*Environmental Conservation* 24 (2): 139–148 © 1997 Foundation for Environmental Conservation

# Trampling associated with bait-collection for sandprawns *Callianassa kraussi* Stebbing: effects on the biota of an intertidal sandflat

RACHEL P. WYNBERG* AND GEORGE M. BRANCH**
*Coastal Ecology Unit and Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7700, South Africa*

Date submitted: 30 October 1996 Date accepted: 1 May 1997

## Summary

Previous studies have inferred that the side effects of physical disturbance associated with bait-collecting for the sandprawn *Callianassa kraussi* are more deleterious than the actual removal of the prawns. The present study was specifically designed to disentangle the side-effects of trampling and disturbance associated with using suction pumps for bait-collecting. Separate areas were sucked over with a prawn pump at three different intensities, and the prawns collected from these areas subsequently returned to them. A parallel treatment involved trampling the sediment at levels comparable to the 'sucking' intensities, without removing the prawns. The responses of the meiofauna, macrofauna and microflora were assessed six weeks after this disturbance.

Prawn densities were depressed six weeks following both sucking and trampling but recovered by 32 weeks. The meiofauna responded positively to some of the disturbance treatments; macrofaunal numbers on the other hand, declined in most treatment areas, and similarity analysis and multidimensional scaling showed that macrofaunal community composition in the most-disturbed areas was distinct from that in other areas. Chlorophyll levels were reduced at the more intensely-disturbed sites.

The results corroborate the conclusion that trampling *per se* has almost the same effect as sucking for prawns, on both the prawns and on the associated biota. This has important implications in terms of managing the use of lagoonal and estuarine ecosystems.

*Keywords*: trampling, disturbance, *Callianassa*, estuaries, sandprawn, bait collection

## Introduction

The thalassinid prawn *Callianassa kraussi* Stebbing is used for fish-bait extensively in southern Africa and is widely distributed in sheltered coastal habitats where it is often the dominant macrofaunal organism (Day 1981). *C. kraussi*, like many other thalassinids, constructs temporary, deep burrow systems and continuously processes large amounts of sediment to extract organic material (Forbes 1973). The intensive bioturbation which results from the burrowing activities of *Callianassa* species has been shown to modify sediment (Aller & Dodge 1974; Roberts *et al*. 1981; Suchanek *et al*. 1986), increase oxygenation and mineralization (Hines & Jones 1985), and have a range of effects on microalgae, bacteria, meiofauna, seagrasses and algae (e.g. Yingst & Rhoads 1980; Brenchley 1981, 1982; Posey 1986; Branch & Pringle 1987). More specifically, *C. kraussi* has been shown to play an important role in the structuring of benthic communities by positively influencing bacteria and having negative effects upon meiofauna and microalgae (Branch & Pringle 1987).

Concern has long been expressed over the vast quantities of mudprawns (*Upogebia africana*) and sandprawns (*C. kraussi*) being harvested from southern African estuaries and lagoons, and the effects which this could have on the prawns and on the associated biota (Hill 1967). In light of this growing concern, experiments were undertaken at Langebaan Lagoon, part of a national park on the west coast of South Africa, to investigate whether prawn populations are reduced in areas where bait-collecting is permitted, and to measure the side-effects of avian predation associated with bait-collection (Wynberg & Branch 1992). In addition, studies were conducted on the long-term effects of high-intensity bait-collecting on mud- and sandprawns, their associated bacteria, microflora, meiofauna and macrofauna, and the composition of the sediment (Wynberg 1991; Wynberg & Branch 1994).

These investigations strongly inferred that the side-effects of intense physical disturbance associated with bait-collecting were more deleterious to the prawn populations and their associated biotic communities than the actual removal of mud- and sandprawns. Sandprawns are generally collected by using a hand-operated suction pump, and the manner in which the pump is used unavoidably involves deep trampling of the adjacent sediment, and potentially causes the collapse of burrows whilst bait is being collected. This possibility led to the present investigation of the effects of bait-collecting, versus the effects of trampling *per se*, on sandprawns and the infauna of lagoonal sediments. As Langebaan Lagoon is intensively used for recreational purposes, negative effects associated with human trampling on the sandflats could have a number of implications for managing use of the area.

---

* Present address: Environmental Evaluation Unit, University of Cape Town, Private Bag, Rondebosch, 7700, South Africa. ** Correspondence: Professor George Branch Tel: +27 21 6503604 Fax: +27 21 6503301 e-mail: GMBranch@pop.uct.ac.za

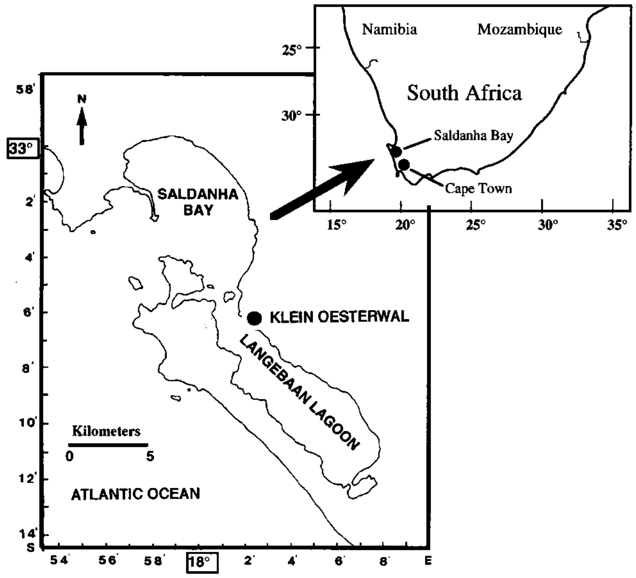

Figure 1 Langebaan Lagoon, showing the Klein Oesterwal sampling station. The inset shows the location of the study area within South Africa.

The rationale of the experiments was to compare the density of prawns and associated biota at control sites and at sites disturbed at three different intensities, all of which fell within the range normally associated with bait-collecting. This was in contrast to earlier work involving harvesting at an unrealistically high intensity. A parallel treatment involved trampling the sediment in order to disturb it at levels comparable with those in the three 'sucked' treatments, but without removing the prawns.

