
**EXPLOITATION OF THE BAIT ORGANISM *UPOGEBIA AFRICANA*
(CRUSTACEA: ANOMURA) IN THE KNYSNA ESTUARY**

THESIS

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requirements for the Degree of
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by

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The Knysna estuary (at high and low tide).

This work forms part of the Knysna Basin Project which co-ordinates scientific and socio-ecological research by specialist researchers around the country to provide a basis for future environmental management protocol for the Knysna Basin.

ABSTRACT

In South African estuaries the anomuran mud prawn, *Upogebia africana* (Ortmann), is the main organism exploited as bait by recreational and subsistence anglers. In the Knysna estuary, three groups of bait collectors were identified on the basis of their source of income: subsistence fishermen who rely on bait-collecting and fishing for their income, supplementary anglers who catch fish to supplement their income and leisure anglers who draw no income from fishing. Two groups were identified based on the methods used: leisure anglers who collect bait using a prawn pusher or pump and fish using a fishing rod and tackle, and non-leisure anglers who collect mud prawns using tin cans and fish with handlines.

The hypothesis was erected that bait-collecting does not affect the *U. africana* populations in the Knysna estuary. The approach adopted was to assess the distribution, density, population structure and reproductive patterns of the bait stock and to estimate the intensity of bait collection, to test the validity of the hypothesis.

U. africana has an extensive distribution, occupying 62 % of the available intertidal area of the Knysna estuary. Mud prawns have a broad intertidal distribution from the high water level (*Spartina* zone) to the shallow subtidal. The density, biomass and population structure of the mud prawns vary significantly with distance up the estuary and with tidal height on each shore. The Invertebrate Reserve supports very low densities of *U. africana* ($x = 11.7 \text{ m}^{-2}$), whereas a relatively inaccessible centre bank in the middle reaches of the estuary appears to be a very effective natural mud prawn reserve as it supports the highest densities ($x = 176.5 \text{ m}^{-2}$). The mud prawn stock of the estuary is estimated to be 2.19×10^8 prawns (82.7 tonnes dry mass).

The numbers of bait collectors present per mudbank is highest on public holidays ($x = 34$) and higher during the summer holidays ($x = 16$) than during the winter ($x = 4$). A total of 1.858×10^6 *U. africana* or 700.53 kg (dry mass) are removed by bait collectors annually from the 6 popular bait-collecting sites studied. This represents 8.49 % of the mud prawn stocks at these sites and 0.85 % of the entire estuary stock. 85 % of the *U. africana* taken as bait annually, is removed by the 77.12 % of bait collectors who are non-leisure anglers. Recreational or leisure anglers are responsible for removing 14.2 %.

The reproduction of female *U. africana* in the Knysna estuary is seasonal and occurs from

late July to April. There is evidence that this breeding season consists of two merging breeding cycles. The largest percentage (63 %) of ovigerous females is found in the middle reaches of the Knysna estuary at the Oyster Bank where the highest numbers of stage 1 larvae (165 m^{-3}) are released. Larvae were exported from the estuary on the crepuscular ebb tide with peaks in abundance of nearly 1500 m^{-3} in November 1995 and January 1996. Although numbers caught are not significantly higher, larvae are nearly twice as abundant on crepuscular neap tides following a new moon (waxing quarter) than on those following a full moon (waning quarter). Recruitment of juvenile *U. africana* to populations in the estuary was highest in December (45 m^{-2}) and decreased over the summer. The highest numbers of recruits (31 m^{-2}) were found at those sites closest to the mouth or on the main channel. Recruitment to the Leisure Isle and Thesens sites which are intensively exploited by bait collectors is high (20 - 32 m^{-2}). The number of juveniles recruiting to *U. africana* populations is estimated to be four times as high as the numbers of mud prawns taken by bait collectors.

Legal methods of bait collection used in the Knysna estuary by the majority of anglers appear to cause minimal sediment disturbance and are not likely to affect the associated infauna. Illegal bait-collecting methods are however highly destructive and must be prohibited. It is concluded that the null hypothesis is acceptable, as mud prawn stocks of the Knysna estuary are not over-exploited and appear to be naturally regulated. The recruitment rate of juvenile *U. africana* is estimated to be sufficiently high to sustain the present levels of exploitation.

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CHAPTER ONE

GENERAL INTRODUCTION

RATIONALE

In South African estuaries the anomuran mud prawn, *Upogebia africana* (Ortmann), is the main organism exploited as bait. In the Knysna estuary, the mud prawn is exploited by subsistence fishermen as well as resident and visiting leisure anglers. This study was carried out to assess whether present levels of bait collecting have an effect on the bait stocks.

The null hypothesis was erected that bait collection has no effect on the density and population structure of *U. africana* in the Knysna estuary. In order to test this hypothesis, it was necessary to:

- (1) assess the present status (density and biomass) and population structure of *U. africana* in the Knysna estuary,
- (2) estimate the extent and intensity of the recreational and particularly the subsistence bait fisheries in this estuary, and
- (3) assess rate of recruitment to the mud prawn stocks in order to estimate the potential sustainability or recovery of bait stocks.

It is anticipated that this research will be of use in planning the sustainable use and management of bait resources not only in the Knysna estuary, but in South African estuaries in general.

South African estuaries tend to be small, shallow, microtidal and relatively turbid, and few systems are truly estuarine. Of the 289 river mouths, only 37 (12.8 %) maintain permanent tidal inlets with the sea (Reddering and Rust, 1990). The Knysna estuary has a deep rocky mouth which is permanently open to the sea and is the second largest estuary in South Africa (Day, 1981b). Although Watling and Watling (1975) suggested that the Knysna estuary is one of the most, if not the most, biologically productive estuaries in South Africa, the productivity of this estuary has not

temperate estuary, and has the highest invertebrate species diversity of all South African estuaries with 310 species recorded (Day, 1981a). The flora and fauna of this estuary were last surveyed in detail by Day and colleagues in 1952. Since then, considerable urban and industrial development has taken place around the estuary and anthropogenic pressure on the estuary has increased.

The Knysna estuary is used for commercial, recreational and subsistence purposes by various sectors of the community as well as by tourists. Commercial activities include oyster farming, passenger transport and cruise operations, speedboat, cruiser and houseboat hire as well as diving and fishing charters. The estuary is also used as a source of industrial cooling water and for waste effluent disposal. Recreational activities are popular with local residents and tourists. These include fishing, waterskiing, sailing and swimming.

There are many subsistence fishermen and women who rely to a lesser or greater extent on the estuary for a living. A number of people are resident at the edge of the estuary and rely on it completely for a living, while others visit the estuary to fish every day to feed their families. A few men and women collect and sell bait and fish to supplement an irregular and inadequate income. Thus, fishing in the Knysna estuary is a popular and economically important practice.

Within the estuary, many species of invertebrate are exploited as bait, including the sandprawn, *Callianassa krausi* Stebbing, the cracker shrimp, *Alpheus crassimanus* Heller, the bloodworm *Arenicola loveni* Kinberg, the estuarine nereid worm *Marphysa sanguinea* (Mont.), the nemertean worm, *Polybrachiorhynchus dayi* Gibbons, red-bait, *Pyura stolonifera* (Heller) and the mud prawn *Upogebia africana*. Of these species the mud prawn is the most extensively used as bait. It is the most abundant of the infauna of the intertidal flats (Siegfried, 1962; Day, 1981a) and the easiest bait species to collect.

Upogebia africana, is found in sheltered bays and estuaries from Langebaan Lagoon on the west coast to Inhambane on the east coast of South Africa (Fig. 1.1). Hill (1967) established that temperature is a major factor limiting their distribution around southern Africa with conditions on the east coast being too warm further north and with cold water possibly limiting distribution up the west coast. *Upogebia africana* is particularly abundant in many permanently open east and south Cape estuaries (Hill, 1967; Day, 1981b; Hodgson, 1987; Hanekom, Baird and Erasmus, 1988) and is an important prey item for a variety of bird and fish species (Day, 1981b; Marais, 1984; Hanekom *et al.*, 1988; Martin, 1988; Whitfield, 1988). In terms of biomass consumed, *U.africana* is the most important prey of the five major bird species of the Swartkops estuary, in the Eastern Cape. In this estuary, 92 % of estuarine birds feed from the intertidal mud at low tide. *Upogebia africana* makes up 99 % of prey items for the common tern, *Sterna hirundo*; 58 % of the diet of the kelp gull, *Larus dominicanus*; 21 % for the grey plover, *Pluvialis squatarola*; and 48 % for the whimbrel, *Numenius phaeopus* (Martin, 1988). Fish have access to subtidal and submerged intertidal prawn beds and *U. africana* is an important prey item (Marais, 1984) of the spotted grunter, *Pomadasys commersonni*, sea catfish, *Galeichthys feliceps*, and the cape moony, *Monodactylus faliciformis*.

Callianassa spp. and *Upogebia* spp. have been referred to as "promoter" species (Reise, 1985) because of their capacity to increase sediment oxygenation and mineralisation (Ott, Fuchs, Fuchs and Malasek, 1976; Hines and Jones, 1985), and to change the community structure of soft bottom estuarine habitats by having diverse effects on microalgae, bacteria and meiofauna (Brenchley, 1981; Flint and Kalke, 1986; Posey, Dumbauld and Armstrong, 1991; Wynberg and Branch, 1994). Hence, disturbance or removal of populations of "promoter" species (*e.g.* through over-exploitation by bait collectors) could therefore have implications beyond the disturbance of the organism *per se*.

A few studies have assessed the effects of bait collecting on various macrobenthic bait organisms of soft substrata. Blake (1979a, 1979b) studied the exploitation of the bait worms, *Arenicola marina* and *Neries virens*, from the north-east coast of England and concluded that the spawning stocks of the worm populations were not threatened by the existing levels of exploitation. Jackson and James (1979) studied the influence of bait digging on cockle, *Cerastoderma edule*, populations in North Norfolk (in the United Kingdom) and McLusky, Anderson and Wolfe-Murphy (1983) described the population recovery of *Arenicola marina* and other benthic fauna after bait digging in the Forth estuary, Scotland. These studies all indicate that systems exploited respond resiliently.

In South Africa, work on bait collecting was initiated by Hill (1967) who noted that mud prawn densities were lower in exploited areas of the Kowie estuary and that bait collection resulted in a decrease in the numbers of larger mud prawns. The only detailed studies on bait collecting in South Africa have been those of Wynberg and Branch (1991, 1994) in the Langebaan Lagoon in the Western Cape. They quantified the removal of sand- and mud prawns and the amount of disturbance caused by bait collectors. It was estimated that 80 % of disturbed macrofauna were consumed by birds. The recovery of the macrofauna after the disturbance associated with bait collecting was found to be protracted and it was suggested that sedimentary disturbance and compaction have a greater impact than the actual removal of sand- and mud prawns. Martin (1988) has briefly discussed the possible impact of bait collecting on the birds of the Swartkops estuary in the Eastern Cape, but no studies have examined bait collecting in detail nor assessed the impact of bait collecting in a South African estuary. The importance of *U. africana* populations as burrowing, filter-feeding, primary consumers at the base of the estuarine food chain is clear. Disturbance or over-exploitation of the mud prawns by bait collecting may therefore have a ripple effect, influencing other components of the ecosystem (Wynberg and Branch, 1991).

THE KNYSNA ESTUARY

The Knysna estuary (34° 04' S; 23° 03' E) is situated on the south coast of the Western Cape, South Africa (Fig. 1.1).

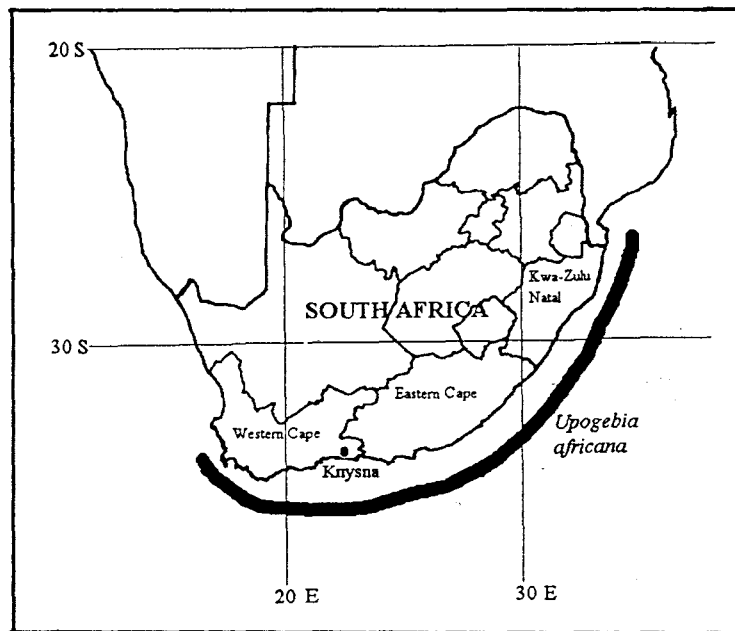


Figure 1.1. Map of southern Africa showing the location of the Knysna estuary on the south coast of South Africa and the distribution of *Upogebia africana*.

The estuary is approximately 19 km long (Day, 1981b) with a tidal reach of about 10 km (Reddering and Esterhuysen, 1984). Freshwater input into the estuary is from the Knysna River, which has a catchment of approximately 315 km² (Reddering and Esterhuysen, 1984). The river rises in the Outeniqua mountains where the annual rainfall exceeds 1000 mm (Grindley, 1985). Since most of the catchment has natural vegetation and the river runs through a gorge in the Tsitsikama forest, erosion is minimal and the river water entering the estuary is clear though peat-stained (Day, 1981b). Mean annual run-off has been calculated to be between 110×10^6 m³ and 70×10^6 m³ (Grindley, 1985) and river flow during inter-flood periods is not strong (Day, Millard and Harrison, 1952).

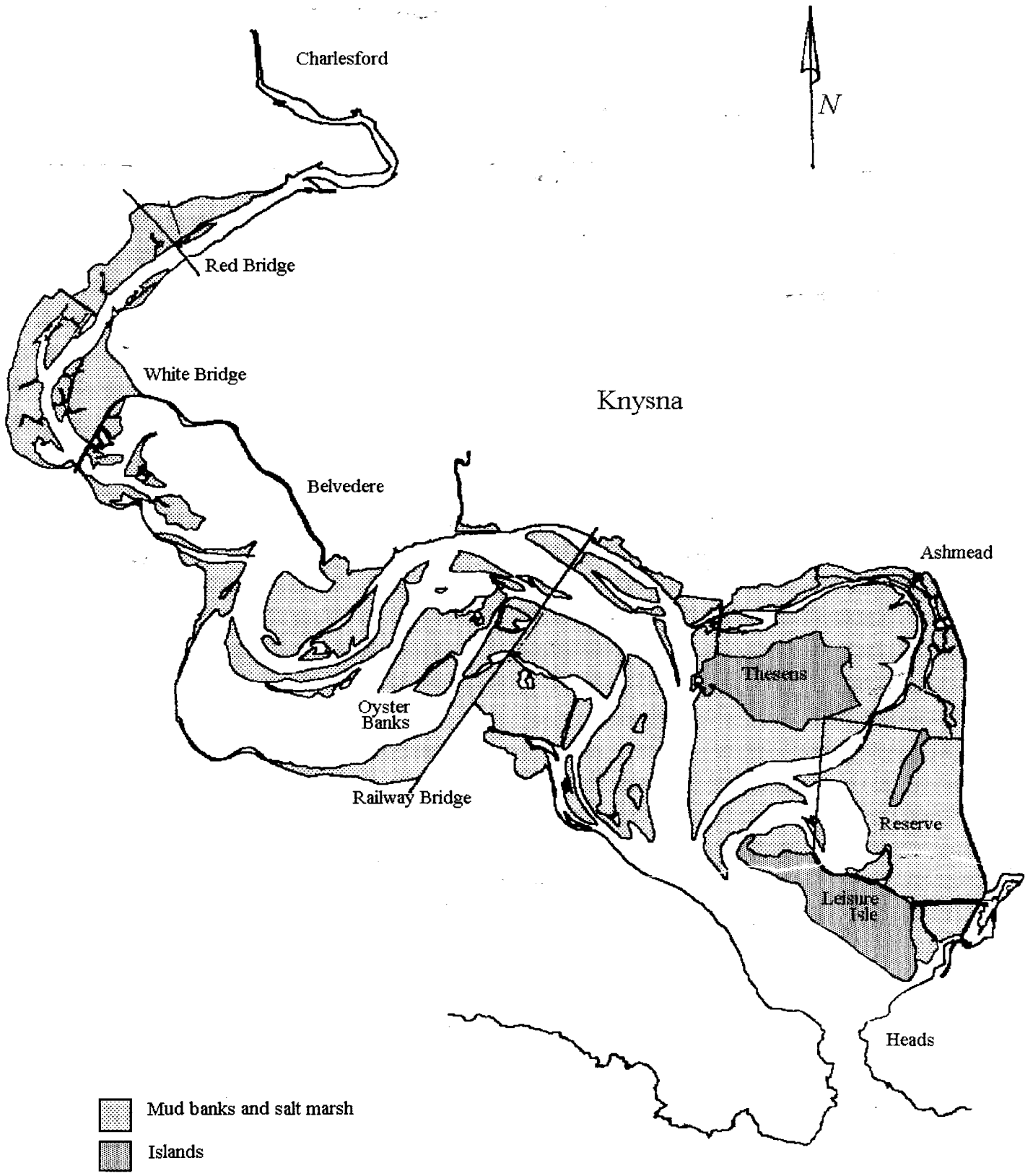


Figure 1.2. The Knysna estuary (scale: 1 : 50 000).

Tidal rise and fall at spring tide at the mouth of the Knysna estuary is approximately 1.8 m which is maintained up to Red Bridge (Fig. 1.2). Above this point the river rises over a series of rapids up to Charlesford, where the tidal range is about 30 cm (Day *et al.*, 1952). The estimated mean flow through the mouth is $0.9 \text{ m}\cdot\text{s}^{-1} \pm 0.0 - 1.6 \text{ m}\cdot\text{s}^{-1}$ and the tidal prism is $19 \times 10^6 \text{ m}^3$ (Proposed Braamkraal Marina, 1974). The channel widens into a broad S-shaped estuary up to 3 km wide and 6 m deep, with extensive intertidal mud flats between Red Bridge and Leisure Isle. The estuary includes two islands, Leisure Isle, a residential area, and Thesens Island which has industrial developments, both being connected to the mainland by causeways. It is also crossed by two road bridges and a rail bridge (Fig. 1.2).

The Knysna estuary is regarded as a clear water estuary (Day, 1981b). Within the estuary, conditions are normally marine up to the railway bridge with salinities between 30 - 35 ‰ and estuarine, in being partially mixed, up to Charlesford weir where the Knysna River flows into the estuary (Fig. 1.2). Salinities range from freshwater to slightly hypersaline (36.7 ‰) (Day *et al.*, 1952). Temperatures near the mouth of the lagoon range from 15.3°C to 22.4°C (Day, 1981b) with temperatures dropping sharply (as low as 9 - 11°C) during periods of upwelling which, as a rule, follow a south easterly wind.

The intertidal area of the mudbanks typically has three main zones based on the vegetation. The eel grass, *Zostera capensis* Setchell, dominates the lower intertidal areas, sometimes occurring mixed with *Halophyllia ovalis* (R. Br.) and bare patches of mud. Usually a broad band of *Z. capensis* in the mid-intertidal is separated by a narrow band of bare sand or mud before the stands of *Spartina maritima* (Curtis) Fernald and higher salt marsh vegetation is reached. In the upper reaches of the estuary *S. maritima* is replaced by *Juncus kraussi* Hoschst. Day (1981b) reports that the biomass of these macrophytes is high but primary production in the Knysna system has not been determined.

The distribution, density and population structure of *U. africana* are described in Chapter 2 and discussed in relation to the physical characteristics of the estuary. Chapter 3 describes the methods and extent of the exploitation of *U. africana* by various groups of anglers. In Chapter 4, mud prawn reproduction and the recruitment of juveniles to the bait stock is investigated. A general discussion on the role of bait collectors as mud prawn predators, as well as some possible considerations for management of bait resources are presented in Chapter 5.

CHAPTER TWO

THE BAIT ORGANISM:

Distribution, density, biomass and population structure

INTRODUCTION

The thalassinidean prawns *Callinassa kraussi* and *Upogebia africana* are dominant members of the macrobenthos in many South African estuaries and make a large contribution to the total biomass of the macrobenthos (Day, 1981a). These animals dominate distinct communities in an estuary (McLachlan and Grindley, 1974). Where the substratum is sandy, *C. kraussi* is dominant. The mud prawn is absent from sandy areas, and occurs predominantly where the substratum consists of muddy sand (Day, 1981a).

Considerable information exists on the density of *U. africana* in South African estuaries (Table 2.1). Densities of 600 m⁻² in the Kowie estuary, and up to 500 m⁻² in the Swartkops estuary were recorded by Day (1981b) and Hodgson (1987) recorded similar densities of 120 - 500 m⁻² in the Kariega estuary. In the Swartkops estuary, *U. africana* was estimated to comprise over 78 % of the shell-free dry biomass of macrobenthos (Hanekom, 1980) and is the most abundant macrobenthic species (Hanekom *et al.*, 1988).

Table 2.1. Comparative ranges of *Upogebia africana* densities in some South African estuaries.

Estuary	<i>U. africana</i> m ⁻²	Reference
Bushmans	120	Hodgson, 1987 (Unpublished data)
Kariega	120 - 500	Hodgson, 1987
Knysna	20 - 220	Present study
Kowie	600	Day, 1981b
Kromme	100 ± 70	Hanekom, 1982
	10 - 100	Baird <i>et al.</i> , 1980
Langebaan	63 ± 16.4	Wynberg & Branch, 1991
Sundays	121 ± 79	du Preez, 1978
	90 - 180	Day, 1981b
Swartkops	218 ± 166	Hanekom <i>et al.</i> , 1988
	156 - 500	Day, 1981b

Hill (1977) compared the size compositions of *U. africana* populations from several South African estuaries. The inter-estuarine differences in the size of adult mud prawns noted by Hill (1977) were not as great as the intra-estuarine variations in size composition found by Hanekom and Erasmus (1988) in the Swartkops estuary. They discussed the nature of these variations and the factors which may have caused them. The factor suggested to account for the variations in the size of adult mud prawns, was the relative distance of the populations from the estuary mouth, with smaller mud prawns found towards the head of the estuary. In addition, the size of adult mud prawns tended to increase with decreasing tidal height (Hanekom and Erasmus, 1988). They suggested that differences in water movement and the associated transport of oxygen and food material within the estuary influenced the growth of *U. africana*.

Within South African estuaries, *U. africana* has its normal upper intertidal limit in the *Spartina* zone, is most abundant in the lower intertidal area and becomes uncommon below the *Zostera* belt (Day, 1981a). In the Swartkops estuary for example, the largest mud prawn populations (comprising c. 85 % of the macrobenthic numbers and biomass) were found in the muddy intertidal areas of the lower reaches of the estuary (Hanekom *et al.*, 1988). Hanekom and Baird (1992) have taken this work further and described the growth, production and consumption of mud prawns in the Swartkops estuary. An estimated 13 %, 5 % and 2 % of the annual somatic production of the entire estuarine population was consumed by birds, fish and man respectively. It was concluded however that the greatest contribution of *U. africana* to the Swartkops estuary ecosystem is by exuviae loss through the scavenger and detritus food web.

In the Knysna estuary, no specific studies on the macrobenthos or the effects of the increasing human pressure on the estuary have been carried out. In order to test the hypothesis that exploitation by bait collectors has no influence on the density and population structure of *U. africana* in the Knysna estuary, the present status of the mud prawn population in the estuary

was examined. The aims of this chapter were, therefore, to describe and compare the distribution, density, biomass and population structure of *U. africana* within the Knysna estuary in order to estimate the standing stock of mud prawns as a bait resource. The physical characteristics of the mud prawn habitats and other factors which may result in variation in density, biomass and population structure are assessed. These include sediment size structure and organic content and water temperature and salinity.

METHODS

Following a preliminary survey of the distribution of *Upogebia africana* within the Knysna estuary, six sites were chosen to assess mud prawn density, biomass and population structure (Fig. 2.1). These sites vary in distance from the estuary mouth and in the intensity of their exploitation by bait collectors. The first site was the Invertebrate Reserve (referred to as Reserve) which is a protected area where bait collecting is prohibited. However the area adjacent to the Reserve, at Leisure Isle, is a popular bait collecting site and was chosen to serve as a comparison. No sites were sampled south of Leisure Isle as this is the downstream limit of the distribution of *U. africana*. The Ashmead and Thesens sites are also exploited by bait collectors. The Ashmead site is in a protected channel east and north of Thesens Island, whereas the Thesens site is on the main channel of the estuary. In the middle reaches of the estuary, above the Railway Bridge, Oyster Bank was identified for study as it is only accessible by boat and is therefore relatively unexploited. The Red Bridge site in the upper reaches of the estuary, was sampled as it is near the up-estuary limit of mud prawn distribution. In addition to sampling the mud prawn populations at each of these sites, the sediment, water temperature and salinity were sampled. Hanekom and Erasmus (1988) have suggested that these factors may influence mud prawn density, biomass and population structure. The water at the Heads was sampled to gain an idea of the conditions at sea and of the water entering the estuary mouth.

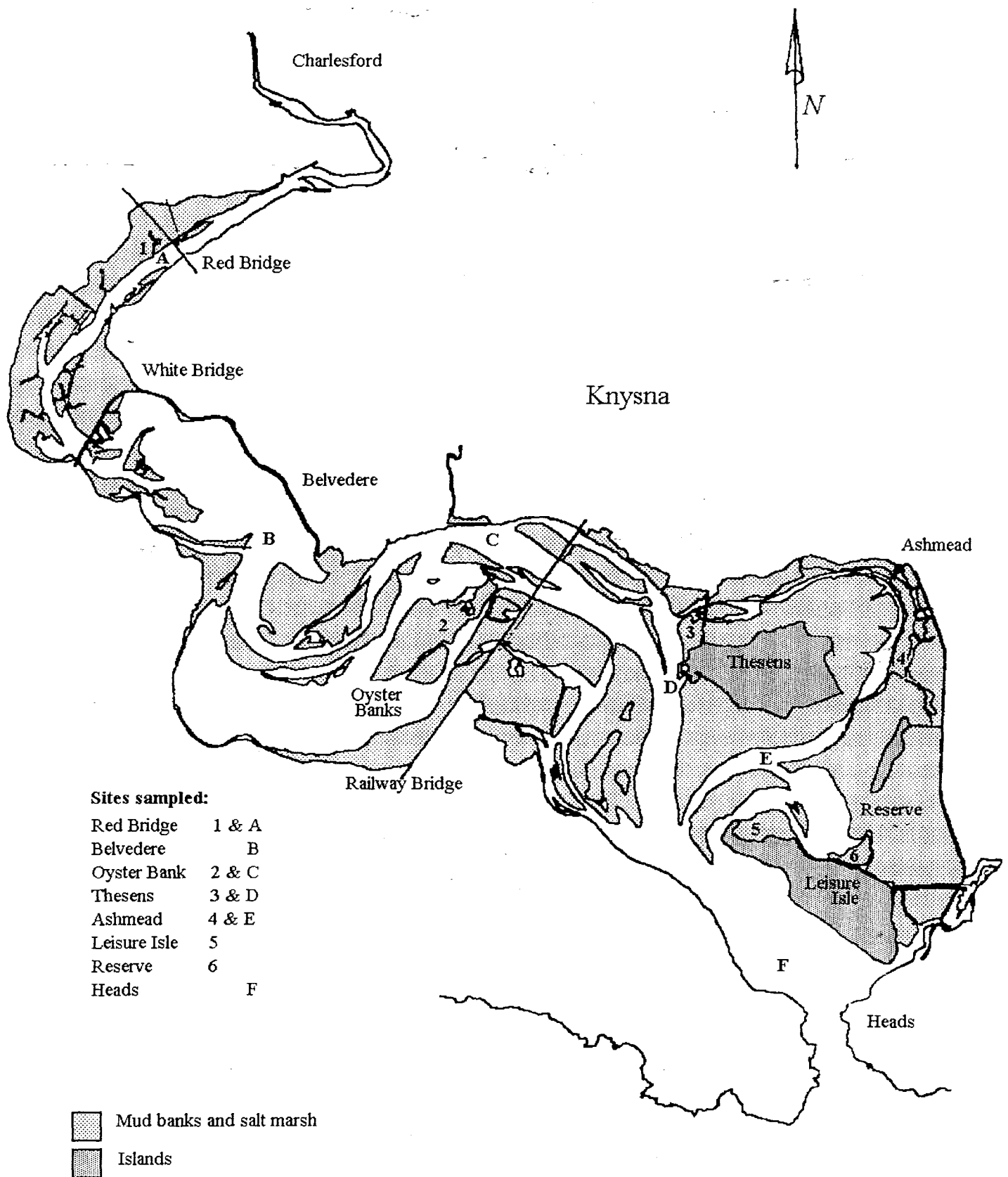


Figure 2.1. The Knysna estuary, showing the locations of the sites sampled for physical data (A - F) and the mud prawn populations studied (1 -6).

Scale: 1 : 50 000

Physical characteristics of the sites

Sediment composition

Sediment samples were collected from seven sites in the Knysna estuary. These included: northern and southern areas in the Invertebrate Reserve, the popular bait collecting sites of Leisure Isle, Ashmead and Thesens and the relatively unexploited areas of the Oyster Bank in the middle reaches and at Red Bridge in the upper reaches of the estuary (Fig. 2.1). At each site the *Spartina*, upper *Zostera* and lower *Zostera* zones were sampled. A core (10 cm diameter PVC pipe) of sediment was collected to a depth of 30 cm and dried to constant weight at 55°C. Sub-samples of 500-1000 g were disaggregated using a mortar and pestle and weighed in a weigh boat to the nearest 0.01 g.

