2002). Pillay (2006) demonstrated that in the presence of *C. kraussi*, microalgal consumption by the filter-feeding bivalve *Eumarcia paupercula* was significantly reduced, culminating in a reduction in its condition.

A third potential outcome of sediment deposition by *C. kraussi* is the enhanced erodability of sediment deposited at the interface between sediment and water. Paterson and Hagerthey (2000) have shown that biofilms on sediments serve to bind the topmost sediment layer, promoting smooth laminar flow of water over the sediment bed. In bioturbated sediments, where natural sediment stabilizers such as bacteria (Dade et al. 1990), diatoms (Madsen et al. 1993) and EPSs (Paterson 1997) are reduced, the sediment bed resists water flow over it, and flow becomes turbulent, increasing the erodability of the bed. Organisms that inhabit these sediments are therefore more prone to being swept into the water column than organisms inhabiting non-bioturbated, stable sediments, increasing exposure to predators such as fish, shrimp or crabs (Flach 1993). This effect is likely to be most severe for small organisms, including larvae and recruits.

A secondary consequence of increased erodability of sediments is the possibility that re-suspended sediments will clog and interfere with the filtration mechanisms of suspension feeders. An increase in suspended sediments has been shown to reduce filtration rates of several suspension-feeding bivalves (Murphy 1985; Rhoads and Young 1970; Ellis et al. 2002). These observations can theoretically be extrapolated to include sub-surface fauna that switch between deposit and filter feeding. If filter feeding becomes impossible, some organisms may switch to deposit feeding, but they will then encounter a second difficulty because of the negative influence of *C. kraussi* on this source of food. Pillay (2006) demonstrated that bioturbation by *C. kraussi* reduces the abundance of microalgae, bacteria and the carbohydrates they exude by 50–70% relative to habitats where *C. kraussi* is rare. The implication is therefore that even if suspension feeders switch to deposit feeding, they will still suffer reductions in food availability.

Sessile filter-feeding epifauna associated with the sediment surface, and sedentary sub-surface fauna that switch between deposit and filter feeding may therefore be excluded or negatively affected by *C. kraussi* because: (1) species with limited mobility cannot escape sediment disturbance associated with bioturbation (Brenchley 1981), (2) those that are sufficiently mobile can escape smothering, but may face reduced food availability because of the scarcity of bacteria, diatoms and EPSs, or increased predation as they emigrate, (3) the filtration apparatus of filter feeders may become clogged by expelled sediments (Rhoads and Young 1970) or (4) small organisms may be washed away into the water column because of increased erodability of sediments. Burrowing infauna are unaffected by bioturbation by *C. kraussi* because they do not rely on the sediment surface to feed, and they do not face the problems of reduced food supply, being eroded into the water column, or being buried by sediments expelled by *C. kraussi*. Indeed, if anything, they may be promoted by bioturbation because destabilisation of the sediment will aid their burrowing activities.

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