## Methods

### Study Area

Studies were conducted at Klein Oesterwal, Langebaan Lagoon on the west coast of South Africa (33°10´S: 18°05´E) (Fig. 1). Langebaan Lagoon forms part of the West Coast National Park and is approximately 15 km in length with a maximum width of 4 km. It is entirely marine, and has a rich fauna typical of most South African estuaries with open mouths (Day 1959). The intertidal sediments are composed principally of $SiO_2$ and range from coarse on the exposed beaches to fine, muddy sands at the head of the lagoon (Flemming 1977). Klein Oesterwal falls within the national park but is a 'multi-purpose recreational area' where bait-collection is permitted. There is presently a nation-wide quota of 50 prawns per person per day. The mean density of prawn holes in the area used for experiments was 88 $m^{-2}$.

### Experimental design

Six areas of 3 × 4 m were randomly positioned and marked out at Klein Oesterwal in March 1989 to determine the effects of low-intensity disturbance and trampling on populations of *C. kraussi* and associated macrofauna, meiofauna and microalgae. Previous experiments had revealed temporary and only minor differences in sediment composition between disturbed and control sites (Wynberg & Branch 1994). A preliminary study showed that the pre-disturbance sandprawn populations were homogeneous between the sites selected for manipulation. On the basis of three 5 × 1 m transects across each area, mean densities of prawn holes ($m^{-2}$ ± SE) in the six areas were 89 ± 6, 92 ± 9, 94 ± 7, 88 ± 11, 95 ± 9, 89 ± 11: no significant differences existed between these values (ANOVA, $p > 0.5$). Once the experimental sites had been marked out, three areas were chosen at random between them for control samples. Homogeneity of prawn-hole densities in both experimental and control areas was then confirmed once again prior to experimentation (10 replicate 0.1 $m^2$ samples per area, ANOVA $F = 0.21$; d.f. 2,81; $p > 0.7$). No initial macrofaunal or meiofaunal samples were taken from either the experimental or control areas because sampling was destructive and would have created additional disturbances in the plots, particularly from trampling.

Three of the selected experimental areas were sucked over with a prawn pump, consisting of a 75-cm long, 9-cm diameter stainless-steel cylinder containing a hand-operated diaphragm pump (Hailstone & Stephenson 1961), until 25, 50 and 100 prawns respectively had been removed. To simulate the behaviour of bait-collectors, only prawns with a body length >*c.* 40 mm were counted. Since the aim of this experiment was to determine only the effects of the physical disturbance inflicted during bait-collecting, all prawns which had been removed were returned to the same area once counted. The numbers of footsteps taken during removal of each of the three respective prawn quotas were counted. Three adjacent, but physically separate, experimental areas were then trampled to an identical intensity without any prawns being sucked out of the sediment. The two sets of experimental areas are hereafter referred to as the 'sucked' and 'trampled' sites, the sucked areas being labelled S25, S50 and S100 and the trampled areas T25, T50 and T100; the numbers being an index of the disturbance generated to obtain 25, 50 and 100 prawns respectively.

Three cordoned-off areas of approximately 3 × 4 m, randomly interspersed in-between these sites acted as independent multiple controls and remained completely undisturbed. The experiment was situated within an area where visitors did not harvest prawns, and signs were installed as an additional precaution to warn people not to enter the area.

Pseudoreplication (Hurlbert 1984) is contained within this experimental design. This arose because large experimental areas were essential to prevent prawns from immigrating into the experimental plots, and for logistical reasons these large areas could not be replicated. This difficulty did not apply to control sites, of which there were three independent replicates. Homogeneity of prawn-hole densities in experimental and control areas was confirmed prior to experimentation (see above). While this does not eliminate the statistical difficulties associated with the pseudoreplication, it does demon-

**Table 1** Mean macrofaunal numbers ($m^{-2}$) six weeks after low-intensity sucking (S) and trampling (T).

| *Species* | *Treatment* | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Control* | *T25* | *T50* | *T100* | *S25* | *S50* | *S100* |
| Bivalvia | | | | | | | |
| *Carditella rugosa* Sow. | 238 | 180 | 230 | 270 | 250 | 150 | 190 |
| *Tellimya trigona* | 130 | 110 | 90 | 210 | 120 | 60 | 120 |
| *Lasaea adansoni turtoni* Bartsch | 3 | 8 | 3 | 23 | 3 | 18 | 10 |
| Gastropoda | | | | | | | |
| *Turritella capensis* Krauss | 30 | 100 | 50 | 40 | 40 | 60 | 80 |
| *Crepidula porcellana* Lam. | 3 | – | – | – | – | – | – |
| *Marginella capensis* Krauss | 5 | 5 | 8 | – | 5 | 5 | 10 |
| Polychaeta | | | | | | | |
| *Scoloplos johnstonei* Day | 2160 | 1500 | 1940 | 2420 | 2730 | 1640 | 1420 |
| *Orbinia angrapaquensis* (Aug.) | 88 | 65 | 60 | 118 | 3 | 108 | 30 |
| *Nephthys capensis* Day | 5 | – | 3 | – | – | 5 | |
| *Euclymene* sp. | 258 | 58 | 198 | 420 | 198 | 163 | 108 |
| *Notomastus latericeus* Sars | 248 | 170 | 223 | 265 | 113 | 110 | 205 |
| *Marphysa depressa* (Schm.) | 20 | 13 | 15 | 10 | 3 | 13 | 18 |
| *Glycera tridactyla* (Schm.) | 40 | 18 | 18 | 30 | 35 | 10 | 148 |
| *Lysidice* sp. | 28 | 30 | 15 | 15 | 53 | 10 | 5 |
| *Telothelepus capensis* Day | 95 | 58 | 48 | 58 | 98 | 48 | 43 |
| *Ceratonereis erythraensis* Fauvel | 10 | 3 | – | – | 8 | – | |
| *Syllis* sp. | 5 | – | 3 | – | – | – | – |
| *Scolelepis squamata* (Müll) | 5 | – | – | – | 10 | 5 | – |
| *Arabella iricolor* (Mont.) | 8 | – | – | – | – | – | – |
| *Platynereis dumerilii* (Aud. & M. Edw.) | – | 3 | – | – | – | – | – |
| *Eunice* sp. | – | – | – | – | – | 8 | – |
| *Thelepus* sp. | – | – | – | 3 | – | – | – |
| Isopoda | | | | | | | |
| *Cirolana hirtipes* M. Edw. | – | 5 | 18 | 3 | 20 | 3 | 5 |
| Amphipoda | | | | | | | |
| *Urothoe grimaldi* Chevr. | 2293 | 1390 | 1633 | 2570 | 1518 | 1798 | 1960 |
| *Ampelisca palmata* Brnrd. | – | 8 | 3 | 10 | 3 | 8 | 15 |
| Mysidacea | | | | | | | |
| *Gastrosaccus brevifissura* O. Tattersall | 3 | – | 15 | – | 8 | – | – |
| Decapoda | | | | | | | |
| *Betaeus jucundus* Brnrd. | 8 | 3 | 3 | 3 | – | 3 | 3 |
| *Diogenes brevirostris* Stimps. | 25 | 8 | 38 | – | 53 | 8 | 8 |
| *Upogebia africana* (Ortm.) | 3 | – | 5 | – | – | – | 5 |
| *Cleistostoma edwardsii* McLeay | 10 | 13 | 23 | 35 | 10 | 23 | 8 |
| *Thaumastoplax spiralis* Brnrd. | 5 | 3 | – | 3 | 5 | – | 5 |
| *Hymenosoma orbiculare* Desm. | 3 | 5 | 3 | 20 | 8 | 3 | 5 |
| Ostracoda | – | – | 3 | – | – | 3 | – |
| Total numbers | 5718 | 3808 | 4663 | 6533 | 5283 | 4245 | 4278 |
| Species richness | 27 | 24 | 25 | 20 | 23 | 23 | 22 |