In the analysis of sediment particle size, the range of particle diameters can cover orders of magnitude and therefore particle size is frequently represented on a logarithmic scale (in phi units). Samples were shaken through a series of Endecott sieves with mesh sizes of 2 mm, 1 mm, 500 μm , 250 μm , 125 μm and 63 μm (*i.e.* at whole phi unit intervals) for 10 minutes. Sieving is the most widely used method of determining particle sizes of sand-grade materials and the results have been shown to be highly reproducible (British Standards, 1975). The fraction of material remaining in each sieve was collected and weighed to 0.01 g. The particle size distribution data from each site were plotted as histograms and as cumulative frequencies (Zar, 1996).

Organic content of sediment

A procedure for the estimation of organic content by loss on ignition (British Standards, 1975) was used to estimate the organic content of the sediment samples. Numbers were etched onto crucibles, which were fired in a furnace to ensure that none of the loss of mass was due to loss of contaminants on the crucible. Sub-samples of 30-50 g were dried for 24 hours in a numbered crucible. The samples were allowed to cool in a desiccator and weighed to 0.001 g. The samples

were then fired in the furnace at 400°C for 12 hours. Samples were again allowed to cool in a desiccator, weighed to 0.001 g and the changes in mass calculated.

Temperature and Salinity

Every month water temperature and salinity were measured at six sites from the Red Bridge up-estuary, down to the Heads at the mouth (Fig. 2.1). Water samples were taken from the surface waters (0 - 0.5 m) and the measurements were made in the field using a mercury thermometer and hand-held optical refractometer respectively. Sampling commenced at the start of the ebb tide at the Red Bridge site and continued throughout the ebb tide down to the mouth.

Mud prawn distribution, density and biomass

Upogebia africana has characteristic burrow openings (Zoutendyk & Bickerton, 1988) making it possible to assess mud prawn distributional limits within the estuary by inspection of the holes. Intertidal banks from the mouth of the estuary at the Heads to the head of the estuary at the Charlesford rapids were visited and examined for the presence of mud prawns. The area of mud bank in the estuary and the area populated by the mud prawns was estimated from GIS (Geographic Information Systems) maps and aerial photographs of the estuary as well as ground truthing measurements.

At the five sites in the middle and lower reaches of the estuary, five habitats could be identified on each shore based on the vegetation present: The high salt marsh, *Spartina* zone, upper and lower *Zostera* zones and the subtidal zone, below low water springs (LWS). From preliminary observations on the distribution of the prawn burrows up the shore it was found that *U. africana* is distributed from within the *Spartina* zone to the subtidal. Up-estuary at the Red Bridge site, *Juncus* replaces the *Spartina* and the mud prawns are found from just below the *Juncus* zone to the subtidal area. Four different zones were identified for sampling: the *Spartina* zone (or just

below the *Juncus* at the Red Bridge site), the upper *Zostera* zone, the lower *Zostera* and bare mud patches (near the spring tide low water) and the subtidal zone. When a zone of sand was present this was also sampled.

Transects from the *Spartina* zone to the spring tide low water mark were carried out on two occasions. The Leisure Isle, Red Bridge and Thesens sites were sampled from the 6 - 8 November 1995 and the Bait Reserve, Ashmead and Oyster Bank sites were sampled on the 4 and 5 April 1996. Five 0.25 m² quadrats were dug to about 50 cm in each of the three zones present in the intertidal area at each site. Hanekom *et al.* (1988), from depth-stratified sampling found that 89 % of mud prawns were found in the top 25 cm of substratum and that a sampling depth of 30 cm was therefore adequate. A metal frame 50 cm high was forced into the substratum and the contents removed with a spade. The top 10 cm of mud were removed first and sieved through a 1mm mesh so that juvenile and newly settled individuals would not escape collection. The remaining approximately 40 cm of mud was sieved through a 3 mm mesh and all the prawns found were counted and preserved in 4 % formaldehyde in sea water.

Subtidal prawn densities were assessed using SCUBA diving equipment. A weighted line was placed perpendicular to the shore and every 5 m the number of burrow openings in ten 0.0625 m² quadrats were counted and the water depth recorded. Subtidal counts were carried out from the spring tide low water level to the distributional limit of the prawn burrows. A ratio of 2:1 (holes:prawns) was suggested for *U. africana* by Wynberg and Branch (1991) for the Langebaan lagoon and this conversion factor has been used in this study.

To express mud prawn densities as biomass, approximately 700 prawns were collected and measured. The tip of the rostrum to the hind margin of the carapace was measured to the nearest 0.01 mm using Vernier calipers (Hill, 1967; Hanekom and Erasmus, 1988). Siegfried (1962)

established that carapace length (hereinafter abbreviated as CL) is a reliable method of measure of prawn size with males having a slightly longer rostrum than female mud prawns. Wet masses were determined and the mud prawns were then dried to constant mass at 55°C. Dry masses were measured to the nearest 0.01 g. A linear regression of carapace length against dry mass was carried out on the data for male and female mud prawns and the equations derived were used to convert all prawn sizes to dry mass (Appendix I).

Population structure

The sexes of the prawns collected in the quadrat samples were used to calculate the ratio of male, female and juvenile prawns. Prawns less than 10 mm carapace length were classed as juveniles, as the smallest ovigerous females found have been in this size class (Hill, 1977). The lengths of the same prawns collected in the quadrat samples were grouped into 1 mm size classes and size frequency histograms were constructed for each zone and each site.

Data Analysis

To test the hypothesis erected in Chapter 1, it was necessary to collect measurements of mud prawn density, biomass and size as well as measurements of the physical characteristics of the environment, in three zones on each shore and at a number of sites up the estuary. This type of multisample hypothesis, with sampling from three or more populations, requires a multisample analysis (Zar, 1996). An Analysis of Variance (ANOVA) assumes that the variances of the populations sampled are equal and that the data are normally distributed. ANOVA tests whether the population means are equal, if they are not, then H_0 is rejected. The ANOVA is robust, even with considerable heterogeneity of variances. It is also robust with respect to the underlying assumption that the data are from a normal population and its validity is affected only slightly by large deviations from normality (Zar, 1996). An ANOVA tests for the effect of a single factor on a variable (*e.g.* sediment composition on prawn density). A Multifactor Analysis of Variance

(MANOVA) is a simultaneous analysis of the effect of more than one factor on the population means (Zar, 1996). Measurements of biological and physical data collected from different zones and sites were tested for differences in their population means by an ANOVA or MANOVA (depending on the number of factors affecting the variable).

An Analysis of Variance tests the null hypothesis, but the rejection of the null hypothesis does not imply that all population means are different from one another. In order to determine where the differences are located among the population means if the null hypothesis is rejected, an ANOVA is often followed by a Multiple Comparison Test (Zar, 1996). Scheffe's Multiple Range Test is an example of a multiple comparison test which can be used to compare combinations of groups (Zar, 1996). This method is particularly useful for testing unplanned contrasts between means as it tests for significant differences between all possible pairs of means (Sokal and Rohlf, 1981). In cases where a significant difference was found between population means, a Multiple Range Test was carried out to determine where the differences occurred. Statgraphics version 7.0 was used to perform statistical analyses and SigmaPlot (Jandel Scientific Software) was used to represent data and statistical results graphically.

Size frequency histograms of the *U. africana* population were analysed using FISAT (Fisheries Stock Assessment Tools). The means of the distributions were estimated by Bhattacharya's method. Hasselblad's NORMSEP analysis then used these means to separate the size frequency distributions into their component normal distributions (Sparre and Venema, 1992; Gayanilo, Sparre and Pauly, 1996). The maximum likelihood principle is applied in these analyses, in which the measure of goodness of fit is closely related to the chi-squared criterion. The separation of length frequency data into their components is an iterative process. An exposed or uncontaminated slope of a normal distribution on the left side of the total distribution is determined. The normal distribution of the first cohort is determined by transformation to a

straight line. The number of mud prawns per length group belonging to the first cohort are subtracted from the total distribution. These steps are repeated until no more normal distributions can be found (Sparre & Venema, 1992; Gayanilo *et al.*, 1996). This method is based on the same principle as Cassie's method (1954) used by Hanekom & Baird (1992) to determine the growth curve of *U. africana* from the Swartkops estuary.

RESULTS

Physical characteristics of the sites

Sediment composition

The results of the particle size distribution of the sediment are not conclusive as the sediment was not wet sieved prior to dry sieving. The finer estuarine mud may have formed conglomerates and influenced the sieving results. The general trend is however unlikely to be affected. At all the sites, except the Red Bridge, the modal particle size of the sediments was 0.125 mm - 0.250 mm diameter (Fig. 2.2). The sediment at the Red Bridge was coarser than at the other sites, with a modal particle size of 0.5 mm - 0.1 mm. Figure 2.3 illustrates that the sediment structure at the six sites in the lower reaches of the estuary is very similar, whereas at the Red Bridge sediment structure is different.

As there were no significant differences between the percentages of subsieve particles ($< 63\mu\text{m}$) in the three zones sampled on each shore ($p > 0.05$, MANOVA; Table 2.2), the data from each site was pooled and the means (\pm S.E.) plotted in Figure 2.4. The Bait Reserve (south), Oyster bank and Ashmead sites show slightly higher mean percentages (4.3 - 6 %) of particles $< 63\mu\text{m}$ in diameter, than the other sites (1.3 - 2.8 %). The only significant differences in percentage subsieve ($p < 0.005$, MANOVA; Table 2.2) however, are between the Bait Reserve (south) and Leisure Isle and Thesens sediments ($p = 0.0017$ MANOVA) (Table 2.3).

Table 2.2. Results of a Multifactor Analysis of Variance to determine whether there are any significant differences in the percentage subsieve sediment between zones (over all sites) and between sites sampled (over all zones).

Variation	Sum of squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECTS					
Zone -	12.30	3	4.10	2.925	0.0772
Site	62.23	6	10.37	7.402	0.0017
RESIDUAL	16.81	12	1.40		
TOTAL	99.40	21			

Table 2.3. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the percentage of subsieve particles between the seven sites sampled.

Site	n (samples)	Mean %	Homogeneous groups	
Leisure Isle	3	0.98	X	
Thesens	4	1.07	X	
Red Bridge	3	1.72	X	X
Reserve (north)	3	2.42	X	X
Ashmead	3	3.94	X	X
Oyster Bank	3	4.82	X	X
Reserve (south)	3	5.61		X

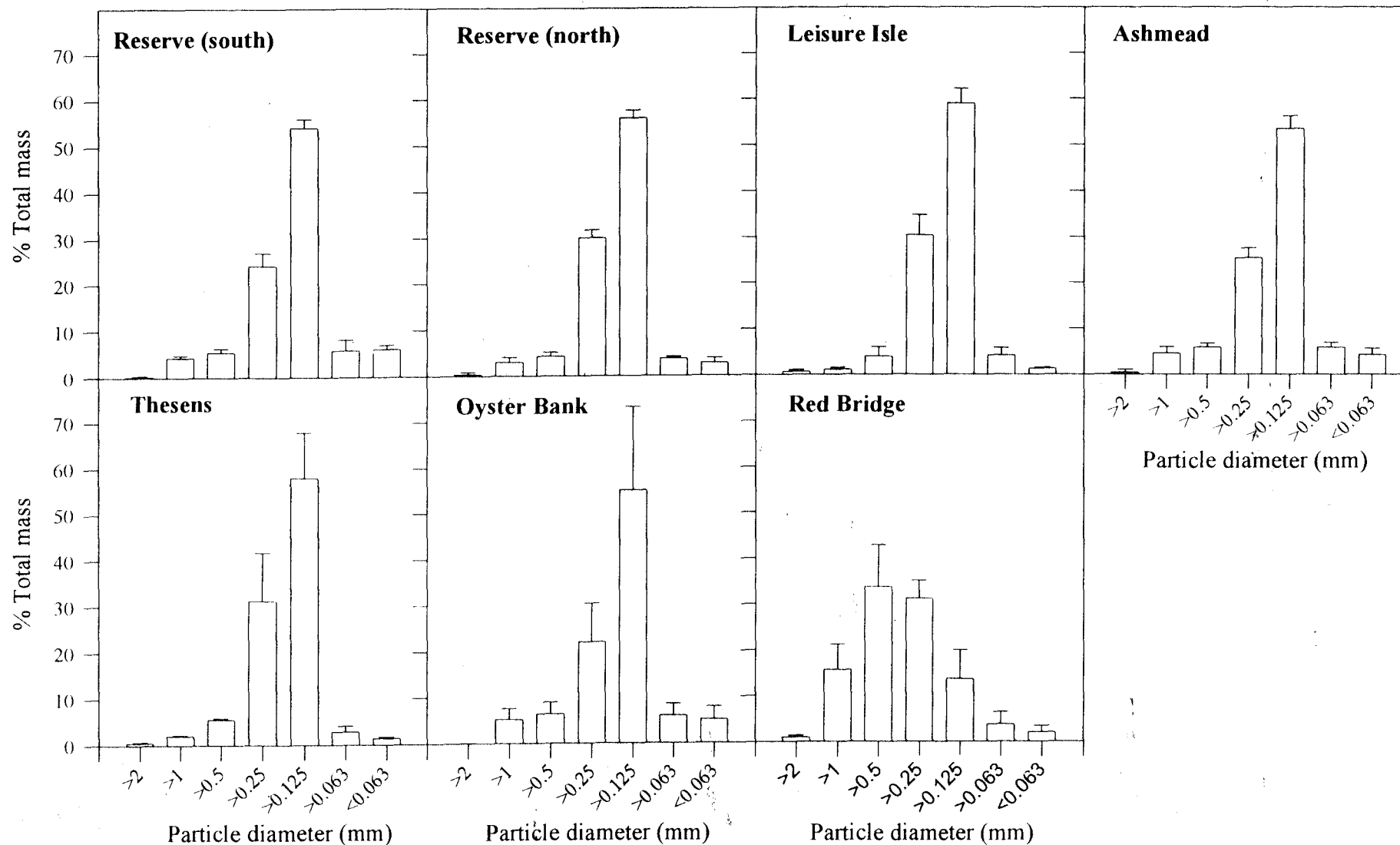


Figure 2.2. Particle size distribution of sediment where the mass of material (as a percentage of the total sample mass) is plotted as a size fraction coarser than each size. Size classes are based on whole phi units.

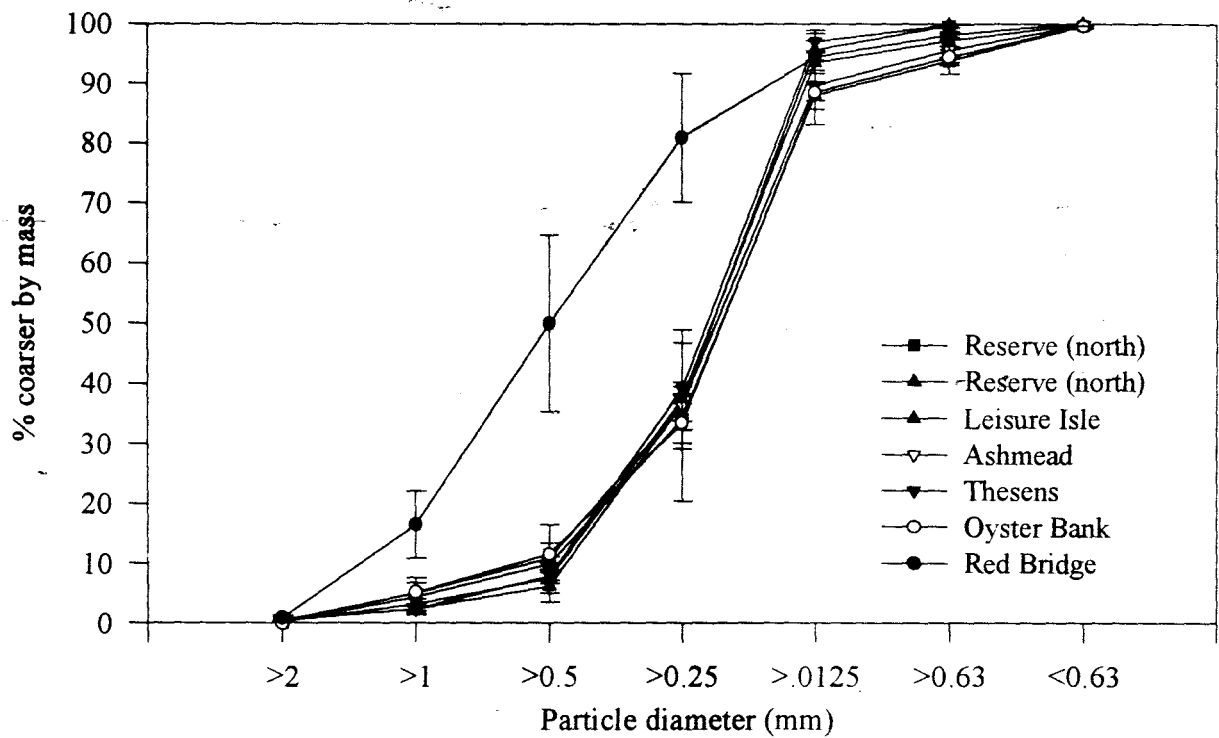


Figure 2.3. Mean percentage sediment (by mass) plotted as cumulative frequencies against particle sizes. Size classes are based on whole phi units and standard errors of the means are shown.

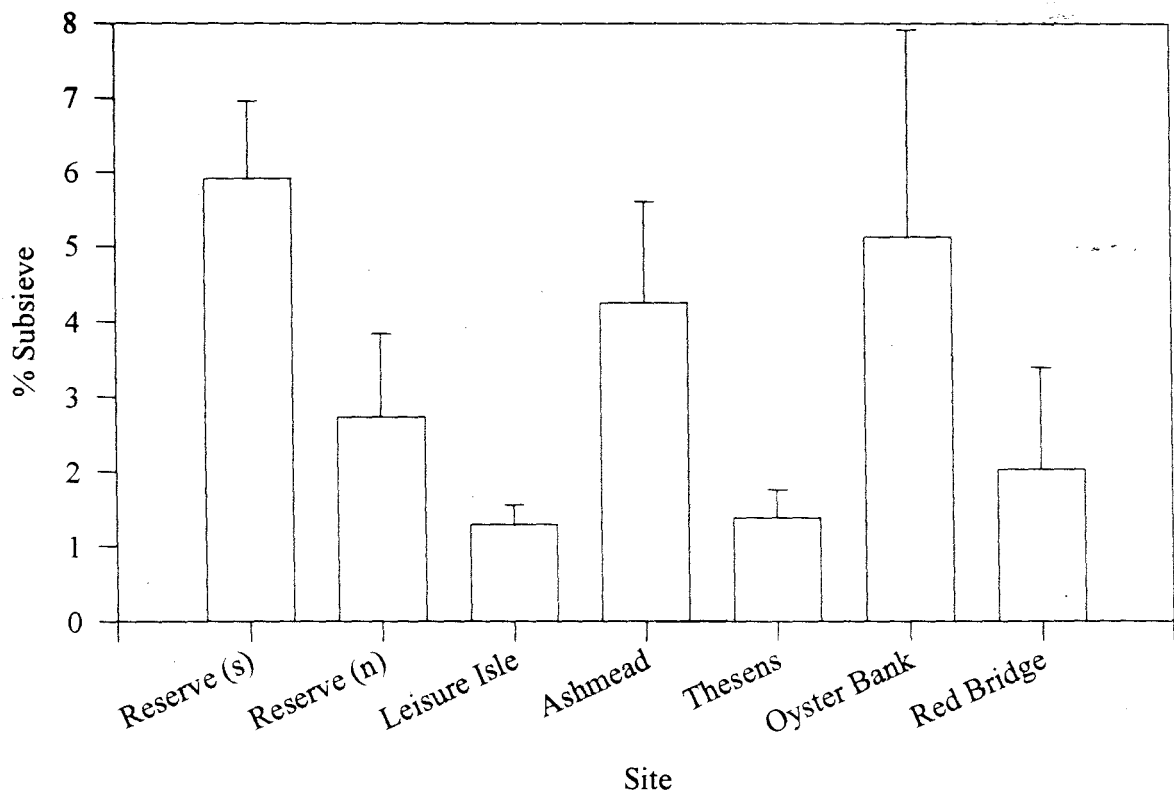


Figure 2.4. Mean percentage subsieve of all three zones per site (with standard error bars) at seven sites in the Knysna estuary.

Organic content of sediment

No significant difference was found in the 'organic content' of the sediment from each of the three zones sampled at each site ($p > 0.05$, MANOVA; Table 2.4). The mean percentages are illustrated in Figure 2.5. The Red Bridge sediment has a slightly higher ($\bar{x} = 2.7\%$), and significantly, different ($p = 0.0491$, MANOVA) percentage of combustible material, than that of the other five sites ($\bar{x} = 0.9 - 1.5\%$) (Table 2.5).

Table 2.4. Results of Multifactor Analysis of Variance to determine whether the percentages of combustible material are significantly different between zones (over all sites) and between sites (over all zones).

Variation	Sum of squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECT					
Zone	2.1422085	3	0.7140695	1.626	0.2354
Site	7.9453390	6	1.3242232	3.015	0.0491
RESIDUAL	5.2698936	12	0.4391578		
TOTAL	15.870352	21			

Table 2.5. Results of Scheffe's Multiple Range Analysis to determine whether the percentages of combustible material are significantly different between sites (over all zones).

Site	n (samples)	Mean %	Homogeneous groups
Leisure Isle	3	0.787	X
Reserve (north)	3	0.825	X
Thesens	4	0.865	X
Ashmead	3	0.923	X
Reserve (south)	3	1.005	X
Oyster Bank	3	1.532	X
Red Bridge	3	2.618	X

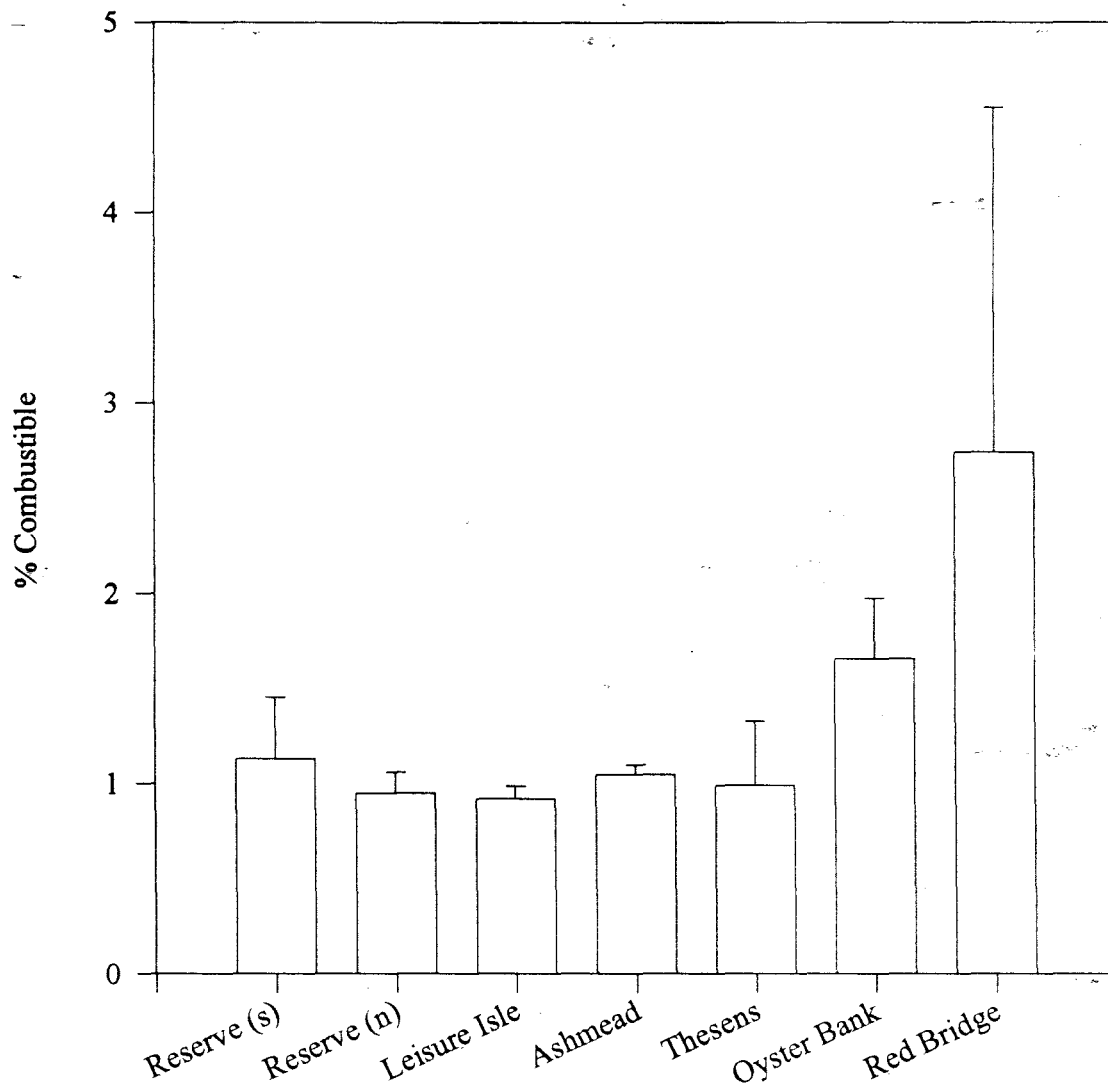


Figure 2.5. Mean percentage of combustible material of all three zones per site (with standard error bars) at seven sites in the Knysna estuary.

Temperature and Salinity

The monthly variations in water temperature at all sites were similar (13°C - 25°C; Fig. 2.6a & b), however on a shorter time scale large fluctuations occurred due to upwelling (e.g. April 1996). Following an upwelling event the temperature of the sea may drop by as much as 10°C over a few hours (Schumann, unpublished data). These conditions cause the water temperature to fall to approximately 10°C at the Heads, Ashmead and Thesens, but have less influence on sites above the Railway Bridge where temperatures remain above 15°C (April 1996; Fig. 2.6 a & b). Since the flow of fresh water from the Knysna river into the estuary is the major factor influencing salinity, the opposite is true for variations in salinity. The Red Bridge and even Belvedere sites can experience a wide range of salinities (9 - 34 ‰ and 23 - 35 ‰ respectively; Fig. 2.6 a). Salinities at sites from the Railway Bridge seaward are relatively stable and remain close to the salinity of the seawater of the surrounding coast at 35 ‰ (Fig. 2.6 b).

Mud prawn distribution, density and biomass

The mud prawn is present in the intertidal region of most mud banks from the *Spartina* belt down to the *Zostera* zone at the spring tide low water level. This represents a fairly narrow band (approximately 50 - 80 m wide) of the total area of mudbank in the Knysna estuary. As expected *Upogebia africana* is absent from the sandy marine areas at the mouth of the estuary as well as the channels between mud banks (Fig. 2.7). The mud prawns are also absent from the more estuarine areas above Red Bridge. Possible explanations for this distribution are presented in the discussion which follows. The total area of intertidal mud bank (sand flats and high saltmarsh were excluded) in the estuary was estimated to be 5669122 m² or 566.9 ha and the area inhabited by *U. africana* to be 3468872 m² or 346.9 ha. From these estimations, 61.2 % of the intertidal mud bank area is inhabited by mud prawns.

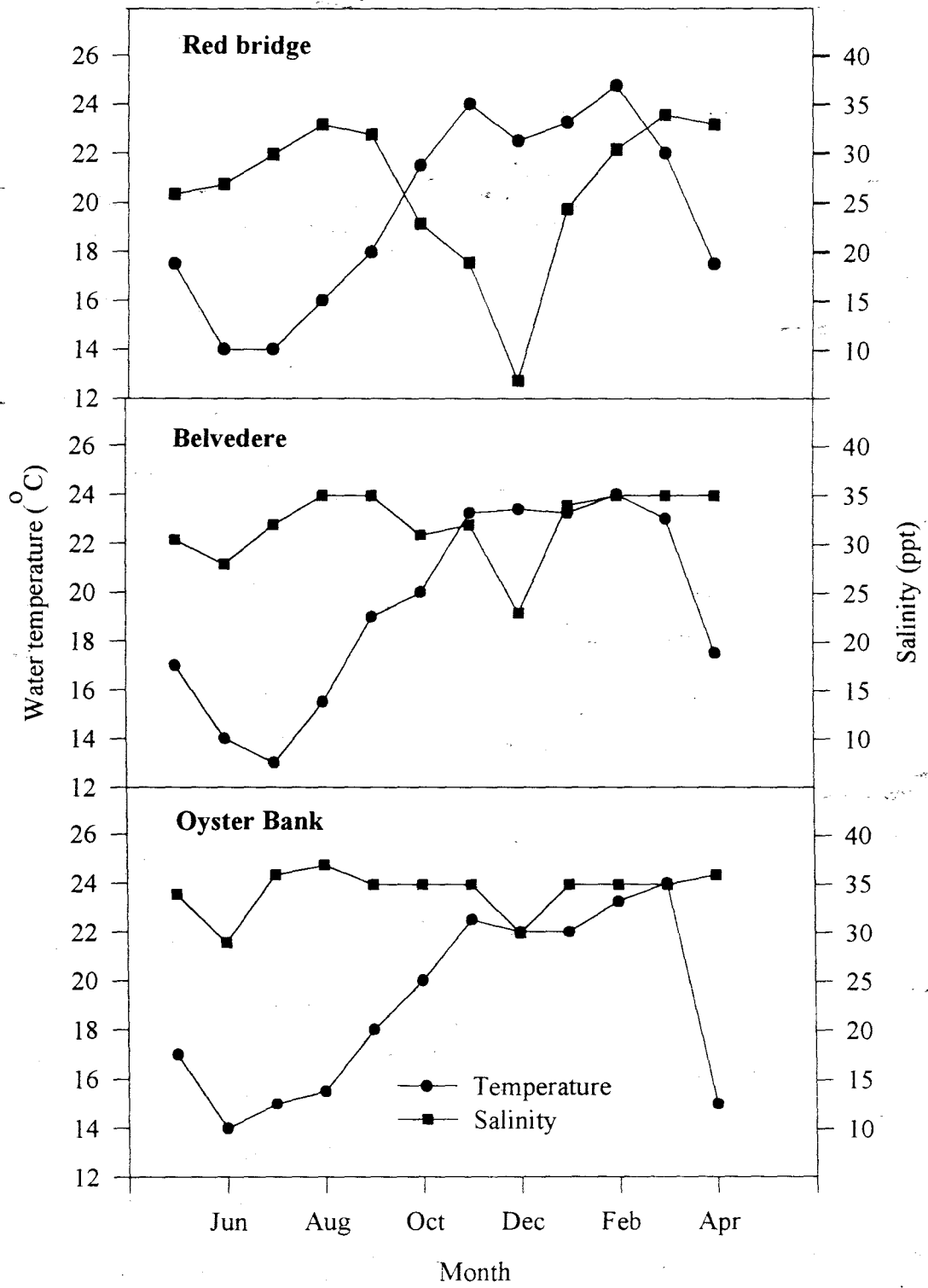


Figure 2.6a. Water temperature and salinity at Red Bridge, Belvedere and Oyster Bank over 12 months.

