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Exploitation and biology of the bait organism *Callinassa kraussi* Stebbing (Crustacea: Decapoda: Thalassinidae) in Langebaan Lagoon

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Thesis presented for the Degree of Master of Science
in the Department of Zoology, University of Cape Town,
February 2006

Declaration

This thesis documents original research carried out in the Department of Zoology, University of Cape Town. It has not been submitted in whole, or in part for any other degree at any other University. All of the work presented in this thesis is my own, except where otherwise stated in the text. Any other sources are fully acknowledged.

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Pierre L. Nel

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Date

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ABSTRACT

The effects of the exploitation of prawns (*Callinassa* & *Upogebia* spp.), in Langebaan Lagoon, primarily for bait collecting, were assessed using field experiments and observations. Langebaan Lagoon has been a proclaimed National Park for 20 years and a proclaimed Marine Protected Area since 2000. The area is zoned for different human uses, about one third being reserved as a sanctuary, one third for non-extractive visitation and one third for extractive purposes including bait-collecting and fishing.

Four species of prawns were identified in Langebaan Lagoon – *C. kraussi*, *C. rotundicaudata*, *U. africana* and *U. capensis*. Densities were assessed for these species in the intertidal and subtidal areas of the lagoon. *C. kraussi* was broadly distributed, occupying a large part of the intertidal area, whereas *U. africana* was confined to the head of the lagoon or beds of eelgrass in the upper sections of the intertidal zone. *U. capensis* was particularly prominent in the subtidal areas, occupying deeper areas below the zonation of *C. kraussi*. The distribution of the different species of prawns was related to sediment characteristics, which are in turn dictated by shore height and distance from the lagoon mouth. For the whole of Langebaan Lagoon, the stocks of *C. kraussi*, *U. africana* and *U. capensis* were estimated to be 8 861 million, 383 million and 663 million animals respectively.

The number of people visiting the sand flats to collect bait was highest during the summer and on weekends ($\bar{x} = 48$ per day). An estimated 676 597 *C. kraussi* are removed annually from the Center Banks and Klein Oesterwal areas of the lagoon. This represents 0.08 % of the sand prawn stock from these areas and 0.008 % of the estimated total stock present in the entire lagoon. On average each bait-collector removed 86 prawns per outing, which is 36 more than the legal daily limit. The amount of sediment disturbed annually by these bait-collecting activities is estimated as 6 189 tonnes. The surface area disturbed by trampling caused by bait-collectors and people accompanying bait-collectors amounts to 285 590 m².

The reproduction of *C. kraussi* in Langebaan Lagoon is seasonal and consists of one breeding cycle per year. Disturbance caused by bait-collecting significantly decreased sand prawn densities in localities where harvesting takes place. However, disturbance by bait pumping did not reduce fecundity significantly. Overall, sand prawns were smaller in the sanctuary area and hence quantitative reproductive output was lower there.

An experimental study of interactions between *C. kraussi* and *U. africana* failed to detect any negative effects of either species on the other, but did show that survival of *U. africana* was less in sandy areas (32.6 %) than in muddy habitats (93.8 %). For *C. kraussi* survival was never significantly different between sites.

As Langebaan Lagoon is part of a national park and an MPA, there is little doubt about its conservation importance. The current zoning scheme is established and generally adhered to. However, bait-collectors regularly exceed bag limits, partly in an attempt to increase their chances of achieving the fish bag limit. This raises another important issue that if bait bag limits were to be adhered to, it would dramatically improve adherence to fish bag limits. This is an emerging conservation principle not highlighted in preceding work.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

The thalassinidean prawns *Callinassa kraussi* Stebbing and *Upogebia africana* (Ortmann) occur in intertidal and shallow subtidal soft substrata, particularly in coastal marshes, tidal channels and estuarine embayments (Day 1981a). The habitats and geographical distribution of these two organisms differ, with *C. kraussi* being more common in sandy areas and extending from the Orange River to San Martinho in Mocambique, whereas *U. africana* occurs in finer, muddier sediment and is confined to an area between Saldanha Bay on the west coast and Inhambane on the east coast (Hill 1971; Forbes 1973a; Jackson & McGibbon 1991).

In 1982, the South African National Committee for Oceanographic Research (SANCOR) identified Langebaan Lagoon as a system 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, Yssel 2000).

Within Langebaan Lagoon, many species of invertebrates are exploited as bait, including the sandprawn *C. kraussi*, the blood worm *Arenicola loveni*, red bait *Pyura stolonifera*, the black mussel

Choromytilus meridionalis, the Mediterranean mussel, *Mytilus galloprovincialis* and the mudprawn *U. africana*.

Work on prawns in Langebaan Lagoon by Wynberg & Branch (1991, 1994, 1997) was initiated as a response to concerns expressed about apparent declines in the abundances of sandprawns and mudprawns, the amounts of removal and the effects thereof. The central focus of this thesis falls on the sandprawn *C. kraussi* as this is the species most affected by harvesting, but comparative studies were also undertaken on other species of sand and mudprawns present.

1.2 Study Area

Langebaan Lagoon (33° 10' S: 18° 5' E) is situated on the west coast of South Africa. The lagoon is an enclosed arm of Saldanha Bay and can also be described as a parallel extension of the Atlantic Ocean. It is approximately 15 km long with a maximum width of 4 km. The lagoon is entirely marine in that it lacks riverine input. Water movement is driven by strong tidal action, in contrast to Saldanha Bay where the system is chiefly wave-driven. The velocity of these tidal movements may reach 1 m/sec during spring tides (Christie 1981). The only wave action that is present occurs near the mouth of the lagoon. During spring low tides, vast areas of intertidal sandflats are exposed (Shannon & Stander 1977). There is a clinal, but variable, salinity gradient in the lagoon. Salinity is almost constant at the mouth of the lagoon (34.5 to 35.0 ‰) and due to evaporation fluctuates increasingly further south. A maximum salinity of 38.0 ‰ has been recorded at the head of the lagoon (Day 1959). Christie (1981) reported small amounts of freshwater seepage into the lagoon due to rain, which has led Whitfield (2005) to classify it as a 'coastal embayment' estuary. During late winter this seepage results in a reduction of salinity to 33.9 ‰, but the variations in salinity are nevertheless small. The mean monthly sea-temperature varies from 19.5°C during the warmest months to 14°C during winter (Wynberg &

Branch 1991). 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 Sea Fisheries Act 58 of 1973 resulted in the division of Langebaan Lagoon into three zones (Wynberg & Branch 1991). In 1985 the West Coast National Park was proclaimed and included Langebaan Lagoon. In 1991 legislation was passed in terms of the National Parks Act, which again recognized the three zones in the lagoon. The principle reasons for zoning were to maintain traditional activities exercised in the lagoon whilst reducing the levels of disturbance from north to south, where there are sensitive salt marsh habitats and large populations of wading bird species.

The northern-most zone is a multi-purpose recreational area, in which the use of motorboats, sailboats and sailboards is permitted. Water-skiing, rowing, diving, swimming, bait-collecting and fishing are also permitted in this zone. The zone to the immediate south of this is a limited recreational area. This area may be used for swimming, sailing, kite boarding and boardsailing, but no extractive harvesting is permitted. The southern-most zone is a “wilderness” area to which entry is prohibited without a permit. In 1992, in terms of the Ramsar Convention, the lagoon was declared a wetland of international importance, a *Ramsar Site*. Ramsar sites are areas deemed to be of global significance for wetland bird species. In terms of the Marine Living Resources Act of 1998, Langebaan Lagoon and an area adjacent to the north were proclaimed a marine protected area (see Government Gazette 29 December 2000). This legislation recognizes the zoning scheme of 1973 and 1991, and allows line fishing in the northern zone. No reference is made to bait collecting in this zone, which to date remains a point of contention.

1.3 Rationale and thesis layout

Following this introductory chapter, Chapter 2 explores the density and distribution of prawns inhabiting the Lagoon, and provides background information against which biological interactions and harvesting are later assessed. It documents their distribution around the lagoon, their patterns of zonation in the intertidal and subtidal zones, seasonal variations in intertidal density of *C. kraussi* specifically, and any correlations of abundance among the species. It also explores in an observational manner whether prawn densities are related to harvesting intensity.

The aim of chapter 3 is to estimate the effect of bait collecting by humans on the prawn stocks in the lagoon. Surveys were made of the numbers of people harvesting sandprawns and the amounts they take, based on field surveys and questionnaires. This chapter also tests hypotheses originally proposed by Wynberg (1991). She argued that neither *C. kraussi* nor *U. africana* constitute heavily exploited populations, due to the bulk of these prawn populations occurring within the *no take* zones. However, she stated further that a quadrupling in recreational activities could be expected over a 20-year period spanning 1991 – 2011. This chapter thus investigates the situation 10 years after this view was expressed.

Chapter 4 determines growth and reproductive patterns of *C. kraussi* in the field, comparing areas where bait harvesting occurs with 'no take' areas.

Chapter 5 describes a simulation of the activity of bait collectors and test the effects of harvesting. In part, this is achieved by comparisons among different parts of the lagoon, but also by establishing experimental areas in which the intensity of harvesting was regulated. Both treatments test the

hypothesis that negative associations should exist between reproductive output and disturbance levels (Wynberg & Branch 1991, Cretchley 1996, Contessa & Bird 2004).

Given that *C. kraussi* and *U. africana* both commonly occur in intertidal and shallow soft substrata and are dominant inhabitants of sheltered lagoonal sandflats and estuarine embayments (Edgecumbe 1980, Day 1981a, Wynberg & Branch 1991, 1994), interactions among them are a likely scenario (Branch 1984). Chapter 6 follows a more academic line and adopts an experimental approach used in many other caging experiments (Tamaki 1988, Angel 2002) to examine interactions between *C. kraussi* and *U. africana* by using cages that held the two species either together or separately.

All the work in the above chapters is then evaluated in a final chapter that puts forward management recommendations. It aims to evaluate the current conservation measures to protect the species, whether they are adequate, or whether additional measures are necessary.

CHAPTER 2

ASSESSMENT OF THE CURRENT STATUS OF *CALLIANASSA KRAUSSI* AND *UPOGEBIA AFRICANA* IN LANGEBAAN LAGOON.

2.1 Introduction

The thalassinidean prawns *Callianassa kraussi* and *Upogebia africana* are dominant members of the macrobenthos in many South African estuaries and make a large contribution to the total biomass, but predominate in different substrata. Where the substratum is sandy, *C. kraussi* is dominant, whereas *U. africana* is generally absent from sandy areas, and occurs predominantly where the substratum consists of muddy sand (Day 1981a).

Considerable information exists on the density of *C. kraussi* and *U. africana* in South African lagoons and estuaries. 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). Densities for *U. africana* of 600 m⁻² in the Kowie estuary, and up to 500 m⁻² in the Swartkops estuary were recorded by Day (1981b). Hodgson (1987) recorded densities of 120-500 m⁻² in the Kariega estuary. Christie & Moldan (1977) found that *C. kraussi* and *U. africana* together constituted approximately 48 % of the total benthic biomass of Langebaan Lagoon, although Wynberg & Branch (1991) noted that prawn densities decreased from the head towards the mouth of the lagoon. They recorded the highest densities in the Schrywershoek area – approximately 350 m⁻². In Sepia Bay, in the northern part of the lagoon, which is intensively utilised for prawn collecting, densities were noticeably lower than elsewhere – approximately 50 m⁻².

Preliminary surveys in the Langebaan Lagoon showed the presence of two species of sand prawns – *Callinassa kraussi* and *C. rotundicaudata*, and two species of mud prawns – *Upogebia africana* and *U. capensis*. The present survey concentrated on *C. kraussi* and to a lesser extent on *U. africana* as they were by far the most abundant and widespread of the four species. Nevertheless, where the other two species were encountered their status is reported.

The aim of this survey was to determine the density and distribution of the different species in the lagoon, in both intertidal and subtidal areas. For the intertidal areas, sampling was done in four seasons of the year to test if there were significant differences of *C. kraussi* density at different times of the year. The sites chosen for sampling were selected to cover the whole lagoon, but also to represent areas exploited by bait collectors and areas where no exploitation is permitted.

Specifically, this chapter probes the following questions:

1. Where do the four species occur and what is their abundance?
2. What zonation patterns are displayed by *C. kraussi* and *U. africana*?
3. How are the species distributed around the lagoon?
4. What is the size structure and sex ratio of *C. kraussi*?

These questions provide a framework designed to generate information for management of prawns as bait organisms in the following ways:

It will allow selection of time of year for optimal monitoring of the species in relation to seasonal effects.

It provides information on abundance and distribution patterns that can in future be used to assess changes in stock.

It establishes base-line data against which the effects of harvesting can be gauged in areas where bait collecting is permitted.

2.2. Material and methods

2.2.1 Study Area

Following a preliminary survey of *Callinassa kraussi* and *Upogebia africana* in Langebaan Lagoon, ten sites were chosen to assess prawn density and population structure (Figures 2.1 & 2.2). These sites were spaced around the lagoon circumference to span all types of soft sediments present. Both areas that are exploited for bait and areas closed to bait collectors were examined. Figure 2.2 shows the position of transects and the zones into which the lagoon was divided when describing the zonation patterns of prawns.

The first two sites, Sepia Bay and Yacht Basin, border on Langebaan Town and are exploited for both *U. africana* and *C. kraussi*. Further south, Klein Oesterwal is exploited for *C. kraussi* by people who access the area on foot. The Center Banks occur in the center of the lagoon and are separated from Klein Oesterwal by a deep channel; they are usually accessed by boat, and are also exploited for *C. kraussi*.

Moving south along the lagoon's eastern shore, Oesterwal falls in the B zone, where bait collecting is prohibited. Further south, Bottelary, Geelbek and Schrywershoek fall in the C zone where entry is prohibited.

On the eastern shore, Churchhaven is situated in the B zone. Here, limited access is allowed on the beach but no resource collection is permitted. Further north, Kraal Bay lies in the A zone, but little prawn exploitation occurs there. The area does, however, have large number of beach-goers in the summer season.

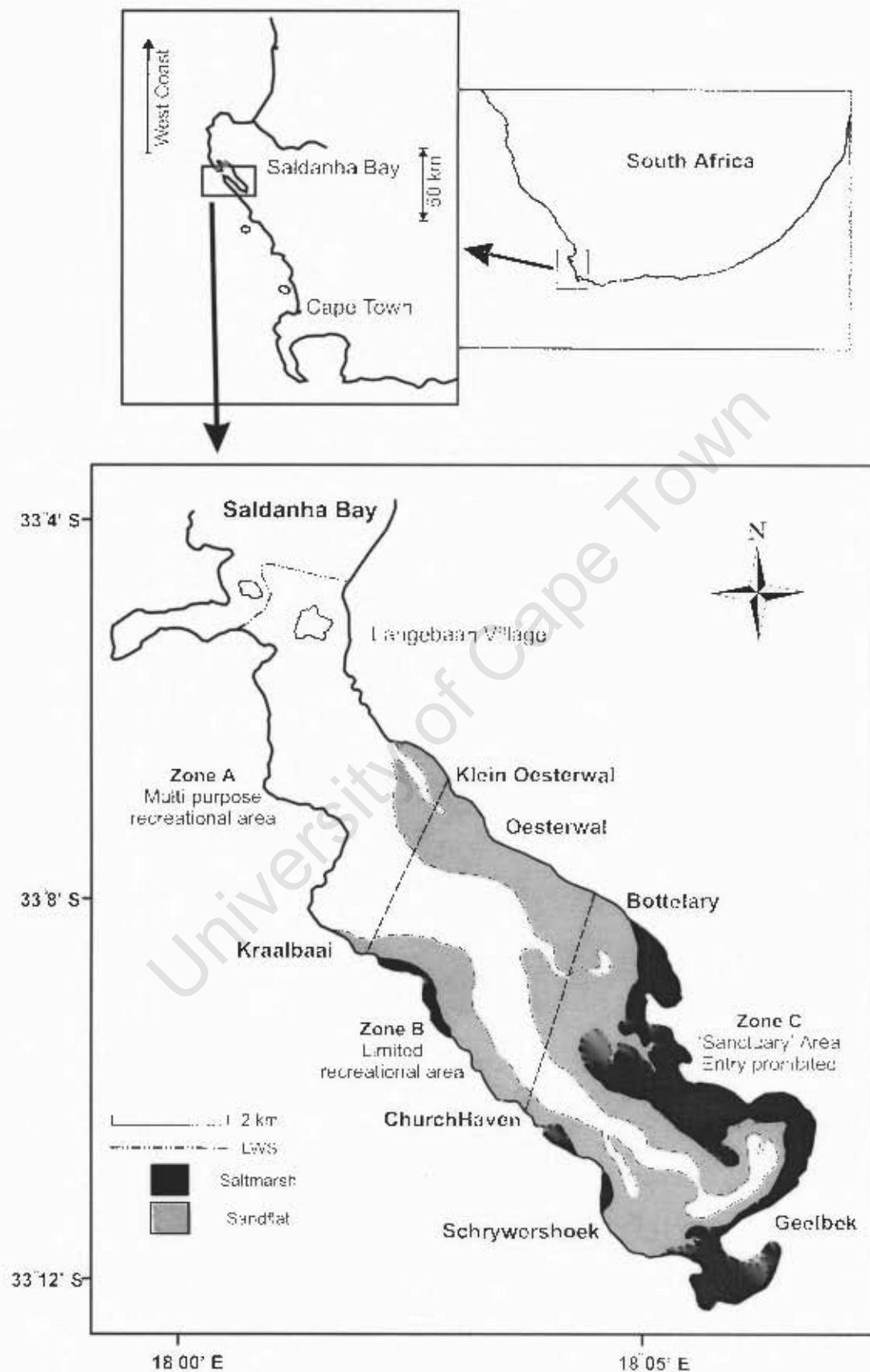


Figure 2.1 Map showing study area.

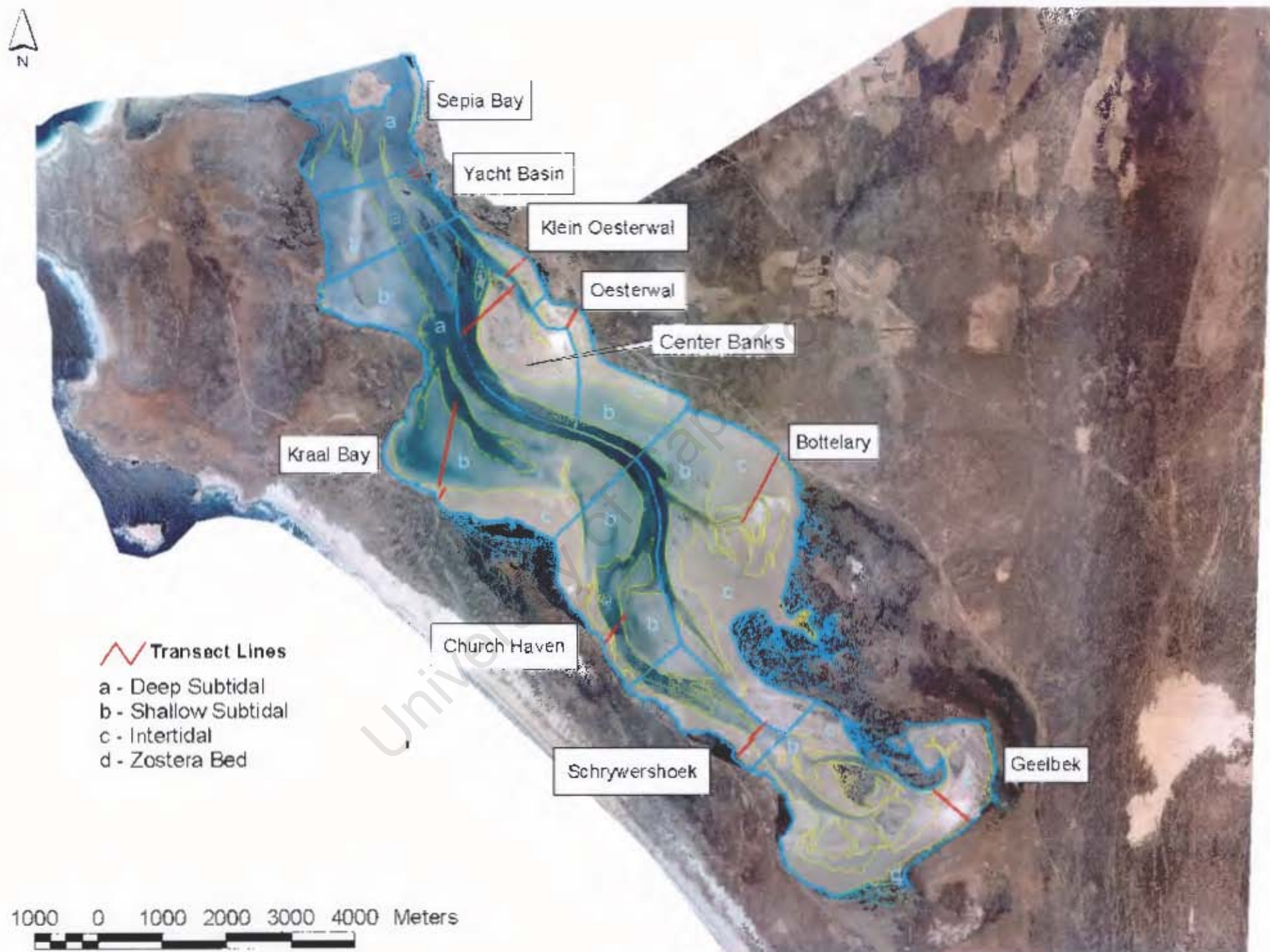


Figure 2.2 Aerial photograph of Langebaan Lagoon showing the zones in which, prawns were sampled in this study.

2.2.2 Particle-size analysis

Sediment samples were collected from up to six zones at each site. A core of sediment was removed from the substratum and a sub-sample of 10 g extracted and dried overnight at 90 °C, after which the weight of the dried bulk sample was recorded. Water was added and the sample was left to stand overnight. The bulk sample was then wet sieved using a 63µm sieve. The subsieve fraction (>63µm) was dried overnight at 90 °C. The >63µm dry fraction was dry sieved using a 2-mm sieve to remove the gravel. The weights of the gravel fraction (>2 mm) and the sand fraction (63µm – 2mm) were recorded. The percentage mud was calculated as the difference between the bulk weight and the >63µm fraction. The sand fraction was split using a sample splitter and a 3 g sub-sample was collected for a grain size analysis using a settling column (Flemming 1975).

2.2.4 Prawn sampling density, size structure and sex ratios

Dug/Sucked Samples

Ratio of prawns to holes

In the surveys of the 10 sites, the densities of prawn holes were taken as a surrogate measure of prawn densities. Before these surveys were undertaken, a pilot study was completed to establish the ratio of prawn holes to prawns. This pilot study also allowed assessments of the size structure and sex ratios of the prawns.

At eight of the ten identified sites, prawn holes were counted in two 50x50 cm areas in the midshore region. Sepia Bay and the Yacht Basin were excluded as the intertidal area was small and often rocky, making effective digs impossible and sandprawns were, in any case, scarce or absent there. At each of the sampled sites one area was dug to a depth of 1 m. The contents were removed with a spade and sieved through a 2-mm sieve and all prawns collected. The second area was sucked

using a prawn pump (Hailstone & Stephenson 1961) and the sediment again sieved through a 2-mm sieve. All prawns removed from these samples were counted and preserved in 4% formaldehyde in seawater. Subsequently they were sexed and their carapace lengths were measured to an accuracy of 0.01 mm. This provided data on the sex ratios and size frequency distribution of prawns at each site.

A Chi-square test was performed on the data for both the dug and sucked samples to determine if the ratio of the number of *C. kraussi*: number of holes departed significantly from 1:1, using a chi-square test on pooled data and a chi-square test for heterogeneity (Zar 1999). When the dug data were tested with a chi-square for heterogeneity, the null hypothesis of a 1:1 ratio was rejected ($P < 0.001$) and hence a 1:1 ratio could not be assumed for the dug data, although the actual ratio of 1:1.09 was very close to the predicted 1:1 ratio. The same goodness of fit was performed on the data obtained from the sucked areas and the result yielded a 1:1.02 ratio, which did not significantly depart from 1:1 ($0.90 \leq P \leq 0.95$). This result was also tested using the chi-square test for heterogeneity and yielded $0.25 \leq P \leq 0.01$; hence, the null hypothesis was not rejected and a ratio of 1:1 could be assumed for the sucked data (Zar 1999). This conforms to the 1:1 ratio obtained for *C. kraussi* by Forbes (1973a) and Wynberg & Branch (1991), for areas with sheltered conditions and constant salinity. As result, I assumed that a 1:1 ratio would be applicable to all my samples of *C. kraussi*. A ratio of 2:1 (holes:prawns) was used for *Upogebia africana* based on Wynberg & Branch (1991), and I assumed that it would apply to *U. capensis* as well.

Size structure

All prawns in the dug and sucked samples were measured to allow comparisons of the size structure of *C. kraussi* among sites, and also allowed a preliminary comparison between samples in exploited versus unexploited areas.

Biomass

Subsamples of prawns (minimum $n = 25$) obtained from dug and sucked samples from Bottelary, Center Banks and Klein Oesterwal were measured and dried at 55°C until a constant weight was achieved. Calibration curves were constructed between carapace length and body mass, and used to calculate the total prawn biomass in Langebaan Lagoon as well as the total biomass removed by bait collectors, from data on prawn densities and size compositions.

Sex ratios

The sexes of the prawns collected in the dug and sucked quadrats were used to calculate the ratio of male, female and juvenile prawns. Prawns less than 7 mm in carapace length could not be effectively sexed and were classed as juveniles (Forbes 1973a).

General Distribution and Density

Zonation

Using aerial photographs of each site and field inspections, the shores were divided into different zones. The zones identified were (1) a vegetation zone (on the upper shore) and four unvegetated zones: (2) the upper intertidal shore, (3) the lower intertidal shore, (4) the shallow subtidal area and (5) the deep subtidal area. The vegetation zone was defined as areas covered by the eelgrass *Zostera capensis* or the cord grass *Spartina maritima*. The intertidal area was subjectively divided in half to define the upper and lower shore areas. The subtidal area was also divided in two, using half the maximum depth encountered as the mid point. Beach profiles were constructed using heights above mean sea level, obtained using a differential GPS placed along a transect of the intertidal area at fixed distances. Table 2.1 records the co-ordinates of the top and bottom of each intertidal transect. The underwater profiles were obtained from water depths measured during the subtidal transects (see method below). Depending on the site, the zones encountered, and their lengths, differed. In certain areas some of the zones were absent.

Table 2.1 Decimal degree co-ordinates of intertidal zones of the ten sample sites analysed.

SITE	ZONE	TOP OF TRANSECT	BOTTOM OF TRANSECT	LENGTH
Sepia Bay	Intertidal	33.10217;18.03075	33.10234;18.03038	50 m
Yacht Basin	Intertidal	33.10248;18.03149	33.10286;18.03131	50 m
Kraal Bay	Upper shore	33.1489;18.03242	33.1483;18.03344	100 m
	Lower shore	33.1483;18.03352	33.1476;18.03428	100 m
Klein Oesterwal	Vegetation zone	33.1166;18.04479	33.1165;18.04491	20 m
	Upper shore	33.1165;18.04491	33.1156;18.04568	160 m
	Lower shore	33.1156;18.04568	33.1142;18.0474	175 m
Oesterwal	Vegetation zone	33.1222;18.05617	33.1224;18.05604	20 m
	Upper shore	33.1225;18.05593	33.1236;18.05487	200 m
	Lower shore	33.1236;18.05487	33.1249;18.05324	210 m
Center Banks	Intertidal	33.12766;18.04123	33.12212;18.04735	850 m
ChurchHaven	Upper shore	33.1776;18.06909	33.1771;18.06966	70 m
	Lower shore	33.1771;18.06966	33.1766;18.07012	65 m
Schrywershoek	Vegetation zone	33.1856;18.08193	33.1855;18.08212	20 m
	Upper shore	33.1855;18.08212	33.1846;18.0835	140 m
	Lower shore	33.1846;18.0835	33.184;18.08472	145 m
Bottelary	Vegetation zone	33.1429;18.08976	33.143;18.08958	20 m
	Upper shore	33.143;18.0894	33.1438;18.08826	140 m
	Lower shore	33.1439;18.08809	33.1447;18.08717	140 m
Geelbek	Vegetation zone	33.1946;18.12109	33.1944;18.12072	40 m
	Upper shore	33.1944;18.12072	33.1937;18.11941	140 m
	Lower shore	33.1937;18.11941	33.1929;18.11823	140 m

During April 1999, three transects were laid out during low spring tides at all ten sites across the width of the exposed intertidal banks from the vegetation zone to the low water mark. On each transect prawn burrow openings were counted every ten meters in 0.0625 m² quadrats. The subtidal transects were performed during the Summer (December – February) of 2000/2001, using SCUBA diving equipment. At nine of the ten sites a weighted line was placed perpendicular to the shore as an extension of the intertidal transect and every 10 meters the number of burrow openings in three replicate 0.0625 m² quadrats were counted and the water depth recorded. The subtidal counts were carried out from the spring tide low-water level to the maximum depth of the channel. In areas such as Kraal Bay where there was no channel close to the beach, the transect was terminated at a distance of 500 m. No subtidal count was done for the site at Oesterwal as there was no significant subtidal area between there and the Centre Banks. Information obtained from these transects was used to estimate the distribution, density and biomass of prawns species in Langebaan Lagoon. The sizes of intertidal and subtidal areas corresponding to each transect were calculated using maps, bathymetric data, differential GPS measurements and field inspections. For each of the ten areas represented by the transects, calculations were made of the areas of the upper shore, lower shore, shallow subtidal and deep subtidal. The distribution and density measurements obtained from the transect data were extrapolated to estimate the density and biomass for prawn species in each zone in each area, and then for the entire lagoon.

Seasonality

Further to the above, the intertidal transects (covering the upper and lower shore) were repeated on four different occasions, during summer, autumn, winter and spring in 2000/2001, allowing an assessment of whether there were significant differences in prawn-hole densities among seasons.

Overall abundance

To estimate overall numbers of prawns, the lagoon was divided into sections representative by each of the sampling sites, and the areas of intertidal shore, shallow subtidal and deep subtidal within each sector calculated by GIS (see Figure 2.2 for sectors and Table 2.5 for estimations of areas).

Data for prawn abundances within these zones and sectors were scaled up from the transect data and summed to estimate numbers in Zone A where prawn harvesting is permitted, and for the lagoon as a whole.

Statistical Analysis

Levene's test and Komolgorov-Smirnov one-sample test were employed to test data for normality and homogeneity of variances (alpha set at 0.05). When possible non-normal data were transformed to achieve normality, and heteroscedastic data were transformed to achieve equality of variance. Nonparametric statistical tests were applied when normality could not be achieved but equality of variance could be attained.

For *U. capensis*, mean densities and standard deviations were calculated from transect data based on hole counts. The identity of this species at the various sites was verified by sampling using SCUBA and a spate pump. Two 0.5m X 0.5m grids were placed at each site and the sediment was pumped out of these areas into 1 mm mesh bags and all prawns collected, identified and counted.

For *U. africana* and *C. kraussi*, each site was treated separately and a One-Way ANOVA was used to test for differences in densities between the different zones at each site.

For *C. kraussi* only, a Two-Way ANOVA was used to test for differences in densities between seasons and sites, with seasons as a fixed factor and sites as a random factor. Sepia Bay was omitted from this analysis as *C. kraussi* was not recorded there.

2.3. Results

2.3.1 Sediment Analyses

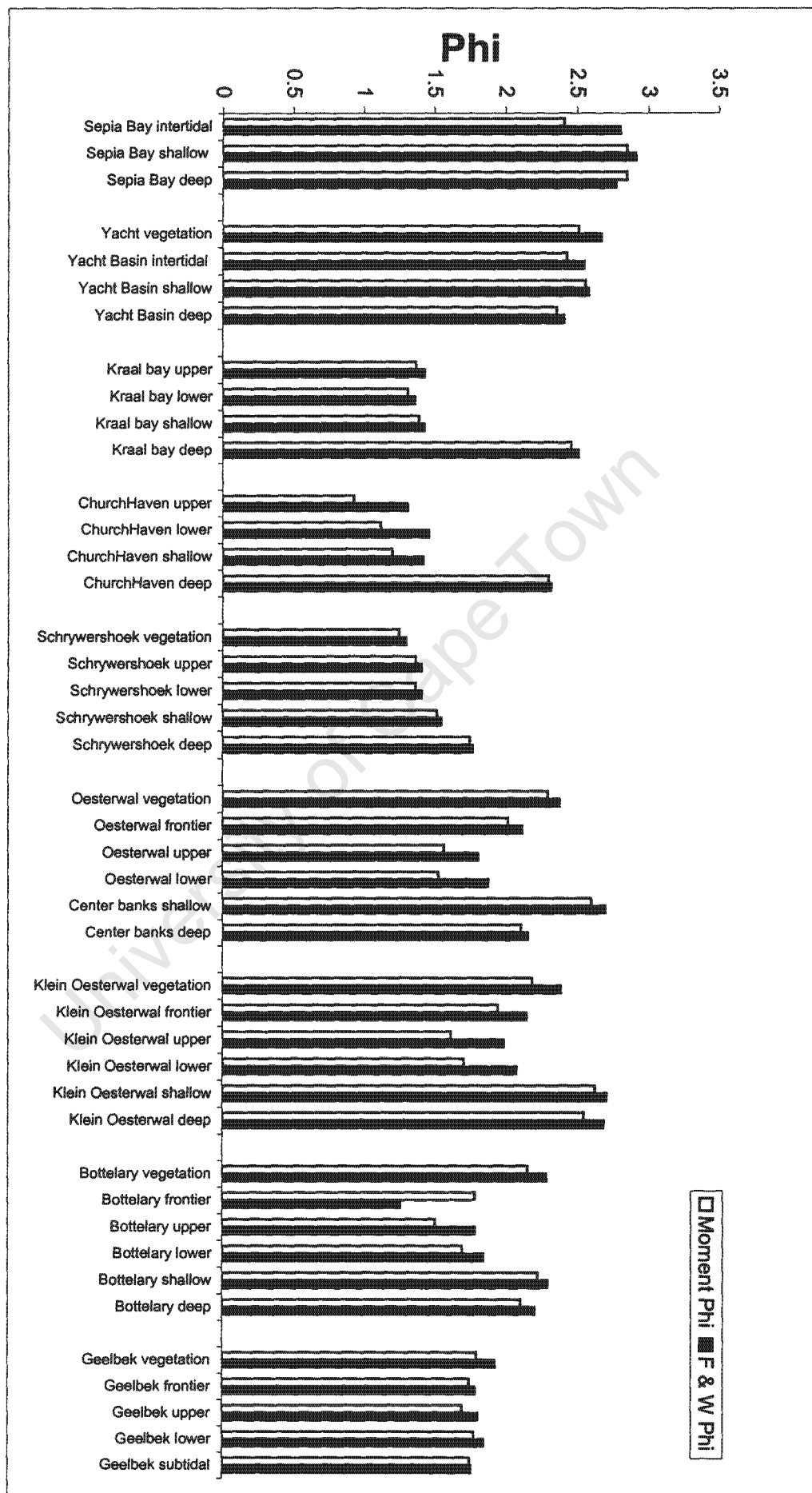
Figure 2.3a shows both Folk & Ward Mean and Moment Mean Phi values for sediment samples obtained from the study sites in this project. Figure 2.3b shows the percentages of clay and gravel at the various study sites. Sediment characteristics differed both up and down the shore and between western and eastern shores. Overall there was a gradient from coarser to finer material as one moved from the upper shore down to the lower shore and into the subtidal, with fine material being prominent in the deeper channel areas. However, wherever vegetation and frontier zones were present, the sediment was finer there than in the remainder of the intertidal zones. Further to this, sites on the western shore had finer sands, slightly more gravel and lower amounts of mud than those on the eastern shore, rendering them 'coarser' than sites on the eastern shore. Sepia bay and Yacht Basin, at the mouth of the lagoon, had substantially more gravel than elsewhere. Geelbek, situated at the head of the lagoon, showed the highest levels of mud and lower levels of sand thus constituting a 'muddy' environment.

Based on the proportions of gravel, sand and mud and the median particle size of the sand, the sites were subjectively ranked from most coarse to most fine in the following sequence: Sepia Bay, Yacht Basin, Kraal Bay, Klein Oesterwal, Oesterwal, Center Banks, Churchhaven, Schrywershoek, Bottelary and Geelbek.

2.3.2. Distribution of sand and mudprawns

Four species of prawns were encountered: two sandprawns, *C. kraussi* and *C. rotundicaudata*, and two mudprawns, *U. africana* and *U. capensis*.

Figure 2.3a Chart showing Phi values for all sediment samples analysed.



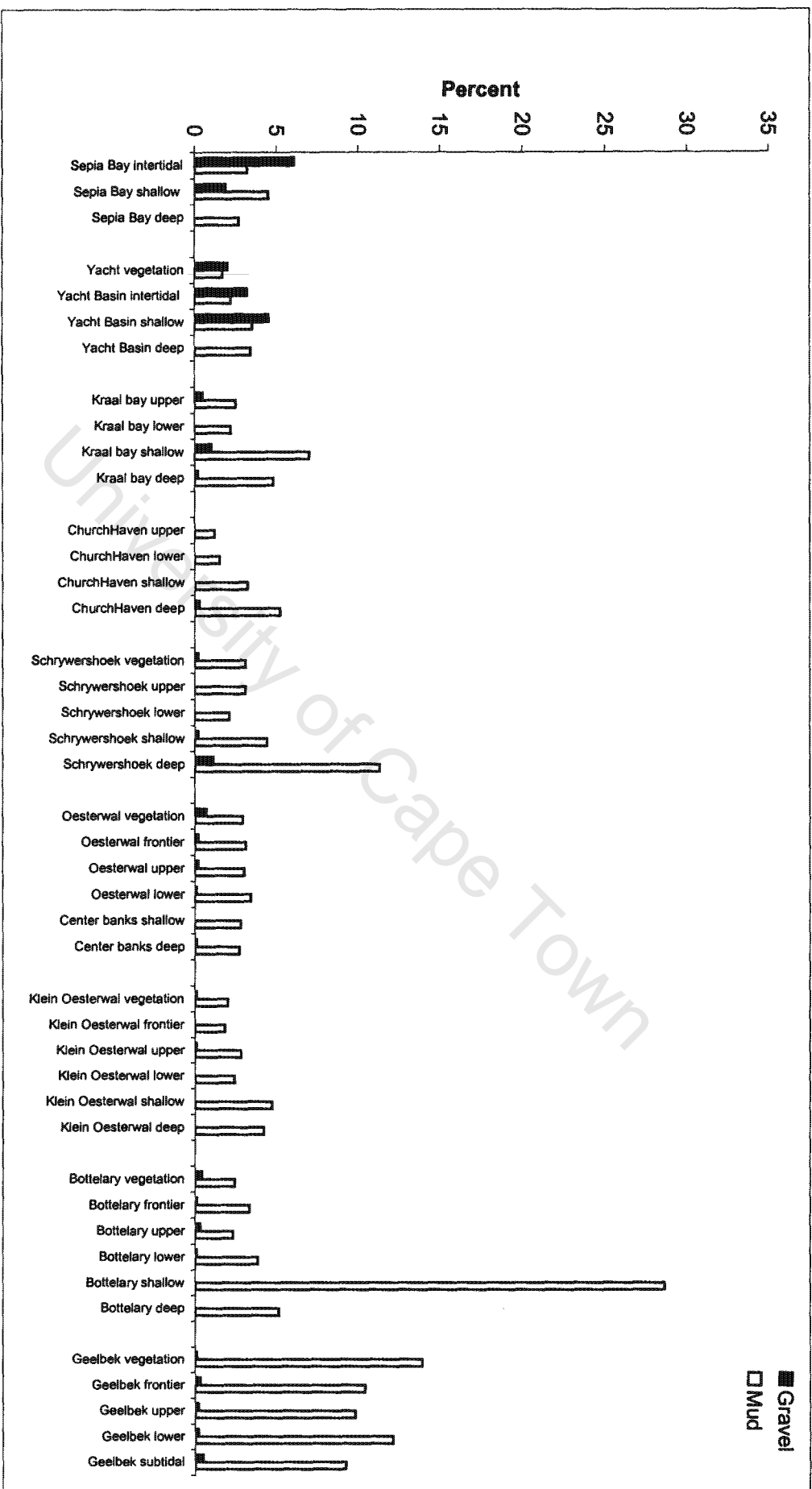


Figure 2.3b Chart showing the percentages of clay and mud present in the sediment at the 10 study sites. Bottelary deep had anomalously high gravel content (17%) because it coincided with a fossilised oyster bed, and was excluded from the analysis.

C. rotundicaudata was never encountered regularly, but a few isolated individuals were found at Oesterwal. This species has never been recorded in the Langebaan system before and it is thought that the area is extralimital for it. It co-existed with *C. kraussi* in very low densities, but was never found consistently enough to estimate its density.

C. kraussi was, however, widely distributed and occurred throughout the lagoon including small numbers in vegetated areas and high densities in unvegetated intertidal and subtidal areas. It appeared to be absent only from the deep subtidal channels where sediments were more fine than elsewhere, and tidal flow strong.

Neither of the two mudprawn species was as widely distributed as *C. kraussi*. *U. africana* was dominant in beds of the eelgrass *Zostera capensis* on the upper shore of the eastern banks of the lagoon. Isolated individuals were also found in the non-vegetated sandy intertidal areas throughout the lagoon, but at very low densities. *U. capensis*, by contrast, was entirely limited to the fine sediments in subtidal channels.

2.3.3. Prawn size structure, sex ratios, biomass, density and distribution:

Dug/Sucked samples

Size structure

Figure 2.4 represents *C. kraussi* size frequencies for the eight sites, based on pooled data from the dug and sucked quadrats. Table 2.2 represents the results of the Kruskal-Wallis ANOVA, and post-hoc Tukey-type test, to determine if there were significant differences in *C. kraussi* sizes, among sites.

