

**The Ecological Effects of Collecting Callianassa kraussi Stebbing and
Upogebia africana (Ortmann) for Bait: Impacts on the Biota of an
Intertidal Sandflat**

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**A thesis submitted to the Department of Zoology, University of Cape Town, in the
fulfilment of the requirements for the degree of Master of Science.**

February, 1991

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The prover proves what the thinker thinks

**Robert Anton Wilson,
Prometheus Rising**

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Abstract

The ecological effects of collecting the sandprawn *Callinassa kraussi* and the mudprawn *Upogebia africana* for bait were assessed at Langebaan Lagoon, South Africa, through surveys, observations and long-term experimental analyses. While only a small proportion of the prawns is removed from the lagoon annually, amounting to no more than 0.01% for the total lagoon, the physical disturbance inflicted by collecting is likely to be more detrimental and longer-lived than the actual removal of the prawns. Bait-collecting activities are concentrated on the centre sandbanks where some 400 000 prawns are removed annually - less than 5% of the total prawn population on these sandbanks. In terms of numbers removed, bait-collecting is thus no threat to the prawn populations at Langebaan Lagoon although there are signs that sandprawn densities and modal body sizes have been reduced in areas of intense bait-collecting activities.

Massive quantities of sediment are disturbed through bait-collecting activities and this, inadvertently, results in the disturbance of other components of the biota. It is estimated that approximately 543 g of macrofauna are disturbed with each bag limit of prawns (50) removed, amounting to approximately 10 000 kg of macrofauna being disturbed annually. While the fate of this macrofauna is not completely determined, approximately 80% is subsequently preyed upon by scavenging gulls.

The long-term effects of high-intensity disturbance on the biota of a sandflat were assessed through simulated bait-collecting activities, viz "digging" and "sucking" for *C. kraussi* and *U. africana*. The recovery of both *C. kraussi* and *U. africana* was far more protracted than predicted - probably being completed only 18 months after the initial disturbance. Meiofaunal and macrofaunal numbers decreased immediately following the initial disturbance. In the case of the meiofauna, this depression was followed by an explosive increase and subsequent levelling out of densities. The macrofauna was slower to recover and still showed signs of depression 18 months after the initial disturbance. Only a single macrofaunal species, the hermit crab *Diogenes brevisrostris*, responded positively to the disturbance. After the disturbance of *C. kraussi*, chlorophyll levels increased above control levels, whereas bacterial numbers were temporarily reduced. Conversely, the disturbance of *U. africana* resulted in nett decreases in chlorophyll levels and initial slight increases in bacterial numbers.

Following the disturbance, *C. kraussi* and *U. africana* densities were reduced by approximately 75%. As only 10% of the original *C. kraussi* population and 46% of the original *U. africana* population was removed during the sampling, the subsequent declines are ascribed to the disturbance of the sediment, particularly its compaction, rather than to the removal of the sand- and mudprawns *per se*.

This conclusion is strongly substantiated by the results from a further set of experiments involving less intense disturbance, which showed the clear negative effect which even trampling has upon the sandflat biota. Indeed, no differences existed between the effects of low-intensity "sucking" and those of trampling. The biota showed similar, but shorter-lived responses to the high-intensity disturbance.

The current status of *C. kraussi* and *U. africana* populations in southern Africa is reviewed through assessments of their respective distributions and biology, and a procedure for drawing up site-specific regulations for the conservation of these species is suggested. Whilst prawn stocks at Langebaan Lagoon appear to be relatively healthy, densities in the unprotected mainland areas of the lagoon may require amendments to the present restrictions. However, at present, the current restrictions are perceived to be adequate. The enormous negative impact which disturbance has on several major components of sandflats has many implications and reemphasises the importance of retaining pristine areas within estuaries.

CHAPTER 1

General Introduction

INTRODUCTION

The thalassinidean prawns *Callinassa kraussi* Stebbing and *Upogebia africana* (Ortmann) are dominant members of the macrofauna in many southern African estuaries, often forming dense beds of over 350 and 400 individuals m^{-2} respectively (Hanekom 1980). Occurring in intertidal and shallow subtidal soft substrata, these fossorial species are adapted to sheltered habitats of coastal marshes, tidal channels, and estuarine embayments (Day 1981a). Because they are extremely popular bait organisms, large numbers are removed from estuaries or sheltered lagoons by digging or by pumping with a suction pump (Hailstone & Stephenson 1961).

The habitats and geographical distribution of the two organisms differ, with *C. kraussi* being more common in sandy areas and extending from the Orange River to San Martinho in Moçambique, whereas *U. africana* burrows in finer, muddier sediment and is confined to the area between Langebaan Lagoon on the west coast and Inhambane on the east coast (Hill 1967; Forbes 1973a). Both species are typically estuarine in that they are osmoregulators (Hill 1971; Forbes 1973a) and have broad tolerances to hypoxic conditions (Hanekom & Baird 1987).

Burrow structure and feeding methods also differ between the two species. The burrow system of the sandprawn (*C. kraussi*) has one or more opening to the surface and typically consists of a series of long shafts with short, blind-ending side-branches (Forbes 1973a). As callianassids are active burrowers, they process large amounts of sediment and selectively remove particles suitable for consumption. The sediment is funnelled into subsurface galleries, gleaned for organic material and sorted (Forbes 1973a). Grains finer than approximately 1 mm diameter are then pumped back up to surface-forming mounds; coarser grains are stored in deep chambers extending > 1.5 m below the sediment surface (Suchanek 1983; Suchanek *et al.* 1986). Sedimentological evidence can therefore be used as an indicator of *Callinassa* activity when interpreting the geological record (Weimer & Hoyt 1964; Shinn 1968; DeWindt 1974; Tudhope & Scoffin 1984). Mudprawns (*U. africana*) build more permanent U-shaped tubes with two surface openings through which they circulate water, filtering out particles in the process (Hill 1967; Schaefer 1970; Branch & Branch 1981).

Burrowing activities by thalassinideans result in intensive bioturbation which has been shown to contribute significantly to sediment transportation (Roberts *et al.* 1981; McMurtry *et al.* 1985, 1986; Suchanek & Colin 1986; Suchanek *et al.* 1986), and to increase oxygenation and mineralisation (Dye 1978; Hines & Jones 1985), alter sediment

geochemistry (Aller & Dodge 1974), enhance bacterial numbers (Yingst & Rhoads 1980; Koike & Mukai 1983; Branch & Pringle 1987; Tamaki 1988), bury and alter the depth-distribution of microalgae (Branch & Pringle 1987) and reduce the meiofauna (Alongi 1986; Branch & Pringle 1987). Bioturbation may also have indirect effects on the community structure, resulting in the possible exclusion of certain groups of organisms and diminished productivity and cover by seagrasses and algae (Rhoads & Young 1970; Brenchley 1981, 1982; Roberts *et al.* 1981; Suchanek 1983; Murphy 1985; Posey 1986). Moreover, *C. kraussi* and particularly *U. africana* constitute an important food source for long-billed waders such as grey plovers (*Pluvialis squatarola*), whimbrels (*Numenius phaeopus*) and common terns (*Sterna hirundo*) (Martin & Baird 1987) and for many species of fish, specifically white steenbras (*Lithognathus lithognathus*), spotted grunter (*Pomadasys commersonni*) (Day 1981a) and sandsharks (*Rhinobatus blochii* and *Rhinobatus annulatus*) (Day 1981a; Harris *et al.* 1989).

Previous work on sand- and mudprawns has focused on their biology (Hill 1967; Forbes 1973a,b; Hanekom 1980; Hanekom & Baird 1987; Hanekom & Erasmus 1988) and their distribution throughout Cape estuaries (Cockcroft & Tomalin 1987; Gaigher 1987; Hanekom *et al.* 1988). Although these authors highlighted the extensive utilisation of the prawns for bait, to date no conclusive experiments have been conducted to determine the effects of bait-collecting on the prawns and on the networks of their associated communities.

BACKGROUND TO THE PROJECT

In 1982, the South African National Committee for Oceanographic Research (SANCOR) identified Langebaan Lagoon as an 'estuary' that should receive high priority in terms of the need for future research. This rating was based partly on the prediction that the area would become a focal point for development. Subsequently, human activities have indeed intensified in the area. Activities that impinge directly on the lagoon include pollution from the iron-ore harbour, boating and water-skiing, fishing, bait-collecting, and less obvious activities such as the trampling of salt marshes (Henderson 1985).

Over the past 20 years, the popularity of coastal sport-fishing has risen rapidly and, with it, the demand for live bait. This study was initiated as a response to concerns expressed about apparent declines in the abundances of sand- and mudprawns. A primary role of this investigation was to examine the implications of their removal for

bait and to follow patterns of recovery within the prawn populations and associated communities.

STUDY AREA

Langebaan Lagoon (33°10'S:18°5'E) is situated on the west coast of South Africa and is approximately 15 km in length with a maximum width of 4 km. Being an extension of Saldanha Bay it is entirely marine, but has a rich fauna typical of most South African estuaries with open mouths (Day 1959). The lagoon experiences minimal wave action apart from the channels near the mouth of the lagoon, where a velocity of 1 m sec⁻¹ can be reached by tidal movements during spring tides (Shannon & Stander 1977). Approximately half the volume of the lagoon passes through these channels into the bay during spring tides, leaving vast areas of intertidal sandflats exposed at low water springs (LWS) (Shannon & Stander 1977). The intertidal sediments are composed principally of SiO₂ and range from coarse on the exposed beaches to fine, muddy sands at the head of the lagoon (Flemming 1977). The mean monthly sea surface temperatures vary between 19.5°C during the warmest summer months and 14°C during the winter (Maritime Weather Office, D.F. Malan Airport, Cape Town).

The proclamation of parts of Langebaan as a national park has resulted in the division of the lagoon into three distinct zones (see Figure 2.1). Zone A is a multi-purpose recreational area, in which the use of motorboats, sailboats and windsurfers is permitted, as well as activities such as waterskiing, rowing, diving, swimming, and angling. This is the only zone in which bait may be collected. Current restrictions allow 50 prawns per person per day to be harvested although this is not specific to Langebaan Lagoon. Zone B of the lagoon is a limited recreational area which was zoned chiefly for the use of sailboats and windsurfers. Powerboating and angling are prohibited here. Zone C is a 'wilderness' area in which no persons are allowed without a permit.

Study sites were chosen at Klein Oesterwal, Geelbek and the centre sandbanks (Figure 2.1). Klein Oesterwal lies just within zone A, but is used infrequently for bait-collecting. The sediment there consists of fine sand at LWS (Md ϕ 2.5) with a low organic content (1.72%) and a low silt and clay component (3.3%) (Mazure & Branch 1979). The intertidal benthic biomass of Klein Oesterwal is dominated by *C. kraussi*; the eel-grass *Zostera capensis* Setchell and, to a lesser extent, the red algae *Gracilaria verrucosa* (Huds.) are the dominant plant forms.

Geelbek, at the head of the lagoon and situated within the sanctuary zone, has

a substrate consisting of fine anaerobic muddy sand at LWS (Md ϕ 3.62; 8% silt and clay) with a high organic content (4%) (Puttick 1977). *Zostera capensis* occurs in large patches at low water neap (LWN) and below. In terms of biomass, *U. africana* is the dominant intertidal benthic organism in this system. Geelbek has recently been purchased by the National Parks Board and functions as an environmental education centre. As such, it remains completely inaccessible to bait-collectors.

The centre sandbanks (Figure 2.1) support enormous numbers of *C. kraussi* and are the hub of bait-collecting activities at Langebaan Lagoon. As these banks fall within both zones A and B, bait may only be collected in the northern half. When exposed at LWS, they are approximately 270 m wide and 740 m long; during high tide they become completely submerged and are surrounded by a 10-m deep channel. The substrate here consists of fine sand (Md ϕ 3) with a low silt component (2%) (Flemming 1977). Extensive stretches of *Zostera capensis* grow on the centre sandbanks at LWN.

THESIS OUTLINE

The two complementary approaches of this thesis, embracing both applied research and pure science, are integral to effective, holistic, environmental management. Chapter 2 is by nature of its aims observational and pragmatic. In it, an attempt is made to quantify both the intensity of prawn harvesting through human activities, and the incidental effects on the discarded organisms which are left exposed after bait-collecting activities. This, together with surveys amongst anglers and regular enumerations of bait-collectors, serve as tools to assess existing bait regulations, calculate the nett harvest of prawns from the sandbanks and, hence, assess the total impact of bait-collecting upon Langebaan Lagoon.

Chapters 3 and 4 on the other hand, follow a more academic line and adopt the experimental approach used in many other disturbance studies. Chapter 3 forms the essence of the thesis and examines the long-term effects of experimental high-intensity disturbance on *C. kraussi* and *U. africana* and their associated macrofaunal, meiofaunal, bacterial and microfloral communities. The high intensity of harvesting in this experiment necessitated the initiation of another, lower intensity study which incorporated the short-term effects of bait-gathering and of physical trampling on *C. kraussi* and associated sandflat organisms. This work is reported in Chapter 4. Chapter 5 consolidates the above aspects in an attempt to formulate a comprehensive management policy which can be used to implement informed conservation measures.

CHAPTER 2

**An Assessment of the Current Status of Callianassa kraussi
and Upogebia africana as Bait Organisms in Langebaan Lagoon**

INTRODUCTION

Callinassa kraussi and *Upogebia africana* together constitute approximately 48% of the total benthic biomass of Langebaan Lagoon (Christie & Moldan 1977). In the Swartkops estuary, *U. africana* and *C. kraussi* comprise 82% and 11% respectively of the total macrofaunal biomass and may reach densities of over 350 and 400 individuals m^{-2} respectively (Hanekom 1980). These two species are thus important components of intertidal mud- and sandflat communities and their exploitation for bait could have serious repercussions.

As early as 1967, concern was expressed over the vast quantities of prawns being harvested from southern African estuaries (Hill 1967). This has undoubtedly been directly related to the introduction of the prawn pump. Prawns had previously been collected either by digging or by being forced out of their burrows using a tin can. A prawn pump consists of a 75-cm long, 9-cm diameter stainless-steel cylinder, containing a hand-operated diaphragm pump (Hailstone and Stephenson 1961) and is efficient and easy to use. Prawn pumps may be operated in either of two ways: firstly by sucking up a core of sediment and examining it for prawns, and secondly by forcing air or water into the burrows to a depth of 50-70 cm. The resultant upward water currents drive the prawns to the surface where they can be easily collected.

Disruption of the sediment and attendant benthic organisms is inevitable when a prawn pump is used to extract bait. Large prawns are removed from the core and the remnants discarded. Immediately after the bait-collector has moved on to another area, opportunistic gulls (*Larus dominicanus* Lich.) flock into the disturbed area. Organisms which have been physically damaged by the prawn pump or have not managed to successfully burrow back into the sediment are consequently preyed upon.

Over the last two decades there has been a surge in sport fishing and this, together with the ease with which prawns can now be harvested, has resulted in the vastly expanded utilisation of both mud- and sandprawns. Although frequently recognised as a problem (Hill 1967; Forbes 1973a; Hanekom 1980; Gaigher 1987; Baird 1988), to date there has been no definitive work on the effects of bait-collecting, nor any effective management scheme completed for the conservation of these prawns. Consequently, serious concerns, although recognised, have not been researched sufficiently to make management recommendations.

In an attempt to formulate appropriate management proposals, two primary aims were identified. Firstly, to assess the impact of bait-collecting on *Callianassa* and *Upogebia* at Langebaan Lagoon and, secondly, to assess the indirect effects which bait-collecting is having on organisms which are inadvertently disturbed through collecting activities. The first aim was pursued through density assessments of the prawn populations at Langebaan Lagoon and comparisons of *Callianassa* size-frequency distributions and densities, between exploited and unexploited areas. In addition, anglers were regularly monitored and their bait requirements surveyed in order to assess the expediency of current bait-collecting restrictions.

Indirect effects on organisms disturbed through bait-collecting activities were assessed through the quantification of the amount of sediment and macrofauna disturbed with each bag limit. Experiments were conducted to assess what proportion of this macrofauna is consumed by birds.

METHODS

The impact of bait-collecting on *Callianassa* and *Upogebia*

Prawn densities: Estimates of population densities were determined from *Callianassa* and *Upogebia* hole counts. Holes were counted in 20 duplicated 0.1 m² quadrats evenly spaced between HWS (high water spring) and LWS (low water spring) at selected sites along the lagoon (Figure 2.1). Sampling sites included Sepia Bay, Klein Oesterwal, Oesterwal, Bottelary, Schrywershoek, Churchhaven, and Kraalbaai.

Prawn holes were initially counted in four 0.5 m² areas which were subsequently dug to a depth of 1 m and all prawns removed. This procedure yielded a ratio of 1.05 holes per adult *Callianassa*, conforming to the 1:1 ratio previously described by Forbes (1973a) for areas with sheltered conditions and constant salinity. A 2:1 ratio (holes:prawns) was obtained for *U. africana*.

On the centre sandbanks (Figure 2.1), transects were laid out across the width of the exposed bank at low tide, and prawn holes within duplicated 0.1 m² quadrats were counted at 10 m intervals. The transects varied from 270 m to 740 m in length. Using these transects, the area of the centre sandbanks at LWS was determined.

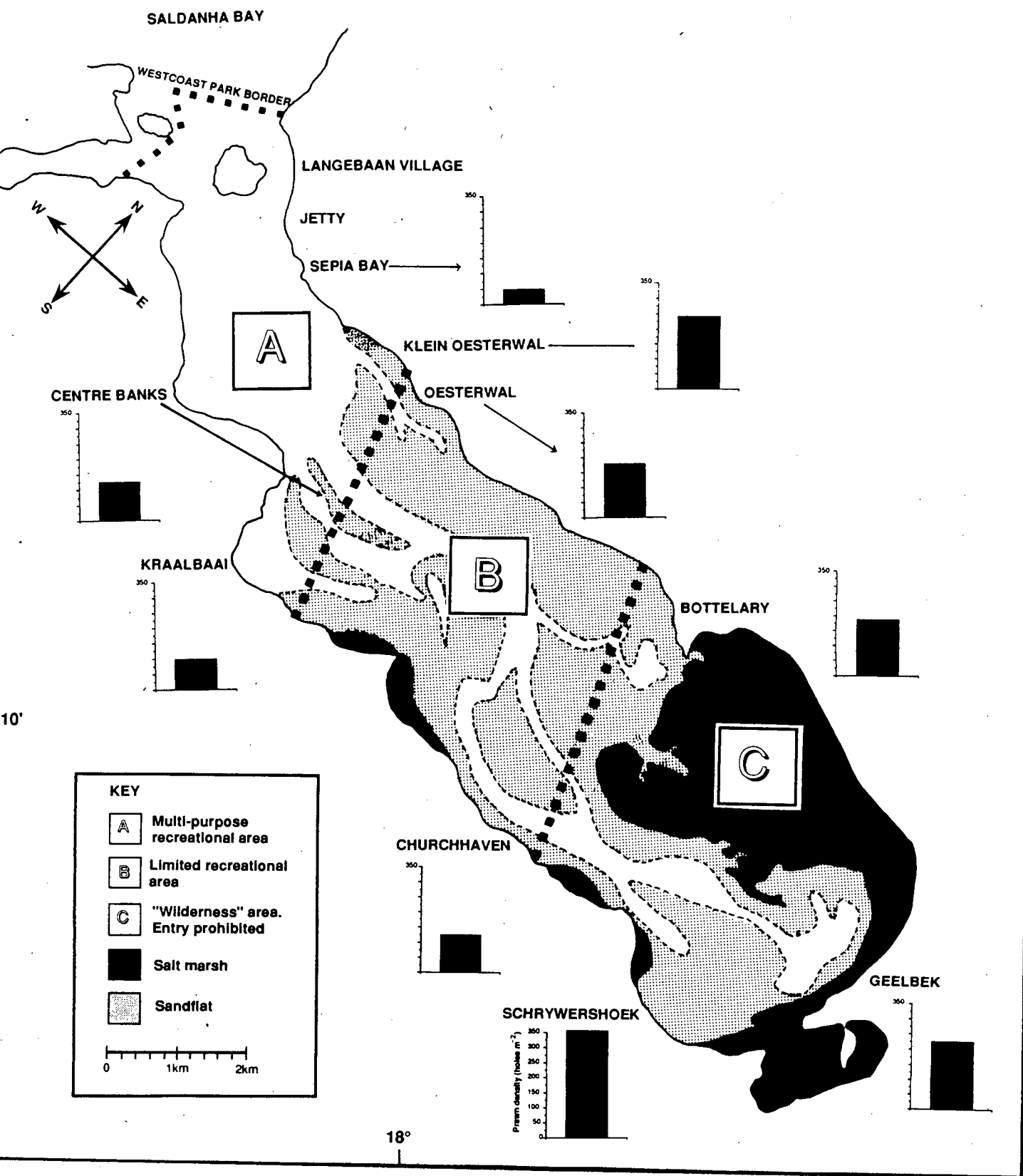


Figure 2.1. Langebaan Lagoon, showing park boundaries, sampling stations and prawn densities. Prawn densities (holes m^{-2}) generally represent mixed *Callinassa kraussi* and *Upogebia africana* populations, although populations at Geelbek and Schrywershoek are predominantly *U. africana*, and the remaining stations are predominantly *C. kraussi*. (Map reference: South Africa 1:50 000, 3317BB & 3318AA Saldanha, third edition).

Sandprawn size-frequencies: A comparison of size-frequency distributions was made between samples of *Callinassa* from exploited and unexploited areas, together with samples of bait obtained from anglers. 100-150 prawns were collected from both the northern centre sandbanks (heavily exploited) and the southern centre sandbanks (unexploited) in November 1989. 50-75 prawns were collected from Klein Oesterwal (lightly exploited) and a similar number of prawns purchased from bait-collectors in the vicinity.

When collecting prawns, juveniles (body length <20 mm) readily escape and are easily overlooked. Since attempts to sieve large quantities of sand to obtain juveniles were unsuccessful, prawns of 0-20 mm body length were excluded from the comparison. Body lengths of *Callinassa* were measured to the nearest 0,2 mm from the tip of the rostrum to the posterior end of the telson, using vernier calipers. Measurements were grouped into 10 mm size classes and size-frequency histograms were constructed for the populations sampled at each site.

The behaviour of bait-collectors: The numbers of bait-collectors active at Langebaan Lagoon were monitored periodically during 1989. Interviews were conducted among a total of 63 anglers at various fishing and bait-collecting sites in the Lagoon, including the yacht basin, Sepia Bay and the centre sandbanks (Figure 2.1). In addition, bait-collectors were interviewed during peak (Easter and Christmas) and off-peak periods of the year. Anglers who fished more than once monthly were regarded as regulars. A copy of the questionnaire circulated is presented in Table 2.1.

Calibration

A calibration curve was computed to determine the average number of prawns removed for each suck of the prawn pump. Bait-collectors were observed on a regular basis at different times of the year. The number of sucks required to obtain specific numbers of prawns was counted and both figures cumulatively added until either the bait-collector had moved on to another area or had collected a sufficient number of prawns. This exercise was repeated 27 times on the centre sandbanks and 10 times on the mainland. Different bait-collectors were assessed on each occasion.

To estimate the mass of sediment disturbed by bait-collectors, the sediment density was determined by its displacement in water. The mean volume removed per 'suck' of the prawn pump was then converted to a mass:

Table 2.1. Questionnaire circulated amongst anglers at Langebaan Lagoon.

BAIT COLLECTION SURVEY

We are at present running a series of experiments to determine the effects of bait digging/pumping on the sand prawn *Callinassa kraussi* and the mud prawn *Upogebia africana*. A knowledge of the intensity of digging/pumping and use of the bait is obviously important and we would greatly appreciate your help in this regard by filling in this questionnaire. Please feel free to add any comments you think necessary. Thank you very much for your help.

- * *Town/City of residence:*
 - * *Which animals do you use most frequently as bait?*
 - * *When you collect mud- and/or sandprawns, how many on average do you collect per day?*
 - * *Which fish are caught with mud- and/or sandprawns?*
 - * *What is your method of collection? (e.g. prawn pump, digging, tin cans etc.)*
 - * *Where is your main site of collection of sand/mudprawns in Langebaan Lagoon?*
 - * *How frequently do you fish? (e.g. only on holidays, every weekend, daily, monthly)*
 - * *50 prawns are allowed to be removed per day. Is this more than adequate/adequate/inadequate for your purposes?*
 - * *How do you rate sandprawns as a bait organism?*
Excellent/Good/Fair/Poor
 - * *How do you rate mudprawns as a bait organism?*
Excellent/Good/Fair/Poor
 - * *Comments:*
-

The indirect effects of bait-collecting

A quantification of the immediate damage inflicted by a bait-collector was assessed in the following way. Three 1 m X 1 m sheets of plastic were staked out at widely-spaced intervals on the centre banks. A thin layer of sediment, previously defaunated by sieving through a 1 mm mesh sieve, was spread over the plastic sheets to act both as a camouflage and as a substrate for burrowing organisms. 10 cores were sucked out with a prawn pump from an area adjacent to each plastic sheet, and placed on top of the defaunated sediment after which they were left undisturbed for 30 minutes to allow time for the gulls to feed. A further 10 cores from an adjacent area were sucked out and placed in an empty bucket. These latter cores acted as the control and were processed immediately by sieving through a 1 mm mesh sieve and removing, identifying and counting the organisms retained. After the 30 minute period, the 'predated' sediment on each of the plastic sheets was collected and processed in a similar manner to that of the controls. 7 samples were obtained for each replicate. Once enumerated and identified, samples were dried and subsequently ashed in a muffle furnace at 480°C for 8 hours.

Data analysis

Differences between prawn densities on the centre sandbanks were assessed using a one-way analysis of variance (ANOVA). Bartlett's test, as described in Zar (1984) was employed to test for homogeneity of variances. Heteroscedastic data were transformed using an appropriate transformation and then evaluated using ANOVA (Zar 1984). The Tukeys HSD test (Tukey 1953 *in* Zar 1984) was employed when analysing multiple differences between samples. Paired t-tests (Zar 1984) were used to determine differences between control and predated samples on the centre sandbanks. Results were computed using STATGRAPHICS (STSC, Inc.) software. The calibration curves were computed using a linear regression on SYSTAT (SYSTAT, Inc.) software.

RESULTS

The impact of bait-collecting on *Callianassa* and *Upogebia*

Prawn densities: Mean prawn densities from selected sites around Langebaan Lagoon are given in Figure 2.1. Prawn densities decreased from the head towards the mouth of the lagoon, with the highest densities being recorded at Schrywershoek. Sepia Bay, an intensively utilised prawn collection area had noticeably lower prawn densities than elsewhere. Although it was difficult to distinguish between *Upogebia* and *Callianassa* burrow holes, densities in the southern, restricted parts of Langebaan Lagoon represent *Upogebia* populations.

The area of the centre sandbanks was estimated to be 199 800 m², with a mean adult prawn density (holes m⁻²) of 126.3 m⁻² (\pm 16.4 S.E.). The total adult sandprawn population on the centre sandbanks at LWS was thus estimated at 25 238 736. *Callianassa* populations showed clear differences between exploited and unexploited areas of the centre sandbanks (Figure 2.2). Comparisons between the northern, exploited areas and the southern, unexploited areas of the sandbank revealed marked reductions in prawn densities in the heavily pumped localities (ANOVA, $F=12.654$, $P<0.005$, d.f. = 6, 345).

Prawn size-frequencies: Size-frequencies on the centre sandbanks and at Klein Oesterwal are illustrated in Figure 2.3. Clear differences exist both within and between the sites. The sample of sandprawns from the northern, exploited centre banks had a modal size of 20-30 mm body length. The modal size of the population on the southern, unexploited centre banks tended to be shifted towards a body length of 30-50 mm and contained the largest *Callianassa* recorded for Langebaan Lagoon (70-80 mm body length). There was a marked difference between the distribution of the prawns on the centre sandbanks, with prawns in the southern areas displaying a normal distribution and those in the northern areas being skewed towards small individuals.

Sandprawns at Klein Oesterwal were generally smaller than their centre sandbank counterparts, although their modal size was still 30-40 mm body length. Bait-collectors clearly preferentially selected large prawns in the 40-60 mm body length range.

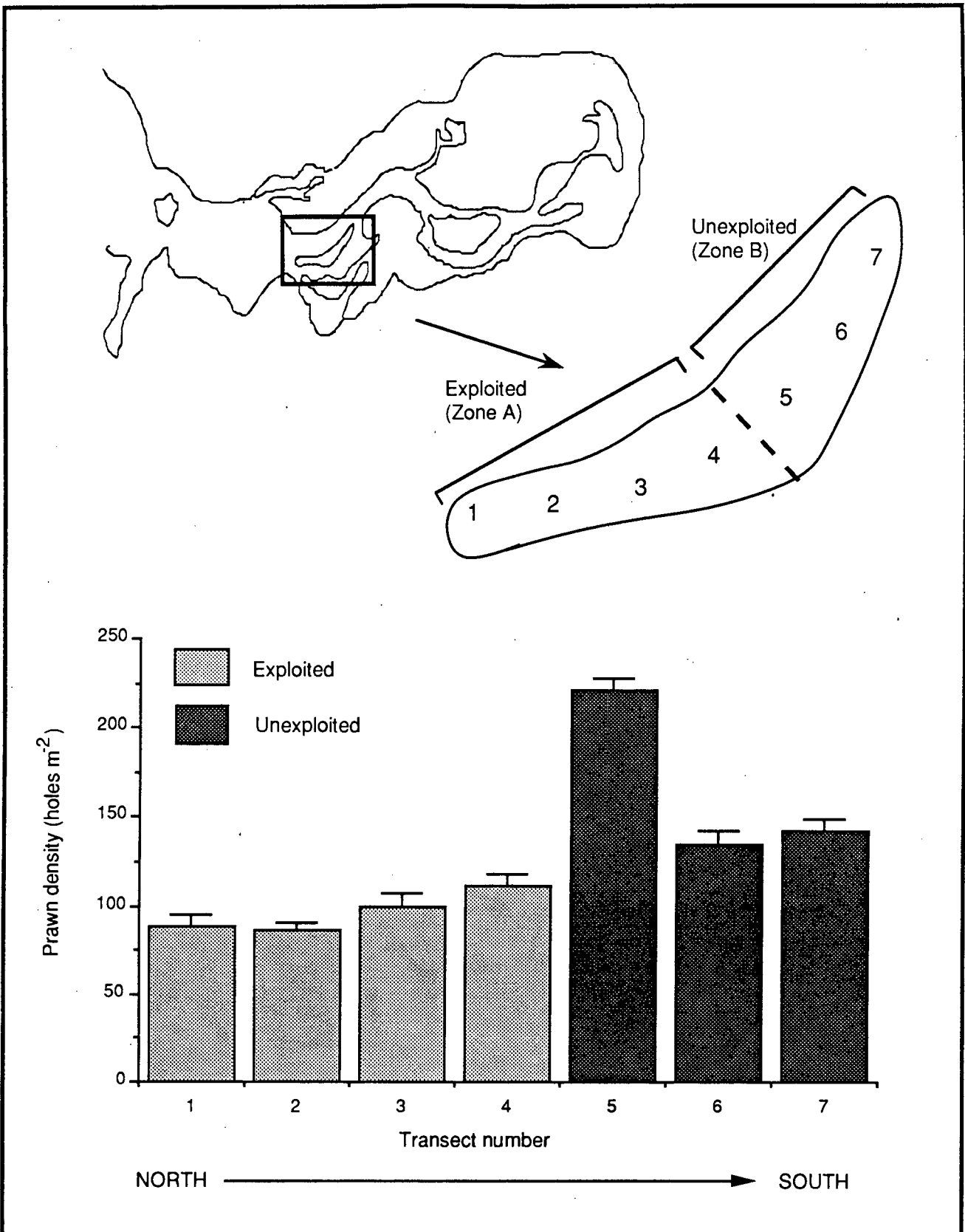


Figure 2.2. Longitudinal distribution of *Callinassa kraussi* on the centre sandbanks at Langebaan Lagoon. S.E. are shown above the mean values.