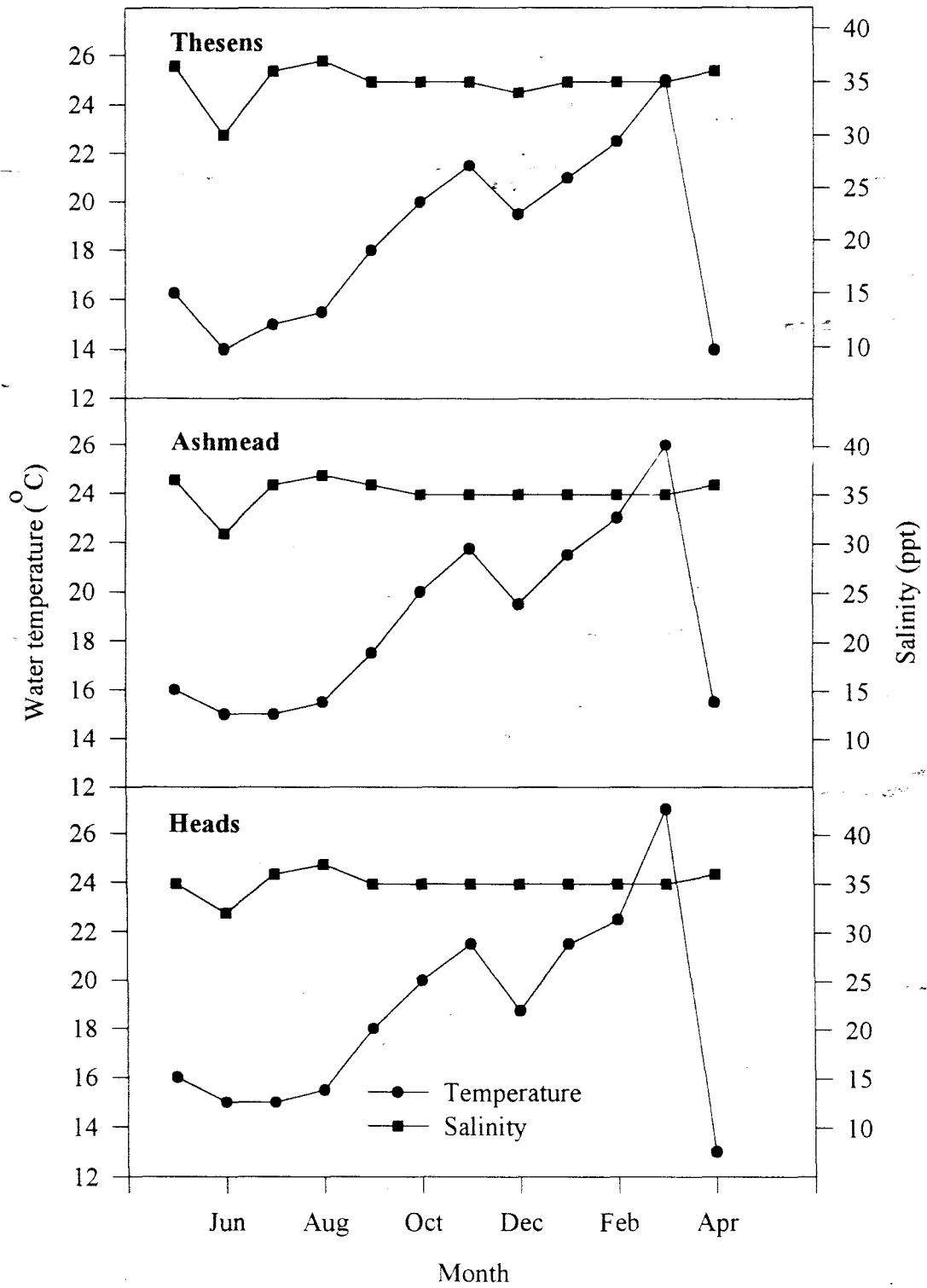


Figure 2.6b. Water temperature and salinity at Thesens, Ashmead and the Heads over 12 months.

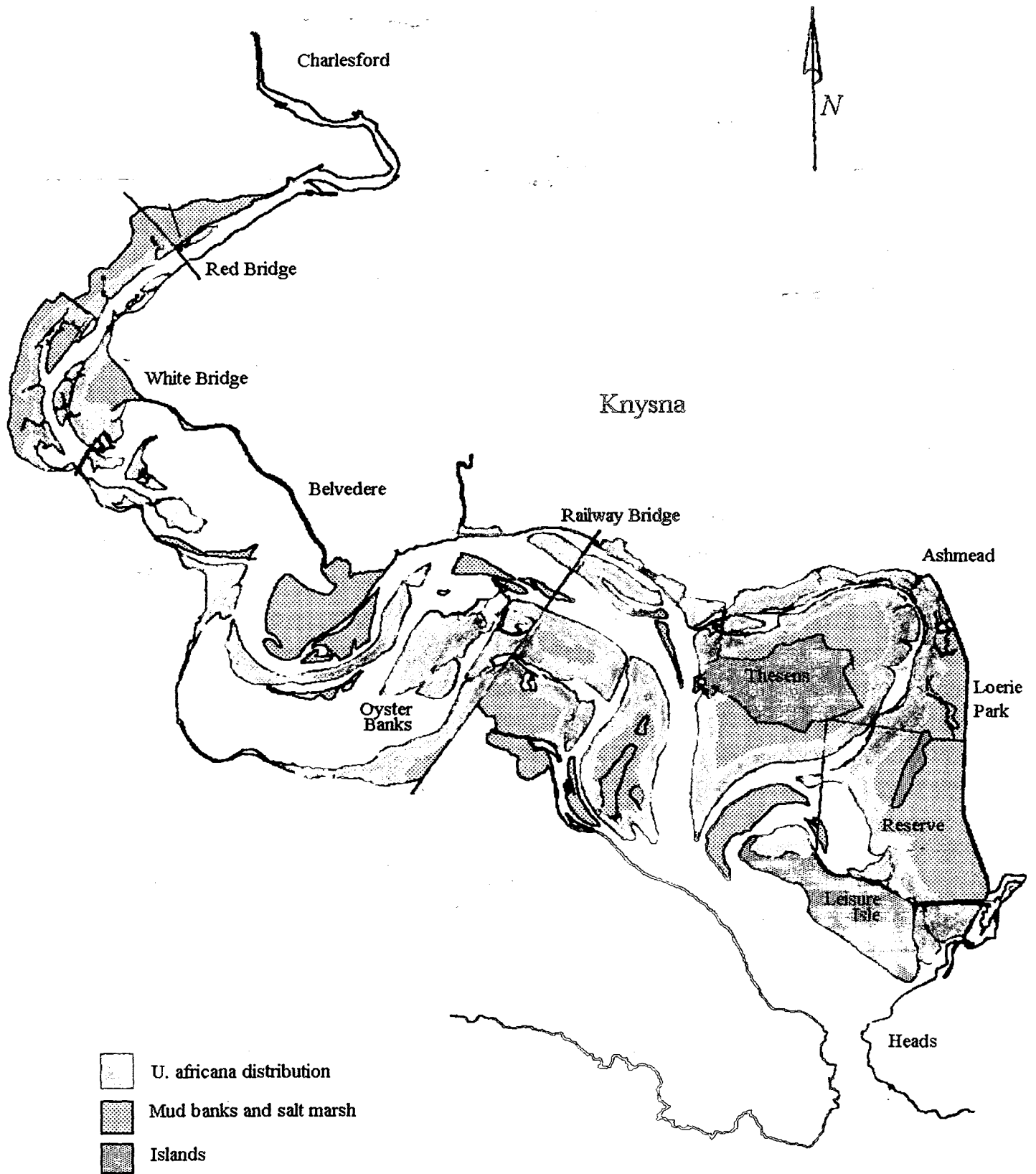


Figure 2.7. The Knysna estuary, showing the intertidal distribution of *U. africana* (Scale 1 : 50 000).

In the lower, middle and upper reaches of the estuary the density and biomass of *U. africana* was very variable. Mean densities and biomass in the intertidal zone ranged from less than 20 m⁻² and 5 g.m⁻² (dry mass) in the Reserve and 50² m and 2² g.m (dry mass) at Red Bridge, to approximately 220 m⁻² and more than 60 - 70 g.m⁻² (dry mass) at Oyster Bank (Figs. 2.8 & 2.9). Both the density (Table 2.6) and biomass (Table 2.7) of mud prawns at the Oyster Bank are significantly higher ($p < 0.0001$, MANOVA) than at Leisure Isle, which in turn has a significantly greater density and biomass than the other four sites (Table 2.8).

Table 2.6. Results of a Multifactor Analysis of Variance to determine whether prawn densities are significantly different between the zones sampled (over all sites) and between the sites sampled (over all zones).

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECTS					
Zone	28828.28	2	14414.14	17.467	0.0000
Site	312455.55	5	62491.11	75.726	0.0000
RESIDUAL	75921.06	92	825.2300		
<hr/>					
TOTAL	405900.00	99			

Table 2.7. Results of a Multifactor Analysis of Variance to determine whether prawn biomass varies significantly different between the zones sampled (over all sites) and between the sites sampled (over all zones).

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECTS					
Zone	2049.52	2	1024.76	5.984	0.0036
Site	50402.65	5	10080.53	58.866	0.0000
RESIDUAL	15754.45	92			
<hr/>					
TOTAL	66804.55	99			

Table 2.8. Results of Scheffe's Multiple Range Analysis to determine any significant differences in the density and biomass of *U. africana* at six sites in the Knysna estuary.

Site	n (samples)	Mean Density (m ⁻²)	Mean Biomass (g.m ⁻²)	Homogeneous groups	
Reserve	20	11.75	3.91	X	
Red Bridge	15	21.87	1.73	X	
Ashmead	15	35.47	13.61	X	
Thesens	15	37.33	15.58	X	
Leisure Isle	20	96.61	42.96		X
Oyster Bank	15	176.53	65.29		X

There is no obvious relationship between intertidal density or biomass with height above LWS at each site (Figs. 2.8 & 2.9). At the Reserve and Ashmead, density increased in the lower intertidal zones (*Zostera* zones), while at the Thesens and Oyster Bank sites, prawn density was highest in the *Spartina* zone. When the data from all sites were combined and compared using a Multifactor Analysis of Variance, the mean density (Table 2.6) and mean biomass (Table 2.7) of prawns are significantly lower ($p < 0.0001$ and $p < 0.005$ respectively) in the upper *Zostera* zone (39.2 m⁻² and 17.5 g.m⁻²), than in the *Spartina* zone above it (74.3 m⁻² and 26.1 g.m⁻²) and the lower *Zostera* zone below (76.3 m⁻² and 27.9 g.m⁻²; Table 2.9).

Table 2.9. Results of Scheffe's Multiple Range Analysis to determine any significant difference in the density and biomass of *U. africana* in three zones of the intertidal mudbanks.

Zone	n (samples)	Mean Density (m ⁻²)	Mean Biomass (g.m ⁻²)	Homogeneous groups	
Upper <i>Zostera</i>	35	39.24	17.54	X	
<i>Spartina</i>	30	74.27	26.09		X
Lower <i>Zostera</i>	35	76.27	27.91		X

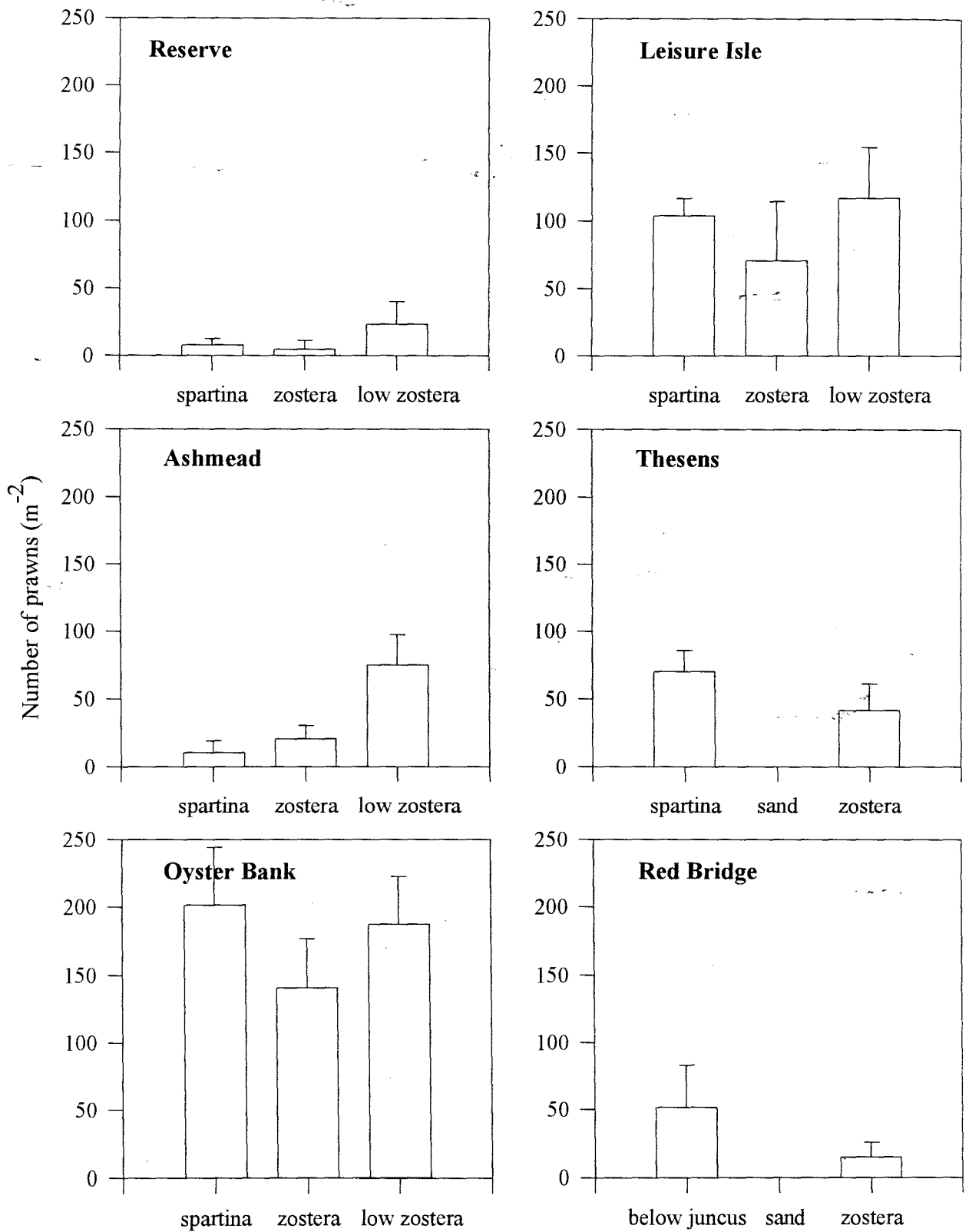


Figure 2.8. Mean density (numbers m⁻²; with standard error bars) of *U. africana* in three intertidal zones at six sites in the Knysna estuary.

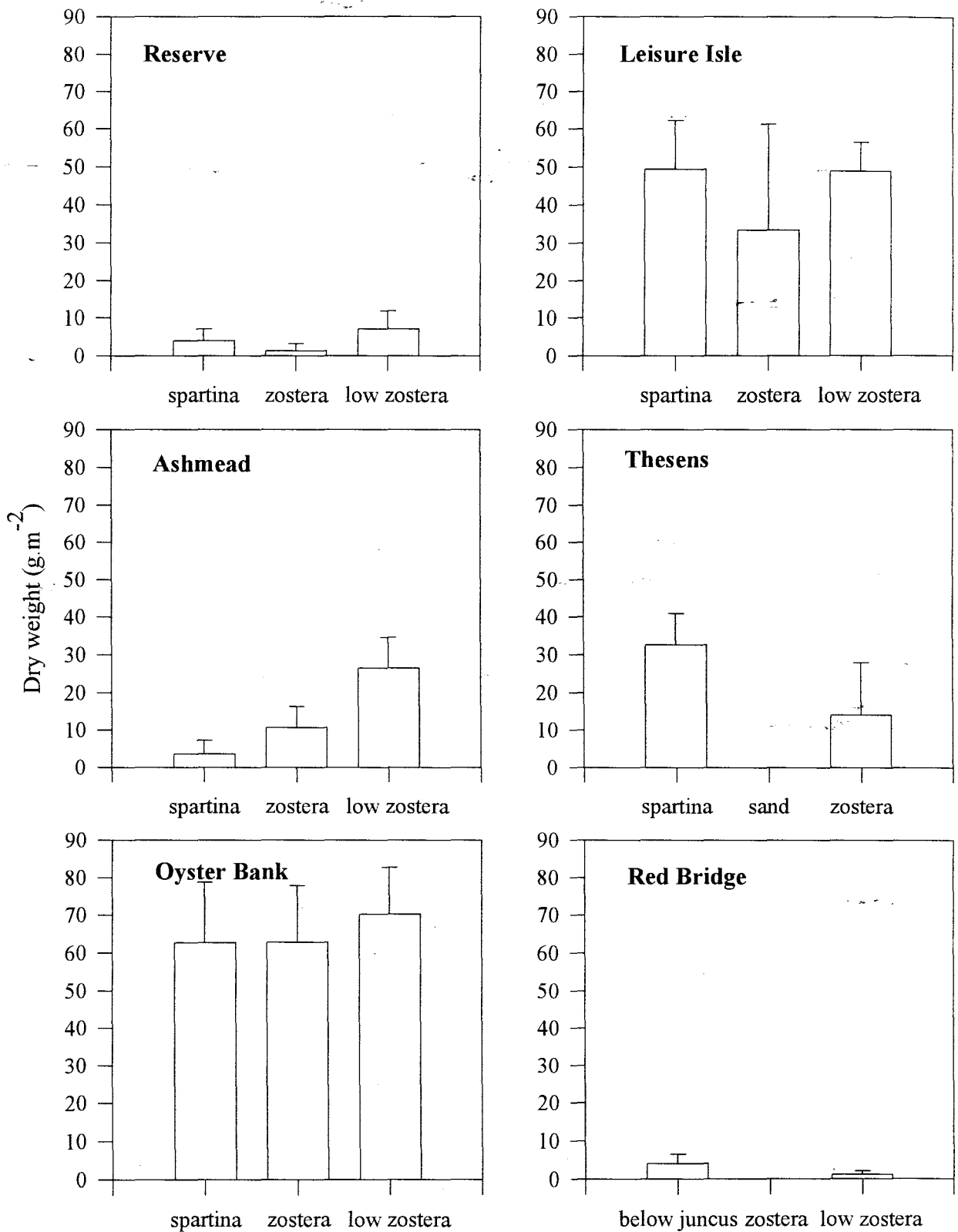


Figure 2.9. Mean biomass (g m^{-2} ; with standard error bars) of *U. africana* in the three intertidal zones at six sites in the Knysna estuary.

Subtidal mud prawn densities were highest in the shallow areas within 5 m of LWS, which are possibly exposed at equinox spring low tides (Fig. 2.10). The subtidal area within 10 m of LWS at the Oyster Bank has prawn densities of 60 - 75 m⁻² and up to 35 m⁻² were recorded subtidally within 5 m of LWS in the shallow channel at Ashmead. At all sites, as the depth and the distance from LWS increased, mud prawn density decreased (Fig. 2.10). The variability in densities was high as subtidal mud prawn distribution was patchy. No mud prawn burrows were found below the low water spring tide level at Leisure Isle and Red Bridge.

Population structure

The percentage of females (52.1 %) found in the *U. africana* population in the Knysna estuary is similar to that found by Hill (1977) for the Knysna estuary, although these percentages are slightly lower than those found in the Swartkops and Uilenkraal estuaries (Table 2.10).

Table 2.10. The percentage that is female of various populations of *U. africana* from some South African estuaries.

Site	% female	Reference
Kowie estuary	50 %	Hill (1977)
Knysna estuary	52.1 %	Present study
Knysna estuary	50.4 %	Hill (1977)
Knysna heated pond	67.5 %	Hill (1977)
Swartkops estuary	56 - 60 %	Hanekom & Baird (1992)
Swartkops lower reaches	62 %	Hanekom & Erasmus (1989)
Swartkops middle reaches	56 %	Hanekom & Erasmus (1989)
Uilenkraal estuary	%	Hill (1977)

The percentages of male, female and juvenile mud prawns varied from 19.5 - 45 %, 10.9 - 52 % and 9.3 - 69.5 %, respectively (Table 2.11). The percentages of male and female *U. africana* in each population are however not significantly different ($p > 0.05$ at all sites, Chi-square statistic). The percentage of mud prawns less than 10 mm carapace length (CL) at Red Bridge (69.51 %) is significantly higher than at the other 5 sites sampled ($p < 0.005$, Chi square statistic; Table 2.11).

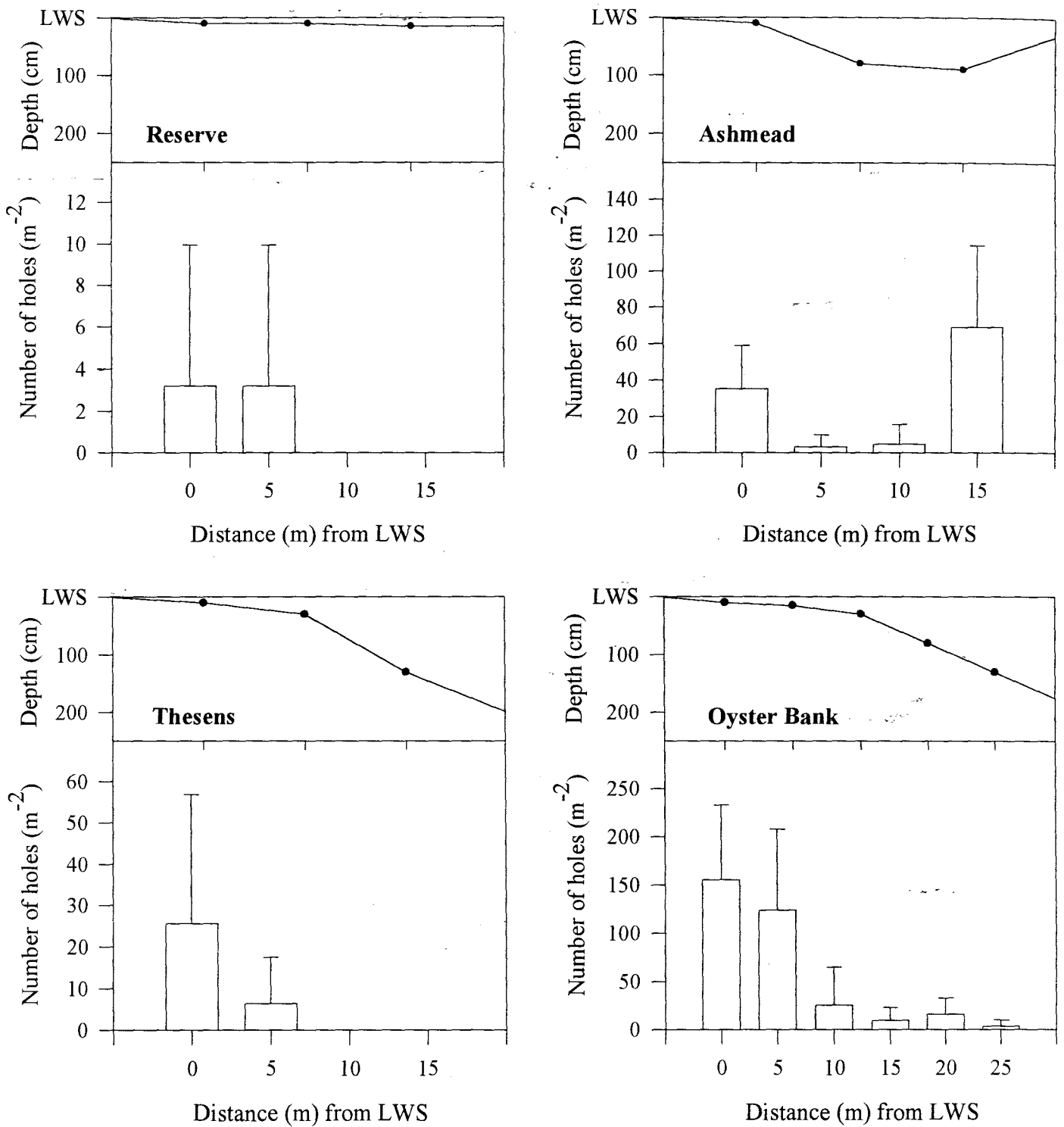


Figure 2.10. Mean number of prawn holes (with standard error bars) at 5m intervals from low water spring (LWS) at four sites (Leisure Isle and Red Bridge sites have no mud prawns subtidally). Above each histogram is a plot of the profile of the shore.

Table 2.11. The percentages of male, female and juvenile prawns at each of six sites in the Knysna estuary.

Site	Male	Female	Juvenile
Reserve	38.67	52.00	9.33
Leisure Isle	39.69	48.68	11.62
Ashmead	42.42	47.72	9.85
Thesens	44.68	34.75	20.57
Oyster Bank	39.47	41.97	18.56
Red Bridge	19.51	10.98	69.51

Sizes of adult *U. africana* (CL > 9.9 mm) vary significantly between the three zones sampled ($p = 0.005$, MANOVA; Table 2.12) and are highly significantly different between the six sites up the estuary ($p < 0.0001$, MANOVA; Table 2.12). Mud prawns from the *Spartina* zone are significantly smaller than those from the upper *Zostera* zone (Table 2.13). Table 2.14 shows that the mean adult mud prawn size from Red Bridge (10.9 mm CL) is significantly smaller than those from the all five of sites lower down the estuary (14.4 mm - 15.9 mm CL).

Table 2.12. Results of Multifactor Analysis of Variance to determine whether adult prawn sizes are significantly different between the three zones sampled and between the six sites sampled in the Knysna estuary.

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECTS					
Zone	100.60	2	50.30	5.2990	0.005
Site	505.04	5	101.01	10.641	0.0000
RESIDUAL	10983.11	1157	9.49		
TOTAL	11631.00	1164			

Table 2.13. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in adult prawn size between the three zones sampled on each shore.

Zone	(n) prawns	Mean Size (mm)	Homogeneous groups	
<i>Spartina</i>	440	14.22	X	
Lower <i>Zostera</i>	405	14.75	X	X
Upper <i>Zostera</i>	320	14.95		X

Table 2.14. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in adult prawn size from different sites in the Knysna estuary.

Site	(n) prawns	Mean size (mm)	Homogeneous groups	
Red Bridge	19	10.90	X	
Reserve	63	14.41		X
Oyster Bank	499	15.39		X
Ashmead	96	15.57		X
Leisure Isle	377	15.67		X
Thesens	111	15.91		X

At all sites sampled, more juvenile prawns were found in the *Zostera* zones than higher up the shore (Fig. 2.11 a, b & c). At some sites, e.g. Leisure Isle, Thesens, Oyster Bank and Red Bridge, the *Spartina* zone contained more large adults (> 20 mm CL) than the *Zostera* zones.

When the length frequency data for each site were combined (Fig. 2.12 a & b), at the sites in the lower reaches, the mud prawns ranged in size from 3 mm CL to 25 mm CL. The largest mud prawns found at Red Bridge in the upper reaches were however less than 12 mm CL. Each distribution of length frequency data was fitted with component normal distributions so that the expected composite distribution was not significantly different ($p > 0.05$) to the observed total distribution. The results of Hasselblad's NORMSEP analysis (FiSAT) are illustrated in Figure 2.13 and summarised in Table 2.15. The separation index was calculated by dividing the difference between two successive means by the difference between their estimated standard deviations. As a guideline, this value should be equal to or greater than two (Gayanilo *et al.*, 1996).