Apart from Schrywershoek, none of the sites differed significantly from each other with respect to mean prawn sizes. Schrywershoek differed significantly ($P < 0.005$) from Kraal Bay, Oesterwal

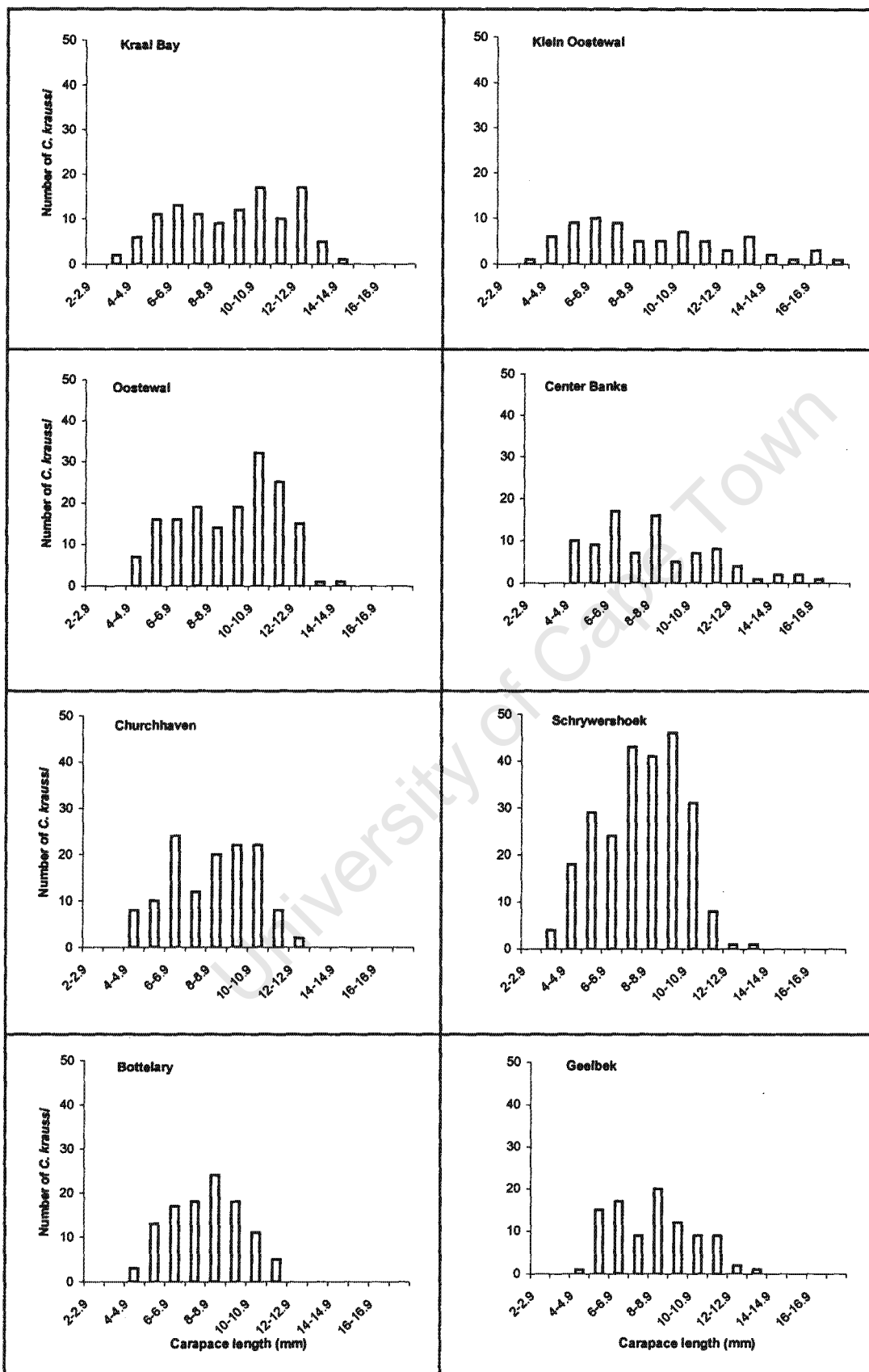


Figure 2.4 Length frequency distributions of *C. kraussi* populations from 8 sites in Langebaan Lagoon. Samples were taken from areas of 0.5 X 0.5 m dug or sucked down to a depth of 1m.

Table 2.2 Results from a Kruskal-Wallis ANOVA to determine whether there were any significant differences in *C. kraussi* size at the different sites in Langebaan Lagoon. Sites are arranged in sequence from those with the most coarse to those with the most fine sediments. Significant differences were analysed using a Tukey-type test; sites with shared letters in the homogenous groups were not significantly different.

Kruskal-Wallis test: $H(7, N = 1001) = 29.80, p = 0.001$.

Tukey-type test:

Number	Site	Sediment composition	(n)	Max size (mm)	Mean size (mm)	Homogenous groups
1	Sepia Bay	5% gravel	<i>no data</i>			
2	Yacht Basin	5% gravel	<i>no data</i>			
3	Kraal Bay	>50% medium sand	110	13.2	8.60	b
4	ChurchHaven	>50% medium sand	245	11.7	7.82	ab
5	Schrywershoek	>50% medium sand	125	12.6	7.50	a
6	Center Banks	>50% fine sand	89	16.1	7.87	ab
7	Oesterwal	>50% fine sand	161	14.3	8.52	b
8	Klein Oesterwal	>50% fine sand	73	16.1	8.60	b
9	Bottelary	>50% fine & v.fine sand	103	11.3	7.62	ab
10	Geelbek	10% mud	95	12.9	7.80	ab

and Klein Oesterwal (Table 2.2). There was a trend for both mean and maximum sizes to be low at the head of the lagoon where the sediments were most fine (Table 2.2).

Too few individuals of *U. africana* were encountered to do an effective analysis of size composition for this species.

Biomass

Figure 2.5 shows the mean biomass per individual and the total biomass per unit area for *C. kraussi* in the intertidal areas of the eight sites where it occurred. There were significant differences among sites (Kruskal-Wallis test: $H(7, N = 940) = 38.17, P < 0.0001$). Four sites (Klein Oesterwal, Center Banks, Churchhaven, Geelbek) did not differ significantly from any other sites, but Schrywershoek and Bottelary had animals with a significantly smaller mean biomass than Kraal Bay, Klein Oesterwal and Oesterwal. Overall, there was a tendency for the mean individual biomass to be less at sites with finer sediment.

Total dry biomass.m⁻² was calculated from mean density and mean biomass per individual. Oesterwal had the highest dry biomass (68.4 g.m⁻²) and the two lowest values were for Bottelary and Geelbek (~ 26 g.m⁻²). The average total biomass.m⁻² for all sites was calculated as 42.2 g.m⁻².

Sex ratios

Prawns that had a carapace length > 7 mm could be sexed. Table 2.3 represents the sex ratios of *C. kraussi* obtained from the dug and sucked quadrats. On average, females made up 58.8% of the sexually mature population, but at the three sites nearest the head of the lagoon, the proportion of females was low.

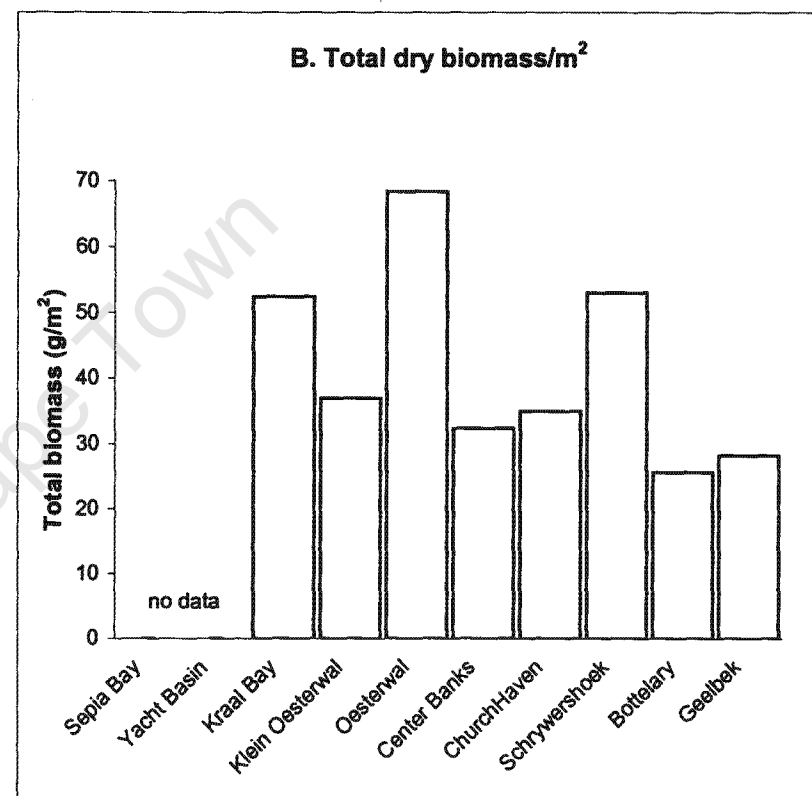
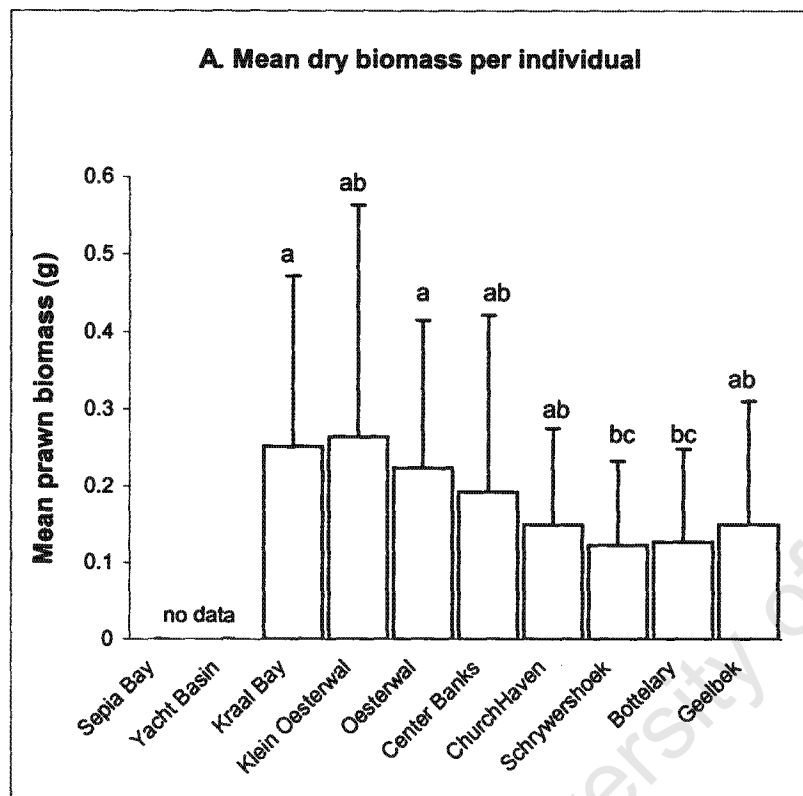


Figure 2.5 Charts showing (A) the mean biomass per individual (+1sd) and (B) total biomass per m² of *C. kraussi* for the 10 sample sites at Langebaan Lagoon. The sites are arranged from coarsest to finest particle size (Flemming 1977). Sites that share common letters do not differ significantly (Tukey-type tests, $p > 0.05$).

Table 2.3 The percentages of male, female and juvenile prawns at each of 8 sites in Langebaan Lagoon, arranged from coarser to finest sediments.

Number	Site	(n)	Male	Female	M:F ratio	Juvenile
1	Sepia Bay	<i>no data</i>				
2	Yacht Basin	<i>no data</i>				
3	Kraal Bay	110	24.07	36.11	1:1.5	39.81
4	Klein Oesterwal	73	15.94	30.43	1:1.9	53.62
5	Oesterwal	161	25.32	39.24	1:1.6	35.44
6	Center Banks	89	16.39	40.98	1:2.5	42.62
7	Churchhaven	245	21.14	34.96	1:1.7	43.9
8	Schrywershoek	125	21.21	23.81	1:1.1	54.98
9	Bottelary	103	30.84	28.04	1:0.9	41.12
10	Geelbek	95	20.43	27.96	1:1.4	51.61

General distribution and density

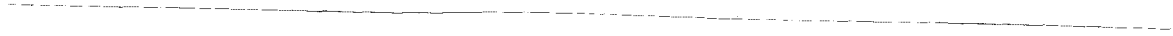
Zonation

Figure 2.6 a & b represents the cross-sectional profiles of the transects at all ten sample sites. A maximum of five zones could be identified at any particular site, namely the vegetation zone, the upper shore, the lower shore, the shallow subtidal and the deep subtidal channel. The lower shore could broadly be separated from the upper shore because it was only fully exposed at Spring Low tide. Because of variation in the structure of the shore and intertidal area, not all of these zones were clearly identifiable at each site. Three trends emerged. Near the mouth of the lagoon and for much of the western bank, the intertidal zone was short, but it widened increasingly towards the head. Second, the subtidal area extended into deep channels near the mouth but became flattened and shallow at the head. Third, the vegetation zone was present only on the eastern bank, extending from about one third of the way down the lagoon to the head.

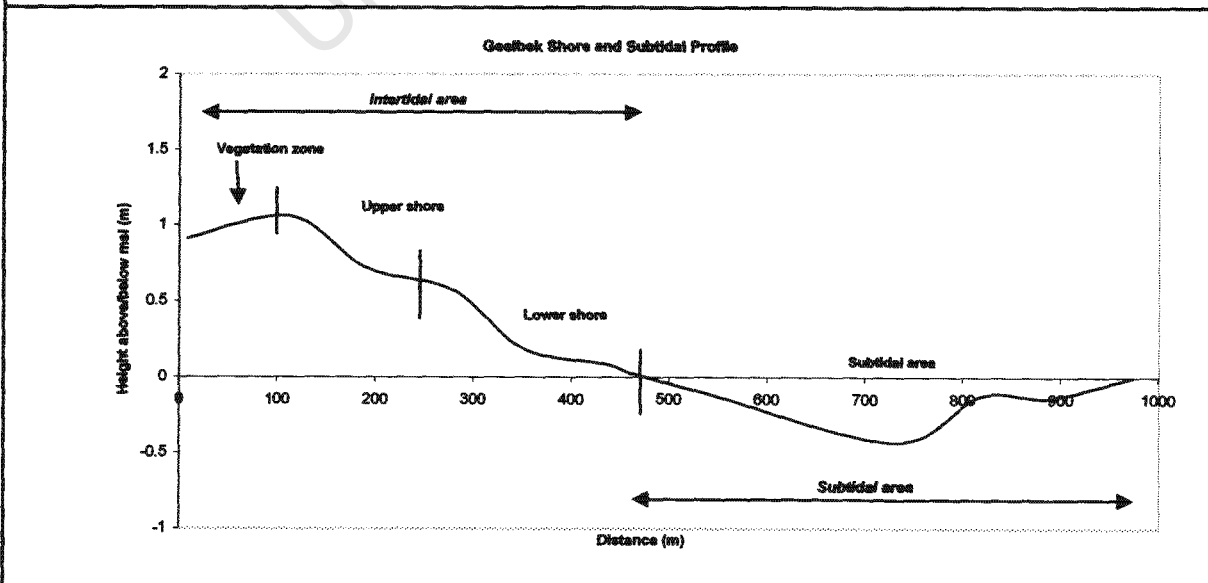
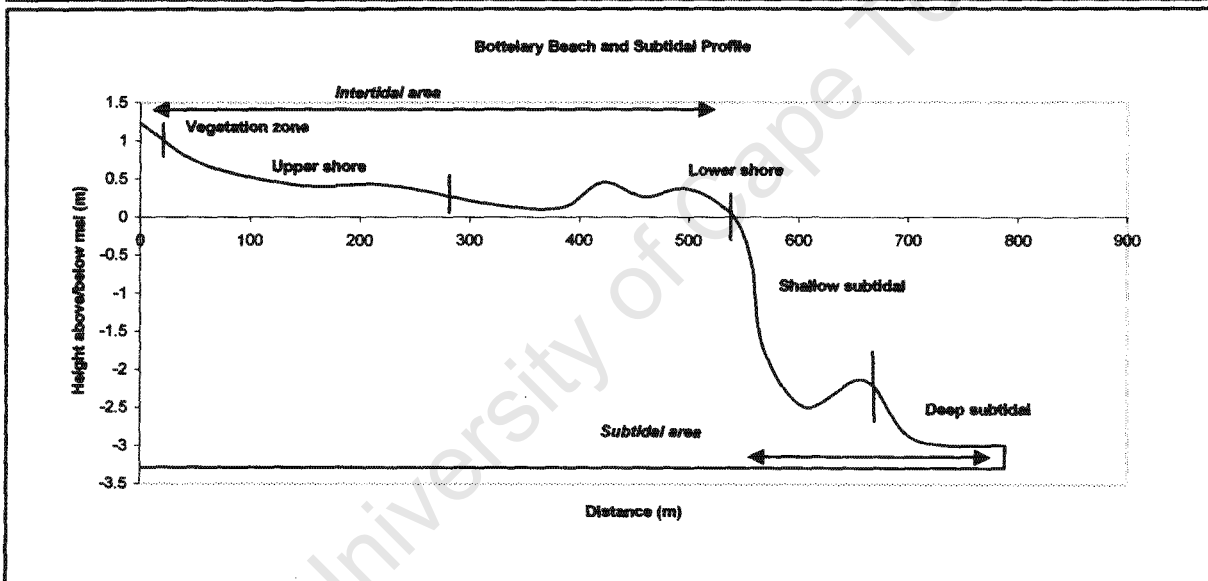
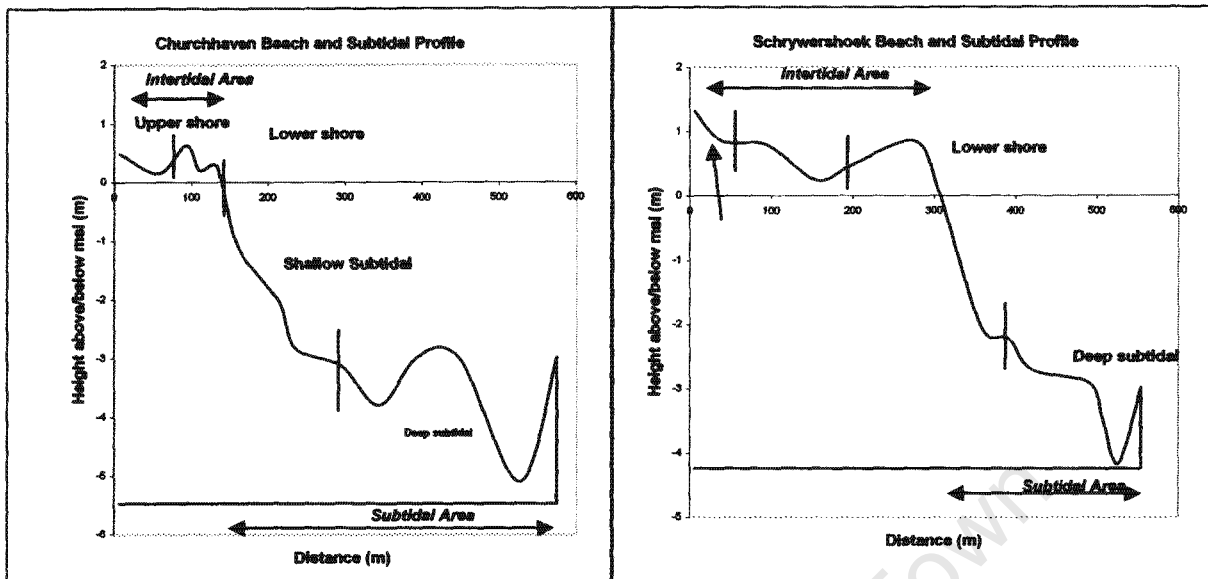
Upogebia capensis

U. capensis was encountered only in the deep subtidal areas off Kraal Bay, Klein Oesterwal, Center Banks, Schrywershoek and Bottelary, and in the shallow subtidal at Sepia Bay and Yacht Basin. It was absent from all intertidal areas (Figure 2.7).

Figure 2.6 a & b Cross-sectional profiles of the shore for the different study sites in Langebaan Lagoon.



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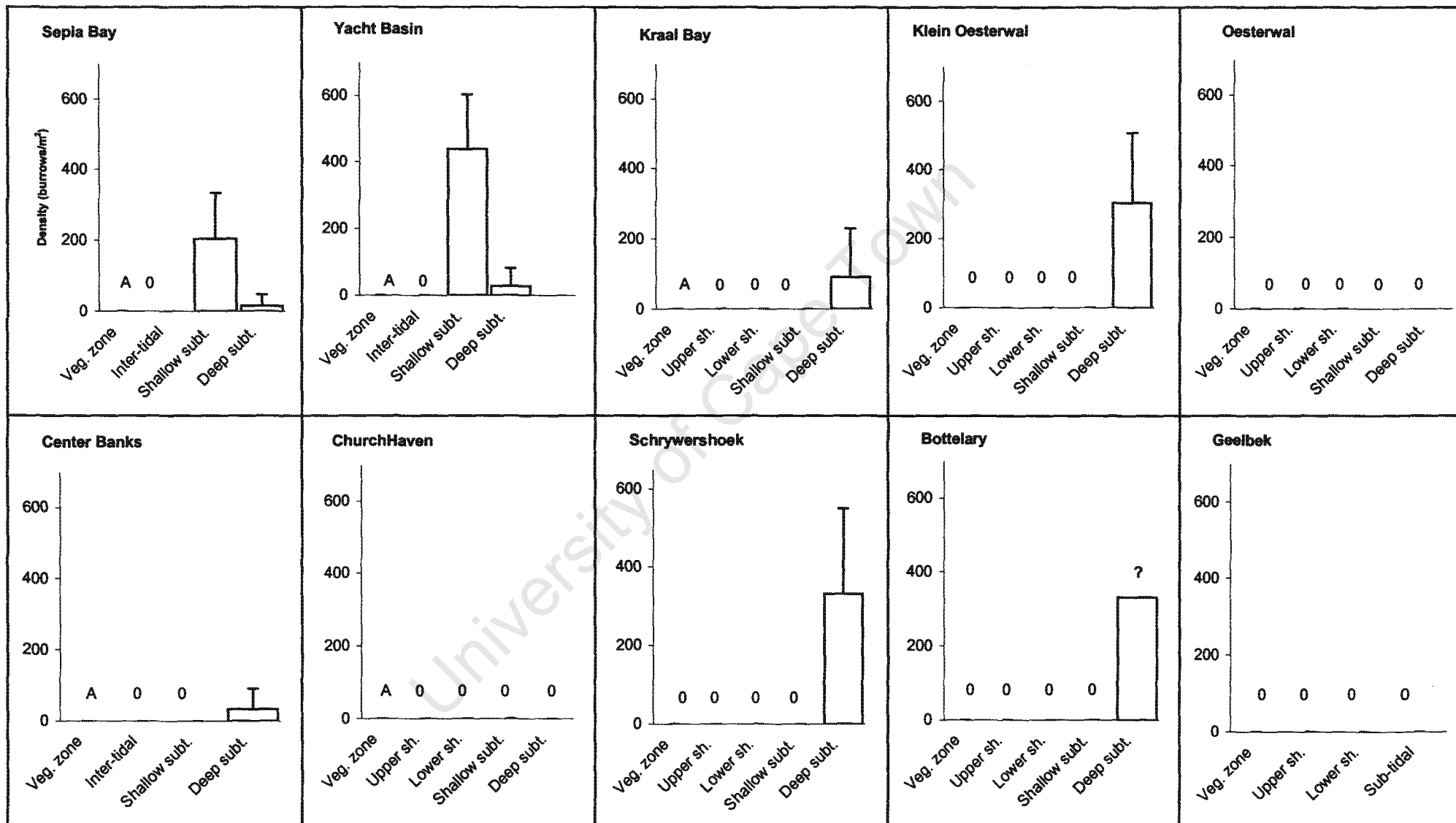


Figure 2.7 The mean density/m² (+ 1 sd) of *U. capensis* for the different zones at the different sample sites in Langebaan Lagoon. 'A' indicates absence of a zone; '0' indicates absence of *U. capensis* from a zone; '?' indicates an estimate.

A Kruskal - Wallis ANOVA and post hoc Tukey-type tests revealed significant differences in densities of *U. capensis* between the deep subtidal channels of all the sites except between Schrywershoek and Klein Oesterwal (Kruskal-Wallis test $H(5, N = 330) = 155, P < 0.0001$; Tukey-type tests $P < 0.0001$ in all cases). The highest density for the species was recorded at the Yacht Basin – 430 burrows.m⁻². At the Yacht Basin and Sepia Bay the species occurred on both the shallow subtidal and in the channel. Densities there were highest in the shallows and significantly less so in the adjacent channels ($P = 0.00002$ for both sites).

Upogebia africana

At sites where there was a vegetation zone present on the upper shore, *U. africana* consistently reached its highest numbers in this zone (Figure 2.8). These sites all occurred on the eastern shore of the lagoon. At all the sites where *U. africana* was present or sufficiently abundant to warrant statistical tests, Kruskal-Wallis ANOVAS detected highly significant differences among zones within sites ($P < 0.0001$ in all cases). In most instances post-hoc Tukey-type tests revealed that this was due to the vegetation zone having significantly greater densities than other zones (which did not differ from each other). The exception was Geelbek where *U. africana* extended down the shore in numbers greater than at other sites, and where all the zones differed significantly from each other (Figure 2.8). *U. africana* was never recorded in the subtidal zone at any of the sites.

There were significant differences in the densities of *U. africana* in the vegetation zone among sites. The densities of mud prawns in the vegetation zones varied from 139 burrows.m⁻² at Geelbek to 549 burrows.m⁻² at Oesterwal. Geelbek and Bottelary did not differ significantly with respect to mud prawn density (Tukey HSD test, $P > 0.05$). All other sites were significantly different from each other ($P < 0.05$). The sites on the western shore mostly lacked *U. africana*: it was only recorded at Kraal Bay at very low densities and, on a single occasion at Churchhaven in the

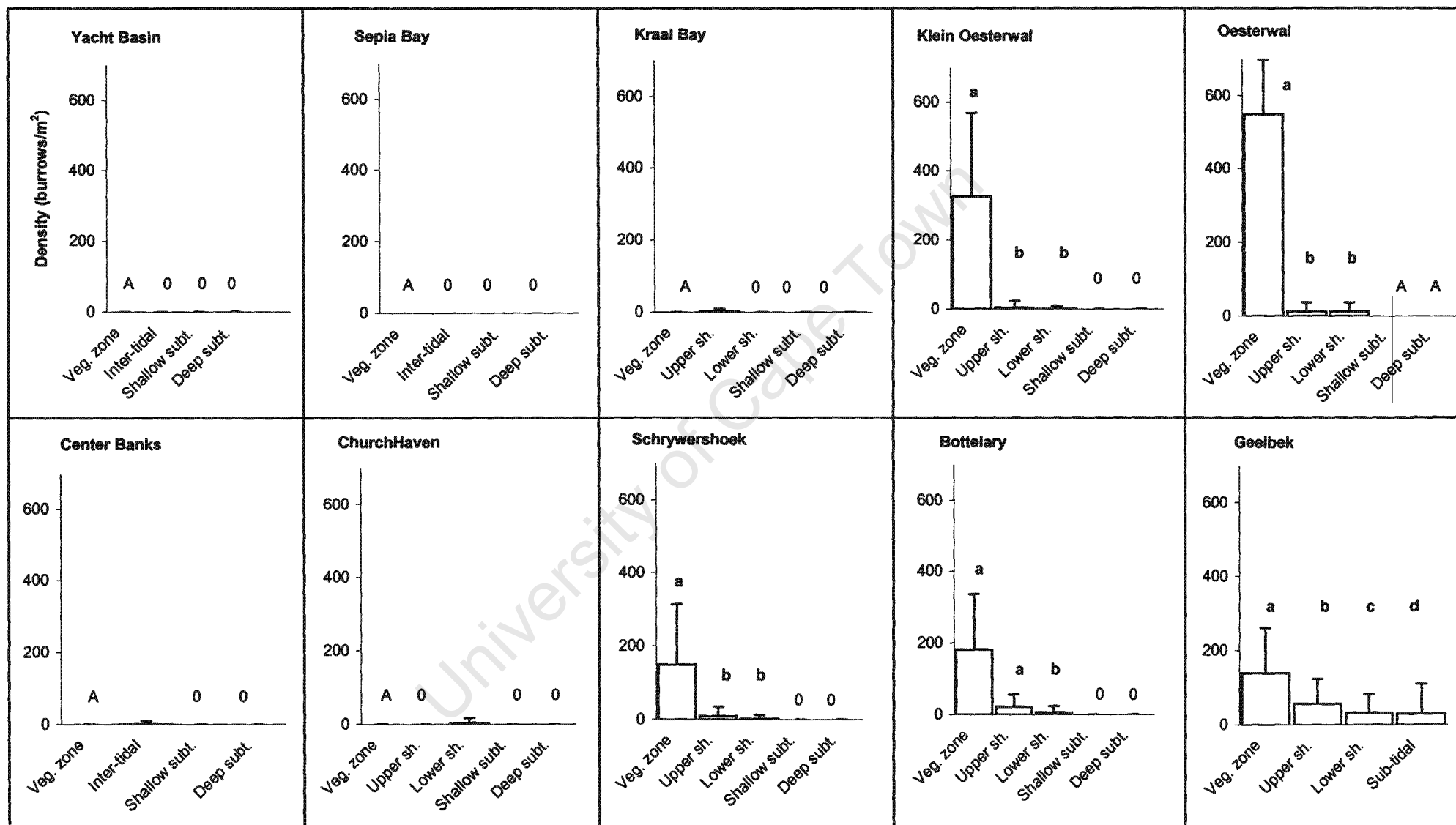


Figure 2.8 The mean density/m² (+ 1 sd) of *U. africana* for the different zones at the different sample sites in Langebaan Lagoon. 'A' indicates absence of a zone; '0' indicates absence of *U. africana* from a zone. Lower case letters placed above bars indicate which zones were significantly different from each other within sites.

intertidal area. Apart from Geelbek, the species was not recorded at any of the sites in either of the two subtidal areas.

Callinassa kraussi

C. kraussi was recorded at all sites with the exception of Sepia Bay (Figure 2.9). At the Yacht Basin the densities were low: in the intertidal area the density measured only 7 burrows.m⁻². The general trend at all other sites was that densities were low in the vegetation zone (if this zone was present), increased down-shore and into the subtidal zone, but often decreased in the deep subtidal zone, most strikingly at Klein Oesterwal and Schrywershoek where *U. capensis* became dominant. The highest density on the lower shore was recorded at Geelbek, 447 burrows.m⁻².

Kruskal-Wallis tests demonstrated that there were significant differences among zones at all sites ($P < 0.001$) except the Yacht Basin, where densities were uniformly low. Post-hoc Tukey-type tests showed that most zones differed significantly from each other (Figure 2.9). The most obvious exception to this generality was that shallow and deep subtidal zones were only significantly different from each other at two sites, namely Klein Oesterwal and Schrywershoek where *U. capensis* replaced *C. kraussi* as the dominant prawn species in the deep zone.

Overall, densities were lowest at the mouth of the lagoon, rose progressively down the lagoon to peak at Bottelary and Schrywershoek but were slightly lower at Geelbek at the head of the lagoon.

Seasonality

Mean densities for intertidal *C. kraussi* differed among seasons and sites (Figure 2.10; Table 2.4). There was a significant interaction between site and season but sites contributed more strongly to the variability ($F = 101.6$) than did seasons ($F = 11.6$).

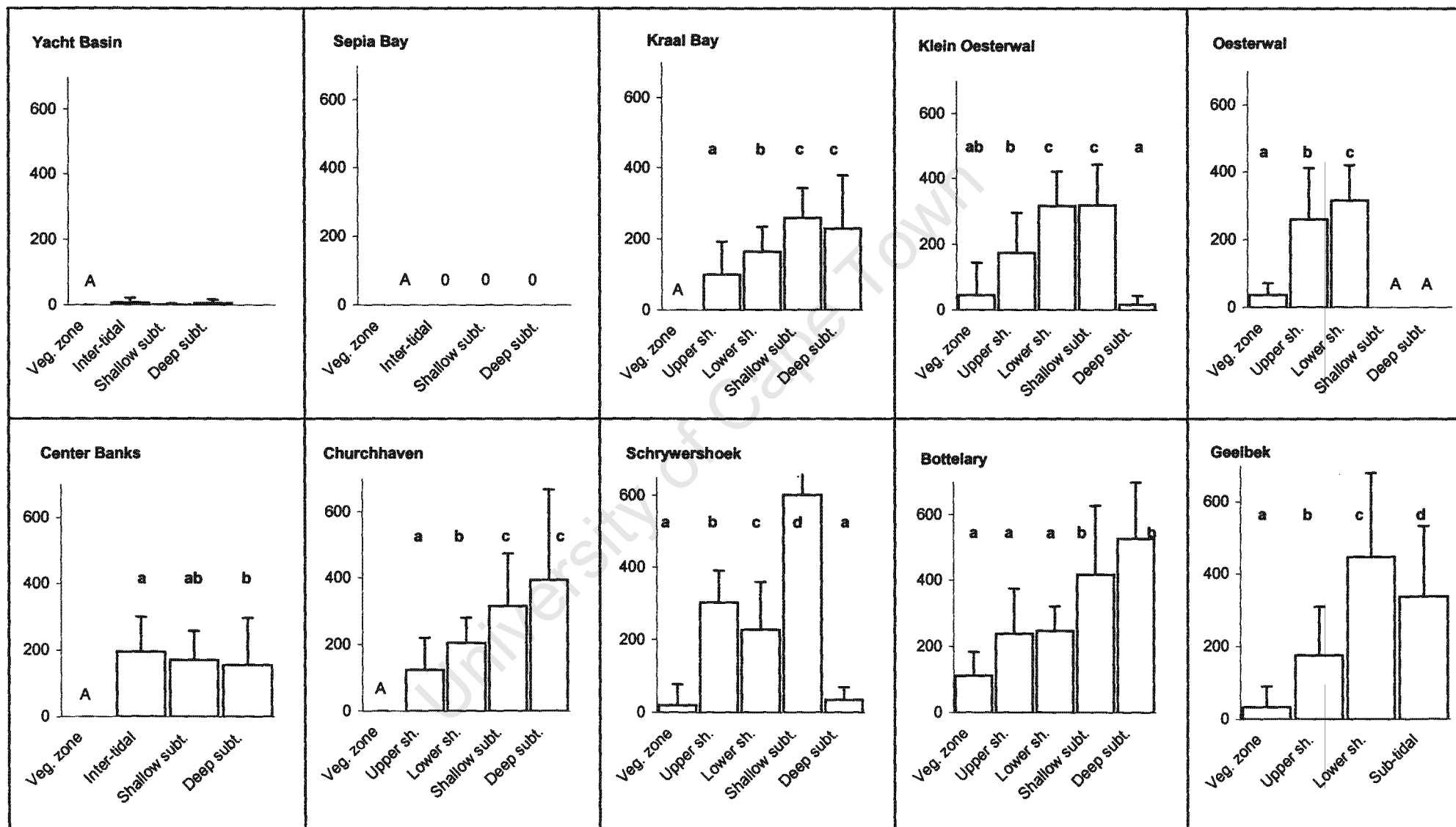


Figure 2.9 The mean density/m² (+ 1 sd) of *C. kraussi* for the different zones at the different sample sites in Langebaan Lagoon. 'A' indicates absence of a zone.

0' indicates absence of *C. kraussi* from a zone. Zones that share lower case letters, placed above bars, were not significantly different from each other within sites.

Table 2.4 Two-Way ANOVA of the effects of site and season (Spring, Summer, Autumn, Winter) on the densities of *C. kraussi*. Significant results were further analysed using Tukey HSD test and are shown with lower case letters in Figure 2.10.

	SS	Df	MS	F	P - level
Site	17433.2	8	2179	101.69	
Season	745.7	3	249	11.6	
Site*Season	5419.9	24	226	10.54	< 0.0001

Densities between the different sites were highly variable and ranged from 9 burrows.m⁻² at the Yacht Basin to 375 burrows.m⁻² at Geelbek. Four groups could be recognised. The Yacht Basin differed from all other sites in having very low densities and could sensibly be combined with Sepia Bay where *C. kraussi* was absent. Kraal Bay, Churchhaven and Center Banks had moderate densities averaging 100-230m⁻². The remaining sites formed two statistically overlapping groups: Klein Oesterwal, Bottelary and Schrywershoek (190-330 m⁻²) and Schrywershoek, Oesterwal and Geelbek (180-380 m⁻²).

Four sites showed no significant seasonal differences and at the remaining five, there were no patterns in terms of which season had peak values. Significant seasonal within-site differences ($P < 0.05$) are shown with lower case-letters in Figure 2.10). Densities between the different seasons at any given site were not very variable, most spanning a range of no more than 80 m⁻², much less than the span of 375m⁻² for inter-site differences.

Estimations of total abundance

The areas of the different zones and the densities of *U. africana*, *U. capensis* and *C. kraussi* in them are presented in Table 2.5 and were used to estimate the total numbers of prawns in (a) the entire lagoon, and (b) for areas that could be exploited because they fell in Zone A where harvesting is permitted and are currently accessed by harvesters.

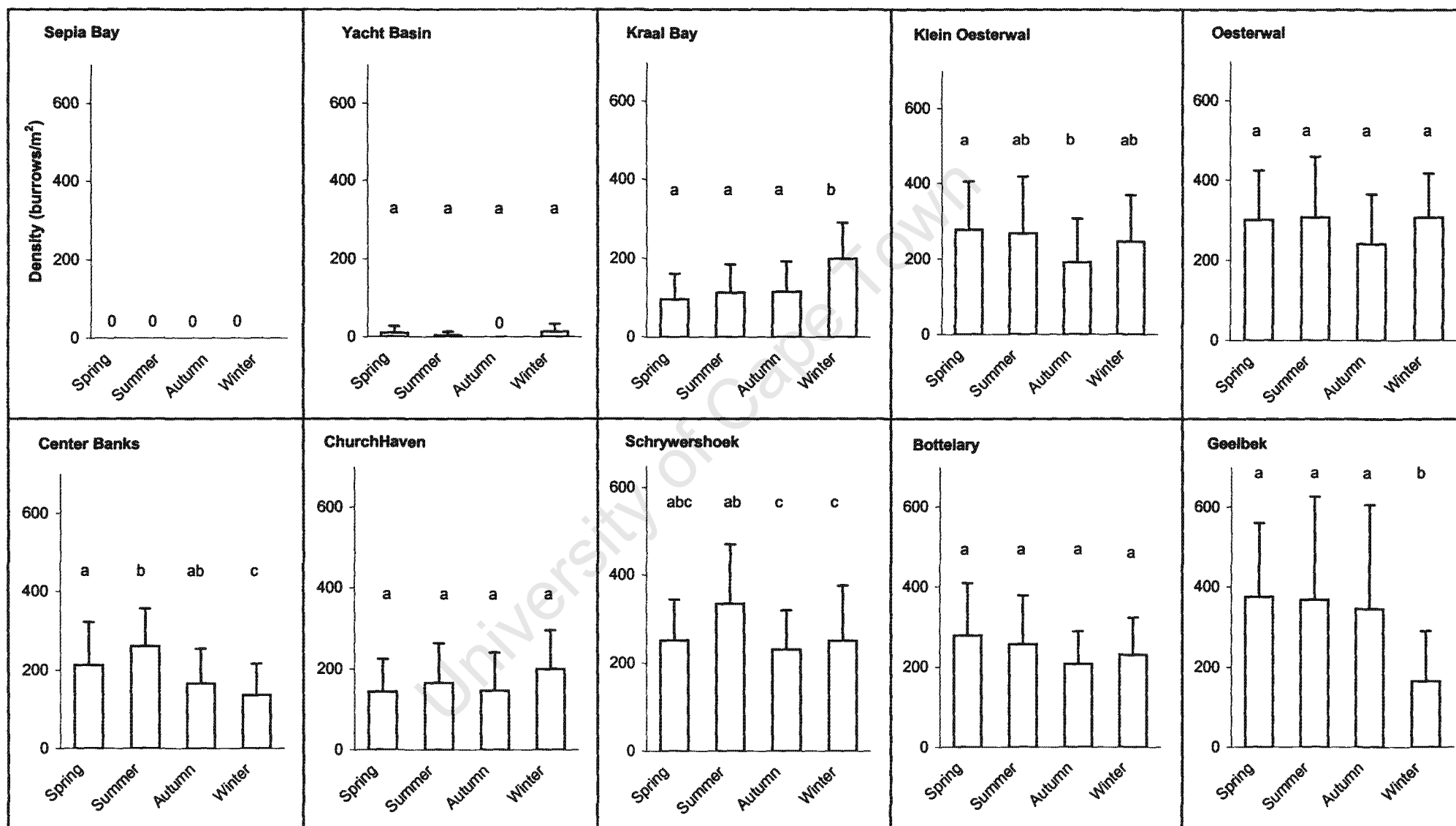


Figure 2.10 The mean density/m² (+ 1 sd) of *C. kraussi* for the inter-tidal zone at the different sample sites the Langebaan lagoon, over the different seasons. Seasons that share the same letters (a, b, c) did not differ significantly from each other.

Table 2.5 Size of zones analysed in Langebaan Lagoon with corresponding densities of prawn burrows expressed per meter square, and total estimated density. Highlighted cells are exploitable areas.

		Area (m ²)	Densities/m ²			Total numbers		
			<i>C. kraussi</i>	<i>U. africana</i>	<i>U. capensis</i>	<i>C. kraussi</i>	<i>U. africana</i>	<i>U. capensis</i>
Sepia Bay	Intertidal	1088	0	0	0	0	0	0
	Shallow subtidal	579791	0	0	204	0	0	118277271
	Deep subtidal	1642896	0	0	15	0	0	24643434
Yacht Basin	Intertidal	6863	7	0	0	48038	0	0
	Shallow subtidal	7161	1	0	437	7161	0	3129545
	Deep subtidal	14298	6	0	28	85787	0	400341
Klein Oesterwal	Vegetation zone	1000	46	325	0	46000	325000	0
	Intertidal	768153	246	3	0	188965579	1920382	0
	Shallow subtidal	168727	319	0	0	53823916	0	0
	Deep subtidal	296117	17	0	304	5067992	0	90627622
Oesterwal	Vegetation zone	500	37	549	0	18500	274500	0
	Intertidal	768153	288	13	0	221227995	9601910	0
Center Banks	Intertidal	1520299	195	2	0	296456350	3040598	0
	Shallow subtidal	929188	170	0	0	157982042	0	0
	Deep subtidal	1004942	155	0	34	155768035	0	34168034
Bottelary	Vegetation zone	9831	112	181	0	1101070	1779408	0
	Intertidal	4350751	243	14	0	1055057174	60910517	0
	Shallow subtidal	2608944	417	0	0	1087929491	0	0
	Deep subtidal	795521	527	0	330	419238350	0	262521794
Geelbek	Vegetation zone	347750	33	139	0	11475736	48337191	0
	Intertidal	4353716	312	46	0	1356182622	198094091	0
	Subtidal	1707590	337	31	0	575457719	52935280	0
Schrywershoek	Vegetation zone	0	20	149	0	0	0	0
	Intertidal	657060	266	6	0	174449423	3613830	0
	Shallow subtidal	980402	602	0	0	590202140	0	0
	Deep subtidal	182559	35	0	331	6389559	0	60426976
Church Haven	Intertidal	685806	165	2	0	112815131	1371613	0
	Shallow subtidal	64441	315	0	0	20298855	0	0
	Deep subtidal	1138157	394	0	0	448433913	0	0
Kraal Bay	Intertidal	1235659	133	1	0	163724778	617829	0
	Shallow subtidal	4826419	259	0	0	1250042566	0	0
	Deep subtidal	2221340	229	0	31	508686967	0	68861555
Total exploitable areas						861 028 703	5 903 810	121 406 816
Total lagoon		33877121				8860963891	382822148	663066670

From these figures it was estimated that the total numbers of *U. capensis* for the whole lagoon and for the exploited section were respectively 663×10^6 and 121×10^6 . For *U. africana* the respective figures were 383×10^6 and 6×10^6 , and for *C. kraussi*, $8\,861 \times 10^6$ and 861×10^6 . These figures provide an important context against which the recorded rates of removal (Chapter 3) can be evaluated.

2.4 Discussion

My survey, together with those of other authors, describes and advance reasons for the current distribution and densities of *Callianassa* and *Upogebia* species in Langebaan Lagoon.

Physical environment

Langebaan Lagoon is almost entirely marine, although minor freshwater inputs take place via seepage. Consequently, salinity varies little throughout the lagoon (Day 1959, Shannon & Stander 1977) and plays no role in regulating the distribution of the benthos, unlike the situation for estuaries where there are longitudinal gradients of salinity that strongly influence distribution patterns and abundance. Christie & Moldan (1977), in analysing benthos in Langebaan Lagoon, classified the occurrence of species into three areas, namely channels, sand bank areas and 'island areas' (in close proximity to Meeuw and Schaapen Islands near the mouth). The channel areas were composed of fine sand with a low percentage of mud due to high current velocity there. The 'island area' had narrow intertidal areas and deep channels and comprised coarser sediments driven by strong currents. The sediments on the sandbanks were of finer texture due to lower current velocity. Mazure & Branch (1979) showed that biological effects also enter into the picture, with high-shore vegetation such as *Zostera capensis* trapping very fine sand and mud and therefore reducing the median particle size.