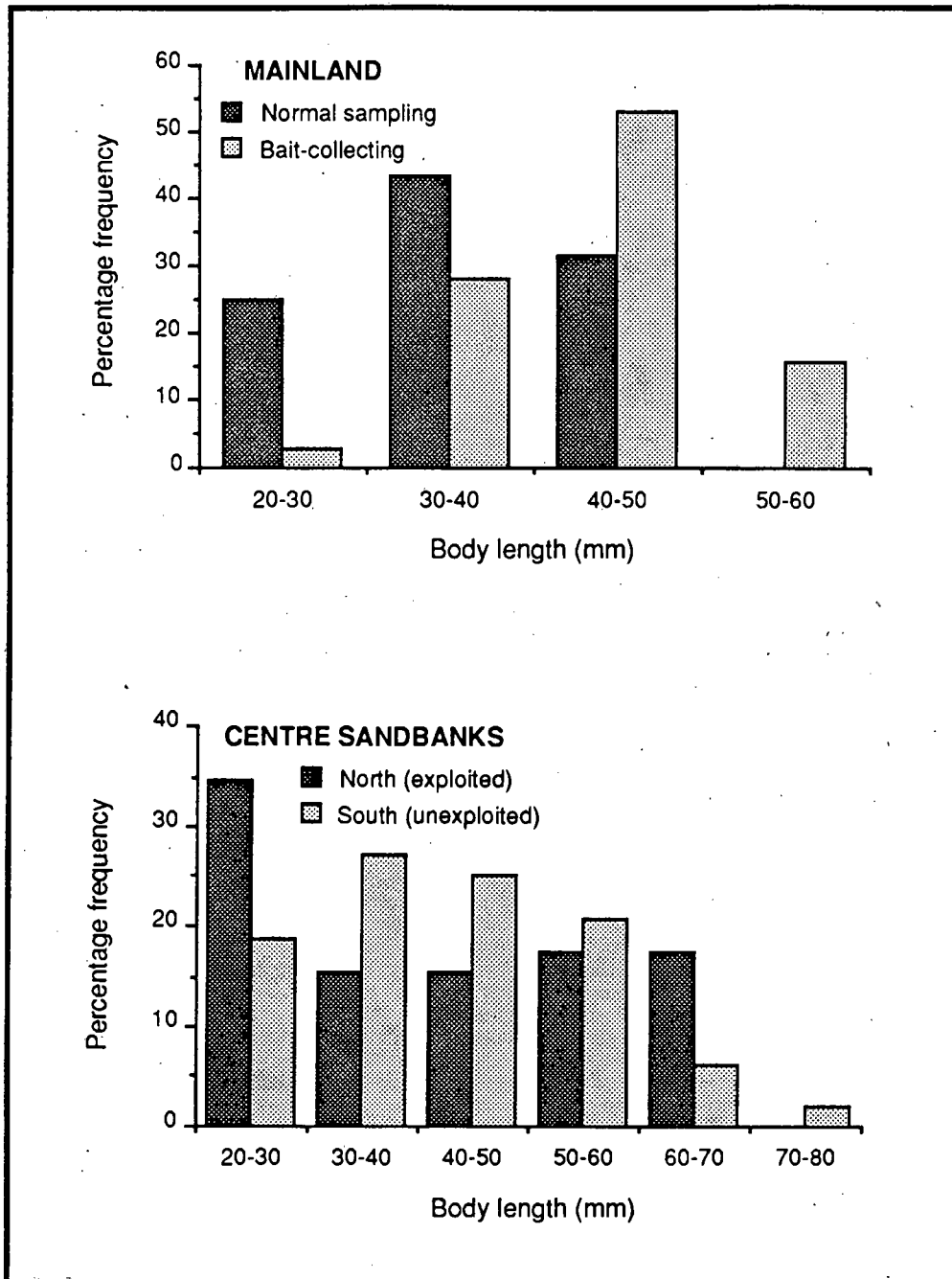


Figure 2.3. Size-frequency distribution of adult (> 20 mm body length) *Callianassa kraussi* at two bait-collecting sites at Langebaan Lagoon.

Bait-collector behaviour: Four categories of bait-collecting activity were seasonally differentiated: peak holiday seasons such as Christmas and Easter, summer weekends and public holidays, winter weekends, and weekday periods. On a daily basis, approximately 300, 150, 75 and 30 people per respective category were observed collecting prawns at Langebaan Lagoon. Approximately two-thirds of these numbers were located on the centre sandbanks at any one time, the remaining one-third being collectors on the mainland who had no access to a boat. This amounts to a crude estimate of 24 450 bait-collectors per annum at Langebaan Lagoon. This is a liberal approximation as these figures include attendant family and friends who are not necessarily anglers or prawn-pumpers. Halving this figure to approximately 12 225 gives a more conservative and perhaps more realistic estimate of the potential exploitation. Assuming each collector takes the maximum quota of 50 prawns per day, the annual removal of prawns in Langebaan Lagoon is between 611 250 and 1 222 500.

Approximately 27% of the anglers interviewed fished on a regular basis and lived in neighbouring areas. The remaining 73% comprised holiday makers (57%) and those who fished monthly (16%). The latter two groups use the lagoon primarily as a recreational facility, whereas the regular anglers probably use the captured fish as a basic food resource.

94% of the anglers interviewed included both *Callianassa* and *Upogebia* amongst the bait they most frequently used in Langebaan Lagoon. Only 6% of the people questioned used bait other than prawns, including bloodworm (*Arenicola loveni* Kbg.), redbait (*Pyura stolonifera* (Heller)), white mussel (*Donax serra* Röding) and sardine (*Sardinops ocellata* (Pappe)). A total of 55% of the respondents used *Callianassa* and *Upogebia* as their only bait, with 35% using *Callianassa* exclusively as bait. The common fish caught in the lagoon using sand- and mudprawns as bait include white steenbras (*Lithognathus lithognathus* (Cuv.)), white stumpnose (*Rhabdosargus globiceps* (Cuv.)), bloukop (*Pachymetopon aeneum* (Val.)), sandshark (*Rhinobatus annulatus* (Müller & Henle)), kabeljou (*Argyrosomus hololepidotus* (Lac.)), hottentot (*Pachymetopon blochii* (Val.)), and steentjies (*SpondylIOSoma emarginatum* (Cuv)).

The excellence of *Callianassa* as a fish bait was undisputed amongst 67% of the anglers interviewed, 28% of them assessing it as "good" and a minority (5%) rating it as "fair" or "poor" bait. The merit of *Upogebia* on the other hand, was more questionable and met with varied responses. Approximately 21% and 15% of bait-collectors regarded the mudprawn as excellent or good bait respectively. A "fair" or "poor" assessment was given by 10% and 6% respectively of those interviewed. 48% were either unaware of the

quality of *Upogebia* as bait or felt its relative inaccessibility in the lagoon did not facilitate its collection.

The numbers of prawns taken per collection are given in Figure 2.4. Most collectors were aware of the present restrictions (50 prawns per person per day) and tended to collect between 30 and 50. Quotas were only surpassed in 4% of the cases studied. 97% of the anglers interviewed used a suction pump to collect prawns, the remaining 3% either digging the prawns out or purchasing the bait from an outlet.

Of the anglers interviewed, 53% considered the present restrictions to be more than adequate to supply their needs for bait, with 33% and 14% considering them respectively adequate and inadequate. Approximately 10%, 8% and 10% of these respective people fished on a regular basis.

Anglers with access to a boat used the centre sandbanks as their principal prawn collection site. The predominant prawn collection sites on the mainland were Sepia Bay and the banks in front of the Yacht Club (Figure 2.1). Other collection sites in the immediate vicinity included Langebaan beach, Milnerton Lagoon (Langebaan) and Saldanha Lagoon. Approximately 10% of the people interviewed used the protected areas of Churchhaven and Oesterwal as prawn collection sites and were uninformed as to the limits of the reserve. This, however, does not imply that the boundaries of the protected areas were recognised amongst the remaining 90%, but simply that the unprotected area is closer to the village of Langebaan.

Calibration

Calibration curves for bait-collectors on the mainland and centre sandbanks are presented in Figure 2.5. From these, it can be determined that an average bait-collector needs to execute 122 sucks with a prawn pump to obtain 50 prawns on the centre banks. On the mainland, 72 sucks are required to obtain the allotted 50 prawns.

The dry mass of sediment that can be contained by a standard prawn pump is approximately 3.25 kg. However, the average bait-collector does not usually fill the pump completely, but to approximately 75% of its capacity. Thus a mean dry mass of 2.45 kg of sediment is disturbed with each suck. Bait-collectors will therefore turn over approximately 297 kg (dry mass) of sediment on the centre sandbanks and 175 kg (dry mass) on the mainland to obtain a bag limit of 50 prawns. This figure will vary with the type of method utilised; experienced collectors on the mainland, for example, tend to collect prawns in shallow water and hence suck up more water than sediment. Further extrapolations, based on the mean number of bait-collectors per annum at Langebaan

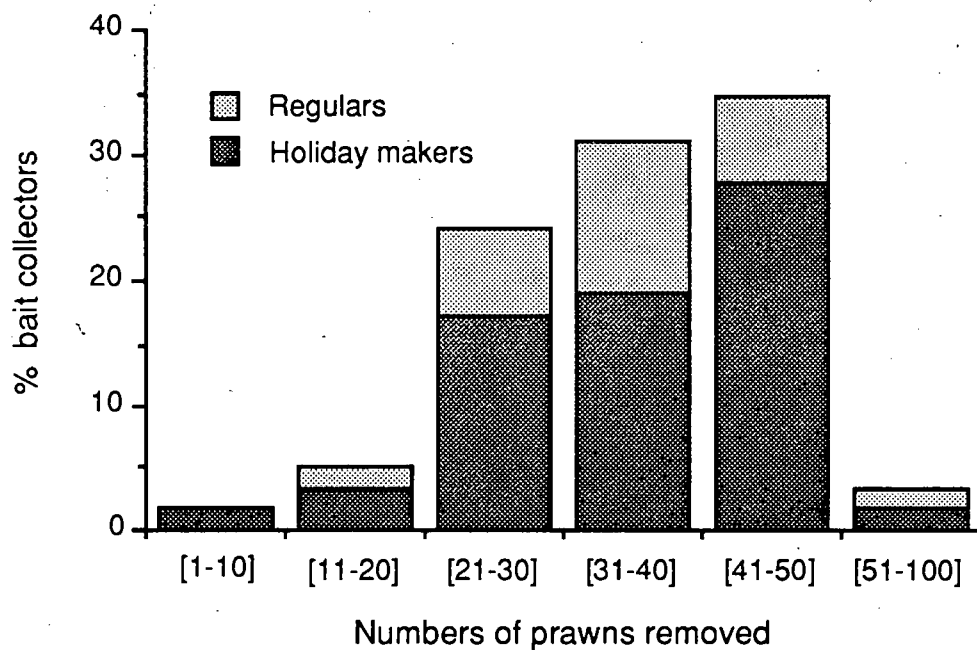


Figure 2.4. Average numbers of mud- and sandprawns removed per collection by anglers at Langebaan Lagoon. Numbers are expressed as a percentage of the total number of anglers interviewed.

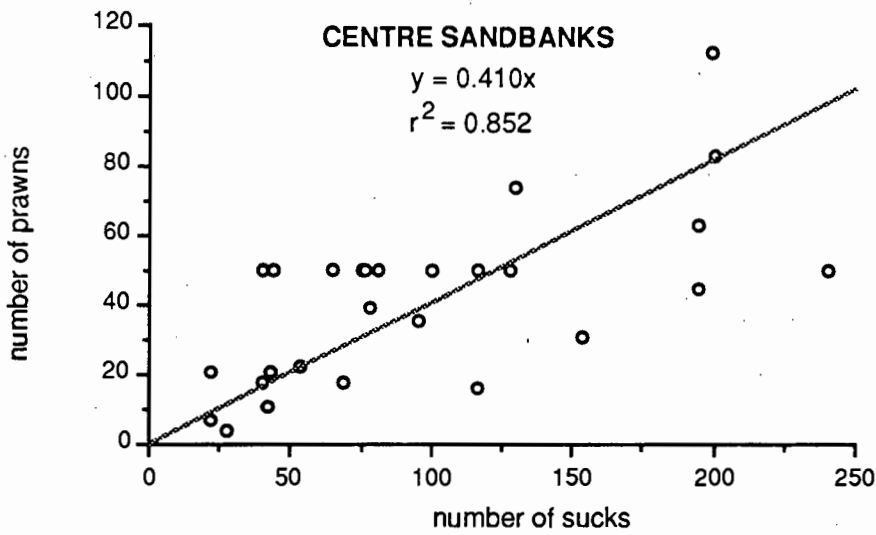
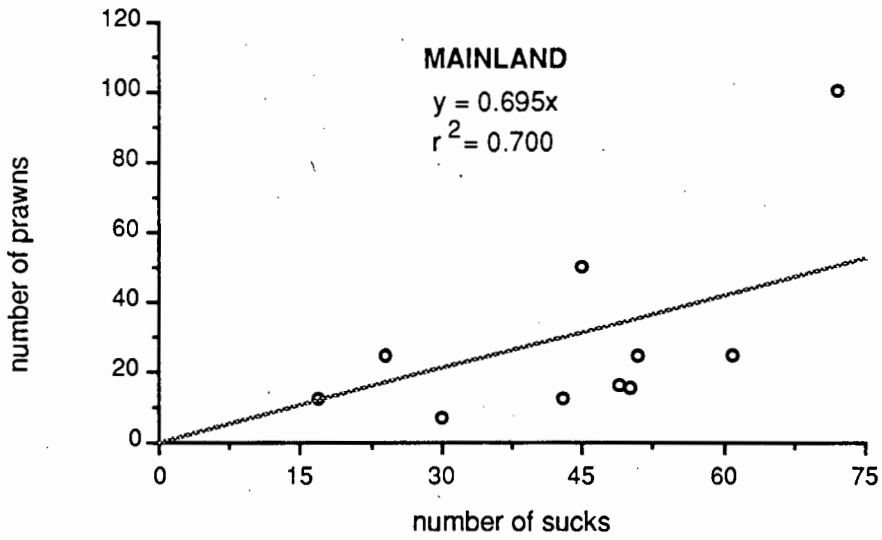


Figure 2.5. Linear regressions calculating the calibration of the number of sucks with a prawn pump against the number of prawns obtained on the mainland and centre sandbanks at Langebaan Lagoon.

Lagoon, result in nett figures of 2 420-4 840 tons (low and high projections) on the centre sandbanks and 713-1 427 tons dry sediment on the mainland being turned over by bait-collectors per annum. It must be stressed that calibration curves are specific to the sites from which they are derived. The development of similar, unique curves for distinct areas would therefore be crucial to the implementation of any bait-collecting measures in other lagoons and estuaries. Comparisons with similar calibration curves (Forbes 1973a) for estuaries in the Eastern Cape have revealed enormous discrepancies in yield per unit effort between sites.

The indirect effects of bait-collecting

In the process of removing a legal limit of 50 prawns, bait-collecting also disturbs other macrofauna. Quantitative estimates of this disturbance are given as 'control' samples shown in Figure 2.6. Density and biomass values were multiplied from their original values (mean value per core) by a factor of 122 (derived from the calibration curve established for the centre banks) so that the data reflect the average amount of damage inflicted during the collection of 50 prawns. The total biomass disturbed amounts to 543 g ash-free dry mass, comprising 451 g *Callianassa* and 102 g of the remaining macrofauna. The numbers of animals disturbed are reflected in Figure 2.6 and Table 2.2 for individual species. Total numbers disturbed amounted to approximately 10 000 - 15 000 macrofaunal organisms with each bag limit.

The fate of animals inadvertently disturbed during bait-collecting is difficult to determine, but an attempt was made to quantify the proportion eaten by gulls scavenging on the remnants left by bait-collectors. The clear patterns which emerged from this experiment are illustrated in Figure 2.6. and Table 2.2. The most discerning predation appeared to be upon *Callianassa* with up to 86% of the initial biomass and 55% of the initial numbers being removed by gulls. Polychaetes were significantly preyed upon, particularly the commoner and more obvious species such as *Antinoe lactea* Day, *Orbinia angrapequensis* (Aug.) and *Euclymene* sp.; more active burrowers such as *Glycera tridactyla* Schm. appeared to escape predation. Smaller organisms such as the common amphipod *Urothoe grimaldi* Chevr. and the sedentary polychaete *Notomastus latericeus* Sars. were also selected as prey items. Other organisms on the centre banks which showed some evidence of being preyed upon but which occurred too infrequently to analyse statistically included the polychaetes *Cirriformia* sp., *Arabella iricolor* (Mont.), *Lumbrinereis tetraura* (Schm.) and *Prionospio sexoculata* Aug. The gastropods *Marginella capensis* Dnkr., *Nassarius scopularcus* Brnrd., *Carditella rugosa* Sow. and an unidentified

white bivalve showed no evidence of being predated upon but also occurred too infrequently to test conclusively.

Predation therefore appeared to be selective, with large, visible, soft-bodied and usually mobile (and hence more obvious) organisms being most heavily preyed upon. Thin-shelled organisms whose shells had been damaged by the prawn pump, such as the bivalve *Tellina trilatera* Gm., were immediately devoured by the gulls; undamaged molluscs on the other hand were not preyed upon. The anenome *Isanthus capensis* Carlg. was avoided by the gulls, presumably because of its unpalatability.

Given that an average of 543 g (ash-free biomass) of macrofauna is disturbed with each bag limit of prawns on the centre sandbanks, the annual mass of disturbed organisms approximates 6 638-13 276 kg. Of this 543 g, 435 g (ca. 80%), including 385 g of *Callianassa*, was subsequently preyed upon. If *Callianassa* is excluded, 53% (or 50 g) of the remaining macrofauna was preyed upon (Figure 2.6; Table 2.2). It was surmised that the remaining animals either recovered sufficiently to burrow back into the substratum, died after being damaged by the pump, or remained exposed and were consequently consumed by fish at high tide.

It should be emphasized that the above results may overestimate the consumption of *Callianassa* by gulls. Normally, large prawns are removed by bait-collectors. Since this was not done in the present experiment, predation intensity upon the remaining macrofauna might therefore be disproportionately low with gulls preferentially feeding upon large, available *Callianassa* rather than the customary macrofaunal species. Nevertheless, it is clear that massive disturbance of macrofauna does occur during bait-collecting and that gull predation accounts for a significant proportion of the disturbed animals.

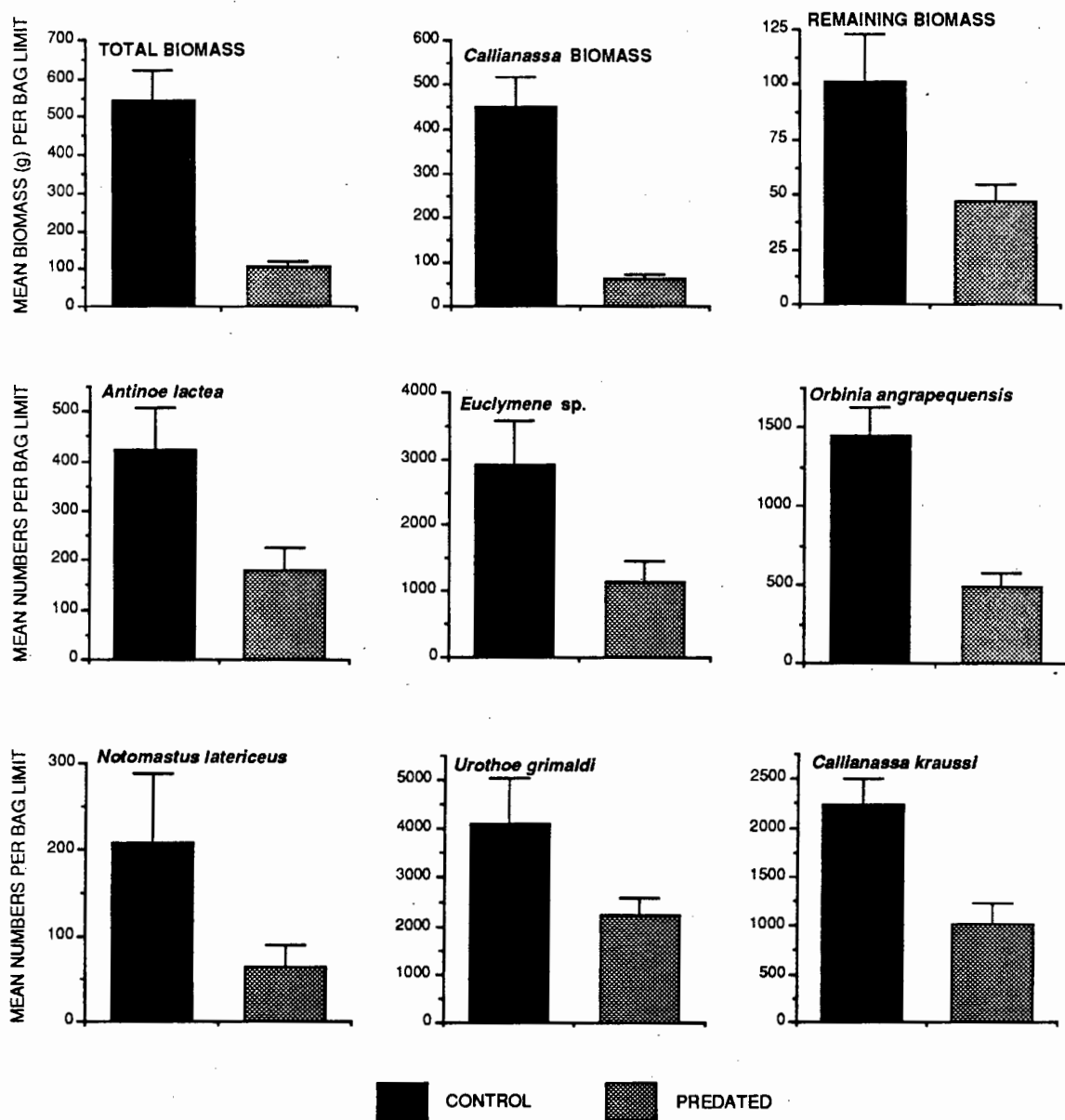


Figure 2.6. Nett disturbance and predation intensity on macrofauna during bait-collecting. Values are calculated per average collection (bag limit = 50 prawns). Data represent the mean values from 3 replicates (n=21). S.E. appear above the mean values.

Table 2.2. Disturbance and predation intensity on macrofauna disturbed during bait-collecting. Values are calculated per average collection (Bag limit = 50 prawns). n = 7 for each te.

SPECIES	MEAN DENSITIES											
	SITE 1			SITE 2			SITE 3			TOTAL		
	Con	Pred	P	Con	Pred	P	Con	Pred	P	Con	Pred	P
ACTINOPTERA:												
ACTINOPTERA: <i>Actinaria</i>												
ACTINOPTERA: <i>Anthus capensis</i> Carlg.	279	244	NS	105	87	NS	139	192	NS			
ACTINOPTERA: <i>Bivalvia</i>												
ACTINOPTERA: <i>Trilateria</i> Gn.	209	105	NS	366	174	*	17	70	**			
ANIMALIA: <i>Polychaeta</i>												
ANIMALIA: <i>Actinoptera</i>	366	87	**	476	157	**	505	296	**			
ANIMALIA: <i>Actinoptera</i> <i>lactea</i> Day	244	209	NS	227	331	NS	105	52	NS			
ANIMALIA: <i>Actinoptera</i> <i>tridactyla</i> Schm.	558	209	*	383	314	NS	471	314	NS			
ANIMALIA: <i>Actinoptera</i> sp.	1952	959	*	4932	1865	**	1882	610	*			
ANIMALIA: <i>Actinoptera</i> <i>angraperquensis</i> (Aug.)	1743	453	**	1481	680	**	1115	349	**			
ANIMALIA: <i>Actinoptera</i> <i>latericeus</i> Sars.	174	35	NS	279	17	NS	173	139	NS			
ANIMALIA: <i>Actinoptera</i> <i>squamata</i> (Müll)	924	1133	NS	192	227	-	17	17	-			
ANIMALIA: <i>Actinoptera</i> <i>johnstonei</i> Day	139	70	*	244	105	NS	488	70	NS			
ANIMALIA: <i>Amphipoda</i>												
ANIMALIA: <i>Amphipoda</i> <i>grimaldi</i> Chevr.	2789	2423	NS	6571	2039	**	3033	2266	*			
ANIMALIA: <i>Amphipoda</i> <i>brachyura</i>	157	279	NS	192	261	NS	157	35	**			
ANIMALIA: <i>Amphipoda</i> <i>orbiculare</i> Desm.	1760	784	**	2388	976	**	157	35	***			
ANIMALIA: <i>Amphipoda</i> <i>kraussi</i> Stebb.												
MEAN BIOMASS (g)												
total	362	68	**	519	169	**	743	96	**			
Amphipoda	287	38	**	414	87	***	640	69	**			
Other	100	33	NS	113	80	NS	91	29	*			

Legend: Con = control; Pred = Predated; P = Probability of significant difference between control and predated samples, with *, **, *** indicating significance at P<0.1, P<0.05 and P<0.005 respectively; NS = not significant; - = not enough data for statistical representation.

DISCUSSION

The impact of bait-collecting on *Callinassa* and *Upogebia*

The tendency for numbers of *Callinassa* and *Upogebia* to increase from the mouth towards the southern, upper end of Langebaan Lagoon (Figure 2.1) has been documented several times and is closely related to sediment textural characteristics and increased shelter (Day 1959; Christie & Moldan 1977). Therefore, the possibility that decreased *Callinassa* populations within the northern, non-reserve, areas are not related to bait-collecting activities cannot be discounted. Nevertheless, the sharp distinction between prawn densities in the physically similar southern conserved and northern non-conserved areas of the centre sandbanks (Figure 2.2) suggests that bait-collecting activities are having an effect.

Similarly, heavily pumped mainland areas such as Sepia Bay possess noticeably reduced prawn densities when compared to adjacent reserve areas. This is corroborated by perceptions amongst anglers and previous researchers who expressed concern over the decline in the numbers of prawns in the lagoon and their scarcity in areas such as Sepia Bay where they were previously abundant. The depletion of prawn stocks from the exploited mainland areas could have severe social implications since many of the local anglers are sustenance anglers who do not have access to boating facilities.

In other parts of the world, bait-collecting for various species has had a range of effects. In Australia, over-exploitation of *Callinassa australiensis* was earlier noted by Hailstone and Stephenson (1961) and was so severe that experimental sampling had to be discontinued. Jackson & James (1979) reported declines in cockle (*Cerastoderma edule*) densities in areas of heavy bait-digging and it has been intimated that lugworm (*Arenicola loveni*) populations in southern Africa have declined through bait-collecting (Gaigher 1979). However, on the North-East coast of England, densities of the lugworm *Arenicola marina* did not differ significantly between exploited and unexploited areas (Blake 1979a) or recovered in exploited sites within 3 months (McLusky *et al.* 1983).

There appears to be some indication that the sandprawn size-composition is being altered in Langebaan Lagoon by the selective removal of large individuals (Figure 2.3). Similar reductions in the numbers of large, 'bait-sized' individuals have been recorded for *U. africana* (Hill 1967). Concomitant increases of smaller individuals have also been shown for the common cockle (Jackson & James 1979). However, Blake (1979a) could not determine significant differences in size-frequency distributions between an exploited and an unexploited lugworm population.

It has been suggested that access to the sea (Forbes 1973a), in addition to decreased temperatures on the West coast (Hill 1967), play major roles in the size determination of thalassinids. Both inter- and intra-estuarine variations in size frequencies reemphasize the vast array of potential overriding factors which might be involved in determining growth rates (Hanekom & Erasmus 1988). The size-frequency data presented in this chapter should thus be regarded as preliminary; monthly measurements and the inclusion of juveniles would be prerequisites to conclusively determine any change in size-composition amongst exploited populations.

The results of the survey conducted amongst anglers suggest that the present restriction of 50 prawns per person per day is, in most cases, more than sufficient to supply their needs. Indeed, it appears that after a days fishing, a surplus of prawns is the norm. The only case where the present restrictions are perceived to be too restrictive is during angling competitions.

Bait preferences vary amongst anglers depending on their individual priorities. By virtue of its colour and flaccidity, *Callianassa* makes a good bait which is extremely visible and easy for fish to bite. Nevertheless, most anglers who have used *Upogebia* prefer it to *Callianassa* because of its durability, sturdiness and subsequent longevity on and off the hook. The scarcity of *Upogebia* in unprotected areas is the factor which restricts its utilisation in Langebaan Lagoon.

The indirect effects of bait-collecting

The present study presents clear evidence that massive numbers of macrofaunal organisms are being disturbed in the process of bait-collecting (Figure 2.6; Table 2.2). In addition, there is clearly a predatory 'scavenging effect' by gulls on the residues left by bait-collectors. Previous work has suggested that this is a fairly common phenomena within areas of heavy bait-collecting (Peterson 1977; Blake 1979a) although its intensity obviously varies depending on the structure, size and appeal of the organisms being disturbed and the nature of the predators present (Jackson & James 1979). Logic dictates that large, soft-bodied, organisms such as *Callianassa* would provide easier meals than small, sedentary molluscs and the present results are not surprising in this light.

Although predation obviously plays a large role in the eradication of disturbed organisms, the damage inflicted by the bait-collectors is not limited to the isolated cores deposited from the prawn pump. Excavation down to a potential depth of 80 cm must cause enormous sedimentary instability and in all likelihood results in the burial and consequent suffocation of trapped organisms. Peterson (1976), for example, reported the

depletion of *Cryptomya californica*, a commensal bivalve living in the burrows of *Callianassa californiensis*, through suffocation during *Callianassa* harvesting.

Mechanical damage from the prawn pump is a third factor which may affect disturbed organisms. Large, thin-shelled organisms such as *Tellina trilatera* could be particularly vulnerable to this type of damage.

Conclusions

The average annual proportion of sandprawns removed by bait-collectors at Langebaan Lagoon is 2.5-4.9% of the total prawn population on the entire centre bank and 4.3-8.6% on the legally exploited portion of the centre bank. This is not particularly high when compared to other fisheries. There are records of approximately 80-90% of bloodworms (*Glycera dibranchiata*) (Klawe & Dickie 1957), 23% of ragworms (*Nereis virens*) (Blake 1979b) and 7.8% of lugworms (*Arenicola marina*) (Blake 1979a) being removed annually by bait-collectors. Nevertheless, the secondary effects of prawn harvesting such as gull predation, disturbance of the sandflat fauna and removal of the primary food source for many fish and birds (Martin 1988) could have serious implications for future harvesting and sedimentary stability. In addition, there is some evidence that prawn pumping reduces the density of the common eelgrass *Zostera capensis* (unpubl. data). As *Zostera* hosts an enormous number of epiphytic organisms which may be uniquely associated with the eelgrass (Thayer & Phillips 1977; Fitzhardinge 1983), its depletion could have several indirect effects.

While this chapter has concentrated exclusively on the depletion of prawns and the short-term disturbance of macrofauna, it should be stressed that the disturbance of meiofauna, bacteria and microalgae may be equally important. In addition, the long-term recovery of disturbed systems needs to be understood. These aspects are developed in Chapters 3 and 4.

CHAPTER 3

The Long-Term Effects of High-Intensity Disturbance on the Biota of an Intertidal Sandflat

INTRODUCTION

Disturbance has been implicated frequently as a major force structuring marine soft-bottom communities and has been extensively reviewed (e.g. Connell & Slayter 1977; Whittaker & Levin 1977; Paine & Levin 1981; Thistle 1981; Woodin 1981; VanBlaricom 1982; Dayton 1984; Probert 1984; Sousa 1984; Picket & White 1985). In soft-sediment environments, disturbance may result either from physical causes (see review by Probert 1984), biological processes (VanBlaricom 1982; Reise 1983; Thrush 1988) or human activities (Blake 1979a,b; Conner & Simon 1979; Jackson & James 1979; McLusky *et al.* 1983; Bonvicini *et al.* 1985; Hruby 1987).

The resilience of a system has been defined as "the degree, manner and pace of restoration of initial structure and function in an ecosystem after a disturbance" (Westman 1978). In most communities, resilience will play a major role, together with the magnitude, frequency and predictability of the disturbance, in determining the response to a perturbation (Sanders *et al.* 1980; Sherman & Coull 1980; Thistle 1980,1981; Boesch & Rosenberg 1981; Woodin 1981; VanBlaricom 1982).

Although few in number, most studies that address the question imply that systems which have been exploited for bait are highly resilient (Blake 1979a; Conner & Simon 1979; Jackson & James 1979; McLusky *et al.* 1983; Hruby 1987). Although the extensive utilisation of *Callinassa* and *Upogebia* (Thalassinidae) species for bait has frequently been addressed (Hailstone & Stephenson 1961; Hill 1967; Forbes 1973a; Hanekom 1980; Baird 1988), only Peterson (1977) tested the effects of removing *Callinassa californiensis* through field manipulations. In addition to following patterns of recovery amongst experimentally harvested populations of the common southern African prawns *Callinassa kraussi* and *Upogebia africana*, the present study incorporates repercussions upon the sediment and associated macrofaunal, meiofaunal, microbial and microalgal communities following removal of the prawns.

The pivotal role which thalassinids play in the functioning of systems in which they are dominant aptly qualifies them as "foundation species" as described by Paine (1969, 1980) and Virnstein (1977), i.e. species which are much more important than others in their ability to control and structure the community.

Extreme bioturbators such as *Callinassa* and *Upogebia* have more specifically been referred to as "promoter" species (*sensu* Reise 1985) because of their capacity to enhance components of an ecosystem through sediment turnover and consequent oxygenation and nutrient exchange with the overlying water column (Dye & Furstenberg

1978; Rhoads & Boyer 1982; Tamaki 1984; Hines & Jones 1985; Flint & Kalke 1986). It was thus predicted that reduced oxygen conditions would result within the sediment from which *C. kraussi* and *U. africana* had been removed and that this would lead to a concatenation of events.

Suchanek (1985) hypothesized that morphological variation in thalassinid burrows could be classified into three major trophic groups. Although this classification is perhaps too simplistic (Griffis & Chavez 1988; Scott *et al.* 1988), *C. kraussi* conforms to one of Suchanek's groups, i.e. that group of detritivore-deposit feeders which typically constructs temporary, deep, architecturally complex burrow systems and continuously processes vast amounts of sediment to extract organic material (Forbes 1973a; Branch & Pringle 1987). *U. africana* on the other hand, belongs to the filter-feeding group which typically builds simple U-shaped burrows through which water is pumped and particles subsequently filtered (Hill 1967; Schaefer 1970).

Rates of sediment reworking for *C. kraussi* have been estimate at $12.14\text{kg.m}^{-2}\text{.day}^{-1}$ (Branch & Pringle 1987), a considerably higher figure than that reported for other *Callianassa* species (Aller & Dodge 1974; Ott *et al.* 1976; Roberts *et al.*, 1981; Suchanek 1983; Riddle 1988). This, together with previous studies showing the ability of callianassids to rapidly return disturbed sediments to pre-disturbance conditions (Riddle 1988) directed the hypothesis that disturbances generated from bait-collecting would have a short-lived effect on *C. kraussi*, with the sandprawns quickly reestablishing themselves in treated areas.