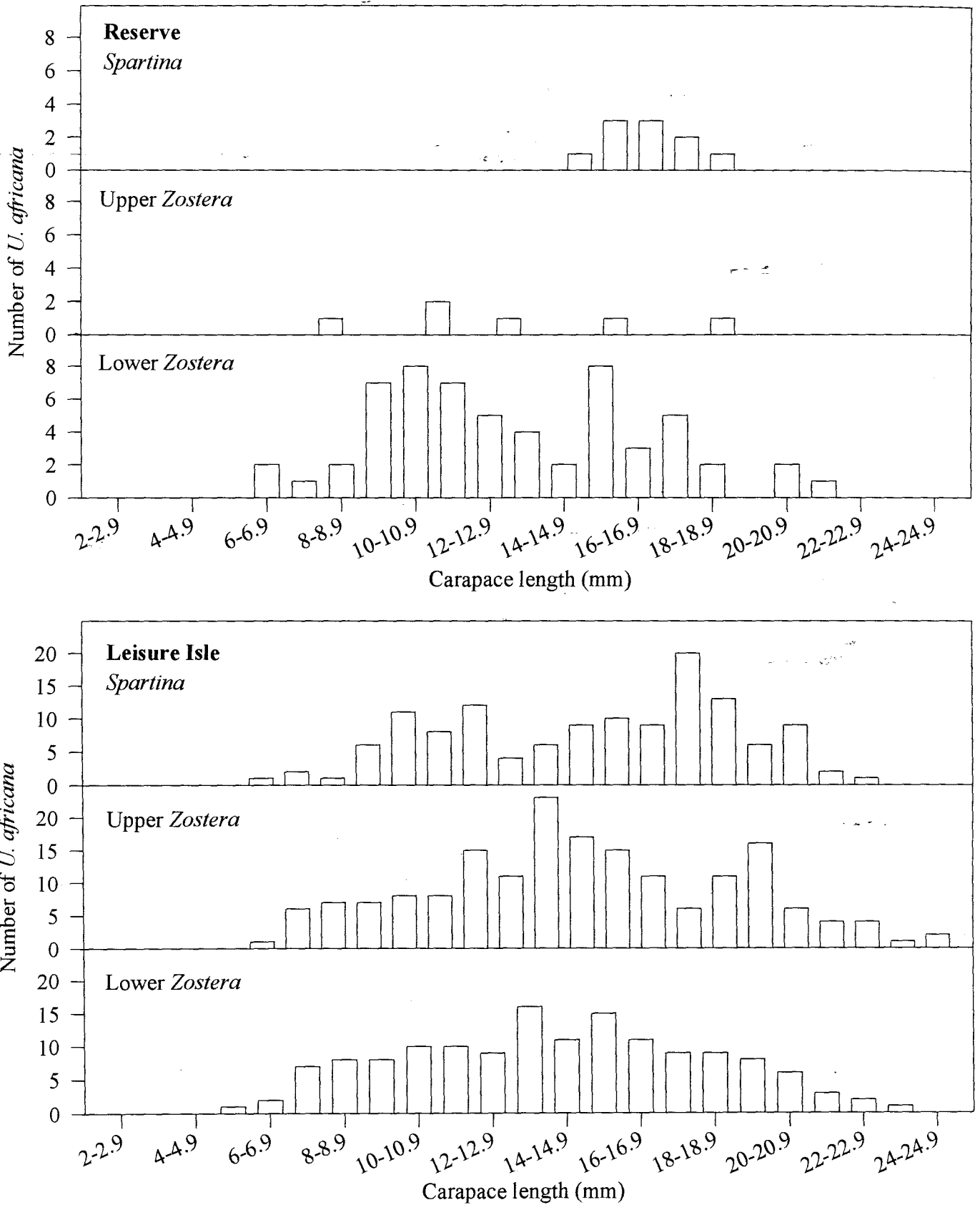


Figure 2.11a. Length frequency distributions of the prawn populations from 3 zones at the Reserve and Leisure Isle sites.

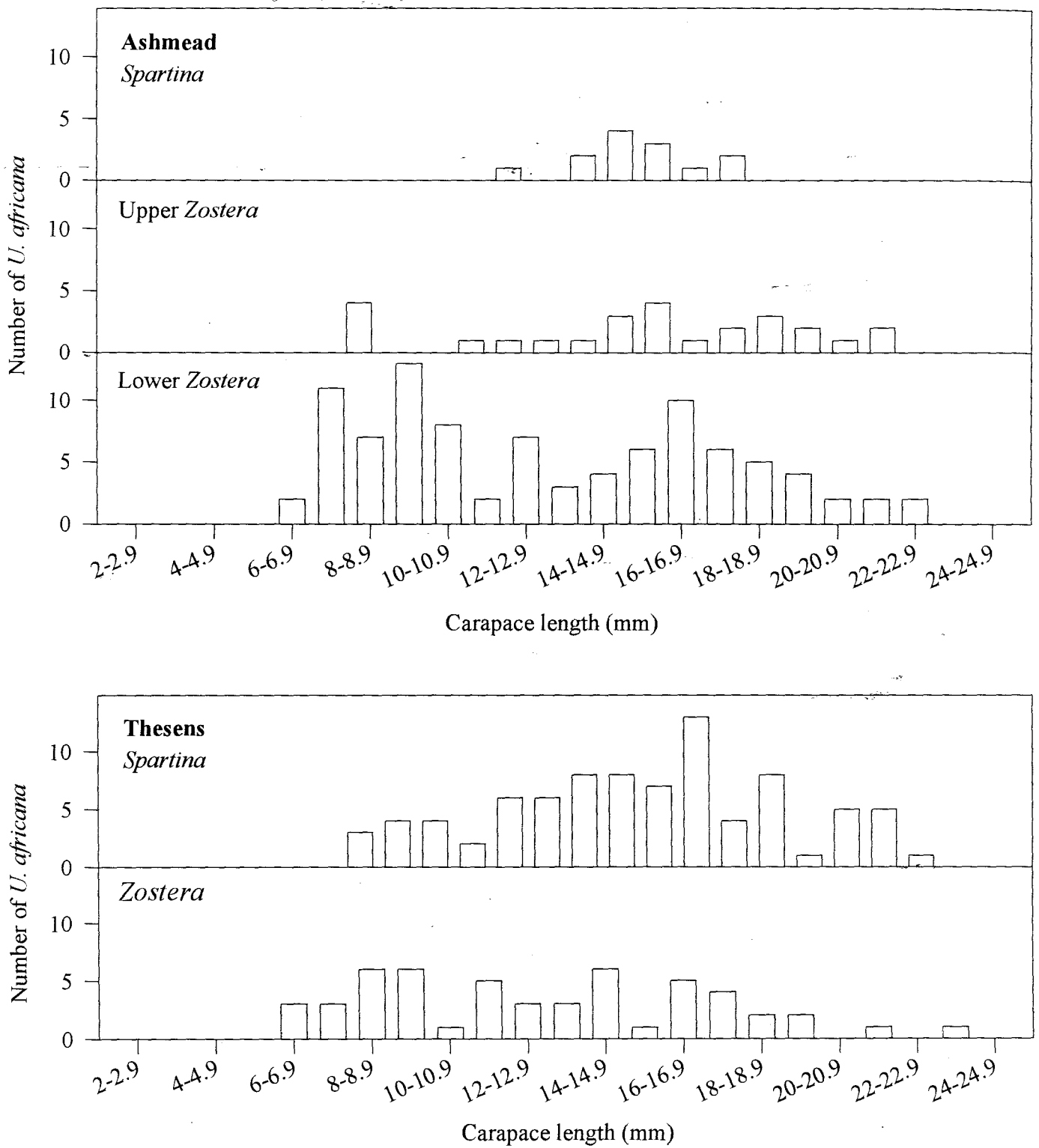


Figure 2.11b. Length frequency distributions of the prawn populations from 3 zones at Ashmead and 2 zones at Thestens sites.

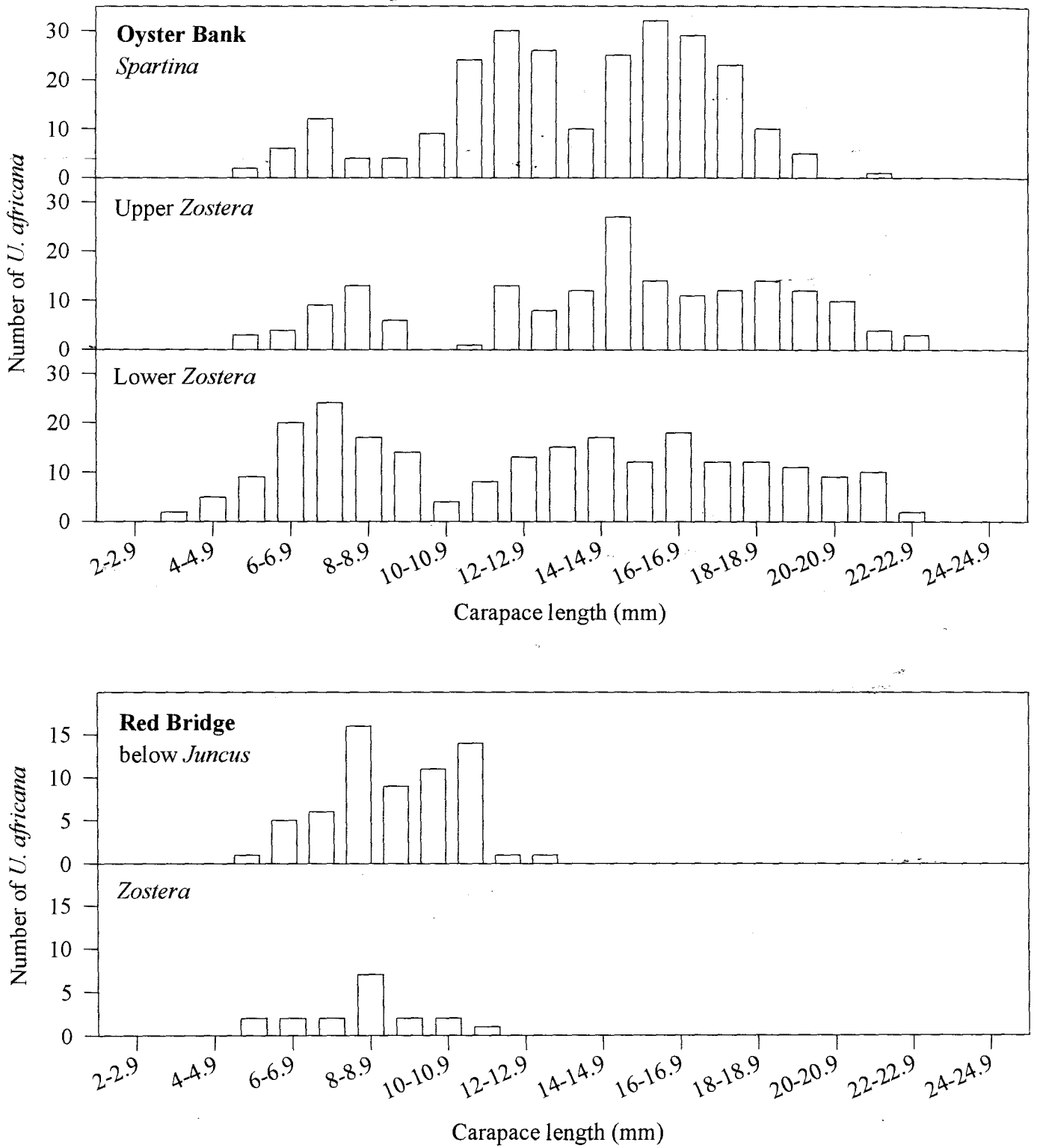


Figure 2.11c. Length frequency distributions of the prawn populations from 3 zones at the Oyster Bank and 2 zones at the Red Bridge site.

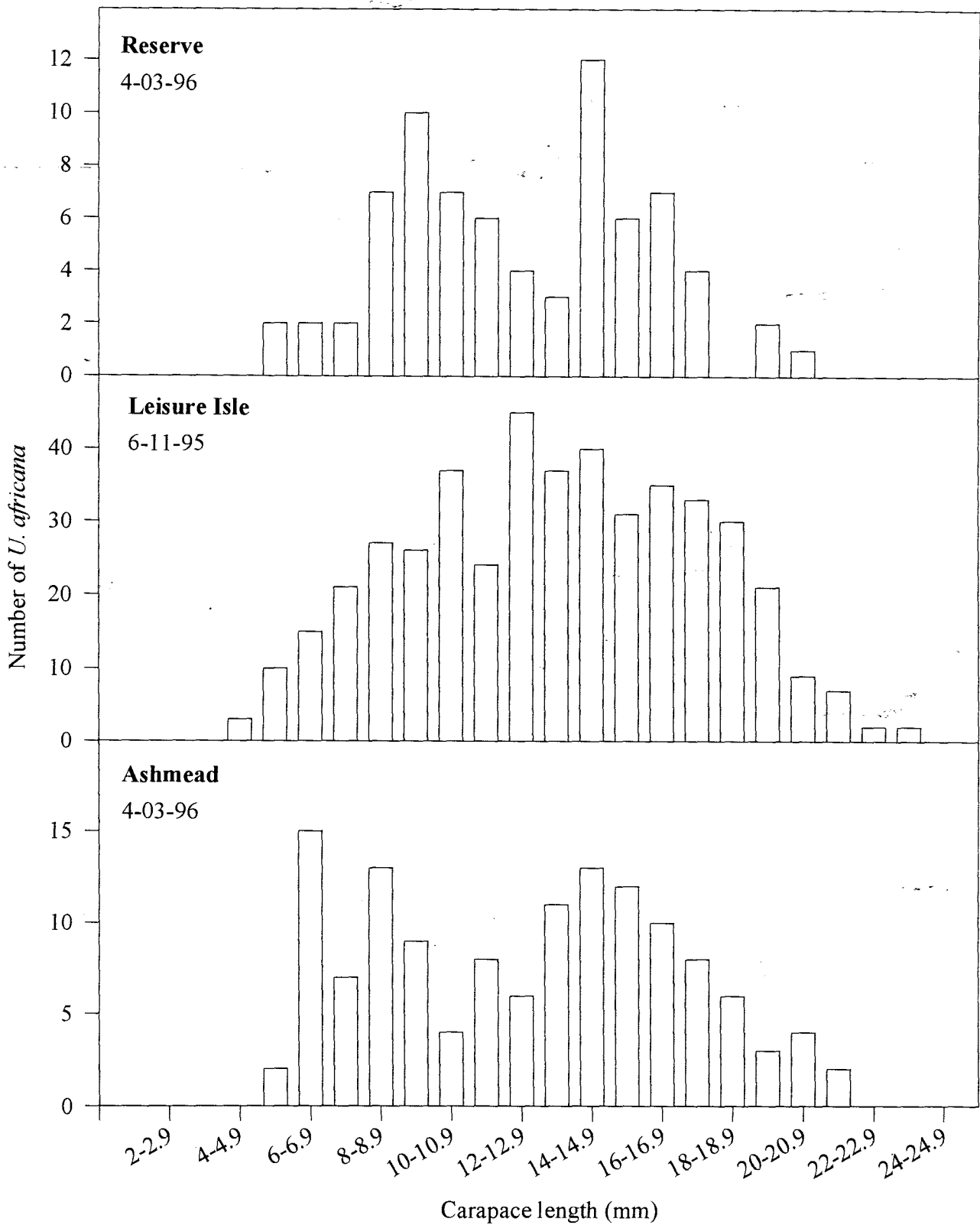


Figure 2.12a. Length frequency distributions of the prawn populations from three sites in the Knysna estuary.

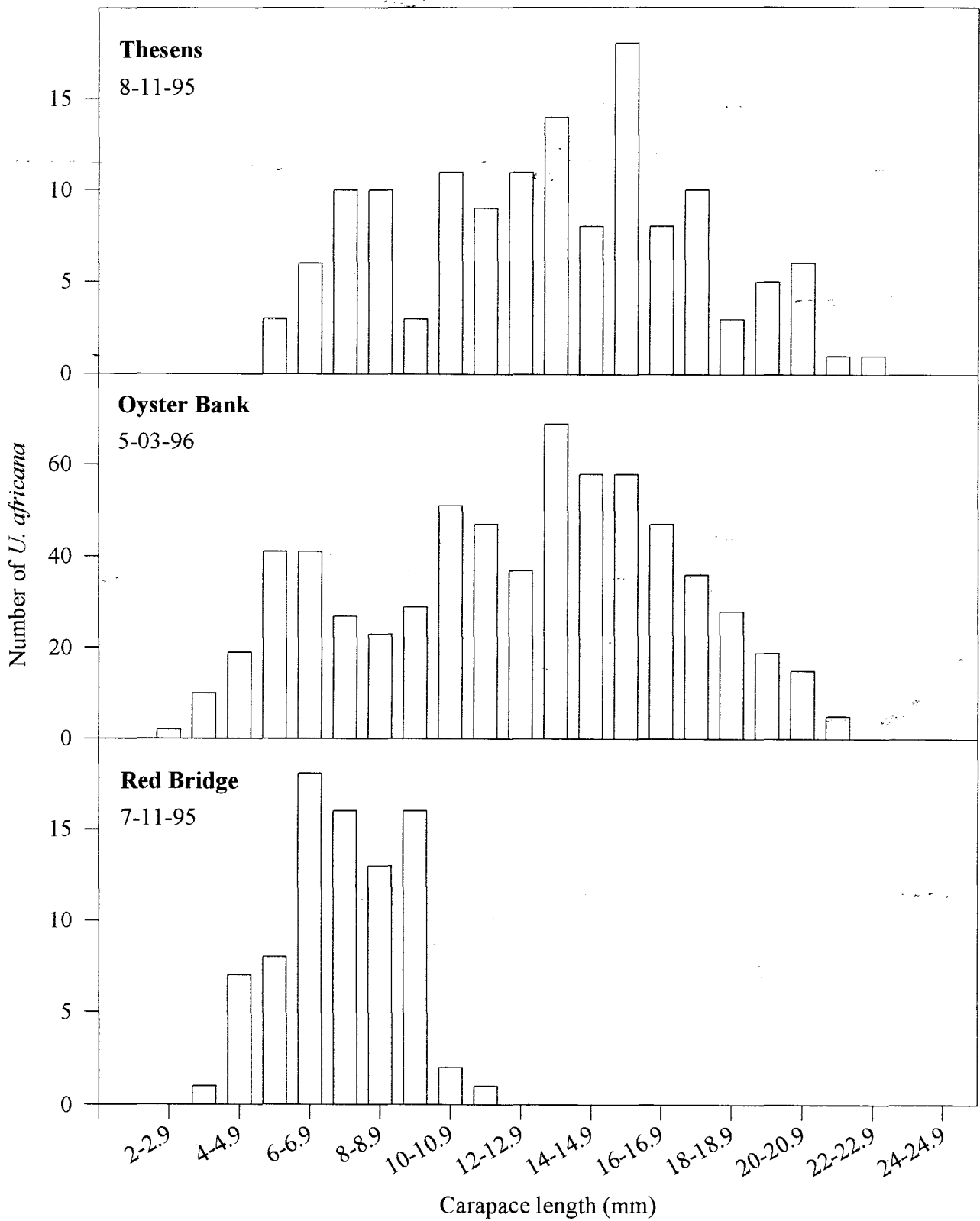


Figure 2.12b. Length frequency distributions of prawns populations from three sites in the Knysna estuary.

These analyses reveal that the *U. africana* populations are all composed of four normal distributions (Fig. 2.13). These are statistically derived components which may represent age groups or cohorts in the populations. The first cohort has a mean size of approximately 6.8 - 8 mm carapace length (CL). This group would represent mud prawns up to 12 months old, recruited to the population earlier during this breeding season. The second cohort has a mean size of between 9.45 and 12.5 mm CL and would represent individuals recruited during the previous breeding season. The female mud prawns in this group would become reproductively active this season. *U. africana* with a mean carapace length of between 13.5 and 16.5 mm CL make up the third age group and those with a mean of greater than 17 mm CL, the fourth. The third cohort represents the majority of the breeding stock of the populations at each site. The fourth cohort is made up of large mud prawns which are likely to be over three years old. Since the life-span of *U. africana* has been estimated at 3 - 4 years, it is likely that the fourth age group is in most cases smaller than the third due to natural mortality. At the Reserve, the three larger size groups overlap and the third cohort was not separable (group 3; Table 2.15). The separation index (SI) value for the fourth cohort of the Ashmead population was slightly below the recommended value of 2, but all the expected composite distributions fit the observed length frequency distributions significantly (Table 2.15). The Red Bridge sample is not included as the sample size is not adequate for this type of analysis.

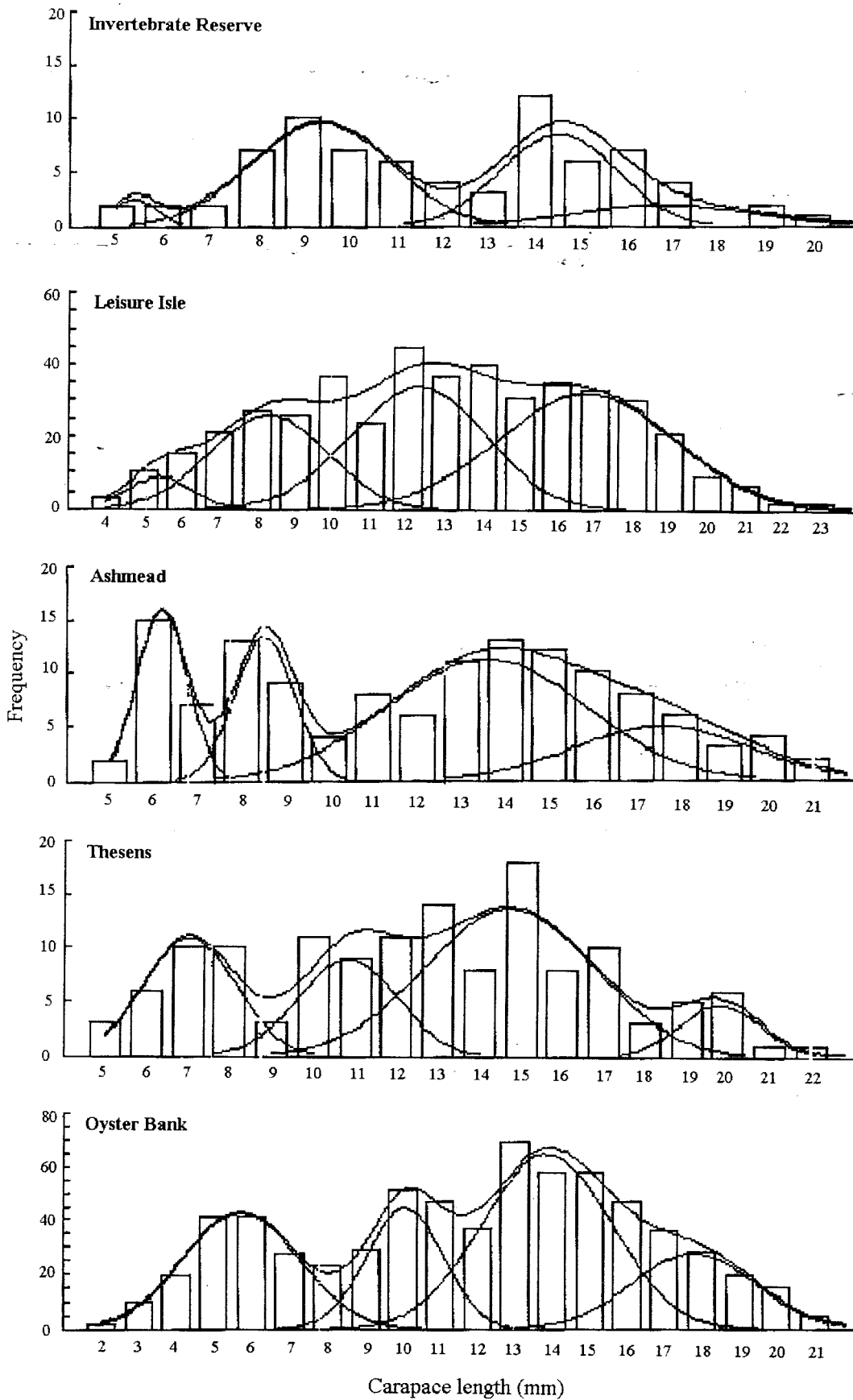


Figure 2.13. Normal distributions fitted to length frequency distributions of the *U. africana* populations at the Invertebrate Reserve, Leisure Isle, Ashmead, Thesens and Oyster Bank, using Hasselblad's NORMSEP Analysis (FISAT).

Table 2.15. Summary of Hasselblad's NORMSEP analysis (FiSAT) to separate the normally distributed components of the size frequency distributions of the prawn populations at each of six sites (refer to Figure 2.14). SI = Separation Index.

Site	Group	Mean \pm s.d.	Population (n)	SI	Significance level
Reserve	1	6.867 \pm 0.501	3.20	-	p = 0.662
	2	10.863 \pm 1.487	35.62	4.0182	
	3	15.975 \pm 1.238	26.27	3.751	
	4	18.28 \pm 1.993	18.28	1.8472	
Leisure Isle	1	7.11 \pm 1.171	38.490	-	p = 0.716
	2	10.35 \pm 1.678	125.260	2.278	
	3	13.95 \pm 1.373	113.710	2.357	
	4	17.95 \pm 2.194	177.540	2.243	
Ashmead	1	7.12 \pm 0.574	22.780	-	p = 0.842
	2	9.45 \pm 0.675	22.450	3.725	
	3	14.57 \pm 2.246	63.720	3.509	
	4	18.61 \pm 2.011	24.050	1.89	
Thesens	1	7.95 \pm 1.087	28.940	-	p = 0.942
	2	12.32 \pm 1.540	42.950	3.326	
	3	16.23 \pm 1.596	52.260	2.496	
	4	20.70 \pm 1.006	12.850	3.437	
Oyster Bank	1	6.68 \pm 1.516	160.34	-	p = 0.804
	2	11.0 \pm 1.014	113.67	3.415	
	3	14.8 \pm 1.698	275.38	2.799	
	4	18.75 \pm 1.652	112.60	2.359	

DISCUSSION

Upogebia africana are distributed throughout the muddy intertidal areas of the lower, middle and upper reaches of the Knysna estuary (Fig. 2.2). The mud prawns were absent from areas near the mouth (south of Leisure Isle) and from the areas up-estuary, above the Red Bridge. A variety of physical and biological factors have been suggested to limit the distributions of *U. africana*. Macnae (1957) and McLachan & Grindley (1974) demonstrated and discussed 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 & Grindley (1974) found that substratum is by far the most important factor influencing the distribution of the macrobenthos as it limits successful burrow construction. *U. africana*, construct permanent burrows lined with silt (Hill, 1967), and cannot colonise areas where strong tidal currents result in clean, sandy and relatively unstable sediments (McLachan & Grindley, 1974) like those south of Leisure Isle. Above the Red Bridge the sediment is cleaner and coarser than at the sites lower down the estuary as it has a component of coarse river sand.

Within this distribution, the density, biomass and population structure of *U. africana* varies with distance up the estuary and with vertical height on each shore. Sediment structure (Ferber & Lawrence, 1976; Lawrence & Murdoch, 1977) and organic content (Longbottom, 1970) have been shown to affect the distribution, biomass and size of macrobentic organisms. Particle size or diameter is one of the most widely used methods of investigating sediment characteristics. Substrata where *Upogebia* predominates have been found to contain a higher percentage of subsieve particles (<63 μm diameter) than sediments where *Callianassa* occurs. Densities of *U. africana* between 50 and 250 m^{-2} are common in sediment with 3 - 20 % of silt and clay (Wooldridge, 1968). In sediments with more than 20 % subsieve particles the mud prawn becomes less common (McLachan & Grindley, 1974; Day, 1981a). In this study the percentage

within this preferred range of *U. africana* (Wooldridge, 1968; McLachan & Grindley, 1974). Although there is little variation in the percentages of subsieve sediment between the sites, prawn biomass differs significantly between these sites. This suggests that the percentage of subsieve sediment does not influence intertidal prawn biomass in the Knysna estuary and that some other factors are involved.

On each shore, mud prawn densities were found to be highest in the lower *Zostera* zone just above the spring tide low water level, and decreased with depth below this point. Moving into the tidal channel, the substratum changes from muddy sand to coarser sandier sediments (Reddering & Esterhuysen, 1984). In some areas, e.g. the shallow Ashmead channel, where currents are not strong and the subtidal substratum remains muddy and fine, prawns are distributed throughout the subtidal channel (Fig. 2.10). In the Swartkops estuary a similar pattern was found where numbers of *U. africana* were much lower towards the subtidal channels where strong currents resulted in a coarse substratum (Wooldridge, 1968). In sheltered creek areas of this estuary where currents were not strong and the subtidal substratum was finer, mud prawns were distributed throughout the subtidal area (Hanekom *et al.*, 1988). Densities of $51 \pm 37 \text{ m}^{-2}$ *U. africana* were recorded at some subtidal stations in the Swartkops estuary (Hanekom & Erasmus, 1988) in comparison to $39 \pm 50 \text{ m}^{-2}$ in shallow subtidal areas in the Knysna estuary. This evidence of low mud prawn densities subtidally, suggests that the subtidal areas which are inaccessible to bait collectors do not represent large reserves of *U. africana*.