strate that any differences arising between experimental areas cannot be simply ascribed to initial differences between such areas prior to the commencement of the experiment.

## Post-disturbance sampling

Responses of the microflora, meiofauna, and macrofauna were quantified from samples taken six weeks after the disturbance. Prawn densities were assessed at six weeks and 32 weeks post-disturbance.

### *Prawn densities*

Previous studies have demonstrated an average ratio of one burrow hole per adult *C. kraussi* (Forbes 1973) and prawn densities were thus assessed by counting burrow holes, using 25 random 0.1 $m^2$ quadrats within each of the experimental and control areas. There was, however, day-to-day variability in the number of holes (documented in Wynberg & Branch 1994), related to the amount of activity by the prawns on a given day. During rainy weather, for example, prawn holes tended to be closed (Hanekom 1980). Despite day-to-day

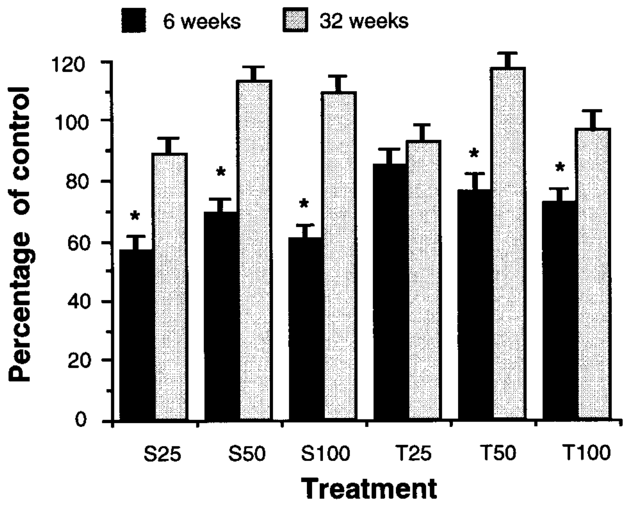

Figure 2 Prawn densities (given as a percentage of the controls), six weeks and 32 weeks after low-intensity sucking (S) and trampling (T). *Indicates a significant difference of $p < 0.001$ between control and treatment. The standard error was comparable for all treatments at approximately 6% of the value. Control values (mean numbers of holes $m^{-2}$) were as follows. After six weeks: for treatments S25, S50, T25, T50, control = 85; for treatments S100, T100, control = 124. After 32 weeks: For treatments S25, S50, S100, control = 66; for treatments T25, T50, T100, control = 56.

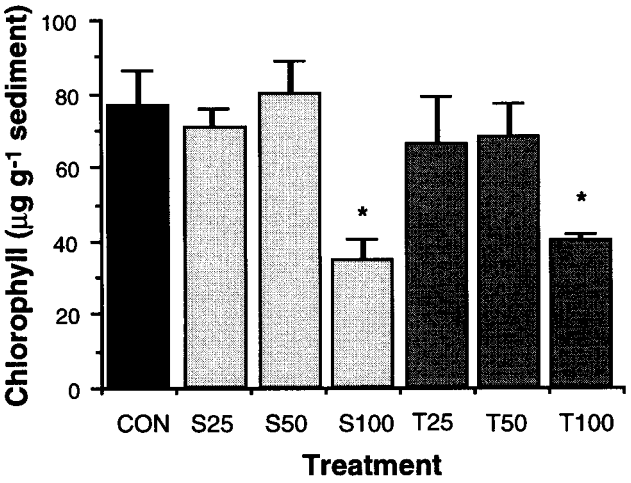

Figure 3 Levels of chlorophyll six weeks after low-intensity sucking (S) and trampling (T). *Indicates a significant difference between control (CON) and treatment at $p < 0.005$. Standard errors appear above the mean values.

variability, control samples were always relatively homogeneous, as demonstrated by their small standard errors. Because of the temporal variability, control counts were undertaken on each of the days on which experimental areas were monitored, and the number of holes counted in each treatment plot expressed as a percentage of the mean control values. ANOVAs were accordingly run separately for each treatment group and its corresponding control.

### *Microflora*

Four random samples of the sediment of approximately 5 g each (*c.* 5 $cm^3$) were collected from the surface, placed in aluminium foil, and stored at −20°C (253 K) in the dark for a maximum of 7 days. The sediment was then wet-weighed before the addition of 10 ml of 90% acetone and a pinch of $MgCO_3$. The sediment was ground for three minutes inside stainless steel cylinders and held at 4°C (277 K) for 24–48 hours to extract the chlorophyll. The samples were then centrifuged until clear, and total chlorophyll determined by measuring optical density at 750, 664, 647 and 630 nm in a spectrophotometer. Data are expressed in µg total chlorophyll $g^{-1}$ dry sediment, derived from the equations of Jeffrey and Humphrey (1975).

### *Meiofauna*

Four 85 ml samples of sediment were taken with a cylindrical core of 60 mm diameter from the surface to a depth of 50 mm, from each treatment and control area and preserved in 4% saline formalin. The meiofauna was extracted from the sediment using a 63-µm mesh sieve through which a jet of water was directed to suspend the lighter particles (i.e. meiofauna). The sieved sediment was oven-dried for three days and then weighed. The meiofauna was stained with Rose Bengal and preserved in phenoxotal until counted. Three subsamples of 10 ml were taken from each sample, and the meiofauna counted.