Although there has been no conclusive work conducted on the bioturbating effects of *U. africana*, logic dictates that sediment processing by it will be minimal, and associated effects, if present, considerably reduced over those of *C. kraussi*. Moreover, as the burrows of *U. africana* function as dwelling-burrows, they probably represent more permanent structures than the feeding-burrows of *C. kraussi* (Ott *et al.* 1976; Dworschak 1983; Tunberg 1986). In this regard, the adverse effects of bait-collecting upon *U. africana* were expected to be both more exaggerated and longer-lived than those affecting *C. kraussi*.

The ability of callianassids to influence grain size is well known (e.g. Suchanek *et al.* 1986). Fine grained particles are pumped to the surface (Suchanek 1983) and only the coarser particles ($> ca. 1\text{ mm}$) enter the 'permanent deposits' of sub-surface galleries (Tudhope & Scoffin 1984). The fine-grained processed material either accumulates as mounds or, in the presence of tidal and wind-driven water movements such as those existing at Langebaan Lagoon, is smoothed to surface levels (Suchanek *et al.* 1986).

Callianassa bioturbation thus produces a better-sorted, virtually gravel-free upper layer (Tudhope & Scoffin 1984). Although it is difficult to predict changes in mean particle size in the absence of *C. kraussi*, a decrease in the sorting coefficient was expected within areas in which *C. kraussi* had been removed.

In contrast to *C. kraussi* bioturbation, *U. africana* does not appear to greatly modify the nature of sediment grain sizes and its burrow entrances are always flush with the sediment surface (Hill 1967). Any sediment changes that might occur probably involve the selective processing of fine particles through its filtering apparatus (Schaefer 1970). Changes in sediment composition with the removal of *U. africana* were therefore foreseen to be negligible.

The bioturbation of sediment implies that benthic microalgae are continually being turned over and effectively buried. Consequently, it stands to reason that diatoms in the presence of *C. kraussi* are commonly found at depths of up to 40 cm (Fielding *et al.* 1988), whereas in the absence of *C. kraussi* they accumulate on the surface (Branch & Pringle 1987). It was therefore hypothesized that the removal of *C. kraussi* through bait-collecting would increase the chlorophyll on the surface, whereas the removal of the more inert *U. africana* would have no effect on surface chlorophylls.

The hypothesis that bacterial growth rates in highly bioturbated sediment should be enhanced over those in sediments with low rates of biogenic reworking was formulated by Yingst & Rhoads in 1980. They and other workers (Aller & Yingst 1978; Koike & Mukai 1983) have shown that the oxidation and consequent nutrient enriching of subsurface deposits by bioturbators attracts and enhances the growth of microbial and meiofaunal communities. Previous work has shown both *C. kraussi* and *C. japonica* to have a profound influence on the distribution and abundance of bacteria, raising both the overall numbers and, more specifically, the numbers in the immediate vicinity of the burrow (Branch & Pringle 1987; Tamaki 1988). Aller *et al.* (1983) have similarly shown burrows of *Upogebia affinis* to be sites of intense nitrification and denitrification which are associated with high bacterial numbers. Based on this knowledge, the microbial populations in the disturbed sites were expected to diminish with the removal of either *C. kraussi* or *U. africana*.

Previous investigations have shown callianassids to depress meiofaunal numbers (McIntyre 1969; Alongi 1986; Branch & Pringle 1987) and it was accordingly postulated that meiofaunal numbers would increase with the removal of *C. kraussi*. As *U. africana* has a less intrusive lifestyle, the premise was formed that meiofaunal numbers in harvested areas should remain unaffected or, alternatively, decrease if they are highly

associated with the burrow structure (*sensu* Reise 1981a).

Several researchers have experimentally demonstrated the negative effect which mobile burrowers have on sedentary organisms (Brenchley 1981,1982; Wilson 1981; Suchanek 1983; Murphy 1985; Posey 1986). Experimental removals of *C. californiensis* have resulted in higher survivorship and recruitment of a more sedentary bivalve (Peterson 1977). Conversely, bioturbation may have potential promoting effects, including the enhancement of colonisation by infaunal species (Flint & Kalke 1986). The complexity of these patterns and the interdependence between the above-mentioned components of the sandflat made it difficult to confidently formulate any concise, plausible hypotheses regarding the effects of the removal of *C. kraussi* and *U. africana* upon the macrofaunal community. In general, however, it was thought that the physical disturbance involved would initially decrease the macrofaunal biomass, numbers and richness. Previous disturbance studies have suggested rapid recolonisation of the macrofauna (Bell & Devlin 1983; Frid 1989) but this would obviously be dependent on the magnitude of the disturbance and the colonising ability of the disturbed organisms.

METHODS

Experimental design

Two sites, Klein Oesterwal and Geelbek, dominated respectively by *C. kraussi* and *U. africana* were selected within Langebaan Lagoon (see Chapter 1 - Figure 2.1). The homogeneity of the prawn populations was ascertained prior to the experiment by counting prawn holes within areas designated for the experiments (Figures 3.1,3.8). No initial macrofaunal, bacterial or meiofaunal samples were taken from the experimental areas because the methods involved are destructive and would have created additional disturbances in the plots, especially from trampling. However, previous sampling in the immediate vicinity of selected areas had shown the macrofaunal, meiofaunal and bacterial communities to be homogeneous ($P > 0.05$). Experimental removal of *C. kraussi* and *U. africana* was accomplished during April 1988, when areas of 3 m X 4 m, approximately 10 m apart, were either exhaustively dug-over with a spade to a depth of 30 cm, or sucked-over repeatedly with a prawn pump, all prawns revealed by either treatment being simultaneously removed. Ropes attached to four wooden stakes were placed around each of the experimental areas which are hereafter referred to as the 'dug' and 'sucked' sites. The surrounding, untouched areas functioned as controls. The nature of the sampling negated re-use of fixed control sites and virgin control areas were

sampled each time. Controls were taken from random, undisturbed areas at the same tidal level and within a few metres of the experimental sites.

Methodological inadequacies related to pseudoreplication (Hurlbert 1984; Stewart-Oaten & Murdoch 1986) are contained within this experimental design. These arose because large experimental areas were essential to prevent prawns from simply immigrating from adjacent areas into the experimental plots. The labour-intensive nature of the treatments prevented erection of multiple experimental sites (establishment of each site taking 120 human-hours). This logistic difficulty did not apply to the control sites which were accordingly independently replicated and taken from separate areas each time. Confirmation of the homogeneity of the experimental and control areas prior to initiation of the treatments does offset some of the statistical difficulties attending the pseudoreplication. Moreover, the treated areas were large enough to permit several small replicates. Further confidence in the results is provided by species responses, with identical species from different experimental areas responding similarly to the disturbance and showing equivalent differences from the control.

POST-DISTURBANCE SAMPLING

Samples were collected 1, 2, 3, 18, 44, 72, 149, 296 and 606 days after the disturbance (referred to in some figures and tables as 1 day, 2 days, 3 days, 18 days, 1 month, 2 months, 4 months, 9 months and 18 months respectively) over the period 1 April 1988 - 22 November 1989.

Prawn densities

Prawn holes were initially counted in four 0.5 m² areas which were subsequently dug to a depth of 1 m and all prawns removed. This procedure yielded a ratio of 1.05 holes per adult *C. kraussi*, conforming to the 1:1 ratio previously described by Forbes (1973a) for areas with sheltered conditions and constant salinity. Estimates of population densities were thus determined from *C. kraussi* hole counts. *U. africana* constructs a typical U-shaped burrow consisting of two holes which usually contain only one animal and hole counts were halved to estimate population densities (Hill 1967).

Prawn densities were thus non-destructively assessed by counting burrow holes in 25 random 0.1m² quadrats within each experimental and control area.

Microflora

Four subsamples of the sediment of approximately 5 g each, were collected from the surface, placed in aluminium foil and stored at 0°C in the dark for a maximum of two weeks. As the amount of sediment collected varied, it was wet-weighted before being placed in stainless-steel cylinders with approximately 10 ml of 90% acetone and a small pinch of MgCO₃. The sediment was then ground for three minutes inside the cylinders and placed at 4°C for 24-48 hours to extract the chlorophyll. The samples were then centrifuged until clear and the total chlorophyll determined by measuring optical density (OD) at 750, 664, 647 and 630 nm in a spectrophotometer. Data are expressed in µg chlorophyll.g dry sediment⁻¹ derived from the equations of Jeffrey & Humphrey (1975):

$$\text{chl a} = 11.85 (\text{OD}_{664}) - 1.54 (\text{OD}_{647}) - 0.08 (\text{OD}_{630})$$

$$\text{chl b} = 21.03 (\text{OD}_{647}) - 5.43 (\text{OD}_{664}) - 2.66 (\text{OD}_{630})$$

$$\text{chl c} = 24.52 (\text{OD}_{630}) - 1.67 (\text{OD}_{664}) - 7.60 (\text{OD}_{647})$$

$$\text{Total chl} = \text{chl a} + \text{chl b} + \text{chl c}$$

Sediment

Three 85 ml cores of sediment were taken between 0-5 cm at each of the experimental and control sites. Animals and pieces of vegetation were carefully removed before wet sieving the sediment to remove the silt and clay fraction (<63 µm). The remaining coarse fraction was oven-dried at 60°C, weighed and sieved using a mechanical shaker through a series of sieves graded at 0.5ϕ intervals. The silt and clay fraction was allowed to settle until the supernatant was clear. The supernatant was then decanted and the remaining sediment oven-dried at 60°C, weighed and then ashed in a muffle furnace at 480°C. Fractions were expressed as percentages of total dry mass. Particle size was plotted in cumulative percentages, using the phi-scale. Percentiles were read from each curve to calculate median particle size (Mdϕ), phi quartile deviation (QDϕ) and phi quartile skewness (Skqϕ) (Morgans 1956).

Soon after the disturbance, it became apparent that the treated sediment was notably anoxic. As reduced layers are stained black by the occurrence of FeS, the redox potential discontinuity (RPD) layers were easily recognised by the abrupt change in the colour of the sediment layers from the oxidized brown to black. The depth of this layer was measured periodically at Klein Oesterwal and the Eh-values recorded at both sites 18 months post-disturbance using a standard redox electrode at 5 cm depth.

The penetrability of the sediment was measured in the experimental and control areas immediately following the disturbance by dropping a penetrometer from a height

of 1 m and recording the depth to which it penetrated the sediment. The penetrometer consisted of a 1-m rod, 2 mm in diameter, with a lead weight of 50 g attached one-third up from its lower end.

Bacteria

Three 1-5 g subsamples of sediment were taken at depths of 10 and 30 cm, suspended in sterile sea water and preserved with 2% formalin. Numbers of bacteria were determined by epifluorescence microscopy after staining with Acridine Orange. Counts were made of 10 microscopic fields for each determination. Details of the technique are outlined in Mazure & Branch (1979).

Meiofauna

Four 85 ml cores of sediment were obtained between 0-5 cm depth 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). This seemingly crude method is as efficient as the more sophisticated meiofaunal separators and results in approximately 99% extraction of soft-bodied organisms (J. Stenton Dozey, pers. comm.). The disadvantage of this method is that hard bodied organisms (e.g. gastropods and bivalves) are not suspended and tend to be overlooked. However, the relative scarcity of this meiofaunal component in intertidal sandflats justified their omission. As the volume of sediment collected varied, the sieved sediment was oven-dried for three days and then weighed. Meiofauna were stained with Rose Bengal and preserved in phenoxotal until counted. Three replicates were taken from each subsample, and the meiofauna divided into the following groups: nematodes, adult copepods, copepod nauplii, polychaetes, turbellarians, kinorhynchans (at Geelbek) and 'other' (which included ostracods and the occasional organisms which did not fall into the above categories). As the meiofauna was preserved in unbuffered formalin, foraminiferans were largely unidentifiable (Gibbons 1988) and therefore excluded. Moreover, previous work has revealed that non-living foraminiferans stained with Rose Bengal are indistinguishable from living forams (Sherman & Coull 1980). The term 'meiofauna' is taken to include not only species which will remain within the category throughout their whole life-span, but also juveniles of larger forms, which must sooner or later outgrow the meiofaunal size limits.

Macrofauna

Three 0.1 m² samples, dug to a depth of 10 cm, were obtained for all treatment and control sites. 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, following identification to species level using the nomenclature of Day (1967; 1981b), Griffiths (1976), Kensley (1972) and Kilburn & Rippey (1981), dried and ashed. The nocturnal behaviour of the common hermit crab, *Diogenes brevis* Stimps., and its profusion in the dug and sucked-over areas at Klein Oesterwal following disturbance, necessitated independent night counts. Total counts of the crabs were made within each experimental site and in adjacent control areas during the evening low tide.

Data analysis

Differences between control and treatment groups were assessed using a one-way analysis of variance (ANOVA). Bartlett's test, as described in Zar (1984), was the method employed to test for homogeneity of variances. Heteroscedastic data were either transformed and then evaluated using ANOVA, or the nonparametric Kruskal-Wallis test procedure was applied (Zar 1984). The absence of some species from a sampling location on certain dates (resulting in zero variances for that cell) was not considered to be a major problem since recalculation of the ANOVA substituting small artificial variances in these cases did not yield noticeably different results. The Tukeys HSD test (Tukey 1953 in Zar 1984) was employed for multiple comparisons when analysing differences between samples. 'Contrast' (Wilkinson 1987), a statistical technique which utilises several types of comparative tests, was used in cases where large standard deviations and small sample sizes occurred (e.g. patchy meiofauna). Although this statistical technique is less stringent than Tukeys, it can be used confidently to confirm trends (L. McNeill, pers. comm.). Significant differences detected between samples by 'Contrast', but which were not recorded by the ANOVA, can be accounted for by the tendency for ANOVA to average the differences being tested. All statistical analyses were conducted using SYSTAT software.

RESULTS

KLEIN OESTERWAL

Effects on *C. kraussi*

The baseline pre-disturbance study showed that the sandprawn populations (O day) were homogeneous between the experimental and control sites ($P > 0.05$) (Figure 3.1; ANOVA analyses in Table 3.1). In the dug-over plot, 244 prawns were removed, representing 6.7% of the numbers estimated from pre-disturbance hole-counts. In the sucked-over area, 478 prawns were removed, 13.1% of original numbers. 1 day after the disturbance, hole-counts of *C. kraussi* inside the experimental areas had been reduced sharply, and remained at reduced levels for the 18 months of the experiment (Figure 3.1). Although the only statistically discernable difference between the two types of treatments (dug and sucked) was at 18 months, the sucked-over areas showed consistently lower prawn densities than those of the dug-over areas. After 18 months, the dug-over sites had begun to approach control levels ($P > 0.05$) whilst the sucked-over sites were still reduced ($P < 0.005$) (Table 3.1; Figure 3.1).

Table 3.1. Effect of disturbance on *Callinassa kraussi*. ANOVA comparisons of control, dug and sucked-over areas. 0d indicates a comparison of prawn densities (holes m^{-2}) between experimental and control areas before the treatment.

TIME	0d ^a	1d ^a	18d	1m	2m ^b	4m	9m	18m ^b
F	0.24	169.36	94.24	52.65	67.57	195.04	111.98	17.42
DF	2,57	2,57	2,57	2,57	2,57	2,57	2,57	2,57
P	0.784	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

d=days, m=months. a denotes $\sqrt{x+0.5}$ transformation; b denotes $\log(x+1)$ transformation

Effects on the sediment

Table 3.2 summarises the results of the sediment analysis. $Md\phi$ indicates the mean particle size of the sediment cores. $QD\phi$ indicates the degree of sorting of a sediment, i.e. the proportion of particles with a similar size to $Md\phi$. $Skq\phi$ indicates which fraction, coarse or fine, is better sorted (Newell 1970). $Md\phi$ values were consistently larger (i.e. finer) in the disturbed sediment than in the control. Both $QD\phi$

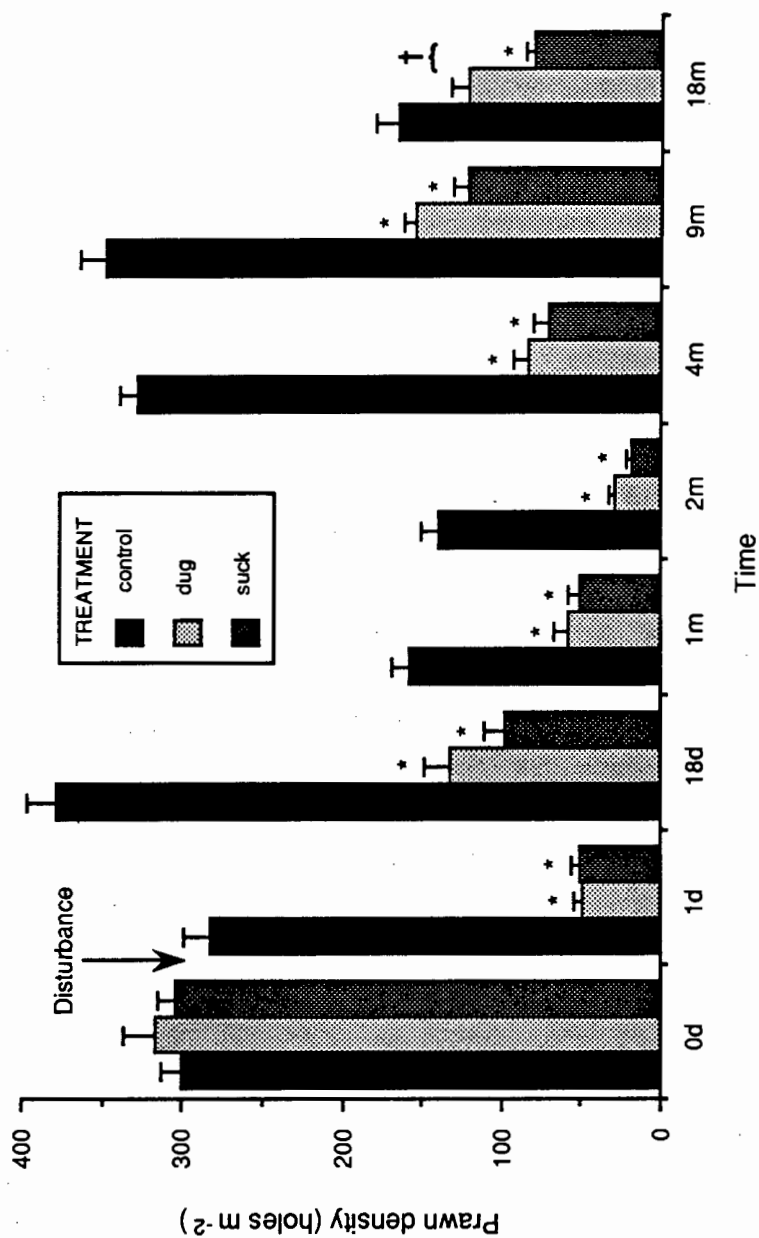


Figure 3.1. Number of *Callinassa kraussii* holes (m^{-2}) in control, dug and sucked-over areas, in relation to time after disturbance. S.E. appear above the mean values. d = days, m = months. 0d shows prawn densities in experimental and control areas before disturbance. * indicates a significant difference between control and treatment at $P < 0.0001$. † indicates a significant difference between dug and sucked treatments at $P < 0.05$. Tukeys is the multiple comparison procedure utilised.

and $Skq\phi$ declined noticeably in the disturbed areas. This indicates that the treatment sediment was less well sorted than the control sediment. Negative values were obtained for all $Skq\phi$, indicating that the fine particles are better sorted than the coarse particles at Klein Oesterwal. This effect was exaggerated in experimental areas by the disturbance administered. The organic fraction of the sediment appeared to be discernably lower in the experimental areas 18 days after the treatment. This trend had apparently reversed itself by the first month, with organic and mud components generally remaining higher than control levels in the treatment areas up until 4 months.

Table 3.2. Table showing the median particle diameter, phi quartile deviation, phi quartile skewness, percentage organics and percentage mud of control and treatment samples after disturbance of *Callianassa kraussi*. d=days, m=months.

TIME	18d	1m	2m	4m
MDϕ				
CONTROL	2.590	2.495	2.715	2.725
DUG	2.790	2.805	2.880	2.815
SUCK	2.745	2.830	2.880	2.820
QDϕ				
CONTROL	0.725	1.008	0.708	0.723
DUG	0.620	0.748	0.608	0.620
SUCK	0.683	0.653	0.515	0.583
Skqϕ				
CONTROL	-0.530	-0.005	-0.675	-0.775
DUG	-0.680	-0.905	-0.775	-0.690
SUCK	-0.555	-0.835	-0.780	-0.655
% Organics				
CONTROL	0.250	0.150	0.160	0.195
DUG	0.205	0.190	0.175	0.150
SUCK	0.180	0.175	0.215	0.200
% Mud				
CONTROL	4.200	7.100	2.355	2.270
DUG	6.380	6.030	3.515	3.555
SUCK	2.885	4.525	3.765	3.270

A marked feature of the experimental areas was that the sediment deflated, the surface becoming depressed about 10 cm below that of the surrounding areas. Penetrability decreased markedly after removal of the prawns, declining from a control value of 119 (± 32.4) mm to 83.9 (± 33.7) mm in the dug-over area, and 76.8 (± 11.9) mm in the sucked-over area.

In the disturbed areas, a black sulphide layer occurred at depths below 3.4 cm. Grey-coloured areas, an indicator of slightly reduced conditions, existed in-between the oxidized, surface layers and the completely reduced, black, deeper layers. The sediment in the control areas was a uniform light colour underlain at varying depths from 50-60 cm by a black sulphide layer. The depth of the oxidized layer in the disturbed sites increased steadily with time, but black, poorly oxygenated sediment remained visible in deeper sections of the cores up until 18 months. Thereafter, an Eh-value approximating 0 mV was recorded for all treatment and control areas when readings were taken at 5 cm.

Effects on the microflora

Chlorophyll levels did not display any obvious changes ($P > 0.05$) until 1 month after the disturbance (Figure 3.2). Thereafter, a one-way ANOVA revealed significant increases in chlorophyll levels in the dug, and particularly in the sucked-over sediment ($F = 32.633$, $P < < 0.001$, d.f. = 2,9; $F = 19.445$, $P < 0.001$, d.f. = 2,8 for 1 month and 2 months after treatment respectively). There was a clear reversion to control chlorophyll levels within the experimental areas 4 months subsequent to the initial disturbance ($P > 0.05$).

Effects on the bacteria

Total bacterial numbers in the treatment areas appeared reduced for up to 1 month following the disturbance (Figure 3.3). However, no significant differences existed between the experimental and control areas ($P > 0.05$) at either surface or depth measurements. A more detailed analysis of the composition of the bacteria revealed significant differences (ANOVA, $F = 5.642$, $P = 0.042$, d.f. = 2,6) 18 days after the disturbance between the rods of the treatment and control areas at 30cm depth (Table 3.3). This reduction was not long-lived and the numbers of rods and cocci within experimental areas had apparently normalised within 2 months of the disturbance (Table 3.3). There were no clear differences between the two types of treatment administered. Substantial variability existed even at the control sites.

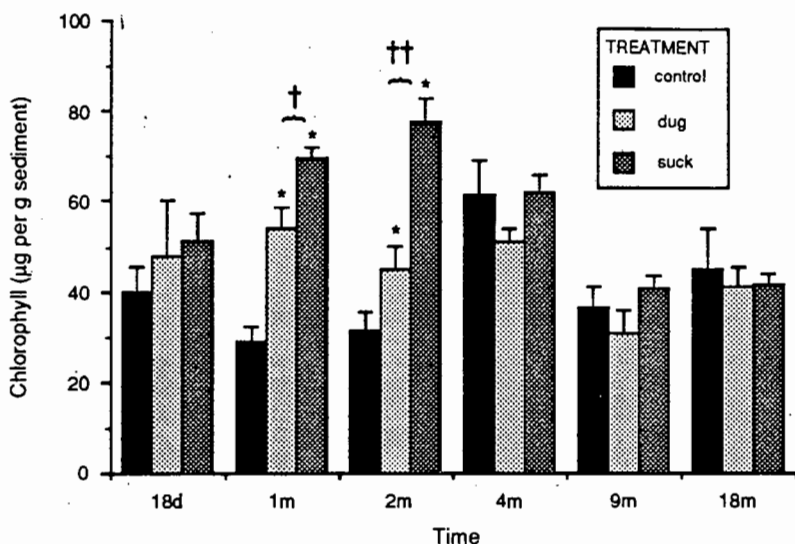


Figure 3.2. Chlorophyll levels in control and treatment areas, in relation to time after disturbance of *Callianassa kraussi*. d=days, m=months. S.E. appear above the mean values. * indicates a significant difference between control and treatment at $P < 0.001$. †, †† indicate a significant difference between dug and sucked treatments at $P < 0.05$ and $P < 0.005$ respectively. Tukeys is the multiple comparison procedure utilised.

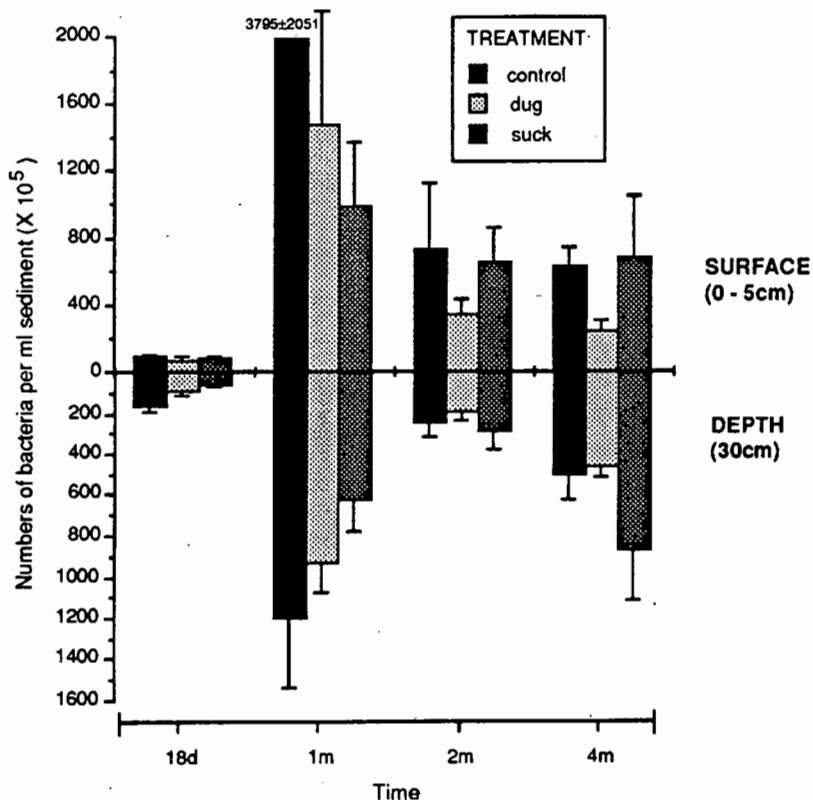


Figure 3.3. Bacterial numbers in control, dug and sucked-over areas in relation to time after disturbance of *Callianassa kraussi*. S.E. appear above mean values. d=days, m=months.

Table 3.3. Bacterial numbers in relation to time after disturbance of *Callianassa kraussi* in control, dug and sucked-over areas. ** indicates a significant difference between control and treatment at $P < 0.05$. d=days, m=months.

Type	Treatment	No. of bacteria per ml sediment ($\times 10^5$)			
		18d	1m	2m	4m
Cocci	<i>Surface</i>				
	Control	33.72	1890.20	365.98	293.45
	Dug	24.01	642.84	110.92	314.22
	Suck	37.11	455.97	326.70	273.75
	<i>Depth</i>				
	Control	69.72	555.28	107.78	189.52
Dug	45.02	406.78	91.23	149.44	
Suck	32.66	350.77	117.92	202.37	
Rods	<i>Surface</i>				
	Control	52.29	1616.60	285.09	250.77
	Dug	37.14	747.03	173.60	207.98
	Suck	27.10	446.79	256.83	302.50
	<i>Depth</i>				
	Control	81.80	548.63	112.88	212.81
Dug	39.48**	465.15	90.79	128.04	
Suck	18.18**	226.50	135.80	132.83	
Other	<i>Surface</i>				
	Control	98.48	289.43	83.28	88.70
	Dug	60.79	82.24	57.43	139.78
	Suck	10.27	80.89	170.30	99.38
	<i>Depth</i>				
	Control	89.04	90.14	21.48	46.15
Dug	73.20	58.52	15.14	43.73	
Suck	5.77	48.83	31.60	59.03	

Effects on the meiofauna

Meiofaunal numbers for each treatment, expressed as a percentage of the control, are displayed in Figures 3.4 a,b,c,d and the corresponding statistics in Tables 3.4 a,b,c,d. This expression was used in order to overcome logistical problems in plotting highly variable, seasonal data, and to illustrate recolonisation patterns within the disturbed areas. Meiofaunal numbers were dominated by nematodes and periodically by copepods. Adult and nauplii copepods displayed similar trends throughout and were accordingly grouped together, nauplii numbers being approximately double those of the adults.

Similar trends were exhibited amongst different groups. An initial depression within the disturbed areas was followed by a peak in the second month (week 8), surpassing control numbers. Thereafter, nematode and copepod numbers in the experimental areas were depressed, but subsequently slowly increased, approximating control levels by the eighteenth month (week 72) (Figures 3.4a,b; Tables 3.4a,b). A similar initial depression was observed for the polychaetes, but this decline was perpetuated for the duration of the experiment (Figure 3.4c) although none of the differences were significant after the eighth week due to high variability (Table 3.3c). Turbellarians responded extremely positively to the disturbance, attaining levels of up to 1100% of the control within 8 weeks of the disturbance but decreasing to control levels by week 36 (Figure 3.4d; Table 3.4d).

Nematodes were abundant in all seasons, showing a minimum in winter months whereas copepods showed marked seasonal variation, developing explosively in May and June. Despite seasonality, the trends observed were consistent from month to month.

Effects on the macrofauna

Biomass: Figure 3.5 presents the ash-free total biomass, with and without the swamping effect of the dominant hermit crab, *D. brevis*. The inclusion of *D. brevis* increased the treatment biomass by up to 7000% compared to a maximum increase of 100% exhibited by the control. Significant differences were recorded between control and treatments for the total biomass up until the fourth month (Table 3.5). Contrary trends emerged if *D. brevis* was excluded from consideration - treatment values were then significantly reduced below control levels and remained depressed for 9 months following the disturbance (Table 3.5). Although biomass values were consistently lower in the dug-over areas than in the sucked-over areas, this was not statistically discernable for all cases.

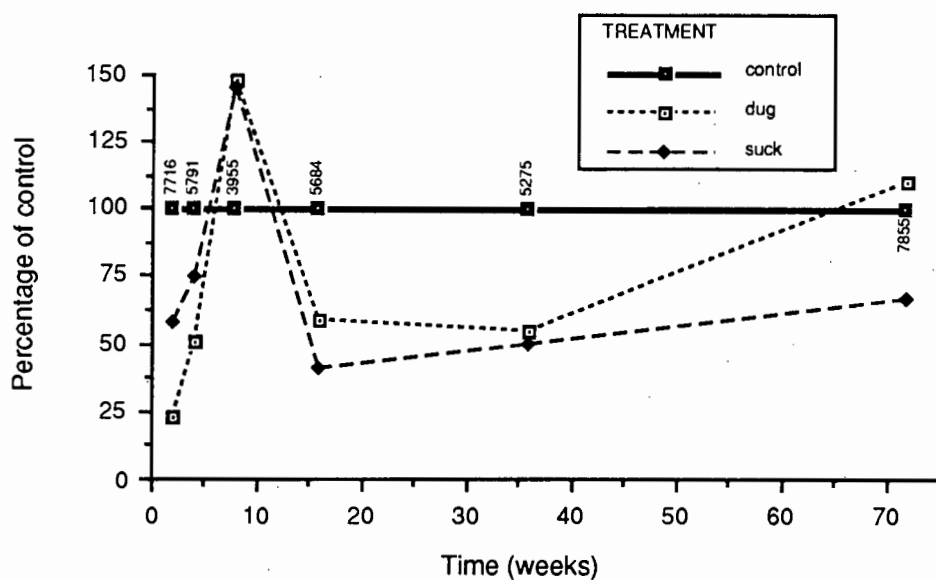


Figure 3.4a. Nematode response in relation to time after disturbance of *Callianassa kraussi*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.4a. Nematode response in relation to time after disturbance of *Callianassa kraussi*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck.

TIME	2 wk	4 wk	8 wk	16 wk	36 wk	72 wk
<u>ANOVA</u>						
F	10.185	4.055	0.754	4.693	2.844	7.824
DF	2,5	2,6	2,5	2,5	2,5	2,9
P	**	*	NS	*	NS	**
<u>CONTRAST</u>	A**, B**	A**	NS	A**	A*	B***

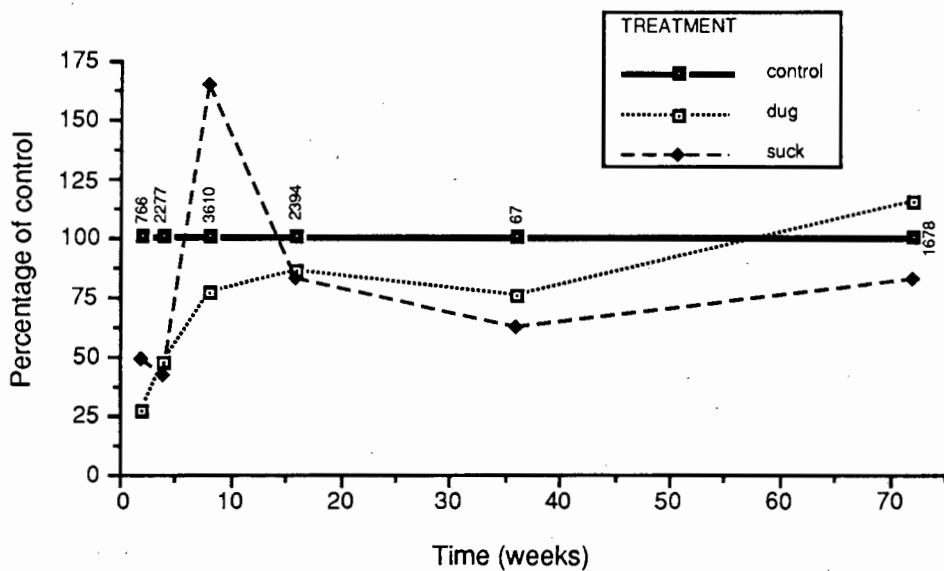


Figure 3.4b. Copepod response in relation to time after disturbance of *Callianassa kraussi*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.4b. Copepod response in relation to time after disturbance of *Callianassa kraussi*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a $\log(x+1)$ transformation.