The population structure of *U. africana* also varied within the Knysna estuary. Hanekom & Erasmus (1988) found significant differences in the size ranges of adult mud prawns at different tidal heights in the intertidal zone and along the length of the Swartkops estuary. Adult mud prawn size tended to increase with decreasing tidal height and to decrease with distance from the estuary mouth. The variations in size of the adult *U. africana* in the Knysna estuary follow a

similar pattern. The adult mud prawns from the Red Bridge site up-estuary were found to be significantly smaller than those from all five sites closer to the estuary mouth (Tables 2.12 & 2.14). *U. africana* from the *Spartina* zone were significantly smaller than those from the upper *Zostera* zone (Tables 2.12 & 2.13). The four sites with the larger adult mud prawns (Thesens, Leisure Isle, Ashmead and the Oyster Bank) also have the highest density and biomass of prawns (Fig. 2.8 & 2.9). In the Swartkops estuary, adult *U. africana* also tended to have larger sizes in areas with the greatest biomass (Hanekom & Erasmus, 1988), this indicates that growth in *U. africana* is probably not density dependent. In the Swartkops estuary, significant differences in the sizes of ovigerous females from the different populations indicated that variations in size composition were a result of differences in growth of the mud prawns and not a spatial separation of adults and juveniles (Hanekom & Erasmus, 1988). No ovigerous female *U. africana* were found at the Red Bridge in the Knysna estuary throughout the 18 month study period.

Hill (1967) estimated the lifespan of *U. africana* to be 3.5 to 4 years. This is comparable with life spans (> 3 years) estimated from size frequency distributions for *U. deltaura* by Gustafson (1934), as well as by Tucker (1930; cited in Dworschak, 1988) and Popovici (1940; cited in Dworschak, 1988) for *U. pusilla*. Hanekom & Baird (1992) identified cohorts from size frequency histograms of *U. africana* from the Swartkops estuary and fitted the resulting modal means to the von Bertalanffy growth model. The four possible cohorts or age classes identified in the mud prawn populations in this study are comparable with the four cohorts identified by Hanekom & Baird (1992). The modal means of the cohorts vary slightly between the sites in the Knysna estuary (Table 2.15). This may be a result of the two sampling occasions being five months apart, although in the same breeding season of *U. africana*. Alternatively, because breeding occurs over seven months of the year, the distribution may be "smoothed out" to some extent. It is possibly due to a similar effect that the growth curve obtained for *U. africana* by Hanekom & Baird (1992) is smooth, despite the fact that crustaceans have discontinuous growth.

Siegfried (1962) found that the size frequency distribution for a population of *U. africana* from the Uilenskraal estuary did not show a regular progression of peaks and he determined that the growth rate could not be determined by size frequency analysis alone. Caution is needed when evaluating size frequency data and particularly cohort structure.

The variability in the density and biomass of *U. africana* in the Knysna estuary and the peak in abundance at the Oyster Bank (Figs. 2.8 & 2.9) could be due to the presence of a more favourable habitat, the inaccessibility of this site to bait collectors or a combination of both factors. Factors contributing to the favourability of the habitat at the Oyster Bank, may include water temperature (Fig. 2.6a & b) which is less variable above the Railway Bridge than closer to the mouth of the estuary. In addition, the salinity in the middle reaches is also less variable than higher up the estuary and the percentages of subsieve sediment and organic matter of the substratum are slightly higher (Fig. 2.4 & 2.5). Hanekom & Erasmus (1988) found a significant positive correlation between the salinity of the water column and mean adult prawn size, but found that temperature and population density had no significant influence on prawn size in the Swartkops estuary. Nutrient content of the water may influence prawn biomass in the Knysna estuary. Korringa (1956) suggested that oyster spat and older oysters might thrive above the Railway Bridge because of the high food content of the water. This suggestion is supported by data which shows that this area has high chlorophyll a concentrations (Knysna Basin Project, unpublished data). This particularly productive area supports the highest density and biomass of mud prawns in the Knysna estuary.

The total area of intertidal mudbank inhabited by *U. africana* can be used to estimate the total prawn stocks of the Knysna estuary. If the mean density and mean biomass of the six sites sampled (63.26 m^{-2} and 23.85 g.m^{-2}) is taken as representative of the entire estuary, the prawn stock is estimated to be 2.19×10^8 prawns or a dry weight of 82732,597 kg (82.7 tonnes).

Observations made by Hanekom *et al.* (1988) in the Swartkops estuary suggest that the size of predatory bird populations and, to a lesser extent, those of the fish may be linked to the magnitude of the *U. africana* populations. This information, combined with studies on production, could indicate the importance of *U. africana* as a potential food resources of an estuary and the value of bait regulations (Hanekom *et al.*, 1988). Exploitation by bait collectors can have an effect on the density and population structure of prawn populations. Wynberg & Branch (1991) found that sand prawns, *Callinassa kraussi*, were significantly less dense and had a smaller modal size, in areas of the Langebaan lagoon exploited by bait collectors than in unexploited areas. A knowledge of the distribution, density biomass and population structure of the bait organism is therefore essential and is important in determining conservation measures for bait stocks. From the density and biomass values obtained in this study (Figs. 2.8 & 2.9) it is clear that the Invertebrate Reserve, although it supports high densities of other invertebrates (pers. obs.), does not conserve large stocks of *Upogebia africana*. The Oyster Bank on the other hand, acts as an effective "natural bait reserve" as it is fairly inaccessible to bait collectors and it supports the highest biomass of mud prawns in the Knysna estuary. Bait collecting in the Knysna estuary is investigated in the following chapter and will be discussed in relation to information presented here on the prawn stocks of the estuary.

Summary

1. A large percentage (62 %) of the available intertidal area of the Knysna estuary is inhabited by *U. africana*. The bait stock of the estuary is estimated to be 2.19×10^8 prawns (82.7 tonnes dry mass).
2. Mud prawn density, biomass and population structure vary throughout the estuary as well as with tidal height on each shore.
3. Various characteristics of the habitat, particularly sediment composition and distance from the estuary mouth, as well as exploitation by bait collectors may affect the distribution, density and sizes of *U. africana*.
4. The Invertebrate Reserve supports very low mud prawn densities. The Oyster Bank appears to be a very effective "natural reserve" as it supports the highest densities of mud prawns in the Knysna estuary and is relatively protected through its' inaccessibility to bait collectors.

CHAPTER THREE

BAIT EXPLOITATION

Bait collectors, their methods and the disturbances caused

INTRODUCTION

In the Knysna estuary, the mud prawn, *Upogebia africana*, is exploited for bait by subsistence fishermen and women, and by resident and visiting leisure and sports anglers. These various groups of anglers employ different methods of collection and their activities and the extent of their use of this bait resource differ widely. This chapter deals with socio-ecological issues and aims to determine the present extent and intensity of the exploitation of *U. africana* in the Knysna estuary and to describe the use of the bait resource by the various sectors of the fishing community. Knowledge of both the resource and the resource users is essential in establishing management recommendations to ensure the sustainable use of the resource.

Despite concerns expressed over the large numbers of mud prawns removed from South African estuaries in general (Siegfried, 1962; Hill, 1967), no studies have quantified the effect of bait collecting on bait stocks and their replenishment in South African estuaries. Present management strategies and bait regulations are, therefore, not based on empirical data. Martin (1988) briefly described the possible secondary effects of illegal bait harvesting on the birds of the Swartkops estuary. The most detailed studies on bait exploitation were by Wynberg and Branch (1991, 1994) who assessed bait collecting for *Callinassa kraussi* and *U. africana* in Langebaan Lagoon on the west coast of South Africa, and the effect of this disturbance on the biota of the intertidal sand flats. Although these studies were carried out in a tidal lagoon, the findings are applicable to estuaries.

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). These studies suggest that systems which have been exploited, respond resiliently. Research on bait collecting has

focused on the holistic analysis of the disturbance associated with bait collecting (Jackson and James, 1979; McLusky *et al.*, 1983; Reise, 1985; Hruby, 1987; Wynberg and Branch, 1994). Wynberg and Branch (1991) monitored the numbers of bait collectors at Langebaan Lagoon and conducted interviews with the anglers and Blake (1979 a, b) has described the numbers of diggers collecting bait worms, their selectivity, efficiency and effort in harvesting bait worms in England.

METHODS

Data Collection

As bait collection occurred throughout the Knysna estuary, during the entire day and to a lesser degree at night, it was not possible to monitor the whole estuary. Six popular bait-collecting sites were chosen from those observed to be frequently exploited (Fig. 3.1), and were monitored during the daylight low-tide periods. This sub-sample of collecting activity was used to estimate the extent of bait collection in the Knysna estuary. At each site the activities and numbers of bait collectors were monitored over four-hour periods of low tide on 60 occasions over 14 months (February 1995 - April 1996). In order to determine which sectors of the population were using the bait resource, observations recorded included demographic details *e.g.* the race, sex and approximate age group (child, adult or elderly) of the collector. The method of bait collection (implement used), catch per unit effort or efficiency (number of pumps needed to catch a mud prawn) and time spent collecting bait (minutes active on the mud bank) were also recorded for each bait collector. Collectors' were interviewed to gain more information about their activities and their mud-prawn catches were measured and counted. A questionnaire (see appendix 1) was compiled with the assistance and advice of the Environmental Evaluation Unit at the University of Cape Town and the Rhodes University Sociology Department. The types of questions included, and their relevance, are summarised in Table 3.1. Forty-six local anglers and thirty-one tourists were interviewed at various popular bait collecting sites while they were gathering bait.

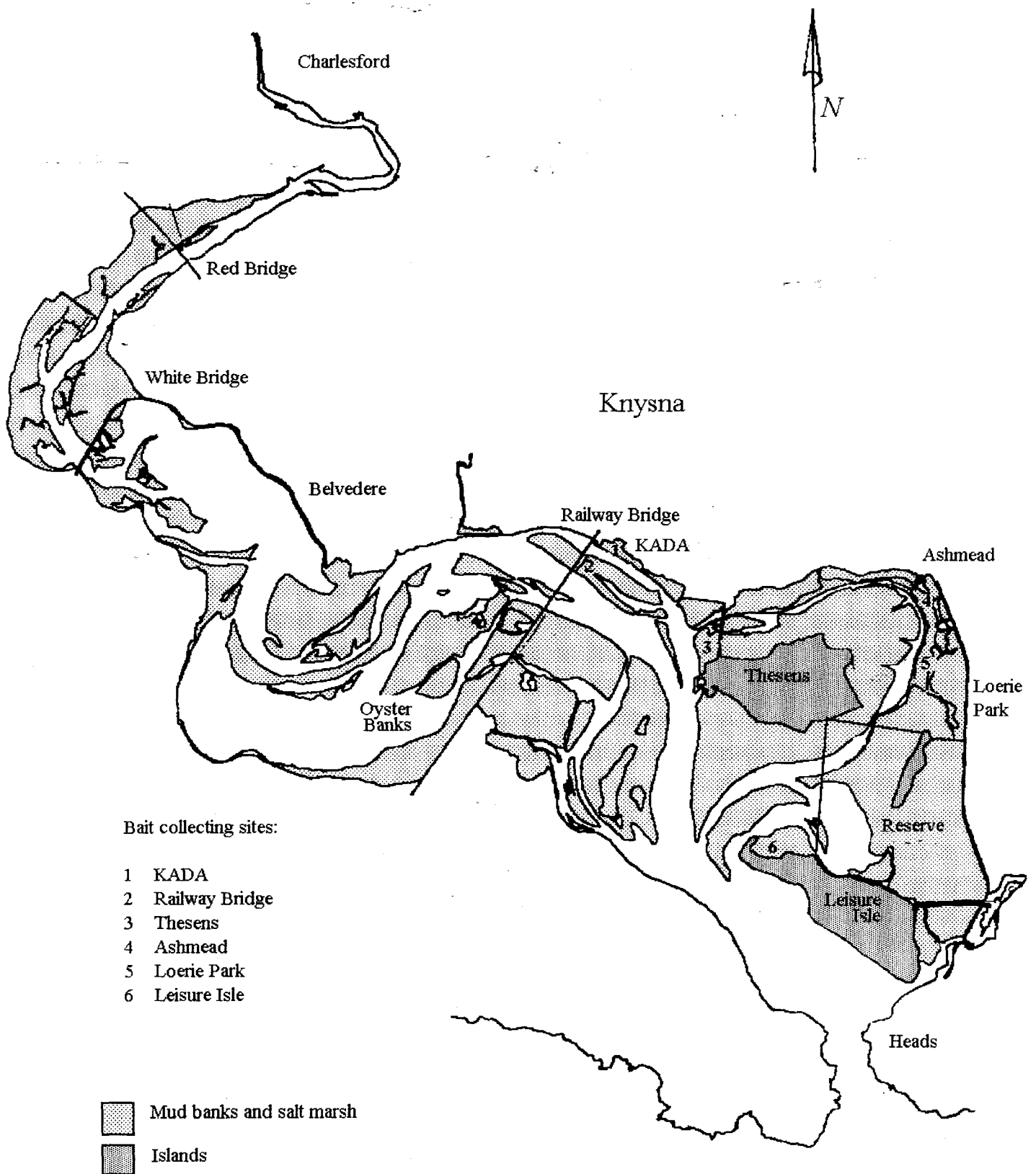


Figure 3.1. The Knysna estuary showing the six popular bait collecting sites studied (1 - 6) (Scale 1 : 50 000).

Data Analysis

Questionnaire responses were analysed using Principal Components Analysis (PCA). A PCA projects a multidimensional swarm of data points into two-dimensions. Data with many variables are summarised into a few components (abstract variables), so that they can be displayed on a graph which uses the components as axes (James and McCulloch, 1990). Although this statistic is intended mainly for the analysis of continuous data (James and McCulloch, 1990), a correlation matrix of ranked data (questionnaire responses) was analysed in this study. This simple ordination technique is suited to the analysis of questionnaire data as the replies of each respondent constitute a set of data points with many variables. A PCA summarises these into a few variables which can be plotted to produce a "profile point" for each respondent on the graph. Respondents who answer a particular group of questions (*e.g.* on fishing and bait collecting methods used) in a similar way, appear as a group of points on the graph.

Table 3.1. Types of questions included in the questionnaire and their relevance.

Category of question	Relevance
Demographic	To determine which sectors of the population are using the bait resource and to what extent
Geographic	To determine whether the respondent lives locally or is a visitor to Knysna (ie. tourist)
LOCALS	
Employment situation	To investigate the means of subsistence of the respondent
Fishing activities	To investigate the fishing preferences and methods used by the various categories of fishermen and women
Bait collecting activities	To investigate bait preferences and uses and collecting methods used by the various categories of fishermen and women
Role of fishing and bait	To determine whether fishing and bait collecting play a role in the collecting means of subsistence of the respondent
Opinion on bait restrictions	To investigate the needs of the fishermen and women and their opinions on bait restrictions and the amount of bait allowed
Impact on estuary	To evaluate what impact the fishermen and women think their bait collecting and fishing activities have on the estuary
Comments	Allowed respondents to air their views on the use of the resources of the Knysna estuary
TOURISTS	
Fishing activities	To investigate the fishing preferences and methods used by the tourist fishermen and women
Bait collecting activities	To investigate bait preferences and uses and collecting methods used by the tourist fishermen and women
Economic	To roughly estimate the amount of money spent by tourists on fishing and related items in Knysna
Opinion on bait restrictions	To investigate the needs of tourist fishermen and women and their opinions on bait restrictions and the amount of bait allowed
Impact on estuary	To evaluate what impact the tourists think their bait collecting and fishing activities have on the Knysna estuary
Comments	Allowed respondents to air their views on the use of the resources of the Knysna estuary

The "factors" listed in Tables 3.2 & 3.3 are those questions relating to a specific issue, used in each PCA. Each factor or question is represented (axis title) on the PCA plots as an axis. The "attributes" are the possible responses to each question. The responses determine where on the graph the profile point of each interviewee falls, relative to the principal component axes. The relationships of the profile points to the principal component axes, are plotted as axes within the distribution of points on the graph, where each axis represents a factor or question. The orientation of these axes within the graph, reveals which factors separate the data points along the principal component axes (Figs. 3.2 & 3.3).

The data obtained on the role that fishing and bait collecting play in the respondents' income (Table 3.2) were analysed by PCA to determine whether or not separate groups of bait collectors could be identified on the basis of their economic status (which is related to their motivation for using the bait resource). A PCA was also carried out on the bait collecting and fishing practices of respondents (Table 3.3) in order to summarise questionnaire responses on the methods used by anglers. The distribution obtained is examined for groups of points, which are interpreted as groups of respondents who gave similar answers to specific questions.

Table 3.2. A list of the socio-economic factors and attributes analysed by PCA to summarise data on the anglers source of income (axes titles refer to Figure 3.2).

Factor	Axis title	Attributes			
Is fishing and/or bait collecting a source of income?	income	Yes	Partly	No	
Are these your only means of subsistence?	other-cash	Yes		No	
Do you have a job?	have-job?	Yes	Sometimes	No	
How many days a week do you work?	days-worked	< 1	1 2 3 4 5 6 7 days		
Do you sell bait?	sell-bait	Yes	Sometimes	No	
Do you sell or eat your catch?	sell-eat	Eat	Eat mostly, sell big fish	Sell	

Table 3.3. A list of the factors and attributes analysed by PCA to summarise questionnaire responses on the fishing and bait collecting methods used by anglers interviewed (axes titles refer to Figure 3.3).

Factor	Axis title	Attributes		
What method do you use to collect mud prawns?	method	Tin cans	Prawn pusher	Prawn pump
What fishing method do you use?	fish-method	Plant lines	Hand lines	Rod & tackle
Do you make use of a boat?	use-boat	No	Sometimes	Yes
Is the allowed amount of bait enough?	enough?	Not enough	Enough	Too much
How long do spend collecting bait per outing?	time-bait	5-15, 15-30, 30-60, 60-120, >120 min, low tide		
How long do you spend fishing per outing?	time-fished	5-30, 30-60, 60-120, 120-240, >240min, all day		

Spearman's rank correlation procedure (Zar, 1996) was used to test the strength of the correlations between the principal component variables generated by the PCA and the factors investigated in each PCA analysis. This robust, non-parametric test of association, describes the relations between two variables (Sokal and Rohlf, 1981). Factors with a strong correlation to the principal component are good indicators of differences between the groups identified. Graphically, these factors are identified as those with axes closest to parallel with the principal component axis.

RESULTS

Based on questionnaire responses, three income groups of anglers could be identified (PCA; Fig. 3.2). The first principal component, the x-axis, summarised the majority of the variation (65 % cumulative variance) and was found to be strongly associated with socio-economic factors and particularly the respondents' source of income (correlation coefficient = 0.9177, $p < 0.0001$, Spearman's Rank Correlation; Table 3.4).

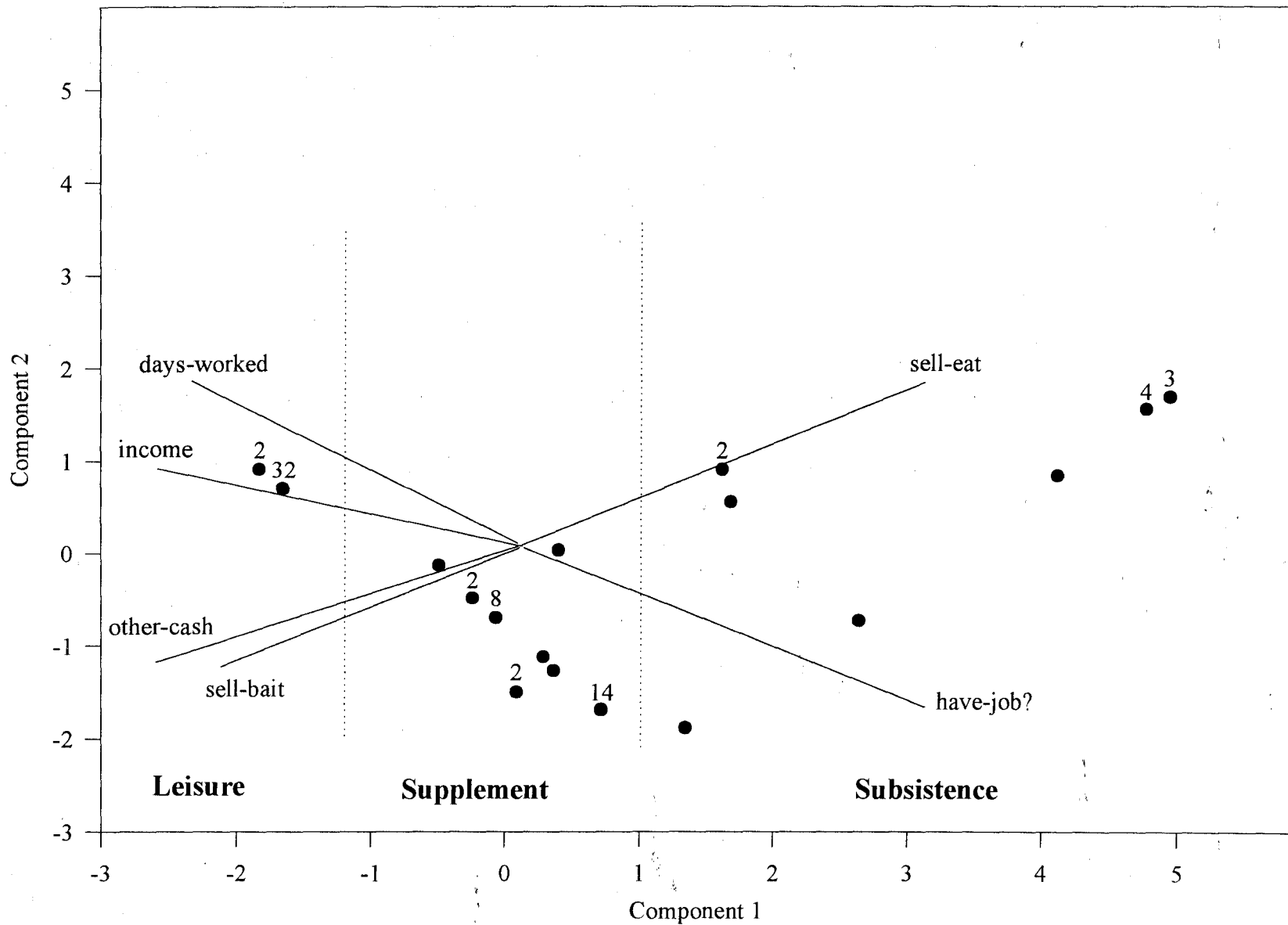


Figure 3.2. Plot of Principal Components Analysis of the source of income of anglers. Numbers above points represent the respective number of anglers, while un-numbered points represent a single angler.

Table 3.4. Results of Spearman's Rank Correlation to determine the correlation between the first principal component (from PCA) and the source of income of anglers.

Factor	Correlation coefficient	Sig. level
Fishing and bait collecting as source of income	0.9177	$p \leq 0.0001$
Have a job or not	0.8757	$p < 0.0001$
Number of days worked per week	0.9505	$p < 0.0001$
Whether have another source of income	0.5799	$p < 0.0001$
Is bait sold	0.6227	$p < 0.0001$
Is the catch sold or eaten	0.5750	$p < 0.0001$

Those anglers who replied that fishing and bait collecting were their only means of income were classed as subsistence fishermen. Those whose income was partly supplied by fishing and bait collecting were grouped as supplementary fishermen, and those who drew no income from angling were classified as recreational fishermen. The factors which differentiate the subsistence anglers from the supplementary and recreational anglers, are that subsistence fishermen and women sell their catch and sell bait and have no other source of income whereas the supplementary and recreational anglers eat their catch (sell-eat, sell-bait and other-cash axes in Fig. 3.2). The number of days worked per week differentiates the recreational anglers who have full time jobs, from the supplementary anglers who have part time employment and supplement their income by fishing (days-worked and have-job axes in Fig. 3.2).

The associations between the categories of angler identified and the demographic details of the collectors interviewed were determined using a Chi-squared Contingency Table. There is a strong correlation between the race of bait collectors and the category of angler, based on economic factors ($p = 7.62 \times 10^{-13}$; Table 3.5). All of the black, and the majority of the coloured (71 %) bait collectors interviewed, were subsistence anglers, while the majority of the white people interviewed (87.1 %) were found to be recreational fishermen (Table 3.5). Most of the women who were interviewed were subsistence (75 %) and supplementary (15 %) fisherwomen,

fisherwomen, while the men were mainly recreational (49 %) and subsistence (40 %) fishermen.

All the youths (< 21 years) interviewed were recreational anglers (Table 3.5).

Table 3.5. Summary of the demographic details of subsistence, supplementary and recreational bait collectors interviewed (p values indicate the significance level of the economic categories to the responses to a specific question; Chi-squared Contingency Table).

		% Subsistence	% Supplement	% Recreational	Sig. level
Race	Black	100	0	0	p = 7.62 x 10 ⁻¹³
	White	0	12.9	87.1	
Sex	Male	40.35	10.52	49.12	p = 4.67 x 10 ⁻⁴
	Female	75	15	10	
Age	Elderly	33.33	16.67	50	p = 6.32 x 10 ⁻⁴
	Adult	59.01	13.11	27.87	
	Youth	0	0	100	

The three categories of angler identified from their source of income, cannot be identified by their bait collecting and fishing methods. A Principal Components Analysis of the methods used by fishermen and women reveals only two categories of angler with different methods of collecting prawns and different fishing practices, *i.e.*, leisure fishermen and non-leisure (Fig. 3.3). This is because subsistence and supplementary anglers use the same methods of bait collecting and fishing. In general, the recreational anglers fish with rods and tackle and use stainless steel or plastic prawn pumps to collect mud prawns. The subsistence and supplementary fishermen and women fish with a “tol” or handline, and use tin cans to collect mud prawns (Plate I). A tin is inverted and, in the same way as a prawn pump or pusher is used, placed over a burrow opening and forced quickly down to blow the prawn and water out of the burrow. The first component (x-axis) again contained the most information (43 % Cumulative Variance) and was strongly associated with the fishing and bait collecting methods used, as well with the socio-economic category of angler (Table 3.6).

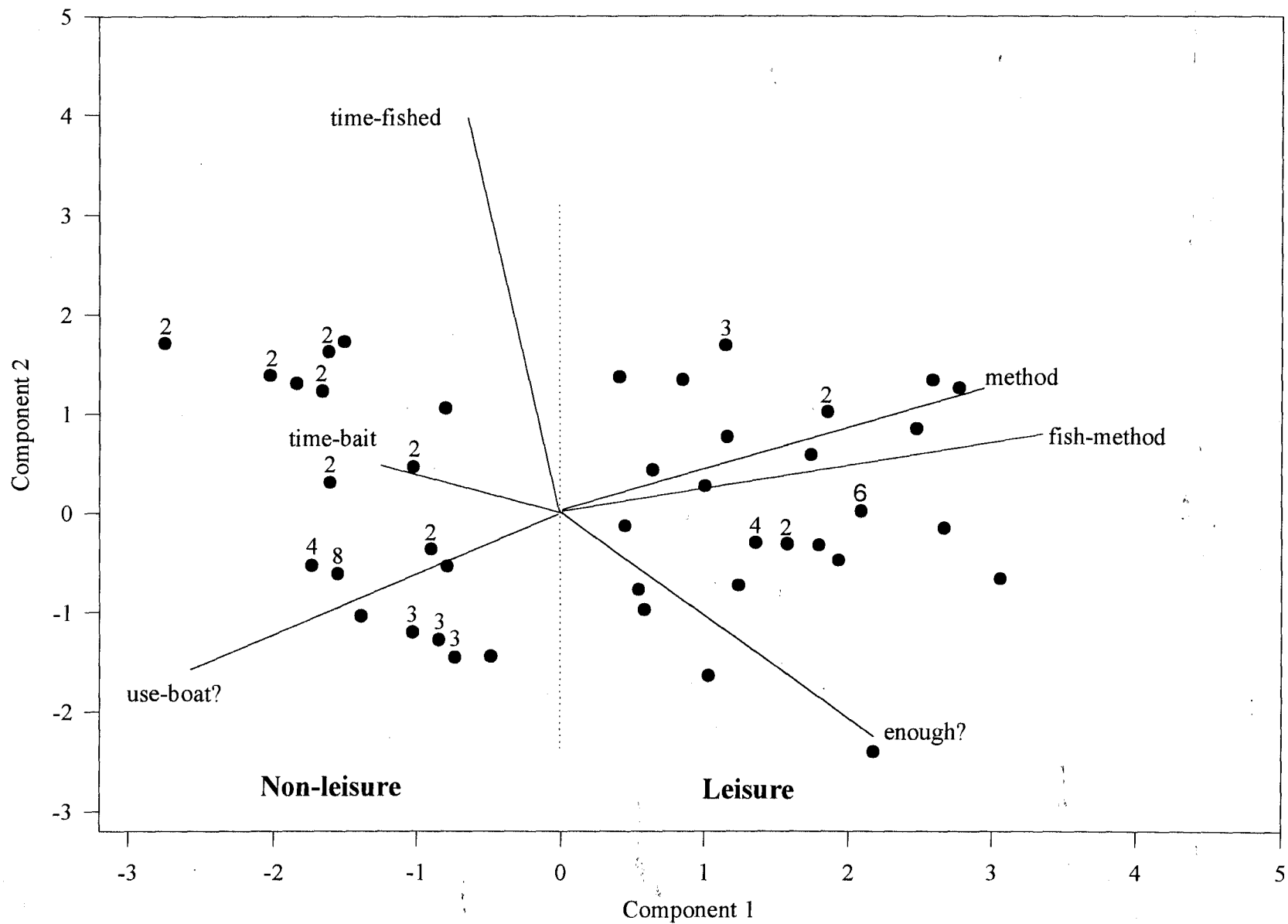


Figure 3.3. Plot of Principal Components Analysis of the bait collecting and fishing methods of anglers. Numbers above points represent the respective number of anglers, while points without numbers represent a single angler.