### *Macrofauna*

Three 0.1 $m^2$ samples, dug to a depth of 10 cm, were obtained for each treatment and control site. The sediment was sieved through 1-mm mesh sieves after first swirling it in buckets to suspend most of the macrofauna. Organisms were preserved in 4% saline formalin and were identified to species level, dried and ashed at 480°C (753 K) to obtain ash-free dry biomass.

## Data analysis

Differences between control and treatment groups were assessed using a one-way analysis of variance (ANOVA). Bartlett's test was employed to test for homogeneity of variances. Heteroscedastic data were transformed and then evaluated using ANOVA. The Tukeys HSD test was employed for multiple comparisons when analysing differences between samples. 'Contrast' (Wilkinson 1987), a statistical technique which utilizes several types of comparative tests, was used in cases where large standard deviations and small sample sizes occurred (e.g. patchy meiofauna). All statistical analyses were conducted using SYSTAT software.

CLUSTER and MDS analyses were performed on macrofaunal densities, using the PRIMER software package (Plymouth Marine Laboratory, UK). Analyses followed the procedures advocated by Field *et al.* (1982) and Clarke (1993), with data being root-root transformed and all species contributing <1% to all samples being discarded. Similarities were determined using the Bray-Curtis similarity coefficient

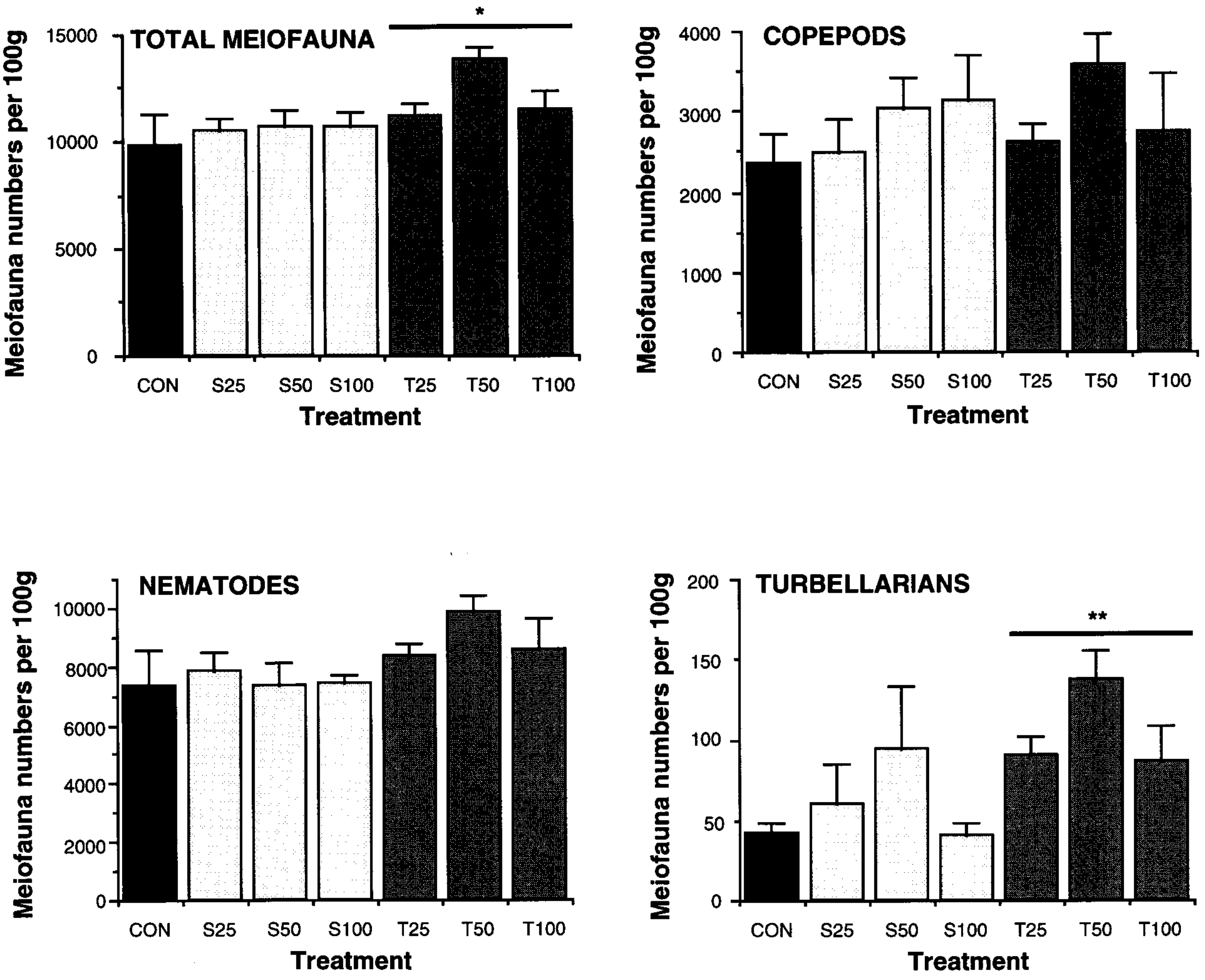

Figure 4 Meiofaunal numbers six weeks after low-intensity sucking (S) and trampling (T). Numbers are per 100 g dry sediment. Significant differences between controls (CON) and treatments are indicated by * and ** for $p < 0.05$ and $p < 0.005$ respectively. Standard errors appear above the mean values.

with group-average linking, and were displayed as a dendrogram and an ordination plot, the latter being generated by non-parametric multidimensional scaling.

As meiofaunal species were not identified beyond being grouped into higher-level taxa, it was not possible to undertake multivariate analysis of their community composition.

## Results

### Prawn density

Both trampling and low-intensity sucking had marked short-term effects on the sandprawns (Fig. 2). With the exception of T25 ($p > 0.05$), all treatment groups had significantly lower prawn densities than the controls after six weeks (ANOVA, Tukeys, $F = 13.38$, $p < 0.001$, d.f. = 4,120 for T50, S25, S50; ANOVA, Tukeys, $F = 25.15$, $p < 0.001$, d.f. = 2,72 for T100, S100). Although the sucked treatments had consistently lower prawn densities than the trampled treatments, these differences were significant only between S25 and T25 ($p < 0.005$). Six weeks after the disturbance, prawn densities in the sucked and trampled sites had respectively dropped to approximately 55% and 80% of those in the controls. After 32 weeks, prawn densities within all treatment areas had returned to background levels, disturbed sites no longer being significantly different from controls (ANOVA, $p > 0.05$) (Fig. 2).