TIME	2 wk	4 wk	8 wk ^a	16 wk	36 wk	72 wk
<u>ANOVA</u>						
F	4.330	5.235	34.259	0.690	0.223	0.489
DF	2,5	2,5	2,5	2,5	2,5	2,9
P	*	**	***	NS	NS	NS
<u>CONTRAST</u>	A**	A**	B***	NS	NS	NS

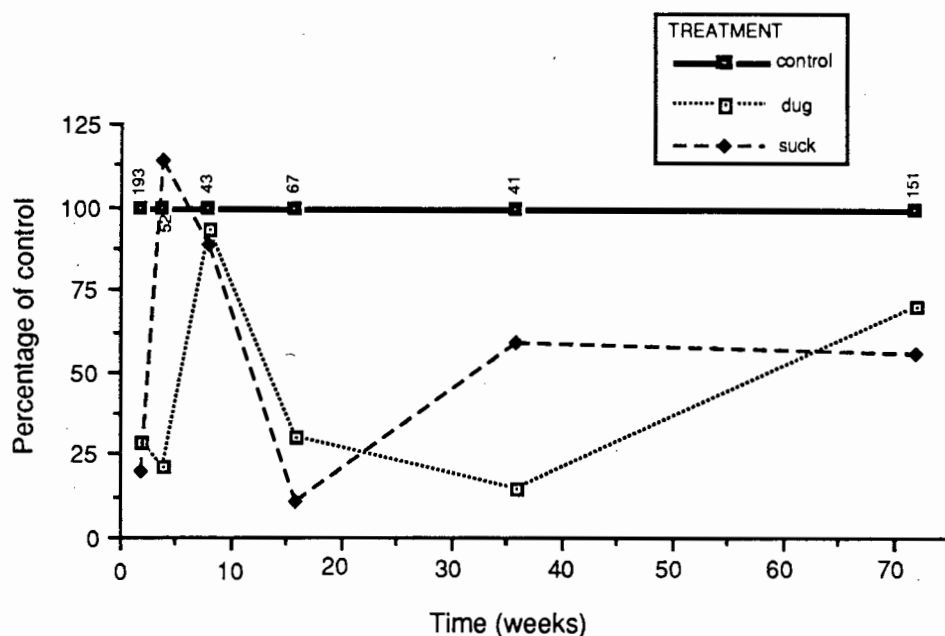


Figure 3.4c. Polychaete response in relation to time after disturbance of *Callianassa kraussi*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.4c. Polychaete response in relation to time after disturbance of *Callianassa kraussi*. ANOVA table: *** represents significance at $P < 0.005$, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a log (x+1) transformation.

TIME	2 wk	4 wk ^a	8 wk	16 wk ^a	36 wk	72 wk
ANOVA						
F	9.219	13.267	0.028	1.794	0.583	0.962
DF	2,5	2,6	2,5	2,5	2,5	2,9
P	***	***	NS	NS	NS	NS
CONTRAST	A***	A***, B***	NS	NS	NS	NS

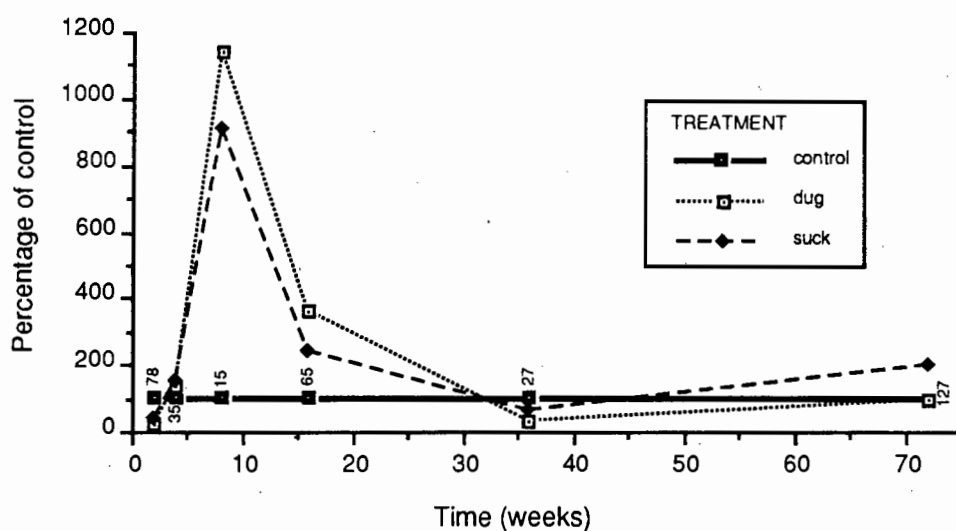


Figure 3.4d. Turbellarian response in relation to time after disturbance of *Callianassa kraussi*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.4d. Turbellarian response in relation to time after disturbance of *Callianassa kraussi*. ANOVA table: *, ** represent significance at $P < 0.1$ and $P < 0.05$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a $\log(x+1)$ transformation.

TIME	2 wk	4 wk	8 wk	16 wk ^a	36 wk	72 wk
ANOVA						
F	6.122	0.885	6.823	6.928	0.799	2.441
DF	2,5	2,6	2,5	2,5	2,5	2,9
P	*	NS	**	**	NS	NS
CONTRAST	A**	NS	A**	A**	NS	B*

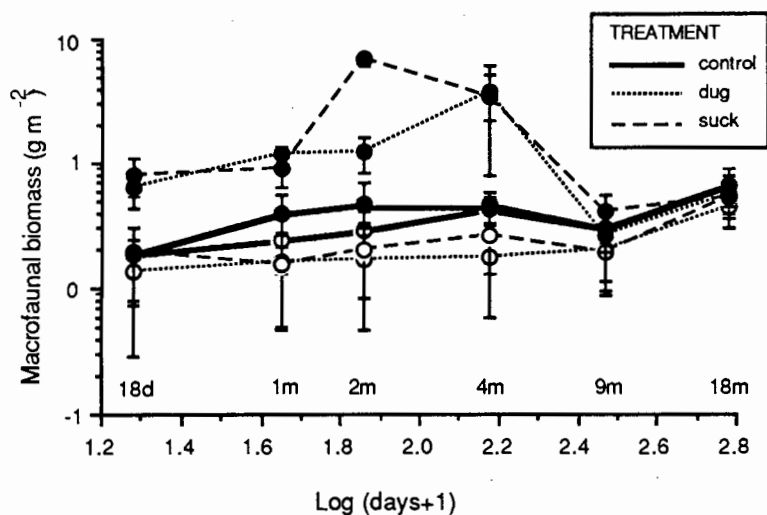


Figure 3.5. Mean macrofaunal biomass (\pm S.E.) in control, dug and sucked-over areas in relation to time after disturbance of *Callianassa kraussi*. Biomass values are plotted on a logarithmic scale. ● including *Diogenes brevirostris*, ○ excluding *D. brevirostris*. d=days, m=months.

Table 3.5. Macrofaunal biomass in relation to time after disturbance of *Callianassa kraussi*. d=days, m=months. ANOVA table: **, *** represent significance at $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Tukeys is the multiple comparison procedure utilised. A denotes a significant difference between control and dug, B denotes a significant difference between control and suck, C denotes a significant difference between dug and suck. ^a indicates the use of a log (x+1) transformation, ^b indicates Kruskal Wallis statistics with Tukeys on ranked data.

LOGTIME	1.28	1.65	1.86	2.18	2.47	2.78
Including <i>Diogenes</i>						
TIME	18d ^a	1m	2m	4m ^b	9m	18m
F	17.905	11.368	72.000	(5.42)	3.158	0.551
DF	2,6	2,6	2,6	2,6	2,6	2,6
P	***	***	***	**	NS	NS
TUKEYS	A [*] , B [*]	A [*] , B [*]	B [*] , C [*]	A [*] , B [*]	NS	NS
Excluding <i>Diogenes</i>						
TIME	18d	1m	2m	4m	9m	18m
F	9.493	13.470	6.65	32.728	31.271	1.825
DF	2,6	2,6	2,6	2,6	2,6	2,6
P	**	***	**	***	***	NS
TUKEYS	A ^{**} , C ^{**}	A ^{**} , B ^{**}	A ^{**}	A ^{**} , B ^{**}	A ^{**} , B ^{**}	NS

Species Richness: An initial decline in the number of macrofaunal species present in the experimental areas relative to the control, was evident within the first 4 days after the disturbance (Figure 3.6; Table 3.6). Thereafter, species richness in the disturbed areas increased but had approached control levels only by the 18th month (week 72). The post-disturbance species richness was not grossly different from that of the control area or the pre-disturbance system.

Numbers: 40 species were collected at Klein Oesterwal during the course of this study. Of these, 19 were selected for further analysis based on at least 3 occurrences in either set of control or treatment samples. Of these 19, those depicting obvious trends are illustrated in Figures 3.7a,b and the corresponding statistics in Tables 3.7a,b respectively. The remaining 11 are listed in Table 3.8 - where their numbers are sufficiently high, statistics have been included.

Scarce organisms which were too rare to include in Figures 3.7a,b or Table 3.8, but which were incorporated in the species richness analyses, included the following: *Crepidula porcellana* Lam., *Hydrobia* sp., *Nassarius scopularcus* Brnrd., *Littorina knysnaensis* Phil., *Natica gualteriana* Récluz, *Clionella sinuata* (Born), an unidentified turrid, *Lysidice* sp., *Nephtys capensis* Day, *Ceratonereis erythraensis* Fauvel, an unidentified terebellid, *Syllis* sp., *Mediomastus capensis* Day, *Nematonereis unicornis* (Grube), *Scolecopsis squamata* (Müll), *Antinoe lactea* Day, *Lumbrinereis tetraura* (Schm.), *Paridotea unguata* (Pallas), *Cirolana* sp., *Gastrosaccus brevifissura* O. Tattersall and *Betaeus jucundus* Brnrd.

The responses of individual species to the disturbance were highly variable and recolonisation trends varied substantially. During the 18 month study, the macrofaunal community at Klein Oesterwal was numerically dominated by two species - *Urothoe grimaldi* Chevr., a detritivorous amphipod which lives just below the sediment surface, and *Scoloplos johnstonei* Day., a tubicolous polychaete which feeds on organic particles in the sediment. These same organisms remained dominant, albeit in diminished numbers, in the disturbed areas; both were significantly depressed relative to the control, from the start of the experiment until its termination 18 months later (Figures 3.7a,b respectively). Similar trends were observed for the sedentary polychaetes *Orbinia angrapequensis* (Aug.) (Figure 3.7b), *Telothelopus capensis* Day (Table 3.8) and the 'unidentified white bivalve' (Figure 3.7a). In each case, there was a significant quantitative reduction during the first 9 months after disturbance. Thereafter, a general trend of recovery was apparent. All except *S. johnstonei* exhibited patterns which were

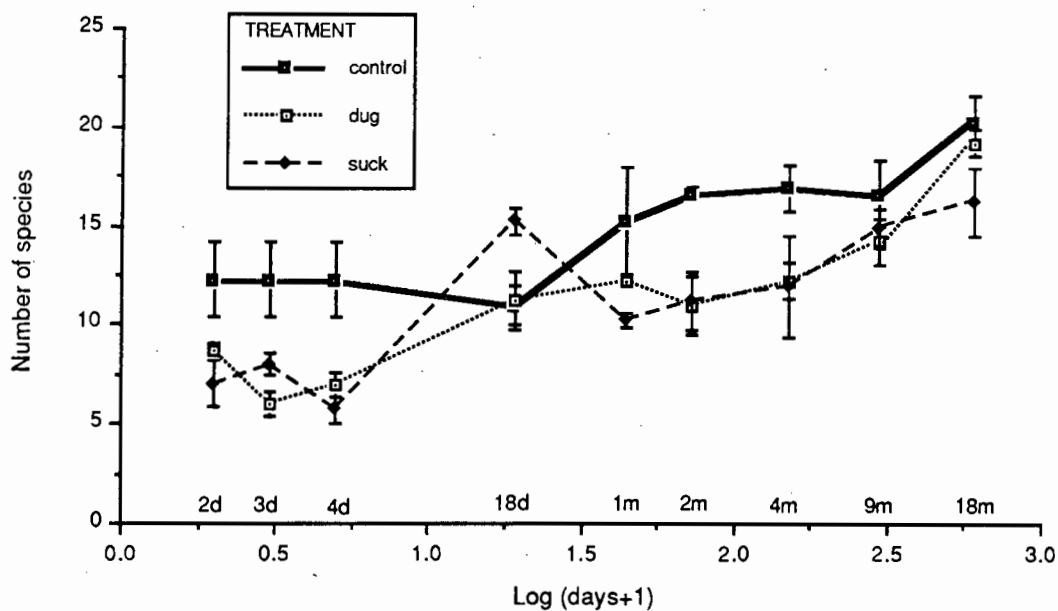


Figure 3.6. Mean number (\pm S.E.) of macrofaunal species in control, dug and sucked-over areas in relation to time after disturbance of *Callianassa kraussi*. d=days, m=months.

Table 3.6. Macrofaunal species richness in relation to time after disturbance of *Callianassa kraussi*. d=days, m=months. ANOVA table: *, ** represent significance at $P < 0.1$ and $P < 0.05$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates Kruskal Wallis statistics.

LOG TIME	0.30	0.48	0.70	1.28	1.65	1.86	2.18	2.47	2.78
TIME	2d	3d	4d	18d	1m	2m	4m	9m	18m
ANOVA									
F	4.568	7.649	8.842	4.906	3.430 ^a	6.659	2.776	0.830	2.850
DF	2,6	2,6	2,6	2,6	2,6	2,6	2,6	2,6	2,6
P	*	**	**	*	NS	**	NS	NS	NS
CONTRAST									
	A**	A**	A**	B**	NS	A**	A*	NS	NS

divorced from any effects due to recruitment.

Delayed responses to the disturbance were exhibited by the polychaetes *Notomastus latericeus* Sars and *Euclymene* sp. (Figure 3.7b) -both of which feed on organic particles in the sand, and by the other bivalves present in sizeable quantities, *Carditella rugosa* Sow. (Figure 3.7a) and *Kellya rubra* (Mont.) (Table 3.8). These organisms showed no effect initially, but after 4 or more months displayed a delayed depression; distinct recruitments in control samples were not matched by increases in the treatment areas, implying that recruitment had in some way been affected. This inference is based on increases in density in control areas which were not matched by corresponding increases in treated areas; comprehensive data on size-frequency distributions would be required to confirm that recruitment of juveniles was responsible. These delayed depressions in abundance were generally perpetuated beyond the termination of the experiment. The filter-feeding gastropod *Turritella capensis* Krauss. showed similar but more ambivalent trends, probably as a result of its clumping behaviour and consequent patchiness (Table 3.8).

Diogenes brevirostris proved to be the only macrofaunal organism which increased disproportionately in treatment plots compared with controls after the disturbance; numbers of crabs soared 2 weeks following the disturbance and peaked at 2-4 months (Figure 3.7a). During this peak, night counts of *D. brevirostris* ranged from 12 m⁻² (control) to 151 and 209 m⁻² (dug and sucked-over areas respectively). Thereafter, densities slowly returned to background abundances. At the termination of the experiment, nocturnal hermit crab counts still remained marginally higher in the experimental areas (39 and 84 individuals m⁻² in the dug and sucked-over sites respectively) than in the control sites (3 m⁻²). *Hymenosoma orbiculare* Desm., a scavenging crab common on the sandflats at Langebaan Lagoon, showed no clear-cut patterns although the density of the other common crab, *Cleistostoma edwardsii* McLeay was reduced in treatment areas from the initiation of the experiment up until month 18 (Table 3.8).

In conclusion, the immediate effects of disturbance on the soft-bottom community at Klein Oesterwal were approximately 50% reductions in species richness, macrofaunal numbers and total invertebrate biomass. By the termination of the experiment, these percentages had been modified to a 13% reduction in species richness, a 50% reduction in numbers and a 32% reduction in biomass. Only one species benefited from the disturbance - the hermit crab *D. brevirostris*.

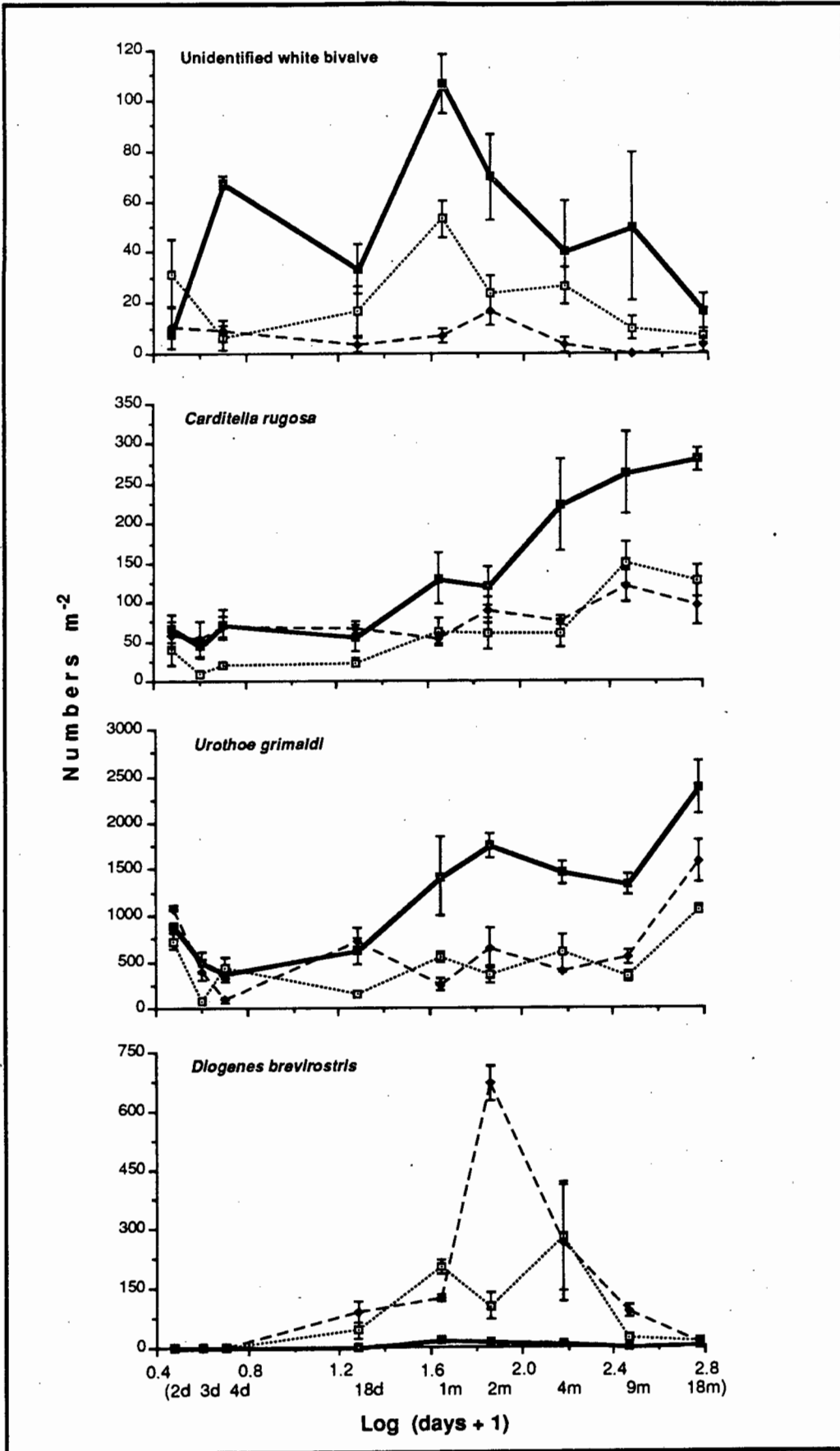


Figure 3.7a. Macrofaunal numbers (mean \pm S.E.) in relation to time after disturbance of *Callianassa kraussi* in control (—■—), dug (····□····) and sucked-over (---●---) areas. d=days, m=months. Corresponding statistics are given in Table 3.7a.

Table 3.7a. Macrofaunal numbers in relation to time after disturbance of *Callinassa kraussi*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. d.f. = 2,6. ^a indicates the use of a log (x+1) transformation.

LOG TIME	0.48	0.60	0.70	1.28	1.65	1.86	2.18	2.47	2.78
TIME	2d	3d	4d	18d	1m	2m	4m	9m	18m
<i>Unidentified bivalve</i>									
<u>ANOVA</u>									
F	1.266	-	32.339	2.259	25.037	4.560	5.059 ^a	1.575	1.444
P	NS	-	***	NS	***	*	**	NS	NS
<u>CONTRAST</u>	NS	-	A***	NS	A***, B***	A**	B**	NS	NS
<i>Carditella rugosa</i>									
<u>ANOVA</u>									
F	0.320	1.617	7.65 ^a	2.317	2.418	1.350	4.114 ^a	3.002	15.359
P	NS	NS	**	NS	NS	NS	*	NS	***
<u>CONTRAST</u>	NS	NS	A*, B**	NS	A*	NS	A**	A**	A***
<i>Urothoe grimaldi</i>									
<u>ANOVA</u>									
F	6.504	11.715 ^a	7.092 ^a	13.964 ^a	9.423 ^a	14.634	12.829	27.290	6.452
P	**	**	**	**	**	***	**	***	**
<u>CONTRAST</u>	B**	A**, B**	B**	A*, B**	A**, B*	A***	A***	A***	A**
<i>Diogenes brevisrostris</i>									
<u>ANOVA</u>									
F	-	-	-	28.321 ^a	37.587	84.076	5.038 ^a	9.526 ^a	2.333
P	-	-	-	***	***	***	**	**	NS
<u>CONTRAST</u>	-	-	-	A***	A***, B**	A***, B***	A**	A**, B**	NS

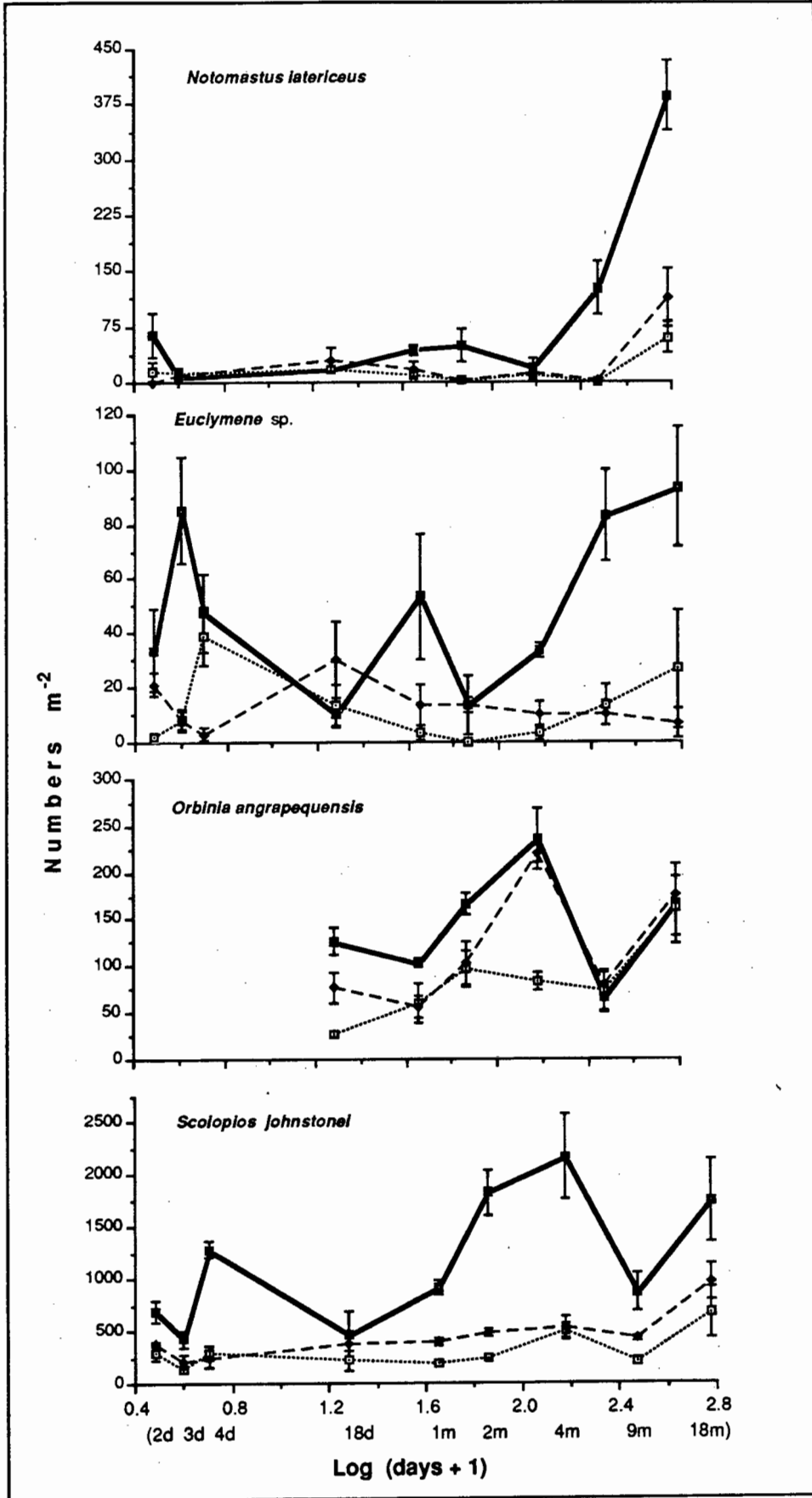


Figure 3.7b. Macrofaunal numbers (mean \pm S.E.) in relation to time after disturbance of *Callianassa kraussi* in control (—■—), dug (---■---) and sucked-over (-♦-) areas. d=days, m=months. Corresponding statistics are shown in Table 3.7b.

Table 3.7b. Macrofaunal numbers in relation to time after disturbance of *Callianassa kraussi*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. d.f. = 2,6. ^a indicates the use of a log (x+1) transformation.

LOG TIME	0.48	0.60	0.70	1.28	1.65	1.86	2.18	2.47	2.78
TIME	2d	3d	4d	18d	1m	2m	4m	9m	18m
<i>Notomastus latericeus</i>									
<u>ANOVA</u>									
F	2.220	0.074	-	0.076 ^a	4.200	1.283 ^a	0.175	8.133	14.573
P	NS	NS	-	NS	*	NS	NS	**	***
<u>CONTRAST</u>	A*	NS	-	NS	A**	NS	NS	A**, B**	A***
<i>Euclymene</i> sp.									
<u>ANOVA</u>									
F	2.208 ^a	4.621 ^a	3.902	0.838	2.333	0.941	13.400	10.523	4.212
P	NS	*	*	NS	NS	NS	**	**	*
<u>CONTRAST</u>	NS	A**	B*	NS	A*	NS	A***	A***	A**
<i>Orbinia angrapequensis</i>									
<u>ANOVA</u>									
F	-	-	-	9.783	2.287	2.858	11.046	0.101	0.031
P	-	-	-	**	NS	NS	**	NS	NS
<u>CONTRAST</u>	-	-	-	A**	A*	A*	A**, B**	NS	NS
<i>Scoloplos johnstonei</i>									
<u>ANOVA</u>									
F	5.415	4.195	30.029	0.500	41.887	46.668 ^a	9.961	14.095 ^a	2.467
P	**	*	***	NS	***	***	**	***	NS
<u>CONTRAST</u>	A**	A**	A***	NS	A***, B**	A***, B**	A***	A***, B**	A*

Figure 3.8. Response of less dominant species in relation to time after disturbance of *Callianassa* in control, dug and sucked-over areas. Numbers are mean densities (n=3) per m². ** indicates significant difference between control and treatment at P < 0.05. d=days, m=months, ND=no data.

Species	1d	2d	3d	18d	1m	2m	4m	9m	18m
Decapoda									
<i>Callinectes sapidus</i> (Mont.)									
CONTROL	-	-	-	-	17	13	50	110	56
	-	-	-	13	27	13	17	43**	27
	-	-	-	17	7	10	10	43**	43
Decapoda									
<i>Libinia capensis</i> Krauss									
CONTROL	34	57	51	7	13	30	77	100	257
	34	2**	39	10	20	23	20**	60	43**
	58	21	63	50	33	43	40**	233**	100**
<i>Libinia capensis</i> Krauss									
CONTROL	6	2	6	3	10	7	13	13	3
	21	-	-	-	7	-	-	17	3
	-	-	-	10	-	3	7	3	10
Decapoda									
<i>Libinia depressa</i> (Schm.)									
CONTROL	117	ND	ND	3	-	3	10	3	20
	13	ND	ND	3	3	7	-	3	-
	35	ND	ND	-	3	10	3	-	3
<i>Libinia tridactyla</i> (Schm.)									
CONTROL	6	-	-	23	10	37	60	7	43
	19	2	-	3	7	13**	17**	10	23
	6	10	6	13	3	7**	3**	13	30
<i>Libinia capensis</i> Day									
CONTROL	9	14	5	23	33	37	97	7	20
	4	-	-	13	7**	3	7**	7	23
	12	4	-	10	3**	10	23**	3	27
Decapoda									
<i>Libinia hirtipes</i> M.Edw.									
CONTROL	11	-	-	13	-	3	10	-	10
	-	8	-	-	-	-	-	-	7
	6	-	-	3	-	-	-	-	13
Decapoda									
<i>Libinia palmata</i> Brnrd.									
CONTROL	8	-	3	3	3	-	23	27	10
	2	-	-	-	3	-	-	80**	13
	2	-	-	7	-	-	3	50	27
Decapoda									
<i>Libinia edwardsii</i> McLeay									
CONTROL	15	10	9	10	10	10	3	53	3
	-	-	-	-	-	-	-	7	10
	-	-	-	3	-	-	3	7	-
<i>Libinia spiralis</i> Brnrd.									
CONTROL	-	-	-	-	7	-	-	-	23
	-	-	-	3	3	-	-	-	7
	-	-	-	-	-	-	3	-	10
<i>Libinia orbiculare</i> Desm.									
CONTROL	-	6	-	-	-	23	17	10	67
	-	-	-	-	-	-	13	60**	47
	-	-	-	3	-	-	10	27	117

GEELBEK

Effects on *U. africana*

Preliminary observations showed that the pre-disturbance mudprawn populations were homogeneous between the selected sites ($P > 0.05$) (Figure 3.8; ANOVA analyses in Table 3.9). In the dug-over area, 726 *U. africana* were removed, representing 49.4% of the prawns originally present (on the basis of a hole-count of 2945 and assuming 2 holes per animal). In the sucked-over area, 491 were removed, approximating 46.7% of the total present. Immediately after removal of the prawns, and for 4 months following the disturbance, numbers of *U. africana* within the experimental areas were markedly lower than in control samples (Figure 3.8). Whilst the dug-over areas initially appeared more affected than the sucked-over areas, this trend evidently reversed with time; sucked treatments remained lower from 18 days until 4 months after the disturbance. However, this difference was statistically significant only at 2 months. The presence of impervious mats of *Zostera capensis* Setchell at month 18, and consequent concealment of mudprawn holes in both control and experimental sites, precluded further quantification of prawn densities.

Table 3.9. Effect of disturbance on *Upogebia africana*. ANOVA comparisons of control, dug and sucked-over areas. 0d indicates a comparison of prawn densities (holes m^{-2}) between experimental and control areas before the treatment.

TIME	0d	1d ^a	18d	1m ^a	2m ^a	4m	9m
F	1.87	49.08	39.22 ^b	15.25	40.78	77.54	1.05
DF	2,57	2,57	2,57	2,52	2,58	2,47	2,40
P	0.164	0.0001	0.0001	0.0001	0.0001	0.0001	0.359

d=days, m=months. a denotes $\log(x+1)$ transformation; b denotes Kruskal Wallis statistics.