The distribution of sediments

The distribution of different types of sediment in Langebaan Lagoon clearly plays a central role in determining where species occur. Within the lagoon there are three main gradients in sediment composition. The first of these is an east-west gradient due predominantly to the prevailing winds that move across the lagoon and deposit finer particles on the eastern shore. On these grounds, Flemming (1977) distinguished two distinct areas in Langebaan Lagoon on the basis of sediment texture: an eastern and western unit. The eastern half was characterised by fine sands (0.125 – 0.25 mm), whereas the western half consisted of medium sands (0.25 – 0.5 mm).

The second gradient is a north-south one and is related to the strength of currents which are maximal on either side of Schaapen Island at the mouth of the lagoon and diminish progressively towards the head. This results in relatively coarse particles including gravel at the mouth and extremely fine, more muddy sediments at the head (Flemming 1977). Very coarse (1 – 2 mm) and coarse (0.5 – 1 mm) sediments are limited to the outflow channels between Donkergat and Langebaan and some areas on the north-western shoreline.

The third gradient is related to vertical height on the shore. At any particular position in the lagoon particles are fine in the channels but become more coarse as one moves up the intertidal area. At the top of the shore, on the eastern banks, beds of *Zostera capensis* and *Spartina maritima* concentrate silt and clay, abruptly reducing the particle size (Mazure & Branch 1979, Siebert & Branch 2005a, in press), as do other seagrasses elsewhere (Terrados & Duarte 2000).

An important question that remains to be answered is the extent to which particle size *per se* influences the distribution of the benthos, relative to the effects of biological interactions. Sediment structure (Ferber & Lawrence 1976, Lawrence & Murdoch 1977) and organic content (Longbottom 1970) have both been shown to affect the distribution, biomass and size of macrobenthic organisms.

Macnae (1957a, b) and McLachan and Grindley (1974) demonstrated the importance of substratum in limiting the distribution of bottom fauna. In the Swartkops Estuary where salinity is usually very similar to that of the sea, McLachan and Grindley (1974) found that substratum is by far the most important factor influencing the distribution of the macrobenthos as it limits successful burrow construction.

Recognition of physiognomic areas.

The division of South African lagoons and estuaries into biotically distinct areas and zones has been documented for several systems (Christie & Moldan 1977, Flemming 1977, Cretchley 1996, Siebert 2003). In surveys done by Siebert (2003) in Langebaan Lagoon, three zones were defined: (1) a vegetation zone on the upper part of the shore (dominated by *Z. capensis*), (2) a zone directly below the *Z. capensis* bed where above-ground seagrass was absent, but below-ground rhizomes were still present, termed the 'Frontier Zone'; and (3) the intertidal sand flat dominated by *C. kraussi*.

Siebert's analysis was restricted to the intertidal zone whereas my survey covered the entire shore and the permanently submerged channels. I recognized six physiognomic units that supported different densities and species of prawns. The criteria used to distinguish these follow Flemming (1977), Cretchley (1996) and Siebert (2003), and are based largely on the presence of vegetation, particle size of the sediments and tidal inundation. They also reflect differences in prawn densities and distribution.

(1) At the top of the intertidal area is a narrow band of sand, bounded above by salt marshes in parts of the lagoon. It is rarely covered with water and never supports any prawns. (2) Directly below this is a narrow vegetation zone dominated by *Zostera capensis* which is patchily distributed and confined to the eastern bank. Immediately below the *Z. capensis* zone lies a short frontier zone (Siebert & Branch 2005a) in which subsurface root/rhizomes of *Z. capensis* extend for about a meter

but there is no above-ground growth of eelgrass. This gives way to an intertidal flat, which is fully exposed only at spring low tide and is divisible into (3) upper and (4) lower portions. The upper intertidal sandflat is exposed during all tides, whereas the lower intertidal is not exposed during neap tides. Below the lower shore, there are subtidal sandflats, always covered by water, and again divisible into (5) shallow subtidal sandflats and (6) deep channels. The shallow subtidal zone experiences intense tidal currents but the floor of deeper subtidal channels experiences slow velocities. The subtidal flat is particularly large at Kraal Bay and Bottelary. Superimposed on these vertical zones, there are marked differences between the eastern and western shores. On the western shore, *Z. capensis* is absent and sediments are courser (Flemming 1977).

Distribution and density of prawns in Langebaan Lagoon

Four species of sand prawns and mud prawns were recorded in my surveys. *Callinassa rotundicaudata* was too infrequently encountered to draw conclusions about its habitat requirements, but *Upogebia capensis*, *U. africana* and *C. kraussi* were all abundant and occupied distinctly different habitats.

Highest densities of *U. africana* were associated with *Zostera* beds on the eastern and southern shores where medium sands and coarse sands are absent and where *Z. capensis* traps and stabilises fine, organic-rich particles (Mazure & Branch 1979). Low densities were recorded on the upper and lower shores at most sites but *U. africana* was absent from the subtidal flats and channel areas except at Geelbek where the sediment is finer than elsewhere and water movements minimal (Day 1959, Flemming 1977). *U. africana* constructs permanent burrows lined with silt (Hill 1967) and cannot colonise areas where strong tidal currents result in clean, sandy, relatively unstable sediments (McLachan and Grindley 1974) like those of the exposed sandy shores near the mouth of the Langebaan Lagoon (Flemming 1977). Cretchley (1996) found that substrata where *U. africana*

dominates contain a higher percentage of subsieve particles (<64 μm diameter) than sediments where *C. kraussi* occurs. Wooldridge (1968) and McLachlan & Grindley (1974) consider that the preferred range for *U. africana* is between 1% and 8% subsieve fraction (< 64 μm). In Langebaan Lagoon, the percentage of fine sand and mud in the intertidal flats is low compared to the vegetation zone (Flemming 1977), and this may be an indication that these areas are subject to more sand movement, making it difficult for *U. africana* to survive there. I also found that on the western shore (Kraal Bay and Churchhaven) where the vegetation zone is absent and sediments are also more coarse and unstable (Flemming 1977, Siebert 2003), *U. africana* is virtually absent.

My research is the first to document in detail the distribution of *Upogebia capensis* in Langebaan Lagoon. Its distribution was diametrically opposite to that of *U. africana*, in terms of zonation. *U. capensis* was entirely absent from the intertidal zone but was abundant in the shallow subtidal zone at Yacht Basin and Sepia Bay, and achieved densities of 30-340 m^{-2} in most of the deep channels. It was, however, absent from the subtidal zone at Geelbek (where the sediment is very fine) and at Churchhaven. Its absence from Churchhaven may be more apparent than real because of the difficulties in sampling the deep subtidal channel there due to the presence of fossil oyster shells. All areas where *U. capensis* was present had fine sediments due to current scour.

This distribution pattern is similar to that found by Christie & Moldan (1977) who reported *U. capensis* in channels in the most northern part of the lagoon on the eastern side, and further south on the western side. Little is known about the biology of *U. capensis*, making it difficult to advance reasons for its distribution patterns. Studies on its burrow structure, mode of feeding, sedimentary requirements and any potential interactions with *C. kraussi* would add much to our understanding of its ecology.

Upogebia capensis and *U. africana* differ in their ability to osmoregulate and in their tolerance of low salinities. *U. africana* can maintain normal salt levels in its blood even when external salinity drops as low 1.7‰ whereas *U. capensis* lacks this ability below 18‰ and dies at 15‰ (Hill 1967). As a consequence, *U. capensis* is absent from estuaries and occurs on open coasts where the sediments is relatively coarse. Its penetration into Langebaan Lagoon is related to the fact that salinities there are consistently close to those of the open sea. Both species of *Upogebia* thus show preference for fine sediments in Langebaan Lagoon: *U. africana* for those associated with *Z. capensis* in the high shore, and *U. capensis* for those in subtidal channels.

Callinassa kraussi had by far the widest distribution of the four species of prawns present in Langebaan Lagoon. It was absent only from Sepia Bay. It is possible that it does occur there at low densities, but was simply never recorded because rocks in the sediment made sampling difficult and because of the small size of the intertidal area.

Despite being distributed throughout the lagoon, significant differences did occur in *C. kraussi* densities among sites. Burrow densities were as low as 2 m⁻² at the Yacht Basin and as high as 602 m⁻² at Schrywershoek. Similar among-site differences in densities were also found for *U. africana* in Knysna Estuary (Cretchley 1996) and in Swartkops Estuary (McLachan & Grindley 1974). In Langebaan Lagoon, there were strong vertical gradients. *C. kraussi* was largely absent from the high-shore eelgrass and *Spartina* beds and from the 'frontier zone' immediately below the eelgrass beds. From there downwards its densities increased progressively, only to decline precipitously in the deeper portions of subtidal channels. In general, *C. kraussi* was most abundant wherever fine sand was prevalent, declining in high-shore vegetated zones, at the head of the lagoon and in deep channels where the silt and clay fraction rose and median particle size diminished. Densities were also generally higher on the eastern than the western bank and increased towards the

southern end of the lagoon, which may indicate that *C. kraussi* prefers sediments containing fine sands.

Population structure of *C. kraussi*

Sizes and biomass per individual *C. kraussi* also varied around the lagoon, declining at sites near the head. Three possible factors may contribute to this. First, the decrease in particle size from the mouth to the head may for some reason be detrimental to *C. kraussi*. Compounding this, however, densities varied around the lagoon and high densities may have resulted in competition, with consequent reductions in size and individual biomass. Finally, harvesting has the potential to influence size. However, the largest maximum sizes were recorded at Klein Oesterwal and Center Banks, where harvesting is most intense. Thus, density (including the effects of harvesting on density) remains the most likely explanation for differences in size among sites. Females made up 58.5% of the sexually mature population for the whole of the lagoon, which is slightly higher than the figure of 50.2% recorded by Hanekom (1980) in Swartkops Estuary. The percentages of females declined towards the head of the lagoon where sediments were finest, in parallel with size and individual biomass. As egg production is energetically more expensive than sperm production, either energy demands of burrowing in fine, stable sediments, or density-driven competition may have influenced the sex ratios.

Seasonal differences in abundance and activity are the norm for callianassids (Berkenbusch *et al.* 2000). Seasonal differences in the abundance of *C. kraussi* were relatively minor compared to differences among sites, but abundance tended to be greatest in summer. However, the estimates of densities were based on hole counts and it is quite possible that activity varies among seasons. Actual densities may vary less than hole counts. Nevertheless, seasonal differences in hole counts do have practical implications. If holes are to be used to monitor populations, they need to be done in a fixed season to avoid seasonal effects clouding inter-annual comparisons.

The upper shore is likely to be a relatively harsh environment for *C. kraussi* for several reasons. First, during low tide it will be impossible for the sand prawns to circulate water through their burrows, so that oxygenation is probably limited to high-tide periods. The further up the shore, the greater this effect. Second, this may translate into reduction in feeding time if activity is limited by oxygen supply. Third, in the *Zostera* zone (and in beds of *Spartina maritima*) in the high shore, stabilisation of sediment will hinder burrowing by *C. kraussi* (Siebert & Branch 2005a), as discussed below. Abrupt reductions in density of *C. kraussi* coincided with the vegetation zone at sites where high-shore vegetation was present, whereas more gradual upshore reductions in density occurred where the vegetation zone was absent. Fourth, very high on the shore, above the vegetation zone, desiccation will become an issue because the water table drops well below the surface (Angel *et al.* 2006). In the bare zone above the vegetation zone, *C. kraussi* (and *U. africana*) were completely absent. Finally, the feeding intensity of wading birds that actively seek out and utilise the macrobenthos in the lagoon will increase from the low to the high shore (Puttick 1977, Wynberg 1991).

Callinassa kraussi has an unusually broad vertical zonation. Forbes (1973a) recorded it at subtidal depths of up to 9 m in the open sea in Algoa Bay, but noted that it avoided areas of strong water movement. In Swartkops Estuary, the number of *C. kraussi* burrows decreased at depths greater than 6 m and were absent beyond 8 m but it extended upwards to close to the top of the intertidal zone (Forbes 1973a). Its depth range is thus substantial. In addition, *C. kraussi* is able to survive in a variety of substrata and is able to burrow in substrata ranging from clean sand through muddy sand to mud silt and clay (Forbes 1973a), although showing a preference for fine sand.

Callinassa kraussi was first considered an osmoconformer although possessing some tolerance to low salinities (Thompson & Pritchard 1969, Forbes 1973a). However, its distribution in southern

African estuaries and the wide range of salinities over which it is found indicate a marked degree of euryhalinity (Day 1959). Salinity variations are of course, not an issue in the Langebaan Lagoon. Unlike *U. africana*, *C. kraussi* is capable of surviving in closed estuaries in southern Africa (Forbes 1973a).

Potential interactions among species

Mixed populations of *C. kraussi* and *U. africana* are rare (Millard & Scott 1953, Macnae 1957a, b, Hill 1967, Forbes 1973a) although I did find them co-existing at substantial densities at Geelbek. Siebert & Branch (2005 a, b) extensively studied interactions between *Zostera capensis*, *U. africana* and *C. kraussi*. They found a negative correlation between *C. kraussi* and *Z. capensis* and argued that *Z. capensis* stabilises the sediment to the extent that eelgrass beds exclude *C. kraussi*, whereas bioturbation by *C. kraussi* destabilises and suspends the sediment, smothering *Z. capensis*. Subsequent experiments (Siebert & Branch in press) found a positive correlation between the abundance of *Zostera* and *U. africana*. This relationship may simply be a direct one based on eelgrass beds trapping fine sediments, thus stabilising the sediment and enhancing the organic content (Mazure & Branch 1979), creating sedimentary conditions suitable for *U. africana*. Eelgrass may also indirectly benefit *U. africana* by excluding *C. kraussi*, as bioturbation by *C. kraussi* has the potential to disrupt the semi-permanent burrows formed by *U. africana*. I found that wherever *C. kraussi* was dominant, *U. africana* was absent or rare. The only exception to this was at Geelbek, where the two co-existed in the fine and relatively muddy sediments of the intertidal sandbanks below the eelgrass beds.

Finally, another potential interaction may occur between *U. capensis* and *C. kraussi*. Abundance of the latter declined abruptly in deep subtidal areas wherever *U. capensis* was abundant. Whether this reflects a biological interaction, or simply preferences for different sediment type remains unresolved.

Estimates of total stock of *U. capensis* amount to 3.5 % of all prawns in the lagoon. Of this stock approximately 18.3 % is available in legally exploitable areas. *U. africana* makes up 2.1 % of the total prawn stock in the lagoon and of this 1.5 % falls in areas that are harvested by bait-collectors. *C. kraussi* made the largest contribution to the prawn stock, comprising 94.4 % of all the prawns in the lagoon. Approximately 9.7 % of this is available to bait-collectors.

The total area of the intertidal sandbank inhabited by *C. kraussi* can be used to estimate an important part of the prawn stocks of the Langebaan lagoon (see Table 2.8). If the mean density and mean biomass of the 10 sites sampled ($203.\text{m}^{-2}$ and 332.9 g.m^{-2}) is taken as representative of the whole intertidal area, the prawn stock (for the intertidal area) is estimated to be 6 425 629 441 (6.4×10^9) prawns or a dry weight of 10 537 399 kg (10 537 tonnes).

The effects of disturbance

Although the effects of human disturbance are dealt with in Chapter 3, several authors consider it as a contributing factor influencing prawn densities in lagoons and estuaries. The tendency for numbers of *Callinassa* and *Upogebia* to increase from the mouth towards the eastern, upper end of Langebaan Lagoon has been well documented and is closely related to sediment textural characteristics and increased shelter (Day 1959, Christie & Moldan 1977, Wynberg 1991, Siebert 2003). Bait collecting activities may, therefore, not be the cause of lower *C. kraussi* densities in the western areas where bait harvesting is allowed. However, Wynberg (1991) and my surveys show that a distinction occurs between prawn densities in areas where harvesting is not allowed and areas where bait collecting may occur, even when the areas have similar sediment characteristics (e.g. Klein Oesterwal vs Oesterwal). A more detailed particle-size analysis of the different areas, analyses of the size and density of prawns, monitoring and experimental alteration of harvesting are all logical measures that would help clarify this issue. Exploitation by bait collectors can have an effect on the density and population structure of prawn populations (Cretchley 1996). Wynberg &

Branch (1991) found that *C. kraussi* populations were significantly less dense and had a smaller modal size in areas of Langebaan Lagoon exploited by bait collectors than in equivalent unexploited areas. A knowledge of the distribution, density and population structure of the bait organism is, therefore, essential to assess and predict harvesting effects to determine conservation measures for bait stocks. Hanekom & Erasmus (1988) suggest that predatory bird populations and, to a lesser extent, those of fish may be linked to the size of prawn populations. This highlights the importance of prawns as a food source for other species and the value of bait regulations and zoning the lagoon. From the density and distribution information obtained from this study it is clear that the protected areas support high densities and conserve large stocks of *U. africana*, *U. capensis* and *C. kraussi*. Most of the shorebased collecting tends to take place at Klein Oesterwal or on the eastern section of the Center Banks. As a result Kraal Bay and the western shores of the Center Banks are less visited and prawn populations there are relatively well conserved even although they fall within the multi-use zone of the lagoon where bait collecting is permitted. Nevertheless, demonstrations by Wynberg & Branch (1991) that bait collecting not only depletes prawns but negatively affects the biota as a whole due to sediment compaction and increased avian predation, make it important that bait collecting be regulated.

In summary, the distribution patterns of *U. africana*, *U. capensis* and *C. kraussi* are influenced by abiotic factors such as vertical height on the shore (Siebert 2003) and particle size distribution (Wynberg 1991, Siebert 2003), but biotic factors including bioturbation (Branch & Pringle 1987), sediment stabilisation by *Z. capensis* (Siebert 2003, Siebert & Branch 2005a, b) and human exploitation (Wynberg 1991) may also play roles in affecting their distribution and abundance. In the chapter that follows I examine patterns of human utilisation, which can be matched against the measurements of stock size described here to assess the magnitude of harvesting.

CHAPTER 3

THE EFFECT OF BAIT COLLECTORS ON PRAWN STOCKS IN LANGEBAAN LAGOON

3.1 Introduction

In Langebaan Lagoon, the sand prawn *Callinassa kraussi* is the bait organism targeted most by resident and visiting leisure anglers. The mud prawn *Upogebia capensis* is also targeted but only in the Yacht Basin in the town of Langebaan. *U. africana*, which is encountered in its largest numbers in areas associated with *Zostera capensis*, is not really targeted because few people are aware of its narrow habitat (Wynberg & Branch 1991). This chapter deals with socio-ecological issues and aims to determine the present extent and intensity of exploitation of *C. kraussi* in Langebaan Lagoon. Knowledge of both the resource and the resource users is essential in establishing management recommendations to ensure conservation and sustainable use of the resource.

Anglers collecting bait in Langebaan Lagoon use prawn pumps (Wynberg & Branch 1991). These consist of a 75-cm long, 9-cm diameter stainless-steel cylinder that contains a hand-operated diaphragm pump (Hailstone and Stephenson 1961) and is efficient and easy to use. The pump is usually operated by sucking up a core of sediment, pumping it out, and examining it for prawns. The pump can also be applied to force air or water into the burrows to a depth of 50-70 cm, resulting in upward water currents that drive prawns to the surface (Wynberg & Branch 1991). Prawn pumps, together with hand digging, are the only legal methods of removing prawns in Langebaan Lagoon. Digging with spades, although sometimes observed, is illegal in terms of national legislation.

Most studies on bait collecting have been on northern hemisphere species, e.g. the exploitation of polychaete worms (Klawe and Dickie 1957, Blake 1979a & b; McLusky *et al.* 1983) and the influence of bait digging on cockle populations (Jackson and James 1979). Blake (1979 a, b) described the number of diggers collecting bait worms, their selectivity, efficiency and effort in harvesting bait worms in England. All of these authors found that these activities did not pose a significant threat to stocks of these bait organisms.

In South Africa, over the last two decades there has been an increase in sportfishing and this, together with the ease with which prawns can now be harvested, has resulted in a vastly expanded utilisation of both sandprawns and mudprawns (Wynberg & Branch 1991). Various authors (Hill 1967, Forbes 1973a, Hanekom 1980, Gaigher 1987, Baird 1988) have recognised this problem as a threat to the conservation of prawn species in South African estuaries and lagoons.

The most detailed studies on bait exploitation to date for Langebaan Lagoon were by Wynberg & Branch (1991, 1994), for *C. kraussi* and *U. africana*; and in the Knysna estuary by Cretchley (1996), for *U. africana*. Wynberg and Branch (1991) monitored the number of bait collectors at Langebaan Lagoon and conducted interviews with bait collectors/anglers. Cretchley (1996) estimated the number of bait collectors in relation to the tidal cycle and described the number mudprawns taken by them in Knysna Estuary.

To formulate appropriate management proposals for Langebaan Lagoon, the effects of bait collecting on *Callinassa* and *Upogebia* need to be assessed. To achieve this goal, this chapter has the following objectives:

1. To quantify the number bait collectors using Langebaan Lagoon.
2. To assess the total number of prawns removed annually from the lagoon.
3. To estimate the disturbance caused by sediment turnover as a result of use of prawn pumps.

4. To estimate the disturbance associated with trampling by persons accompanying bait collectors.
5. To collect information on the perceptions of bait collectors about bait collecting and its associated consequences, and their awareness of local regulations restricting bait collecting.

3.2 Materials and methods

3.2.1 Areas of data collection

Bait collecting in Langebaan Lagoon is only permitted in Zone A, which is situated in the northern part of the lagoon (see definition in previous Chapter, Section 2.2.1 and Figure 2.1). Preliminary observations showed that bait collecting took place almost exclusively during the daytime low tides and was concentrated at four sites on the eastern shore of the lagoon, (Langebaan beach, Sepia Bay, Yacht Basin and Klein Oesterwal), and at site on the Center Banks of the lagoon (see Chapter 2, Figure 2.1). Surveys were therefore limited to these conditions and places.

3.2.2 Number of bait collectors

During 1999 and 2000, each of the five sites was monitored each month on a weekend or public holiday for 4 hours: from 2 hours before to 2 hours after day-time low tide. During 2001, four weekend and four corresponding weekday samples were taken for similar 4-hour periods at four times in the year to represent the seasons and to compare weekend and weekday activities. These samples of collecting activity were used to estimate the extent of bait collection in the lagoon. At each site, the numbers of bait collectors (also referred to as 'pumpers' in the text, figures and statistical analyses) were counted over the 4-hour periods. The numbers of walkers associated with bait collectors at Center Banks and Klein Oesterwal were also recorded, as was the number of paces taken by these walkers accompanying pumpers, and the duration they spent on the sandflats.

3. 2. 3 Calibration

A calibration curve was computed to determine the average number of prawns removed for each suck of a prawn pump. Bait-collectors were observed on a regular basis at different times of the year. The number of sucks required to obtain a specific numbers of prawns was counted and both figures cumulatively added for a period of ten minutes. This exercise was repeated for 34 collectors on the Center Banks and 36 collectors at Klein Oesterwal. The total amount of time spent collecting prawns and total number of prawns removed was also recorded for 30 individual bait collectors on the Center Banks and 30 at Klein Oesterwal. This information was used together with data on numbers of bait collectors to estimate by extrapolation the total amount of prawns removed annually from Center Banks and Klein Oesterwal, the two sites that proved to be the most intensively harvested.

To estimate the mass of sediment disturbed by bait-collectors, the dry mass of a given volume of sediment was determined. The internal volume of the prawn pump was then converted to sediment mass. Wynberg (1991) calculated the dry mass that can be contained by a standard prawn pump as approximately 3.25 kg. She estimated that the average bait collector does not usually fill the pump completely, but retrieved approximately 75% of its capacity. Thus, a mean dry mass of 2.45 kg of sediment is disturbed with each suck. This figure was used to estimate the total amount of sediment disturbed during bait collecting in one year. The number of paces taken by persons on foot, and the time spent accompanying bait collectors was extrapolated to calculate the total area disturbed by footprints left in the sand.

3. 2. 4 Interviews

Collectors were interviewed to gain information about their activities on the sand flats. A questionnaire (Table 3.1) was compiled and modeled on previous studies (Wynberg 1991, Cretchley 1996). Interviews were conducted among a total of 115 anglers at various fishing and bait-

Table 3.1 Questionnaire for survey of bait collectors and fisherman.

BAIT COLLECTING QUESTIONNAIRE

POPULATION GROUP	Black	White	Coloured
SEX	Male	Female	Asian
AGE GROUP	>35	<35	Youth
WHAT BAIT IS COLLECTED?	Sand prawns	Mud prawns	Sand & Mud prawns
	Sand prawns & other		Blood worm & other
IMPLEMENT USED	Prawn pump	Trampling	Tin can Fork
YOUR FAVOURITE BAIT COLLECTING SPOT?	Center banks	Klein Oesterwal	Yacht Basin
	Sepia Bay	Langebaan Beach	
DO YOU HAVE ACCESS TO A BOAT?	Yes	No	
HOW MANY PRAWNS DO YOU COLLECT?	< 30	30-50	
	50	> 50	
ARE YOU AWARE OF THE BAIT BAG LIMITS & ZONATION REGULATIONS?	Yes	No	
ARE RESTRICTIONS ?	More than adequate?	Adequate?	
WHERE DO YOU FISH?	Inadequate?	What do you suggest?	
WHY DO YOU COLLECT BAIT?	Lagoon	Spreeuwal	
	Saldanha	Leentjiesklip	
WHAT FISH ARE CAUGHT WITH PRAWN BAIT?	To obtain food	To sell bait	
	To sell fish	Recreational use	
HOW DO RATE THE PRAWN BAIT?	White stumpnose	Steentjie	Strepie
	Sandshark	Shad	Dassie
	Hottentot	White Steenbras	Blue Hottentot
DO YOU THINK SANPARKS IS NECESSARY?	Excellent	Good	
	Fair	Poor	
DO YOU THINK YOUR ACTIVITIES HAVE A ON THE SANDFLATS/LAGOON?	Yes	No	
HOW OFTEN TO YOU FISH/COLLECT BAIT?	Positive	Negative	No effect
	Once a week	Twice a week	
	Less than 1 day per week	Holidays only	

collecting sites in the Lagoon, including the Yacht Basin, Sepia Bay, Langebaan Beach, Klein Oesterwal, and the Center Banks. Bait-collectors were also interviewed during peak (Easter and Christmas) and off-peak periods of the year. Following Wynberg (1991), anglers who fished more than once monthly were regarded as 'regulars'.

3.2.5 Statistical Analysis

Assumptions of normality and homogeneity of variances (alpha set at 0.05) for each of the variables were checked using Kolmogorov-Smirnov one sample test and Levene's test (Zar 1999). When possible, heteroscedastic data were transformed to achieve equality of variance and normality. When the latter could not be achieved, nonparametric statistical tests were applied.

The number of bait collectors (pumpers) and persons accompanying them on foot (walkers) was analysed for the differences among sites and seasons using a Two – Way ANOVA, with sites as a random factor and seasons (see definition in chapter 2) as a fixed factor. Differences in the numbers of pumpers between weekend and weekdays were analysed using a dependant t-test (sites as dependant variable, and number of bait collectors as the independent variable) (Zar 1999). A dependant t-test was also applied to test for differences between the Center Banks and Klein Oesterwal with respect to footprints/unit time, sucks/unit time, time spent collecting, total number of prawns removed by collectors, and total number of paces taken by walkers. In each of these tests the site was the dependant variable and the second variable was the independent factor. All analyses were performed with alpha set at 0.05. Statistical Analyses were conducted using Statsoft, Inc. (2000) STATISTICA version 6 for Windows.

3.3 Results

Bait-collector activities

For data collected on weekends and public holidays for 1999 and 2000 the number of bait collectors (pumpers) was high during Summer and often in Autumn, and the lowest numbers were recorded during Winter at all sites (Fig. 3.1). There was no interaction between the effects of site and season, both of which had highly significant effects on the numbers (Table 3.2).

Table 3.2 Results of a Two-Way ANOVA to determine whether there are any significant differences in the number of bait collectors between sites (over all seasons) and between seasons (over all sites) sampled for weekends (1999 & 2000).

Variation	Sum of Squares	d.f.	Mean Square	F-ratio	Sig. level
MAIN EFFECTS					
Site	15.2	4	3.8	41.37	$p < 0.0001$
Season	4.08	3	14.8	14.8	$p < 0.0001$
Site*Season	0.61	12	0.55	0.55	0.871

Post-hoc Tukey tests showed that Center Banks and Klein Oesterwal (no significant difference, $P = 0.97$) had consistently higher numbers of bait collectors (over all seasons), and differed significantly from the other three sites. Yacht Basin did not differ significantly from either Sepia Bay or Langebaan Beach ($P = 0.99$ and $P = 0.08$ respectively). However, Langebaan Beach was significantly different from Sepia Bay ($P = 0.025$), and had consistently greater numbers of bait collectors. Center Banks had the highest average measurement namely 48 ± 22.61 bait collectors per 4-hour period.

The number of 'walkers' at Klein Oesterwal and Center Banks followed the same pattern as the bait-collectors, with a peak in Summer and early Autumn (Fig. 3.2). The overall ratio of 'walkers' to bait-collectors per day was calculated as 1: 0.89.

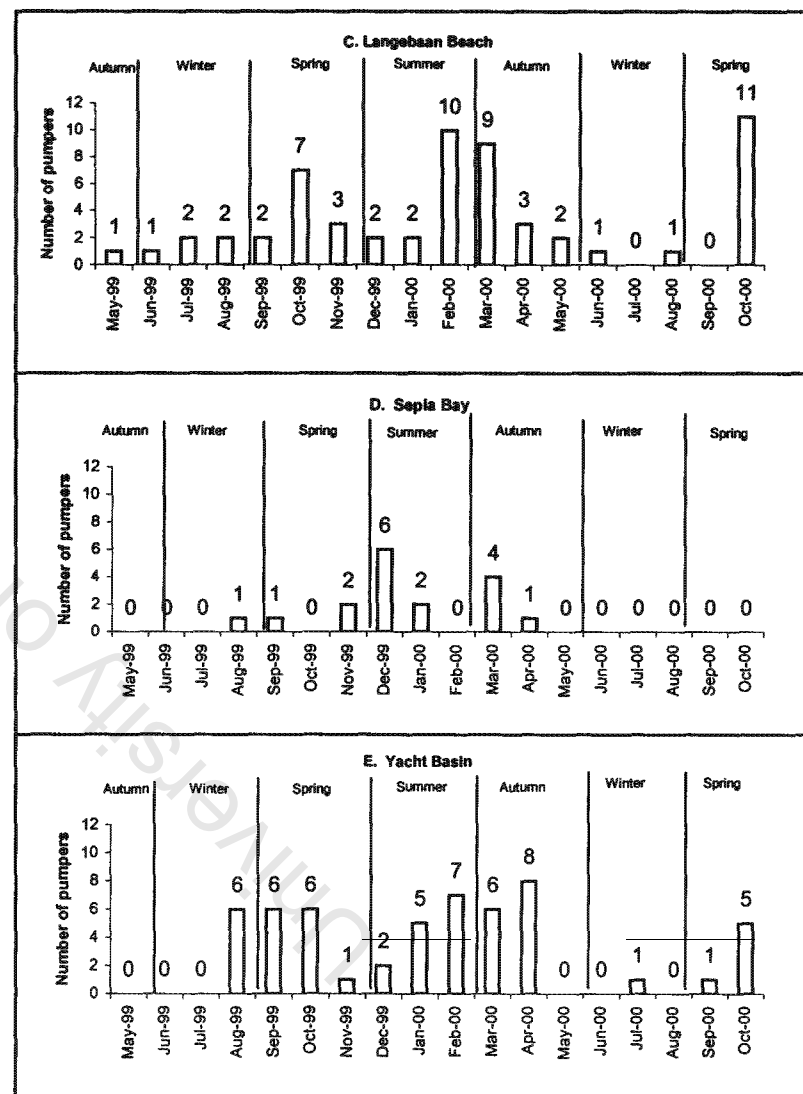
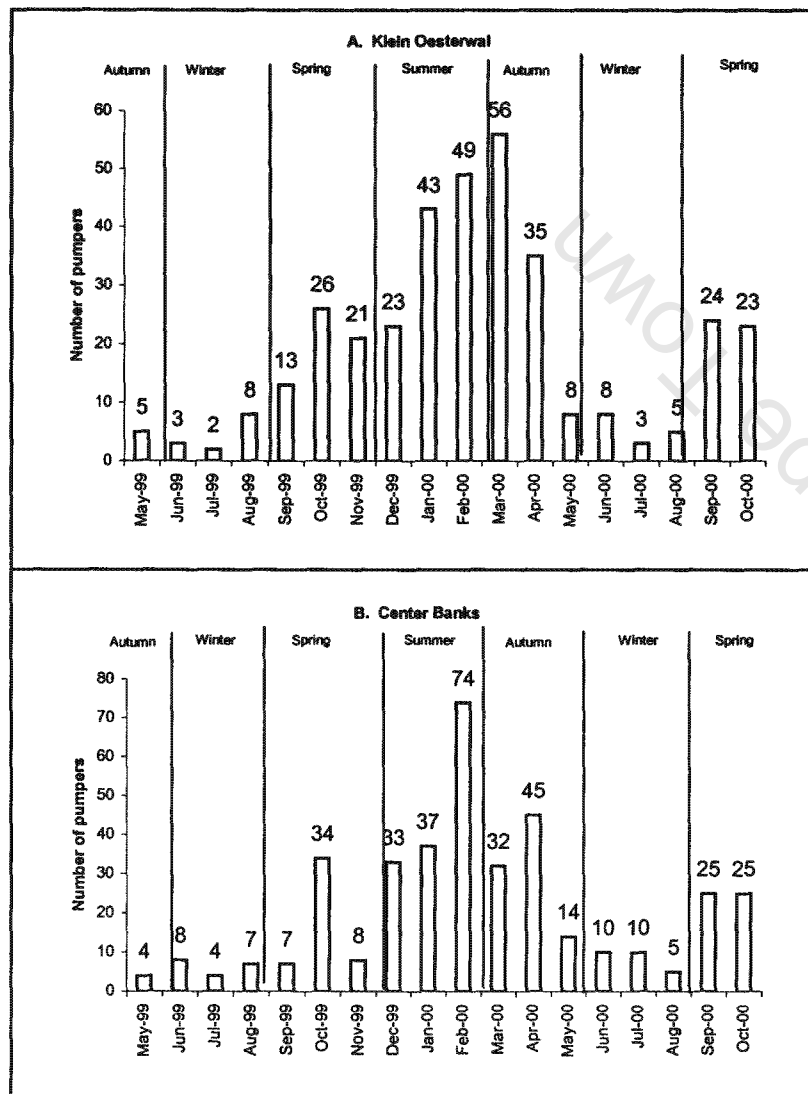


Figure 3.1 Number of pumpers observed per 4 hours at A) Klein Oesterwal, B) Center Banks, C) Langebaan Beach, D) Sepia Bay and E) Yacht Basin.

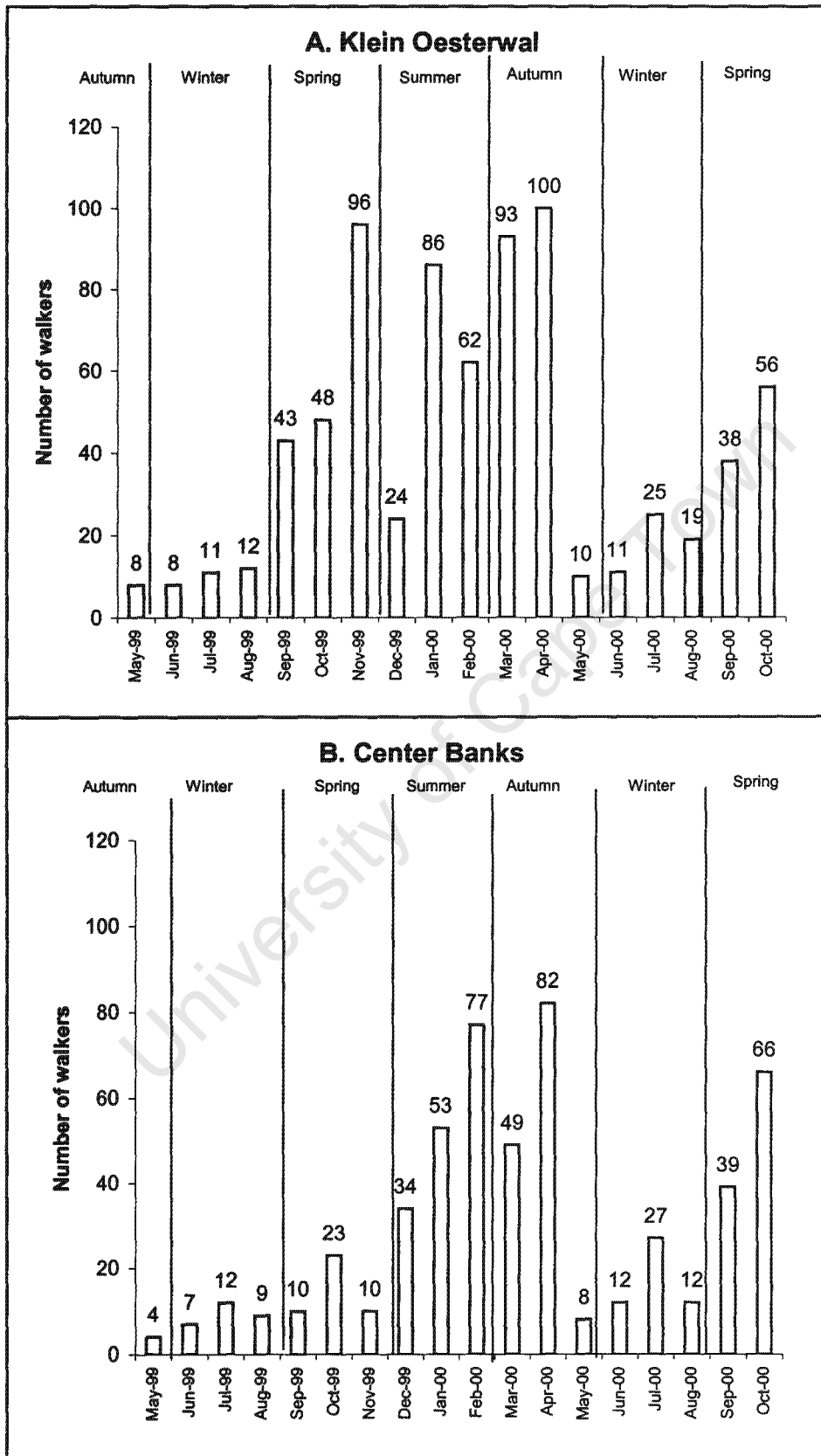


Figure 3.2 Number of walkers observed per 4 hours at A) Klein Oesterwal and B) Center Banks

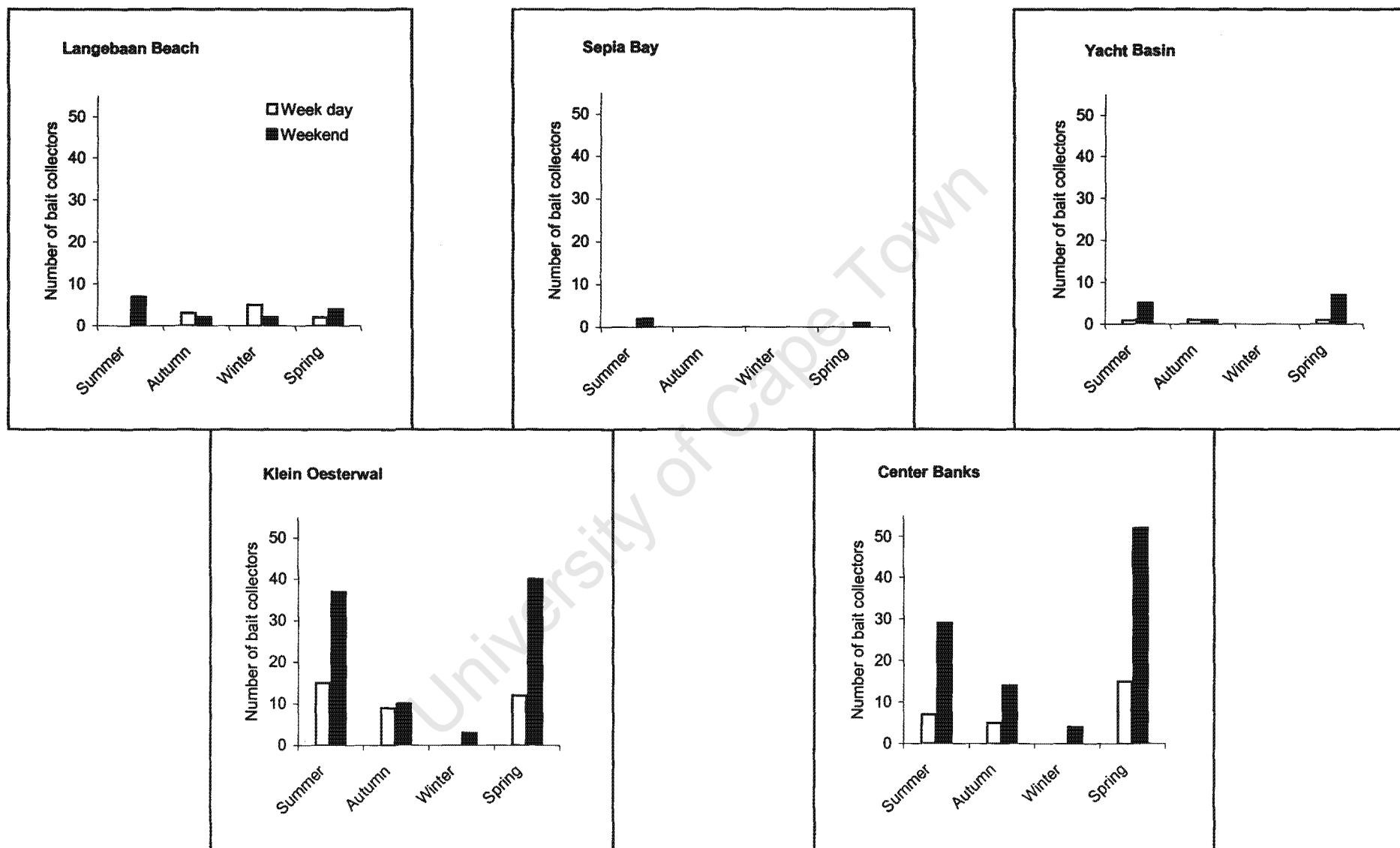


Figure 3.3 Numbers of bait collectors per site observed per 4-hour period on week days and corresponding weekends over 12 months in 2001.