### Microflora

Six weeks after disturbance, chlorophyll levels were lower than the control samples in all but one of the disturbed sites (Fig. 3), although differences were significant only in sites with the highest intensity of disturbance (S100 and T100; ANOVA, Tukeys, $F = 4.448$, $p < 0.005$, d.f. = 6,21). The nature of the disturbance (i.e. trampling or sucking) had no bearing on the chlorophyll levels ($p > 0.05$).

### Meiofauna

Total meiofaunal numbers displayed modest but consistent and statistically significant increases in the trampled areas in comparison with control sites (ANOVA, Contrast, $F$ =

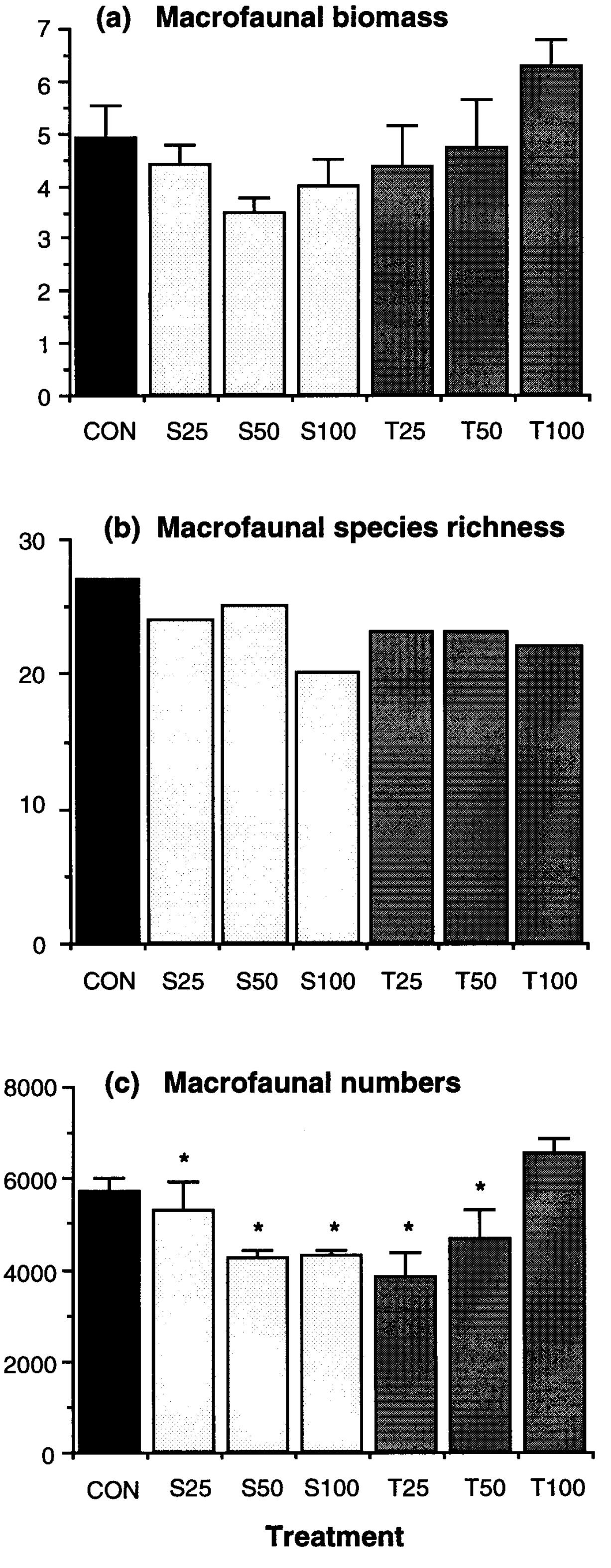

Figure 5 (*a*) Macrofaunal ash-free dry biomass per gram (*b*), total species richness per control and treatment and (*c*) total numbers per m$^2$ six weeks after low-intensity sucking (S) and trampling (T). Standard errors appear above the mean values. * Indicates a significant difference between control (CON) and treatment at $p < 0.05$.

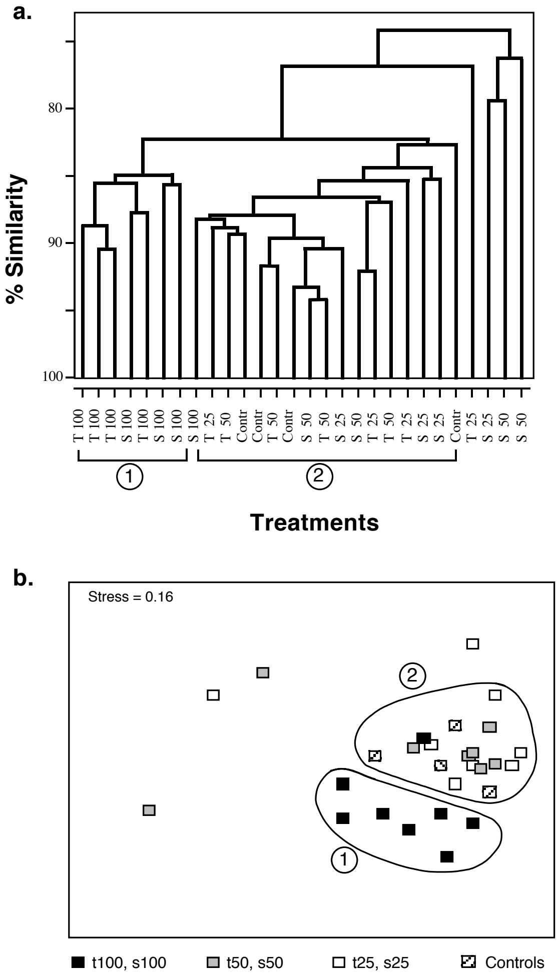

Figure 6 (*a*) Bray-Curtis similarity analysis of macrofaunal numbers at control and treatment sites disturbed by trampling (T) or sucking (S) to intensities equivalent to the removal of 25, 50 or 100 prawns. (*b*) Ordination plot of the same data obtained by non-parametric MDS.

4.548, $p = 0.05$, d.f. = 3,12). Although numbers were also lower in the control areas than in the sucked areas, this difference was not statistically discernible ($p < 0.1$, $>0.05$) (Fig. 4). All three meiofaunal groups had higher densities in the disturbed areas than the controls, but this difference was significant only for turbellarians in the trampled treatment (Fig. 4).