Effects on the sediment

Md ϕ values were generally lower (i.e. coarser) in the disturbed sediment than in the control (Table 3.10). QD ϕ had decreased in the experimental areas within the first month after the disturbance. Thereafter, no detectable differences in QD ϕ were observed. Skq ϕ in the disturbed areas did not appear to be notably modified. The low Skq ϕ values imply that the sediment at Geelbek is well sorted. There were no obvious

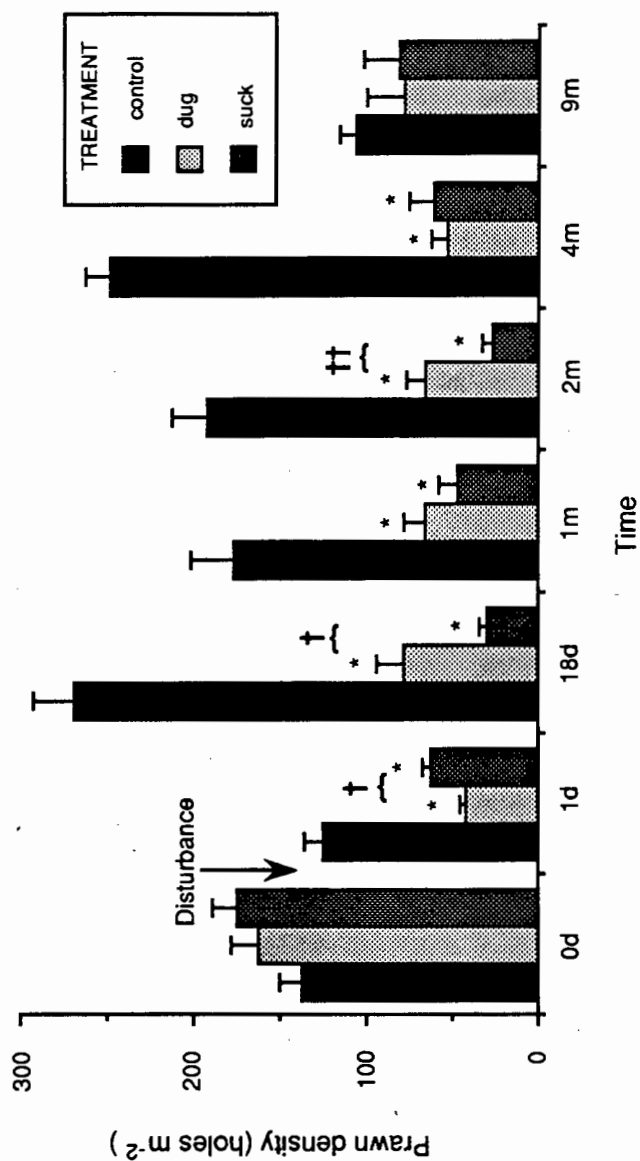


Figure 3.8. Number of *Upogebia africana* holes (m^{-2}) in control, dug and sucked over areas in relation to time after disturbance. S.E. appear above the mean values. d=days, m=months. 0d shows prawn densities in experimental and control areas before disturbance. * indicates a significant difference between control and treatments at $P < 0.0001$. †, †† indicate a significant difference between dug and suck treatments at $P < 0.05$ and $P < 0.005$ respectively. Tukeys is the multiple comparison procedure utilised.

differences in organic content or mud fractions between the experimental and control areas.

Table 3.10. Table showing the median particle diameter, phi quartile deviation, phi quartile skewness, percentage organics and percentage mud of treatment and control samples after disturbance of *Upogebia africana*. d=days, m=months.

TIME	18d	1m	2m	4m
MDϕ				
CONTROL	2.160	2.250	2.145	2.115
DUG	2.165	2.180	2.160	2.070
SUCK	2.065	2.145	2.095	2.080
QDϕ				
CONTROL	0.483	0.495	0.450	0.413
DUG	0.468	0.458	0.445	0.415
SUCK	0.415	0.478	0.450	0.430
Skqϕ				
CONTROL	0.045	0.050	0.050	0.015
DUG	0.075	0.065	0.050	0.070
SUCK	0.040	0.075	0.080	0.040
% Organics				
CONTROL	0.470	0.595	0.330	0.310
DUG	0.590	0.595	0.325	0.180
SUCK	0.325	0.470	0.240	0.520
% Mud				
CONTROL	4.200	7.100	2.355	2.270
DUG	6.380	6.030	3.515	3.555
SUCK	2.885	4.525	3.765	3.270

As at Klein Oesterwal, the surface of the sediment became depressed in the experimental areas, deflating by about 10 cm below the surrounding control areas. In contrast to Klein Oesterwal, there was no change in the penetrability of the sediment after removal of the prawns at Geelbek. Control values of 362.4 (\pm 53.8) mm were not markedly different from values in the dug-over (340.5 \pm 30.6 mm) or sucked-over areas (340.9 \pm 66.6 mm).

The sediment at Geelbek is typically black and sulphurous and remained so throughout the experiment in both control and treatment plots. Redox potential

measurements taken at depths of 5 cm in the 18th month showed experimental and control areas to be similar, approximating an Eh-value of -360 mV.

Effects on the microflora

A one-way analysis of variance revealed chlorophyll levels in the sucked-over sediment to be suppressed within 18 days of the disturbance and for a further month - a similar, less intense trend was observed for the dug-over sediment ($F=5.390, P=0.038, d.f.=2,7$; $F=6.232, P=0.023, d.f.=2,10$ for 18 days and 1 month respectively) (Figure 3.9). Although there subsequently appeared to be a pattern of recovery in the experimental areas ($P>0.05$), in the ninth month chlorophyll levels were still lower than in the control ($F=22.984, P<0.001, d.f.=2,7$), recovering completely by the eighteenth month ($P>0.05$). These trends were in sharp contrast to the increase in chlorophyll levels in the experimental areas exhibited after the disturbance of *C. kraussi*.

Effects on the bacteria

There were no clear trends amongst the bacteria after disturbance of *U. africana* (Figure 3.10; Table 3.11). This was partly due to the tendency of the bacteria to aggregate around fine organic particles such as those found at Geelbek, hence causing enormous variability within the samples. Nevertheless, there was a distinct increase in total surface bacteria 18 days following the disturbance (ANOVA, $F=4.628, P=0.061, d.f.=2,6$) (Figure 3.10). This was particularly marked in the sucked-over areas where all types of bacteria showed similar trends (Table 3.11).

After 1 month, no differences between the control and experimental areas, apart from a slight reduction in the treatment areas were apparent at either surface or depth measurements ($P>0.05$) (Figure 3.10). Nevertheless, after 2 months surface bacterial numbers were significantly reduced in both treatments and particularly in the dug-over areas (ANOVA, $F=4.981, P=0.05, d.f.=2,6$); no corresponding differences were discerned at 30 cm depth ($P>0.05$). Bacterial abundances within experimental areas had resumed control levels by 4 months and sampling was consequently terminated. Thus, although there was an initial increase in surface bacteria in the disturbed areas, there were no consistent responses evident subsequently apart from a reduction in surface bacteria after 2 months.

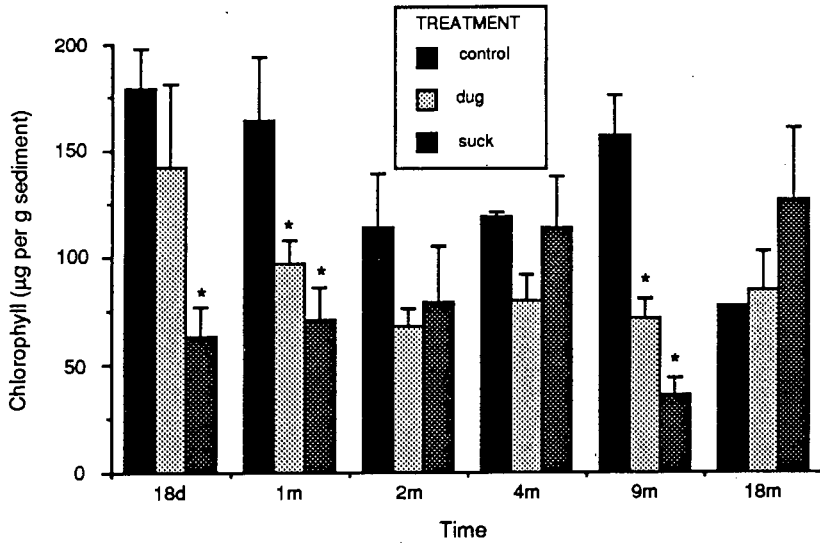


Figure 3.9. Chlorophyll levels in control, dug and sucked-over areas, in relation to time after disturbance of *Upogebia africana*. d=days, m=months. S.E. appear above the mean values. * indicates a significant difference between control and treatment at $P < 0.05$. Tukeys is the multiple comparison procedure utilised.

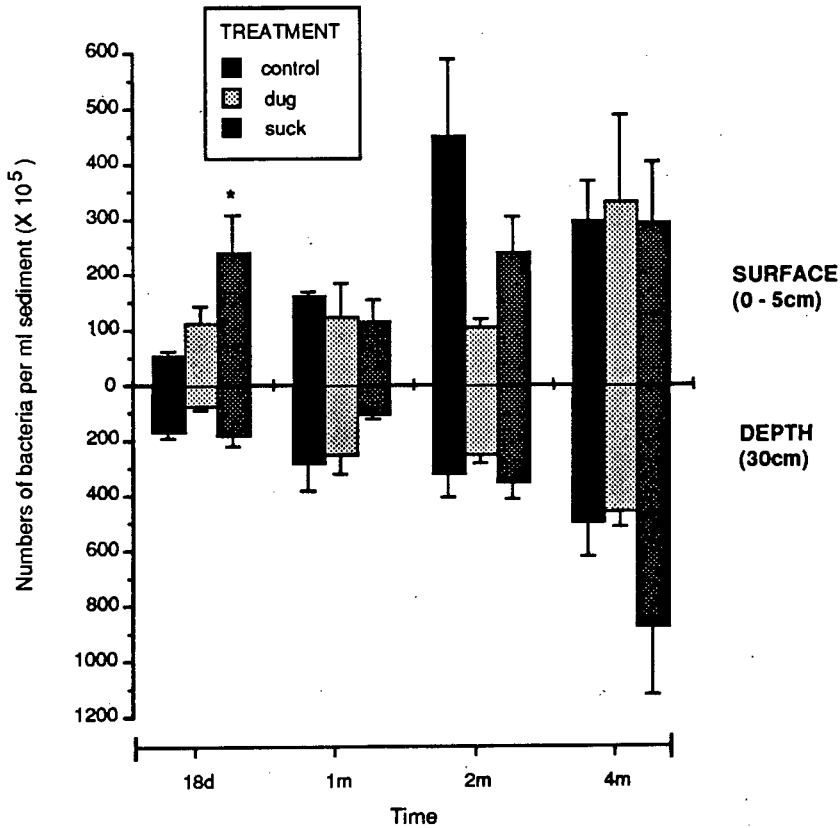


Figure 3.10. Bacterial numbers in control, dug and sucked-over areas in relation to time after disturbance of *Upogebia africana*. S.E. appear above mean values. d=days, m=months. *, ** indicate a significant difference between control and treatment at $P < 0.01$ and $P < 0.05$ respectively. Tukeys is the multiple comparison procedure utilised.

Table 3.11. Bacterial numbers in relation to time after disturbance of *Upogebia africana* in control, dug and sucked-over areas. d=days, m=months.

Type	Treatment	No. of bacteria per ml sediment (X10 ⁵)			
		18d	1m	2m	4m
Cocci	<i>Surface</i>				
	Control	22.58	56.19	254.29	129.54
	Dug	37.84	44.46	58.82	136.79
	Suck	108.20	49.82	74.18	116.32
	<i>Depth</i>				
	Control	64.43	130.28	178.59	195.63
Dug	41.11	121.76	124.62	198.33	
Suck	95.39	35.18	216.38	325.70	
Rods	<i>Surface</i>				
	Control	25.40	83.39	178.59	120.62
	Dug	67.48	59.22	40.87	147.13
	Suck	105.95	52.11	147.56	159.40
	<i>Depth</i>				
	Control	86.35	132.12	140.32	251.75
Dug	26.04	102.90	121.89	192.48	
Suck	61.97	60.06	122.21	364.52	
Other	<i>Surface</i>				
	Control	5.80	20.07	18.92	46.73
	Dug	6.26	20.31	3.43	45.64
	Suck	22.72	14.10	17.79	16.77
	<i>Depth</i>				
	Control	19.75	25.38	7.17	54.73
Dug	8.33	32.19	7.07	74.71	
Suck	24.15	12.15	14.81	186.06	

Effects on the meiofauna

Meiofaunal numbers, expressed as a percentage of the control, are displayed in Figures 3.11 a,b,c,d,e and the corresponding statistics in Tables 3.12 a,b,c,d,e. Meiofaunal numbers were dominated by nematodes and copepods. Both adult and nauplii copepods displayed similar trends throughout and were accordingly grouped together - both were equally represented. Prevalent in the experimental areas amongst all meiofaunal groups, was an initial reduction in numbers within the first 2 weeks of the treatment. A peak in copepod and kinorhynch numbers, surpassing control figures, followed the initial depression (Figures 3.11b,e). Although the statistical results are somewhat ambivalent, all groups except turbellarians were initially reduced in the treatment areas, and copepods, polychaetes and kinorhynchs appeared to be particularly affected. The recolonisation of the nematodes was comparatively rapid, with the turbellarians being little affected by the disturbance. There were no clear-cut differences between dug and sucked-over areas.

Effects on the macrofauna

Biomass: Figure 3.12 presents the ash-free total macrofaunal biomass after the disturbance of *U. africana*. Values in the treatment areas were considerably lower than those of the control and remained significantly depressed for up to 4 months following the disturbance. No significant differences were apparent after this time (Table 3.13). The doubling of biomass at month 18 was associated with an increase in *Zostera* and its associated assemblages of macrofauna in both control and experimental areas. There were no discernable differences in biomass values between dug and sucked-over treatments.

Species Richness: The number of species present declined in the experimental areas relative to the control samples within the first day of the disturbance (Figure 3.13; Table 3.14). This depression was perpetuated for 2 months, thereafter species richness in the disturbed areas increased, approaching background levels by the fourth month ($P > 0.05$). All species recorded in the experimental plots also occurred in the control sites.

Numbers: 48 macrofaunal species were collected at Geelbek during the course of this study. Of these, 21 were selected for further analysis based on their occurrences in either set of control or treatment samples. Of these 21, those depicting obvious trends are

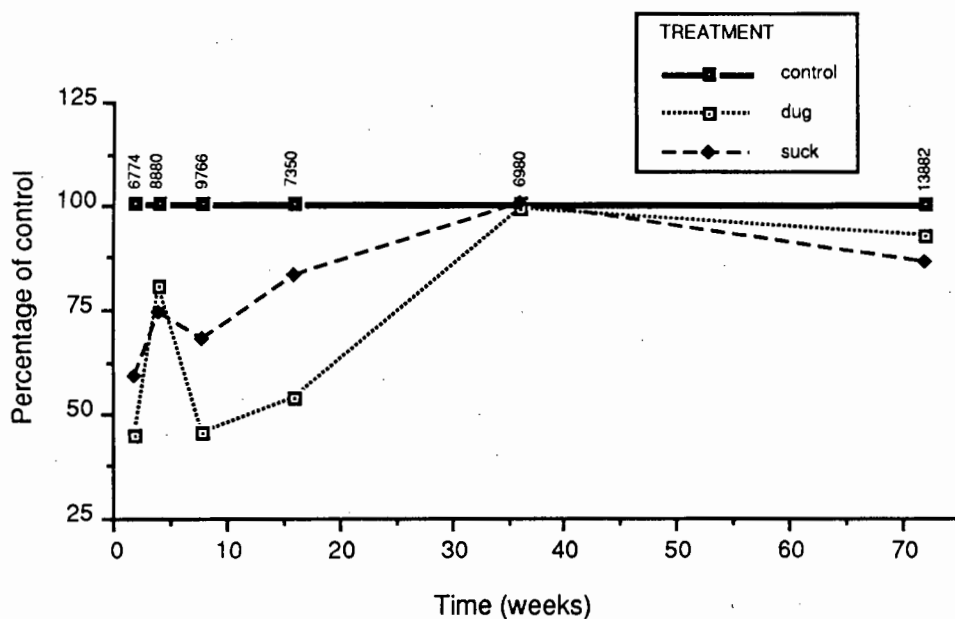


Figure 3.11a. Nematode response in relation to time after disturbance of *Upogebia africana*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.12a. Nematode response in relation to time after disturbance of *Upogebia africana*. ANOVA table: ** represents significance at $P < 0.05$, NS=not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a log (x+1) transformation.

TIME	2 wk ^a	4 wk	8 wk	16 wk	36 wk	72 wk
ANOVA						
F	8.150	0.259	2.004	1.755	0.001	0.105
DF	2,6	2,6	2,5	2,6	2,5	2,8
P	**	NS	NS	NS	NS	NS
CONTRAST	A**	NS	NS	NS	NS	NS

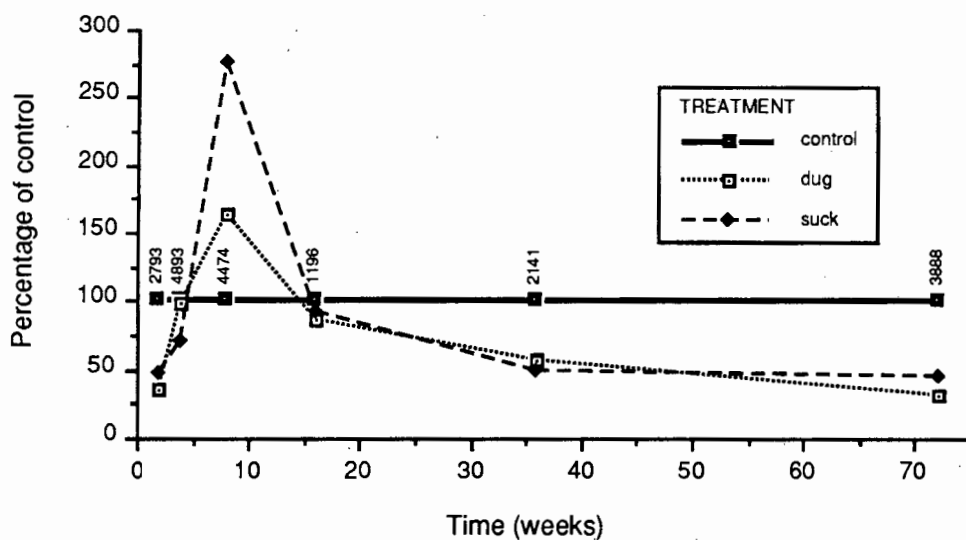


Figure 3.11b. Copepod response in relation to time after disturbance of *Upogebia africana*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.12b. Copepod response in relation to time after disturbance of *Upogebia africana*. ANOVA table: *, ** represent significance at $P < 0.1$ and $P < 0.05$ respectively, NS=not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a log (x+1) transformation.

TIME	2 wk ^a	4 wk	8 wk	16 wk	36 wk	72 wk
<u>ANOVA</u>						
F	5.783	0.710	1.828	0.066	0.488	3.788
DF	2,6	2,6	2,5	2,6	2,5	2,8
P	**	NS	NS	NS	NS	*
<u>CONTRAST</u>	A**	NS	NS	NS	NS	A**

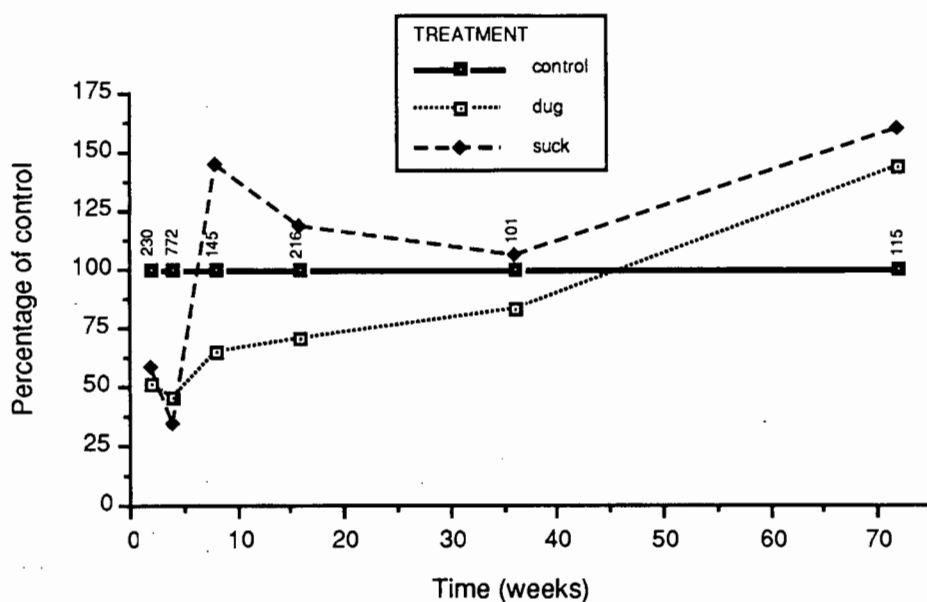


Figure 3.11c. Turbellarian response in relation to time after disturbance of *Upogebia africana*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.12c. Turbellarian response in relation to time after disturbance of *Upogebia africana*. ANOVA table. Contrast is the multiple comparison procedure utilised. NS = not significant.

TIME	2 wk	4 wk	8 wk	16 wk	36 wk	72 wk
<u>ANOVA</u>						
F	1.810	1.023	0.765	0.692	0.065	0.974
DF	2,6	2,6	2,5	2,6	2,5	2,8
P	NS	NS	NS	NS	NS	NS
<u>CONTRAST</u>	NS	NS	NS	NS	NS	NS

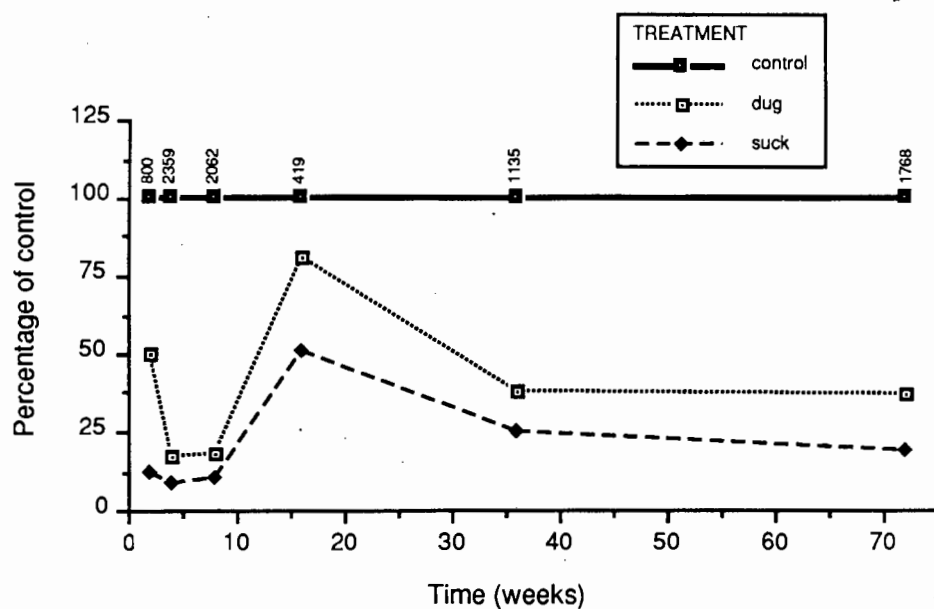


Figure 3.11d. Polychaete response in relation to time after disturbance of *Upogebia africana*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.12d. Polychaete response in relation to time after disturbance of *Upogebia africana*. ANOVA table: ** represents significance at $P < 0.05$, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a log (x+1) transformation.

TIME	2 wk ^a	4 wk	8 wk	16 wk	36 wk	72 wk ^a
ANOVA						
F	7.597	1.381	0.699	0.841	0.507	0.373
DF	2,6	2,6	2,5	2,6	2,5	2,8
P	**	NS	NS	NS	NS	NS
CONTRAST	A**	NS	NS	NS	NS	NS

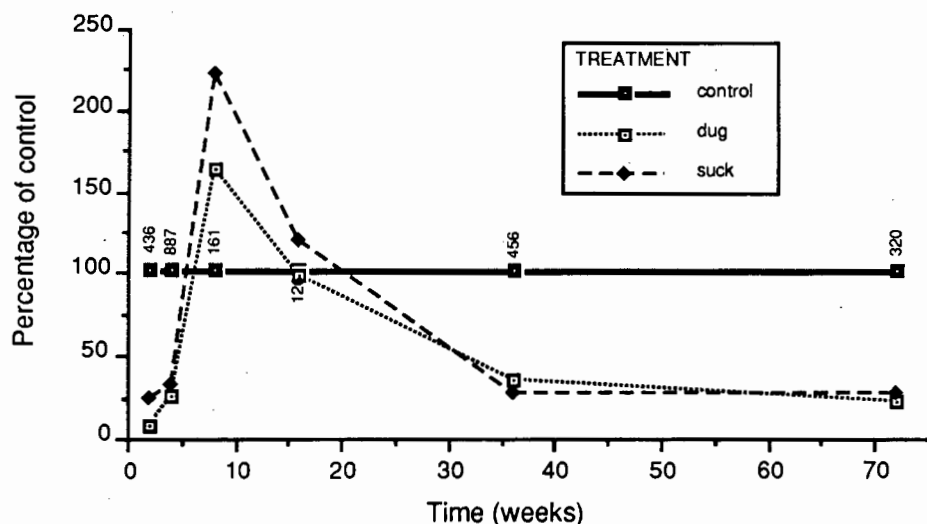


Figure 3.11e. Kinorynch response in relation to time after disturbance of *Upogebia africana*. Experimental values are given as a percentage of the control. Control values are numbers per 100g sediment.

Table 3.12e. Kinorynch response in relation to time after disturbance of *Upogebia africana*. ANOVA table; *, ** represent significance at $P < 0.1$ and $P < 0.05$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. ^a indicates the use of a log (x+1) transformation.

TIME	2 wk ^a	4 wk ^a	8 wk	16 wk ^a	36 wk	72 wk ^a
ANOVA						
F	11.037	2.544	0.608	0.056	0.881	2.299
DF	2,6	2,6	2,5	2,6	2,5	2,8
P	**	NS	NS	NS	NS	NS
CONTRAST	A**, B*	A*	NS	NS	NS	A*

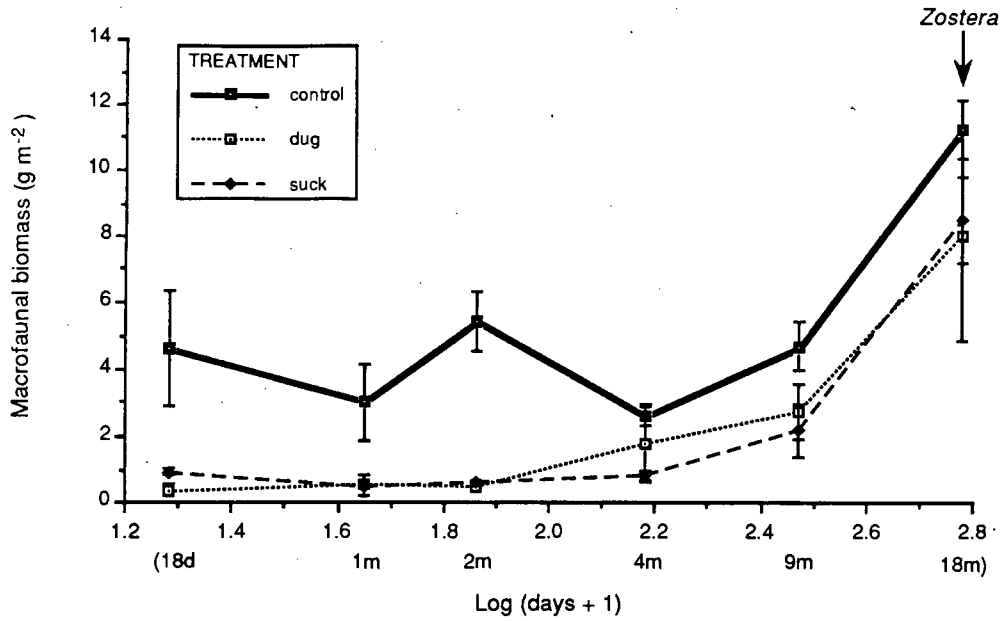


Figure 3.12. Mean macrofaunal biomass (\pm S.E.) in control, dug and sucked-over areas in relation to time after disturbance of *Upogebia africana* d=days, m=months. The period of *Zostera* proliferation is arrowed.

Table 3.13. Macrofaunal biomass in relation to time after disturbance of *Upogebia africana*. d=days, m=months. ANOVA table: **, *** represent significance at $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Tukeys is the multiple comparison procedure utilised. A denotes a significant difference between control and dug, B denotes a significant difference between control and suck. ^a indicates the use of a log (x+1) transformation.

LOGTIME	1.28 ^a	1.65 ^a	1.86 ^a	2.18 ^a	2.47	2.78
TIME	18 d ^a	1 m ^a	2 m ^a	4 m ^a	9 m	18 m
ANOVA						
F	14.920	7.895	88.127	2.279	2.918	0.730
DF	2,6	2,6	2,6	2,6	2,6	2,6
P	***	**	***	NS	NS	NS
TUKEYS						
	A***, B***	A**, B**	A***, B***	NS	NS	NS

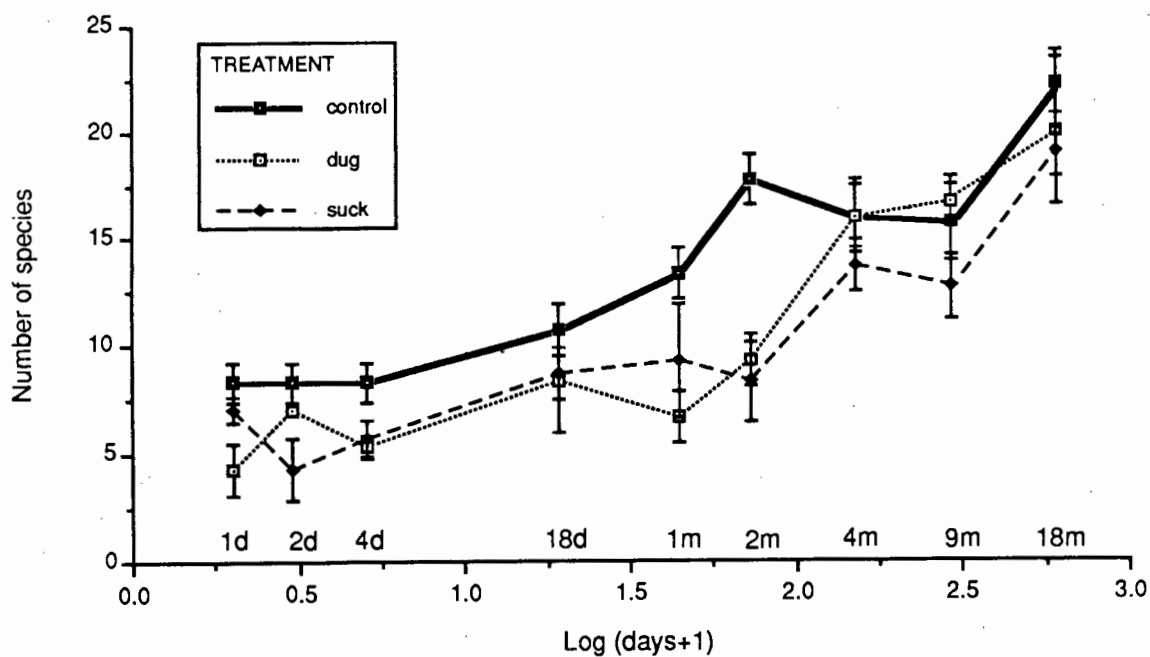


Figure 3.13. Mean number (\pm S.E.) of macrofaunal species in control, dug and sucked-over areas in relation to time after disturbance of *Upogebia africana*. d=days, m=months.

Table 3.14. Macrofaunal species richness in relation to time after disturbance of *Upogebia africana*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. d=days, m=months. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck.

LOG TIME	0.30	0.48	0.70	1.28	1.65	1.86	2.18	2.47	2.78
TIME	1 d	2 d	4 d	18 d	1 m	2 m	4 m	9 m	18 m
ANOVA									
F	4.870	3.558	4.867	0.551	3.494	12.439	0.803	1.950	0.556
DF	2,6	2,6	2,6	2,6	2,6	2,6	2,6	2,6	2,6
P	*	*	*	NS	*	**	NS	NS	NS
CONTRAST	A*, B*	NS	A**	NS	A**	A***	NS	NS	NS

illustrated in Figures 3.14a,b and their corresponding statistics given in Tables 3.15a,b. The remaining 12 are listed in Table 3.16 - as in the case of Klein Oesterwal, statistics for these species have been included where their numbers are sufficiently high.

Occasional organisms which were too scant to include in Figures 3.14a,b or Table 3.16, but which were incorporated in the species richness analyses included the following: 'unidentified white bivalve', *Nassarius scopularcus*, *Scoloplos johnstonei*, *Euclymene* sp., *Glycera tridactyla* (Schm.), *Lysidice* sp., *Perinereis nuntia* v. *vallata* Gr., *Nereis* sp., *Lumbrinereis tetraura*, *Platynereis dumerilii* (Aud & M.Edw.), *Syllis* sp., *Cirriformia tentaculata* (Mont.), *Boccardia ligerica* Ferronière, *Polydora antennata* Claparède, *Arabella iricolor* (Mont.), *Cirolana hirtipes* M. Edw., *Paridotea unguolata* (Pallas), *Urothoe grimaldi*, *Lysianassa ceratina* (Wlkr.), *Lembos* sp., *Paraphoxus oculatus* (Sars), an unidentified talitrid, *Orchestia rectipalma* (Brnr.), an unidentified mysid, *Palaemon pacificus* (Stimps.), *Cyclograpsus punctatus* M. Edw. and tipulid fly larvae.

Dominant species at Geelbek during the 18 month study fluctuated enormously and variations were in some cases undoubtedly related to the presence or absence of *Zostera*. Organisms that were consistently present in abundance included *Nassarius kraussianus* (Dnkr), *Hydrobia* sp., *Cleistostoma edwardsii* and *Ceratonereis erythraensis* Fauvel.

Species responses to the disturbance were highly variable and recolonisation trends varied significantly. Three broad post-disturbance responses could be discerned. Firstly, there were those organisms which were precipitously reduced immediately after the disturbance. These included the sedentary polychaete *Orbinia angrapequensis* (Table 3.16), the omnivorous gastropod *Nassarius kraussianus* (Figure 3.14a) and the detritivorous amphipod *Cymadusa filosa* Sav. (Table 3.16). These organisms displayed a slow but steady increase in density over the course of the experiment and had generally recovered by the termination of the experiment.