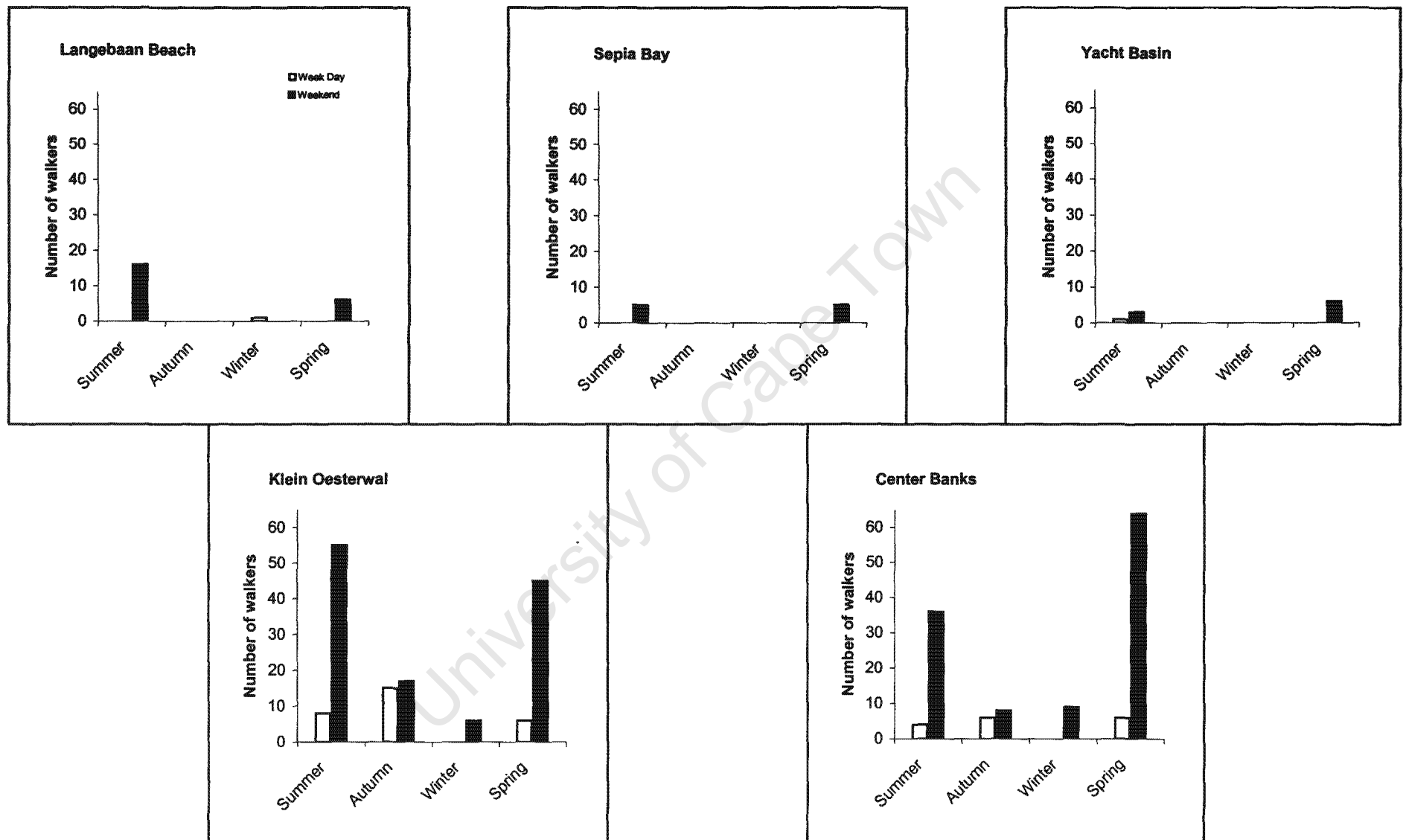


Figure 3.4 Numbers of walkers associated with bait collectors per site observed per 4-hour period on week days and corresponding weekends over 12 months in 2001.

When data for bait-collectors for weekends of 1999 and 2000 were compared with corresponding data collected on weekends and weekdays during 2001, similar results for bait-collector numbers were obtained for weekends in all years, but weekday numbers were 50-100% less than those for weekends (Figure 3.3). The number of walkers during weekdays were even smaller relative to weekends (Fig. 3.4) but followed the same seasonal and spatial patterns as bait collectors.

Integrating the information for weekdays and weekends and weighting the data according to the number weekdays and weekends per season provides an overall estimate of the number of bait-collectors visiting the five sites (Fig. 3.5). During all seasons, bait-collectors focused on Klein Oesterwal and Center Banks, with a peak of Summer/Spring activity and minimal effort in Winter.

At the two sites subject to the greatest activity, Center banks and Klein Oesterwal, bait-collectors undertook an average of respectively 14.06 ± 3.70 and 11.37 ± 4.41 sucks/minute (Fig. 3.6), the difference being significant ($t = 2.756221$, d.f. = 68, $P = 0.008$). The mean number of prawns retrieved per suck was 0.27 on the Center Banks and 0.55 for Klein Oesterwal, the difference again being significant (One-Way ANOVA, $F_{1,68} = 25.34875$; $P < 0.0001$). Hence, it takes 3.7 sucks to retrieve one prawn on the Center banks but only 1.8 sucks at Klein Oesterwal.

The total time spent collecting prawns at the Center Banks and Klein Oesterwal (Figure 3.7) was not significantly different for the two sites ($t = 1.25$, d.f. = 66; $P = 0.021$). The total number of prawns removed from the two sites by bait collectors (Figure 3.8) also did not differ significantly ($t = 0.35$, d.f. = 66; $P = 0.72$).

The number of paces taken per minute by walkers averaged 27.9 ± 16.33 at the Center Banks and 29.0 ± 20.89 at Klein Oesterwal, with no significant difference between the two sites ($t = 0.148798$, d.f. = 9; $P = 0.88$). The total number of paces taken by walkers per visit at the two sites averaged

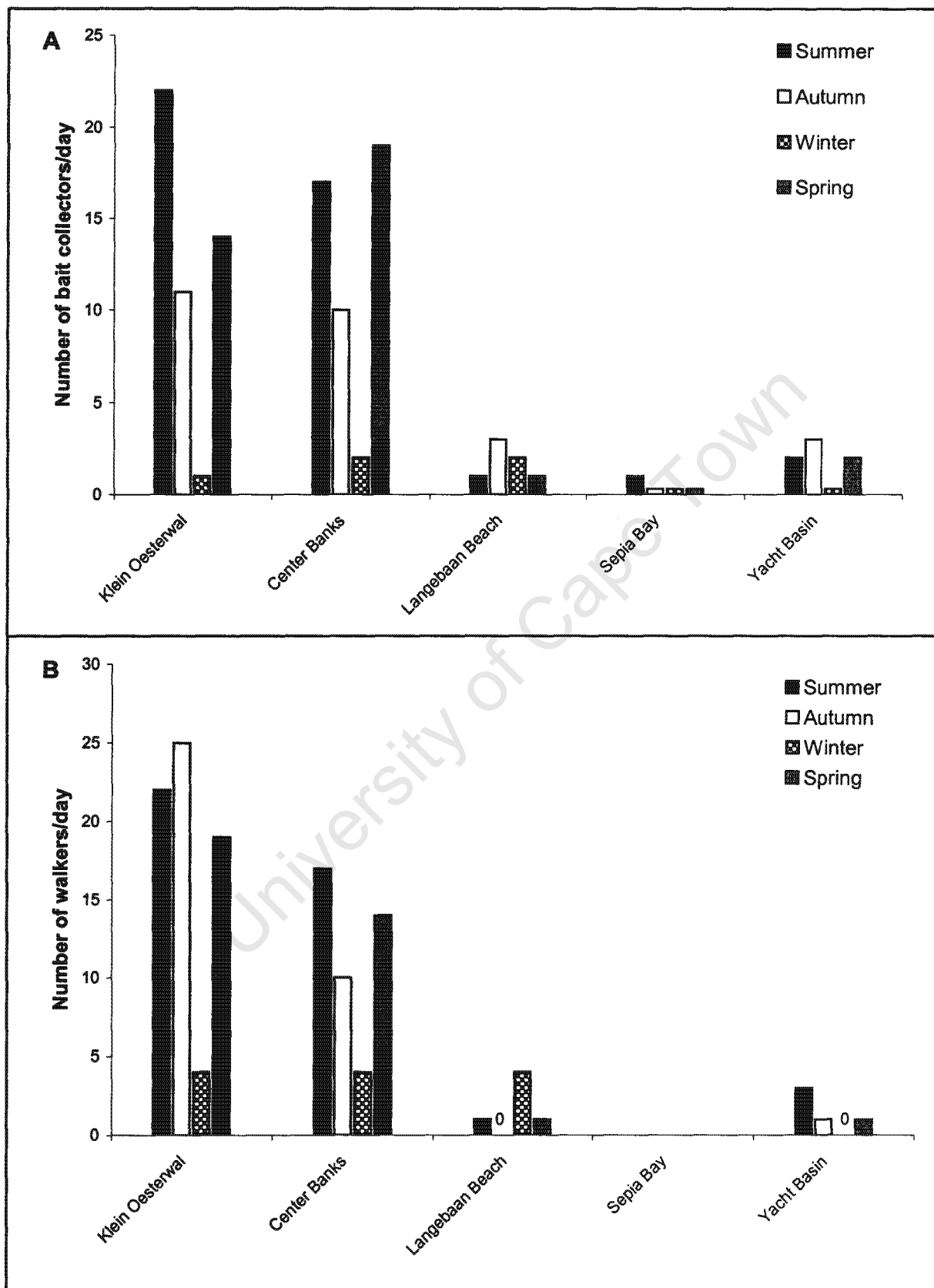


Figure 3.5 Mean number of (A) bait collectors and (B) walkers over four seasons for five sites in Langebaan Lagoon. Information represents data collected over weekdays and weekends for 1999, 2000 and 2001.

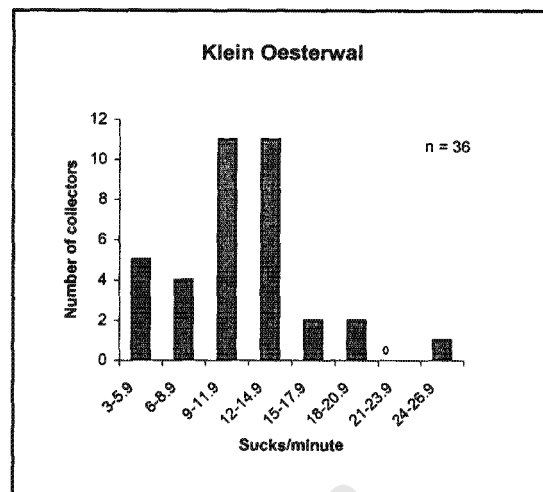
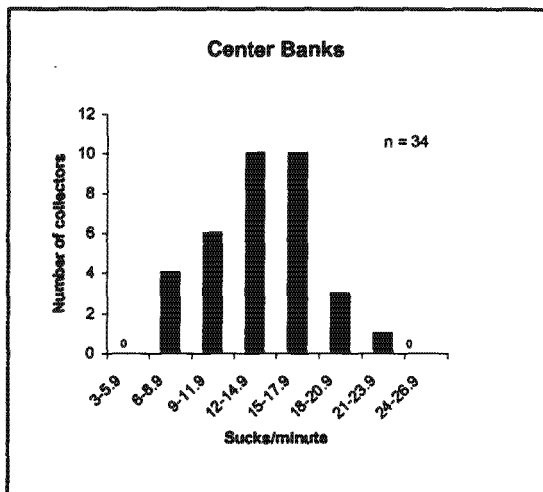


Figure 3.6 The rate at which a prawn pump is applied at two sites in the lagoon.

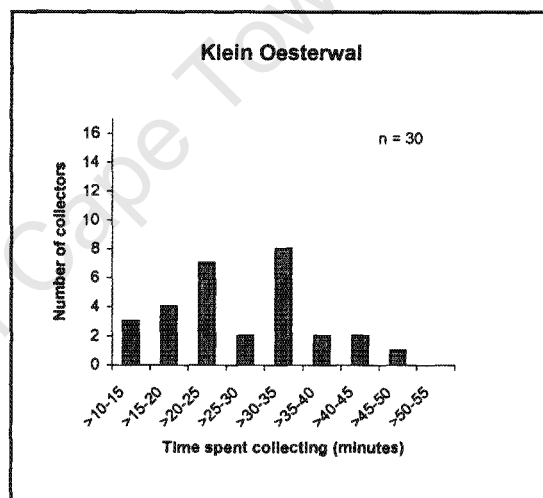
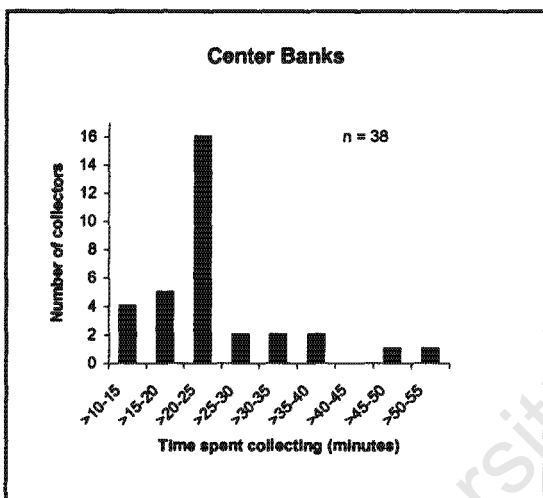


Figure 3.7 The total time spent collecting prawns at two sites in the lagoon.

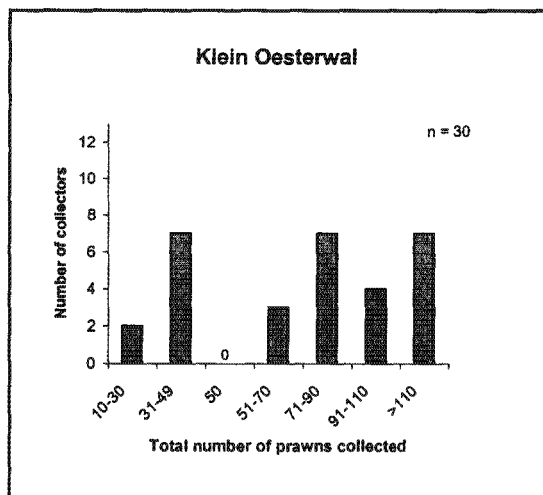
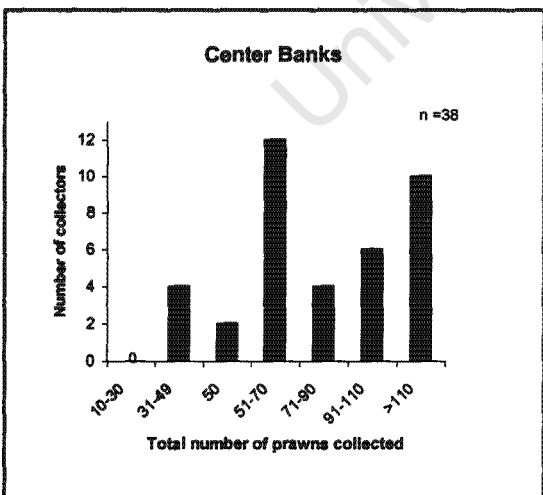


Figure 3.8 The total numbers of prawns collected by bait collectors per visit to two sites in the lagoon.

544 ± 403.54 for Center banks and 905 ± 691.35 for Klein Oesterwal. Again, there was no significant difference between the two sites ($z = 1.64317$, d.f. = 9; $P = 0.10$).

When examining the physical impacts of the bait-collecting activity, the total number of sucks by bait collectors using a prawn pump was estimated at 2 526 254 per annum. Taking the dry mass of sediment displaced by each suck with a prawn pump as 2.45 kg, a total of 6 189.3 tonnes of sediment is disturbed yearly by bait collecting.

On average the bait-collectors at Langebaan removed 86 prawns per bait-collecting outing, 36 more than the legal limit of 50. The total number of prawns removed by bait collectors was estimated at 676 597 per annum for the whole lagoon system. The area from which these prawns are actually removed (Center Banks & Klein Oesterwal intertidal areas) amounted to 1 175 408 m².

The total number of paces taken by walkers accompanying bait collectors to these sites was estimated at 10 199 648 per annum. If this is multiplied by the average size of the footprint left by these walkers (0.028 m²), a total surface area of 285 590 m² is disturbed by this activity.

Bait collector behaviour

All 115 people who were approached responded to the interview. All were white (74.8%) or coloured (25.2%) and males predominated (98.3%).

Approximately 27% of the anglers interviewed fished and collected bait on a weekly or monthly basis (Fig. 3.9A). The rest comprised holiday makers who fished only during their holidays (73%). Of the anglers interviewed, none admitted to selling bait and 13% of them stated that they used the fish caught as a source of food. Approximately 3% had semi-commercial licences to catch and sell

fish at the time of the survey (most of which have since been withdrawn). The bulk of the bait collectors (84%) were therefore recreational (Fig. 3.9B).

The majority of anglers (93.1%) targeted *Callinassa* as bait (Fig. 3.9C). At Yacht Basin where it was rare, attention was directed at *Upogebia*. A small proportion (5.2%) focused on the bloodworm (*Arenicola loveni*). Isolated individuals collected redbait (*Pyura stonolifera*) or other polychaete worms only. All anglers used a prawn pump to collect all types of bait. It depended largely on where harvesters collected bait as to what bait was retrieved: anglers targeted any species of prawn that was accessible in the area they happen to be collecting (Fig. 3.9C). The large majority of anglers (90.3%) rated prawns as good or excellent bait (Fig. 3.9E).

The most common fish caught in the lagoon using prawns as bait was white stumpnose (*Rhabdosargus globiceps*). Other fish caught included steentjies (*Spondyllosoma emarginatum*), strepie (*Sarpa salpa*), dassie (*Diplodus sargus*), white steenbras (*Lithognathus lithognathus*), shad (*Pomatomus saltatrix*), sandshark (*Rhinobatus annulatus*), kabeljou (*Argyrosomus hololepidotus*), hottentot (*Pachymetopon blochii*) and galjoen (*Dichistius capensis*) (Fig. 3.9D). The vast majority of bait collectors fished in the lagoon (78.1%) while the remainder were roughly equally divided between Saldanha Bay and the beach area between there and Langebaan Lagoon.

Center Banks and Klein Oesterwal were by far the preferred sites for bait collecting (Fig. 3.9F). Anglers with access to a boat favoured using the Center Bank area as their primary bait-collecting area. They also visited Klein Oesterwal but sites like Sepia Bay, Yacht Basin and Langebaan Beach were exclusively visited by collectors on foot as they are difficult to access by boat (Fig. 3.9G). Seventy-seven percent of anglers were aware of the zonation regulations in the lagoon and all bait collectors complied with this regulation. This compliance was probably mainly because the multi-use area is closest to the town of Langebaan, and thus most accessible.

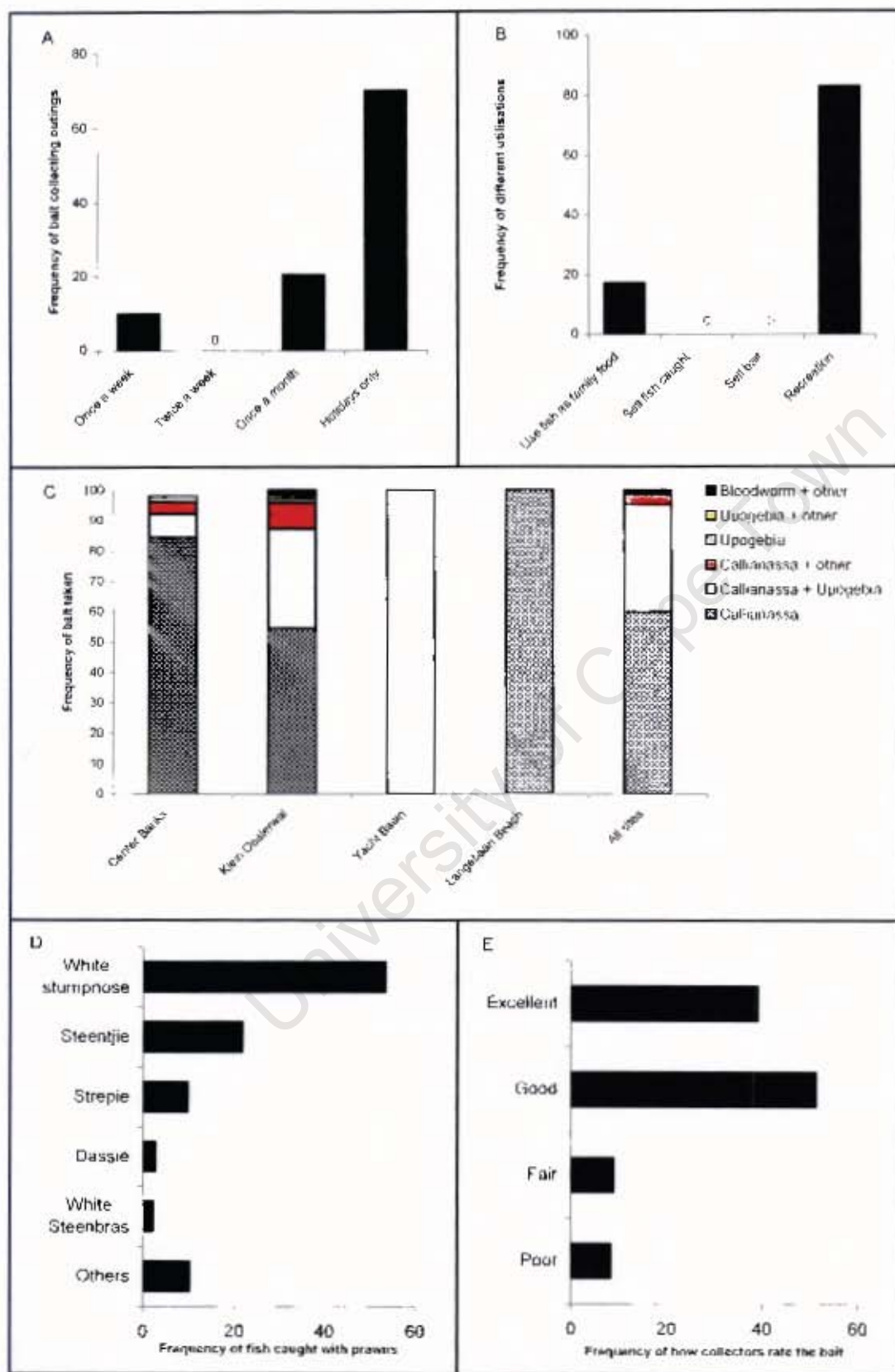


Figure 3.9 A, B, C, D and E Summaries of responses to bait-collecting questionnaires.

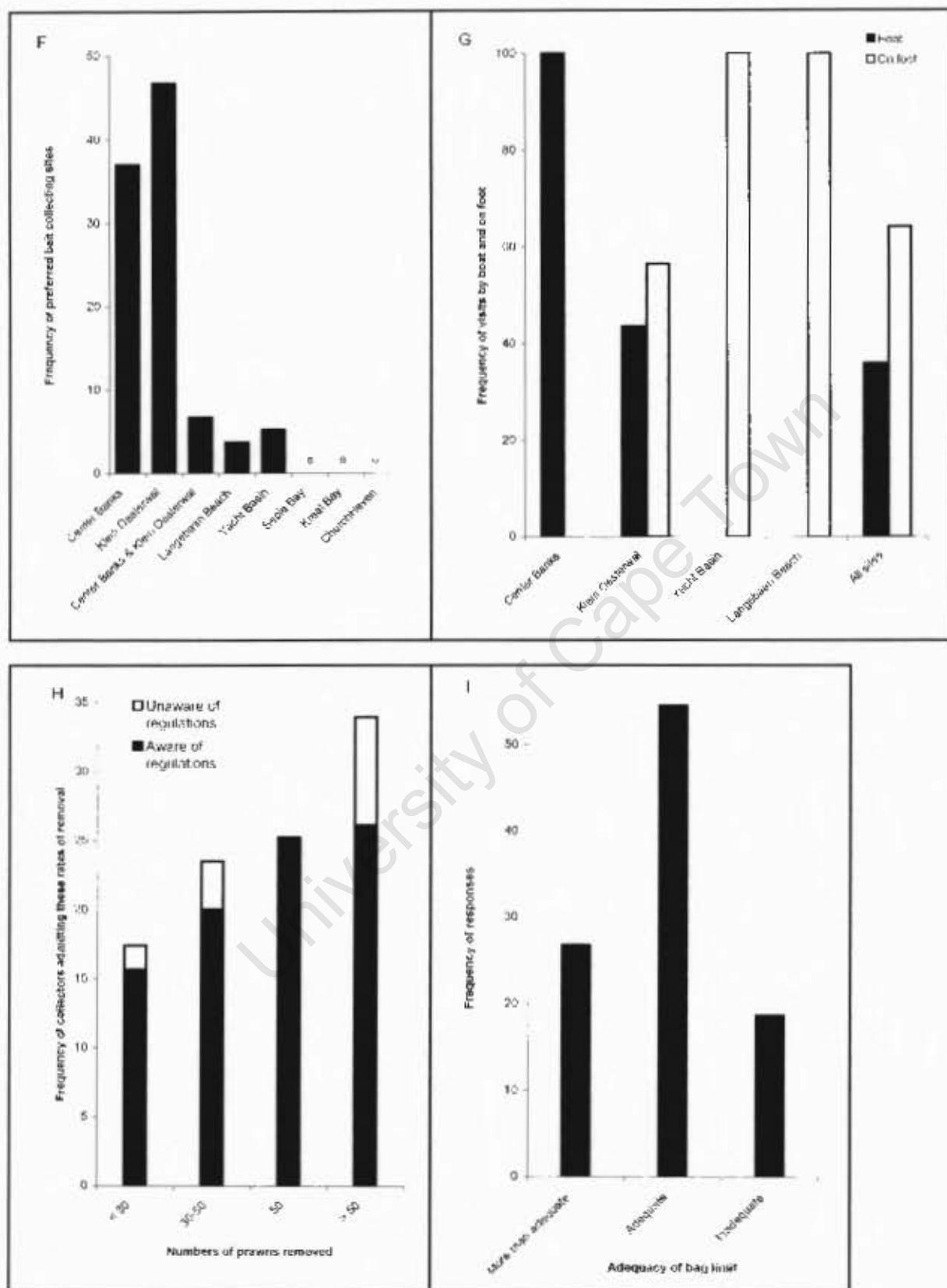


Figure 3.9 Continued F, G, H and I Summaries of responses to questionnaires.

The majority of bait collectors (69%) claimed that they were taking 50 or fewer prawns per outing and were therefore within legal bag limits. However, 31% admitted to taking more than 50 and of these 75% were aware that they exceeding the legal bag limit for prawns (Fig. 3.9H). From the empirical data (Fig. 3.8) the actual proportion exceeding bag limits is substantially greater (81%), the average collector removing 86 prawns per bait-collecting outing. It would thus appear that there is an awareness of the restrictions, but many anglers simply disregard the rules and regulations. Despite this, 92% of the fisherman interviewed regarded the presence of South African National Parks and some form of regulation and control of the area important. Thirty-eight percent considered their activities to have a negative effect on the sandflat environment: 60% felt they had no effect and 2% felt they had a positive effect. A large majority of bait collectors (83.5%) felt that the restrictions are adequate or more than adequate to supply their needs (Fig. 3.9I). Those who disagreed advocated a bag limit of between 50 and 100 prawns.

3.4 Discussion

The data collected allow estimates of the total number of bait collectors that utilise Langebaan Lagoon annually, the total number of prawns taken, where and when they are taken, the magnitude of the collateral damage by trampling and the significance of these activities relative to the size of the prawn stocks. They also allow an assessment of the attitudes of bait collectors with respect to regulations. Collectively, this information allows a review of the efficacy of management measures and whether or not there is a need to revise strategies.

3.4.1 Removal of bait species

The number of collectors observed on the intertidal sandflats in the different seasons was highly variable. Similarly the rate at which prawns were pumped and the numbers removed per visit also varied. Hence, these factors had to be taken into account in calculating the total offtake. The data on bait collector numbers (as was the case in surveys by Wynberg & Branch 1991 and Cretchley

1996) were inevitably under-estimates, as the values used in these calculations are from four-hour periods over low tide. Bait collecting was observed to take place by wading in deeper water, closer to high tide, and even at night in the summer. Nevertheless, it is likely that the magnitude of the underestimate is small because by far the majority of bait-collecting (90%) took place during the hours spanned by the surveys.

Working in Knysna Estuary, Cretchley (1996) distinguished between leisure and non-leisure anglers and estimated that the latter annually removed higher numbers of *U. africana* than the former. Wynberg & Branch (1991) found that in Langebaan Lagoon 27% of bait collectors fished on a regular basis, 57% fished during holidays only and 16% fished monthly. They found that the latter two groups used the lagoon primarily for recreation, whereas the 'regulars' probably use the fish they catch as a basic food source. From interviews conducted in my survey with bait collectors, no persons admitted to selling bait, and I concluded that bait collecting was largely for personal use. Boats displaying 'B' numbers (indicating a semi-commercial licence) were observed in the lagoon, but there was no evidence that the bait was collected for sale. It may be that at the time of the survey the crew of 'B' fishing boats sold their catch of fish, but that fell outside the scope of my survey. At present 'B' licences no longer exist and the only commercial fishing rights granted for Langebaan Lagoon are for netfishing (a total of 11 permits). Of the total number of persons interviewed, 13 % stated that the fish caught were used as a basic source of food. However, there was no other indication that subsistence fishing was taking place, so I classified all bait collecting as being recreational.

Wynberg (1991) estimated as many as 300 people collected bait during busy periods in the lagoon. Observations showed that two-thirds of these collectors visited the Center Banks and the remainder utilised the mainland areas that were accessible by foot. She postulated a crude estimate of 24 450 collectors per annum. However, her estimate included attendant family and friends who are not

necessarily anglers or prawn pumpers. As a result of this she proposed half this figure (12 225) as a more realistic estimate of the potential exploitation. In my survey (approximately 10 years later) observations distinguished 'pumpers' and 'walkers' (analogous with 'attendant family and friends'), and I estimated that 3542 bait-collecting and 6031 walker-visits take place per annum.

a) What species were taken?

Callinassa kraussi is the bait organism collected most. This may in turn largely be because it occurs in large numbers in the bait-collecting areas and is removed with relative ease from the sediment using a prawn pump. In the sites closer the Langebaan Town and, if collectors are willing to wade into the shallows of the shallow subtidal areas of Yacht Basin and Sepia Bay, the more robust *Upogebia capensis* is easily harvested. Although *C. kraussi* will also be pumped out in these shallow areas, no *U. capensis* are present in the intertidal areas so its harvesting requires more targeting.

b) How fast were they taken?

The rate at which the prawn pump was applied by bait collectors was significantly higher on the Center Banks than at Klein Oesterwal. The Center Banks are only accessible by boat and at low tide. There is an apparent urgency among collectors there to remove bait organisms as quickly as possible in order to prevent being caught by the incoming tide. At Klein Oesterwal bait collectors are more relaxed and walk around leisurely whilst pumping bait and hence do not pump as profusely when arriving. However, when the total time spent collecting and the total number of prawns collected is compared between the Center Banks and mainland, there were no significant differences between these sites. This pumping activity results in 2 526 254 sucks in one year over Center Bank and Klein Oesterwal areas, causing 6 189.3 tonnes of sediment to be disturbed.

Wynberg (1991) estimated sediment turn over as between 2 420 – 4 840 tonnes for the Center

Banks, and 713 – 1427 tonnes for mainland areas. When comparing the data of my survey with those of 1991, at Center Banks there has been an increase in sediment turn over of at least 22%.

c) How many prawns were taken?

Importantly, this survey shows that the average bait collector removes 86 prawns (36 more than the national legal limit), on each bait collecting outing. Assuming this for each collector, the annual removal of prawns in Langebaan Lagoon is 676 597. From the areas where bait is collected, this represents 0.08% of the available stock. Expressed relative to the entire lagoon, the figure is 0.008%. (See Chapter 2 for data on prawn numbers available.)

d) Spatial distribution?

The Center Banks and Klein Oesterwal had the highest visitorship by both bait-collectors and 'walkers' with other mainland areas attracting significantly smaller numbers. Yacht Basin and Sepia Bay have a very small intertidal area and most bait-collecting takes place in 45 cm of water. This is less comfortable than at Klein Oesterwal or Center Banks, and Yacht Basin and Sepia Bay are really used only by collectors who fish on the rock outcrops between these sites. Wynberg & Branch (1991) found that two thirds of collectors used Center Banks and the remaining one-third operated on the mainland at Klein Oesterwal because they had no access to a boat.

e) Seasonality?

The summer months had consistently the highest number of bait collectors and walkers. During the winter months bait collecting is at its lowest, and over many weekends at this time no bait collecting takes place. Peak harvesting does not coincide with the reproductive season, which falls in Winter (see Chapter 4). Therefore, there is little danger of harvesting interfering with breeding.

f) Collateral damage by walking?

The total surface area disturbed by walkers accompanying bait collectors is 285 590m². This amounts to 24.3% of the area of 1 175 408m² that is visited for bait-collecting purposes. With a 1:0.89 ratio of 'walkers' to 'collectors', the total disturbance by the two combined amounts to 46% of the area. This estimate does not include the disturbance caused by other people walking in general on sand flats in the Langebaan system. Many people walk and visit the beaches, often for the whole day, to swim, sunbathe and partake in watersports. It, therefore, was not possible to accurately estimate the total impact associated with trampling in the lagoon.

3.4.2 Surveys of bait collectors

a) How often is fishing/bait collecting undertaken?

Whereas fishing and bait collecting were observed most of the year there are distinct "highs" during the warmer months and depressed values over Winter. Fishing is apparently poorer in the colder Winter months although the exact reasons are not clear and subject to a study currently underway by Marine and Coastal Management. Most of the respondents claimed to collecting bait over holidays only (69.9%). The 9.8% of persons collecting bait and fishing more than once a week are probably local anglers who stay close to the lagoon and can plan outings on a regular basis based on favourable weather conditions.

b) What is caught?

White stumpnose, steentjies and strepies make up the bulk of the fish caught using prawn bait, contributing 53.3%, 21.8% and 9.8% respectively. These three species appear to be caught equally well and fairly easily by boat and shore anglers. Other species caught are white steenbras, dassie, galjoen, shad, kob and hottentot. Certain of these species like shad and kob are not caught as easily, requiring more knowledge of the area, and therefore contribute less to the catches. These results are similar to those found by Wynberg & Branch (1991).

c) Species of bait collected?

Bait collectors appear to collect what is available. At the Yacht Basin the intertidal area is small and sediment hard. Collecting takes place in the shallow subtidal area where *U. capensis* dominates. At Center Banks and Langebaan Beach almost only *C. kraussi* is pumped and this species therefore constitutes the bulk of the prawns harvested. *Upogebia africana* is present at Klein Oesterwal and anglers appear to remove this bait if they happen to pump it out whilst collecting *C. kraussi*. Certain anglers target worms, specifically bloodworm.

d) Quality of bait?

Wynberg and Branch (1991) found that *Callinassa* was regarded as an excellent bait by 67% of the anglers interviewed. They also found that *Upogebia* was voted 'excellent' by 21% of anglers and 'good' by 15%. My survey revealed 39% of anglers evaluating prawn bait as excellent and 51.2% stating it was 'good' bait. Although I did not distinguish between the two species with respect to prawn bait, anglers selecting *U. capensis* as bait organism seem to think it is more robust and, therefore, more efficient bait ('it stays on the hook longer').

e) Where is bait collected?

There is no doubt that the different species of prawns have specific habitat preferences (Chapter 2). Anglers who are aware of this may target these habitats to collect a specific species. Thus anglers pumping bait in the shallows of the yacht Basin remove large numbers of *U. capensis* and lesser number of *C. kraussi*. Anglers visiting Klein Oesterwal and Center banks remove mostly *C. kraussi*, as that is what is available there. The *Zostera* beds at Klein Oesterwal support *U. africana* (which is also more robust than *C. kraussi*) but anglers seem to prefer *C. kraussi*. Wynberg & Branch (1991) attributed this favouring of *C. kraussi* to its 'pleasant' pinkish colour and flaccidity.

f) How do collectors get there?

Approximately 60% of bait collectors access the bait collecting areas by foot. All harvesters collecting bait on the Center Banks require a boat to access this area. Although most of the harvesters at Klein Oesterwal access the area by foot, approximately 30% do visit the area by boat.

g) How much is taken?

Out of the four categories of number of prawns harvested per outing (< 30, 30-50, 50 and > 50) the largest proportion of respondents (26.1%) admitted to taking more than 50 prawns per outing. Most of these interviewees were at Klein Oesterwal. Twenty-five percent of respondents admitted to pumping the legal bag limit of 50 prawns. Twenty percent stated they removed 30-50 prawns and 15.7% less than 30 prawns per outing. Records that I made showed that the average collector actually collects 86 prawns per outing, 36 more than the legal limit. Ignorance of regulations is not an explanation for this: 84% of collectors were aware of the legal bag limit. I believe that collectors simply do not count the bag size. They continue collecting until 'they think they have enough'.

h) How much do you need?

Of people interviewed, only 18% felt the legal limit of 50 prawns per day was inadequate to meet their needs. Thus by their own admission, neither needs nor ignorance of the law are excuses for the large numbers of people exceeding the bag limit. Apart from protecting bait stocks, the significance of a bait bag limit is that it indirectly limits catches of fish. Fifty prawns only go so far and, in restricting the number of prawns harvested, the number of fish caught is likely to be restricted. This is postulated as an important conservation measure.

i) Awareness of regulations and perceptions about compliance?

From the interviews conducted with anglers in the bait collecting areas, it would seem that there is an awareness of the bag limit restrictions of prawns and about the zonation regulations. However, a

distinct lack of adherence to the bag limit regulations was evident and reflected peoples' disregard for conservation measures. Some people expressed the view that these bait organisms were diminishing and this must pose a dilemma to them, as the majority of collectors removed in excess of the legal bag limit and did so in a very short time (20-30 minutes). My study contrasts with findings by Wynberg (1991). She found that most anglers removed no more than 50 prawns per outing and that this was more than sufficient to supply their needs. She concluded that after a days fishing, a surplus of prawns was the norm, implying that the bag limit of 50 is not unreasonable in terms of the needs of the fishers. Views expressed in my survey verify the latter.

3.4.3 Significance of bait-collecting

a) Significance relative to availability of prawns

In fished areas

Calculating the amount of prawns harvested in fished areas was not practical as collectors do not seem to target specific areas on the intertidal sandflats. Anglers fishing from rocks would pump closest to that area. Some anglers fish waist deep in water and pump in the adjacent area. Other anglers make an outing of bait collecting travelling by foot or boat to an area where they randomly select a site depending on the local conditions. Further studies relating to impacts of collecting specific fished areas may display elevated impacts of collecting.

In harvesting area

Because of zoning and accessibility, harvesting is concentrated in Zone A. It is estimated that about 0.08 % of the prawns are harvested from Zone A per annum. As more and more day anglers visit the lagoon and as the population of Langebaan grows this will certainly increase.

In total lagoon

Because all of the harvested species occur throughout the lagoon, large sections of the prawn stocks are never subject to harvesting. Seen in the context of the whole lagoon, 676 597 prawns are

removed per annum, less than 0.01 % (0.008 %) of the prawns available in the system. When numbers removed are compared to the 611 250 found by Wynberg in 1991, there has been an increase in exploitation over the last years of approximately 10%.

b) Comparisons with other areas

The level of removal in Langebaan is lower but not dissimilar to that for Knysna Estuary where Cretchley (1996) found that less than 0.01 % of the total prawn stocks are removed by bait collectors. In many cases bait collecting does not pose a direct significant threat to the bait organisms, but instances of severe effects either to the target species or to the associated fauna have been recorded. Studies in the Dutch Wadden Sea showed that less than 1 % of the lugworm (*Arenicola marina*) population is removed annually by mechanical bait digging (McLusky *et al.* 1983). Blake (1979a) found that in the United Kingdom, bait collectors targeting ragworm (*Nereis virens*) posed no threat to its population. In a similar study on the bloodworm (*Arenicola marina*), Blake (1979b) found the bait collectors' selectivity, efficiency and effort for *N. virens* were higher than for *A. marina*, but still the proportion of the population removed annually was lower than for *A. marina*. Studies on the biology of bloodworm *Glycera dibranchiata* in Canada (Klawe & Dickie 1957), showed that spawning stock was not threatened by bait digging even though collectors removed 80 – 90 % of the commercially valuable worms per annum.

However, in Australia, over-exploitation of *Trypaea* (= *Callianassa*) *australiensis* was noted by Hailstone & Stephenson (1961) and required that experimental sampling be ceased to prevent loss of the species. Gaigher (1987) has reported declines in lugworm (*Arenicola loveni*) in southern Africa as a result of bait-collecting. Moreover, bait collecting/digging may indirectly influence other infaunal species. Bait digging for rag- and bloodworms on the Norfolk coast (UK) showed that it caused a decline in cockles, *Cerastoderma edule* (Jackson & James 1979). In Scotland, digging for lugworm causes significant temporary dislocation of *A. marina* without causing

permanent damage (McLusky *et al.* 1983). Experimental exploitation using a prawn pump or digging for *C. kraussi* and *U. africana* species in Langebaan Lagoon by Wynberg & Branch (1994) showed a 6.7 – 13.1 % and 46 – 49 % removal of sand prawns and mud prawns respectively, resulting in a subsequent decline in their numbers by 70 %. Recovery to background numbers took about 32 weeks once the exploitation ceased.

c) Effects on other species

I did not investigate the effects of bait-collecting on other species, but Wynberg & Branch (1994) showed that effects on the associated infauna were substantial and long-lived, especially for species that lacked dispersive larvae. Recovery was incomplete even after 48 months. Cretchley (1996) concluded that sediment disturbance in Knysna Estuary is not as severe as in Langebaan. Although prawn pumps are used in Knysna Estuary, the majority of anglers use “blowing” methods to remove prawns. This involves forcing air into one hole of a prawn burrow using a tin can or ‘pusher’ that is rapidly pressed into the mud over a mud prawn hole, ejecting the prawn through the other hole. This ‘blowing’ method does not disturb the sediment. The majority of prawns removed in the Knysna estuary are by non-leisure fisherman, and these anglers are likely to cause the least disturbance to sediment because they all use tin cans and prawn pushers.

3.4.4 Management relevance

The numbers of prawns removed from Langebaan represent less than 0.001 % of the population of prawns on the intertidal areas in Langebaan Lagoon. Amalgamating the information for different areas and seasons, I estimated that the total number of bait collectors visiting Langebaan Lagoon was 3 081 per annum, which, is a quarter of that estimated by Wynberg (1991). Thus, there appears to have been a significant decrease in the number of people harvesting bait in the lagoon in the 10 years following the work of Wynberg in 1991, although the take has increased by 10%.

Stricter enforcement will certainly awaken the public to the regulations regarding bait collecting in Langebaan Lagoon. The area is not only a national park but also a marine protected area (MPA) and a Ramsar Site, making non-compliance completely unacceptable, particularly given the fact that existing regulations seem fair in terms of meeting anglers needs.

Regular patrols at least during spring low tides, education of harvesters and penalties for those exceeding bag limits are recommended to ensure that harvesters/collectors stick to bag limits. Signage with the necessary regulations/guidelines needs to be posted at access points to the collecting areas.

It is recommended that monitoring of prawns be done once a year at a fixed time of the year, particularly at the sites where collecting takes place, and at selected control sites. Monitoring of bait collecting should also be undertaken but should only be necessary at longer intervals, say, five years.

It is construed that the current zoning structure ensures that prawn stocks are adequately protected, particularly given that only a low proportion is being removed from the areas that can be harvested. However, the indirect effects of sediment disruption by sucking and trampling and consequent effects on the biota remain of concern. The challenge for future conservation, therefore, will be to maintain the status of the protected zones. Recently netfishing rights have been allocated for the 'B' zone, which alters the intent of this zone; any violation of permit conditions will risk impacts on these sandflat areas.