## Macrofauna

### *Biomass*

Figure 5*a* details the mean ash-free biomass for control and disturbed areas. These figures exclude the common hermit crab, *Diogenes brevirostris* which, owing to its relatively large size, tends to swamp the biomass when present and obscure trends amongst the smaller macrofauna. Biomass appeared to be reduced (relative to the control) in all but one (T100) of the disturbed areas, but statistically the samples were not significantly different from the controls (ANOVA, $F = 2.062$, $p = 0.102$, d.f. = 6,21).

### *Species richness*

Although the number of species was lower within all the treated areas in comparison with the controls, the differences between treatments and controls were not statistically significant (Fig. 5*b*).

### *Numbers*

Total macrofaunal numbers were depressed in all the sucked treatments (ANOVA, Contrast, $F = 4.897$, $p < 0.05$, d.f. = 3,12) and two out of three of the trampled treatments, T100 again being the exception (Table 1, Fig. 5*c*). Of the most abundant macrofaunal species, the numbers of *Urothoe grimaldi* (Amphipoda), *Lasaea adansoni turtoni* (Bivalvia), *Euclymene* sp., *Notomastus latericeus*, *Marphysa depressa*, *Telothelepus capensis* and *Glycera tridactyla* (all Polychaeta) were depressed in all but one of the treatment areas but no statistical significance could be attached to this trend. The amphipod *Ampelisca palmata* was recorded only in disturbed areas. The remaining macrofauna appeared little affected by the sucking or trampling (Table 1). The density of the hermit crab *D. brevirostris* was not significantly higher in treatment areas than in controls.

### *Similarity analysis and multidimensional scaling*

Figure 6*a* shows that the samples split into two broad clusters, separable at a level of abut 83% similarity. The first cluster comprised all but one of the samples from the most intensively-disturbed areas (T100 and S100). The second united most of the remaining samples, including those from the controls and the less intensively-disturbed areas. Four samples constituted outliers with no affinities to either of these groups or to each other.

Non-parametric multidimensional scaling (MDS) (Fig. 6*b*) yielded the same groupings. The MDS had a stress level of 0.16, acceptably below the value of 0.20 which Clarke (1993) sets as the limit above which interpretation is of questionable value.

Both methods thus separated the macrofaunal community composition of the most-disturbed areas from that of other areas, but failed to distinguish between the remaining areas. The species contributing most to the similarity within clusters 1 and 2 were all abundant, ubiquitous species; *Scoloplos johnstonei*, *Urothoe grimaldi*, *Carditella rugosa*, and either *Euclymene* sp. (group 1) or *Notomastus latericeus* (group 2) explained >50% of the similarity within the groups. Species contributing most to the dissimilarities between groups 1 and 2 were *Diogenes brevirostris* (which was absent from all group 2 samples) and *Lysidice* sp. (four times more abundant in group 1 than in group 2).

## Discussion

Most studies concerned with bait harvesting imply that systems which have been exploited respond resiliently (Blake 1979; Conner & Simon 1979; Jackson & James 1979; McLusky *et al*. 1983). Although the utilization of thalassinid prawns for bait has frequently been addressed (Hailstone & Stephenson 1961; Hill 1967; Forbes 1973; Hanekom 1980), only Peterson (1977) has tested the effects by way of field manipulations.

Previous studies (e.g. Roberts *et al*. 1981; Suchanek 1983; Posey 1986; Branch & Pringle 1987; Dobbs & Guckert 1988) have shown that callianassids play a pivotal role in the structuring of soft-bottom communities, and intense harvesting of prawns has prolonged effects on the prawns themselves and other components of the macrofauna, as well as shorter-term effects on bacteria, benthic diatoms and meiofauna (Wynberg & Branch 1994; Dittmann 1996). Many early studies on disturbance focused on the target organism only or on individual groups of organisms. More recent studies do take a more holistic approach (see review by Hall 1994; Dittmann 1996), and our present study, together with earlier investigations (Wynberg & Branch 1994), addresses the effects of disturbance both on the target species, *C. kraussi*, and on its associated macrofauna, meiofauna and microflora.

Many of the results of our experiment showed similar, but less obvious patterns to those recorded by us in an earlier experiment involving high-intensity disturbance (Wynberg & Branch 1994). Perhaps the most striking result to emerge from the present study is the impact which trampling has. Indeed, although the sucked-over sites displayed consistently lower prawn densities than did those which had been trampled, the two were statistically indistinguishable. Following both treatments, prawn densities were clearly depressed at six weeks although they had recovered by 32 weeks (Fig. 2). These results corroborate earlier suspicions raised by trends from the high-intensity experiments, which showed that numbers of *C. kraussi* were depressed by 70% following disturbance, despite only 10% of the original *C. kraussi* population being removed experimentally (Wynberg & Branch 1994). The inference is that this disturbance modifies the nature of the environment by collapsing burrows, compacting the sediment and reducing oxygen levels (see Wynberg & Branch 1994), and that this disturbance is in its own a major source of mortality. The present experiment, specifically designed to disentangle the effects of trampling and suction pumps, clearly shows that trampling can be as damaging to the prawn population as sucking.

As in the case of the high-intensity experiments (Wynberg & Branch 1994), the meiofauna as a whole and turbellarians in particular responded resiliently and positively to trampling (Fig. 4). This is the opposite of the result obtained by Dittmann (1996), who recorded lower meiofaunal densities in plots from which *Callianassa australiensis* had been excluded. This difference may, however, reflect contrasts in the methods employed: in our case the sandprawns were pumped out and replaced, or the sediment trampled. In Dittmann's experiments, sandprawns were excluded from the surface layers by inserting a flyscreen at a depth of 5 cm, so that the sediment was scarcely disturbed.

Of the macrofauna, the biomass, species richness, total numbers and the numbers of many individual species were lower in the disturbed areas than the controls. However, of these trends, only the decline in macrofaunal numbers was statistically significant (Fig. 5). Differences in community structure, as reflected by Bray-Curtis similarity analysis and non-parametric multidimensional scaling, only became apparent at the highest level of disturbance (Fig. 6).

Various other forms of disturbance, including scallop-dredging (Currie & Parry 1996, Thrush *et al.* 1995), oyster-shell dredging (Conner & Simon 1979), wave action (Oliver *et al.* 1980, Hall 1994), and bioturbation by a range of organisms including surface-feeding rays (Thrush *et al.* 1994), flamingos (Glassom & Branch 1997), and both infaunal and epifaunal invertebrate burrowers (Brenchley 1981, 1982), all have negative impacts on sediment-dwelling macrofaunal species, particularly those that are relatively sedentary. The common factor in these diverse examples is that sediment is being disturbed, and that this has an effect disproportionately greater than would be predicted by the actual removal of a particular target species.