Secondly, depressions in abundances were sometimes only evident when recruitment took place in control areas but was much reduced in treated areas. This pattern was displayed by the bivalves *Carditella rugosa* and *Kellya rubra*, the limpet *Siphonaria capensis* Q. & G., the gastropod *Hydrobia* sp. (Figure 3.14a), the errant polychaete *Marphysa depressa* (Schm.) (Table 3.16), the common brachyurans *Cleistostoma edwardsii* and *Hymenosoma orbiculare* (Figure 3.14b), the detritivorous amphipods *Paramoera capensis* (Dana) and *Melita zeylanica* Stebb., the mysid *Gastrosaccus brevifissura* and perhaps the polychaete *Ceratonereis erythraensis* and gastropod *Marginella capensis* Krauss. (Table 3.16). In all these cases, distinct

recruitments in control samples were not matched by increases in the treatment areas, implying that recruitment had in some way been affected. These depressions in abundance were perpetuated beyond the termination of this experiment. Of the above-mentioned species only *Hydrobia* sp. (Figure 3.14a) exhibited an delayed depression which was exclusively recruitment-related although numbers of other species were often too low to unequivocally determine trends.

Finally, there were species which apparently showed no effects but occurred too infrequently to test conclusively. These included the isopods *Exosphaeroma truncatitelson* Brnrd. and *E. pallidum* Brnrd., the amphipod *Ampelisca palmata* Brnrd. and *D. brevirostris* (which showed slight, albeit statistically insignificant increases in treatment areas) (Table 3.16).

A large proportion of the above-mentioned organisms showed clear increases in month 18 when *Zostera* beds proliferated. These included *Carditella rugosa*, *Kellya rubra*, *Notomastus latericeus*, *Marphysa depressa*, *Hymenosoma orbiculare*, *Exosphaeroma truncatitelson*, *Cymadusa filosa*, *Paramoera capensis* and *Melita zeylanica*.

In conclusion, the immediate effect of disturbance on the soft-bottom community at Geelbek was a 33% reduction in species richness, a 66% reduction in macrofaunal numbers and an 84% reduction in total invertebrate biomass. At the termination of the experiment, these percentages had been modified to a 13% reduction in species richness, a 25% reduction in numbers and a 26% reduction in biomass.

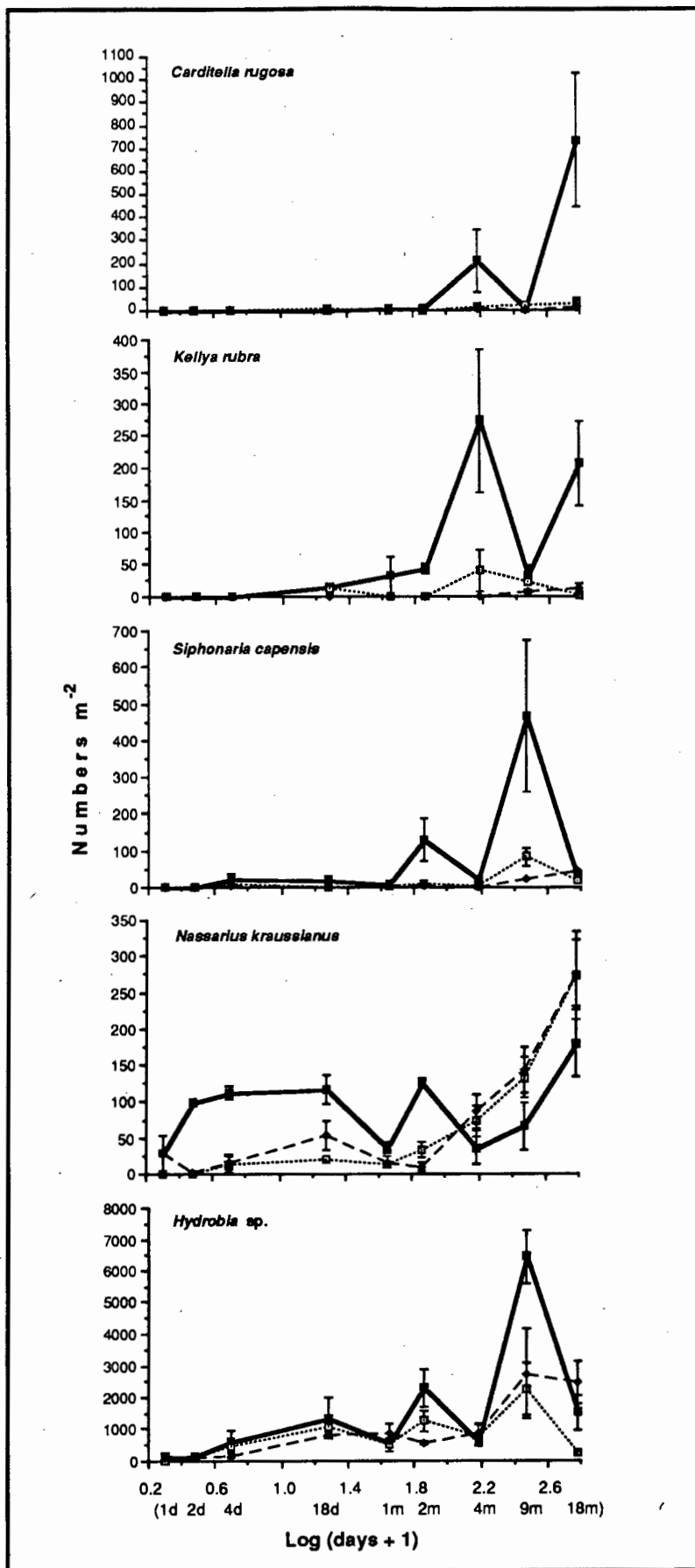


Figure 3.14a. Macrofaunal numbers (mean \pm S.E.) in relation to time after disturbance of *Upogebia africana* in control (—■—), dug (·····○·····) and sucked-over (---◇---) areas. d=days, m=months. Corresponding statistics are given in Table 3.15a.

Table 3.15a. Macrofaunal numbers in relation to time after disturbance of *Upogebia africana*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. d.f. = 2,6. ^a indicates the use of a log (x+1) transformation.

LOG TIME	0.30	0.48	0.70	1.28	1.65	1.86	2.18	2.47	2.78
TIME	1d	2d	4d	18d	1m	2m	4m	9m	18m
<i>Carditella rugosa</i>									
<u>ANOVA</u>									
F	-	-	-	-	-	-	2.675 ^a	-	2.935 ^a
P	-	-	-	-	-	-	NS	-	NS
<u>CONTRAST</u>	-	-	-	-	-	-	A*	-	A*
<i>Kellya rubra</i>									
<u>ANOVA</u>									
F	-	-	-	-	-	24.143	3.219	2.705	8.032 ^a
P	-	-	-	-	-	***	NS	NS	**
<u>CONTRAST</u>	-	-	-	-	-	A***	A**	B*	A**
<i>Siphonaria capensis</i>									
<u>ANOVA</u>									
F	-	-	-	-	-	3.929 ^a	-	4.493 ^a	0.710
P	-	-	-	-	-	*	-	*	NS
<u>CONTRAST</u>	-	-	-	-	-	A**	-	A**	NS
<i>Nassarius kraussianus</i>									
<u>ANOVA</u>									
F	3.185 ^a	2.904	3.284	5.884 ^a	0.843	7.679	1.160	2.355 ^a	0.666
P	NS	NS	NS	**	NS	**	NS	NS	NS
<u>CONTRAST</u>	A*	A**	A**	A**	NS	A**	NS	A*	NS
<i>Hydrobia</i> sp.									
<u>ANOVA</u>									
F	2.271 ^a	0.146	1.609 ^a	0.241	0.509	3.191	0.194	3.150	4.366 ^a
P	NS	NS	NS	NS	NS	NS	NS	NS	*
<u>CONTRAST</u>	NS	NS	NS	NS	NS	A*	NS	A**	B**

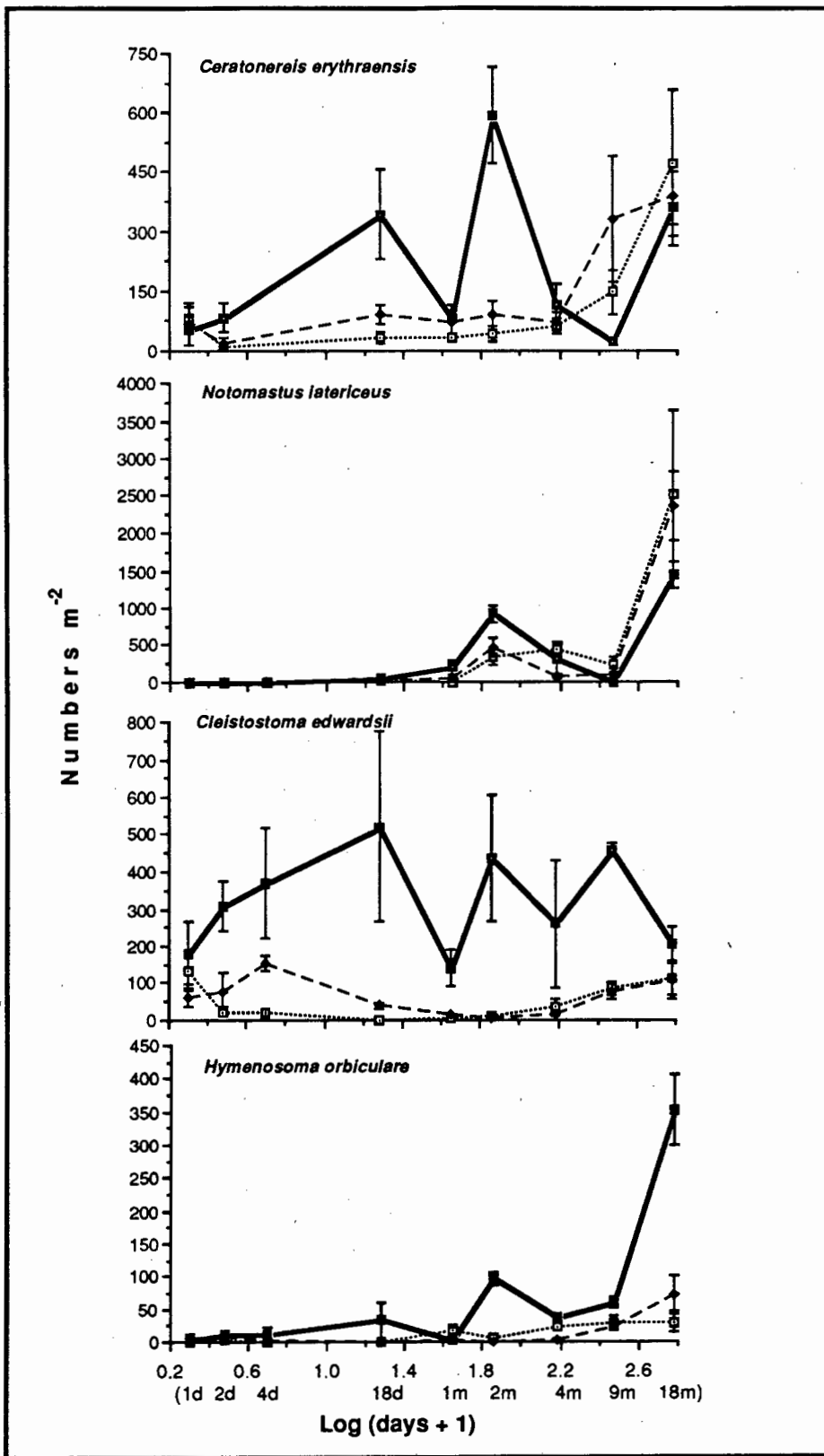


Figure 3.14b. Macrofaunal numbers (mean \pm S.E.) in relation to time after disturbance of *Upogebia africana* in control (—■—), dug (····■····) and sucked-over (---▲---) areas. d=days, m=months. Corresponding statistics are given in Table 3.15b.

Table 3.15b. Macrofaunal numbers in relation to time after disturbance of *Upogebia africana*. ANOVA table: *, **, *** represent significance at $P < 0.1$, $P < 0.05$ and $P < 0.005$ respectively, NS = not significant. Contrast is the multiple comparison procedure utilised. A denotes a significant difference between control and treatments, B denotes a significant difference between dug and suck. d.f. = 2,6. ^a indicates the use of a log (x+1) transformation.

LOG TIME	0.30	0.48	0.70	1.28	1.65	1.86	2.18	2.47	2.78
TIME	1d	2d	4d	18d	1m	2m	4m	9m	18m
<i>Ceratonereis erythraensis</i>									
<u>ANOVA</u>									
F	0.058	1.892	-	6.491 ^a	0.553	11.725	0.377	3.577 ^a	0.142
P	NS	NS	-	**	NS	**	NS	*	NS
<u>CONTRAST</u>	NS	NS	-	A**	NS	A***	NS	A**	NS
<i>Notomastus latericeus</i>									
<u>ANOVA</u>									
F	-	-	-	0.097	3.459 ^a	4.651	1.254	0.827 ^a	0.464
P	-	-	-	NS	*	*	NS	NS	NS
<u>CONTRAST</u>	-	-	-	NS	A**	A**	NS	NS	NS
<i>Cleistostoma edwardsii</i>									
<u>ANOVA</u>									
F	0.640	4.835	7.934 ^a	56.624 ^a	9.376 ^a	10.688 ^a	2.350 ^a	82.765	0.793
P	NS	*	**	***	**	**	NS	***	NS
<u>CONTRAST</u>	NS	A**	A**, B**	A***, B***	A**	A**	A*	A***	NS
<i>Hymenosoma orbiculare</i>									
<u>ANOVA</u>									
F	-	-	-	-	-	39.350	7.594 ^a	3.679	16.056
P	-	-	-	-	-	***	**	*	***
<u>CONTRAST</u>	-	-	-	-	-	A***	A**, B**	A**	A**

Table 3.16. Response of less dominant species in relation to time after disturbance of *Upogebia africana* in control, dug and sucked-over areas. Numbers are mean densities (n=3) per m². *, **, *** indicate significant differences between control and treatment at P<0.1, P<0.05 and P<0.005 respectively. d=days, m=months.

SPECIES	1d	2d	4d	18d	1m	2m	4m	9m	18m
Gastropoda									
<i>Marginella capensis</i> Krauss									
CONTROL	-	3	-	27	10	10	7	13	60
DUG	-	-	-	10	-	-	-	17	13**
SUCK	3	-	-	-	-	-	7	17	37
<i>Littorina knysnaensis</i> Philippi									
CONTROL	3	-	18	-	23	-	10	27	3
DUG	3	15	-	13	17	3	13	-	7
SUCK	-	-	-	23	3	67	10	7	7
Polychaeta									
<i>Arbinia angrapaquensis</i> (Aug.)									
CONTROL	9	54	68	77	17	183	13	30	1313
DUG	3	18	-**	3**	-	3**	23	40	1127
SUCK	-	15	12**	17	3	10**	17	30	490
<i>Parphysa depressa</i> (Schm.)									
CONTROL	44	48	82	20	30	70	73	37	153
DUG	15	23**	74	3*	20	10**	23	17**	-**
SUCK	84	12**	89	7	7*	37	7	10**	13**
Isopoda									
<i>Asophaeroma truncatitelson</i> Brnrd.									
CONTROL	-	-	17	10	17	27	13	63	360
DUG	-	-	3	-	7	-	20	123*	260
SUCK	-	-	-	-	10	-	-	17	320
<i>Asophaeroma pallidum</i> Brnrd.									
CONTROL	-	-	-	-	-	10	-	37	40
DUG	-	-	-	-	-	7	-	43	43
SUCK	-	-	-	-	-	-	-	-	57
Amphipoda									
<i>Ampelisca palmata</i> Brnrd.									
CONTROL	-	-	-	-	-	3	27	-	30
DUG	-	-	-	-	-	7	37	10	40
SUCK	-	-	-	-	3	20	70	-	47
<i>Symadusa filosa</i> Sav.									
CONTROL	12	3	47	53	23	17	40	73	583
DUG	9	-	-***	-***	-	-	7	53	483
SUCK	3	-	-***	-***	27	-	-	33	887
<i>Paramoera capensis</i> (Dana)									
CONTROL	-	-	-	-	-	-	3	-	917
DUG	-	-	-	-	-	-	-	-	130**
SUCK	-	-	-	-	-	-	3	-	347**
<i>Melita zeylanica</i> Stebb.									
CONTROL	-	-	-	-	-	-	-	7	650
DUG	-	-	-	-	-	-	-	40	63**
SUCK	-	-	-	-	-	-	-	93	137**
Myxidacea									
<i>Gastrosaccus brevifissura</i> O. Tattersall									
CONTROL	-	-	-	-	3	77	10	3	23
DUG	-	-	-	3	-	3**	17	-	23
SUCK	-	-	-	-	3	-**	-	-	3
Decapoda									
<i>Diogenes brevirostris</i> Stimps.									
CONTROL	3	-	-	-	-	-	-	-	3
DUG	-	-	-	7	-	3	20	23	3
SUCK	-	-	-	7	3	-	10	3	-

EFFECTS ON:	PREDICTED EFFECTS OF THE REMOVAL OF:		ACTUAL OUTCOME OF THE REMOVAL OF:	
	<i>Callianassa kraussi</i>	<i>Upogebia africana</i>	<i>Callianassa kraussi</i>	<i>Upogebia africana</i>
THE PRAWNS	↓ short-lived	↓ short-lived	↓ prolonged	↓ prolonged
SEDIMENT PROPERTIES	↓ oxygen; minor composition changes	↓ oxygen; minor composition changes	↓ oxygen; minor composition changes	↓ oxygen; minor composition change
CHLOROPHYLLS	↑ short-lived	no change	↑ short-lived	↑ short-lived
BACTERIA	↓ short-lived	short-lived	↓ short-lived	↑ short-lived
MEIOFAUNA	↑ short-lived	or no change	↓ then short lived	↓ then short lived
MACROFAUNA	↓ short-lived	short-lived	↓ prolonged	↓ prolonged
		hermit crabs	hermit crabs	hermit crabs

Table 3.17. Résumé of the predicted effects of the removal of *Callianassa kraussi* and *Upogebia africana* versus the actual outcome of the removals. ↑ = increase; ↓ = decrease, with length of the arrow indicating the strength of the response.

DISCUSSION

Table 3.17 summarises the predicted results of the experimental depletion of prawns, derived from the hypotheses outlined in the introduction, and recapitulates the responses that were actually obtained. Most of the responses conformed to the predictions but three of the more interesting unexpected results were the prolonged depletions of both prawn and macrofaunal numbers, and the initial short-term depressions of the meiofauna.

The effects on *Callinassa* and *Upogebia*

The results presented here strongly indicate that the effects of high-intensity disturbance on *U. africana* and particularly on *C. kraussi* are longer-lived than anticipated. Although a prolonged recovery was predicted for *U. africana*, the development of dense *Zostera* may have further inhibited it - seagrasses have been shown to present physical obstacles to the movement of other thalassinids (Brenchley 1982; Harrison 1987). Activities from callianassids have previously been shown to return disturbed systems to pre-disturbance conditions within a period of six weeks (Riddle 1988) - the prolonged 18-month reduction of *C. kraussi* densities in this study was therefore unexpected. Several reasons can be explored. They include the development of anoxic conditions, changes in the physical composition of the sediment and altered biological interactions.

Former studies have revealed both *U. africana* and particularly *C. kraussi* to be typically estuarine in that they are extremely euryhaline (Hill 1971; Forbes 1973a) and adapted to conditions of hypoxia (Hill 1967; Hanekom & Baird 1987). This implies that anoxic conditions which were present or developed within the sediment after disturbance were not the primary cause of the slow recovery of *C. kraussi* and *U. africana*. The fact that the populations of both *U. africana* and *C. kraussi* declined far more than would have been expected from the numbers of animals removed, suggests that the disturbance as such had a powerful negative effect on their populations.

Similarly, as the modifications in sedimentary particle composition were temporary and relatively minor, they are an unlikely explanation for the slow recovery of the prawns. Indeed, the ability of callianassids themselves to influence grain size characteristics is well-known (e.g. Suchanek *et al.* 1986).

However, other physical properties of the sediment overtly influence the mobility of burrowing organisms (Brenchley 1982). In particular, sediment compaction (which is

related to particle size and sediment sorting) is known to restrict the movement of burrowing organisms (Chapman 1949; Brenchley 1982 and references therein). In general, mobility is reduced in poorly sorted sediments because the sedimentary fabric becomes "tighter" (*sensu* Rhoads 1974) when fine particles rather than water fill spaces between larger grains.

This may explain the slow recovery of the prawns - a suggestion that is supported by the reduced penetrability of the sediment at Klein Oesterwal (but not at Geelbek) after disturbance. Previous records have indicated that densities of both *C. kraussi* and *U. africana* increase in areas in which the substrate has become more easily penetrable through siltation (Gaigher 1987).

The potential complexity of these patterns is further underscored by the fact that the density of other burrowers in the sediment will influence burrowing ability and may either enhance conditions or be detrimental. For example, *Callianassa* itself may increase sediment penetrability, making it easier for other *Callianassa* individuals to burrow. Conversely, by continually reworking the surface sediments, the high numbers of hermit crabs which accumulated in disturbed sites at Klein Oesterwal may have played a major role in preventing the relocation of *C. kraussi*.

Not only does a change in sediment composition affect mobility but it is of paramount importance to the settlement of many invertebrate larvae (Gray 1974; Lee *et al.* 1977), particularly as settlement has been shown to depend on the presence of living microorganisms on sand grains (see Gray 1974; Probert 1984 for a general discussion). Probert (1984) suggests that not only will sediment stability increase during an initial recolonisation phase but disturbance of the sediment may in itself provide a geochemical settlement cue for larvae. Thus, although poorly understood (Dayton & Oliver 1979), processes affecting larval recruitment may powerfully influence the establishment and maintenance of soft-bottom communities (Thorson 1966; Dauer & Simon 1976).

Although it would be tempting to conclude that the prevention of larval settlement is a plausible explanation for the prolonged reductions of the sandprawn, *C. kraussi* is characterised by a markedly abbreviated larval life which has lost its planktonic phase (Forbes 1973a,b). Recruitment of *C. kraussi* occurs by way of post-larval stages which tend to be stronger, faster swimmers and more efficient burrowers than mature prawns (Forbes 1973a,b). *U. africana*, on the other hand, has maintained a planktonic phase (Hill 1967) and inhibited larval settlement may be quite feasible in this case.

Thus the re-establishment of *C. kraussi* and *U. africana* may have been retarded by a host of factors, although sedimentary compaction is most likely to be the primary cause. However, it is clear that the effects of disturbance associated with bait-collecting on prawn populations are far greater than would be estimated from the numbers of prawns removed. At Klein Oesterwal, for example, intense bait-collecting led to the removal of between only 6.7% and 13.1% of the prawns present (dug and sucked-over sites respectively), but the population declined by about 70% as a result - an effect that lasted for at least four months. Evidently the physical disturbance associated with bait-collecting has a far larger impact than the actual removal of the prawns.

The removal of *C. kraussi* and *U. africana* probably resulted in the collapse of a wide network of burrows, possibly accounting for the deflation of sediment in the experimental sites. As well as extending the oxic layer, the burrows of these prawns generally serve as housing for a host of associated bacteria, meiofauna and macrofauna which utilise these nutrient-rich, irrigated micro-environments (Ott *et al.* 1976; Rhoads *et al.* 1977; Reise & Ax 1979; Reise 1981a,b; Bell 1983; Branch & Pringle 1987; Reise 1987). However, *C. kraussi* may also have negative effects on the meiofauna (Branch & Pringle 1987) and a recent report has showed lower meiofaunal densities in *C. trilobata* burrows than in the ambient sediment (Dobbs & Guckert 1988). Removal of the prawns, the collapse of their burrows, and disturbance of the sediment may therefore have a ripple of effects on other components of the biota.

Effects on the microflora

Surface levels of microalgal chlorophyll in the experimental sites predictably rose above control levels within 1 month of *C. kraussi* being removed, and remained elevated for approximately 2-4 months after treatment (Figure 3.2). This confirms previous experiments which showed that *C. kraussi* buries surface-dwelling microflora whilst reworking the sediment (Branch & Pringle 1987); consequently, in the absence of the sandprawns greater amounts of microflora build up on the surface. It was anticipated that surface chlorophyll levels would remain elevated until *C. kraussi* numbers recovered. However, chlorophyll levels returned to control levels within 2-4 months of the initial disturbance despite prolonged reductions of sandprawn numbers. This is most readily explained by grazing - initially by the increased meiofaunal populations and later on by the dense assemblies of *D. brevis* which reworked the sediment and would consequently have reburied and/or grazed the microalgae (Bolt 1961; Schaefer 1970).

Contrasting trends were found after the removal of *U. africana* (Figure 3.9). *U. africana* filter-feeds and, accordingly, has a more permanent burrow than the detritivorous *C. kraussi* (Hill 1967; Ott *et al.* 1976). Consequently, its turnover of sediment is probably minimal. The initial depression of surface chlorophyll levels in treatment areas relative to control areas (Figure 3.9) was probably caused by the burial of surface-dwelling microflora. After the first month, these differences disappeared. (The later recurrence of differences in month 9 remains unexplained, but measurements may by then have been confounded by the growth of *Zostera*).

Few studies have detailed the response of benthic diatoms to disturbances of soft-bottom communities. Available figures suggest that the colonisation of defaunated sediment by benthic microalgae is rapid (Davis & Lee 1983), being generated - at least in shallow-water systems - through transport in the water column (Baillie and Welsh 1980). It thus seems unlikely that bait-collecting could reduce the microalgae for any prolonged period; on the contrary, the removal of large bioturbators should increase surface concentrations of microalgae due to the stabilisation of the sediment (Holland *et al.* 1974).

Effects on the bacteria

As predicted, bacterial numbers initially paralleled the decimation of sandprawn populations in the experimental areas and were accordingly reduced (Figure 3.3). This effect was scarcely discernable in the case of *U. africana* removals (Figure 3.10). Even at Klein Oesterwal, declines in bacterial abundances were short-lived despite the protracted reductions in the numbers of thalassinids. This implies that a secondary controlling factor other than biogenic activity was responsible for the restored bacterial densities.

One of the more obvious manifestations of the treatment was the deflation of the sediment, leading to the formation of large depressions in the disturbed areas. These depressions would have experienced the same physical forces as those described for feeding pits of rays (Cook 1971; Reidenauer & Thistle 1981), currents and wave action causing the edges of the depression to erode toward the centre and decreasing shear stress (Eckman 1983; Savidge & Taghon 1988). Depressions act as catchments for finer sediments, drift algae and other debris (Weinberg 1979; Thistle 1981; VanBlaricom 1982; Tamaki 1984; DePatra & Levin 1989), concentrating the fallen debris into an organic soup which may be an attractive nucleus for bacterial activity. It is possible that the depressions which formed in the experimental areas facilitated recovery of the bacterial

populations, which returned to background levels very shortly after the disturbance.

The resistance of bacterial communities to physical perturbations, at least within salt marsh soils, is well known (Christian *et al.* 1978; Howarth & Hobbie 1982). This resistance does not imply that the species composition will not alter. Indeed, given the change in sediments to increased anoxia, a switch from aerobic to anaerobic forms is implicit (Aller & Yingst 1985) and studies have shown the enormous resilience of anaerobic forms after perturbations (Christian *et al.* 1978).

Several functional groups of organisms affect the chemocline and occupy specific positions with respect to the aerobic-anaerobic gradient (or redox potential discontinuity - RPD) within the sediment. The RPD is known as a site of high microbial activity (see Yingst & Rhoads 1980 and references therein), where bacterial-feeders concentrate (Fenchel & Riedl 1970). At Klein Oesterwal, the RPD was identified as lying at approximately 3.4 cm below the sediment surface of the disturbed areas. Similar blackened, soft patches of substrate, indicative of reducing conditions, appear and remain for some time in areas where prawns have been collected. Their development has previously been associated with *Callinassa* removals (Peterson 1977).

At Klein Oesterwal, a shallow, anoxic, sulphurous sediment developed within days of the disturbance, so a switch to predominantly anaerobic forms amongst the bacteria was probably rapid. Since anaerobic forms are less productive than aerobes (Battersby & Brown 1982; Alongi 1985), this might explain the initial reductions in bacterial numbers at Klein Oesterwal. The substrate at Geelbek is perpetually anoxic and similar reductions were consequently not observed.

Finally, although meiofaunal and macrofaunal predation rates on the bacteria were not determined in this study, previous studies have suggested that the role of larger benthos in controlling bacterial activity is small, particularly under conditions of high organic input (see Alongi 1985 and references therein). Certainly at Klein Oesterwal, large increases in the meiofauna did not apparently have any effect upon the bacteria which, after an initial decline (unrelated to meiofaunal abundance), rapidly returned to background levels. Similarly, substantial increases in the numbers of hermit crabs in the experimental areas at Klein Oesterwal in months 2 to 4 apparently failed to influence bacterial numbers.

Effects on the meiofauna

The resilience of the meiofauna in these experiments was evidenced by the sharp rise in density of all taxa following disturbance (Figures 3.4a-d; 3.11a-e) and is in accordance with previous experiments (Sherman & Coull 1980; Thistle 1981; Hogue 1982; Alongi *et al.* 1983; Sherman *et al.* 1983; Webb & Marcotte 1984; Alongi 1985). This resilience may predispose the meiofauna to resisting anthropogenic stresses (McIntyre 1969; Boesch & Rosenberg 1981) such as those inflicted by bait-collecting.

Numerically, nematodes dominated at both Geelbek and Klein Oesterwal, with turbellarians and copepods proving to be the most resilient taxa. The ability of copepod assemblages to proliferate under optimum conditions is common and has been attributed to flexible nutritional requirements (Hicks & Coull 1983; but see Austen 1989). Since individual meiofaunal species were not considered in this study, it was difficult to conclusively determine whether any single dominant species was affected by the treatment or whether the group responded as a whole. After being initially reduced for 4 weeks at Klein Oesterwal, meiofaunal densities became disproportionately abundant - thereafter falling below control levels. After 18 months, only the nematodes at Klein Oesterwal did not equal background densities. Meiofaunal numbers at Geelbek statistically equalled control levels within 4 weeks of the disturbance.

These results confirm previous experiments which have revealed the tendency for meiofauna to become disproportionately abundant during early stages of recolonisation (see Heip *et al.* 1985). This has been attributed both to the considerable intrinsic growth potentials and highly plastic reproduction strategies of meiofauna (Heip *et al.* 1985).

The ability of meiofauna to recolonise disturbed sediments rapidly has been well documented (e.g. Sherman & Coull 1980; Thistle 1980; Reidenauer & Thistle 1981; Fegley 1988) although estimates are variable. For example, the time taken for meiofauna to recolonise small patches ranges from 1.5 h for spot feeding pits (Billheimer & Coull 1988) to 7 days for decaying organisms (Gerlach 1977), but other recolonisation rates reported for meiofauna are much lower, of the order of months (Coull 1969; 'Olafsson & Moore 1990) and even years (Pequegnat 1975). The present experiments suggest a recolonisation time of at least 1 month.

Given the rapid colonisation rates for meiofauna, the mode of recolonisation is of interest and it seems likely that the meiofauna is more active than previously thought. Conventional views hold that movements of meiofauna into depressions are due to passive transport by currents and erosion from surrounding sediments (Sherman & Coull 1980; Palmer 1984, 1986; Billheimer & Coull 1988). However, contradictory evidence

advocating active migration of meiofauna to sites of low relief (with high concentrations of resources) has been unequivocally demonstrated by a number of researchers (Reidenauer and Thistle 1981; Thistle 1981; VanBlaricom 1982; Fegley 1988; Hicks 1989). If one were to accept colonisation by passive transport, then high numbers of meiofauna should be sustained within the depressions by ongoing passive input. After the initial escalations in meiofaunal abundance in the disturbed areas at both Klein Oesterwal and Geelbek, numbers either returned to control levels or were suppressed below them. It is thus proposed that the colonisation sequence cannot be explained solely by passive advection and may depend on the hydrodynamic environment (Palmer 1988; DePatra & Levin 1989; 'Olafsson & Moore 1990), active movement of the meiofauna, and interactions between species (see Savidge & Taghon 1988 for a more complete review).

The capacity of some macrobenthic species to regulate meiofaunal communities either by predation, physical disturbance or perhaps competition has been confirmed by many reports (McIntyre 1969; Bell & Coull 1978, 1979; Dye & Furstenberg 1978; Gerlach 1978; Bell 1980; Reidenauer & Thistle 1981; Branch & Pringle 1987; 'Olafsson & Moore 1990). However, the overall predation by macrofauna on the meiofauna is still relatively unknown, as is the importance of the meiofauna as prey. Although increases in meiofauna have been documented after experimental reductions of predators/disturbers (Bell 1980; Bell & Woodin 1984; 'Olafsson & Moore 1990), Reise (1979) demonstrated that permanent meiofauna remained unaltered when predators were excluded and hence concluded that permanent meiofauna of the Wadden Sea was only locally and temporarily 'grazed down' by macrobenthos.

The initial reductions of meiofauna in the present experiments were in all likelihood a response to extreme anoxia immediately following the disturbance. Although exceptions do occur, a positive relationship between meiofaunal density and oxygenation exists (Reise & Ax 1979 and references therein). It is proposed that subsequent increases in meiofaunal numbers at both Klein Oesterwal and Geelbek were disturbance-associated phenomena, following the classical post-disturbance peak (Dayton & Hessler 1972). The subsequent suppression of meiofaunal numbers at Klein Oesterwal was concomitant with large increases of hermit crabs into the disturbed areas. As *D. brevis* actively reworks the sediment, it is difficult to separate its potential predation from the disturbance it creates. However, influxes of hermit crabs into the depressions occurred at the same time that the meiofauna was declining from its peaks of abundance, implying that meiofaunal density may have been indirectly or directly

controlled by the hermits. This argument is supported by the trends observed at Geelbek where hermit crabs were scarce; here post-peak meiofaunal numbers rapidly returned to control levels. Although it has been documented that large numbers of meiofauna are 'grazed down' by hermit crabs (Gerlach *et al.* 1976; Lee *et al.* 1976; Reise 1979), the contribution by the meiofauna to their carbon budget is probably negligible and it seems likely that the physical disturbance generated by the hermit crabs reduces meiofaunal abundance, similar to the effects that some *Callianassa* species have on the meiofauna (Alongi 1986; Branch & Pringle 1987).