CHAPTER 4

GROWTH, BREEDING SEASON AND FECUNDITY FOR *CALLIANASSA KRAUSSI* IN LANGEBAAN LAGOON

4.1 Introduction

The success of any species is based ultimately on its ability to reproduce. Marine invertebrates use a wide spectrum of reproductive strategies which are often influenced by onshore – offshore movements of larvae, juveniles or adults of the species.

The genus *Callianassa* is distributed throughout the world, but because of the subterranean habitat of the species and the difficulty of obtaining regular samples of decent proportions, little information was available on the breeding and growth of *C. kraussi* up until Forbes' (1973b, 1977) analysis. Work was, however, done before this on other species on the east and west coasts of North America by MacGintie (1934), Lunz (1937) and Pohl (1946) mainly the general ecology of *Callianassa* species.

Initial work done in the southern hemisphere focussed on population studies (Hailstone & Stephenson 1961, Devine 1966). More recent studies (Wynberg & Branch 1991, 1994, 1997, Cretchley 1996, Siebert 2003, Siebert & Branch 2005a, b) have examined effects of bioturbation related to *Callianassa* as well as the effects of disturbance caused by bait-collecting on the species' density and vigour.

Forbes (1973a, 1977) determined the number of eggs carried by female *C. kraussi* of different size classes, the major breeding seasons and the incubation times of the eggs. Further to this, Hanekom (1980) focussed on the percentage of females in the population, size at which prawns reach sexual

maturity, major breeding season, the number and percentage of the adult females ovigerous during the breeding season and the reproductive potential of the female prawns i.e. the number of eggs carried by females of a specific size. One key aspect of the reproductive biology of *C. kraussi* is that it has no planktonic larval stage, producing juveniles that burrow laterally from the burrows of adults (Forbes 1973b).

The above work, and related work on the mud prawn, *Upogebia africana* (Hanekom & Erasmus 1989, Cretchley 1996), was all conducted on the southern east coast of South Africa. No work has previously been carried out on the breeding and growth of *C. kraussi* on the west coast despite its abundance there (Christie & Moldan 1977, Wynberg & Branch 1991, see Chapter 2 of this thesis).

In my study the following parameters were considered:

1. The size composition of *C. kraussi* on sequential dates.
2. Growth rate deduced from cohort analysis.
3. The number and percentage of females present at each site.
4. The major reproductive season when females are ovigerous.
5. The number and percentage of adult females that are ovigerous.
6. The comparative fecundity of female prawns among study sites.

4.2 MATERIALS AND METHODS

4.2.1 Study sites

Four sites in Langebaan Lagoon were chosen to investigate the breeding cycle, namely Center Banks, Klein Oesterwal, Bottelary North and Bottelary South (see Chapter 2 Figure 2.1 for map of localities). Center Banks and Klein Oesterwal attract a large number of bait collectors (see chapter 3). Bottelary is a sanctuary area and no public access is permitted to this area.

4.2.2 Rationale

At each of the sites, prawns were collected every month to draw conclusions about the length and timing of the breeding cycle for *C. kraussi*. Other measurements (carapace length, dry mass and fecundity) were used to ascertain if differences occurred in the populations of *C. kraussi* between sanctuary and harvested areas.

For all samples, I recorded three responses: (1) the number of ovigerous females; (2) carapace size and dry mass of males and females; (3) the fecundity of ovigerous females measured as dry egg mass relative to dry body mass.

4.2.3 Sampling

Seasonality of reproduction

Fifty prawns were collected monthly from each site by pumping, from April 1999 to September 2000. The prawns were fixed in an 8% formaldehyde solution. All prawns were measured to 0.01 mm carapace length, sexed and the pleopods of the females examined for eggs. A subsample ($n = 203$ for Bottelary North, $n = 247$ for Bottelary South, $n = 229$ Center Banks and $n = 211$ for Klein Oesterwal) was dried at 55°C until a constant mass had been achieved, to determine length-mass regressions, from which the dry mass of the remaining individuals could be calculated.

The seasonal appearance of juveniles was recorded by plotting the percentage of juveniles (individuals < 7.25 mm carapace length) in the population per month. The seasonal appearance of ovigerous females was plotted similarly.

Reproductive capacity

During 2000 all ovigerous females in each sample were analysed. The carapace length and dry mass was measured for each ovigerous female. Eggs were separated, dry egg mass measured and

the number of eggs per brood counted. Fecundity was calculated as dry egg mass $\div$ dry body mass, expressed as a percentage.

Growth rate

Growth was tracked by plotting the modal sizes of cohorts recorded each month against time.

4.2.4 Statistical Analysis

One-Way ANOVAs were used to test for differences in dry mass and fecundity among localities.

Levene's test and Komolgorov-Smirnov one-sample test were employed to test data for normality and homogeneity of variances (alpha set at 0.05). When possible non-normal data were transformed to achieve normality, and heteroscedastic data were transformed to achieve equality of variance. Nonparametric statistical tests were applied when equality of variance could be attained but normality could not be achieved.

4.3 Results

Breeding season

At all four sites, *C. kraussi* exhibited a well-defined single annual peak in breeding over winter (May to early August) (Figure 4.1). The maximum proportion of adult females recorded as ovigerous was 86%, in June 2000 at Bottelary.

Animal size

Figure 4.2 shows the size frequencies of sand prawns from the three study sites from February 1999 to September 2000. At Bottelary the population was normally unimodal with periods of bimodality when recruits were added to the population. At Klein Oesterwal and Center Banks it was nearly always bimodal and sometimes trimodal.

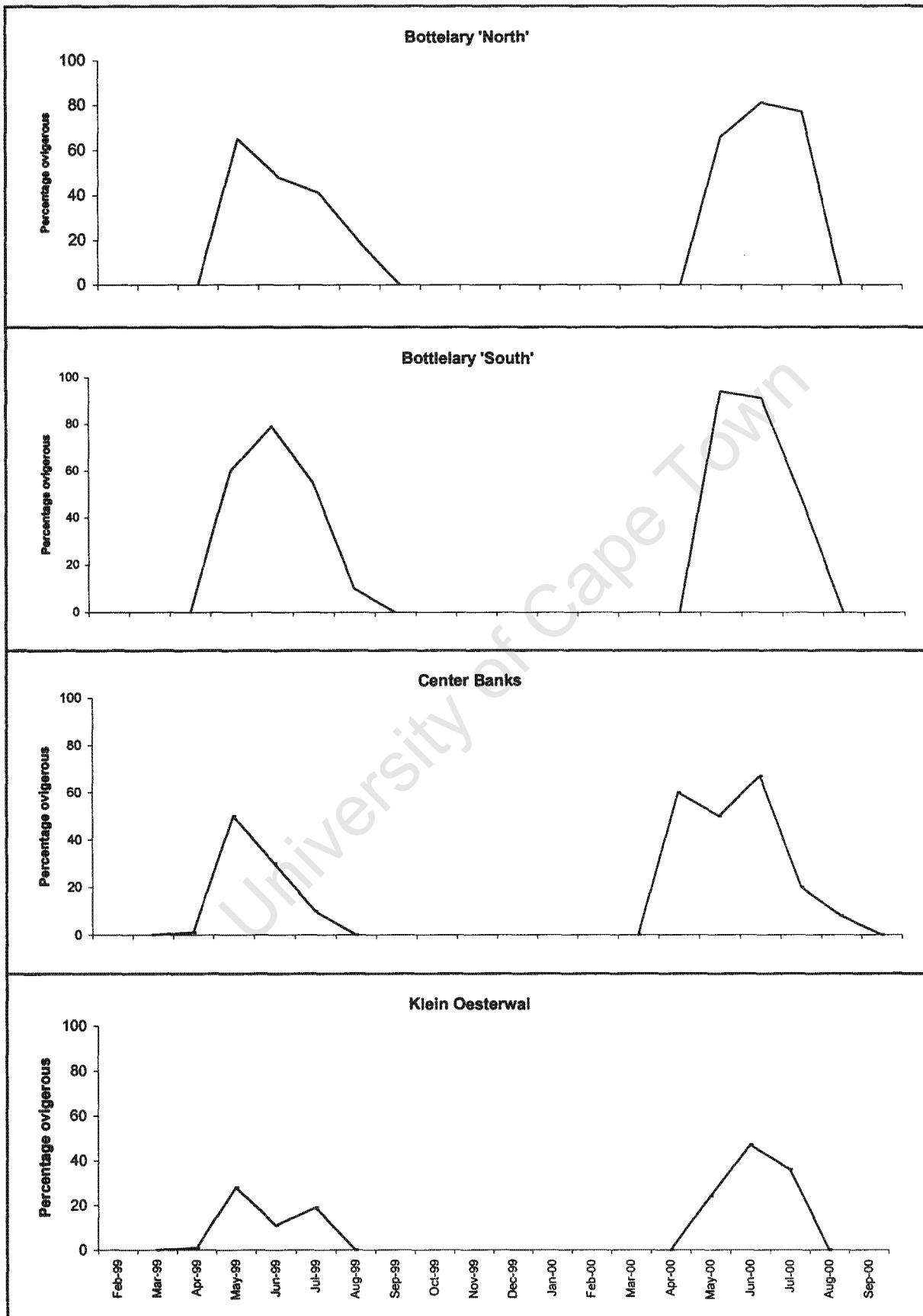


Figure 4.1 The proportion of adult female *C. kraussi* which were ovigerous at Bottelary, Center Banks and Klein Oesterwal in Langebaan Lagoon over the period February 1999 - September 2000.

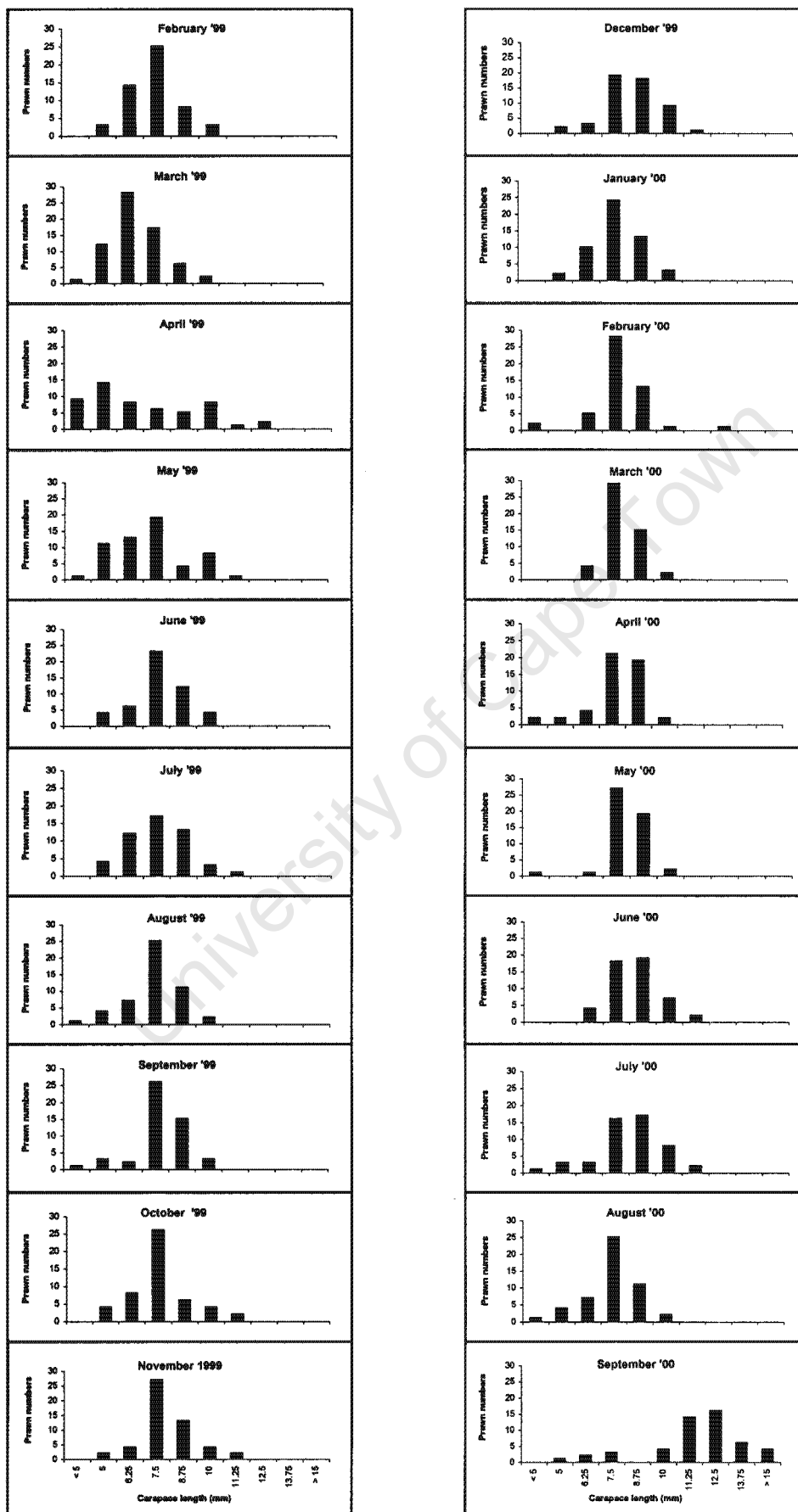


Figure 4.2a Charts showing size frequencies of *C. kraussi* at Bottelary 'North'.

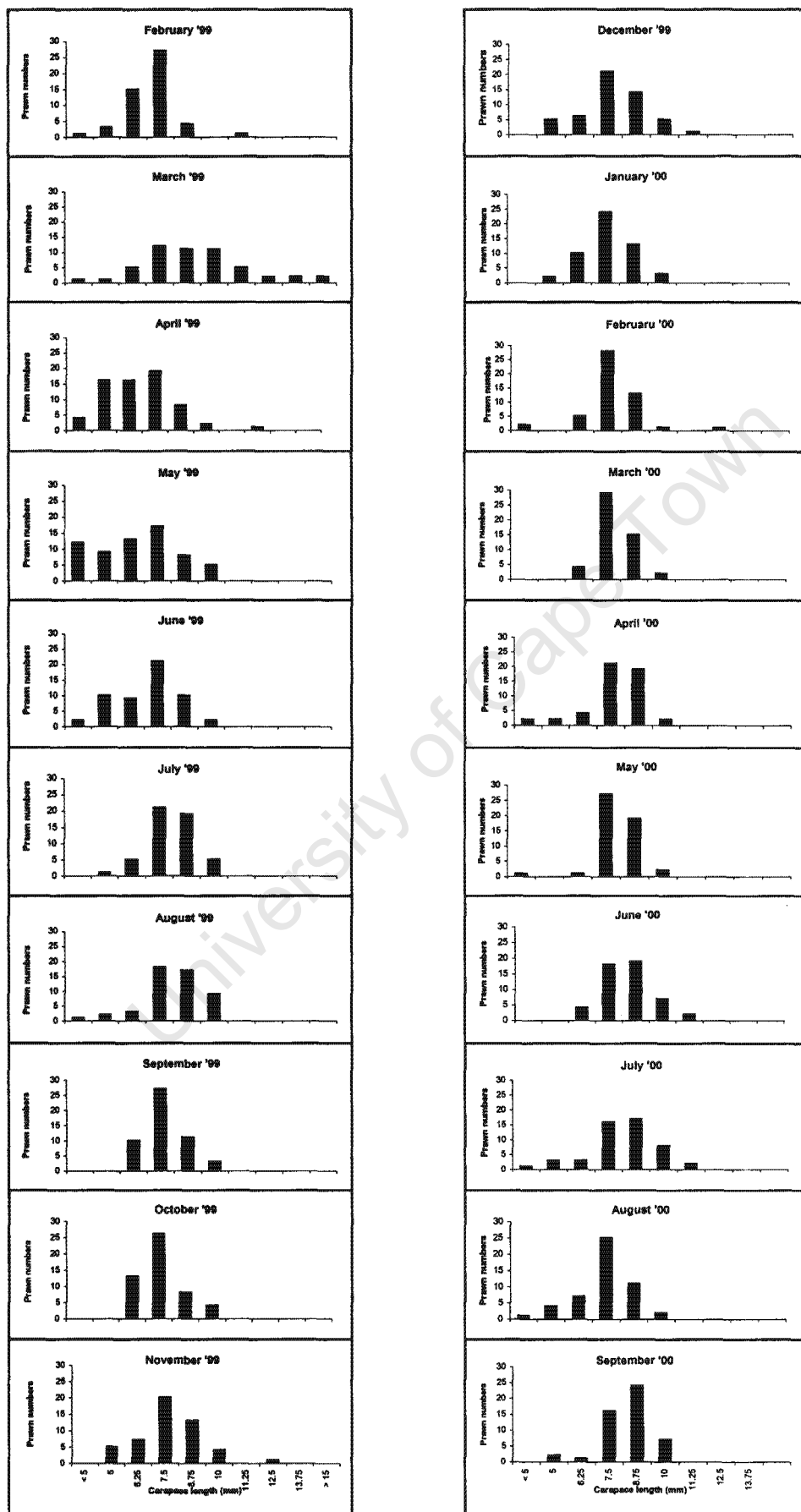


Figure 4.2b Charts showing size frequencies of *C. kraussi* at Bottelary 'South'.

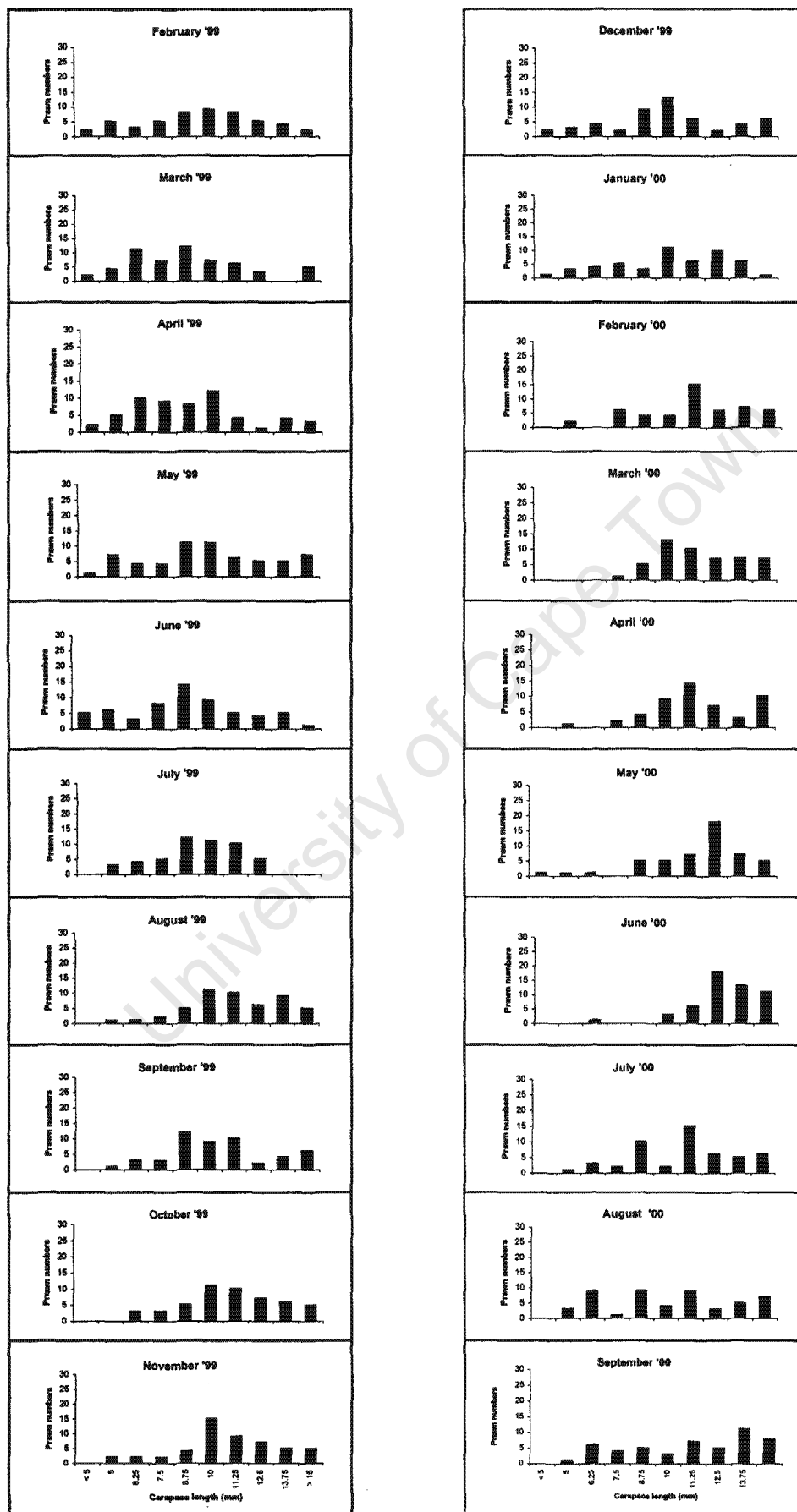


Figure 4.2c Charts showing size frequencies of *C. kraussi* at Center banks.

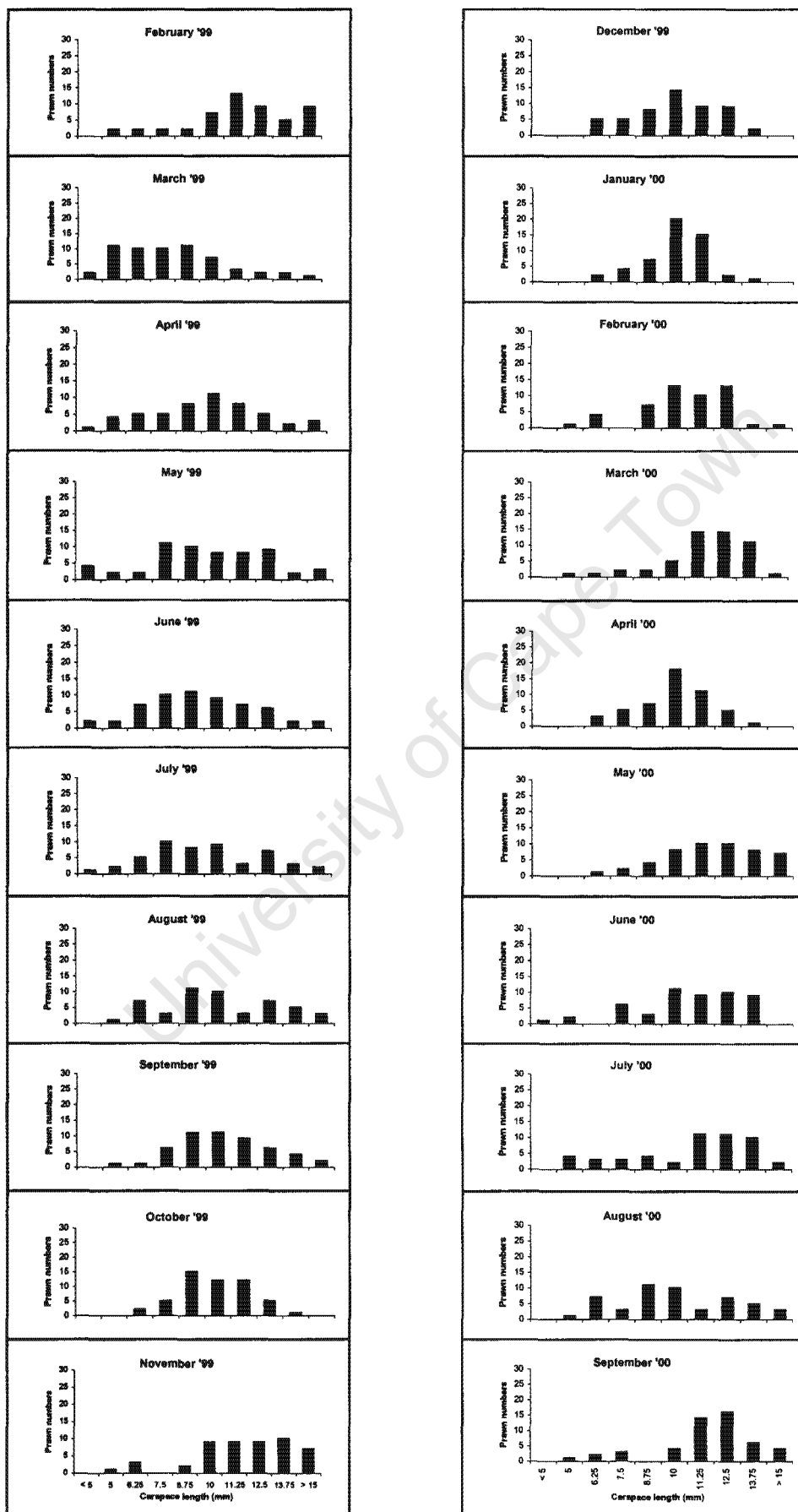


Figure 4.2d Charts showing size frequencies of *C. kraussi* at Klein Oesterwal.

Comparisons between the four localities showed that sand prawns were significantly larger at Center Banks followed by Klein Oesterwal and Bottelary (1 – Way ANOVA $F_{3,4152} = 597.71$, $P < 0.001$) (Figure 4.3). The Bottelary ‘north’ and ‘south’ sites did not differ significantly from each ($P = 0.96$). Figure 4.4 shows the mean mass of ovigerous females during the months of the breeding season in 2000. Comparisons between the four sites showed differences between the two Bottelary sites when compared to Center banks and Klein Oesterwal. The largest ovigerous females were also found at Center Banks (1-Way ANOVA, $F_{2,268} = 878.60$, $P < 0.001$) (Figure 4.5).

A plot of the frequency of juvenile prawns (Figure 4.6) revealed a single peak each year between March and May (except that no peak was detected at Bottelary South in 2000). Detection of juveniles thus lagged approximately nine months behind the time when females were in berry.

Fecundity

Figure 4.7 shows the mean fecundity of ovigerous females at the four study sites for the breeding season of 2000. Comparisons between the four sites (1-Way ANOVA $F_{3,268} = 14.13$, $P < 0.0001$) and Tukey tests revealed no significant differences between the two Bottelary sites and Klein Oesterwal. However, animals at the Center Banks had a significantly lower fecundity than for the other three sites (see Figure 4.8).

Egg numbers

The mean and maximum number of eggs carried by females of a given size classes are shown in Table 4.1. Females at Bottelary matured at substantially smaller sizes than those at Klein Oesterwal and Center Banks. Being smaller, they also carried smaller numbers of eggs per female than at these two sites. Comparisons of sand prawn size and hence the mean number of eggs carried per female shows significant differences between the sites (1-Way ANOVA, $F_{3,268} = 121.87$, $P < 0.001$) (see Figure 4.9 A & B). Tukey test revealed that mean egg numbers per female was

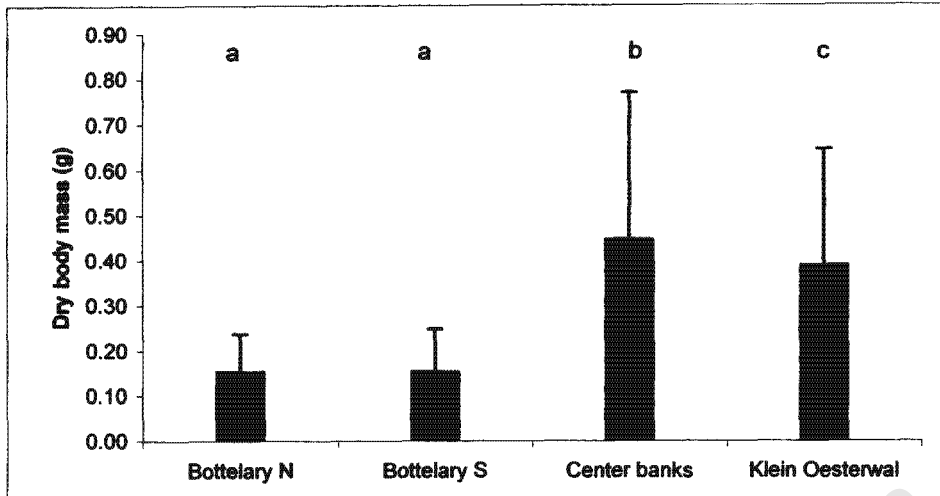


Figure 4.3 Mean dry body mass (+ 1sd) for all sand prawns at the three study sites. Significant differences are shown with lower case letters.

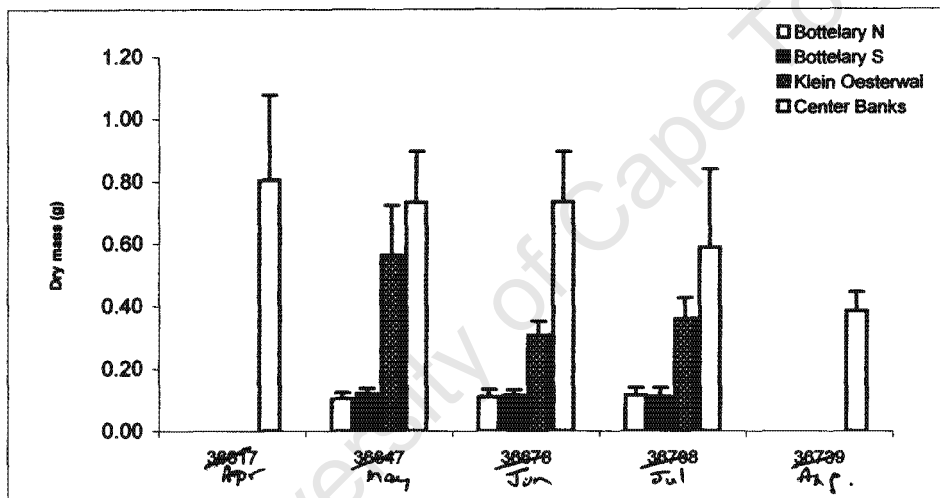


Figure 4.4 Mean dry body mass (+ 1sd) of ovigerous females measured during the breeding season. Only Center Banks had ovigerous females during April and August.

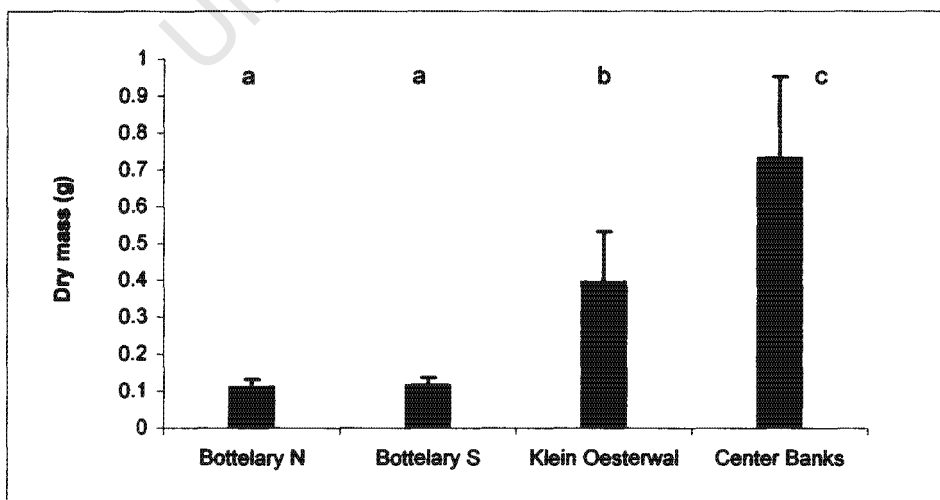


Figure 4.5 Mean dry body mass (+ 1sd) of ovigerous females at the three study sites. Significant differences are shown with lower case letters.

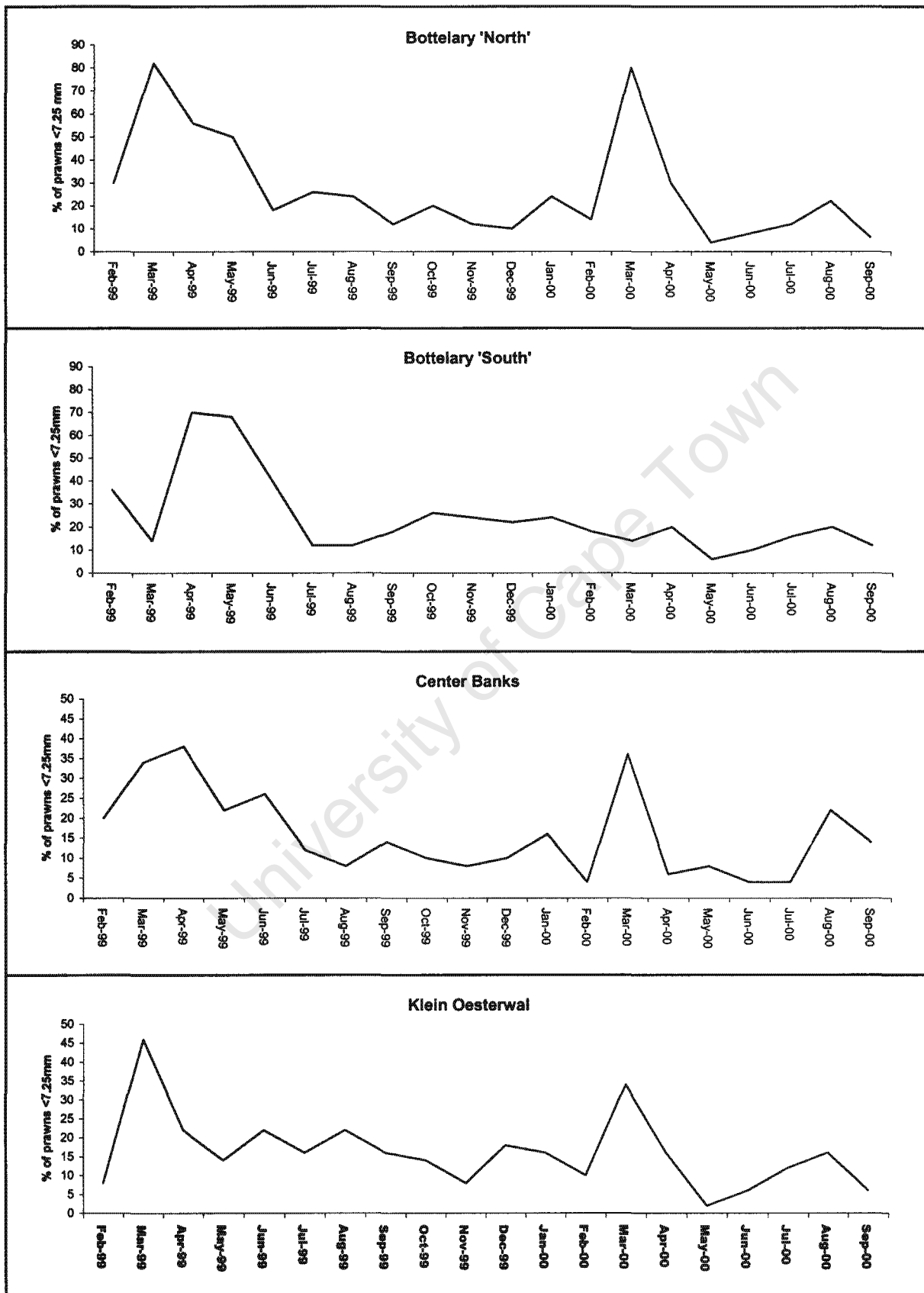


Figure 4.6 Charts showing peaks in juvenile numbers of sandprawns at the four study sites. The y axis measurement depicts carapace length.

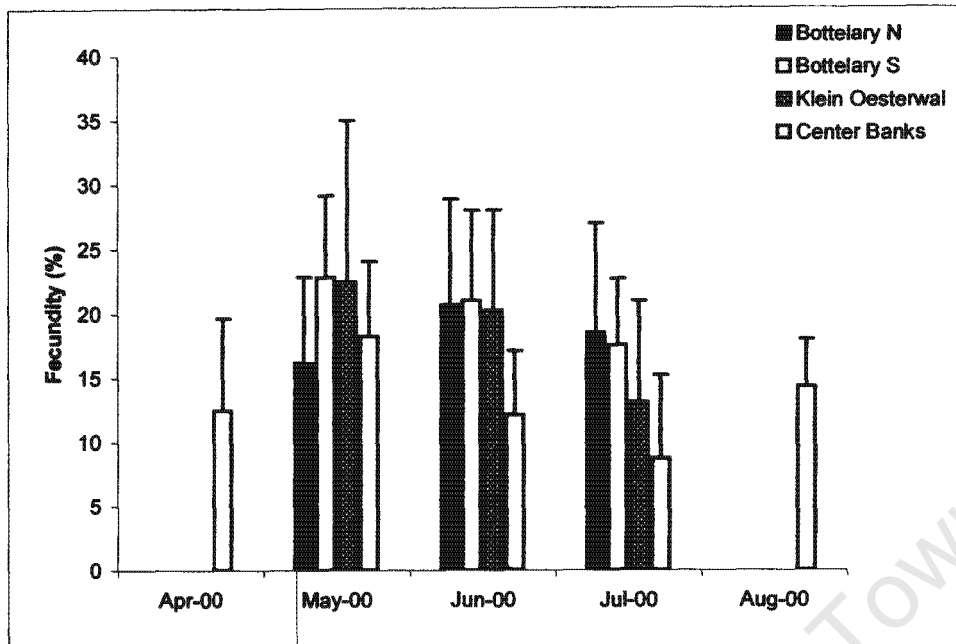


Figure 4.7 Mean fecundity for the breeding season for the three study sites. No ovigerous females were found at Bottelary and Klein Oesterwal during April and August. Error bars show 1 standard deviation.

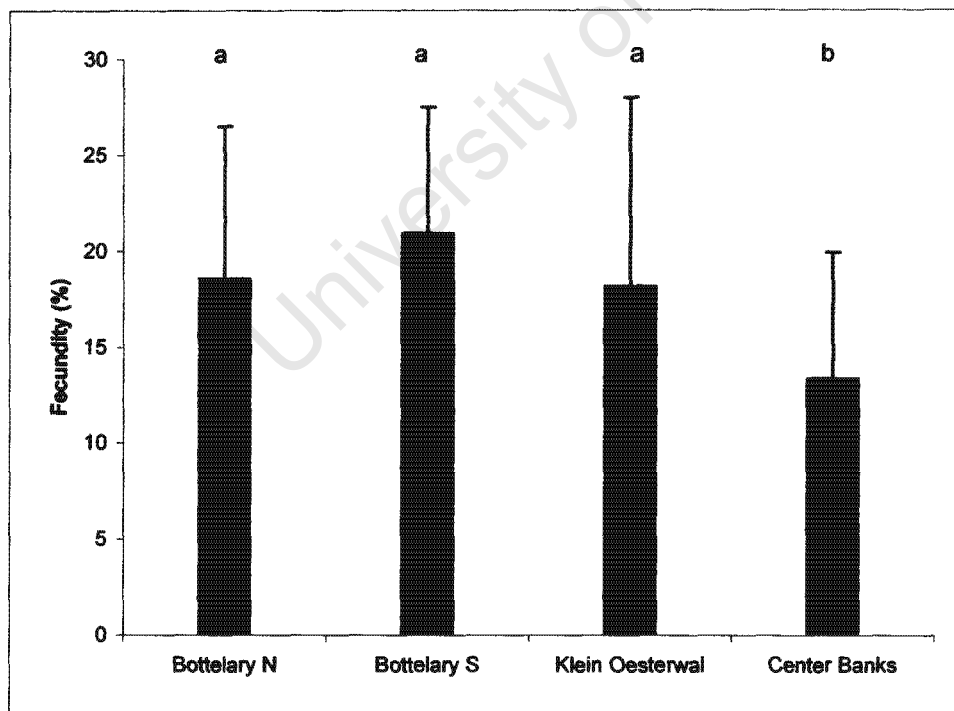


Figure 4.8 Comparisons of mean fecundity (+ 1sd) between the three study sites. Significant differences are shown with lower case letters.

significantly lower at the Bottelary sites than for Center Banks and Klein Oesterwal ($P < 0.0001$)

and no significant difference was found between Center banks and Klein Oesterwal ($P = 0.16$).

Table 4.1 The mean and maximum numbers of eggs recorded for female *C. kraussi* of a given size class. The same classes were used as for Forbes (1973a) and Hanekom (1980).

a) Forbes (1973); b) Hanekom (1980); c) Bottelary; d) Klein Oesterwal; e) Center Banks

Carapace length (mm)	7	8	9	10	11	12	13	14	15	16	17
a) mean	42	86	138	282	76						
max	78	285	500	628	90						
b) mean	60	106	153	254	263						
max	115	153	229	354	385						
c) mean	21	35	41	54							
max	50	64	71	81							
d) mean						50	97	155	151	180	
max						61	217	273	190	180	
e) mean				122	98	117	146	158	221	200	147
max				123	216	280	272	305	317	256	152

Growth rates

Patterns of growth (Figure 4.10) were consistent at all four sites although faster growth and larger sizes were attained at Klein Oesterwal and Center Banks than either of the Bottelary sites. Growth was characterised by a rapid spurt between April and July followed by slower growth or even an absence of growth from about August to January. Normally a single cohort was detectable at any given time at Bottelary whereas up to three simultaneous cohorts could be found at the other sites. Maximum longevities of about 18 months to 2.5 years can be deduced by tracking the cohorts.