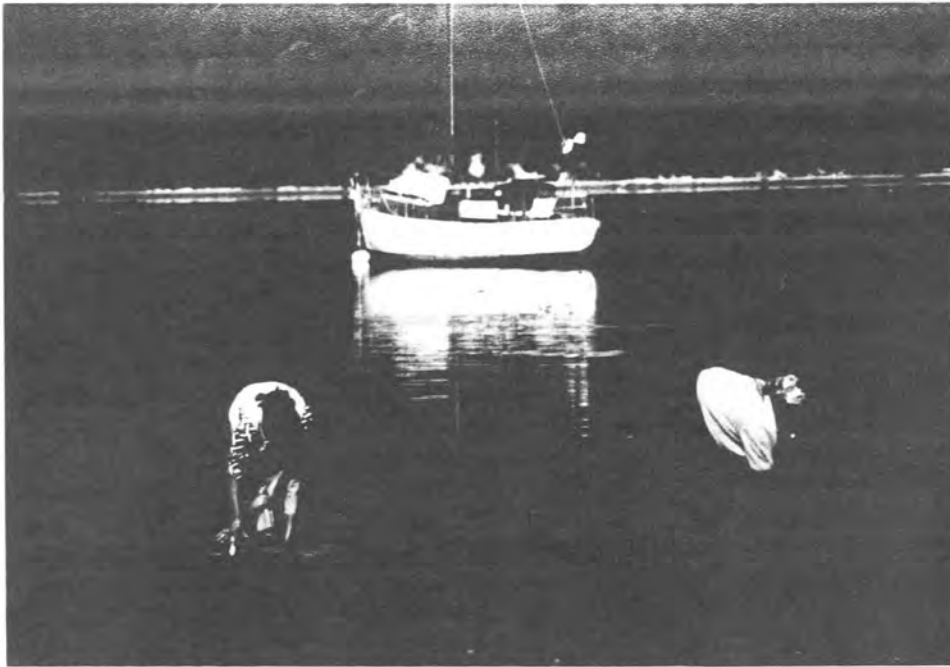


Plate I. Fisherwomen use tin cans to collect mud prawns and fish with handlines from Thesens jetty.

Table 3.6. Results of Spearman's Ranked Correlation to determine the correlation between the principal component and the fishing methods used by anglers.

Factor	Correlation Coefficient	Sig. level
Bait collecting method	0.7904	p < 0.0001
Fishing method	0.8607	p < 0.0001
Category of angler	0.8563	p < 0.0001
Whether a boat is used	0.7158	p < 0.0001
Whether allowed bait is enough	0.6673	p < 0.0001

The recreational anglers are distinguished from the supplementary and subsistence anglers by the implements and methods used (method and fish-method axes in Fig. 3.3). The recreational fishermen and women spend shorter times collecting bait and are more likely to use a boat when fishing than the supplementary and subsistence anglers (time-bait and use-boat axes in Fig. 3.3). The recreational anglers tend to respond that the allowed number of 50 mud prawns per person per day is enough or too much. In contrast, the supplementary and subsistence anglers believe that the allowed amount of bait is too little (enough? axis in Fig. 3.3). The second component (y-axis) has less influence on the distribution of the points on the plot (17 % Cumulative Variance) and is associated with the time spent fishing by various anglers (Correlation coefficient = 0.8456, p < 0.0001, Spearman's Rank Correlation). In general, subsistence anglers spend a longer time fishing than recreational fishermen, who spend longer periods fishing than the supplementary anglers (time-fish axis in Fig. 3.3).

The utility of the bait collecting method employed, for predicting the two groups of angler was tested in a Chi-squared contingency table. There is a highly significant relationship between the bait collecting method used by anglers and the groups identified (p < 0.0001). This indicator was used to categorise all the bait collectors observed using the bait resource, as leisure or non-leisure anglers. Of the bait collectors observed at the six sites studied, 22.16 % were leisure and 77.84 % were non-leisure (subsistence and supplementary) anglers (n = 546). There is a significant

difference in the mean number of *Upogebia africana* taken by leisure ($\bar{x} = 59.03$) and non-leisure ($\bar{x} = 101.37$) bait collectors ($p < 0.05$, ANOVA; Tables 3.7 & 3.8). Although non-leisure anglers collect nearly twice as many mud prawns using tin cans as leisure anglers do using pushers or pumps, there is no significant difference in the time spent pumping by anglers using different implements ($p > 0.05$, ANOVA; Tables 3.9 & 3.10). The majority of anglers take 11 - 20 minutes to collect bait, but occasionally anglers were observed to spend more than two hours gathering bait on a mud bank (Fig. 3.4).

Table 3.7. Results of an Analysis of Variance to determine whether there is a significant difference in the numbers of *U. africana* collected by leisure and non-leisure fishermen and women.

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Category	39001.98	1	39001.98	11.002	0.0013
RESIDUAL	347414.78	98	3545.05		
TOTAL	386416.76	99			

Table 3.8. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the numbers of *U. africana* collected by leisure and non-leisure anglers.

Category	n (collectors)	Mean number of mud prawns	Homogenous groups
Leisure	32	59.03	X
Non-Leisure	68	101.37	X

Table 3.9. Results of an Analysis of Variance to determine whether there is a significant difference in the time spent pumping by anglers using tin cans, prawn pushers and prawn pumps.

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Method	1738.04	2	869.02	1.040	0.3546
RESIDUAL	265683.80	318	835.48		
TOTAL	267421.84	320			

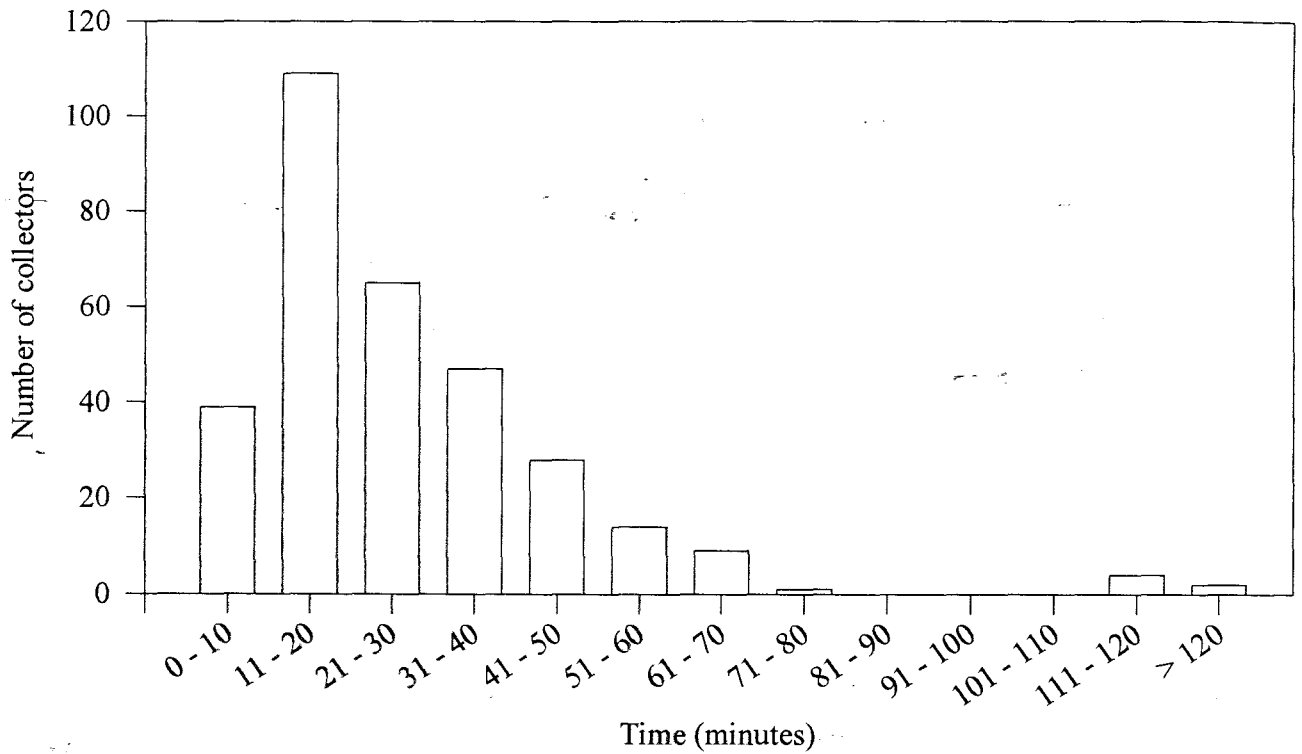


Figure 3.4. Frequency of times spent pumping *U. africana* per collecting outing by bait collectors.

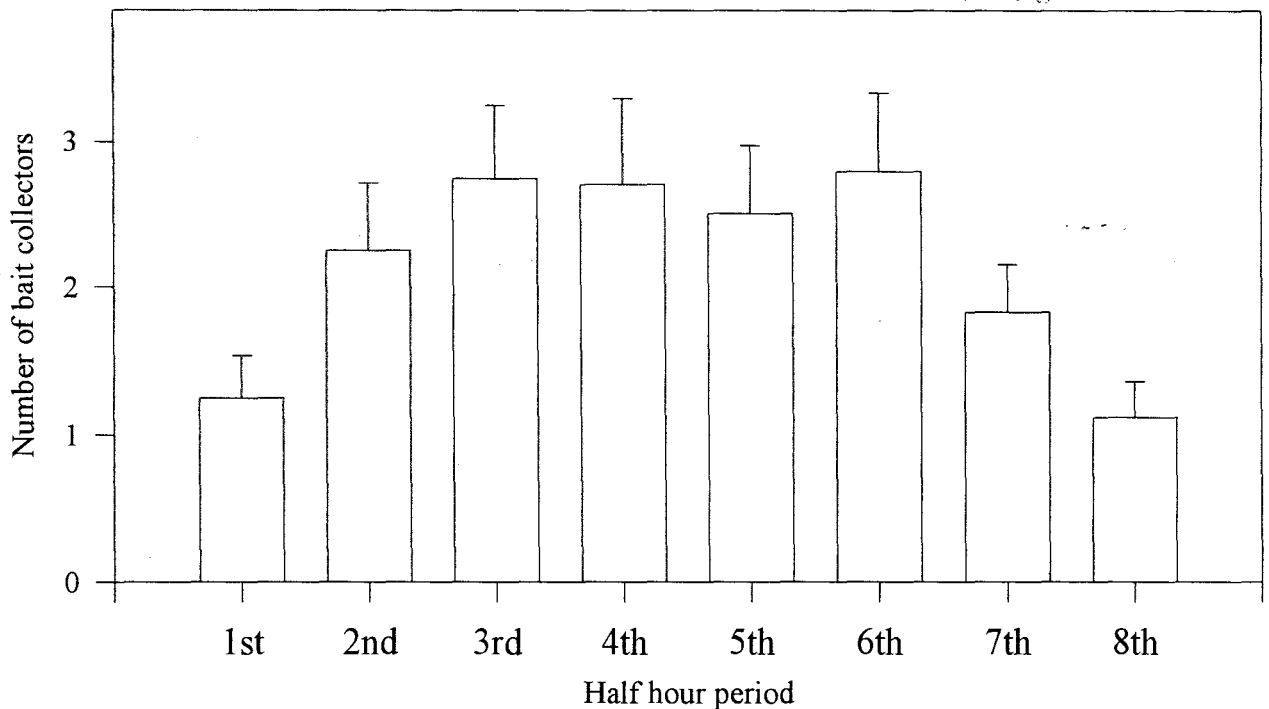


Figure 3.5. The mean number of bait collectors active on each mud bank per half hour period of low tide ($n = 60$ low tide observation periods). Standard errors of the means are shown.

During low tide, the mean number of bait collectors active per mud bank per half hour ranged from 1 to 3, with numbers highest when the tide was at its lowest (Fig. 3.5). The numbers of people collecting *U. africana* varied between spring and neap tides, and during different seasons (during summer and winter days, summer holidays and public holidays; Table 3.10). The numbers of bait collectors active throughout the year varies considerably with three peaks of bait collecting activity on public holidays (14 March 1995 - Good Friday, 31 May 1995 - Republic Day, 21 March 1995 - Human Rights Day; Fig. 3.6). On the 21 March 1996, numbers of collectors reached a peak of 58 people on a single mudbank (Fig. 3.6).

Table 3.10. Numbers of bait collectors observed collecting *U. africana* per site per low tide.

	Mean number of collectors	n (days)
Summer (November - April)	9.1	21
Winter (May - October)	4.7	22
Holidays (December & January)	15.4	9
Public Holidays	48.3	3
Neap tides	7.5	27
Spring tides	13.5	28

Mean numbers of bait collectors present per mud bank during the summer ($x = 8.55$), were double those present during the winter months ($x = 4.60$). During the summer holiday periods, mean numbers of bait collectors per mud bank ($x = 16.5$) were again double the number present during the summer months and are significantly higher than numbers present during the winter ($p < 0.0001$, MANOVA; Tables 3.11 & 3.12). The mean numbers of bait collectors were highest on public holidays ($x = 43.5$) and significantly higher than during any other season ($P < 0.0001$, MANOVA; Tables 3.11 & 3.12).

There is also a significant difference in the number of bait collectors active per site ($p < 0.005$, MANOVA; Table 3.11). The mean number of anglers collecting *U. africana* per low tide at Thesens ($x = 26.5$) is significantly higher than at Ashmead ($x = 15.5$), although there was high variability in the numbers of bait collectors active per site (Table 3.12). There is no significant difference in the numbers of anglers collecting bait on neap and spring tides ($p > 0.05$, MANOVA; Table 3.11).

Table 3.11. The results of a Multifactor Analysis of Variance to determine whether there are any significant differences in the numbers of bait collectors present per mud bank in different seasons, at different sites and between neap and spring tides.

Variance	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECTS					
Season	3428.68	3	1142.89	29.875	0.0000
Site	797.23	5	159.45	4.168	0.0038
Tide	19.00	1	19.00	0.497	0.4925
RESIDUAL	1530.25	40			
TOTAL	7742.72	49			

Table 3.12. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the numbers of bait collectors present per mud bank in different seasons.

Season	n (days)	Mean number of collectors	Homogeneous groups		
Winter	16	4.60	X		
Summer	24	8.55	X	X	
Summer holidays	10	16.49		X	
Public holidays	3	43.45			X

Table 3.13. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the number of bait collectors present per site.

Site	n (low tides)	Mean number of collectors	Homogeneous groups		
Ashmead	9	14.46	X		
KADA	7	16.09	X	X	
Railway Bridge	8	16.76	X	X	
Loerie Park	7	17.42	X	X	
Leisure Isle	9	18.42	X	X	
Thesens	10	26.51			X

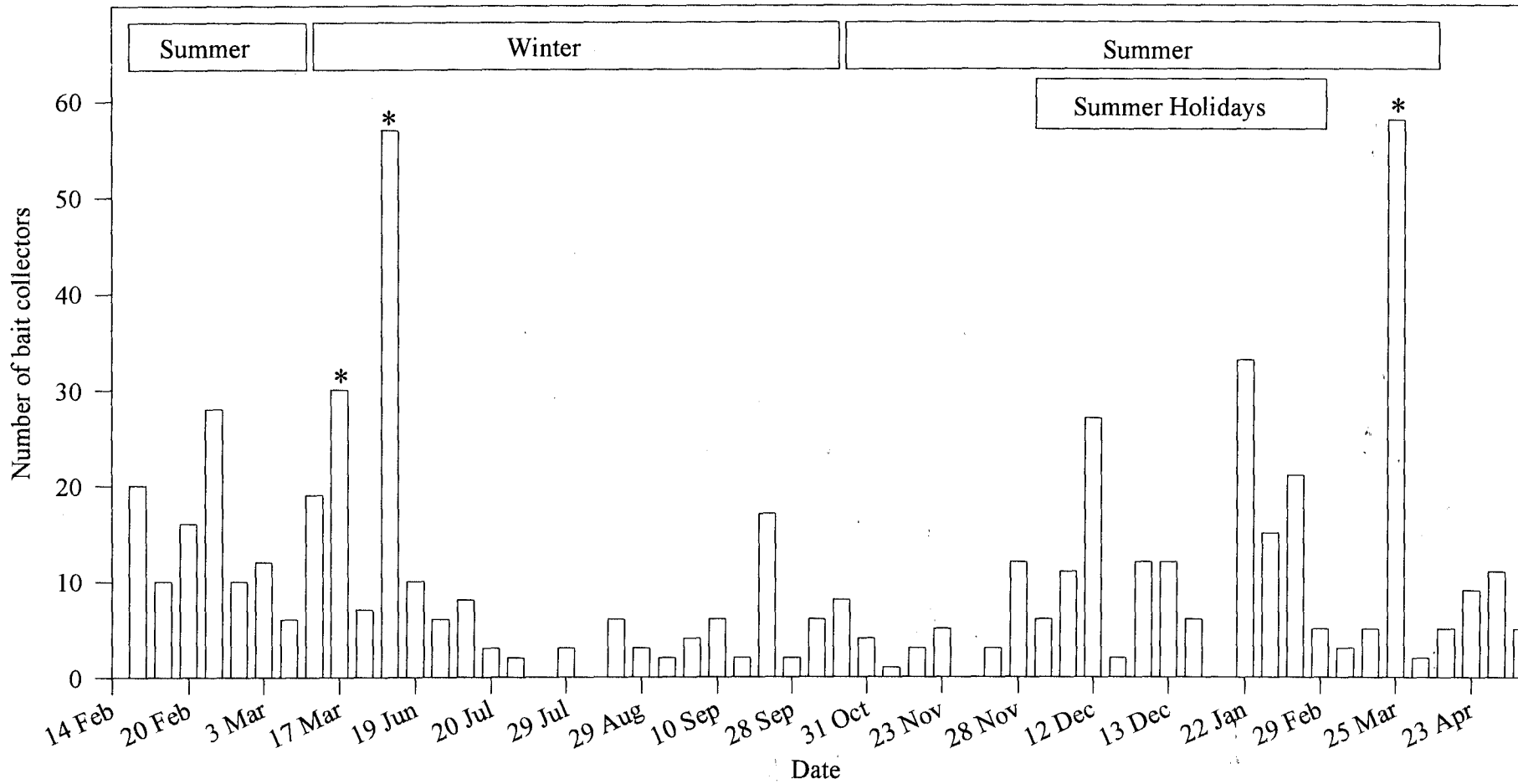


Figure 3.6. Numbers of bait collectors per site observed over 14 months. The seasons are shown above the histogram and public holidays (14 April, 31 May & 21 March) depicted as *.

Disturbances caused by bait collectors

Illegal bait collecting practices appear to be far more destructive than legal pumping methods. Of the legal bait collecting methods, sucking with a prawn pump disturbs the most sediment. Unskilled or unpractised collectors sometimes remove a plug of *Zostera* covered sediment in the tin or pusher and displace it. This leaves behind small mounds and hollows (Plate II). The only visible damage done by skilled bait collectors "blowing" or "popping" prawns is pressing some *Zostera* strands into the sediment and in some cases cutting them with the tin can or prawn pump edge. Illegal bait collecting in the Knysna estuary usually takes place at night and involves digging shallow, often circular, "trenches" with a garden fork or spade (Plate II). These are 8 - 20 cm deep and are approximately 2 - 3 m long and 0.5 - 1.5 m wide, but trenches 7 m by 2 m have been recorded. Uprooting *Spartina maritima* is another illegal method of obtaining bait used in the Knysna estuary (Plate II).



Plate II. a) "Plugs" and hollows left by an inexperienced or unskilled bait collector using a prawn pusher, b) large, shallow "trenches" dug by illegal bait collectors using a garden fork or spade (black and white scale bars are 10 cm), and c) *Spartina maritima* up-rooted by illegal bait collectors (metal quadrat is 25 cm x 25 cm).

DISCUSSION

From the data collected, an estimate of the total numbers of *Upogebia africana* taken by bait collectors at the six sites studied, was calculated. Since the numbers of bait collectors present per mud bank in different seasons and the numbers of prawns taken by leisure and non-leisure anglers was highly variable, these factors were taken into account in the calculations. The number of bait collectors in all these data are, if anything, under-estimates, as the values used in these calculations are from observations during four hours over low tide. Bait collectors were observed to collect bait during high tide in the *Spartina* beds, during the early outgoing and later incoming tides and even during the night.

If the mean number of bait collectors present per site per low tide during winter, summer, summer holidays and public holidays (Table 3.13) are multiplied by the number of days in each "season", a total of 3367 anglers are estimated to collect *U. africana* at each site annually. For the six sites studied, the number of bait collectors per annum is 20200. Since it has been determined that 77 % of collectors are non-leisure anglers who remove a mean of 101 prawns per person per day, the number of mud prawns taken annually by this group is estimated as 1.59×10^6 . The 23 % of bait collectors who are leisure anglers remove an estimated 2.64×10^5 mud prawns per annum. A total of 1.85×10^6 or 700 kg (dry weight) *U. africana* were collected as bait from the six sites studied over one year.

Non-leisure anglers, who make up 77 % of bait collectors, used 86 % of the prawns taken, while recreational anglers were responsible for removing 14 % of the prawns. The total numbers of mud prawns removed from the sites monitored therefore represent 8.5 % of the prawn stocks at these six sites. Although mud prawns are harvested at other sites, if this figure for the six sites monitored is applied to the whole estuary, 0.85 % of the whole estuary stock is harvested per annum (see Chapter 2).

This level of exploitation in the Knysna estuary is greater than at Langebaan Lagoon, where bait collectors were found to remove less than 0.01 % of the sand- and mud prawn populations annually (Wynberg & Branch, 1991). However at Langebaan, on the centre banks where most bait collecting activity took place, about 800 000 mud- and sand prawns were removed per annum which amounts to about 3.2 % of the population (Wynberg & Branch, 1991). Less than 1 % of the lugworm population in the Dutch Wadden Sea was calculated to be removed annually by mechanical bait digging (McLusky *et al.*, 1983). In the United Kingdom, bait diggers collecting polychaete worms were found to be selective predators and were rarely more than 50 % efficient in capturing potentially useful *Nereis virens* (Blake, 1979a) and it was found that the exploited ragworm populations were not threatened by such a level of exploitation (Blake, 1979a). In a similar study on the bloodworm, *Arenicola marina*, Blake (1979b) found that although the diggers selectivity, efficiency and effort were higher, the annual proportion of the population removed was lower for *N. virens* than for *A. marina*. Klawe and Dickie (1957) studied the biology of the bloodworm, *Glycera dibranchiata*, in relation to the bloodworm fishery in Maritime Provinces of Canada. They concluded that the spawning stock was not threatened by bait digging, even though the diggers turned over 460 m² of sand and removed 80 - 90 % of the commercially valuable worms per tide.

These studies on polychaete worm digging did not include data on the effects of digging on other infauna. Jackson and James (1979) showed that bait digging can affect other species and attribute the decline in the cockle, *Cerastoderma edule*, populations on the Norfolk coast to the effect of digging for rag- and bloodworms. McLusky, Anderson and Wolfe-Murphy (1983) described the distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging in the Forth estuary, Scotland. They concluded that bait digging by sport fishermen for lugworm causes substantial dislocation of *Arenicola* populations but that this disruption was temporary, rather than permanently damaging. In contrast to the study by Jackson and

James (1979), McLusky *et al.* (1983) found no deleterious effects on *Macoma balthica* and *Hydrobia ulvae* populations. These studies have suggested that bait collecting is not a threat to the populations of bait organisms.

Historically, it is not known over what time period bait collecting for *U. africana* has occurred in the Knysna estuary, although mud prawns are recorded as being exploited for bait since at least the 1960's (Siegfried, 1962; Hill, 1967). No studies have quantitatively assessed the density of mud prawns in the Knysna estuary, and it is therefore not possible to compare present densities with empirical data from the past. There is however no evidence to suggest that densities of *U. africana* have declined over the past 30 years. Bait collectors do not experience trouble collecting sufficient large mud prawns for bait and the "seasoned" anglers interviewed had not noticed a decline in the numbers of mud prawns at the popular bait collecting sites. In Langebaan Lagoon, a sharp distinction in prawn densities was found between physically similar conserved and non-conserved banks. Heavily pumped areas possessed noticeably lower prawn densities which suggests that bait collecting has an impact on these populations (Wynberg and Branch, 1991). However, there is no evidence to suggest that bait exploitation has a deleterious effect on the *U. africana* populations of the Knysna estuary. The impact of bait collecting on the bait stocks of *U. africana* will be discussed further in Chapter 5.

Disturbance by bait digging has been found to have far greater effects on prawn populations than would be estimated from the numbers removed. Disturbance of the sediment which results in compaction has been suggested as the most likely agent responsible (Wynberg and Branch, 1994). Intense bait collecting of the sand prawn, *Callinassa kraussi*, and mud prawn, *U. africana*, in the Langebaan lagoon resulted in the removal of 6.7 - 13.1 % of the sand prawns and 46 - 49 % of the mud prawns, but both populations subsequently declined by 70 % as a result (Wynberg and Branch, 1994). These populations were experimentally exploited by sucking (using a prawn

pump) and digging (with a spade to a depth of 30 cm) over a specific area. This scale of sediment disturbance is similar to that caused by illegal bait-diggers in the Knysna estuary.

The legal bait collecting methods used in the Knysna estuary do not result in the same physical sediment disturbance caused by digging in the Langebaan Lagoon. Some recreational anglers use a prawn pump to collect bait. This consists of a 75 cm long, 6 cm diameter stainless steel or plastic cylinder, containing a hand operated diaphragm pump (Hailstone and Stephenson, 1961) and is efficient and easy to use. It can be operated by pulling the plunger up, placing the pump over the opening of a prawn burrow, forcing the plunger down and the water and prawn out of the burrow, or by sucking up a core of sediment and examining it for prawns. Some anglers utilize commercially bought or home-made "prawn pushers" which are simpler, but operate on the same principle of hydraulic pressure as the pump and as the tin cans used by subsistence and supplementary anglers.

These "blowing" methods used by the majority of bait collectors do not disturb the sediment. They are in fact similar to the method used by the white steenbras, *Lithognathus lithognathus*, and spotted grunter, *Pomadasys commersonni*, which are often called "blowers" as they hang vertically in the shallow waters covering mud banks and blow down one opening of a prawn burrow so that the prawn is ejected from the other (Day, 1981a). The different categories of anglers identified in this study may have varying effects on the prawn populations and associated benthic fauna due to the varying degrees of disturbance caused by their methods of bait collecting. Although the majority of the prawns removed (85 %) are taken by non-leisure fishermen and women, these anglers are likely to cause the least disturbance of sediment using tin cans and prawn pushers.

There are three main indirect effects of bait collecting on macrofaunal organisms associated with sand- and mud prawns. Firstly, organisms left or exposed and overlooked by bait collectors are often preyed upon by scavenging birds (Jackson and James, 1979; Martin, 1988; Wynberg and Branch, 1991). Secondly, excavation down to a potential depth of 80 cm by prawn pumps or digging, must cause sediment instability which could result in the burial and suffocation of trapped organisms (Wynberg and Branch, 1991). Thirdly, physical damage of organisms can occur from prawn pumps and spades or forks. Of these three indirect effects of bait collecting, only the first applies to the legal methods of bait collection in the Knysna estuary. "Blowing" mud prawns from their burrows results in minimal disturbance to the sediment or damage to infaunal benthic organisms. It is suggested that the secondary effects of bait collecting by digging identified in other studies are not as of yet an important factor in the Knysna estuary.

Summary

1. Three groups of bait collectors can be identified on the basis of their source of income: subsistence fishermen and women who rely on bait collecting and fishing for their income, supplementary anglers who catch fish to supplement their income and leisure anglers who draw no income from fishing.
2. These three groups are not reflected in the bait collecting and fishing methods used by anglers. Two groups can be identified based on the methods used: leisure anglers who collect bait using a prawn pusher or pump and fish using a rod and tackle, and non-leisure anglers who collect mud prawns using tin cans and fish with handlines.
3. The number of bait collectors present per mudbank, is highest on public holidays ($x = 34$) and greater during the summer holidays ($x = 16$) than during the winter ($x = 4$).
4. A total of 1.858×10^6 *U. africana* or 700 kg (dry mass) are removed by bait collectors annually from the 6 popular bait collecting sites studied. This represents 8.5 % of the mud prawn stocks at these sites and 0.85 % of the entire estuary stock.
5. 85 % of the *U. africana* taken as bait annually, is removed by the 77 % of bait collectors who are non-leisure anglers. Leisure anglers are responsible for removing 14 % of the mud prawns collected annually.
6. Legal methods of bait collection do not cause sediment disturbance or destruction of the habitat. The secondary effects of bait collecting appear not to be a threat to the macrofauna of the mud banks in the Knysna estuary.

CHAPTER FOUR

REPLENISHMENT OF STOCKS OF *UPOGEBIA AFRICANA*

Reproductive cycle, larval transport and recruitment

INTRODUCTION

The success of any species is based ultimately on its ability to reproduce. Marine and estuarine invertebrates are known to use a wide spectrum of reproductive strategies. The most common of these is planktotrophic development whereby larvae are free in the plankton and prey on other species for nourishment as they develop (Epifanio, 1988). For estuarine species, use of this strategy results in the dispersal of larvae to coastal waters by tidal currents (Epifanio, 1988; McConaugha, 1988). Many authors have shown that there is considerable onshore - offshore movement of both adults and larvae amongst the Decapoda in relation to spawning and recruitment (Sandifer, 1975; Staples, 1980a, b; Christy & Stancyk, 1982; Johnson & Gonor, 1982; Emmerson, 1983; Wooldridge, 1991, 1994) and there is ample evidence that the larvae of some decapod species inhabiting the lower reaches of estuaries are exported (see McConaugha, 1988 for review). For planktotrophy to be an advantageous strategy, larvae must be released when conditions are optimal for their survival (McConaugha, 1988).