Effects on the macrofauna

The experiments described here clearly demonstrate that a variety of macrofaunal species was adversely affected by disturbance in the experimental areas, and that rates of macrofaunal recolonisation were markedly slower than anticipated. The fact that macrofauna recovers slowly when compared to meiofauna has been well documented (Bell 1980; Thistle 1980, 1981; Woodin 1981; Bell & Devlin 1983; Bell & Woodin 1984) and can be ascribed to both shorter generational times of meiofauna (e.g. McIntyre 1969, Gerlach 1971 for meiofauna; Sellmer 1967 for macrofauna), and the greater rapidity with which meiofauna can move through sediments (through 'resuspension') (Bell & Coen 1982; Savidge & Taghon 1988). Nevertheless, macrofaunal recolonisation rates have been recorded to be as short as 7 hours (Bell & Devlin 1983) and 24 hours (Frid 1989), while Thrush & Roper (1988) noted considerable colonisation by adult infauna within 20 days.

In the present experiments, responses of the macrofauna could be broadly categorised into three patterns: species which were initially reduced by the treatments and were then slow to recolonise; species which appeared to have their recruitment suppressed relative to the control areas - even long after the treatment; and species which were unaffected by the treatment. Only a single species, the hermit crab *D. brevis*, increased its numbers in response to the disturbance.

Examples of the first response are provided by the orbiniid *Orbinia angrapequensis* and the crab *Cleistostoma edwardsii*, both of which declined in the experimental areas following the disturbance, and took at least 9 months to recover. As *C. edwardsii* is highly mobile, its prolonged depression in disturbed sites implies ongoing active avoidance of these areas. Densities of *Carditella rugosa* and *Kellya rubra* remained low in the experimental sites at both Klein Oesterwal and Geelbek up until the termination of the experiment. Considerable increases in control samples were not matched by

increases in the disturbed areas, suggesting recruitment failure within the disturbed areas. All of these species exhibited the same responses at both Klein Oesterwal and Geelbek. Such identical responses under different physical conditions are strong pointers to disturbance being responsible, rather than local environmental conditions.

Urothoe grimaldi, *Nassarius kraussianus* and *Cymadusa filosa* were initially affected by the treatment, but none showed signs that their subsequent recruitment was affected. A clear explanation for this may be found in their mode of reproduction. All three species retain their eggs in brood pouches or egg cases, releasing larvae at a later and less vulnerable stage (Griffiths 1976; Palmer 1980).

Species which were most sensitive to disturbance in these experiments were sedentary, shallow-dwelling, tubicolous deposit feeders. For example, the fragile *Euclymene* sp. and *Notomastus latericeus*, both sedentary surface dwellers, were considerably reduced after the disturbance and also showed clear recruitment effects. At Geelbek, mobile organisms such as *Hydrobia* sp. displayed extremely rapid recolonisation rates by adults but diminished recruitment.

The disturbance affected *D. brevis* positively at Klein Oesterwal (Figure 3.7a) and probably also at Geelbek (Table 3.16). Dense aggregations of hermit crabs have previously been noted by Walters & Griffiths (1987), who recorded densities of up to 632 individuals m⁻² of *D. brevis* in seagrass-free depressions at Langebaan Lagoon. Asakura (1987) observed large conglomerations of migratory *D. nitidimanus* in creeks or tide pools, implying that moisture confers some advantage to the crabs. However, further experimentation would be required to elucidate why *D. brevis* aggregates in depressions, including those generated by the disturbance.

Walters & Griffiths (1987) ascribed the aggregation of *D. brevis* at natural depressions to an absence of *Callianassa* and seagrass rhizomes. Asakura & Kikuchi (1984) have noted that the hermit crab *Diogenes nitidimanus* is rare in areas where *Callianassa japonica* densities are high. However, it is possible that hermit crabs actively migrate to micro-sites where food resources are concentrated (Bauer 1985; Asakura 1987). Passive settlement of detritus into the depressions created by the disturbance may result in a detritus-rich resource as discussed earlier. The ability of *D. brevis* to use its antennae to feed by filtering fine particles in addition to its typical scavenging behaviour, was observed by Boltz (1961) and Schaefer (1970) and has been further documented for *Pagurus bernhardus* (Gerlach *et al.* 1976). Thus, in addition to enhancements of organic debris, microbes and meiofauna in the depressions, increases in surface chlorophylls (arising from a reduced amount of sediment reworking by *C.*

kraussi) may provide an additional source of food to the foraging crabs. The reduction in *D. brevis* abundance after 18 months coincided with a levelling-out of the depressions, a reversion of meiofaunal numbers and surface chlorophylls to ambient levels, and increased recolonisation by *C. kraussi*.

Biological interactions

Although physical characteristics of the environment, food availability, predation and larval recruitment all may affect the composition of benthic communities, several researchers have suggested that indirect interactions between groups of functionally similar organisms may also play important roles in determining distribution patterns.

The concept of "trophic group amensalism" (*sensu* Rhoads & Young 1970) has been widely used to explain negative interactions between soft-sediment organisms, for example between filter and deposit feeders and between tube-dwellers and burrowers (e.g. Rhoads & Young 1970; Bloom *et al.* 1972; Levinton 1972; Aller & Dodge 1974; Woodin 1976; Myers 1977; Weinberg 1984; Jensen 1985).

Revisions of the hypothesis have been offered by Brenchley (1981, 1982) who concluded that mobility rather than feeding type determined the nature of interactions among biota, because of the effects that different species have on the stability of the substrata (Gallagher *et al.* 1983; Thrush 1988; McCann & Levin 1989). Further elaborations of the model have drawn attention to the incompatibility between sediment stabilisers and destabilisers (e.g. *Zostera* and *Callianassa/Upogebia*) (Brenchley 1982; Suchanek 1983; Murphy 1985; Reise 1985; Harrison 1987; Posey 1987).

C. kraussi has a clear negative effect on diatoms (Branch & Pringle 1987). Increases in surface diatoms following removal of *C. kraussi* (Figure 3.2) were therefore predicted. This was probably the only biological response directly attributable to reductions of *C. kraussi*. All other responses were more likely to have been induced by the disturbance of the sediment and its subsequent compaction - this overriding any potential biological interactions structuring the communities during its recovery.

Severe environmental disturbances generally tend to be followed by a 'noninteractive' phase of recolonisation (Simberloff & Wilson 1969; Schoener 1974; Dauer & Simon 1976; Reise 1985) during which densities are relatively low and competitive and predatory pressures are minimal. However, the build-up of large numbers of *D. brevis* in the later stages of colonisation at Klein Oesterwal must have had effects on other species. Occurrences of this kind, in which *D. brevis* aggregates in extremely high densities, are however likely to be chance events, related

to local disturbance. They will probably cease when sedimentary movements stabilise the topography and eliminate the depressions - as occurred at Klein Oesterwal in the closing stages of the experiment (Figure 3.7a). Thus, indirectly, the alteration of the sediment by compaction was the factor responsible for the aggregation of hermit crabs and their subsequent dispersal coincided with a levelling of the depressions.

The role of physical disturbance

Models of soft-bottom community structure have emphasised the importance of disturbance in producing a mosaic of habitat types, and consequently, local areas of available resources (e.g. the concentration of drift organic matter) (Grassle & Sanders 1973; Thistle 1981; VanBlaricom 1982; Grant 1983). This pattern is particularly apt for the meiofauna, where short life-cycles, adaptive reproductive strategies and opportunistic behaviour patterns are preadaptive to stress situations, including anthropogenic disturbance. However, what appears to be a disturbance for one benthic group may have little impact, or only a short-lived effect, on another and while one component may be resistant, others may not be.

The effects of bait-collecting have previously been demonstrated by Peterson (1977) who observed declines in the numbers of some previously abundant species in areas of *Callinassa californiensis* exploitation. Conversely, the removal of *C. californiensis* resulted in high recruitment of *Sanguinolaria nuttallii*, and increased *C. californiensis* densities were followed by a decrease of *Cryptomya californica* (Peterson 1976). Blake (1979a) concluded that due to the relative inefficiency of diggers, lugworm (*Arenicola marina*) populations are not threatened by their activities, but bait-digging may be detrimental to other benthic species, as was shown by Jackson and James (1979) for the common cockle, *Cerastoderma edule*. On the other hand, McLusky *et al.* (1983) showed no deleterious effects on populations of benthic animals other than *Arenicola* itself which did not recover for over 3 months after digging.

Effects comparable to bait-digging (following sedimentary disturbance) have been shown by Canadian workers (Levings *et al.* 1978 in McLusky *et al.* 1983) who reported macrofaunal reductions in areas adjacent to a dug-out ditch, but also the creation of new micro-habitats for some species utilising plant debris which accumulated in the ditch. Hruby (1987) has shown bait-digging to have an impact on areas dug more than once. Conner & Simon (1979) and Bonvicini *et al.* (1985) have described enormous macrofaunal reductions after dredging operations, but a rapid return to pre-dredging conditions within 6-12 months, and concluded that in the absence of other disturbances

interacting to cause unpredictable effects, dredging may take place without long-lasting or irreversible environmental impact.

These trends strongly indicate that the disturbance induced by bait-collecting is more deleterious than the removal of mud- and sandprawns *per se*. Nonetheless, the impact which the disturbance inflicts upon the prawns themselves still implies that on a large enough scale, bait-collecting could orchestrate changes in the community structure. On the small, patchy, scale on which bait-collectors currently operate this is unlikely. Nevertheless, large, active burrowers such as thalassinids do reduce the abundances of smaller tube-builders and bivalves (Stevens 1928; Peterson 1977; Thayer 1979; Dorsey & Synnot 1980; Brenchley 1981, 1982; Suchanek 1983; DeWitt & Levinton 1985; Tamaki 1985, 1988; Posey 1986; Riddle *et al.* 1990). Their removal may consequently have a ripple of indirect effects. There is, however, little indication that such changes will be irreversible. None of the species which is indirectly affected by a reduction in the prawns has the capacity to subsequently inhibit re-invasion by the prawns.

Conclusions

Much of the information on forces organising soft-sediment communities has been inferred from a 'black box' approach using single field experiments or short-term monitoring of communities. Temporal variability (Zajac & Whitlatch 1982a) and current demographic states (Zajac & Whitlatch 1989) have often been overlooked. Zajac & Whitlatch (1982b) have further emphasised the importance of the timing of the disturbance, the habitat in which the disturbance takes place and the reproductive periodicity of the infauna in determining succession.

The role of chance in determining experimental results has been highlighted by Reise (1983) who conducted a 3 year study on the removal of *Arenicola marina*. Depending on the events which happened to strike the sites (e.g. algal mats, geese, seagrass and polychaete invasion), removal of the lugworms had positive, neutral or negative effects on the benthic community. Caution must therefore be exercised in extrapolating beyond primary effects - patterns revealed in this study are similarly unique in space and time. At Geelbek, for example, increases in the amount of *Zostera* resulted in a marked increase in species richness and a change in species composition of both experimental and control sites. The initiation of the experiments at this time may have revealed completely different trends from those observed, as has been demonstrated by Zajac & Whitlatch (1982b). The influx of an unprecedented number of hermit crabs at

Klein Oesterwal was completely unpredicted and probably resulted in a chain reaction of events which are difficult to separate from the effect of the disturbance - this ideally should comprise a study in itself, as the scale of the present experiment is insufficient to differentiate between singular and general relationships.

Despite these complications, the results clearly show that intense harvesting of mud- and sandprawns had a prolonged detrimental effect on the prawns, the magnitude of which was far greater than would have been predicted from the actual proportion of the population removed. Disturbance of the sediment, resulting in compaction, seems the most likely agent responsible. Unambiguous side-effects included a long-lived decrease in macrofaunal numbers, biomass and richness; short-term depressions of meiofaunal numbers, followed by rapid increases and later declines; and brief increases in surface microflora - at least in the case of *Callianassa* removals. Deflation of the sediment also led to increases in the numbers of hermit crabs, with unknown effects on other components of the biota.

On a final note, the concept of tidal flats serving as an "ecological turntable" (*sensu* Reise 1985) between two adjoining ecosystems - land and sea - provides a forewarning of the potential risks involved in destroying large parts of these flats through bait-collecting. A holistic approach, revolving around the principles of Gaia (Lovelock 1982, 1989) and consequently accounting for all ecosystem components, their complex interactions, and the long-term effects of deforming the sandflats, is imperative to effective management of these fragile ecosystems.

CHAPTER 4

The Short-Term Effects of Low-Intensity Disturbance and Trampling on the Biota of an Intertidal Sandflat

INTRODUCTION

The preceding chapter demonstrated that the effects of intense physical disturbance are more deleterious than the removal of mud- and sandprawns. However, the unrealistic intensity of these perturbations prompted a further set of experiments which would more closely simulate disturbance inflicted by bait-collectors and, hence, be directly applicable to the formulation of any management proposals.

The manner in which a prawn pump is used unavoidably involves deep trampling of the contiguous sediment and, potentially, burrow destruction whilst bait is being collected. With even slight sand movement burrows tend to close up and this may be as damaging as the physical removal of the prawns. This possibility led to an assessment of the side-effects associated with trampling, as part of the investigation.

Since sandprawns represent the most available and hence principal form of bait at both Langebaan Lagoon and most other southern African estuaries (Gaigher 1987), this chapter focuses predominantly on the response of *Callinassa kraussi* and its associated communities to low-intensity harvesting and to trampling inflicted at an intensity approximating that imposed during bait-collecting.

METHODS

Experimental design

Areas of 3 m X 4 m were 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 macrofaunal, meiofaunal and microalgal communities. A preliminary study showed that the pre-disturbance sandprawn populations were homogeneous between the selected sites ($P > 0.05$). No initial macrofaunal or meiofaunal samples were taken from either the experimental or control areas because the method was destructive and would have created additional disturbances in the plots, particularly from trampling. However, previous sampling in the immediate vicinity of selected areas had shown the macrofaunal and meiofaunal communities to be homogeneous ($P > 0.05$).

Three areas were sucked over with a prawn pump until 25, 50 and 100 prawns respectively had been removed. To simulate the behaviour of bait-collectors, only prawns with a body length $> ca.$ 40 mm were counted. Since the aim of this experiment was to determine 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

number of footsteps taken during removal of each of the three respective prawn quotas was counted. Three adjacent areas were then trampled to a similar 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. Cordoned-off areas of approximately 3 m X 4 m in-between these sites acted as independent multiple controls and remained completely undisturbed. After the experimental areas had been disturbed, they were left for a period of six weeks before sampling.

Post-disturbance sampling

Prawn densities were assessed by counting prawn holes, as described in Chapter 3. Holes were counted at 6 weeks and 32 weeks post-disturbance, using 25, random 0.1 m² quadrats within each experimental and control area. Responses of the meiofauna, macrofauna and microflora were quantified from samples taken after 6 weeks, also using the methodology described in Chapter 3.

Data analysis

The day-to-day variability of hole counts necessitated taking independent control quadrats on each of the two consecutive days over which the treatment sites were sampled. Accordingly, a one-way ANOVA was run separately on prawn densities for each control and treatment group. Statistical methods used were as for Chapter 3.

RESULTS

Prawn density

Both trampling and low-intensity sucking had marked short-term effects on the sandprawns (Figure 4.1). With the exception of T25 ($P > 0.05$), all treatment groups had significantly lower prawn densities than the controls after 6 weeks (ANOVA, Tukeys, $F=13.382$, $P < 0.001$, d.f. = 4,120 for T50, S25, S50; ANOVA, Tukeys, $F=25.157$, $P < 0.001$, 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 ($P > 0.05$) (Figure 4.1).

Microflora

Six weeks post-disturbance, chlorophyll levels were lower in all disturbed sites than in the control samples (Figure 4.2), although differences were significant only in sites with the highest intensity of disturbance (S100, T100) (ANOVA, Tukeys, $F=4.448$, $P < 0.005$, d.f. = 6, 21). This trend is in sharp contrast to that discerned for the high-intensity disturbance experiments where chlorophyll levels increased markedly after disturbance (Figure 3.2). 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, $F=4.548$, $P=0.05$, d.f. = 3, 12). Although this pattern also consistently existed in the sucked areas, it was not statistically discernable ($P > 0.1$) (Figure 4.3). If the meiofaunal groups are considered separately, then repeated positive responses to the disturbances were recorded for nematodes, copepods and turbellarians (Figure 4.3). Additional details for less prevalent groups (polychaetes and 'other' meiofauna) are provided in Table 4.1.

Table 4.1. Less prevalent meiofaunal groups not represented by Figure 4.3 six weeks after low-intensity trampling and sucking. Values (mean numbers \pm S.E.) are expressed per 100g, but derived from four 85 ml samples. $P > 0.1$ for all comparisons with controls.

TREATMENT	Numbers of meiofauna per 100 g	
	POLYCHAETES	OTHER
CONTROL	77 \pm 11	10 \pm 11
T25	81 \pm 11	61 \pm 15
T50	123 \pm 40	158 \pm 93
T100	56 \pm 14	57 \pm 19
S25	37 \pm 11	6 \pm 6
S50	180 \pm 85	49 \pm 42
S100	88 \pm 38	23 \pm 8

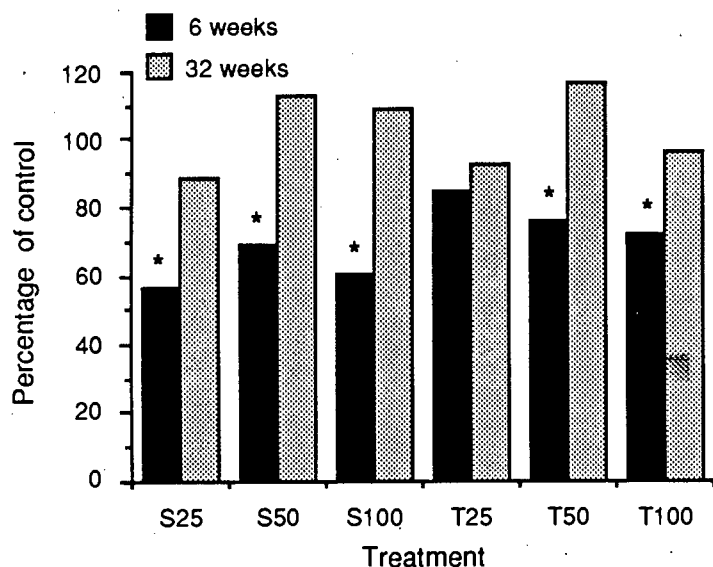


Figure 4.1. Prawn densities (given as a percentage of the control), 6 weeks and 32 weeks after low-intensity sucking (S) and trampling (T). * indicates a significant difference of $P < 0.001$ between control and treatment. S.E. remains constant for all treatments at approximately 6% of the value. Control values (holes m^{-2}) were as follows:
6 weeks - S25,S50,T25,T50 = 85; S100,T100 = 124;
32 weeks - S25,S50,S100 = 66; T25,T50,T100 = 56.

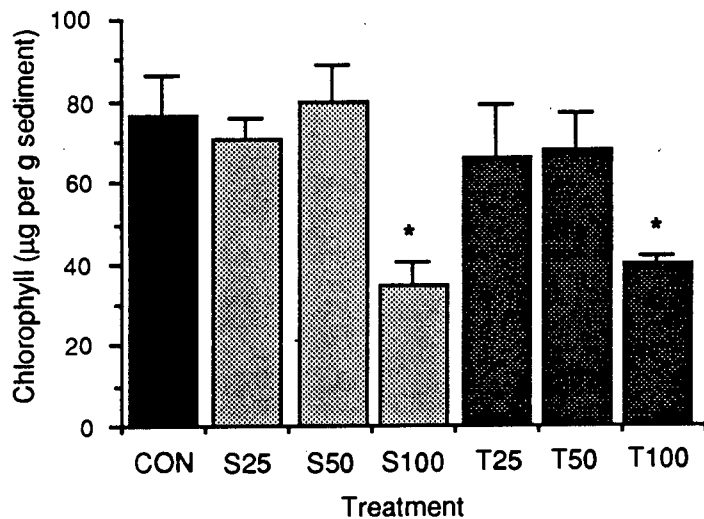


Figure 4.2. Levels of chlorophyll 6 weeks after low-intensity sucking (S) and trampling (T). * indicates a significant difference between control and treatment at $P < 0.005$. S.E. appear above the mean values.

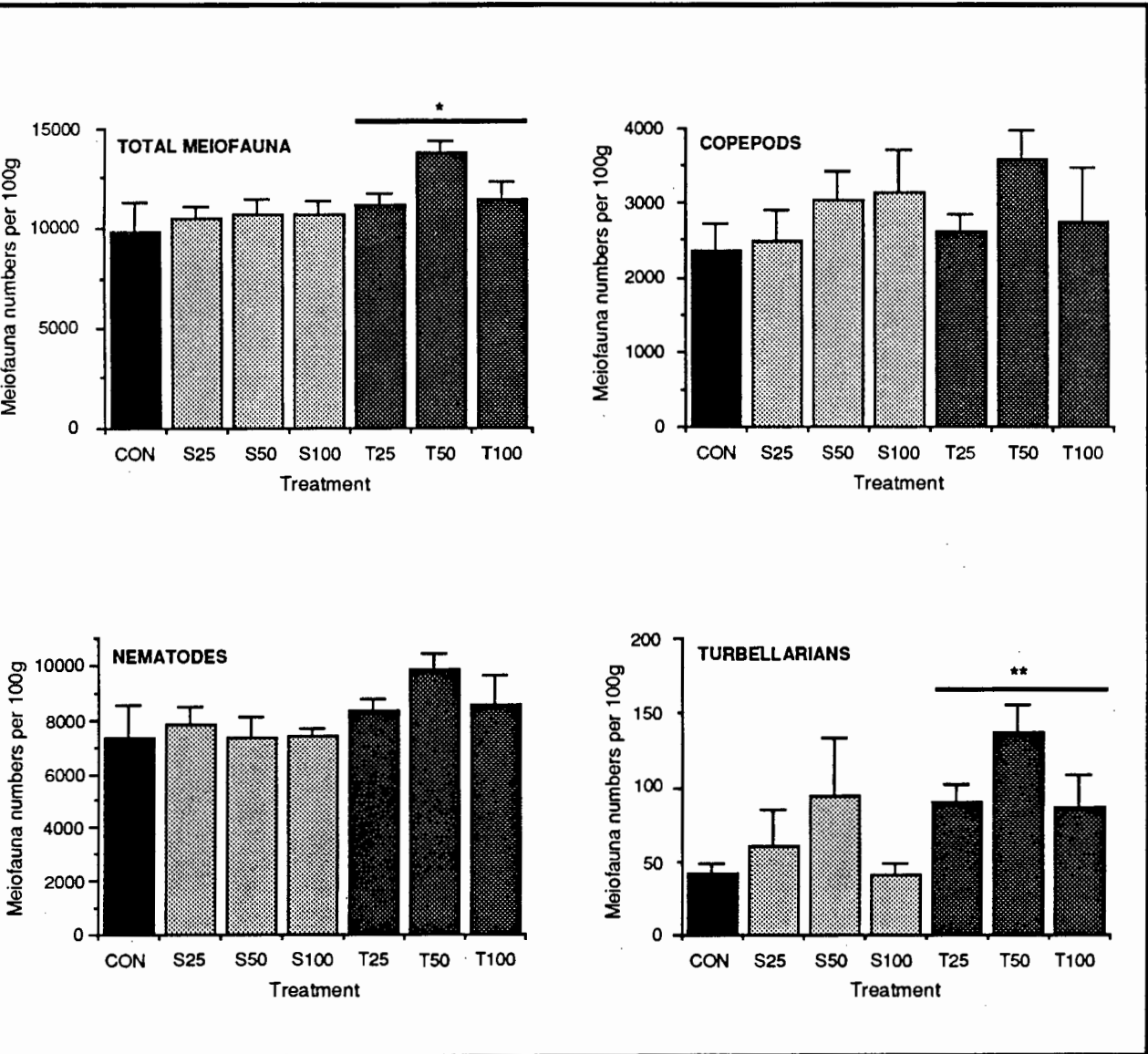


Figure 4.3. Meiofaunal numbers 6 weeks after low-intensity sucking (S) and trampling (T). *, **, indicate a significant difference between control and treatment at $P < 0.05$ and $P < 0.005$ respectively. S.E. appear above the bars.

Macrofauna

Biomass: Figure 4.4 details the mean ash-free biomass figures for control and disturbed areas. These figures exclude the common hermit crab, *Diogenes brevis* which, owing to its relatively large size, tends to swamp the biomass when present and obscure trends amongst the smaller macrofauna. Biomass was 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 declined within all the treated areas in comparison with the controls, the discrepancies between treatments and controls were too small to be statistically conclusive (Table 4.2).

Numbers: Total macrofaunal numbers were depressed in all the sucked treatments (ANOVA, Contrast, $P<0.05$) and two out of three of the trampled treatments, T100 again being the exception (Figure 4.5). Of the dominant macrofaunal species, only *Urothoe grimaldi* and *Scoloplos johnstonei* responded negatively to the sucked treatments (Figure 4.5). The remaining macrofauna appeared little affected by the sucking or trampling (Table 4.2). Although the numbers of *Euclymene* sp., *Notomastus latericeus*, *Marphysa depressa*, *Telothelopus capensis* and *Glycera tridactyla* (all polychaetes) were depressed in all but one of the treatment areas, their small numbers prevent statistical significance being attached to this trend. Unlike the high-intensity disturbances, no depressions were created in the surface of the substratum by the disturbance, nor was the density of *D. brevis* any higher in treatment areas than in controls.

DISCUSSION

Many of the results showed similar, but less striking patterns to those recorded for the high-intensity experiments. For this reason, a discussion of the trends is by necessity brief, highlighting the differences between the two experiments only.

Perhaps the most striking result to emerge from this study is the large 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 the treatments, prawn densities were clearly depressed at 6 weeks although they had recovered by 32 weeks. As in the case of the high-intensity

experiments, the meiofauna responded resiliently and positively to the disturbance; both turbellarians and copepods in particular responded positively. Of the macrofauna, total numbers and the numbers of many individual species exhibited declines associated with the disturbance, as did most of those species affected by the high-intensity treatment. Species richness was also reduced and the only difference between these low-intensity treatments and those described in the previous chapter lies in the response of the microalgae. In contrast to the high-intensity disturbance, chlorophyll levels were reduced within the more intensely trampled and sucked-over plots, implying that they had been buried by the trampling.

In conclusion, with the exception of the microflora, the above results provide similar, though less obvious trends to those of the high-intensity treatments and serve as validations to the trends previously observed. Both numbers and biomass of the macrofauna were reduced after even the least-intense treatments, as were prawn densities. Most notable, 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.

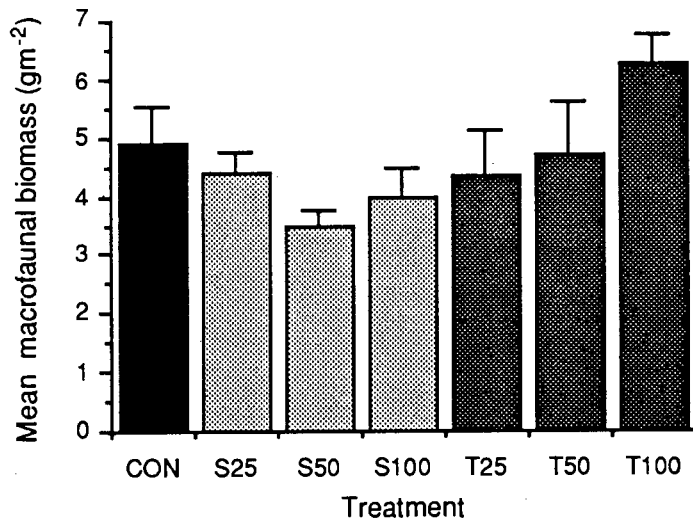


Figure 4.4. Mean biomass values 6 weeks after low-intensity sucking (S) and trampling (T). S.E. appear above the mean values.

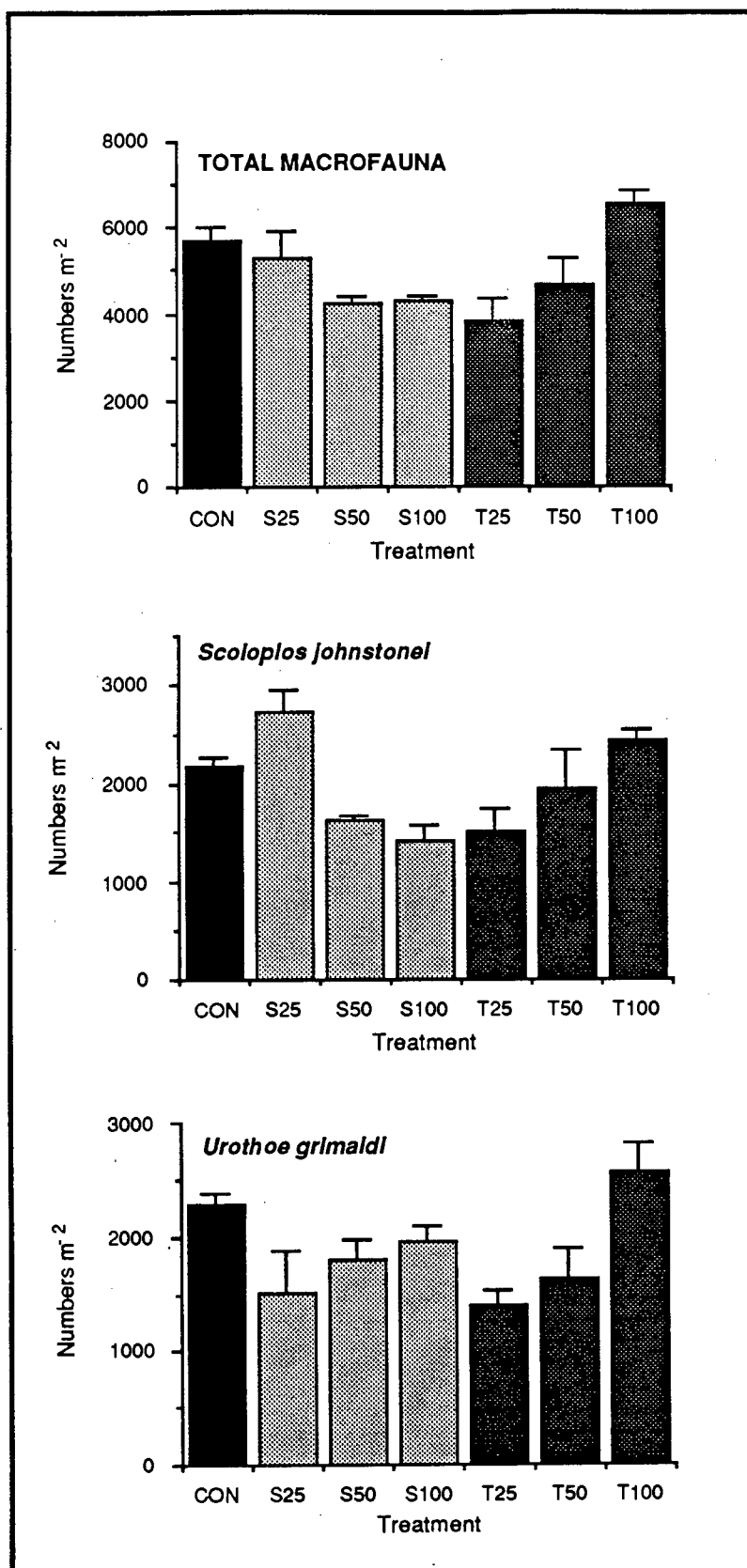


Figure 4.5. Macrofaunal numbers 6 weeks after low-intensity sucking (S) and trampling (T). S.E. appear above mean values.

Table 4.2. Numbers of individuals (per m²) after low-intensity disturbance of *Callianassa kraussi*.