4.4 Discussion

In Swartkops Estuary Forbes (1973a, b) found two peaks of ovigerous females per year: a substantial 'winter peak' during May and June-July and a smaller summer peak from November – January. The delay between winter production of eggs and appearance of juveniles was about four months; after the summer production of eggs the delay was 5-6 months. In my case the delay was up to nine months. Forbes found a similar pattern to the Swartkops Estuary in Kleinemonde

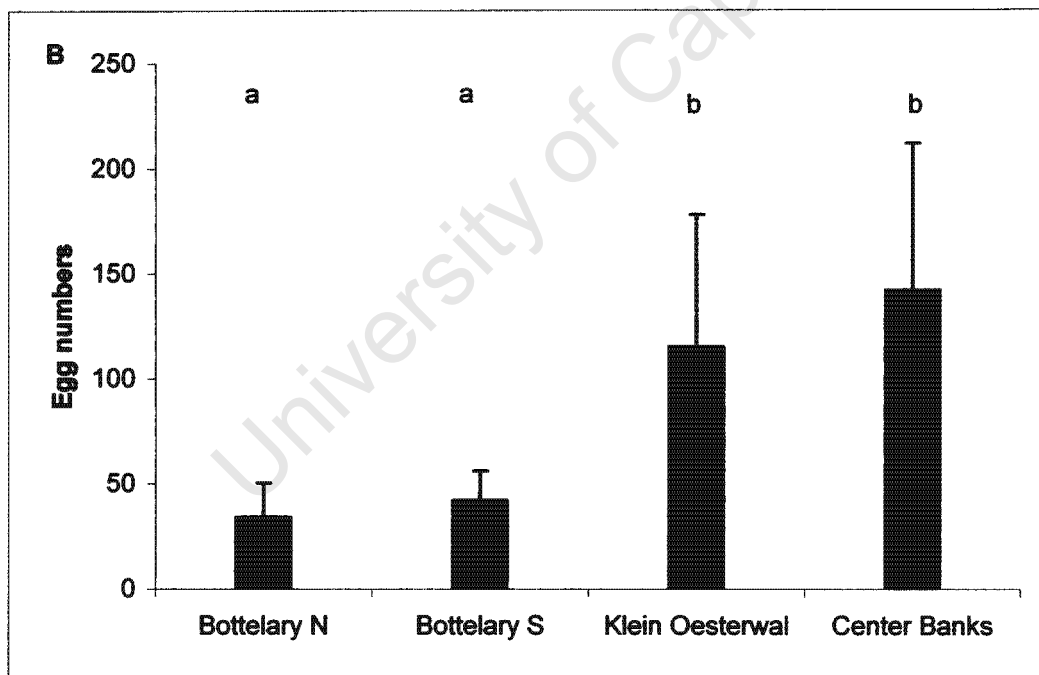
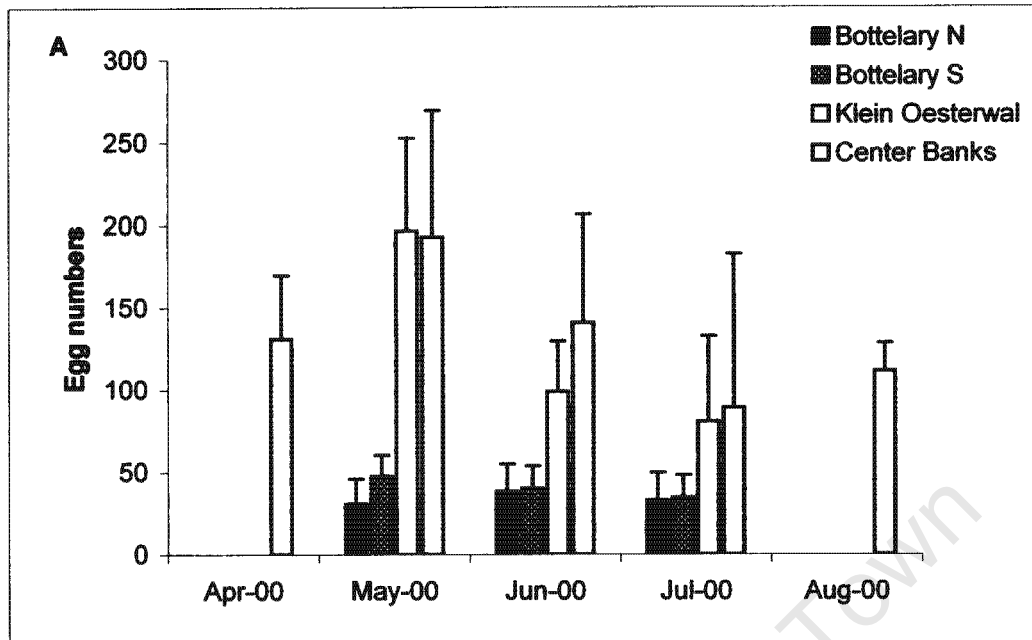


Figure 4.9 Graphs showing mean egg numbers (per female) for the different sites for the months when egg-bearing females were observed (A) and overall comparative mean egg numbers for the three study sites (B). Error bars indicate 1 std deviation and lower case letters indicate homogenous groups.

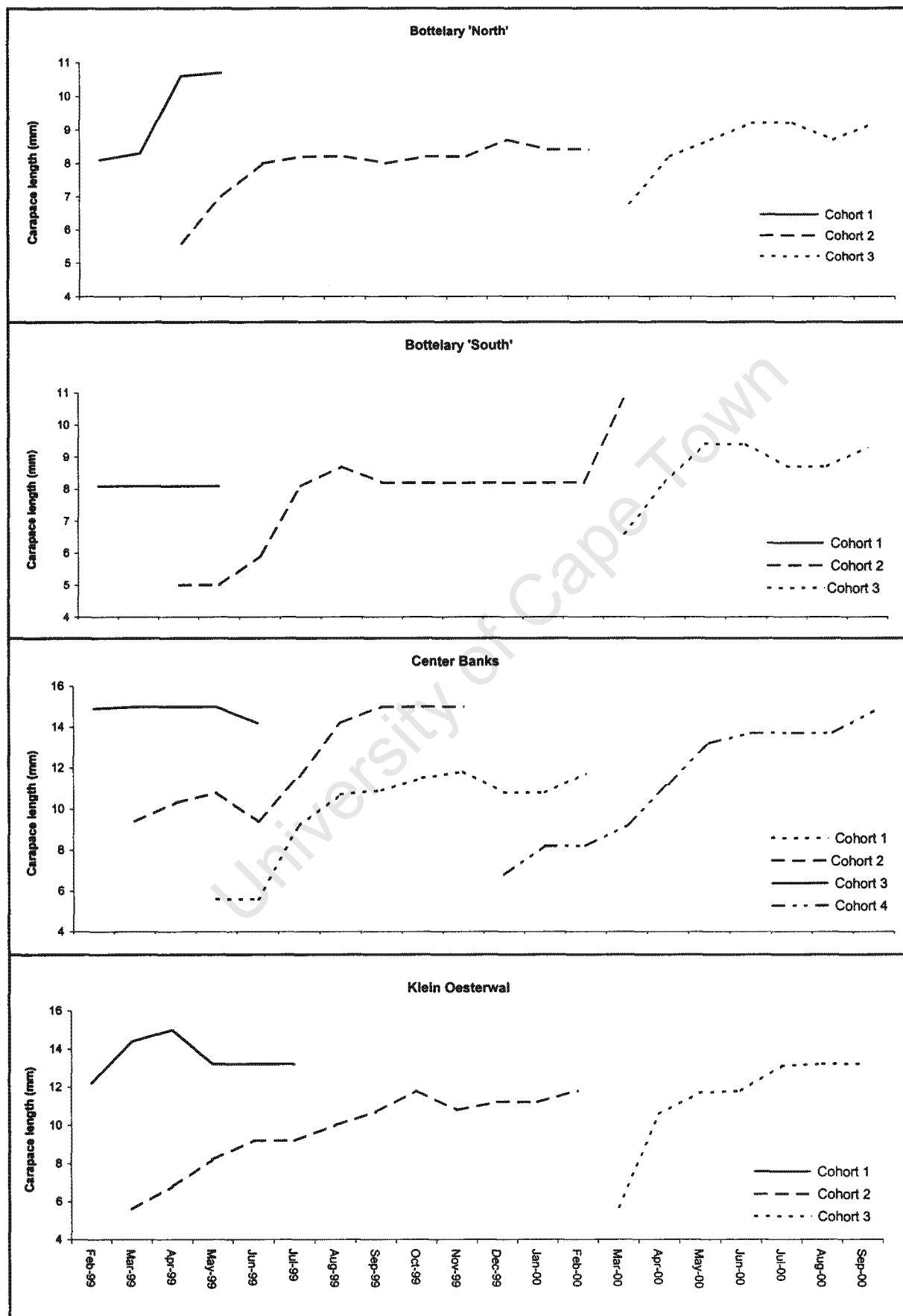


Figure 4.10 Growth rates deduced from cohort-analysis for the four study sites.

Estuary, where there was also a large breeding peak in winter and a small summer breeding effort. He obtained similar results in the Swartvlei system, although small variations occurred in different areas with respect to the timing of the appearance of juveniles after the egg production peaks.

In contrast, Hanekom (1980) recorded a single well-defined breeding peak in winter and a single peak of juvenile recruitment in Swartkops Estuary, pointing to the extrusion of one batch of eggs. He challenges Forbes' (1977) data which point to the production of two batches of eggs, by arguing that the incubation time (ca 42 days) during the peak breeding season (May to September) was slightly longer than the sampling interval (ca 30 days). This would have resulted in some ovigerous females being counted twice, yielding an elevated overall percentage. Forbes (1977) calculated the cumulative values for the sampling periods in 1971, 1972 and 1973 as 120 %, 140 % and 99 %, which again points to one batch of eggs being produced, with double counting of ovigerous females artificially inflating the cumulative percentages. In my experiment the animals were removed when they were sampled, eliminating the potential problem of counting an ovigerous female twice.

I found that reproduction of *Callinassa kraussi* in Langebaan Lagoon is seasonal with females being ovigerous from late April to early August. The Center Banks appeared to have females in berry slightly before Bottelary and Klein Oesterwal. There was also only a single annual peak to the appearance of juveniles, supporting the view that there is only one brood per year.

Both the mean and maximum sizes of prawns at Bottelary were consistently smaller than at Klein Oesterwal and Center Banks and egg production was initiated at a larger size at the latter two sites. Comparisons of the numbers of eggs produced per individual show a smaller output at Bottelary because of their smaller size. However, both Forbes and Hanekom recorded substantially greater outputs per individual when considering animals of comparable size (Table 4.1). This reinforces the view that Bottelary constituted a suboptimal habitat relative to Klein Oesterwal and Center

Banks. Growth was also faster at these latter two sites. The rates of growth recorded were comparable to those recorded by Forbes (1977) in the Swartkops Estuary but the pattern of growth was strikingly different, with initial growth spurts being followed by prolonged periods with little or no growth. It is possible that periods of seeming slow growth were an artefact of following cohort size to determine growth rate, since selective mortality of the largest individuals in the population can yield apparent slow growth. However, as fast growth was again detected in large individuals after periods of slow growth, I consider it unlikely that selective mortality was responsible for the slow-growth phase.

Fecundity appeared reduced at Klein Oesterwal and Center Banks - both sites where bait harvesting takes place. The sanctuary site of Bottelary showed the highest mean fecundity although this was only significantly greater when compared to Center Banks. One possible reason fecundity was higher at Bottelary may have been the slower growth experienced there: energy may have been diverted into growth rather than reproduction at Center Banks and Klein Oesterwal. Because the animals are significantly smaller at Bottelary they carried fewer eggs per individual even although their fecundity per unit mass was greater. The faster growth and greater maximum sizes achieved at Klein Oesterwal and Center Banks relative to Bottelary may simply reflect environmental differences, but it is possible that because bait-collecting there has reduced densities (Chapter 3), competition has been diminished, enhancing growth and size. However, it is almost impossible to distinguish whether these differences are influenced by site-related related environmental conditions or density-dependant consequences of bait-collecting. In the following chapter I undertake a specific experiment to attempt to disentangle these effects.

CHAPTER 5

THE IMPACT OF BAIT PUMPING ON ABUNDANCE, FECUNDITY AND REPRODUCTIVE OUTPUT OF THE SAND PRAWN, *CALLIANASSA KRAUSSI*

5.1 Introduction

Reproductive cycle and reproductive capacity

Forbes (1973a, 1977) found that *C. kraussi* breeds mainly in winter/spring with a smaller peak in summer. Hanekom (1980) recorded a single peak between April and September, and considered that one brood of eggs was produced per annum. He found, however, that the mean and maximum numbers of eggs carried by a female *C. kraussi* of a given carapace length were lower than the values recorded by Forbes (1973a), despite the two studies being done at the same locality. He attributed the difference to disturbance, brought about by physical structures modifying tidal flow, manifested in differences in food transport to the area. This, he argued, resulted in lowered reproductive output. The direct effect of disturbance by bait collecting/harvesting on the reproductive output of *Callianassa* species has never been examined, although its influence on population numbers and biophysical effects on the soft-bottom sediment have been explored (Wynberg & Branch 1991, 1994, 1997, Contessa & Bird 2004). Effects of bait harvesting on several other marine populations and their subsequent recovery have also been documented (for general infaunal intertidal populations see Brown & Wilson 1997, Dernie *et al.* 2003; for *Arenicola marina* see McLusky *et al.* 1983; for the cockle *Cerastoderma edule* see Jackson & James 1979, Ferns *et al.* 2000; for *Arenicola marina* and *Nereis virens* see Blake 1979 a & b, for *Mya arenaria* see Ambrose *et al.* 1998).

Following previous work done on aspects of reproduction of *C. kraussi*, the present study documents the abundance and fecundity (measured as egg mass as a percentage of body mass) of

this species in Langebaan Lagoon at sites experimentally subjected to controlled bait-collecting. Because this species attains different sizes and densities among different areas and among different sites within areas (Forbes 1973a, Hanekom 1980, see Chapter 2 of this project) I also predicted differences in reproductive capacity among sites in Langebaan Lagoon.

Disturbance

In soft-sediment environments, disturbance can be caused by physical processes (Wynberg & Branch 1991, Siebert & Branch 2005a), biological processes (Reise 1985, Branch & Pringle 1987, Thrush 1988, Thrush *et al.* 1991) or human activities (Blake 1979 a, b, Jackson & James 1979, McLusky *et al.* 1983, Wynberg & Branch 1991, Contessa & Bird 2004). In Langebaan Lagoon sand prawns are collected as bait species by recreational fishers using a hand-operated suction pump (Hailstone & Stephenson 1969). The effects of pumping and associated trampling are clearly visible on the sediment surface, and are often very extensive. In the long term, harvesting may influence the numbers of prawns, either as a direct result of their removal by bait-pumping, or due to associated trampling. However, the continued survival of sand prawns depends on successful reproductive output. Harvesting of prawns may not only directly reduce their numbers (Wynberg & Branch 1991) but may also reduce their capacity to reproduce and thus indirectly reduce their densities. Both a reduction in numbers of *C. kraussi* and reduced levels of fecundity were thus expected in areas where *C. kraussi* was exposed to disturbance caused by bait-collecting. I therefore predicted a lower density of prawns and a reduced fecundity of females in areas where harvesting/disturbance is high.

5.2 Materials and methods

5.2.1 Study sites

Three sites in Langebaan Lagoon were chosen to investigate the effect of bait collecting for prawns on density, fecundity and reproductive output, namely Center Banks, Klein Oesterwal and Bottelary

(see chapter 2 for map of localities). Center Banks and Klein Oesterwal attract a large number of bait collectors (see chapter 3). The Center Bank area is only really accessible by boat, whilst the Klein Oesterwal area is accessible by boat and on foot. The third site, Bottelary is a sanctuary area and no access is permitted to this area.

5.2.2 Rationale

At each of the sites, attempts were made to establish up to three experimental treatments (Table 5.1), each replicated two times per site: (1) 'undisturbed controls' where all harvesting and disturbance were prevented; (2) 'experimental disturbance' in which I imposed a known intensity of harvesting; (3) 'fisher disturbance' in which fishers were permitted to continue harvesting at intensities previously recorded in Chapter 3. At Bottelary, this third treatment was not possible as fishers may not harvest there. The experiment was also disrupted at Klein Oesterwal because the control and experimentally harvested plots were disturbed by fishers harvesting in these plots, so for that site I report only results from plots subjected to fisher disturbance.

For all treatments, I recorded four responses:

1. Carapace size and dry mass of male and female prawns.
2. Densities.
3. Individual fecundity of ovigerous females measured as dry egg mass relative to dry body mass.
4. The population reproductive output by ovigerous females (measured as numbers of eggs.m⁻²).

5.2.3 Sampling

Experimental design

At Center Banks and Klein Oesterwal a total of six 3 m x 4 m plots and at Bottelary four 3 m x 4 m plots were established, corresponding in size to the plot sizes used by Wynberg & Branch (1994). The plots were marked using short wooden droppers and signage was erected to inform the public

of the experiment and to control access and activities. Before initiating the treatments, ten replicate background counts were undertaken on three consecutive days in each plot using 0.0625 m² quadrats. These showed that at each site there were no significant differences in the densities of prawn holes among plots designated for different treatments (ANOVA $F_{2, 87} = 3.14$, $P > 0.05$ for Center Banks; $F_{2, 87} = 3.11$, $P > 0.05$ for Klein Oesterwal and $F_{1, 58} = 2.40$, $P = 0.097$ for Bottelary).

From the observations on bait collectors (see Chapter 3) I calculated that the average rate of collection by fishers was 20 sucks/12 m²/month. In two of the six plots per site an 'experimental disturbance' was imposed by excluding fishers and initiating a controlled harvest at a fixed rate of 20 sucks per month. Another two of the six plots were set aside as 'controls' and all disturbance was prevented in these plots. The remaining two plots at Center Banks and Klein Oesterwal were left as 'fisher disturbed' background plots, in which the public could continue to pump and remove prawns. The experiment was started in March 2001 and ran until June 2003. Each month the plots were visited and holes were counted in ten 0.0625 m² quadrats per plot. In June 2003 an area of 0.5 m x 0.5 m was analysed within each plot for each treatment type, as follows.

Measuring differences in prawn density

At the end of the experiment, prawn densities were sampled in all plots by sinking metal sheets into the sand to delineate two replicate areas of 0.5 m x 0.5 m x 1 m deep, and all the prawns in these areas were pumped out using a stainless-steel diaphragm prawn pump (Hailstone & Stephenson 1961). The sediment was sieved through a 2-mm sieve and all prawns removed and fixed in 8% formaldehyde solution. All individuals with eggs were measured and dried until a constant mass was reached. Fifteen other individuals from each 0.5 m x 0.5 m sucked area were measured and dried. These individuals were used for comparisons of length-mass relationships among different sites and treatments. For all other individuals, carapace length was measured.

Reproductive fecundity and reproductive output

Carapace length and dry mass were measured for each ovigerous female. Fecundity was calculated as dry egg mass $\div$ dry body mass, expressed as a percentage. Reproductive output or egg output was calculated as number of eggs per meter square, derived from data for number of eggs per female multiplied the density of females/m².

Statistical Analysis

The experimental design was unbalanced due to the loss of two treatments at Klein Oesterwal and the fact that one treatment could not be established at Bottelary, so it was not possible to undertake a Two-Way ANOVA to test for treatment and site effects simultaneously. As a result, One-Way ANOVAS were used to test for differences in density, dry mass and fecundity among treatments for each site separately, and for differences among sites for each treatment separately (Table 5.1). For analyses of egg output an ANCOVA was used with female dry body mass as the covariate.

Levene's test and Komolgorov-Smirnov one-sample test were used to test for normality and homogeneity of variances ($\alpha = 0.05$). Non-normal data and heteroscedastic data were transformed to meet assumptions of parametric tests, or nonparametric statistical tests were applied

Table 5.1 Description of sites, treatment and the statistical analyses.

	Undisturbed Control	Fisher disturbance	Experimental disturbance	Test of treatment effects
Bottelary	√	Not applicable	√	1-Way ANOVA fixed factor
Center Banks	√	√	√	1-Way ANOVA fixed factor
Klein Oesterwal	No data	√	No data	No analysis possible
Tests of site effects	1-Way ANOVA random effect	1-Way ANOVA random effect	1-Way ANOVA random effect	

5.3 Results

a. Effects of disturbance on densities of C. kraussi.

Densities were significantly reduced within experimental disturbance treatments at Bottelary and Center Banks when compared to control areas, but no difference was found between the fisher disturbance and control plots at Center Banks (Figure 5.1; see Table 5.2). There were, however, no differences among areas when comparisons were made within each treatment (1-Way ANOVA $F_{1,6} = 2.919$, $P = 0.138$ for comparisons of controls at Bottelary and Center Banks; $F_{1,6} = 1.604$, $P = 0.252$ for comparisons of fisher disturbance plots at Center Banks and Klein Oesterwal; $F_{1,6} = 3.611$, $P = 0.106$ for experimental disturbance at Bottelary and Center Banks).

When the densities of ovigerous females alone were compared among treatments within sites (Figure 5.2) there were no significant differences (One-Way ANOVAs, $F_{1,6} = 1.6$, $P = 0.25$ for Bottelary; $F_{2,9} = 2.21$, $P = 0.17$ for Center Banks). There were also no significant differences among sites within treatments (One-Way ANOVAs, $P > 0.15$).

Table 5.2 One-Way ANOVAs of mean numbers of *C. kraussi*, between treatments for (a) Bottelary and (b) Center Banks. Significant results were analysed using Tukey HSD.

(a) Bottelary	df Effect	MS Effect	df Error	MS Error	F	p-level
	1	484128.0	6	8821.333	54.88	0.0003
(b) Center Banks	df Effect	MS Effect	df Error	MS Error	F	p-level
	2	13545.33	9	1766.222	7.67	0.0114
Tukey HSD	Exp. dist.	No dist.	Fisher dist.			
Exp. dist.		0.0097	0.0843			
No dist.	0.0097		0.3748			
Fisher dist.	0.0843	0.3748				

Effects of disturbance on C. kraussi dry body mass

Mean dry body masses of individual prawns were significantly different among treatments at Bottelary (Kruskal-Wallis test: $H(1, N = 192) = 7.089$, $P = 0.0078$) but not at Center Banks (Kruskal-Wallis test: $H(2, N = 243) = 3.86$, $P = 0.1451$). At Bottelary the control treatment showed

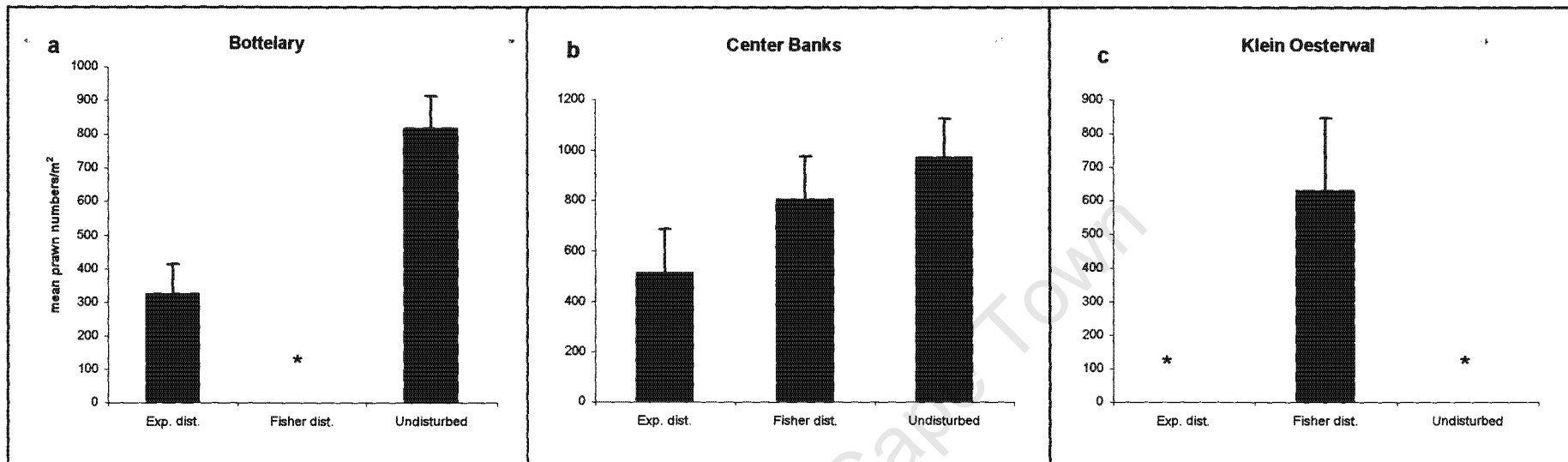


Figure 5.1 Mean individual densities in different treatments at Bottelary, Center Banks and Klein Oesterwal. Asterisks indicate treatments for which data could not be gathered. Error bars show 1 standard deviation.

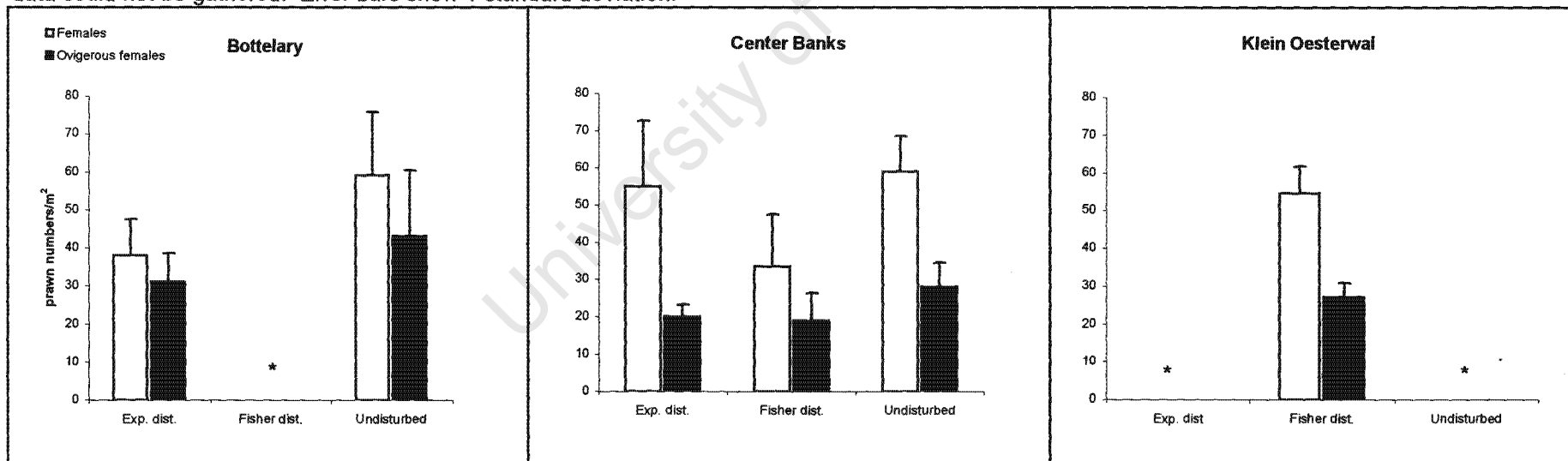


Figure 5.2 Mean individual densities for females and ovigerous females in different treatments at Bottelary, Center Banks and Klein Oesterwal.

significantly higher mean dry mass than the experimentally disturbed treatments (Figure 5.3).

Where treatments could be compared between Bottelary and Center Banks, mean mass was significantly greater for both treatments at Center Banks (1-Way ANOVA $F_{1,166} = 35.8$, $P < 0.0001$ for experimental disturbance and $F_{1,188} = 13.89$, $P = 0.0002$ for controls). For fisher disturbance plots there were no significant differences between Center Banks and Klein Oesterwal (Kruskal-Wallis test: $H(1, N = 122) = 0.186$, $P = 0.666$).

Figure 5.4 illustrates the mean dry mass of the ovigerous females in different treatments at Bottelary, Center Banks and Klein Oesterwal. Comparisons between different treatments within sites showed no significant differences (Bottelary 1-Way ANOVA $F_{1,72} = 0.033$, $P = 0.856$; Center Banks 1-Way ANOVA $F_{1,46} = 2.36$, $P = 0.131$). However, comparisons of the same treatments between different sites did show significant differences. For the 'fisher' treatment, animals were larger at Center Banks than Klein Oesterwal (1-Way ANOVA $F_{1,44} = 29.99$, $P < 0.0001$), for the undisturbed 'control' treatment animals were larger at Center Banks than Bottelary (Kruskal-Wallis test: $H(1, N = 71) = 50.17$, $P < 0.0001$) and for the 'experimentally' disturbed treatment, animals were again larger at Center Banks than Bottelary (Kruskal-Wallis test: $H(1, N = 51) = 35.77$, $P < 0.0001$).

Regressions of dry body mass versus carapace length (Figure 5.5) and Analyses of Covariance (Table 5.3 & 5.4) revealed that there were significant differences among treatments at both Center Banks and Bottelary. At both sites prawns in the control plots had significantly greater body masses relative to carapace length than either the experimentally-disturbed or fisher-disturbed plots. Disturbance thus reduced body size relative to length at both Bottelary and Center Banks. It was also evident that both mean individual mass and mass relative to length were substantially lower at Bottelary than for Center Banks or Klein Oesterwal, so both site and treatment effected size and mass, within implications for reproductive output.

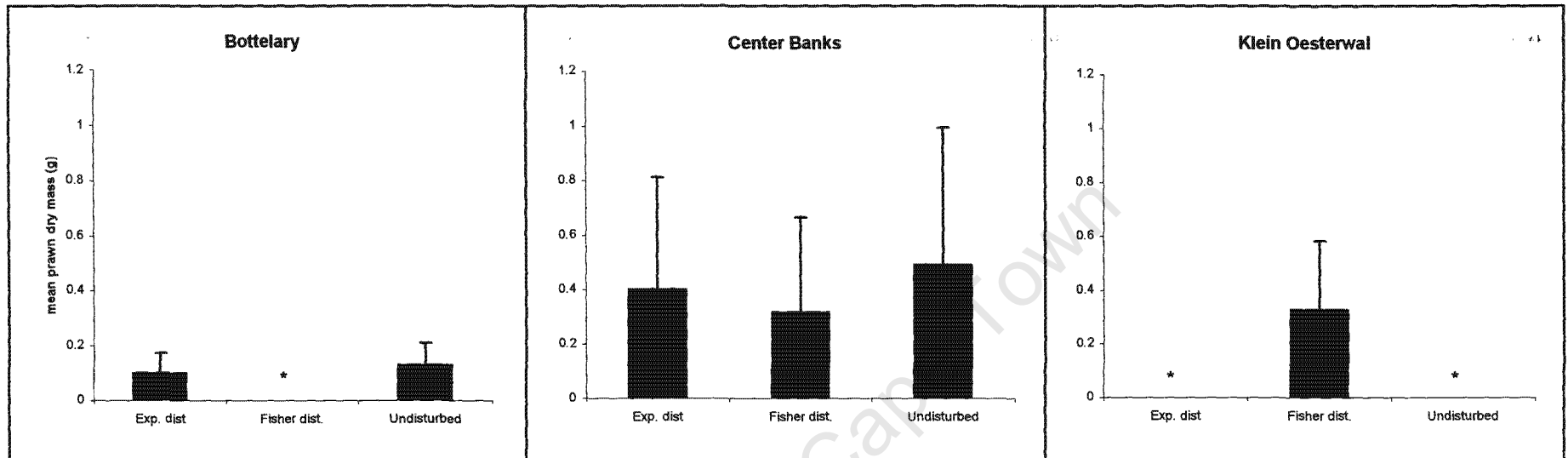


Figure 5.3 Mean dry mass of individuals in different treatments at Bottelary, Center Banks and Klein Oesterwal. Asterisks indicate treatments for which data could not be gathered. Error bars show 1 standard deviation.

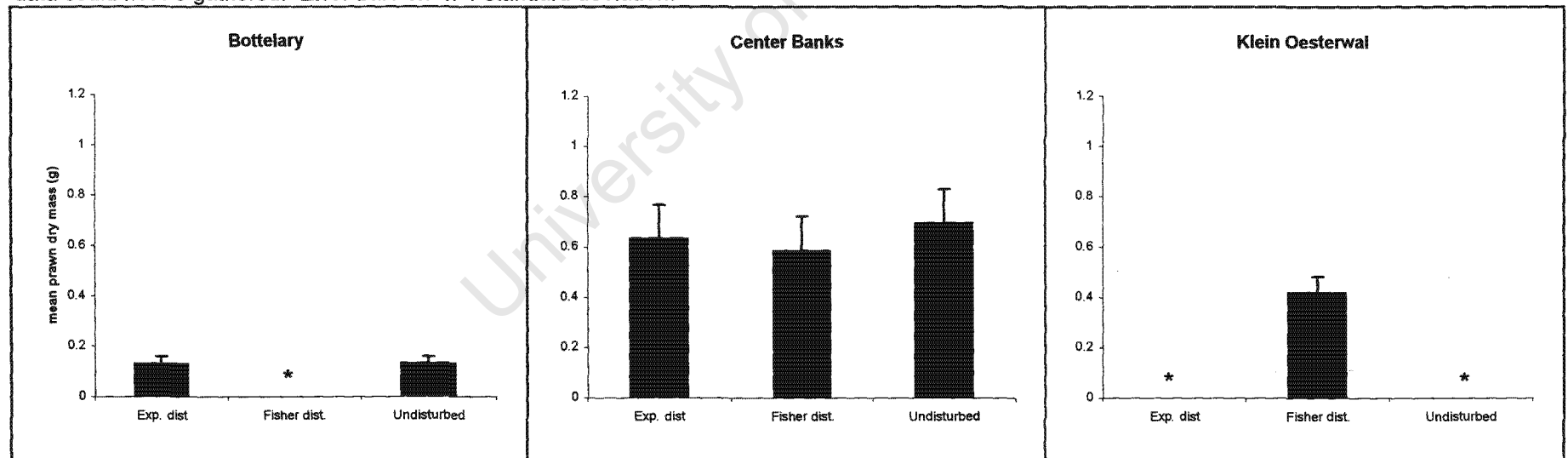


Figure 5.4 Mean dry mass of ovigerous females in different treatments at Bottelary, Center Banks and Klein Oesterwal. Asterisks indicate treatments for which data could not be gathered. Error bars show 1 standard deviation.

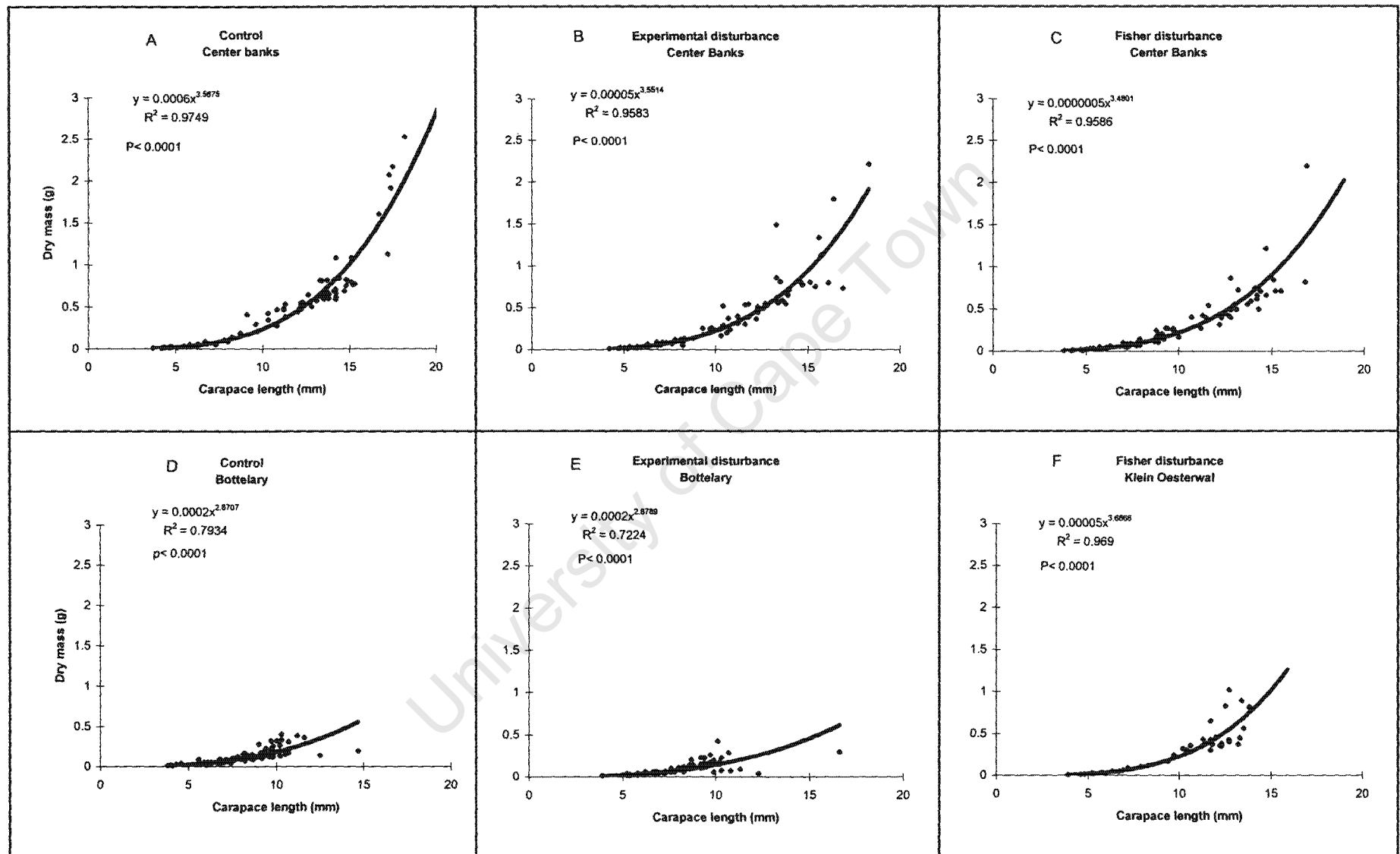


Figure 5.5 Regressions of dry body mass vs carapace length for Center banks, Bottelary and Klein Oesterwal.

Table 5.3 Results of ANCOVA to determine if any differences exist between 'experimental' and 'non disturbed' treatments for *C. kraussi* at Bottelary using carapace length as the covariate. Significant results were analysed with Fisher LSD.

	SS	df	MS	F	P
Length	0.6326	1	0.63	221.10	0.0001
Treatment	0.0294	1	0.03	10.26	0.0016

Fisher LSD

	Exp. disturbance	No disturbance
Exp. disturbance		0.0002
No disturbance	0.0002	

Table 5.4 Results of ANCOVA to determine if any differences exist between 'experimental', 'fisher disturbed' and 'non disturbed' treatments for *C. kraussi* at Center Banks using carapace length as the covariate. Significant results were analysed with Fisher LSD.

	SS	df	MS	F	P
Length	32.5351	1	32.54	646.59	0.0001
Treatment	0.3939	2	0.20	3.91	0.0212

Fisher LSD

	Exp. disturbance	Fisher disturbance	No disturbance
Exp. disturbance		0.0204	0.0102
Fisher disturbance	0.0204		0.0001
No disturbance	0.0102	0.0001	

Effects of disturbance on fecundity and egg output

Expressed in terms of egg mass relative to body mass, fecundity was not influenced by treatment (Figure 5.6). When fecundity was compared between the 'experimental disturbed' and 'undisturbed' treatments at Bottelary, there was no significant differences between treatments (1-Way ANOVA, $F_{1,71} = 0.2800$, $P = 0.598$). Similarly when comparisons were done between the three treatments at Center Banks no significant differences were found ($F_{2,64} = 0.254$, $P = 0.778$).

For any particular treatment there were no significant differences in fecundity between sites (for the 'experimental disturbance treatment' between Bottelary and Center Banks, 1-Way ANOVA, $F_{1,49} = 0.924$, $P = 0.341$; for the 'undisturbed treatment' between Bottelary and Center Banks, $F_{1,69} = 2.082$, $P = 0.154$ and for 'fisher disturbance' between Center Banks and Klein Oesterwal, $F_{1,44} = 0.148$, $P = 0.702$).

The mean egg output (number of eggs produced/m²) was not significantly different between treatments at Bottelary (1-Way ANOVA $F_{1,72} = 0.0032$, $P = 0.955$) or Center Banks ($F_{2,64} = 0.576$, $P = 0.565$) (Figure 5.7). Within treatments, sites did differ ($P < 0.0001$ in all cases) with egg output being greatest at Center banks and least at Bottelary.

5.4 Discussion

Many authors have reported on changes in the habitat of prawns and other intertidal species caused by bait collection using a prawn pump (Wynberg & Branch 1991, 1994, 1997, Contessa & Bird 2004), trampling (Wynberg & Branch 1997), bait-digging for cockles (Jackson & James 1979) or 'raking' for cockles (Kaiser *et al.* 2001). Jackson & James (1979) found that cockles (*Cerastoderma edule* L.) declined drastically in response to bait digging. Digging caused heavy mortality of cockles and was most severe on smaller individuals. Wynberg & Branch (1994) reported that bait collecting for prawns is associated with sedimentary compaction and reductions of

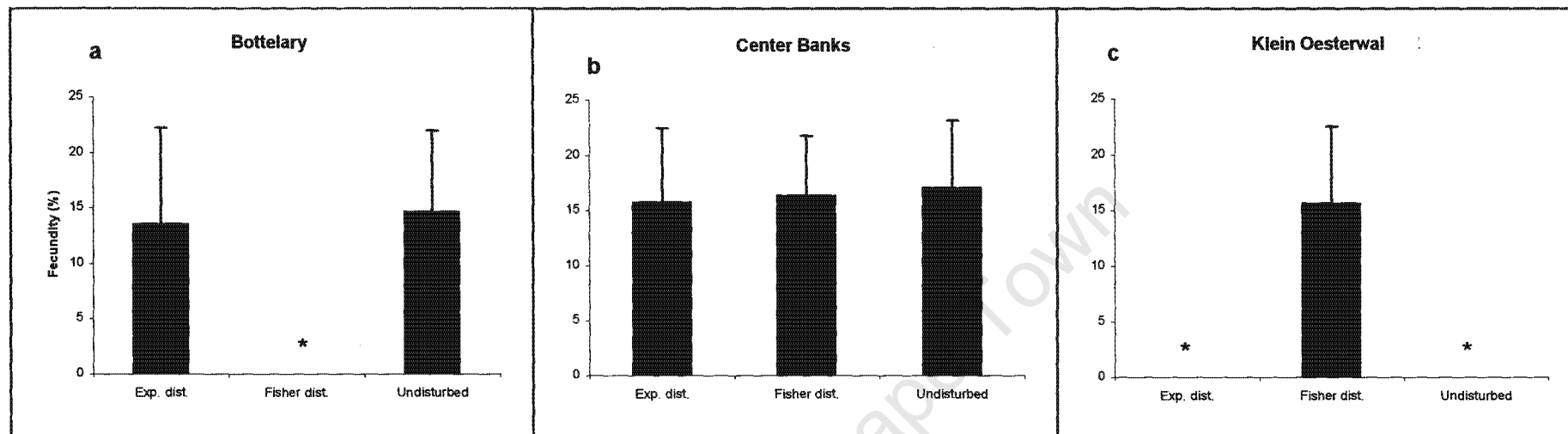


Figure 5.6 a, b, c Graphs showing fecundity for Bottelary (a), Center banks (b) and Klein Oesterwal (c) for the treatments measured at each site.

* Indicates no measurement.

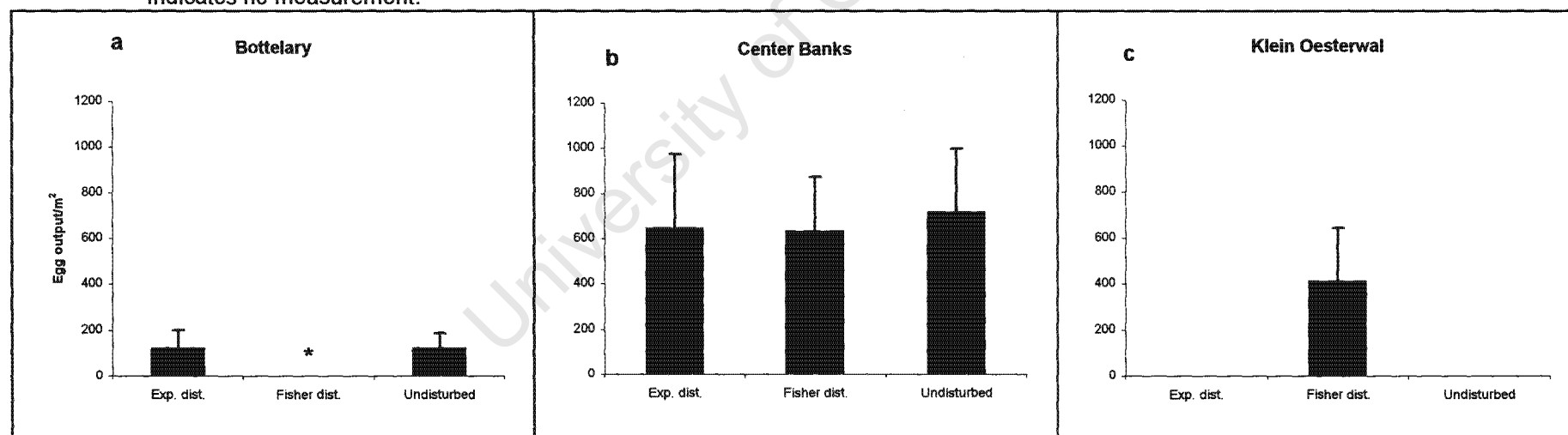


Figure 5.7 a, b, c Graphs showing egg output for Bottelary (a), Center banks (b) and Klein Oesterwal (c) for the treatments measured at each site.