Two clear differences can be distinguished between the present low-intensity treatments and the high-intensity harvesting described in Wynberg and Branch (1994). Firstly, for the low-intensity experiments, the densities of the hermit crab *Diogenes brevirostris* were not statistically different in the treatment areas and in the control areas. One of the most striking results of high-intensity disturbance was the positive effect upon *D. brevirostris*, which aggregated densely in depressions caused by the disturbance. The tendency of *Diogenes* to aggregate in depressions has previously been recorded (Asakura 1987; Walters & Griffiths 1987) and the absence of similar depressions following lower-intensity treatments could account for the fact that the densities remained statistically unchanged. Ramsay *et al.* (1996) have shown that the hermit crab *Pagurus bernhardus* congregates in areas where the sediment is disturbed by trawling, apparently to feed on damaged or disturbed fauna. This is, however, unlikely to explain the concentration of *D. brevirostris* in the high-intensity experiments, because the effect lasted for over four months.

The second difference between the two experiments lies in the response of the microalgae. After high-intensity disturbance, chlorophyll levels increased in the surface sediments, a result that was attributed to the development of surface depressions and the reduction of sediment turnover by *Callianassa*. The present results, by contrast, show reduced chlorophyll levels at the more intensely-disturbed sites (Fig. 3).

Thus, with the exception of the hermit crabs and microflora, the present results provide similar, though less obvious trends to those of the high-intensity treatments and serve as validations to the trends previously observed. Macrofaunal numbers were reduced after even the least-intense treatments, as were prawn densities.

Of greatest significance, however, is the inescapable conclusion that trampling *per se* has almost the same effects as sucking for prawns – both on the prawns themselves and on the associated biota. This has important management implications in light of earlier research which showed the average annual proportion of sandprawns removed by bait-collectors to be only 0.01% of the prawn population in the whole lagoon, and thus no threat to the population (Wynberg & Branch 1992). Earlier work additionally showed that the secondary effects of prawn harvesting, such as gull predation on residual organisms left by bait-collectors, disturbance of the sandflat fauna and human trampling could have a far greater impact on the ecosystem than the direct removal of sandprawns for bait (Wynberg & Branch 1992, 1994). The present study suggests that, in addition to the numbers of prawns removed, a key factor to consider in managing bait-collecting concerns the numbers of people permitted to utilize a designated area and the relative intensity of their trampling. Although the effects of trampling will clearly vary with the nature of the sediment and its associated infauna, these findings have broader implications in terms of managing the utilization of sandflats. At Langebaan Lagoon, this is effected by maintaining three distinct zones. The first is a ‘wilderness’ area, in which no one is allowed without a permit. This lies at the head of the lagoon, where the sediment happens to be very soft (Flemming 1977) and thus particularly sensitive to the impacts associated with trampling. Secondly, there is a limited recreational area which can be entered but in which certain activities such as motor-boating and bait-harvesting are not permitted. Finally, there is a multi-purpose recreational area, in which a wide range of activities is permitted, including bait-collecting. We recommend the retention of this system of zoning, as it succeeds in protecting the bulk of the lagoon and its biota, while still allowing reasonable levels of utilization. Our demonstration that trampling has significant effects provides strong evidence for the need for ‘wilderness’ zones in estuaries and lagoons, serving as a core area for the protection of biodiversity.

Our results show that because of the side-effects of trampling and suction pumps, removal of bait can have much greater effects than would be predicted purely from the numbers of animals removed. Even those animals that are discarded may suffer because of increased levels of predation or because of alterations to the sediment. In the present context, *Callianassa* is an active and deep burrower, well known for its impacts on the composition of sediment and associated biota (Roberts *et al.* 1981, Suchanek *et al.* 1986, Posey 1986, Branch & Pringle 1987, Dobbs & Guckert 1988, Dittmann 1996). Activities associated with harvesting *Callianassa* may collapse its burrows, leading to local anoxia, decreased penetrability and deflation of the surface layers. The magnitude of such effects is likely to be influenced by two primary issues: the nature of the sediment, and the nature of the animals occupying the sediment. Ecosystems dominated by animals with stable burrows are likely to be most severely affected, as the burrows can collapse and the sediment become compacted. Calm-water lagoons and estuaries are most susceptible to these effects, partly because they support burrowing animals, but also because the sediment is fine and water-logged and can be compacted by displacement of the water. Open-coast beaches exposed to wave action will be least influenced as they support few animals with stable burrows, and the coarse sediment there does not become compacted to the same extent. Thus, our findings have most relevance for the management of lagoonal and estuarine ecosystems. In such systems, trampling and the side-effects of bait-gathering will have their greatest impact and be longest-lived.

## Acknowledgements

We are grateful to the 1990 Zoology II students at the University of Cape Town for their assistance with initial field work. Mr Carl van der Lingen provided invaluable help in the field and for this he is warmly acknowledged. Financial support was received from the Foundation for Research Development (FRD), the South African Network for Coastal and Oceanographic Research (SANCOR), the National Parks Board and a postgraduate grant made available to the first author by the FRD.

## References

Aller, R.C. & Dodge, R.E. (1974) Animal-sediment relations in a tropical lagoon – Discovery Bay, Jamaica. *Journal of Marine Research* 32 (2): 209–32.

Asakura, A. (1987) Preliminary observations on the offshore mass migration of the sand-dwelling hermit crab, *Diogenes nitidimanus* Terao (Crustacea: Decapoda: Anomura). *Journal of Ethology* 5: 207–9.

Blake, R.W. (1979) Exploitation of a natural population of *Arenicola marina* (L.) from the North-East coast of England. *Journal of Applied Ecology* 16: 663–70.

Branch, G.M. & Pringle, A. (1987) The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna and benthic microflora. *Journal of Experimental Marine Biology and Ecology* 107(3): 219–35.

Brenchley, G.A. (1981) Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *Journal of Marine Research* 39(4): 767–90.

Brenchley, G.A. (1982) Mechanisms of spatial competition in marine soft-bottom communities. *Journal of Experimental Marine Biology and Ecology* 60(1): 17–33.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–43.

Conner, W.G. & Simon, J.L. (1979) The effects of oyster shell dredging on an estuarine benthic community. *Estuarine and Coastal Marine Science* 9: 749–58.