A considerable amount of information has been published on the rhythms of larval release by decapod crustaceans (see Forward, 1987 for review). Larvae are known to be released rhythmically in relation to lunar, light - dark and tidal cycles (Forward, 1987). There are two distinct dispersal patterns associated with larval advection: larvae can be retained in the nearshore marine waters adjacent to the mouth of the estuary or they can be dispersed over a range of 100 km or more. In all cases, the maintenance of adult estuarine populations depends on the successful reinvasion and recruitment of late-stage larvae or juveniles (McConaugha, 1988).

Upogebia africana is one estuarine species of decapod crustacean which is not confined to this environment. Although the adult prawns are only found in estuaries or sheltered bays (Hill, 1967), they have been shown to utilize inshore marine waters at specific times during their life cycle (Wooldridge, 1991). The reproduction of *U. africana* is well documented (Siegfried, 1962; Hill and Allanson, 1971; Hill, 1977, 1981; Hanekom and Erasmus, 1989). Siegfried (1962) described the reproductive biology and growth of an unexploited natural population of *U. africana* from the Uilenkraals River estuary in the Western Cape, South Africa and summarised a possible life cycle. The smallest ovigerous mud prawns found were 10 mm - 10.9 mm carapace length (CL), therefore prawns greater than 10 mm CL have been classified as adults (Siegfried, 1962; Hill, 1977). Ovigerous female mud prawns have been recorded from late August to March (Hill, 1977; Hanekom and Erasmus, 1989). Eggs are carried and incubated on the pleopods under the abdomen for approximately 40 days before they hatch into the water column (Hill, 1977). It has been suggested that this would allow some females to breed twice during one season, in summer and in spring (Hanekom and Erasmus, 1989).

The larvae of *U. africana* have been found in the plankton from November to early April (Emmerson, 1983; Wooldridge, 1991). Emmerson (1983) has shown that the mud prawn larvae use tidal currents and are dispersed into nearshore marine waters to undergo larval development before re-invading estuaries during the late larval stages. Wooldridge (1991, 1994) established that this marine phase in their development is obligatory, as larvae trapped in a closed estuary or held in estuarine water in the laboratory did not develop further than stage 1. *Upogebia africana* has been shown to exhibit a semi-lunar rhythm of larval release. First stage mud prawn larvae are exported on the nocturnal ebb tide with their release centered on crepuscular high tide. Post larvae invade estuaries on nocturnal flood tides, are dispersed and settle into the mud where they burrow (Emmerson, 1983; Wooldridge, 1991).

Since the reproductive cycle and larval life history of *U. africana* are well documented, this study focused on establishing whether or not the reproductive pattern of females in the Knysna estuary is similar to that documented for *U. africana* in other South African estuaries. In addition, comparisons of the numbers of females reproductively active and the numbers of larvae released, were made between sites in the estuary, to determine whether or not *U. africana* is reproductively active throughout the Knysna estuary. The production of *U. africana* larvae from various areas in the estuary and the transport of the larvae are described. The recruitment of juvenile *U. africana* to the various mud prawn populations throughout the estuary is investigated and the potential of these recruits to sustain exploited populations or to recolonise areas exploited or disturbed by bait collectors is discussed.

METHODS

Seasonality of reproduction

In order to study the seasonality of reproduction in *Upogebia africana*, females were collected by pumping on a monthly basis from February 1995 to April 1996. This relatively rapid and easy method of obtaining mud prawns was used, as more thorough methods such as digging and sieving core samples, were not possible as they are extremely labour and time intensive, as well as destructive. Mud prawns obtained by core sampling (see Chapter 2) and those in bait collectors catches were also examined throughout the year and the data obtained from these sources were included. In total, data were collected from 9 sites along the estuary (Fig. 4.1). Sites sampled varied in distance from the estuary mouth and in the intensity of their exploitation by bait collectors (see Chapter 3). All prawns were measured to 0.01 mm carapace length (CL), sexed and the pleopods of the females examined for eggs.

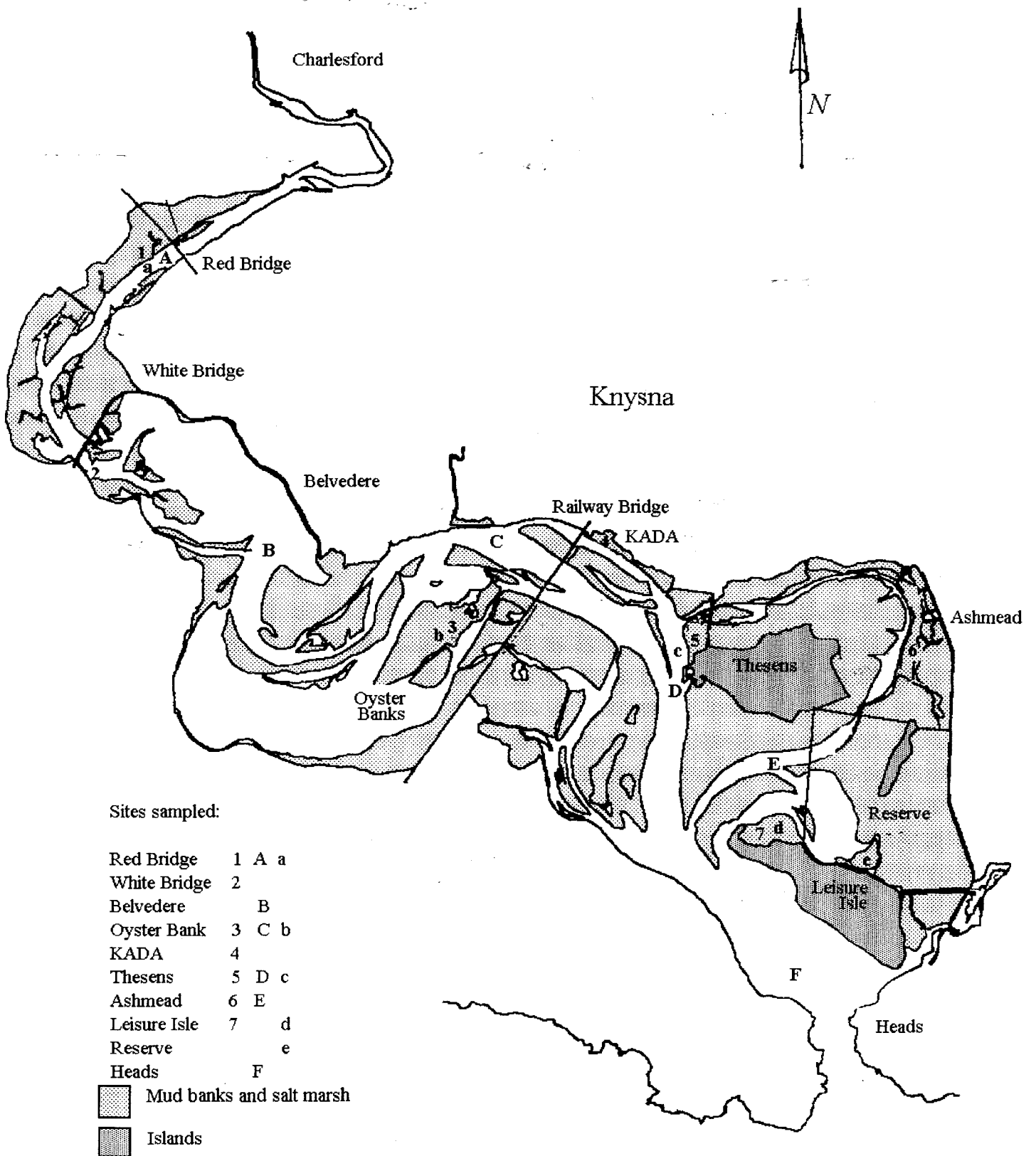


Figure 4.1. The Knysna estuary showing the sites sampled for reproductive data (1 - 7), plankton (A - F) and juvenile recruitment (a - e). Scale: 1 : 50 000.

Planktonic phase

To study the flux of *U. africana* larvae in the Knysna estuary, regular plankton sampling was carried out. To assess where larvae are released and to estimate the numbers of larvae leaving the estuary, six stations were sampled from Red Bridge down to the Heads (Fig. 4.1). Sampling commenced at Red Bridge as this site is near the upper limit of the distribution of *U. africana* in the estuary (Fig. 2.7; Chapter 2). Between this site and the Heads, three stations were chosen at approximately equal intervals: Belvedere, the Oyster Bank area and Thesens. The Ashmead channel was sampled as it runs through areas of extensive intertidal mud flats, including the Invertebrate Reserve and is off the main channel. A site at the Heads was sampled to determine the densities of larvae leaving the estuary.

From August 1995 to April 1996, during the breeding season of *U. africana*, two flood and two ebb tides were sampled each month. In the winter months only one flood and one ebb tide were sampled each month. Along the South African coast, crepuscular tides are neap. Stage 1 larvae are released on the crepuscular high tide and leave the estuary with the early evening ebb tide (Wooldridge, 1991). Sampling therefore commenced at dusk at neap high tide, and continued for at least four hours of the nocturnal ebb tide.

A 12 cm diameter Clarke-Bumpus Automatic Plankton Sampler (No. 012WA300) with Flowmeter (model 012WA300) was used to collect quantitative plankton samples. The flowmeter was calibrated every 2 months. Wooldridge (1991) found that stage 1 *U. africana* larvae were significantly more abundant in surface waters than in sub-surface layers (unpublished data), therefore samples were collected near the surface of the water column. The plankton sampler was fitted with a 90 cm conical net (80 μ m mesh) and was towed 0.5 m below the surface from the bow of a flat bottomed river boat with a 30 hp outboard motor. At each station three 3 minute trawls were collected.

Post larvae are known to re-invade estuaries on the nocturnal flood tide (Wooldridge, 1991) therefore sampling was started at crepuscular low tide and continued for at least four hours of the flood tide. During the flood tide, stations sampled were limited to those at the mouth, to determine the numbers of post larvae entering the estuary, and at the entrance to the Ashmead channel. The Ashmead channel was sampled as it is shallower (2 - 3 m) than the very deep, wide mouth of the estuary and the volumes of water sampled at this site were more representative of the water column. When flood tide sampling for post larvae, the plankton sampler was fitted with a 150 μm mesh and five minute sub-surface (0.5 m) trawls were collected on every half hour in a method similar to that used on ebb tides. A preliminary investigation revealed that post larvae entering the estuary were more elusive than stage 1 larvae leaving the estuary, therefore an additional qualitative plankton net was also towed to increase the volume of water sampled. Bottom and mid-water trawls were also carried out.

All plankton samples were concentrated and preserved in 5 % formaldehyde in filtered seawater before the larvae were counted and identified under a binocular microscope. The larvae of *U. africana* have recently been described by Loubser (1992). Dr. B. Newman and Prof. T.H. Wooldridge, Zoology Department, University of Port Elizabeth and Dr. Nguyen Ngoc-Ho, National Natural History Museum, France assisted with and confirmed larval identifications.

Transport of *Upogebia africana* larvae

A drift bouy was followed up and down the estuary with a spring flood and ebb tide to determine the potential distance that larvae could be transported on a single tide. The bouy was designed with only a flag above the water level so that the wind and other surface conditions had a minimal influence on it's movement. Four vanes, at right angles to each other below the water, ensured that the bouy was always caught by the current. A motor boat was used to follow the drift bouy which was allowed to drift freely in the main channel of the estuary.

Recruitment

Five sites up the estuary (Fig. 4.1) were chosen to assess the numbers of juveniles settling into the mud each month from December 1995 to April 1996. The sites chosen were the Invertebrate Reserve, the adjacent exploited area at Leisure Isle and the exploited Thesens site on the main channel, the unexploited Oyster Bank and a truly estuarine site at the Red Bridge. At each site five 0.25 m² quadrats were dug to approximately 10 cm and all prawns were sieved from the mud through a fine "mosquito mesh" sieve (1 mm mesh). Prawns under 5 mm CL were considered to be newly settled as the post larvae of *U. africana* are described as being 4.5 - 5 mm in length (Loubser, 1992).

RESULTS

Seasonality of reproduction

Ovigerous female *U. africana* were found in the population from late July 1995 to the end of March 1996. The percentage of female prawns that were ovigerous each month varied from 76 % to less than 10 % (Fig. 4.2a), with two peaks of reproductive activity in October 1995 (65 %) and January 1996 (76 %). No females were in berry during the winter period of April, May and June of 1995. The two peaks of breeding activity observed in spring (October) and summer (January / February) indicate that two over-lapping breeding cycles may occur in each breeding season.

The percentage of the female mud prawns that were ovigerous varied between the 9 sample sites within the estuary (Figs. 4.1 & 4.3). With the exceptions of the Oyster Bank and Factory sites, the percentage of ovigerous females tended to decrease with distance from the estuary mouth. The Factory site is where warm water (24°C) from a factory cooling plant is pumped into the estuary. No ovigerous females were found at the White and Red Bridge sites up-estuary.

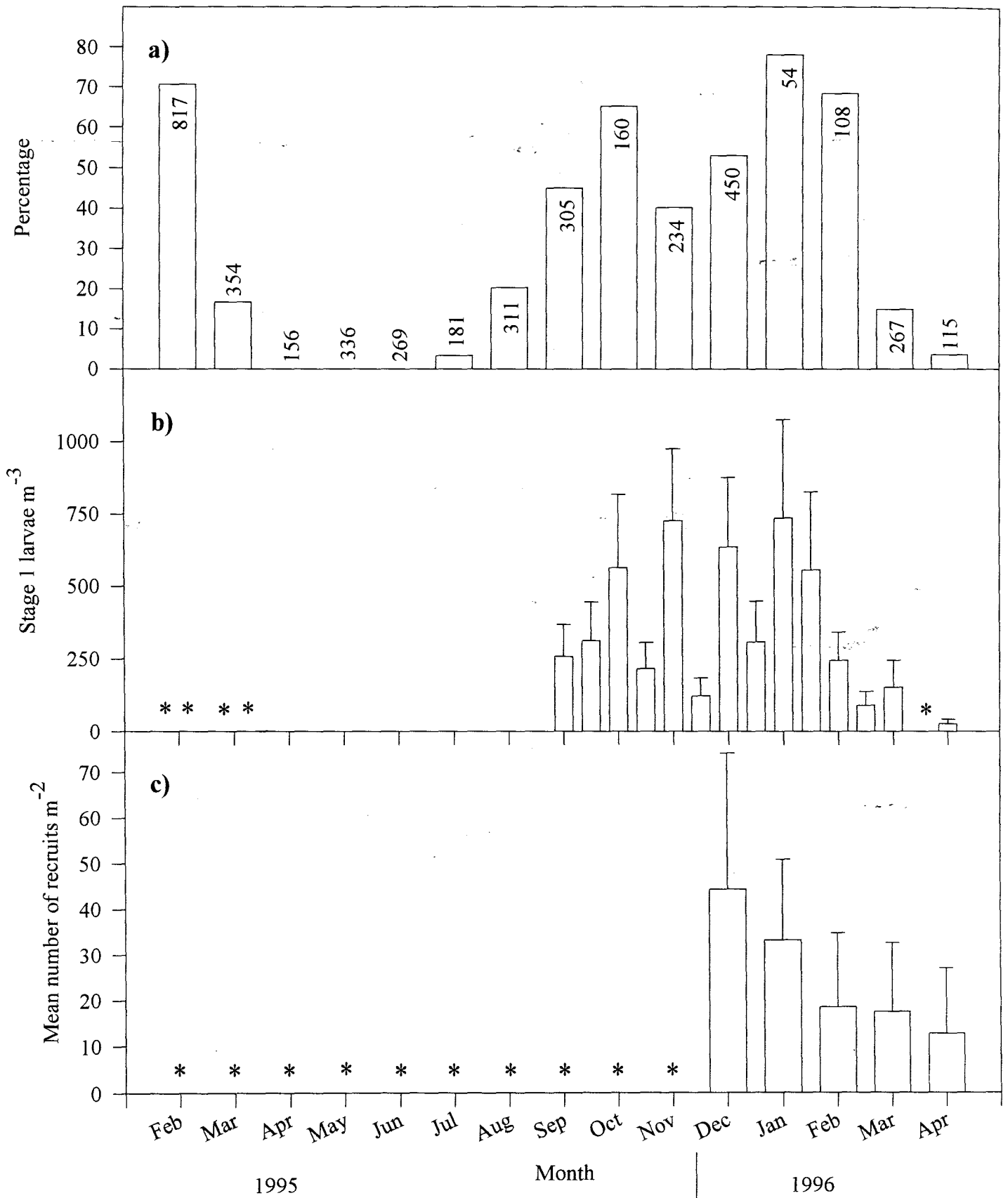


Figure 4.2. a) % females ovigerous (with number of females sampled), b) Mean (of the total at each site) number of stage 1 larvae m⁻³ and c) Mean number of juvenile recruits m⁻² per month (with standard error bars of the means; * No data).

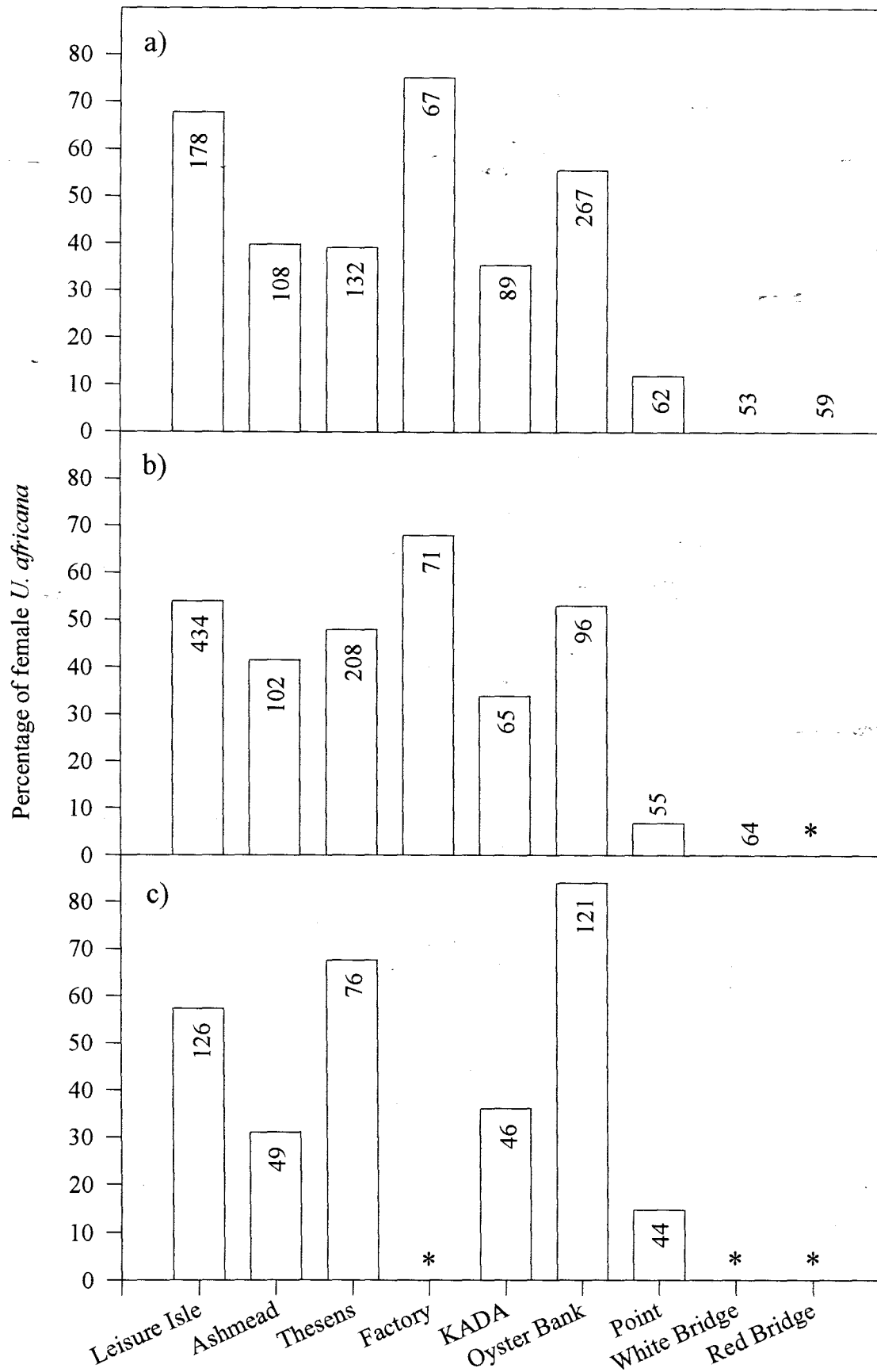


Figure 4.3. Percentage of the female *U. africana* that were ovigerous at each of 9 sites up the Knysna estuary in a) September, b) November and c) December 1995. The number of prawns sampled (n) is shown in the bars. (* No data).

of development are shown in Figure 4.4. When freshly extruded onto the pleopods the eggs are greenish in colour (Hill, 1977), they then change to an orange-brown and eventually brown when eyespots are visible. In October 1995, near the beginning of the breeding season, the proportion of mature eyed eggs was approximately 5 %. This increased to 35 % by November 1995 and remains around 30 % throughout the breeding season. The percentage of freshly extruded eggs, on the other hand, was highest October 1995 (nearly 40 %), decreased in November and December 1995 and rose again to over 20 % in January and February 1996. The two peaks in the percentages of freshly extruded and mature eggs provides more evidence of two overlapping breeding cycles.

Planktonic phase

Plankton sampling confirmed the results of Wooldridge (1991). Larvae were found in the plankton from September 1995 to April 1996. These larvae were found leaving the estuary on the crepuscular ebb tide, and none were found once the tide had turned to flood. The numbers of stage 1 larvae leaving the estuary per month increased from September 1995 to November 1995, with peaks of larval abundance in October (nearly 1200 m⁻³) and in January (over 1000 m⁻³; Fig. 4.2b).

During the peak breeding season, when two ebb tide sampling trips were undertaken per month, large differences were found in the numbers of larvae caught on successive neap tides (e.g. 450 m⁻³ on 14 November and over 1400 m⁻³ on 27 November; Fig. 4.5). Besides during February, the numbers of larvae released during the peak breeding season on the crepuscular ebb tide following the new moon (waxing quarter) were nearly double those released on a crepuscular ebb tide following the full moon (waning quarter). These differences in the numbers of larvae released are however not significant ($p > 0.05$, ANOVA; Table 4.1).

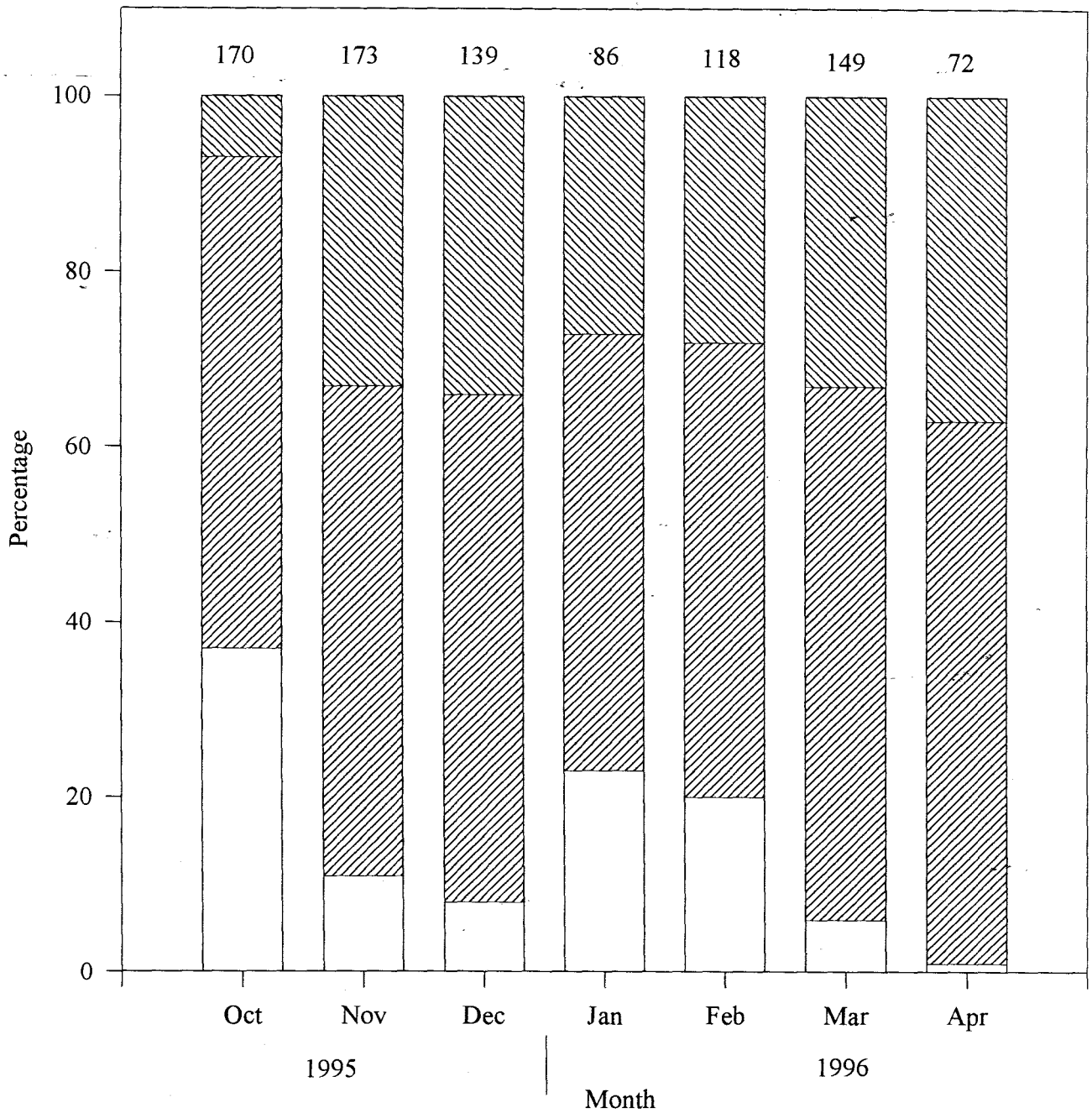
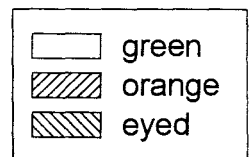


Figure 4.4. The percentages of the ovigerous females bearing freshly extruded (green), mid-term (orange) and developed (brown with eyespots) eggs during the breeding season. The number of females sampled (n) is shown above the bars.



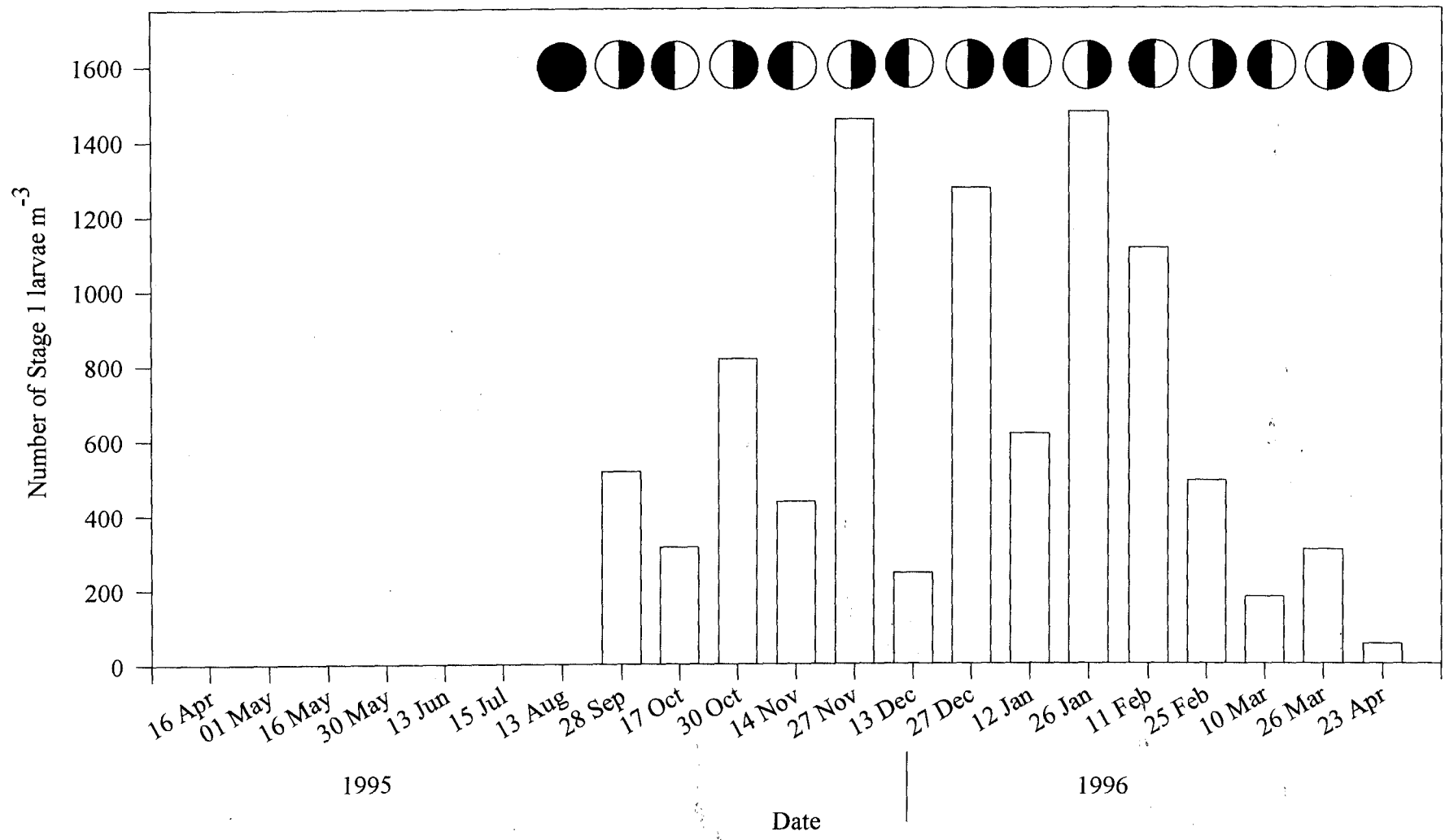


Figure 4.5. Numbers of *U. africana* Stage 1 larvae (m⁻³) leaving the Knysna estuary. The phases of the moon are shown above the graph (● New moon, ◐ waxing, ◑ waning).