* Indicates no measurement.

sandflat biota, including chlorophyll levels and meiofaunal and macrofaunal numbers. They also state that intensive pumping for bait may lead to anoxic conditions which are unfavourable for prawn survival. Further work on cockles by Kaiser *et al.* (2001) showed that 'raking' for cockles altered the sediment structure, although the effects on the habitat were reversed within one year. Contessa & Bird (2004) reported destruction of prawn burrows, compaction of sediment, reduced sediment porosity and more reducing conditions (up to depths of 20 cm) in sediments disturbed by pumping for bait. Begon *et al.* (1995) explain that the 'condition' of an animal is a reflection of its net response to environmental circumstances. Each species will have an optimal set of circumstances where it performs best. The effects of environmental conditions can be seen in reproduction, survival, respiration rate, metabolism and growth rate. Hanekom (1980) argues that the growth rate of *C. kraussi* is strongly influenced by environmental conditions, and that where conditions become altered for whatever reason e.g. current flow, this may effect the animals' growth and survival.

It is important to note that most organisms can survive over a wider range of conditions than those required for them to grow or reproduce. Taking the above into account it may be construed that the lower dry mass of prawns when exposed to physical disturbance reflects a deterioration of conditions.

Forbes (1973a) concluded that closing off burrows by physical destruction such as strong water or sand movement can result in the exclusion of *C. kraussi*. Wynberg & Branch (1994) showed that experimental harvesting of *C. kraussi* resulted in greater reductions in densities than would have been expected from the numbers of animals removed during experimentation. They attributed this to the disturbance and sediment compaction caused by the prawn-pumping and associated trampling.

Wynberg & Branch (1994) attempted to 'disentangle' the effects of prawn pumps and associated trampling, and showed that both types of disturbance caused reduction in prawn densities. They concluded that sucking with a prawn pump has almost the same effect as trampling on both the prawns and the associated biota of the sandflat. It must be noted that the experimental design in their experiments allowed for relatively intense disturbance, equivalent to about 100 sucks /12m², whereas I attempted to impose realistic levels of harvesting approximating the intensities recorded for bait-collecting fishers (Chapter 3).

Contessa and Bird (2004) found similar results for the ghost shrimp, *Trypaea australiensis* Dana, in Coronet Bay, Western Port, southern Australia and reported a reduction in shrimp density due to harvesting, and a slow recovery over the experimental period (six months).

Effect on densities

The above findings point to disturbance on sandflats causing a reduction in the densities of both targeted bait organisms and associated biota, which are slow to recover. In my experiment, I estimated the number of sucks taken by prawn collectors (bait collectors) each month, and used that value to impose a realistic regime of experimental harvesting of *C. kraussi*. However, despite my harvesting regime being less intense than that imposed by Wynberg & Branch (1994), I still recorded significantly reduced densities in the plots that were harvested relative to control plots (Figure 5.1).

Effects on body mass

There were substantial differences in the mean body mass of prawns at different sites with those at Bottelary being significantly smaller than at Center Banks. This was a simple reflection of the fact that prawns were smaller at Bottelary than elsewhere, and overshadowed significant differences that existed among treatments. However, when body mass was standardized by relating it to carapace

length and Analyses of Covariance undertaken, body mass relative to carapace length was significantly greater in control plots than in any of the disturbance plots (Figure 5.4). Thus, not only were densities reduced by disturbance but body mass relative to carapace length was also reduced.

Effects on fecundity and egg output

Working in Swartkops Estuary, Hanekom (1980) found that the mean and maximum number of eggs carried by female *C. kraussi* of a given carapace length were lower than in previous studies there by Forbes (1973a). He attributed the difference to the extension of a bridge in the study area which would have altered tidal flow and therefore food transport, possibly resulting in lower reproductive output. Baird *et al.* (1980) similarly argue that marinas alter water flow and influence prawns.

I could detect no differences in fecundity (egg mass relative to body mass) between either treatments or sites (Figure 5.6). When egg output was considered in terms of number of eggs produced per unit area, there were again no significant differences among treatments, but there were substantial differences among sites (Figure 5.7). This latter difference was entirely attributable to the fact that animals at Bottelary were smaller than those at other sites. When an Analysis of Covariance was applied (using dry body mass as the covariate), there was no difference in fecundity among sites, indicating that animal size at the different sites played the major role in dictating differences in reproductive output.

The effects of prawn pumping are thus not manifested in a reduction of brood size per female, or even in terms of reduced output per unit area (Figure 5.6 & 5.7). Rather, harvesting influenced overall densities (Figure 5.1) and reduced body mass relative to length (Figure 5.5). Curiously, harvesting had no significant effect on the densities of ovigerous females (Figure 5.2) despite

reducing overall density. One possibility is that reductions in density due to harvesting reduced competition, leading to compensatory increases in the proportion of females bearing eggs. When the sex ratios of the animals were compared between sites (Table 5.5), I found more females than males at all the study sites. The differences among sites found in chapter 2 were also not reflected here and there did not appear to be any differences among treatments. Thus, I could not effectively explain why the overall densities were affected by disturbance but the overall densities of females seemed unaffected.

Table 5.5 The percentages of male, female and juvenile prawns at each of 3 sites for the respective treatments.

Number	Site & treatment	(n)	Male	Female	M:F ratio	Juvenile
1	Bottelary exp. dist.	105	15	38	1:2.5	52
2	Bottelary undist.	247	21	59	1:2.8	167
3	Center banks exp. dist.	128	23	55	1:2.4	50
4	Center Banks fisher dist.	212	18	36	1:2.0	158
5	Center banks undist.	271	19	59	1:3.1	193
6	Klein Oesterwal fisher dist.	180	16	58	1:3.6	106

In addition to these treatment effects, there were striking differences in size composition and body mass relative to length among sites, pointing to background differences in environmental conditions that have repercussions for total egg output per unit area.

In short, bait-collecting reduced overall densities and mass relative to length but had no effect on fecundity or egg output/m², and there were strong site effects on mean mass and egg output.

CHAPTER 6

AN EXPERIMENTAL STUDY OF POTENTIAL COMPETITION BETWEEN *CALLIANASSA KRAUSSI* AND *UPOGEBIA AFRICANA* AT TWO SITES WITH DIFFERENT SEDIMENTARY CHARACTERISTICS

6.1 Introduction

Thalassinidean burrowing prawns form an important part of many shallow temperate and tropical marine benthic communities (Suchanek 1983, Posey *et al.* 1991, Cretchley 1996, Siebert 2003) and strongly affect both sediment composition and local community structure (Aller & Dodge 1974, Aller *et al.* 1983, Suchanek 1983, Koike & Mukai 1983, Branch & Pringle 1987, Rowden *et al.* 1998, Berkenbusch & Rowden 2003, Webb & Eyre 2004). In general, callianassid prawns are burrowers and live within relatively impermanent burrow systems where they deposit-feed (Forbes 1973a, Aller & Dodge 1974). Where callianassids are abundant, bioturbation (biological disturbance of sediment) arising from their burrowing activities may reduce numbers of tube-dwelling sedentary organisms (Aller & Dodge 1974, Gray 1974, Peterson 1977, Tamaki 1988, Siebert 2003). *Callianassa* species are burrowing deposit feeders and their activity results in continual reworking of near-surface sediments, altering their composition and causing them to be more easily resuspended and eroded (Aller & Dodge 1974, Suchanek 1983, Tamaki 1988, De Vaugelas & Buscail 1990, Stamhuis *et al.* 1998). These bioturbating activities may affect other macrobenthos either positively or negatively, or insignificantly (Posey 1986). More specifically, bioturbation by *Callianassa* spp may clog the filtering apparatus of filter-feeders such as *Upogebia* spp. and result in burrow destruction (Rhoads & Young 1970, Suchanek 1983). Siebert & Branch (2005a) found that in Langebaan Lagoon, the seagrass *Zostera capensis* and the sand prawn *Callianassa kraussi* are mutually exclusive of each other, because the root

networks of *Zostera* may exclude *Callianassa* spp. by obstructing its burrowing activities, whereas bioturbation of *Callianassa* spp. may result in resuspension of sediments, smothering and fragmenting seagrass beds (Homziak *et al.* 1982, Suchanek 1983, Brenchley 1982, Valentine *et al.* 1994, Townsend & Fonseca 1998, Rowden *et al.* 1998). The beds of *Z. capensis* show a patchy distribution on the high shore in Langebaan Lagoon and *C. kraussi* dominates the rest of the shore. *Upogebia africana* requires stable sediments to construct its permanent U-tubes in which it filter-feeds (Branch & Branch 1984), as has been described for other *Upogebia* species (Dworschak 1983) and it achieves these conditions through co-habitation with *Z. capensis* (Siebert & Branch 2005a). In Langebaan Lagoon *C. kraussi* contributes more than any other species to bioturbation, accounting for 94% of the sediment turnover totaling 4.42 tonnes wet mass.m⁻².y⁻¹. The effects of callianassids on habitat structure are so profound that Berkenbusch & Rowden (2003) have classed them as ecosystem engineers.

Mudprawns (*Upogebia* spp.) occur commonly in temperate shallow waters, but their effects on the distribution and abundance of other species have been poorly studied compared to the work on callianassids (Posey *et al.* 1991). The species of *Upogebia* that have been studied are primarily suspension feeders that live within relatively permanent burrow systems whose walls are hardened by a glandular secretion (Hill 1967, Posey *et al.* 1991). Burrowing activities of *Upogebia* spp. seem restricted primarily to periods of actual burrow construction and expansion, such as occur after moulting (Posey *et al.* 1991). Unlike callianassids, they do not burrow continuously to feed.

Brenchley (1981, 1982) studied the effects of a number of different burrowers, including *Upogebia pugettensis*, on abundances of selected tube-dwelling species in a short term laboratory experiment. Her experiments, together with correlative field data, showed that *U. pugettensis* and *Callianassa californiensis* may have functionally similar effects on community composition despite their

differences in burrowing activity. Because these experiments were of relatively short duration and conducted within laboratory aquaria, they may have over-emphasized bioturbation by *Upogebia*, because under these conditions the mudprawns would have been in the process of actively excavating new burrows and the associated sediment resuspension would have been confined to the relatively small space of the aquarium. In contrast to this, Bird (1982, cited in Posey *et. al* 1991) compared infaunal macrobenthos in *U. pugettensis* and *C. californiensis* beds, and found higher abundances of several tube-dwelling polychaete and crustacean species in the presence of *Upogebia*.

Posey *et al.* (1991) conducted a transplant/exclusion experiment to examine the effects of *U. pugettensis* on the abundance of other macro-infauna in a Pacific Northwest tideflat. They found that several numerically dominant, sedentary crustaceans and polychaetes were less abundant in the presence of *U. pugettensis* as compared to treatments where the mud prawn was absent. However, they found that the overall pattern of faunal response to *U. pugettensis* was similar to *C. californiensis*, which was unexpected given the different burrowing and feeding habits of these two crustaceans.

Peterson (1980) states that soft bottom habitats are difficult to manipulate in the field because infauna cannot be counted or removed without excavation. He found that such removal by digging/excavation destroys sedimentary structures and selectively eliminates many delicate taxa, thus limiting any subsequent experiment to an impoverished biota in an unnatural environment.

A fundamental characteristic of interspecific competition is that individuals of one species suffer a reduction in reproductive capacity (fecundity), survivorship or growth as result of resource exploitation or interference by individuals of another species. Interspecific competition can affect the population dynamics of competing species in many ways (Byers 2000). These dynamics, in turn, can influence the species' distributions and their evolution. Furthermore, competing species may either exclude one

another from particular habitats so that they do not coexist, or may coexist, perhaps by using the habitat in slightly different ways. In interspecific competition, the distinction can be made between interference and exploitation competition. In the latter, individuals interact with each other indirectly, responding to a resource level that has been depressed by the activity of the competitors. In the former, one species “interferes” with the occupation of by another species, excluding it (Begon *et. al* 1995).

The basic approach to the study of interspecific competition is the same for any ecological system. One attempts to vary either the density of a presumed competitor or the abundance of a potentially limited resource. To evaluate the outcome, the effects of the manipulation can be examined in terms of growth, mortality, recruitment, migration or reproductive effort. Most studies of interspecific competition involve only two or sometimes three competing species.

In this study, the potential effects of *Callinassa kraussi* and *Upogebia africana* on each other were investigated experimentally.

The two species were held in cages, either separately or together, and the effects of these treatments evaluated by measurements of survivorship and condition. The effect of depth was investigated by using cages of two different depths, and the experiment was undertaken at two sites with different sedimentary properties. From my field observations (Chapter 2), my expectation was that I would find both site and treatment effects. I hypothesised that at Bottelary, where the sediment is not as fine as at Geelbek, that survival of *U. africana* would be less than at Geelbek, and also less in treatments where it was mixed with *C. kraussi* than when it was held alone. At Geelbek, where the two species naturally co-occur, I expected equal survivorship of both species and that *C. kraussi* would have no effect on the survival of *U. africana*.

6.2 Materials and methods

6.2.1 Experimental design

I used cages that prevented immigration and emigration, to run inclusion experiments. These had two main objectives: first, to force *U. africana* and *C. kraussi* to coexist, to test for any interspecific competition between the two species; second to test this interaction at different depths and sites. I performed the experiment at two different sites to test for the effects of different habitats on survival. In each case survivorship and “condition” (mass relative to length) were used as measures of interspecific competition. To achieve this, 10 individuals of each species were placed in cages together (‘mixed’). As a control, 20 individuals of either species were held alone in cages (‘alone’). The cage construction allowed the organisms to occupy one of two available depths, namely 10 cm or 30 cm. Each treatment was replicated three times in each of the two areas.

From the preliminary analysis of the lagoon, two sites, Bottelary and Geelbek, were chosen, as both *C. kraussi* and *U. africana* occur there naturally. I have previously shown (Chapter 2) that the first site, Bottelary, has low overall densities of *U. africana* and high densities of *C. kraussi* in the sandflat there and that high densities of *U. africana* are limited to high-shore beds of *Zostera capensis*. At Geelbek, *U. africana* is more abundant and *C. kraussi* is also well represented. Conditions are more muddy at Geelbek, whereas Bottelary represents sandy sediment.

6.2.2 Cages

Cages were cylinders 25 cm in diameter and 10 or 30 cm deep. They were made from a steel frame covered with a soft 2-mm plastic mesh. To prevent damage by predators, the soft mesh was reinforced and covered by stiff plastic 5-mm mesh. A bottom seal made of the same mesh was stitched to the bottom of the cage, preventing entry and exit of all animals bigger than 2 mm. Lids for the cages were

made of the same mesh and were made to size so that they fitted snugly over the top of the cage but could be lifted to establish the treatments and to monitor them.

6.2.3 Experimental application

At each of the two sites the cages were randomly positioned approximately in the mid-shore, about 100 m below the spring high-water level. The cages were placed in the sandflats free of any vegetation such as *Z. capensis* or *Gracilaria verrucosa*. To install the cages, a corer slightly larger than the cages was inserted into the sand. The sand inside the corer was dug out and sieved through a 2-mm sieve to remove any sandprawns or mudprawns. The cage was then placed inside the corer and the sieved sediment was deposited back into the cage. Once each cage had been inserted and filled, the corer was removed, lids installed, and the cages were left for 5 days to allow the sediment to stabilise.

Figure 6.1 summarises the sequence of establishment, maintenance and sampling of the cages. After 5 days, *U. africana* was first introduced on its own into both its ‘alone’ and ‘mixed’ cages. At the same time, *C. kraussi* was established on its own in its ‘alone’ cages. This was termed the ‘pre-establishment phase’. During this phase, which lasted 5 days, all dead sand or mudprawns observed on the surface of the sediment in the cages were counted daily, removed and replaced with living individuals. Initial mortalities were high due to the disturbance involved in introducing animals to the cages. In particular, *U. africana* struggled to establish itself and hence it was allowed time to establish itself alone before *C. kraussi* was added to the ‘mixed’ cages after five days. After *C. kraussi* had been introduced into the ‘mixed’ cages, any dead prawns appearing on the sediment surface were replaced for the next three days. This combined period of 8 days ended the “pre-establishment” phase.

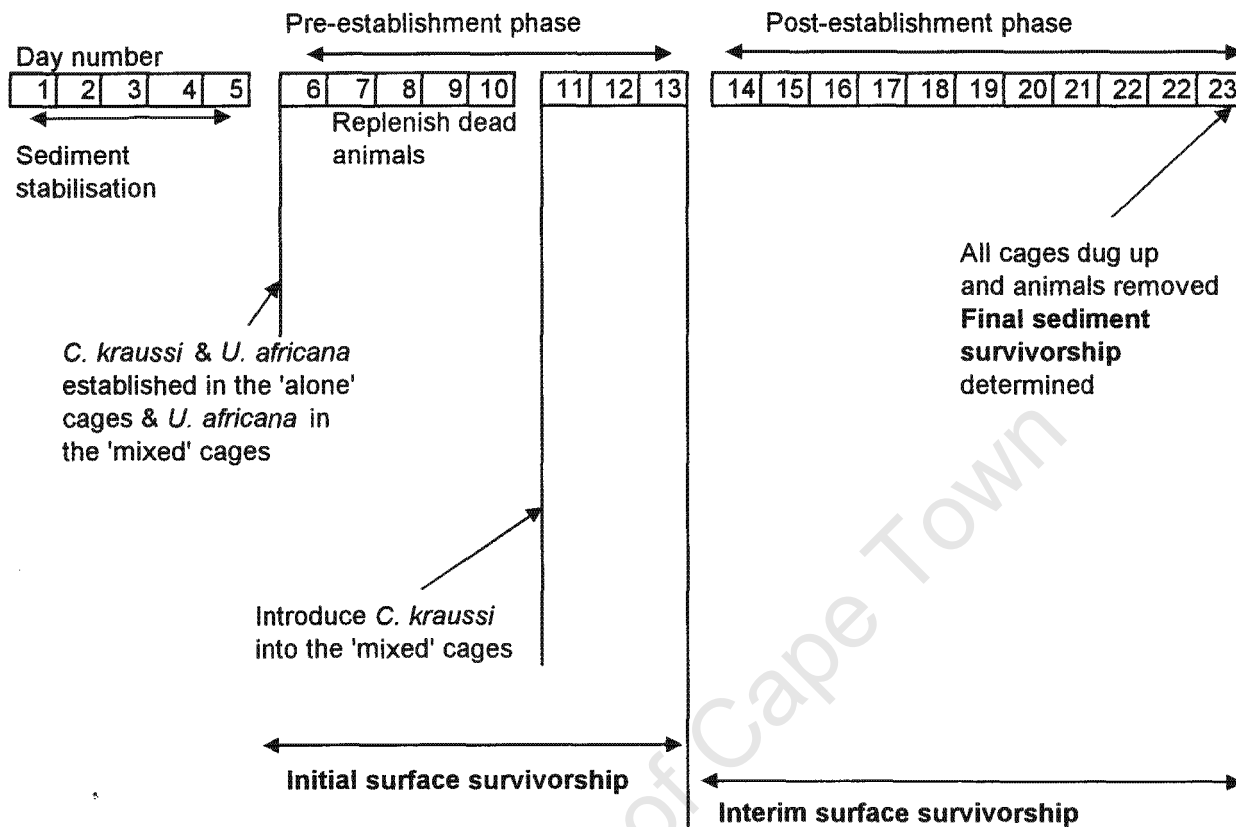


Figure 6.1 Diagram showing the various phases of the experiment and the timing when measurements were made of different survivorship values.

The subsequent stage of the experiment involved a 10-day “post-establishment phase”, during which no further replenishment of dead prawns took place, but any dead prawns appearing on the sediment surface were recorded and removed. At the end of this period, the contents of the cages were dug up and sieved through a 2-mm sieve, and all prawns were removed and preserved in 8% formalin. The carapace lengths of all surviving individuals were measured and they were then dried at 55°C and their dry masses measured.

6.2.4 Survivorship

The experimental design allowed survivorship of the species to be assessed in three ways, namely ‘initial surface survivorship’, ‘interim surface survivorship’ and ‘final sediment survivorship’. Initial surface survivorship was calculated for the pre-establishment phase and relied on counts of dead animals appearing on the surface of the sediment. The procedure assumed that all animals that died did appear on the surface and that none were lost before being counted. Interim surface survivorship relied on the same procedure and same assumptions, but covered the post-establishment phase. Final sediment survival did not rely on these assumptions as the sediment was dug up and a count obtained of the remaining survivors.

Initial surface survivorship was expressed as the total number of animals surviving in each cage divided by the total number of animals that has been introduced in the pre-establishment phase (including replenished animals). The assumption was made that any prawns that had been introduced and not been found dead on the surface had survived. Interim surface survivorship constituted the number of animals calculated to be surviving in each cage divided by the number presumed to have been established at the start of the post-establishment phase. Final sediment survivorship was

calculated as the total number of live animals dug up in each cage divided by the number of animals assumed to be present at the start of the post-establishment phase.

Equations for calculations of survivorship are as follows:

Initial surface survivorship = $(a - b + c)/(a + c)$ during the pre-establishment phase

Interim surface survivorship = $(d - b) / d$ during the post-establishment phase

Final sediment survivorship = e/d at the end of the experiment

where:

a = number of animals introduced initially

b = number of animals dying and found on the surface

c = number of animals introduced to replenish those dying in the pre-establishment phase

d = numbers of animals assumed to be established at the start of the post-establishment phase (20 in 'alone' cages and 10 of each species in 'mixed' cages)

e = number of living animals dug up at the end of the post-establishment phase.

6.2.5 The effect on the condition

Thirty 'control' animals were collected from the natural sediment at each site, their carapace lengths measured and their dry biomass determined. The same measurements were made for all living animals removed from the cages at the end of the experiment. Regressions were constructed for dry body mass vs carapace length and were compared among treatments and with control animals using Analysis of Covariance (ANCOVA) (Dytham 2003), with treatment as grouping variable and carapace length as a covariate.

6.2.6 Statistical analysis

Levene's test and Komolgorov-Smirnov one-sample test were employed to test data for normality and homogeneity of variances (alpha set at 0.05). When necessary, data were arcsin transformed to attempt to achieve normality and equality of variance. Nonparametric statistical tests were applied when normality could not be achieved.

The differences between survivorship of *C. kraussi* and *U. africana* within each treatment were assessed using Mann-Whitney nonparametric tests (Zar 1999).

Differences among treatments in survivorship for each species were analysed using a Three-Way ANOVA with survivorship as the dependant factor, and cage depth (10 cm or 30 cm), treatment ('alone' or 'mixed') and site (Bottelary or Geelbek) as independent fixed factors. Site was treated as a fixed factor as I had *a priori* expectations of different outcomes related to differences in sediment at the two sites.

6.3. Results

Initial Surface Survivorship

Figure 6.2a shows initial surface survivorship for the two sites for both *C. kraussi* and *U. africana*, and Table 6.1 shows the results of Mann-Whitney tests to determine if differences existed between *C. kraussi* and *U. africana*. At Bottelary, all but one treatment ('mixed' 30 cm depth) showed that the survivorship for *C. kraussi* was significantly higher than for *U. africana*. At Geelbek no significant differences were found between the two species.

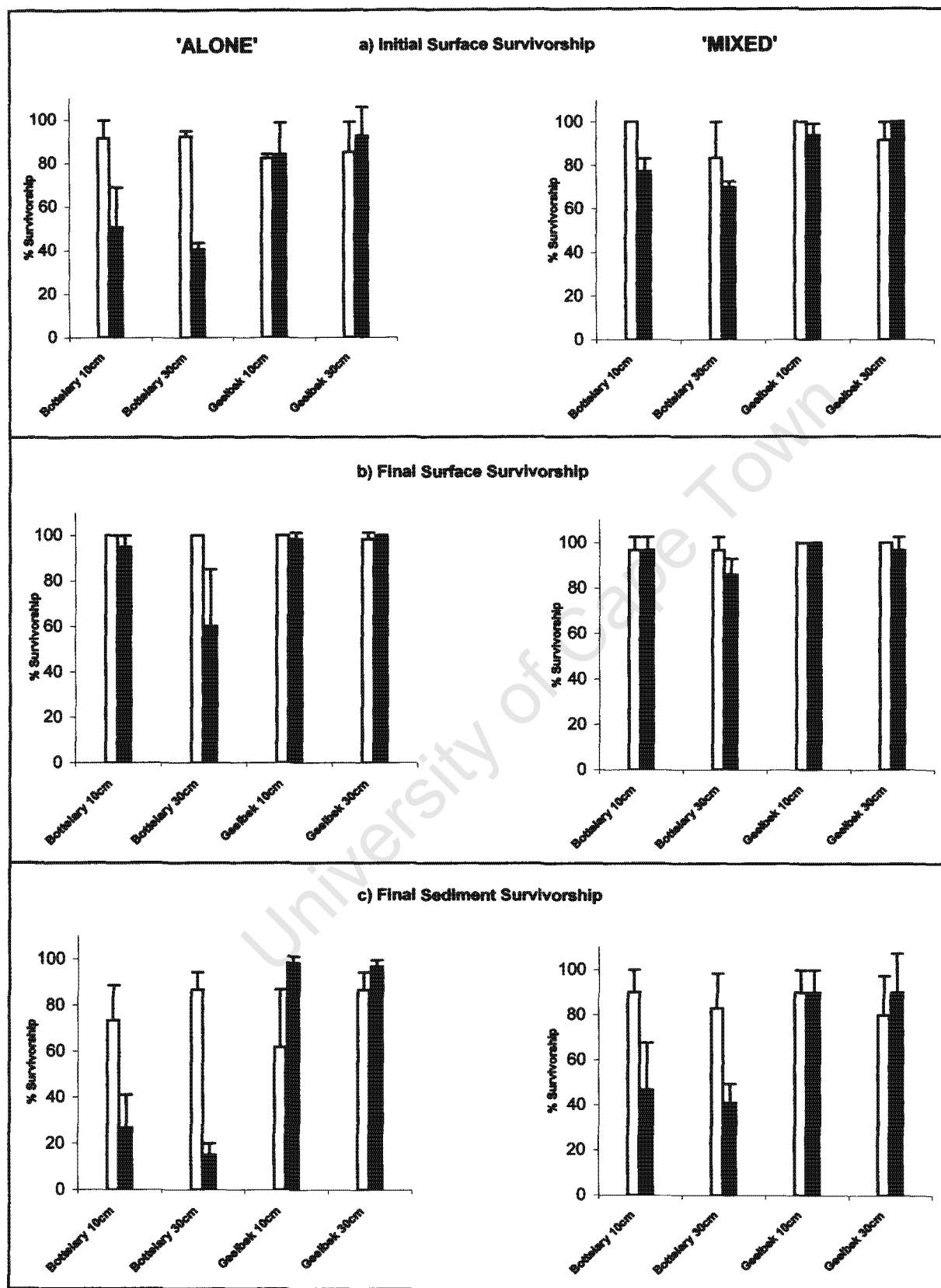


Figure 6.2 Graphs showing Initial and final surface survival and final sediment survival for *C. kraussi* and *U. africana* for two sites (Bottelary & Geelbek), two treatments ('alone' & 'mixed') and two depths (10 cm & 30 cm). Data represents means + 1 SD.

Table 6.1 Mann-Whitney U tests comparing *C. kraussi* and *U. africana* initial surface survivorship within treatments at Bottelary and Geelbek.

<i>Bottelary</i>	U	Mann-Whitney U Z	p-level	Difference between species
10 cm 'alone' cages	0.00	1.9639	0.0495	Significant
10 cm 'mixed' cages	0.00	1.9639	0.0495	Significant
30 cm 'alone' cages	0.00	1.9639	0.0495	Significant
30 cm 'mixed' cages	2.50	0.8728	0.3827	Not significant
<i>Geelbek</i>	U	Z	p-level	
10 cm 'alone' cages	3.50	0.4364	0.6625	Not significant
10 cm 'mixed' cages	1.50	1.3093	0.1904	Not significant
30 cm 'alone' cages	2.00	-1.0910	0.2752	Not significant
30 cm 'mixed' cages	1.50	-1.3093	0.1904	Not significant

Table 6.2 Three-Way ANOVA of the initial surface survival of *C. kraussi* between sites, depths and cage treatments. Significant results within factors were further analysed using Tukey HSD test.

	df effect	MS effect	df Error	MS Error	F	p
Site	1	43.8	16	95.5	0.459	0.5079
Treatment	1	675.9	16	95.5	7.078	0.0171
Depth	1	392.7	16	95.5	4.113	0.0595
Site*Treatment	1	191.4	16	95.5	2.005	0.1759
Site*Depth	1	49.5	16	95.5	0.518	0.4819
Treatment*Depth	1	459.4	16	95.5	4.811	0.0433
Site*Treatment*Depth	1	0.0	16	95.5	0.000	0.9852
Tukey HSD						
Treatment*Depth		Alone 10 cm	Alone 30 cm	Mixed 10 cm	Mixed 30 cm	
Alone 10 cm			0.9995	0.0163	0.9693	
Alone 30 cm		0.9995		0.0206	0.9872	
Mixed 10 cm		0.0163	0.0206		0.0394	
Mixed 30 cm		0.9693	0.9872	0.0394		

Table 6.3 Three-Way ANOVA of the initial surface survival of *U. africana* between sites, depths and cage treatments. Significant results within factors were further analysed using Tukey HSD test.

	df effect	MS effect	df Error	MS Error	F	p
Site	1	4370.76	16	125.88	34.7228	< 0.0001
Treatment	1	693.16	16	125.88	5.5067	0.0321
Depth	1	132.73	16	125.88	1.0544	0.3198
Site*Treatment	1	213.13	16	125.88	1.6932	0.2116
Site*Depth	1	617.12	16	125.88	4.9026	0.0417
Treatment*Depth	1	42.45	16	125.88	0.3373	0.5695
Site*Treatment*Depth	1	27.18	16	125.88	0.2159	0.6484
Tukey HSD						
Site*Depth		Bottelary 10 cm	Bottelary 30 cm	Geelbek 10 cm	Geelbek 30 cm	
Bottelary 10 cm			0.8350	0.0817	0.0010	
Bottelary 30 cm		0.8350		0.0160	0.0003	
Geelbek 10 cm		0.0817	0.0160		0.1417	
Geelbek 30 cm		0.0010	0.0003	0.1417		

When comparing sites, treatments and depths for *C. kraussi* (Table 6.2) significant differences ($P < 0.05$) were found between treatments and for the treatment*depth interaction. Overall, survivorship was higher in the 'mixed' treatment applications ($93.7\% \pm 21.07$) than for the 'alone' treatment ($87.7\% \pm 16.27$) but Tukey tests showed that this was only significant in the 10 cm cages. When comparing the treatment*depth interaction, treatment was significant at 10 cm but not at 30 cm.

When the same comparisons were done for *U. africana*, the most significant differences ($P < 0.0001$) were found between sites, but there were also significant treatment and site*depth effects (Table 6.3). Overall, survival was higher at Geelbek ($90.0\% \pm 24.81$) than at Bottelary ($59.9\% \pm 34.26$). Survival was also higher in the 'mixed' treatment applications ($82.7\% \pm 26.46$) than for the 'alone' applications ($66.8\% \pm 14.45$). When examining the site*depth interaction, survival at Geelbek was higher than Bottelary at the 30 cm depth, but not at 10 cm depth.

Interim surface survivorship

Figure 6.2b shows interim surface survivorship for both *C. kraussi* and *U. africana*, and Table 6.4 shows the results of Mann-Whitney tests comparing the two species. Survival was significantly less for *U. africana* than for *C. kraussi* at Bottelary for both 30 cm treatments but not for 10 cm. At Geelbek no significant differences were found between the species.

For *C. kraussi* there were no significant effects of site, depth or treatment (Table 6.5, $P > 0.05$). Survival was consistently high, spanning 96.7 - 100%.

Significant differences were found for *U. africana* between sites and among treatments (Table 6.6). Between sites, survival was higher at Geelbek ($98.8\% \pm 3.12$) than at Bottelary ($84.4\% \pm 19.17$) but, as

Table 6.4 Mann-Whitney U tests comparing *C. kraussi* and *U. africana* interim surface survivorship within treatments at Bottelary and Geelbek.

<i>Bottelary</i>	Mann-Whitney U			Difference between species
	U	Z	p-level	
10 cm 'alone' cages	1.50	1.31	0.19	Not significant
10 cm 'mixed' cages	2.50	0.87	0.38	Not significant
30 cm 'alone' cages	0.00	1.96	0.049	Significant
30 cm 'mixed' cages	0.00	1.96	0.049	Significant

<i>Geelbek</i>	U	Z	p-level	
10 cm 'alone' cages	3.00	0.66	0.51	Not significant
10 cm 'mixed' cages	4.50	0.00	n/a	Not significant
30 cm 'alone' cages	3.00	-0.66	0.51	Not significant
30 cm 'mixed' cages	3.00	0.66	0.51	Not significant

n/a = not applicable, Z = 0

Table 6.5 Three-Way ANOVA of the interim surface survivorship of *C. kraussi* between sites, depths and cage treatments.

	df effect	MS effect	df Error	MS Error	F	p
Site	1	1.3	16	21.1	0.060	0.8097
Treatment	1	1.3	16	21.1	0.060	0.8097
Depth	1	1.3	16	21.1	0.060	0.8097
Site*Treatment	1	41.0	16	21.1	1.940	0.1827
Site*Depth	1	41.0	16	21.1	1.940	0.1827
Treatment*Depth	1	41.0	16	21.1	1.940	0.1827
Site*Treatment*Depth	1	1.3	16	21.1	0.060	0.8097

Table 6.6 Three-Way ANOVA of the interim surface survivorship of *U. africana* between sites, depths and cage treatments. Significant results within factors, were further analysed using Tukey HSD test.

	df effect	MS effect	df Error	MS Error	F	p
Site	1	1659.0	16	80.4	20.626	0.0003
Treatment	1	771.3	16	80.4	9.590	0.0069
Depth	1	143.0	16	80.4	1.778	0.2011
Site*Depth	1	651.5	16	80.4	8.099	0.0117
Site*Treatment	1	201.8	16	80.4	2.509	0.1327
Treatment*Depth	1	1.6	16	80.4	0.019	0.8910
Site*Treatment*Depth	1	197.3	16	80.4	2.454	0.1368

Tukey HSD
Site*Depth

	Bottelary 10 cm	Bottelary 30 cm	Geelbek 10 cm	Geelbek 30 cm
Bottelary 10 cm		0.0035	0.6363	0.7396
Bottelary 30 cm	0.0035		0.0005	0.0006
Geelbek 10 cm	0.6363	0.0005		0.9980
Geelbek 30 cm	0.7396	0.0006	0.9980	

reflected by the site*depth interaction, the difference was only significant in the 30 cm cages. Among treatments, the 'mixed' applications had higher survival ($94.8\% \pm 7.20$) than the 'alone' treatment ($88.3\% \pm 20.37$).

Final Sediment Survivorship

Figure 6.2c shows final sediment survivorship for the two sites for both species. Mann-Whitney tests (Table 6.7) indicated that at Bottelary, *C. kraussi* had a significantly higher survival than *U. africana* at all depths and treatments ($P = 0.049$), but at Geelbek, there was no significant difference between the two species except for the 10 cm 'alone' cages. This was the only time that differences emerged between species at Geelbek, and the only circumstance in which survival of *U. africana* exceeded that of *C. kraussi*.

For *C. kraussi*, final sediment surface survival was never significantly different between sites, treatments or depths (Table 6.8).

When the same comparison was done for *U. africana* (Table 6.9) there were highly significant differences between sites, with survival at Geelbek ($93.8\% \pm 9.56$) being substantially greater than at Bottelary ($32.6\% \pm 17.28$). Treatment had no significant effect. The fact that site had an effect at 10 cm but not 30 cm accounted for the site*depth interaction.

Combining the three measures of survivorship

Considering all three measures of survivorship, and taking into account the fact that final sediment survivorship is likely to be the most accurate measure, several trends emerge. First *C. kraussi* survival was generally unaffected by site, treatment or depth. Second, there were strong site effects for *U.*

Table 6.7 Mann-Whitney U tests comparing *C. kraussi* and *U. africana* mean final sediment survivorship within treatments at Bottelary and Geelbek.

Bottelary	Mann-Whitney U			Difference between species
	U	Z	p-level	
10 cm "alone" cages	0.00	1.96	0.049	Significant
10 cm "mixed" cages	0.00	1.96	0.049	Significant
30 cm "alone" cages	0.00	1.96	0.049	Significant
30 cm "mixed" cages	0.00	1.96	0.049	Significant

Geelbek	U	Z	p-level	
10 cm "alone" cages	0.00	-1.96	0.05	Significant
10 cm "mixed" cages	4.50	0.00	1.00	Not Significant
30 cm "alone" cages	1.00	-1.53	0.13	Not Significant
30 cm "mixed" cages	3.00	-0.65	0.51	Not Significant

Table 6.8 Three-Way ANOVA of the final sediment survivorship of *C. kraussi* between sites, depths and cage treatment.

	df	MS	df	MS	F	p-level
	Effect	Effect	Error	Error		
Site	1	20.0	16	188.4	0.170	0.686
Treatment	1	462.7	16	188.4	0.391	0.541
Depth	1	54.8	16	188.4	2.733	0.118
Site*Treatment	1	20.0	16	188.4	0.058	0.813
Site*Depth	1	20.0	16	188.4	0.058	0.813
Treatment*Depth	1	619.6	16	188.4	2.983	0.103
Site*Treatment*Depth	1	20.0	16	188.4	0.170	0.686

Table 6.9 Three-Way ANOVA comparing the final sediment survivorship of *U. africana* between sites, depths and cage treatments. Significant differences are shown in bold.

	df	MS	df	MS	F	p-level
	Effect	Effect	Error	Error		
Site	1	12763.25	16	119.5	106.85	0.001
Treatment	1	54.54	16	119.5	0.46	0.509
Depth	1	97.53	16	119.5	0.82	0.380
Site*Treatment	1	47.94	16	119.5	0.40	0.535
Site*Depth	1	675.01	16	119.5	5.65	0.030
Treatment*Depth	1	67.47	16	119.5	0.56	0.463
Site*Treatment*Depth	1	3.51	16	119.5	0.03	0.866

Tukey HSD

		Bottelary	Bottelary	Geelbek	Geelbek
		10 cm	30 cm	10 cm	30 cm
Site*Depth	Bottelary 10 cm		0.7917	0.0002	0.0002
	Bottelary 30 cm	0.7917		0.0002	0.0002
	Geelbek 10 cm	0.0002	0.0002		1.0000
	Geelbek 30 cm	0.0002	0.0002	1.0000	

africana, with survival at Bottelary always being less than at Geelbek. Third, treatment effects for *U. africana* were always absent or much weaker than site effects, and when they did exist, survival of *U. africana* was greater in ‘mixed’ than ‘alone’ treatments. Overall, no direct competitive effect of *C. kraussi* on *U. africana* could be detected.

‘Condition’ measured as mean dry mass

Figures 6.3 & 6.4 show regression curves for carapace length against dry body mass for animals that survived the cage experiment and for ‘control’ animals collected from unmanipulated background sediment.

For *C. kraussi* at Bottelary the ‘alone’ 10 cm treatment was the only one in which mass was significantly different from the control animals (Figure 6.3a; Table 6.10a). Although not significantly different, other caged treatments also had lower mean masses than the control animals.

At Geelbek the control animals’ mean dry mass was significantly greater than that of two of the four caged treatments (Figure 6.3b; Table 6.10b). Thus, caging had an effect on mass (standardized to take into account size). Added to this, at Geelbek, there were significant differences between the ‘alone’ and ‘mixed’ treatments, with alone treatments having lower mean mass – the reverse of what would be predicted if interspecific competition is important.

When comparisons for *C. kraussi* were made between sites, no significant differences in mass ever emerged for any given treatment (ANCOVA followed by Fisher LSD; $P > 0.07$ in all cases).

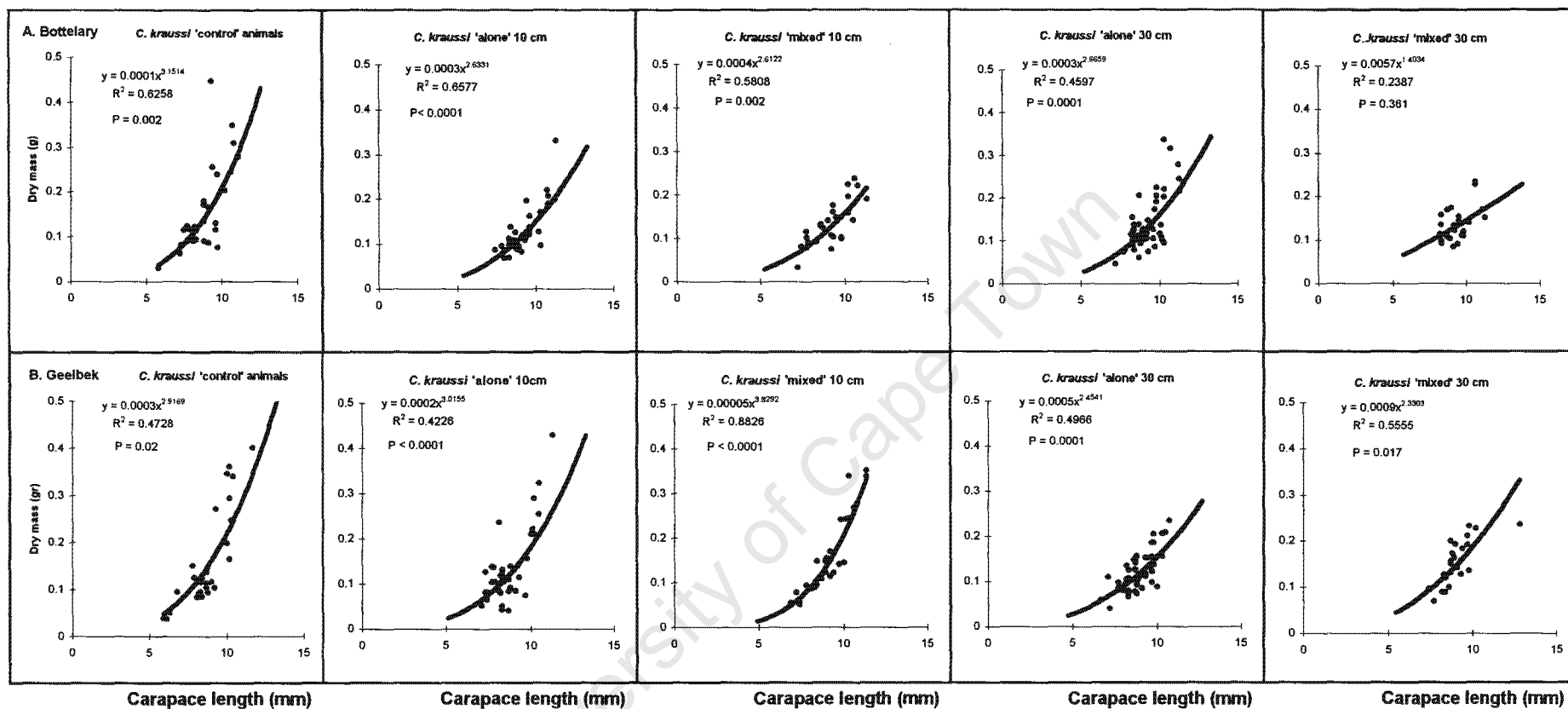


Figure 6.3 Regressions of the mean dry body mass vs carapace length for *C. kraussi* at Bottelary (A) and Geelbek (B). The first graph shows the 'control' animals.

Table 6.10 Results of ANCOVA to determine if any differences exist between the mass of treatment & control animals for *C. kraussi*, with carapace length as the covariate.
Significant results were analysed with Fisher LSD.