Currie, D.C & Parry, G.D. (1996) Effects of scallop dredging on a soft sediment community: a large-scale experimental study. *Marine Ecology Progress Series* 134: 131–50.

Day, J.H. (1959) The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. *Transactions of the Royal Society of South Africa* 35(5): 475–547.

Day, J.H. (1981) The estuarine fauna. In: *Estuarine Ecology with Particular Reference to Southern Africa*., ed. J.H. Day, pp. 147–78. Cape Town, South Africa: Balkema.

Dittmann, S. (1996) Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. *Marine Ecology Progress Series* 134: 119–30.

Dobbs, F.C. & Guckert, J.B. (1988) *Callianassa trilobata* (Crustacea: Thalassinidea) influences abundance of meiofauna and biomass, composition, and physiologic state of microbial communities within its burrow. *Marine Ecology Progress Series* 45: 69–79.

Field, J.G., Clarke, K.R. & Warwick, R.M. (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37–52.

Flemming, B.W. (1977) Distribution of recent sediments in Saldanha Bay and Langebaan Lagoon. *Transactions of the Royal Society of South Africa* 42: 317–40.

Forbes, A.T. (1973) A study of the burrowing sandprawn *Callianassa kraussi* Stebbing (Crustacea: Decapoda: Thalassinidea). Ph.D. thesis, Rhodes University, Grahamstown: 164 pp.

Glassom, D. & Branch, G.M. (1997) Impact of predation by greater flamingos *Phoenicopterus ruber* on the macrofauna of two southern African lagoons. *Marine Ecology Progress Series* 149: 1–12.

Hailstone, T.S. & Stephenson, W. (1961) The biology of *Callianassa (Trypaea) australiensis* Dana 1852 (Crustacea, Thalassinidea). *Papers of the Department Zoology, University of Queensland* 1(12): 259–85.

Hall, S.J. (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology, Annual Review* 32: 179–239.

Hanekom, N. (1980) A study of two thalassinid prawns in the non *Spartina* regions of the Swartkops estuary. Ph.D. thesis, University of Port Elizabeth: 253 pp.

Hill, B.J. (1967) Contributions to the ecology of the Anomuran mud prawn *Upogebia africana* (Ortmann). Ph.D. thesis, Rhodes University, Grahamstown: 201 pp.

Hines, M.E. & Jones, G.E. (1985) Microbial biogeochemistry and bioturbation in sediments of Great Bay, New Hampshire. *Estuarine and Coastal Shelf Science* 20(6): 729–42.

Hurlbert, S.A. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.

Jackson, M.J. & James R. (1979) The influence of bait digging on cockle, *Cerastoderma edule*, populations in North Norfolk. *Journal of Applied Ecology* 16: 671–9.

Jeffrey, S.W & Humphrey, G.F. (1975) New spectrophotometric equations for determining chlorophylls a, b and c in higher plants, algae and natural phytoplankton. *Bio. phys. Pflanz*. 167: 191–4.

McLusky, D.S., Anderson, F.E. & Wolfe-Murphy, S. (1983) Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait-digging. *Marine Ecology Progress Series* 11: 173–9.

Oliver, J.S., Slattery, P.N., Hulberg, L.W. & Nybakken, J.W. (1980) Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. *Fishery Bulletin* 78: 437–54.

Peterson, C.H. (1977) Competitive organization of the soft-bottom macrobenthic communities of southern Californian lagoons. *Marine Biology* 43: 343–59.

Posey, M.H. (1986) Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. *Marine Ecology Progress Series* 31(1): 15–22.

Ramsay, K., Kaiser, M.J. & Hughes, R.N. (1996) Changes in hermit crab feeding patterns in response to trawling disturbance. *Marine Ecology Progress Series* 144: 63–72.

Roberts, H.H., Suchanek, T.H. & Wiseman, W.J. (1981) Lagoon sediment transport: the significant effect of *Callianassa* bioturbation. In: *Proceedings of the Fourth International Coral Reef*

*Symposium, Manila, 1981*, ed. E.D. Gomez, C.E. Birkeland, R.W. Buddemeier, R.E. Johannes, J.A. Marsh & R.T. Tsuda, Vol. 1, pp. 459–66. Quezon City, Philippines: Marine Science Centre, University of the Philippines.

Suchanek, T.H. (1983) Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidae) bioturbation. *Journal of Marine Science* 41(2): 281–98.

Suchanek, T.H., Colin, P.L., McMurtry, G.M. & Suchanek, C.S. (1986) Bioturbation and redistribution of sediment radionuclides in Enewetak Atoll lagoon by callianassid shrimp: biological aspects. *Bulletin of Marine Science* 8(1): 144–54.

Thrush, S.F., Pridmore, R.D., Hewitt, J.D. & Cummings, V.J. (1994) The importance of predators on a sandflat: interplay between seasonal changes in prey density and predator effects. *Marine Ecology Progress Series*. 107: 211–22.

Thrush, S.F., Hewitt, J.D., Cummings, V.J. & Dayton, P.K. (1995) The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Marine Ecology Progress Series* 129: 141–50.

Walters, W.L. & Griffiths, C.L. (1987) Patterns of distribution, abundance and shell utilization amongst hermit crabs, *Diogenes brevirostris*. *South African Journal of Zoology* 22(4): 269–77.

Wilkinson, L. (1987) In: *SYSTAT: The System for Statistics*, ed. I.L. Evanston, pp. 24–35. New York, NY, USA: SYSTAT, Inc.

Wynberg, R.P. (1991) The ecological effects of collecting *Callianassa kraussi* Stebbing and *Upogebia africana* (Ortmann) for bait: impacts on the biota of an intertidal sandflat. M.Sc. thesis, University of Cape Town: 142 pp.

Wynberg, R.P. & Branch, G.M. (1992) An assessment of bait-collecting for *Callianassa kraussi* Stebbing in Langebaan Lagoon, and of associated avian predation. *South African Journal of Marine Science* 11: 141–52.

Wynberg, R.P. & Branch, G.M. (1994) Disturbance associated with bait collection for sandprawns (*Callianassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal sandflats. *Journal of Marine Research* 52(3): 523–58.

Yingst, J.Y. & Rhoads, D.C. (1980) The role of bioturbation in the enhancement of bacterial growth rates in marine sediments. In: *Marine Benthic Dynamics*, ed. K.R. Tenore & B.C. Coull, pp. 407–21. Columbia, South Carolina: University of South Carolina Press.