TREATMENT	CONTROL	T25	T50	T100	S25	S50	S100
ISOPODA							
<i>Callinectes</i>							
<i>Callinectes rugosa</i> Sow.	238	180	230	270	250	150	190
<i>Callinectes rubra</i> (Mont.)	130	110	90	210	120	60	120
Unidentified species	3	8	3	23	3	18	10
<i>Callinectes</i>							
<i>Callinectes capensis</i> Krauss	30	100	50	40	40	60	80
<i>Callinectes porcellana</i> Lam.	3	-	-	-	-	-	-
<i>Callinectes cella capensis</i> Krauss	5	5	8	-	5	5	10
<i>Callinectes</i>							
<i>Callinectes johnstonei</i> Day	2160	1500	1940	2420	2730	1640	1420
<i>Callinectes angrapaquensis</i> (Aug.)	88	65	60	118	3	108	30
<i>Callinectes capensis</i> Day	5	-	3	-	-	5	-
<i>Callinectes</i> sp.	258	58	198	420	198	163	108
<i>Callinectes latericeus</i> Sars	248	170	223	265	113	110	205
<i>Callinectes depressa</i> (Schm.)	20	13	15	10	3	13	18
<i>Callinectes tridactyla</i> (Schm.)	40	18	18	30	35	10	148
<i>Callinectes</i> sp.	28	30	15	15	53	10	5
<i>Callinectes lepus capensis</i> Day	95	58	48	58	98	48	43
<i>Callinectes erythraensis</i> Fauvel	3	10	-	-	8	-	-
<i>Callinectes</i> sp.	5	-	3	-	-	-	-
<i>Callinectes squamata</i> (Müll)	5	-	-	-	10	5	-
<i>Callinectes iricolor</i> (Mont.)	8	-	-	-	-	-	-
<i>Callinectes dumerilii</i> (Aud. & M.Edw.)	-	3	-	-	-	-	-
<i>Callinectes</i> sp.	-	-	-	-	-	8	-
<i>Callinectes</i> sp.	-	-	-	3	-	-	-
<i>Callinectes</i>							
<i>Callinectes hirtipes</i> M. Edw.	-	5	18	3	20	3	5
<i>Callinectes</i>							
<i>Callinectes grimaldi</i> Chevr.	2293	1390	1633	2570	1518	1798	1960
<i>Callinectes palmeta</i> Brnrd.	-	8	3	10	3	8	15
<i>Callinectes</i>							
<i>Callinectes saccus brevifissura</i> O. Tattersall	3	-	15	-	8	-	-
<i>Callinectes</i>							
<i>Callinectes jucundus</i> Brnrd.	8	3	3	3	-	3	3
<i>Callinectes brevirostris</i> Stimps.	25	48	38	-	53	8	8
<i>Callinectes biala africana</i> (Ortm.)	3	-	5	-	-	-	5
<i>Callinectes stomia edwardsii</i> McLeay	10	13	23	35	10	23	8
<i>Callinectes astoplax spiralis</i> Brnrd.	5	3	-	3	5	-	5
<i>Callinectes osoma orbiculare</i> Desm.	3	5	3	20	8	3	5
<i>Callinectes</i>							
<i>Callinectes</i>							
<i>Callinectes</i>							
TOTAL INDIVIDUALS	5718	3808	4663	6533	5283	4245	4278
SPECIES RICHNESS	27	24	25	20	23	23	22

CHAPTER 5

Conservation Measures and Conclusions

INTRODUCTION

Benthic ecology is frequently unable to provide confident answers to many questions. For example, the question of whether the continued removal of *C. kraussi* and *U. africana* will cause any shift in their respective ecosystems could be answered with a range of answers, depending on the ecosystem in question and the magnitude, frequency and predictability of the disturbance. The localised experiments undertaken in Langebaan Lagoon can therefore only be extrapolated to the whole system with difficulty. Nevertheless, there is no doubt that the disturbance through bait-collecting, including the effects of trampling, is more deleterious than is the actual removal of the prawns, and has surprisingly long-lived effects on the macrofauna. While direct responses such as these can be envisaged with confidence, secondary effects arising indirectly from bait-collecting are much more difficult to predict and present an enormous number of complex permutations.

Quantification of the activities of bait-collectors in Chapter 2 has revealed that they remove a relatively small proportion of mud- and sandprawns in Langebaan Lagoon; this amounts to no more than 0.01% for the total lagoon and <5% for the centre banks. Bait-collecting activities are concentrated on the centre banks where some 400 000 prawns are removed per annum (Figure 5.1a). In terms of numbers removed, bait-collecting is thus no threat to the prawn populations at Langebaan Lagoon, although there are signs that sandprawn densities and modal body sizes have been reduced in areas of intense bait-collecting (Figure 5.1b,c). In addition, bait-collecting disturbs massive quantities of sediment and, inadvertently, this results in the disturbance of other components of the biota. In Chapter 2, it is estimated that 543 g of macrofauna is disturbed with each bag limit of 50 prawns, amounting to approximately 10 000 kg of macrofauna being disturbed annually by bait-collectors (Figure 5.1d). While the fate of this disturbed macrofauna is not completely determined, the results of predation experiments suggest that approximately 80% is subsequently preyed upon by scavenging gulls (Figure 5.1d).

In Chapter 3, an experimental long-term analysis was undertaken of the effects of intense bait-collecting on both the prawns and other organisms (see synopsis in Figure 5.2). The results revealed that the recovery of both *C. kraussi* and *U. africana* is far more protracted than previously imagined - probably only being completed 18 months after the initial disturbance. Immediately after disturbance of both *C. kraussi* and *U. africana*, numbers of meiofauna and macrofauna declined. Only a single macrofaunal species, the

hermit crab *Diogenes brevisrostris*, benefited from the disturbance. In the case of the meiofauna, this depression was followed by an explosive increase in densities and subsequent levelling out of densities. The macrofauna was slower to recover and still showed signs of depression 18 months after the initial disturbance. After the disturbance of *C. kraussi*, chlorophyll levels increased above control levels, whereas bacterial densities were temporarily reduced. Conversely, the disturbance of *U. africana* resulted in nett decreases in chlorophyll levels but slight increases in bacterial numbers. As only a proportion of the original prawn population was removed (ca. 10% of *C. kraussi* and 46% of *U. africana*), the above responses were more likely to have been induced by the disturbance of the sediment and its subsequent compaction (and, perhaps, development of anoxia) than by the removal of the sand- and mudprawns *per se*. This prompted the initiation of a further set of experiments to assess the effects of both less intense disturbance during bait-collecting and those of trampling.

The results of these experiments are reported in Chapter 4 which demonstrates the detrimental effects which any physical disturbance, including trampling, may have upon sandflat communities. Indeed, no clear differences existed between the damage inflicted with a prawn pump and that of trampling (Figure 5.3). As in Chapter 3, sandprawn numbers were reduced 6 weeks following the disturbance (Figure 5.3a), but this effect was short-lived and recovery was complete after 32 weeks. Short-lived but slight reductions of the macrofauna and chlorophylls (Figure 5.3b,d) and increases of the meiofauna (Figure 5.3c) were immediate responses to the disturbance. The overriding importance of disturbance and the fragility of the sandflats is further emphasised in these results: the removal of sand- and mudprawns *per se* may not be as important as was previously thought, but the attendant disturbance certainly does have major effects.

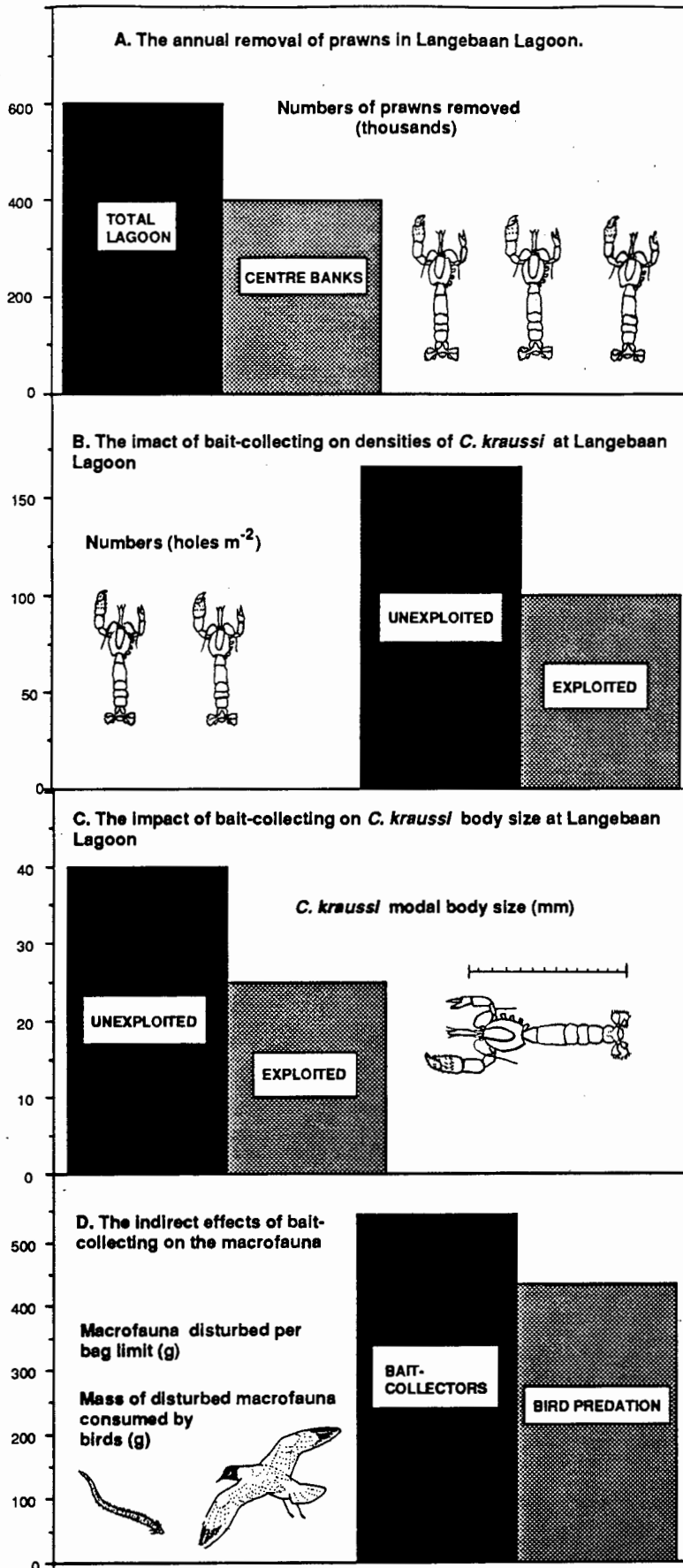


Figure 5.1. Synopsis of the effects of collecting *Callinassa kraussi* and *Upogebia africana* for bait in Langebaan Lagoon.

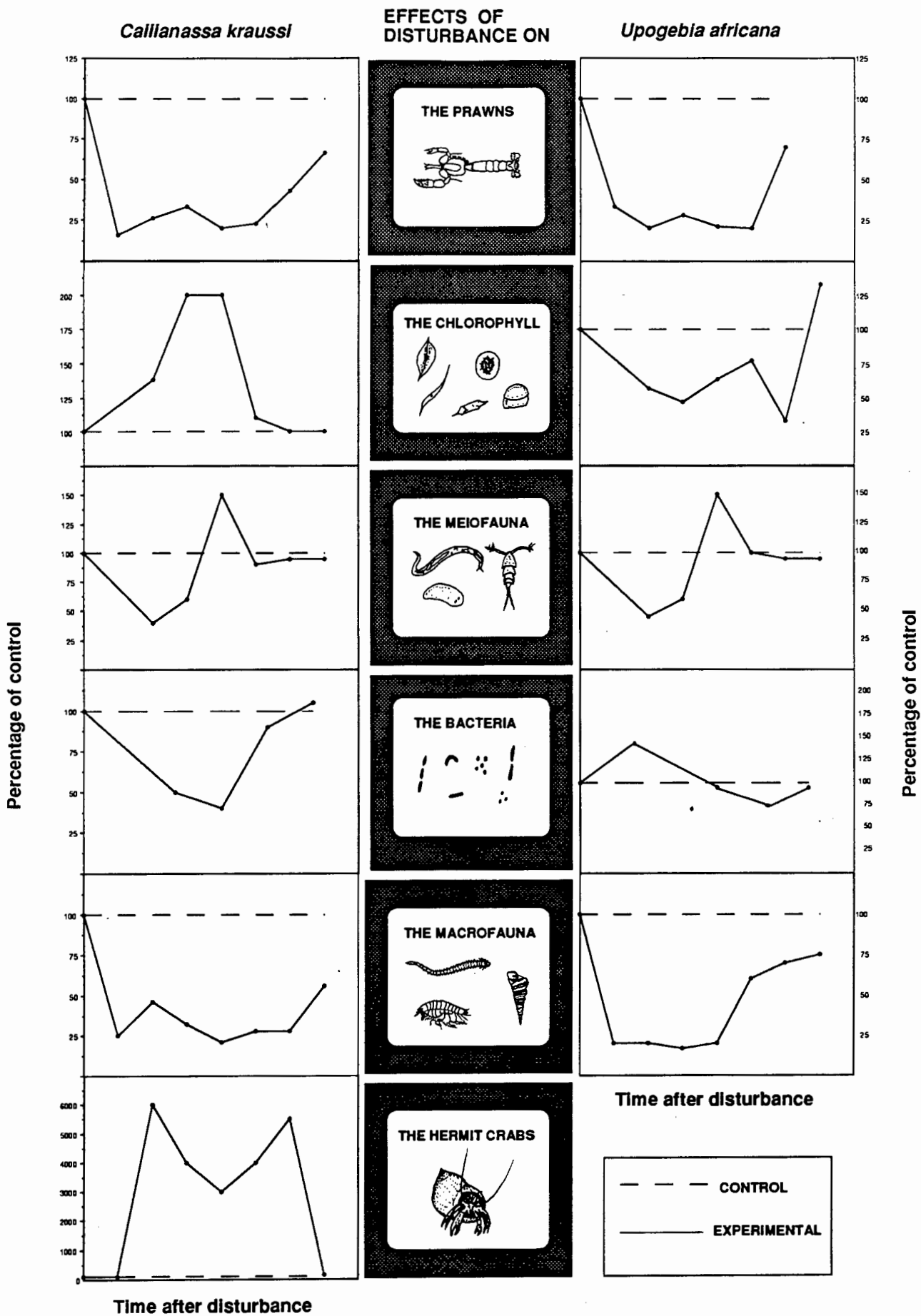


Figure 5.2. Synopsis of the effects of high-intensity disturbance on the biota of an intertidal sandflat. Time is expressed by positioning successive samples equidistantly, irrespective of the time interval and (in some cases) the different depths in the sediment. They express qualitative trends, not absolute values.

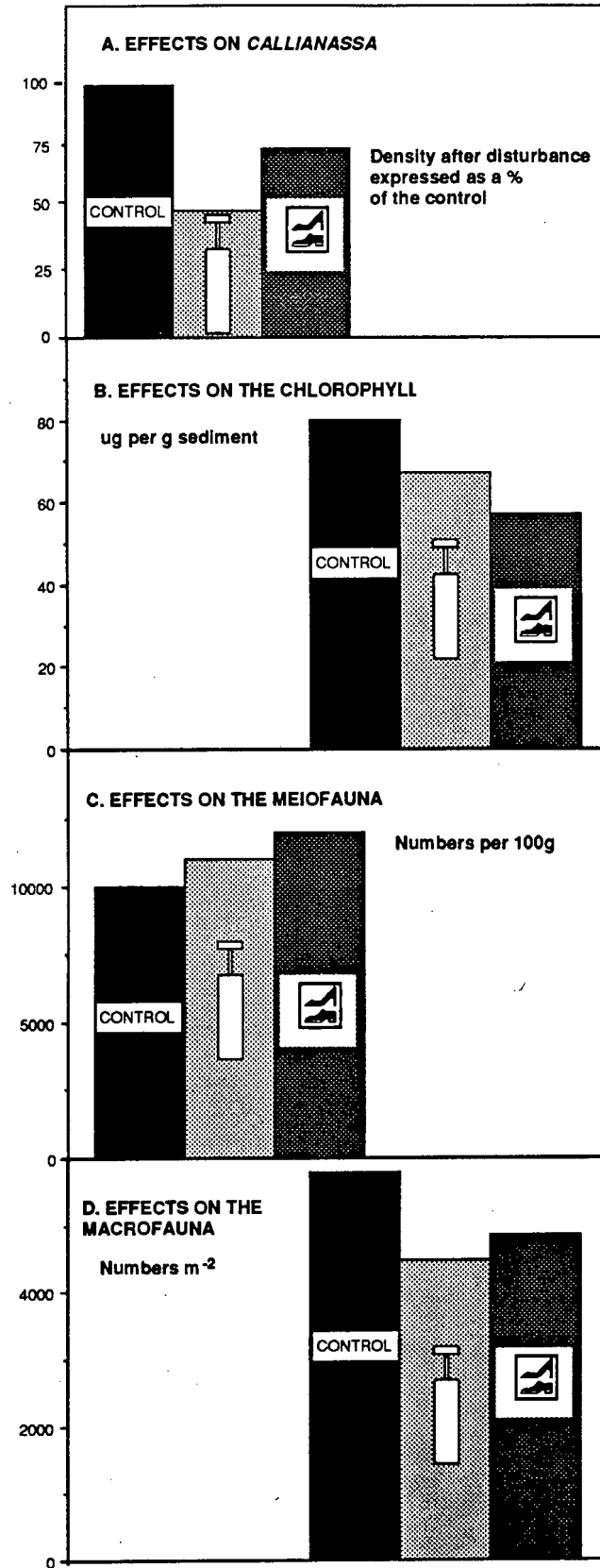


Figure 5.3. Synopsis of the effects of low-intensity sucking (□) and trampling (▣) on the biota of an intertidal sandflat, measured six weeks after the disturbance.

THE CURRENT STATUS OF *C. KRAUSSI* AND *U. AFRICANA* POPULATIONS

The success of *C. kraussi* in colonising estuaries has been described by Gaigher (1987) who surveyed *C. kraussi* populations in the Cape and, based on distribution patterns, concluded that "this species will undoubtedly prove to be the mainstay as a bait resource and ...is not in any way being negatively affected by exploitation". Although this kind of approach is an important part of assessing available stocks, its integration with experimental evidence, such as that presented in this study, is crucial for effective management.

At the present levels of exploitation there do not appear to be any threats of large-scale *C. kraussi* depletions. Gaigher (1987) made particular mention of the proliferation of *U. africana* and, expressly, *C. kraussi* (up to 2 000 individuals m⁻²) in areas which had been disturbed through siltation. Unfortunately, populations in these disturbed areas were not monitored over a period of time. In all likelihood, siltation would have been followed by sediment consolidation and compaction (Postma 1967) which would decrease the penetrability of the substrate considerably, hinder burrowing and, ultimately, reduce the abundances of *C. kraussi*.

Densities of the more sedentary *U. africana*, far from mirroring the healthy populations of *C. kraussi*, appear to be declining in many estuaries (Gaigher 1987). This phenomenon has been most obvious in estuaries which have been invaded by marine sediments, closed to the sea, or subject to intense bait-collecting (e.g. Swartkops estuary) (Hill 1967; Day 1981a; Martin 1988).

ASPECTS OF THE REPRODUCTIVE BIOLOGY OF *C. KRAUSSI* AND *U. AFRICANA* OF SIGNIFICANCE IN CONSERVATION

A knowledge of the dispersal of *C. kraussi* and *U. africana* and their respective life histories is clearly crucial to understanding the long-term effect bait-collecting may have on prawn populations. For example, the blood worm *Arenicola loveni*, a popular bait organism, has been completely eliminated from some southern African estuaries largely because of its limited dispersal, the larval stage being planktonic only for a few hours (Barham 1979).

An abbreviated larval development may not, however, be necessarily detrimental; decreased vulnerability through reductions in the planktonic phase may even confer

some advantages. For example, *C. kraussi* has no planktonic larval stage; dispersion takes place by post-larval stages which tend to be stronger, faster swimmers and more efficient burrowers than mature prawns, and are not as vulnerable to estuarine water movements as a planktonic larval stage. Although offshore populations of *C. kraussi* are known to occur off the coast of southern Africa, the extent and density of these populations is unknown and there is probably little contact between these and estuarine populations (Forbes 1973a). This implies that isolated estuarine areas which have been disturbed by bait-collectors are probably repopulated from neighbouring areas of the sandbanks within the estuary.

The mean number of eggs carried by *C. kraussi* is remarkably low (ranging from 20-600 - Forbes 1973a) when compared to other thalassinids. For example, Pohl (1946) recorded 8 170 eggs on a specimen of *C. major* and Devine (1966) found 660-1 500 in *C. filholi*; *U. africana* has been noted to carry 1 000-4 800 eggs (Siegfried 1962; Hanekom & Erasmus 1989). Despite this low fecundity, the recruitment of juveniles to the population is large and they may constitute 60-70% of the population at certain times of the year (Forbes 1973a).

Both the retention of a planktonic larval stage and the high fecundity of *U. africana* (Hill 1967) imply that it probably more readily achieves recolonisation than *C. kraussi*. Although *C. kraussi* is perhaps better adapted to survive long isolation from the sea, evidence suggests that it still is ultimately dependent on some access to the sea (Forbes 1973a). Careful consideration should therefore be given to whether collection of this species should continue to be permitted in closed estuaries. *U. africana*, on the other hand, rapidly disappears from estuaries that have been closed for a prolonged period, regardless of whether exploitation occurs or not.

The potential life-span of both *C. kraussi* and *U. africana* has been estimated at approximately 2-4 years (Forbes 1973a; Hanekom 1980). Double breeding cycles have been described for both species in the Eastern Cape (Hill 1967; Forbes 1973a; Hanekom 1980). Females breed for the first time at approximately 18 months followed by a second contribution before dying (Forbes 1973a; Hanekom 1980). Marked increases in the numbers of juvenile *C. kraussi* are observed approximately 4 months after breeding (Forbes 1973a). These cycles appear to be strongly temperature-related, with *C. kraussi* populations in Natal and Transkei breeding earlier than their southern counterparts; salinity levels are also known to affect the appearance of juveniles of both species (Forbes 1973a; Hanekom 1980).

THE ROLE OF *C. KRAUSSI* AND *U. AFRICANA* IN ESTUARIES

Previous work has clearly shown that both *C. kraussi* and *U. africana* play central roles in the ecology of estuarine and lagoonal systems (Hill 1967; Forbes 1973a; Hanekom 1980). The impact of thalassinid prawns on the turnover of sediment and consequent oxygenation and nutrient exchange with the overlying water column (Dye & Furstenberg 1978; Rhoads & Boyer 1982; Tamaki 1984; Hines & Jones 1985; Flint & Kalke 1986; Branch & Pringle 1987) and their ability to alter sediment geochemistry (Aller & Dodge 1974), enhance bacterial numbers (Yingst & Rhoads 1980; Koike & Mukai 1983; Branch & Pringle 1987; Tamaki 1988), bury and alter the depth-distribution of microalgae (Branch & Pringle 1987) and reduce the meiofauna (Alongi 1986; Branch & Pringle 1987) must have powerful consequences on energy flow in the ecosystem. In addition, the prawns themselves constitute an important food source for various predators, notably fish and birds. Those fish which appear to feed largely on prawns include white steenbras *Lithognathus lithognathus*, spotted grunter *Pomadasys commersonni* (Day 1981a) and the sandsharks *Rhinobatus blochii* and *Rhinobatus annulatus* (Day 1981a; Harris *et al.* 1989). The removal of prawns for bait could thus potentially limit the amount of food available to these fish.

The effect of bait-collecting on bird populations is difficult to assess. *C. kraussi*, and particularly *U. africana*, constitute some of the most important prey species for a number of bird populations, including kelp gulls *Larus dominicanus*, grey plovers *Pluvialis squatarola*, whimbrels *Numenius phaeopus*, and common terns *Sterna hirundo* (Martin & Baird 1987). On the one hand, some birds, especially kelp gulls, are quick to take advantage of prawns and debris left on the surface by bait-collectors and may thus benefit from bait-collecting. Less opportunistic birds are, however, scared off by bait-collecting activities. Moreover, habitat destruction and consequent declines in prawn densities could potentially limit bird numbers and modify distribution patterns, particularly as some of these birds are territorial, establishing their domain as a direct function of the prawn densities (J. Turpie, pers. comm.). Martin (1988) has shown that birds commonly prey upon large, parasitised mudprawns which surface at low tide. The selection of larger mudprawns by bait-collectors has been shown to reduce their numbers and consequently shorten the mean lifespan in populations of mudprawns (Hill 1967). This suggests that the removal of large prawns for bait could potentially reduce the amount of suitable-sized food available to the birds. Further ramifications are provided by the prolonged depressions of the numbers of *Urothoe grimaldi* (and of the macrofauna

as a whole) after disturbance. As *U. grimaldi* forms a major component of the diet of the curlew sandpiper *Calidris ferruginea* (Puttick 1977), its continued suppression in areas of bait-collecting activities could result in barren 'pockets' of sediment. Implicit in the above details is a concern that the carrying capacity of estuaries may be lowered by intense bait-collecting, particularly when the dependence of predatory fish on prawns (Marais 1984) is incorporated into this analysis.

PRESENT REGULATIONS

Legislation pertaining to the protection of estuarine bait organisms was first promulgated in 1965 by what was then known as the 'Department of Fisheries' (Gaigher 1987). Specific measures to protect this resource comprised a prohibition on the removal of any estuarine bait species for angling in the sea, the stipulation of specific quotas for each species (70 per person per day for any 'prawn'), a ban on the purchasing or selling of any bait species and a prohibition on the use of forks and spades to capture bait organisms.

Amendments to these ordinances have included the lifting of the restriction forbidding the removal of *C. kraussi* (but not *U. africana*) from estuaries for use in the sea, and the lowering of quotas for both sand- and mudprawns. At present, a total number of 50 sand- and mudprawns collectively may be gathered per person per day. There is no limit on size or sex, although a natural size limit is imposed by the anglers who generally collect large prawns only (>40 mm body length at Langebaan Lagoon). Areas in which the collection of prawns is prohibited do exist in a few estuaries although these are usually blanket reserve restrictions.

ADEQUACY OF CURRENT REGULATIONS AND SUGGESTED CONSERVATION MEASURES

Evidence presented by this study has provided a strong case for the introduction of appropriate, independent and flexible regulations particular to the unique conditions of each estuary. Although the problems of blanket edicts have previously been highlighted (Forbes 1973a; Gaigher 1987), to date no site-specific regulations exist. The following procedure is suggested when drawing up regulations:

1. The construction of a calibration curve to assess CPUE (Catch Per Unit Effort).
2. A determination, through hole counts, of the proportion of the population that is concentrated in intertidal or shallow-water, i.e. accessible, exploitable regions, and that which is concentrated in inaccessible, subtidal regions. A large percentage in subtidal areas would obviously imply the use of lenient regulations in the intertidal.
3. An investigation of the annual patterns of the life cycles of the prawns. This should be coupled to an evaluation of the seasonal utilisation of the area by bait-collectors.
4. An estimation of the relative proportion of prawns removed each year.
5. An estimation of the proportion of the macrofauna being disturbed by each collector and the significance of this in terms of total impact upon the estuary.

The above procedure should be incorporated with other considerations regarding the conservation status and nature of the estuary in question. For example, closed estuaries would require more careful monitoring and, if necessary, a prohibition on collection. Stricter regulations could be achieved either by restricting the number of bait-collectors at any one time (including attendant families); by reducing the quota; or by spreading collecting areas over a broad part of the estuary and hence diluting the previously localised, concentrated impact. The latter option does, however, involve the risk of disturbing pristine areas. Because of the clear detrimental effects of digging, sucking or even trampling on many components of the sandflat biota, serious consideration should be given to restricting bait-collecting to specific parts of estuaries to avoid widespread destruction.

It is recommended that a blanket ban be introduced on the removal of any berried females for bait. Many anglers at present are reluctant to remove berried females because they perceive that this may reduce future stocks. The fact that they discard berried females and undersized individuals is not, however, necessarily beneficial, because gulls prey on a high proportion of discarded prawns. Survival of these animals would almost certainly be ensured if they were returned to undisturbed burrows (into which they rapidly dig). While it is impractical to legislate for such action, anglers should be informed of the potential benefits.

Contrary to popular belief and hence current regulations, the removal of prawns with a prawn pump is at least as destructive, and possibly more destructive than digging. However, *C. kraussi* can be collected with much greater efficiency with a prawn pump, implying that a smaller area will be worked over. Moreover, the cost of the prawn pump

restricts broad-scale usage and it is therefore suggested that the present restrictions, preventing the use of a spade or fork, should be maintained (although for different reasons from those for which the regulation was originally introduced).

The attraction of site-specific proposals lies in their flexibility. This is imperative in a situation where the bait demand is seasonal and highly dependent on local fishing conditions. Not only will these considerations allow for more effective estuarine management, but they will instill in the populace conservation-backed notions of the prawns and particularly of the sandflats as being managed, vulnerable entities akin to those of sand dunes.

A complete prohibition of bait-collecting, with the accompanying purchase of bait through registered outlets, should be considered only in severe cases of over-exploitation or disturbance. If this procedure were to be introduced, it should allow for effective harvesting of the prawns and accurate records of removals and CPUE. Problems inherent to this option lie in the 'commodity' nature of commercial bait which may be outside the budget of a sustenance angler. Since part of the 'recreational experience' associated with sport fishing is coupled to the collection of bait, which is also often a social, family event, a total ban on collection would deprive anglers.

BAIT MANAGEMENT AT LANGEBAAN LAGOON

Neither *C. kraussi* nor *U. africana* represent heavily exploited populations at Langebaan Lagoon. This is largely due to the bulk of the population occurring within the boundaries of the fully protected 'wilderness' region of the park (Figure 2.1). However, the scarcity of bait at unprotected mainland areas is a prevailing problem which will be augmented by the predicted 100-200% increase in recreational activities at Langebaan within the next 20 years (Henderson 1985).

The survey conducted suggests that at Langebaan Lagoon the bag limit of 50 prawns is more than sufficient for most angler's purposes. Anglers are more concerned about a perceived decrease in fish size in the lagoon and the quantities of small fish currently being harvested from the lagoon, with the imposition of size limits being viewed as a necessary restriction.

Low prawn exploitation rates on the centre banks (4% per annum), together with high densities (*ca.* 126 m⁻²) indicate that these banks still represent a relatively rich resource of *C. kraussi* which should be maintained as a primary collection site.

Nevertheless, exploited areas display noticeably reduced prawn densities and changes in size-frequency distributions when compared to unexploited areas. Similar trends are illustrated for the heavily-pumped mainland localities (Figure 2.1). By chance, the centre banks lie astride the boundary-dividing regions of the park in which prawns can or cannot be exploited. In view of the slow recovery times recorded after disturbance and the absence of a larval stage in *C. kraussi*, this partitioning of the centre banks may be highly desirable. The division allows for continual stocking of prawns, through juvenile and adult migrations from the unexploited to the adjacent, exploited parts of the centre banks.

Partial restrictions, such as those decreed at Langebaan Lagoon, would be more effective if linked to a rotational system of collecting, where open and closed areas would be alternated, based on the age of the prawns and their breeding cycles. As the longevity of prawns is about 2-3 years, it is suggested that at least two years should pass between rotations, thus allowing perturbed prawn populations to recover and attain a mature size-structure. Since juvenile prawns are highly prone to mortality in the process of bait-collection, either directly through mechanical damage or indirectly through gull predation, the ideal rotational period should be three-yearly, ensuring time for juveniles to reach maturity. The designated areas should be chosen to ensure that prawns have free access between the alternating open and closed areas. These broad principles are forwarded for specific use at Langebaan but can be applied for use in similar situations.

If necessary, some areas of the centre banks which presently fall within the protected portion of the reserve could be opened up as part of the rotational system. In addition, small areas within the mainland reserve which represent sizeable populations of *C. kraussi*, should remain open to those collectors without boats. This would circumvent the complete depletion of those stocks within the currently exploited areas. These areas could be rotated as discussed and situated where they could be easily monitored (e.g. Churchhaven). The present angling population is not regarded as large enough to warrant restrictions additional to those that already exist. However, this may well change with the predicted boom in recreational activities and population.

The enormous negative impact which disturbance has on several major components of sandflats has many implications and emphasises the importance of retaining pristine areas within estuaries. The importance of sanctuary areas is further underlined by the potential impact which trampling *per se* has upon the sandflats, particularly in those areas in which the sediment is very soft, such as those contained by

the sanctuary at Langebaan Lagoon. In maintaining three distinct zones at Langebaan Lagoon - that of a sanctuary, an area for restricted activities and an open recreational area, an unusual balance has been struck between conflicting themes - those of human recreation and environmental conservation. While the centre banks are fortuitously ideal for the concurrent exploitation and protection of *C. kraussi*, only small areas of prawns can be harvested from the mainland. Although this situation is currently adequate, it may in future need to be amended. Not only is the management of bait-collecting activities adequately incorporated into the zoning system at Langebaan Lagoon, but broader recreational activities are too; this system can thus be regarded as a model working example.

Acknowledgements

The sheer drudgery of this project was gratefully farmed out to many unsuspecting (good) friends and undergraduate students. Thanks are due to Ms Sue Burchell, Ms Gill Kerchhoff, Ms Alli Macey, Ms Jacqui MacQueen-Ahrends, Mr Brad Rees, Dr Sha Slater and expressly to Senor Carlos Y Sanchez for endless hours of mud-bath frolicking. The 1988, 1989 and 1990 Zoology II students of the University of Cape Town are gratefully acknowledged for their sweat and toil in establishing and toeing the line in this project. The UCT Maintenance team kindly donated their hard-earned bait to the cause of Quantification.

Thanks are also extended to Mr Geoff Hoy, Mr Steven Tugwell, Mr Carlos Villacastin-Herrero and Dr Patti Wickens for computer assistance; Mr Cedric Meyer for his helpfulness in providing equipment; Mr Ian Davidson for drawing my attention to relevant literature and assistance with disk debugging; Ms Lindsey McNeill for making the statistics intelligible; Professor Alec Brown for providing laboratory facilities and encouragement; Professor Charlie Griffiths for assistance with amphipod identification; Dr Mark Gibbons for deliverance from the malevolent monstrous meiofauna and to the National Parks Board for assistance at Langebaan. I am grateful towards my supervisor, Professor George Branch for help, both in the field and in the laboratory, and for his criticisms and encouragement. I appreciate helpful comments on the manuscript from Mr Carl van der Lingen, Dr Mark Gibbons and Professor George Branch. Mr Chris Gaigher from the Department of Nature and Environmental Conservation of the Cape Provincial Administration kindly contributed unpublished data.

My special thanks go to all the non-zoologists and particularly to Carl and my father for maintaining their healthy, sardonic views and putting Gaia into perspective. The completion of this work would not have transpired without the inspiration of "Ashley Cottage", Jay Gunn and the chickens. It was funded by the National Parks Board and a post-graduate bursary from the Council for Scientific and Industrial Research.

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