A. Bottelary

	SS	d.f.	MS	F	p
Carapace length	0.1444	1	0.1444	193.0005	0.0001
Treatment & group	0.0118	4	0.0029	3.9334	0.0044

Fisher LSD

	Control animals	10 cm alone	10 cm mixed	30 cm alone	30 cm mixed
Control animals		0.0268	0.1735	0.2466	0.5983
10 cm alone	0.0268		0.4971	0.2019	0.1317
10 cm mixed	0.1735	0.4971		0.6861	0.4382
30 cm alone	0.2466	0.2019	0.6861		0.6218
30 cm mixed	0.5983	0.1317	0.4382	0.6218	

B. Geelbek

	SS	d.f.	MS	F	p
Carapace length	0.2098	1	0.2098	182.4454	0.0001
Treatment & group	0.0164	4	0.0041	3.5732	0.0080

Fisher LSD

	Control animals	10 cm alone	10 cm mixed	30 cm alone	30 cm mixed
Control animals		0.0366	0.8746	0.0068	0.6939
10 cm alone	0.0366		0.0284	0.5945	0.0181
10 cm mixed	0.8746	0.0284		0.0053	0.8142
30 cm alone	0.0068	0.5945	0.0053		0.0033
30 cm mixed	0.6939	0.0181	0.8142	0.0033	

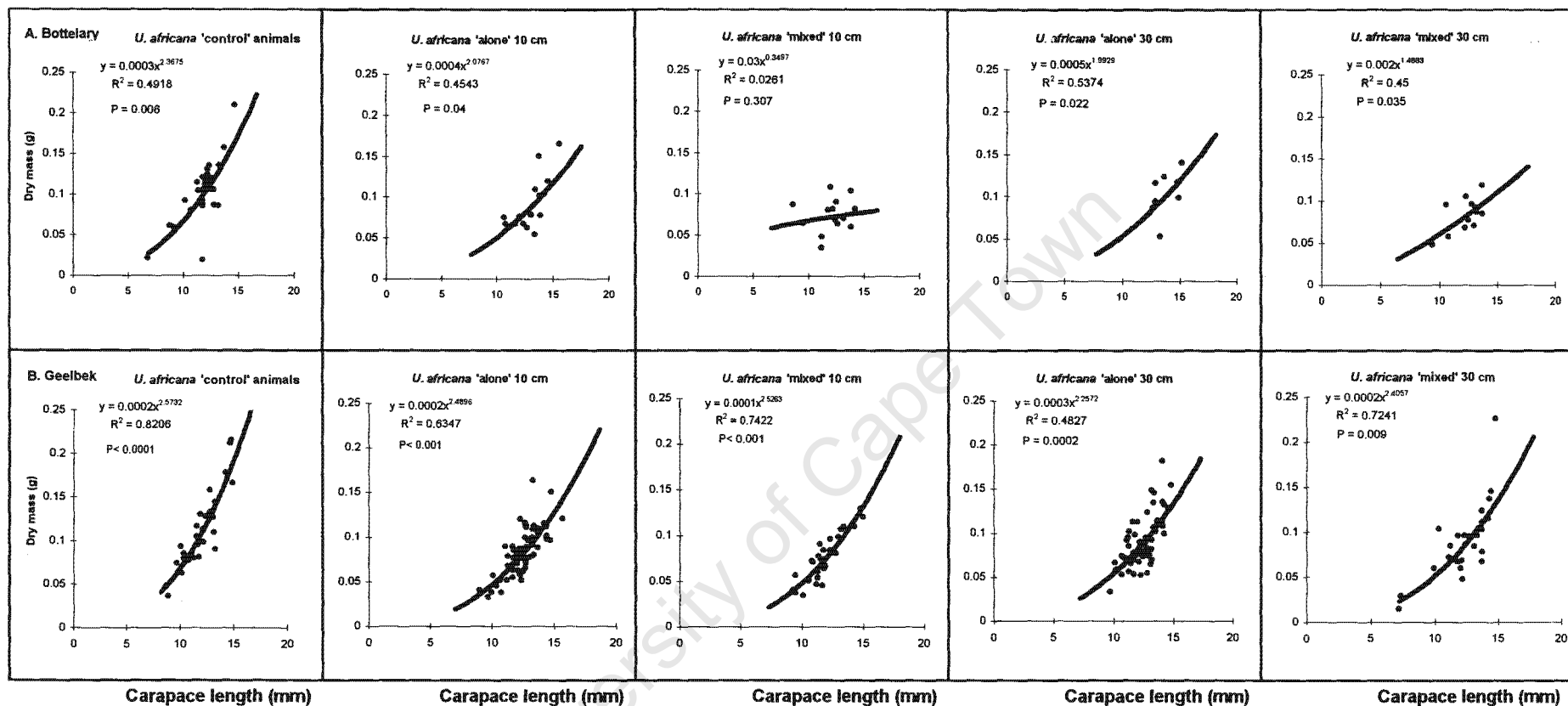


Figure 6.4 Regressions of the mean dry body mass vs carapace length for *U. africana* at Bottelary (A) and Geelbek (B). The first graph shows the 'control' animals.

Table 6.11 Results of ANCOVA to determine if any differences exist between the mass of treatment and control animals for *U. africana*, with carapace length as the covariate.
Significant results were analysed with Fisher LSD.

A. Bottelary

	SS	d.f.	MS	F	p
Carapace length	0.0883	1	0.0883	53.3761	0.0001
Treatment & group	0.0415	4	0.0104	6.2635	0.0002

Fisher LSD

	Control animals	10 cm alone	10 cm mixed	30 cm alone	30 cm mixed
Control animals		0.1370	0.0006	0.5469	0.0040
10 cm alone	0.1370		0.0591	0.5741	0.1677
10 cm mixed	0.0006	0.0591		0.0314	0.6395
30 cm alone	0.5469	0.5741	0.0314		0.0856
30 cm mixed	0.0040	0.1677	0.6395	0.0856	

B. Geelbek

	SS	d.f.	MS	F	p
Carapace length	0.2899	1	0.2899	321.7420	0.0001
Treatment & group	0.0541	4	0.0135	15.0006	0.0001

Fisher LSD

	Control animals	10 cm alone	10 cm mixed	30 cm alone	30 cm mixed
Control animals		0.0001	0.0001	0.0001	0.0006
10 cm alone	0.0001		0.2406	0.0730	0.2191
10 cm mixed	0.0001	0.2406		0.0102	0.0410
30 cm alone	0.0001	0.0730	0.0102		0.8293
30 cm mixed	0.0006	0.2191	0.0410	0.8293	

In the case of *U. africana* (Figure 6.4), at Bottelary, animals in two of the four caged treatments had a significantly lower dry mass than the control animals (Figure 6.4a; Table 6.11a). At Geelbek, all caged treatments showed significantly lower dry mass than the control animals (Figure 6.4b; Table 6.11b).

There were never any significant differences in condition between sites for any given treatment (ANCOVA followed by Fisher LSD; $P > 0.08$ in all cases).

Differences in mean mass (Figure 6.5) followed exactly the same pattern as the length-mass regressions, with control animals being heavier than those in some or all of the caged treatments, and no differences emerging among treatments that could be construed as being due to competition between the two species (i.e. differences between 'mixed' and 'alone' treatments).

Summary of results

Table 6.12 summarises the effects of site, treatment and depth on survival, and of these three factors and the caging effect on condition, together with central conclusions which are amplified in the discussion.

6.4 Discussion

This study was prompted by the fact that there is a strong negative association between the abundances of *C. kraussi* and *U. africana* in the field (Siebert 2003, Siebert & Branch 2005a, and Chapter 2 of this study) and experiments have shown that the eelgrass *Zostera capensis* is associated with high densities of *U. africana* but is negatively correlated with *C. kraussi* (Siebert & Branch in press). There are, however, at least three possible explanations for these observations, which are not necessarily mutually exclusive. First, *C. kraussi* and *U. africana* may simply have preferences for different types of

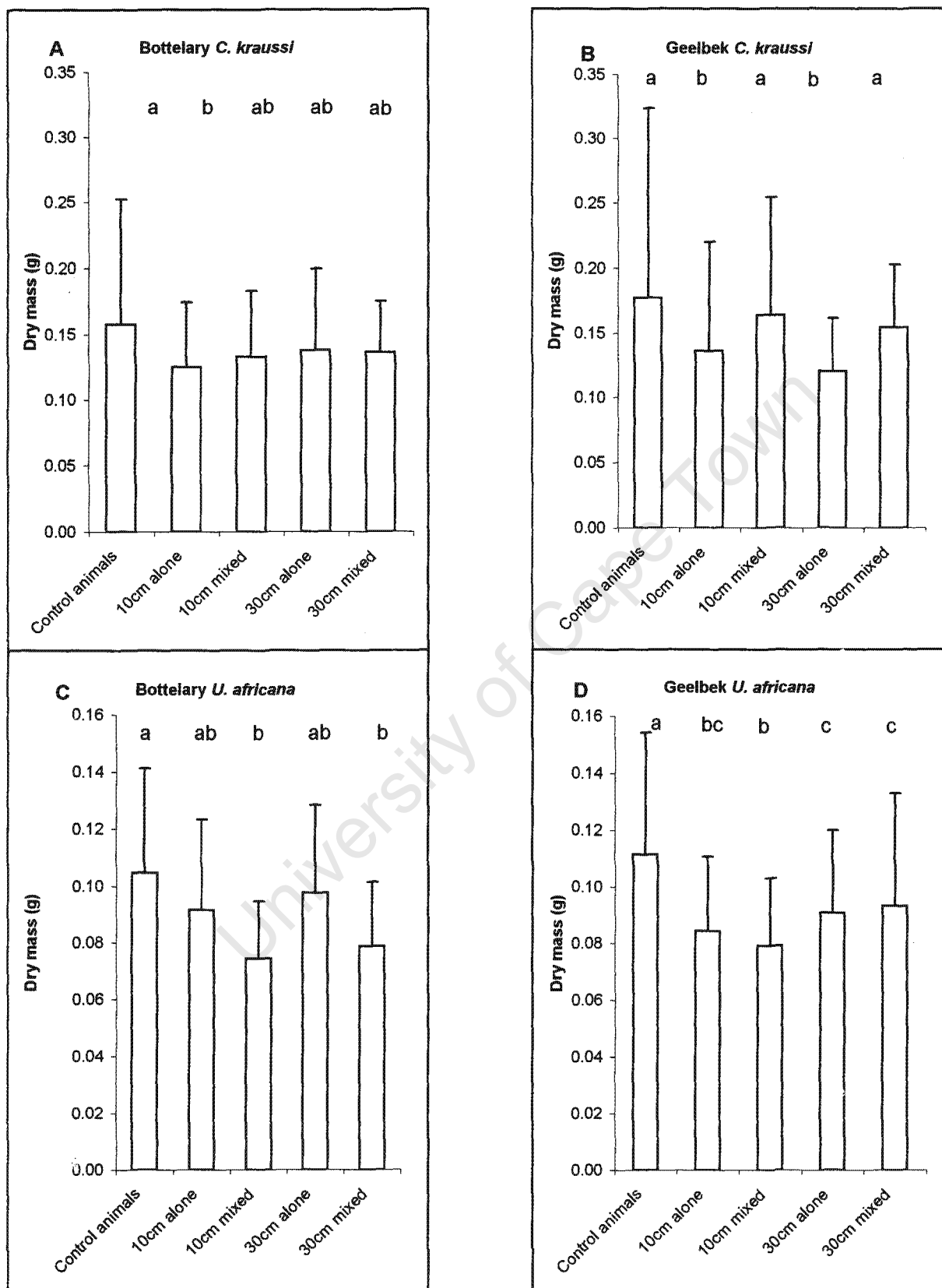


Figure 6.5 Charts showing biomass of prawns including control animals. Error bars show +1 sd. Treatments sharing the same letters did not differ significantly.

Table 6.12 Summary of the effects of site, treatment and depth on survival, and of these three factors and the caging effect on condition.

A. Survival

1. *Callianassa kraussi*

Factors	Initial Surface Survival	Final Surface Survival	Final Sediment Survival	Conclusions
Site (S)	—	—	—	No site effect
Treatment (T)	$P = 0.01$ (only at 10 cm)	—	—	No meaningful treatment effect
Depth (D)	—	—	—	No depth effect

1. *Upogebia africana*

Site (S)	$P < 0.0001$ (Bott < Geel)	$P < 0.0003$ (Bott < Geel)	$P < 0.0001$ (Bott < Geel)	Strong site effect; survival at Bott < Geel
Treatment (T)	$P = 0.03$ (only at 10 cm)	$P = 0.006$	—	No competition; survival 'alone' < 'mixed'
Depth (D)	T effect only at 10cm TxD $P=0.04$	Only at Bott: SxD $P=0.01$	—	Depth effect minor, only seen in interactions

B. Condition

1. *Callianassa kraussi*

Factors	Condition	Conclusions
Cage effect	Control > Cages at 10cm 'alone' at Bott; $P=0.02$ Control > cages at 10 & 30cm 'alone' at Geel; $P<0.03$	Negative cage effects for 3/4 cases
Site (S)	—	No site effect
Treatment (T)	10cm 'alone' < 10cm 'mixed' at Geel; $P=0.02$	No competition; 'alone' < 'mixed' at Geel
Depth (D)	—	No depth effect

2. *Upogebia africana*

Cage effect	Control < cages at 10 & 30cm 'mixed' at Bott; $P<0.005$	Negative cage effect for 2/4 cases
Site (S)	—	No site effect
Treatment (T)	—	No treatment effect
Depth (D)	—	No depth effect

sediment and may therefore seldom co-exist. Indeed, as the names 'sandprawn' and 'mudprawn' imply, they are respectively most commonly found in fine sand and muddy sediments (Hill 1967, Forbes 1973a, Hanekom 1980, Day 1981a, Wynberg & Branch 1991, 1994, Cretchley 1996, Siebert 2003). Second, one or both species of prawn may have negative effects on the other. Bioturbation by *C. kraussi* is one possible means by which it may negatively affect *U. africana*, particularly in sandy sediments where the semi-permanent U-tubes of *U. africana* (Branch & Branch 1984) will be more prone to collapse (Brenchley 1982). Third, *Z. capensis* may indirectly affect the association between the prawns by excluding or inhibiting *C. kraussi* but promoting *U. africana* due to its stabilisation of the sediment (Siebert 2003, Siebert & Branch 2005a, in press).

Observations cannot on their own resolve which of these processes yields the patterns observed in the field. My experiments specifically tested whether the presence or absence of either species of prawn affects the survival or condition of the other species. By repeating the experiment at two sites with different sedimentary properties I could also explore inter-site effects related to sediment type. I did not include *Z. capensis* in my experiments but work by others employing field observations and experimental transplants of *Z. capensis* has explored the interaction of this species with both *C. kraussi* and *U. africana* (Siebert & Branch 2005a, in press) and I have drawn on their work in interpreting my results.

My results indicated that site and to a lesser extent depth and the presence or absence of the other species influenced the survival and condition of *C. kraussi* and *U. africana*.

Experimental design

Natural, laboratory and field experiments are identified by Peterson (1980) as methods of assessing interaction and competition among infauna. My experiments constituted a 'field experiment' where all background factors varied uncontrollably except for the number of animals placed in each cage.

Unfortunately, when such experiments are undertaken on sedimentary habitats they inevitably involve disturbance of both the sediment and its biota (Peterson 1980). In the present case, sediment cores were excavated, sieved to remove all prawns, returned to cages and populated with prawns in the desired combination and densities. Peterson (1980) notes that such "defaunation" will remove a large amount of the sedimentary structure and more delicate fauna, which may be important to the functioning of the system. Added to this, the cages were placed in a specific zone in the center of the intertidal area. The results are thus representative of that zone and take no account of the changes in biological (Berkenbusch & Rowden 1999) and physical condition (Peterson & Andre 1980) that will exist across the intertidal zone.

Mechanisms of competition

Studies done by Peterson (1980) on interspecific competition in marine soft-bottom environments show four mechanisms for competition. These are direct interference competition for space, exploitative competition for food, adult interference with larval settlement and indirect interference through alteration of the physical environment.

Adult interference with larval settlement was not examined in my experiment and a different experimental design would be required for this. However, it is worth noting that *C. kraussi* and *U. africana* have different life-cycles. *U. africana* has a dispersive planktonic larval stage (Hill 1967) whereas *C. kraussi* has direct development and its juveniles form lateral tunnels from the burrows of

adults (Forbes 1973b). This means that *U. africana* is vulnerable to any adult interference with larval settlement that may take place, whereas *C. kraussi* is not. Working on the east coast of South Africa, D. Pillay (unpublished data) has shown that adult *C. kraussi* reduce bacteria and organic films on sand particles. Hypothesising that both bacteria and organic films act as cues promoting larval settlement, he then went on to demonstrate that high densities of *C. kraussi* inhibit the settlement of larvae of several species of macrofauna. Strasser & Felder (1999a, b) discuss how settlement cues affect the ghost shrimp *Callichirus major*.

If adults of *C. kraussi* have any negative effects on adults of *U. africana* by way of interference, competition for food or alteration of the physical habitat, these effects should have been detected in my experiments. From Chapter 2 it is clear that the distribution and habitats of *C. kraussi* and *U. africana* differ in the Langebaan Lagoon, *C. kraussi* having a far wider distribution than *U. africana*, which appears to favour beds of *Z. capensis* and only occurs at very low densities in the open sand flats. This led me to expect that *C. kraussi* would survive better than *U. africana* in the experimental cages, particularly at Bottelary where the sediment consists of unconsolidated fine sand. Added to this, I anticipated that bioturbation by *C. kraussi* (Branch & Pringle 1987) would reduce survivorship of *U. africana* when the two species were held together. Because *U. africana* has a more sedentary lifestyle (Aller & Dodge 1974, Hill 1967, Siebert & Branch 2005a) and because the bioturbating activity of *Upogebia* species is limited to periods of burrow construction and burrow cleaning (Posey 1987, Coelho *et al.* 2000), I expected it to have little or no effect on *C. kraussi* survivorship. I also anticipated that the depth of the cages would influence survivorship. Because *U. africana* generally occurs closer to the surface than *C. kraussi* (Hanekom 1980, Cretchley 1996) the effect of cage depth in the experimental design was expected to influence *C. kraussi* survivorship but not *U. africana* survivorship.

Survivorship

My experiment allowed me to measure survivorship of both species, which I assessed in three ways, namely 'initial surface survivorship' during the pre-establishment phase of the experiment, 'interim surface survivorship' during the post-establishment phase and 'final sediment survivorship' at the end of the experiment. Both measures of surface survivorship relied on counts of dead animals appearing on the surface of the sediment, thus depending on the assumption that these counts recorded all deaths. Final sediment survival was obtained from counts of the remaining survivors, is likely to have provided greater accuracy. I employed all three measures because 'surface survival' provided a record of survivorship during the course of the two phases of the experiment, whereas 'sediment survivorship' generated only a single estimate at the end of the experiment, but I would put most faith in the 'sediment survivorship'.

Three central results emerged from the measurement of survival. (1) Survival of *C. kraussi* was unaffected by site, whereas there were strong site effects for *U. africana*, which suffered greater mortality at Bottelary than Geelbek. (2) Treatment (i.e. the presence or absence of *U. africana*) had no effect on *C. kraussi*. Treatment effects did exist for *U. africana* but were much weaker than site effects and, opposite to my expectations, survival of *U. africana* in the presence of *C. kraussi* (in 'mixed' cages) was greater than in its absence (in 'alone' cages). (3) Depth had no effect on *C. kraussi*, no effect on *U. africana* interim surface survival, and only minor effects on its surface survival in interaction with other factors.

Survivorship of *U. africana* was low at Bottelary when compared to *C. kraussi*. Cages at Bottelary were situated in fine sand normally occupied by high densities of *C. kraussi* but with few *U. africana*.

The amount of sediment disruption by *C. kraussi* was expected to be greater there than at Geelbek where the sediment is more muddy and I anticipated this would reduce the survivorship of *U. africana* at Bottelary relative to Geelbek.

Bioturbation by *Upogebia* is limited to times when these animals enlarge or repair their burrows. Although *Upogebia* would have had to actively bioturbate during the pre-establishment phase of the experiment when the animals were constructing burrows after being introduced into the cages, once established, they would not have undertaken further burrowing. Because of this, I did not expect *U. africana* to have any affect on *C. kraussi* survivorship during the latter part of the experiment, and this was indeed the case. *C. kraussi*, by contrast, would have continued to bioturbate aggressively throughout all stages of the experiment and, hence, might constantly have influenced survivorship of *U. africana*.

At Geelbek the differences in survivorship between the species were not obvious, with the only significant difference being detected in the 10 cm 'alone' cages, where final sediment survival of *C. kraussi* was lower than that of *U. africana*. Conditions at Geelbek are more muddy and it is postulated that any effects of bioturbation on *U. africana* by *C. kraussi* will be reduced because of this.

Unfortunately studies on bioturbation to date do not provide information on its effects in different sedimentary scenarios. However, conditions at Geelbek would appear to favour the lifestyle of *U. africana* which requires a stable substratum to construct its semi-permanent burrows. Geelbek is the only site in Langebaan Lagoon where *U. africana* is abundant outside the high-shore *Zostera* beds (Chapter 2). Both my observations and the present experiments clearly indicate differences in the abundance and survival of *U. africana* in different parts of the lagoon, with differences in sediment being implicated as the cause.

By comparison with these strong site effects on *U. africana*, treatment either had no effect, or when it did, both *C. kraussi* and *U. africana* had higher survival and better condition in ‘mixed’ cages than ‘alone’. Clearly, there was no evidence of interspecific competition between the two species. Indeed, intraspecific effects exceeded any interspecific effects, with survival and condition being lower when either species was held on its own than at the same (combined) density for the two species together.

There were no significant main effects relating to cage depth for either of the species. Only in interaction with other factors did depth have an effect, and then only for *U. africana*. For initial surface survival there was a treatment x depth effect, with treatment being significant at 10 cm, and for interim surface survival a site x depth interaction led to depth having an effect only at Bottelary. It was therefore concluded that depth had no important effect on the survival of either of the species.

The absence of site, treatment and depth effects for *C. kraussi* contrasts with the outcomes for *U. africana* and indicates the latter species has narrower habitat requirements – as reflected in its narrower distribution and zonation compared with *C. kraussi* (Chapter 2).

Condition

Measurements of length-mass relationships as a proxy of ‘condition’ strongly indicated that the caging procedure had negative effects on both species, with free-living ‘control’ animals having higher mass per unit length and higher average mass than caged individuals in most cases. This does not, however invalidate the experiment approach, as both species were held under identical conditions whether they were ‘alone’ or ‘mixed’.

For both species, there were no site or depth effects on the condition of the prawns when comparisons were made for any given experimental treatment (Figure 6.5). Treatment generally had no effect on condition, with one exception: for *C. kraussi* at Geelbek, animals from the 'alone' treatments paradoxically had a significantly lower mean mass than in 'mixed' treatments. This reinforced the view expressed earlier, that intraspecific effects were stronger than any interspecific effects.

Bioturbation

Bioturbation is an important driving force in species interactions in soft sediment environments (Levinton 1972, Aller & Dodge 1974, Suchanek 1983, Posey 1987, Gerino 1990, Hall 1994) and its role seems to be an important one in Langebaan Lagoon (Branch & Pringle 1987, Siebert 2003, Siebert & Branch 2005a, 2005b, in press).

In previous studies it has been found that sedentary taxa are negatively associated with *Callianassa* spp., and the mechanism has been attributed to bioturbation (Branch & Pringle 1987, Aller & Dodge 1974) relating to the feeding and burrowing activities of *Callianassa* spp. (Posey 1987, Stamhuis *et al.* 1998, Berkenbusch & Rowden 1999). However, Posey *et. al* (1991) also found a negative association between *U. pugettensis* and other sedentary taxa, even though *U. pugettensis* exhibits a more sedentary lifestyle than *Callianassa* and contributes less to bioturbation. Wynberg & Branch (1994) found that *C. kraussi* is responsible for a large amount of bioturbation and needs unstable, loose sediments to burrow. Siebert & Branch (2005a) demonstrated that the speed of burrowing of *C. kraussi* is faster in unstabilised sand flats than in *Zostera* beds where the penetrability of the sediment is reduced. Wynberg & Branch (1994) argue that in contrast to *C. kraussi*, *U. africana* requires stable sediments and causes little bioturbation. *U. africana* does burrow and consequently cause bioturbation when building its burrows. Thereafter, however, it forms semi-permanent burrows through which it

circulates water to filter-feed. *C. kraussi* is a deposit feeder and therefore constantly burrows causing sediment turnover down to depths of one meter (Pringle and Branch 1987), and can be expected to interfere with filter feeding by *U. africana*, as predicted by the 'trophic group amensalism' model of Rhoads & Young (1970) who argued that continual turnover of sediment by bioturbating deposit feeders will interrupt, bury and smother filter feeders (see also Levinton 1972, Probert 1984, Gerino 1990, Hall 1994, Kerr & Corfield 1998).

It was these differences that led me to forecast that *C. kraussi* would have negative effects on *U. africana* but not vice versa. In reality, no evidence of negative effects of either species on the other emerged. On the contrary, survival and condition were either no different among treatments or higher in 'mixed' than 'alone' treatments.

The role of *Zostera capensis*

Siebert & Branch (2005a) found that in Langebaan Lagoon *Zostera capensis* was negatively correlated with *C. kraussi*, with *Z. capensis* occurring in a narrow band on the high shore and *C. kraussi* in the sandflats immediately below these eelgrass beds. They also found that the distribution of *U. africana* mirrored that of *Z. capensis*. These patterns were consistent over time and suggestive of a negative amensal interaction between *C. kraussi* and *Z. capensis*, and between *C. kraussi* and *U. africana*. Siebert & Branch (2005a) demonstrated that *Z. capensis* creates stable sediments by trapping fine particles and consolidating the sediment with its root/rhizome system (Terrados & Duarte 2000), hindering burrowing by *C. kraussi*. Conversely *C. kraussi* bioturbation destabilizes sediments and increases suspension of particles (Siebert & Branch in press) and is likely to smother *Z. capensis*. Comparable effects have been recorded elsewhere (Homziak *et al.* 1982, Valentine *et al.* 1994, Stamhuis *et al.* 1997, Townsend & Fonseca 1998, Rowden *et al.* 1998).

Siebert & Branch (in press) performed experimental transplants of *Z. capensis* into areas of the sandflats supporting natural densities of *C. kraussi*. This resulted in rapid deterioration of the transplanted eelgrass. But in areas where bioturbation had been eliminated, the eelgrass increased in cover. *U. africana* was associated with *Z. capensis* and became common in experimentally introduced plots of eelgrass in areas where *C. kraussi* had been eliminated.

Despite the strong inference from these observations and experiments that *U. africana* and *C. kraussi* are negatively associated, my experiments detected no hint of competition between the two. At Bottelary *U. africana* survival was low irrespective of the presence or absence of *C. kraussi*. At Geelbek, where the sediment is more muddy, survival of *U. africana* was high, again independent of the presence or absence of *C. kraussi*. It is postulated that the sedimentary conditions there are more favourable for mudprawns, so *U. africana* is not reliant on *Zostera* there to provide the sedimentary stability it requires. Elsewhere, where sandflat sediments comprise fine sand with little mud or silt, *Zostera* beds may create the only suitable conditions for *U. africana* because their root/rhizome systems stabilize the sediment and trap fine particles (Mazure & Branch 1979 and see Chapter 2).

The effects of sediment type

The distribution of sediments in Langebaan Lagoon is documented by Flemming (1977). Certain areas of the lagoon such as Geelbek are more sheltered and experience weaker tidal exchange, little wave action and, importantly, have a substratum with a higher proportion of silt and clay (Day 1959). These conditions result in more stable sediments where *U. africana* occurs at higher densities by virtue of its need to form stable burrows. My experiment also points to *U. africana* surviving better at Geelbek where these stable sediments occur. *Callinassa kraussi*, however, appears to survive equally well in a wider range of conditions, as reflected in its broad distribution and zonation in Langebaan Lagoon.

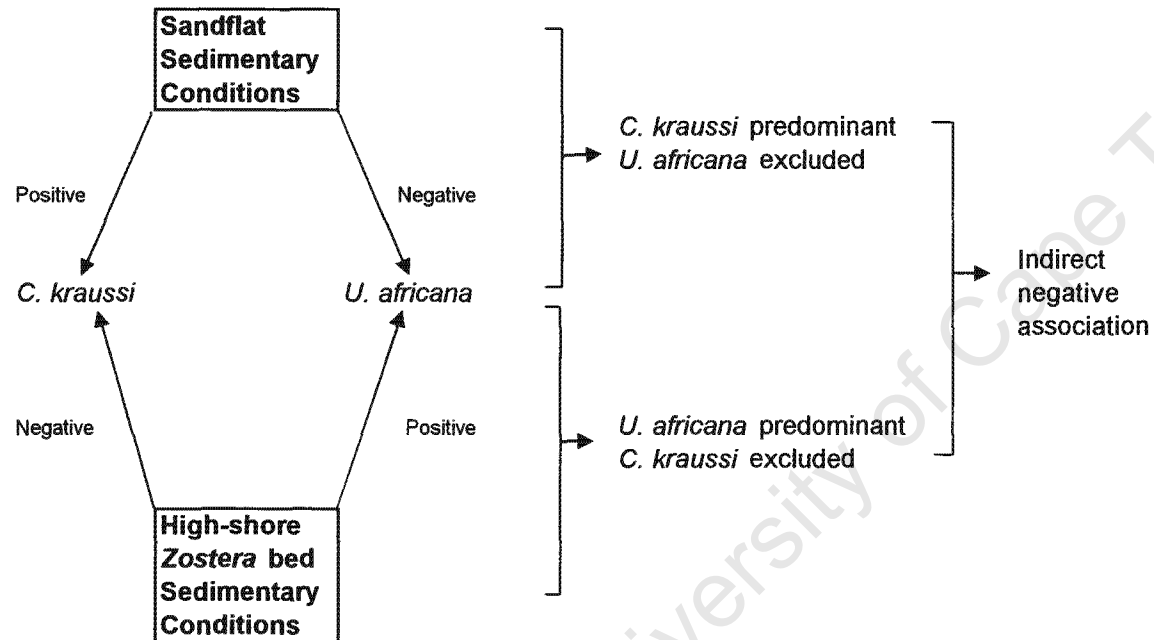
Conclusion

I initially anticipated an inter-specific competitive effect, with *C. kraussi* having negative effects on *U. africana*. I also expected this effect to be strong at Bottelary where the sediments are relatively unstable, and weak or absent at Geelbek where the sediments are more muddy and stable. These expectations were in part based on the fact that *U. africana* requires stable sediment to construct its burrows so that it can filter-feed and that it exists predominantly in the upper levels of the sediment (Hanekom 1980, Branch & Branch 1984). *C. kraussi* bioturbates actively (Posey *et al.* 1991) and makes burrows extending down to depth of ~1m (Pringle & Branch 1987, Siebert & Branch 2005a) and will destabilize the sediments, and I assumed this would make conditions unfavourable for *U. africana*. Further to this, where *Z. capensis* is present, it excludes *C. kraussi*. However, no direct evidence was found of competition between the two species of prawns. Certainly, however, I found strong evidence of site effects for *U. africana*, survivorship of which was significantly lower at Bottelary than Geelbek.

Rather than *C. kraussi* actively excluding *U. africana* because of its bioturbation, it appears that the generally negative association between the two (as exemplified by Bottelary) is due to a combination of (a) exclusion of *U. africana* from sediments that are not sufficiently muddy and stable (b) exclusion of *C. kraussi* and promotion of *U. africana* in *Zostera* beds that stabilize the sediment and trap fine particles and generate a root/rhizome system that hinders burrowing by *C. kraussi*. The negative association between *C. kraussi* and *U. africana* thus emerges as a secondary effect of sedimentary conditions rather than been driven by competition (Figure 6.6). Only in circumstances such as those at Geelbek where the sediment is more muddy do *C. kraussi* and *U. africana* coexist.

Bottelary

Fine sand, little mud & silt



Geelbek

More mud and silt, weak current conditions

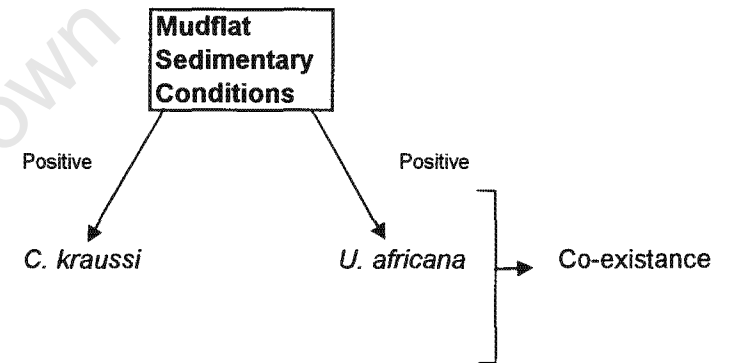


Figure 6.6 Summary of sedimentary and biological factors influencing the relative abundance and coexistence of *C. kraussi* and *U. africana*.

CHAPTER 7

THE CONSERVATION IMPLICATIONS OF BAIT-COLLECTING

7.1 Introduction

This chapter states the importance of Langebaan Lagoon as a 'Protected Area' and of sand- and mudprawns in the functioning of marine ecosystems. It then goes on to summarise recommendations made over the years by researchers regarding their conservation and 'sustainable' use. I then examine the current legislation and evaluate whether it takes into account these recommendations.

7.2 The Area

The conservation importance of Langebaan Lagoon and adjacent area was noted by Fuggle (1977) who argued that we have an international obligation to preserve the most southerly African habitat of many migratory wading birds, and a national obligation to preserve archaeological evidence of early human artifacts known there, as well as evidence of early man's first exploitation of ocean resources. He states further that the area has unique vegetation assemblages, dwindling numbers of African black oystercatchers and the largest breeding colony of African penguins. He also noted the imminent threat of degradation of this natural environment due to increased human pressure.

This human pressure is no longer imminent but a reality today. It is seen in the continuous extension of the port facilities in Saldanha Bay, the increase in heavy industry – Mittal Steel Plant, Duferco Galvanising Plant and the extension of the Namakwa Sands Plant. Housing development is increasing at a rapid rate in Langebaan with a large number of units being built in the Myburgh Park development, Country Club development, Langebaan Country Estate development and coastal developments like the

extension of Club Mykonos, the 'Cove', 'Paradise Beach' and 'Waterfront' developments along the coast between Langebaan Town and Club Mykonos. To supply additional water requirements, water is being drawn from aquifers, the effects of which are still largely unknown. With increased industry and housing come people and boats and outboard motors. Many of these people fish and collect bait and hence increase pressure on fish and bait stocks in the lagoon.

7.3 Sand- and mud-prawns

Previous work by several authors has shown that both *C. kraussi* and *U. africana* have an important role to play in marine systems such as estuaries and lagoons, particularly in terms of sediment turnover, oxygenation and exchange of nutrients with the adjacent water column, sediment geochemistry, as a source of food for fish and various birds (Hill 1967, Forbes 1973a, Aller & Dodge 1974, Hanekom 1980, Day 1981a, Branch & Pringle 1987, Tamaki 1988).

7.4 Conservation measures suggested by Forbes (1973a) and Wynberg (1991)

Forbes (1973a) states that any measures implemented to protect prawns will only be effective if they are underwritten by effective enforcement. The optimal situation is described as one where complete control can be exercised and bait removal activities regulated. This would allow for exact records of removals to be kept and make changes in catch per unit effort detectable. In the event that harvesting is shown in the future to be reducing prawns at an unacceptable rate, a range of control measures is possible. First, bag limits could be reduced. Second, larger areas could be set aside to protect the stocks. Third, a rotation system of collecting with alternate open and closed areas has been suggested by Forbes (1973a). This proposal is based on the reproductive cycle of *C. kraussi*, which has an initial growth period of one year followed by maximum breeding during the second year (Forbes 1977). If areas were to be closed for two years this would allow the population to breed uninterrupted, yielding a

next generation that could be harvested when the area was opened again. Such a system thus ensures the constant availability of one undisturbed portion of the breeding stock. The difficulty with such a system is that it ignores the environmental effects of bait-collecting such as sediment compaction and the long duration of recovery demonstrated by Wynberg & Branch (1994). An alternative is the permanent closure of certain areas to bait collection, a system legislated in Langebaan Lagoon (see Chapter 1). This involves easier control than a rotation system, and migrations from closed areas should re-populate depleted areas, provided that these areas are always linked.

Wynberg (1991) stresses the importance of site-specific regulations to cover unique conditions in specific estuaries or lagoon systems. Her recommendations deal more specifically with the animal itself and include the following: calculation of catch per unit effort; determination of the proportion of the prawn population available for harvesting; estimation of the number of prawns removed annually; assessment of macrofaunal disturbance by bait-collectors and its significance for the system as a whole.

7.5 Current Regulations

In 1965 the then Department of Fisheries promulgated legislation which prohibited the removal of estuarine bait species for the purposes of angling in the sea, a stipulated bag limit of 70 prawns (sand- and mud prawns collectively) per person per day, the prohibition of selling or purchasing any such bait species and banning the use of forks or spades to collect bait organisms (Wynberg 1991).

Amendments to these regulations have seen the removal of the restriction banning the collecting of *C. kraussi* (not *U. africana*) from estuaries for use in the sea and lowering the daily bag limit for sand- and mud prawns to 50 animals per person per day. There are no restrictions on size or sex of the animals collected. In 1985 Langebaan Lagoon was proclaimed a national park under the National Parks Act 57

of 1976 and the Sea Fisheries Act was repealed as far as it applied to the lagoon. In 1991 the National Parks Act was amended and the zoning scheme, first ratified by the Sea Fisheries Act of 1973, was again recognized and bait-collecting and fishing was restricted to an area north of Beacons LB 4 (Oesterwal) and LB 3 (Kraal Bay) (Figure 2.1). This regulation did not stipulate any bag or size restrictions for fish or bait organisms.

After the 1994 national elections the political dispensation changed and in 1998 the Marine Living Resources Act (Act 18 of 1998) (MLRA) was proclaimed. In terms of this fisherman are now allowed to collect 50 prawns of the genus *Callinassa* and 50 of the genus *Upogebia* which presents an increase in quotas for prawns as a whole. In addition to this, Langebaan Lagoon was proclaimed a Marine Protected Area (MPA) (in terms of the MLRA) in 2000. According to the regulations for the Langebaan Lagoon MPA line fishing is allowed only in the area north of Beacon LB 4 and LB 3. However, bait-collecting continues, and is recognised to be a legal activity by officials of Marine and Coastal Management. The precise and correct interpretation of this new law will need to be clarified and if bait-collecting is to be allowed to continue, an amendment to the Act is necessary.

7.6 Recommendations

A key to successful law enforcement in the present day is co-operative governance between responsible authorities. Langebaan Lagoon is a national park and an MPA and an effective management plan will need to be compiled for this area. South African National Parks must ideally sign a management agreement with Marine & Coastal Management (MCM) to ensure effective management of the area (Lemm & Attwood 2003).

In chapter 2 I demonstrated that there are strong links between the distribution of species with the distribution of sediment in the lagoon. This has the implication that any alterations to the sediment by dredging or the construction of harbour walls and breakwaters will have important repercussions for sand and mud prawns. In particular *U. africana* is largely limited to the high shore where it is associated with *Zostera*. There is a strong case to be made for banning the collection of *U. africana* in Langebaan Lagoon because of this. Its limited habitat makes it vulnerable to over-harvesting, and harvesting damages *Zostera* beds with long-lived effects. *Zostera* is on the decline in Langebaan Lagoon (Angel *et. al* in press) and the rare and endangered *Siphonaria compressa* is indirectly threatened because of its association with *Zostera* (Angel *et. al* in press).

The surveys in chapter 2 also provide background information on which recommendations for future monitoring can be based. I recommend that monitoring of prawn densities (i.e. hole counts) should be undertaken once a year at two harvested sites and two control sites. The surveys should be done at a fixed time of the year to avoid seasonal variations confounding inter-annual trends. Monitoring of the numbers of bait-collectors and their catch per unit effort will also be necessary but can take place at longer intervals, say every 5 years.

In chapter 3 I could detect no signs that any of the prawn species are currently threatened by over-harvesting, even in areas where collection is most intense. However, 32 % of bait-collectors remove more than the legal limit of 50 *C. kraussi* per day. Wynberg & Branch (1991) found that 50 prawns per person per day were, in the view of the fishermen themselves, more than sufficient to meet their needs. Therefore, education and law enforcement will need to address this non-compliance in Langebaan Lagoon. There is no doubt that fishermen enhance their chances of catching fish when they have more

bait available and this is the motivation for exceeding the legal limit. Thus, by ensuring compliance in bait-collecting, fish stocks will automatically be more effectively protected.

In chapter 4 I demonstrated a single peak of reproduction each year. Although consideration could be given to implementing a closed season at this time, in practice this seems neither necessary nor desirable. The rate of harvesting currently poses no threat and a closed season would require stringent enforcement which is probably impractical.

The experiments I described in chapter 5 did show that harvesting reduces density but had no effect on fecundity. Moreover the intensity of the effects was too small to raise concerns about current levels of harvesting.

One option for decreasing the effects of bait-collecting would be to insist that small or female animals in berry be returned to the sand. The likelihood of this succeeding would depend on the species of prawn and the effect of the prawn pump on the animals. *C. kraussi* does not always burrow back into the sand effectively once removed. Often flocks of Hautlaub and Kelp gulls can be seen near bait-collectors and they are quick to snatch up any prawns that are not collected. Wynberg & Branch (1991) have also reported on avian predation of discarded prawns. *U. africana* fails to bury itself when left on the surface. Most of the *U. capensis* that are collected occur in the shallow subtidal area.

Returning them into the water column is then the only way of releasing them. Although no research has been done on the success with which they re-establish themselves, I observed them floating around for up to 15 minutes after release and still not finding their way back to the sediment. In short, insistence on the release of small prawns or berried females is unlikely to be an effective means of protection.

I could not find any specific criterion in the literature used by the authorities to set the current bag size of 50 mud prawns and 50 sand prawns per person per day. I could also not find any reference to why originally this limit was 70, then became 50 overall, and then 50 per genus. I was also not able to clarify whether or not bait can legally be collected in Langebaan Lagoon MPA. The regulation as stipulated in the Government Gazette of 2000 clearly disallows this. I strongly recommend that the above two issues at least be clarified. Examining the amount of prawns removed by collectors per annum compared to the stock available, there is no reason to reduce the current bag size limit. To ensure that harvesting does not increase to the point where it is a problem in the future, however, monitoring should be initiated as outlined above.

The zoning scheme in Langebaan Lagoon (see Figure 2.1 and Introduction of this thesis) (as broadly recommended by Forbes 1973a) is very effective as a conservation measure and very seldom are there any reported transgressions in the reserve or sanctuary areas. By nature of the position of zone 'A' close to Langebaan (also noted by Wynberg 1991) the area is very accessible to anglers. Prawns are collected quickly and no real 'desire' exists to breach the zoning regulations in order to collect bait further south. What is unfortunate though, is that MCM has granted 11 netfish permit holders rights to catch harders (mullet) in the 'A' and 'B' zones thus decreasing the protection normally accorded to zone 'B'. Zonation not only protects prawns and fish but all other elements of the ecosystem. In particular it establishes a disturbance-free zone for the important migratory birds that occupy the lagoon seasonally. This zoning scheme must, therefore, be maintained and actively managed to ensure effective compliance and monitoring of prawn stocks in the lagoon.

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