The mean numbers of *Upogebia africana* larvae caught per month at each of the sites sampled also show high variation and reflect the trends in abundance of stage 1 larvae observed over the whole estuary (Figs. 4.6a & b). *Upogebia africana* larvae were never found up-estuary at Red Bridge and when found at Belvedere, numbers were very low ($< 3 \text{ m}^{-3}$; Figs. 4.6a & 4.7). Mean numbers of larvae m^{-3} peaked at Thesens before decreasing again as the mouth of the estuary was neared (Fig. 4.7). The numbers of stage 1 *U. africana* larvae produced at Thesens and Ashmead are significantly higher than the numbers caught further up-estuary at Belvedere and at the Oyster Banks ($p < 0.0005$, ANOVA; Tables 4.3 & 4.4). *U. africana* post larvae were never caught in the Knysna estuary using the equipment available.

Table 4.1. Results of an Analysis of Variance to determine whether there are any significant differences in the numbers of Stage 1 *U. africana* larvae released on the neap tide following a full moon (waning quarter) and a new moon (waxing quarter).

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Between groups	76317.1	1	76317.08	2.797	0.0998
Within groups	1582744.2	58	27288.66		
TOTAL	165959.3	59			

Table 4.2. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the numbers of Stage 1 *U. africana* larvae released on the neap tide following a full moon (waning quarter) and a new moon (waxing quarter).

Lunar conditions	n (sampling occasions)	Mean number of larvae (m^{-3})	Homogeneous groups
Waning quarter	12	118.27	X
Waxing quarter	12	189.59	X

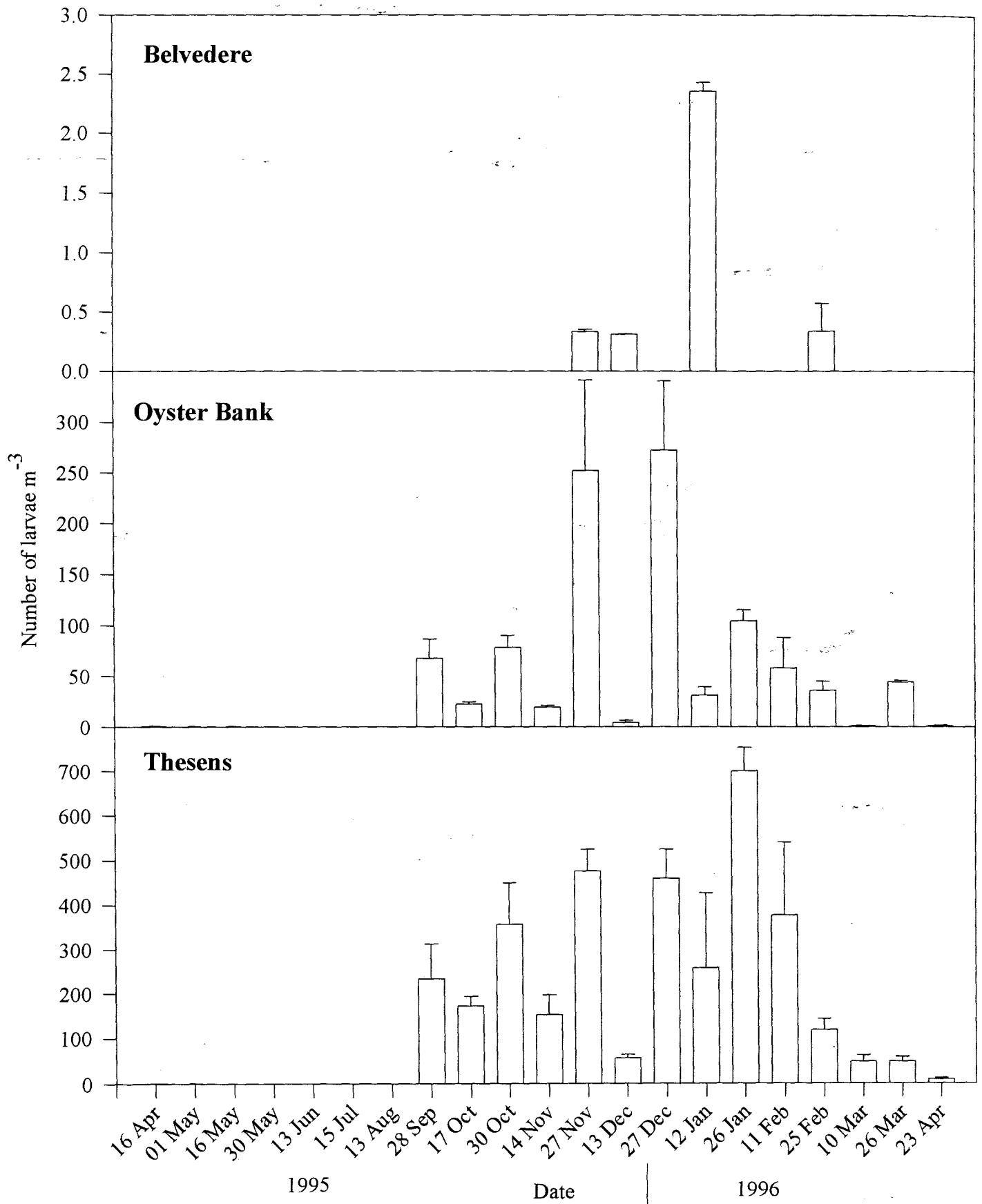


Figure 4.6a. Mean numbers of *U. africana* stage 1 larvae at three sites from April 1995 to April 1996 (standard errors of the means of 3 trawls are shown).

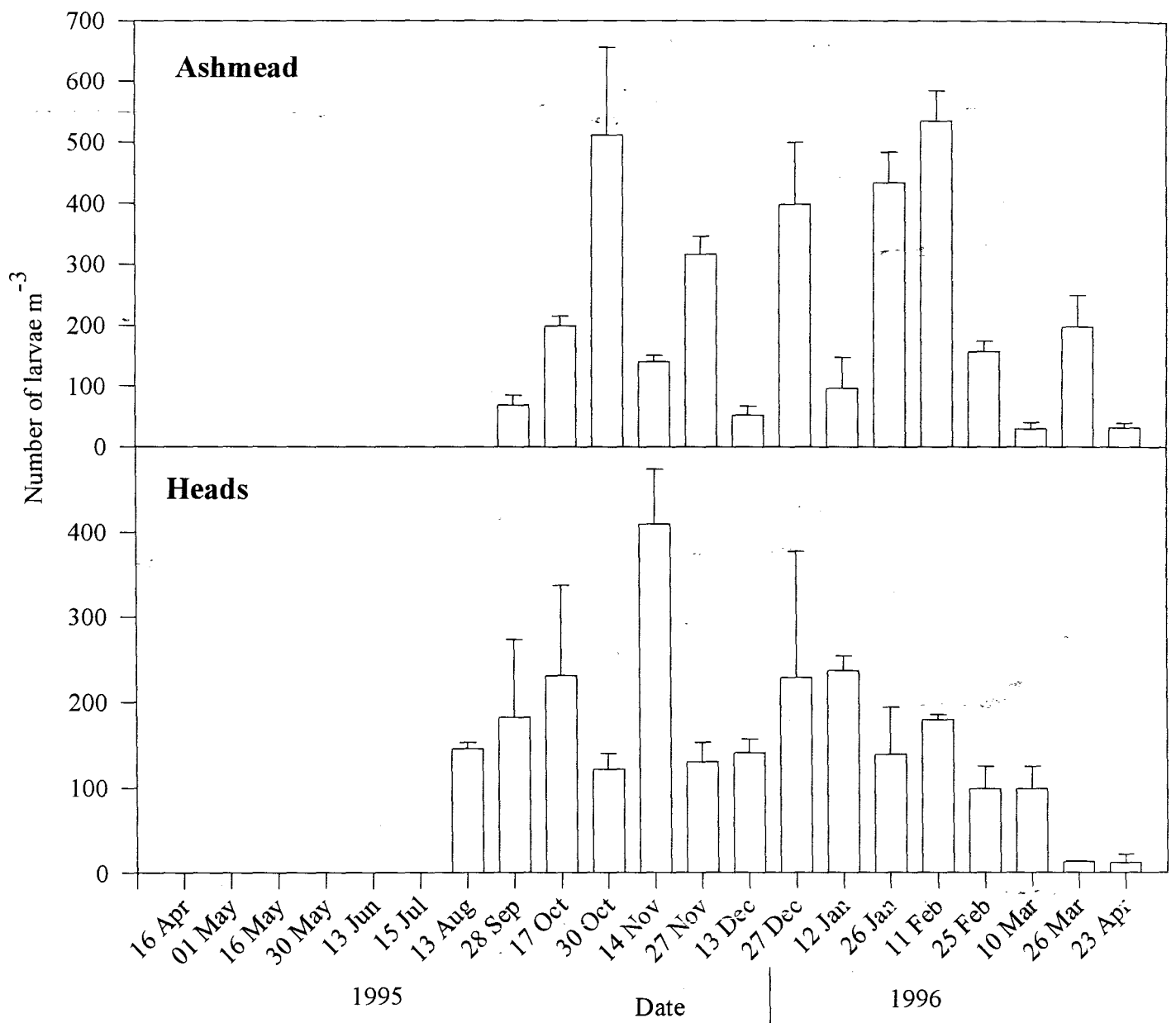


Figure 4.6b. Mean numbers of *U. africana* stage 1 larvae at three sites from April 1995 to April 1996 (standard errors of the means of 3 trawls are shown).

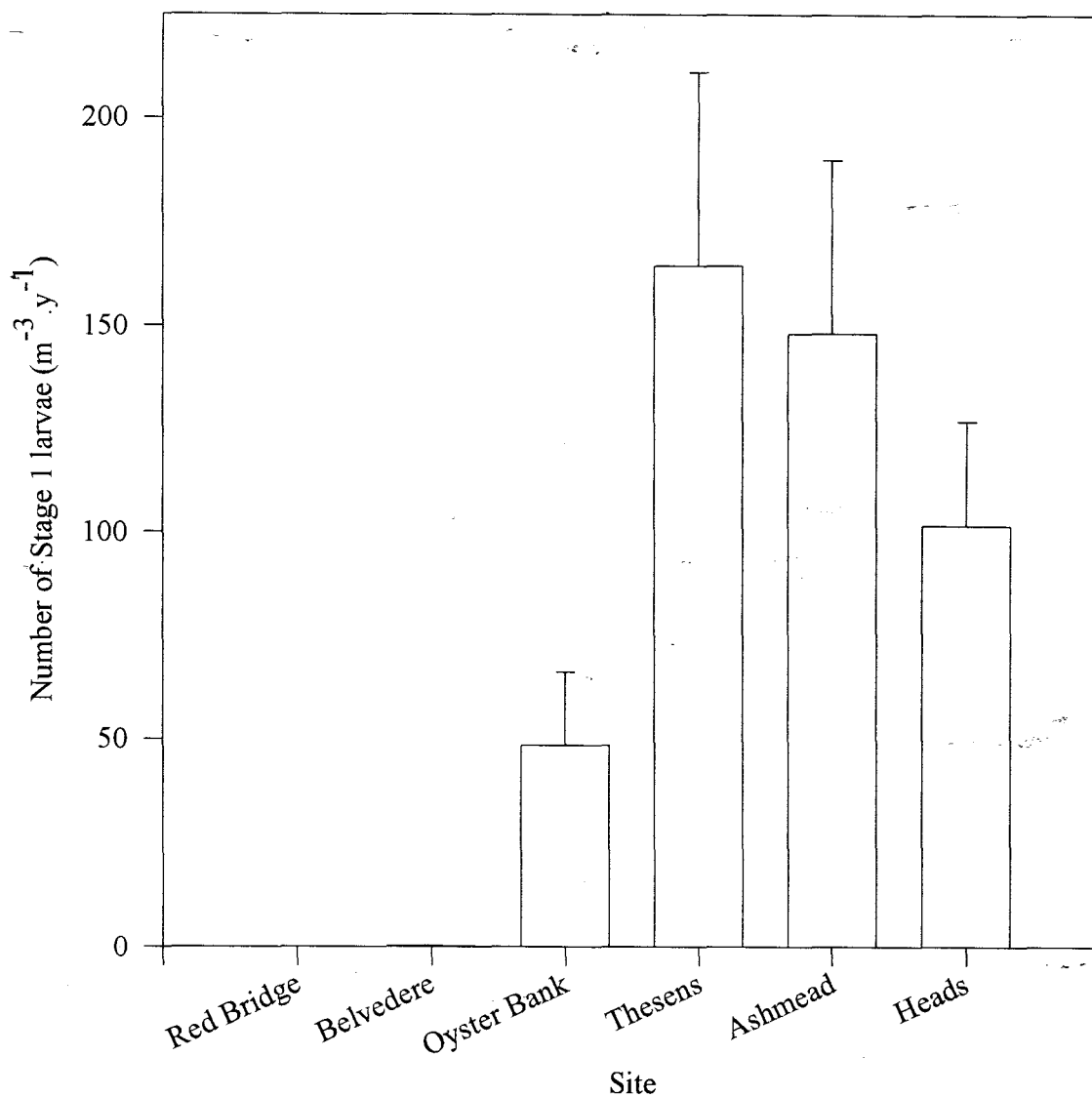


Figure 4.7. Mean numbers (with standard error bars) of *U. africana* Stage 1 larvae leaving the Knysna estuary from each of six sites over the year (April 1995 - April 1996).

Table 4.3. Results of an Analysis of Variance to determine whether there are any significant differences in the numbers of Stage 1 *U. africana* larvae released from different sites in the estuary. The Red Bridge site was excluded as no larvae were found at this site.

Variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Between groups	411223.6	4	102805.9	5.592	0.0004
Within groups	1838461.8	100	18384.62		
TOTAL	2249685.4	104			

Table 4.4. Results of Scheffe's Multiple Range Analysis to determine whether there are any significant differences in the numbers of Stage 1 *U. africana* larvae released from different sites in the estuary. The Red Bridge site was excluded as no larvae were found at this site.

Site	n (sampling occasions)	Mean number of larvae (m ⁻³)	Homogeneous groups		
Belvedere	21	0.159	X		
Oyster Bank	21	47.22	X	X	
Heads	21	112.62		X	X
Ashmead	21	150.68			X
Thesens	21	164.96			X

Transport of *Upogebia africana* larvae

The drift bouy followed from the mouth of the estuary at the Heads, on a spring flood tide, was found to reach White Bridge (Fig. 4.1) in a single tide. On a spring ebb tide, the bouy was transported from Red Bridge to the Heads. This indicates that *U. africana* post larvae entering the Heads have the potential to be transported as far as the upper reaches of the estuary on a single flood tide. Stage 1 larvae released in the upper reaches would, conversely, reach the sea on a single ebb tide.

Recruitment

Throughout the Knysna estuary, the mean number of juveniles (< 5 mm CL) recruited to *U. africana* populations during the summer was 24 m⁻² per month. The highest mean numbers of recruiting juveniles were found at Thesens (31 m⁻²), and the lowest number of recruits at the Oyster Bank (11 m⁻²; Fig. 4.8a). The density of juvenile *U. africana* recruited to the Thesens site is significantly higher than densities found at the Oyster Bank ($p < 0.05$, ANOVA; Tables 4.5 & 4.6).

The mean numbers of recruits per square meter in the estuary decreased from December (45 m⁻²) to April (14 m⁻²; Fig. 4.8b). At the four sites in the lower and middle reaches of the estuary, the number of juvenile mud prawns recruited decreased during the summer (Fig. 4.9). Recruitment of larvae at Red Bridge shows no clear trend (Fig. 4.9), but this may be due to mud prawn sizes at this site being atypical, with most mud prawns smaller than elsewhere in the estuary.

Table 4.5. Results of an Analysis of Variance to determine whether there is any significant difference in the number of juveniles recruited to the five sites sampled.

Variation	Sum of squares	d.f.	Mean square	F-ratio	Sig. level
MAIN EFFECT					
Site	5128.83	4	1282.21	2.862	0.0265
RESIDUAL	51520.64	115	448.01		
TOTAL	56649.47	119			

Table 4.6. Results of Scheffe's Multiple Range Analysis to determine whether there is any significant difference in the number of juveniles recruited to the five sites sampled in the Knysna estuary.

Site	n (samples)	Mean number of recruits (m ⁻²)	Homogeneous groups	
Oyster Bank	20	10.80	X	
Reserve	25	24.96	X	X
Leisure Isle	25	25.44	X	X
Red Bridge	25	27.84	X	X
Thesens	25	31.04		X

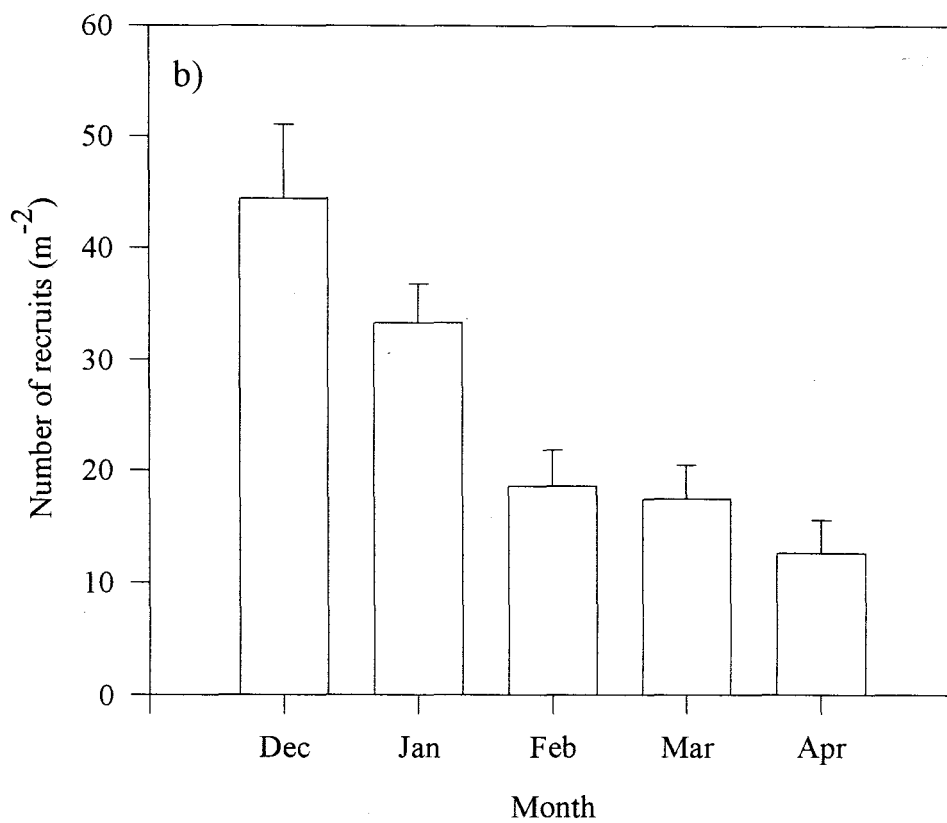
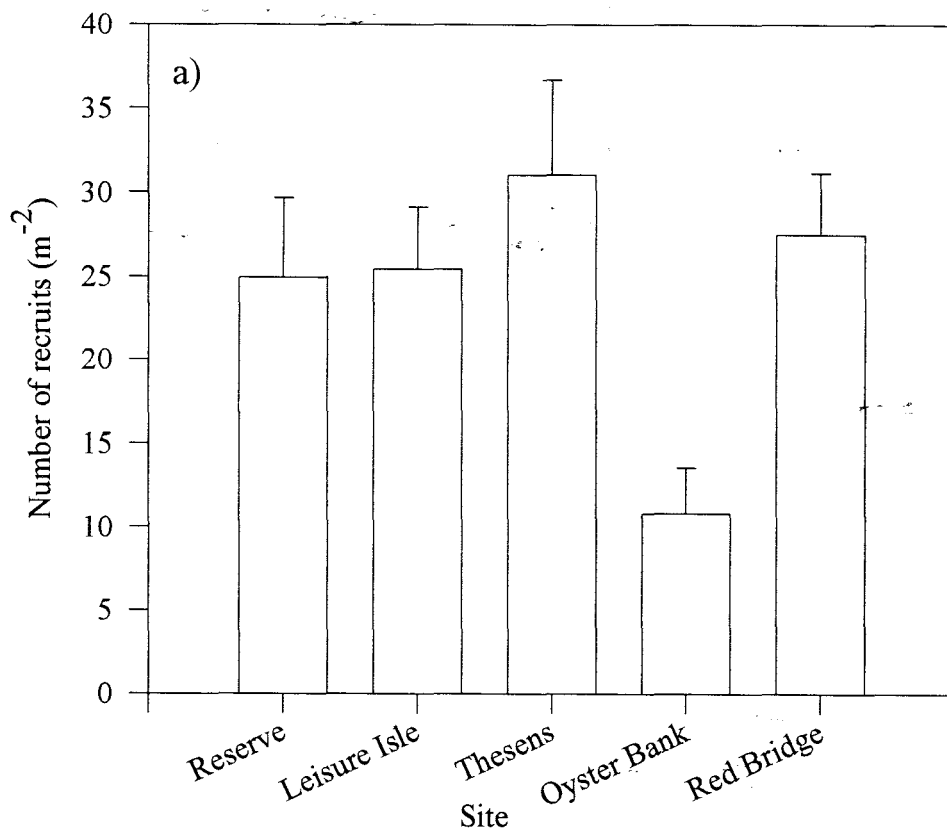


Figure 4.8. a) Mean number of juveniles recruited to each of 5 sites over five months (with standard error bars), and b) mean number of juveniles recruited to all sites during the 5 months sampled (with standard error bars).

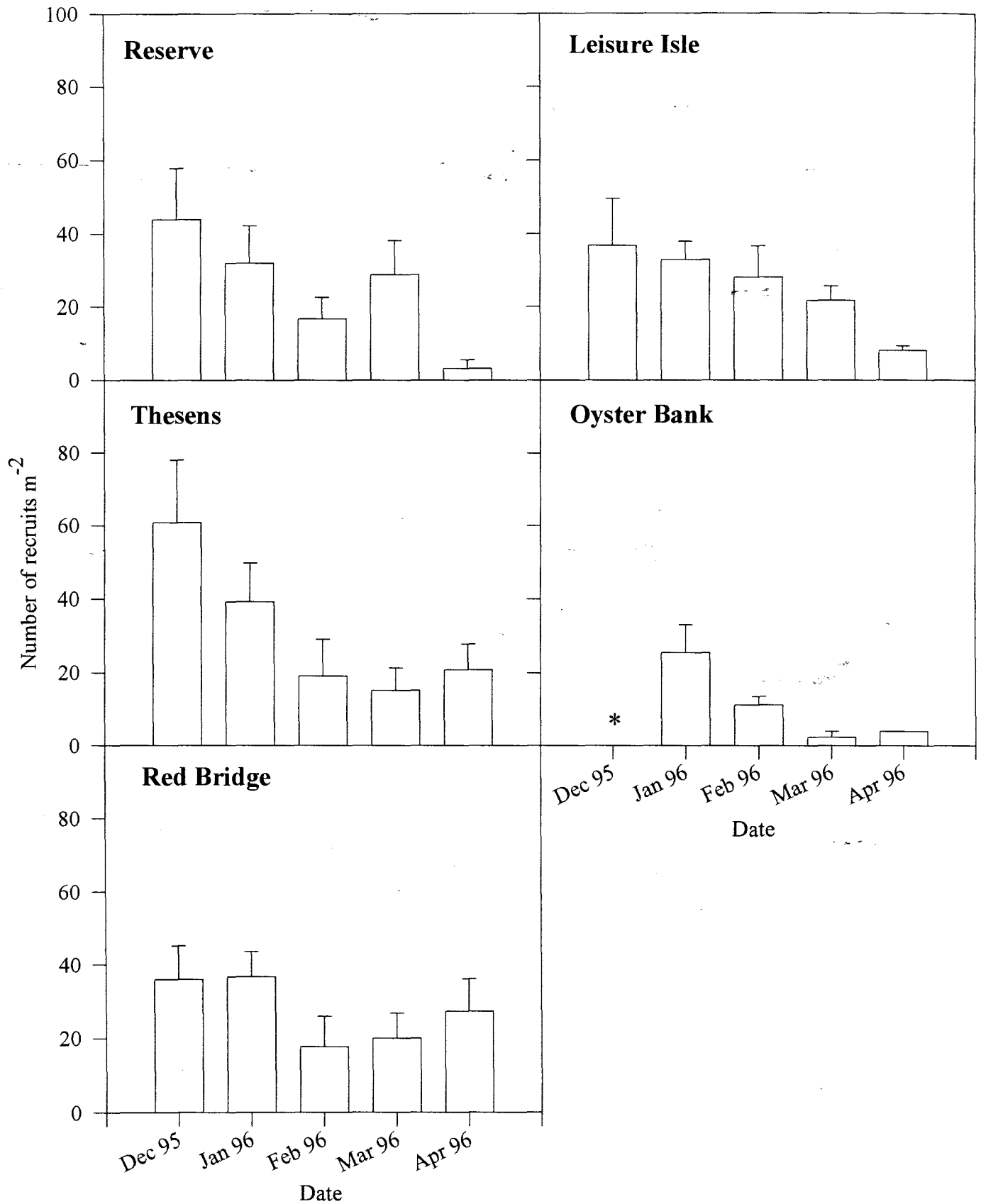


Figure 4.9. Mean numbers of recruits (m^{-2}) (with standard errors) over 5 months at 5 sites in the Knysna estuary (* No data).

DISCUSSION

Reproduction of *Upogebia africana* in the Knysna estuary is seasonal with females being ovigerous from late July to April. In the Kowie estuary (Hill, 1977) and the Swartkops estuary (Hanekom and Erasmus, 1989) the breeding season of *U. africana* was made up of two cycles per year, one in spring (September, October) and one in summer (December to March). In the lower reaches of the Swartkops estuary the two breeding seasons were found to merge with no latent period between cycles (Hanekom and Erasmus, 1989). The pattern at this site in the Swartkops estuary shows similarity to the breeding season recorded in the Uilenkraal and Knysna estuaries, where Hill (1977) found that the breeding season consisted of a single cycle. The two peaks in reproductive activity of *U. africana* (percentage of females in berry with eyed eggs and the numbers of stage 1 larvae in the plankton) found in the Knysna estuary, suggests that the single breeding season may be composed of two overlapping breeding cycles. In all the estuaries mentioned above, *U. africana* were reproductively inactive during the winter months of May and June. It has been suggested that relative temperatures may be important in initiating the breeding cycle, as the numbers of ovigerous females increase as estuarine temperatures increase (Hill, 1977; Hanekom and Erasmus, 1989).

Upogebia africana is not reproductively active throughout the Knysna estuary. With the exception of the Oyster Bank, the percentage of females in berry decreased with distance from the estuary mouth and no ovigerous females were found up-estuary at Red Bridge. The middle area of the estuary, at the Oyster Banks, in addition to supporting the highest biomass of mud prawns, also has the highest percentage of females in berry. This area of the Knysna estuary has the highest chlorophyll *a* concentrations and food rich water (Korringa, 1956; Knysna Basin Project, unpublished data). The mud prawns here may have more food available, or better quality food resources, and therefore have more energy to channel into reproduction. Hanekom and Erasmus (1989) calculated the reproductive output and reproductive biomass ratios (Pr / B) of

U. africana in areas of high water movement, and therefore high food availability, to be much greater than those of stunted mud prawns higher up the estuary. In addition, the reproductive output of female mud prawns is known to increase with prawn size (Hanekom & Baird, 1992).

The mud prawns at the Red Bridge were found to be much smaller than those in the lower reaches of the estuary. The largest mud prawns were 10.9 mm carapace length (Chapter 2, Table 2.9) which is the smallest size recorded as ovigerous. It is therefore not surprising that no females were reproductively active in this "stunted" population. Similar differences in population structure were found by Hanekom & Erasmus (1988) in the Swartkops estuary where the mean size of ovigerous females was smaller, further from the estuary mouth.

As expected, the timing of the onset of reproduction in the females, the appearance of stage 1 larvae in the plankton and the recruitment of juveniles to the population all show similar trends (Fig. 4.9). Ovigerous females were found in the population throughout the year except from April to the winter months. From July (< 2 %) the percentage of females in berry increased to 30 % by January (Fig. 4.9). Since reproduction in *U. africana* females is seasonal, it is likely that oogenesis may follow a similar seasonal pattern with egg production taking place throughout the warmer months and with a break from April to June. In the northern hemisphere, reproduction in *Upogebia pusilla* (Petagna) in the Northern Adriatic Sea occurs over 7 spring and summer months from March to September (Dworschak, 1988), whereas the breeding season of *Upogebia deltaura* (Leach) on the Swedish coast, is restricted to 4 months, from May to August (Tunberg, 1986).

U. africana stage 1 larvae are first found in the plankton in September, two months after the females become ovigerous (Fig. 4.9). This delay would account for the approximately 33 to 45 day suggested incubation period of the eggs on the pleopods of the females (Siegfried, 1962; Hill,

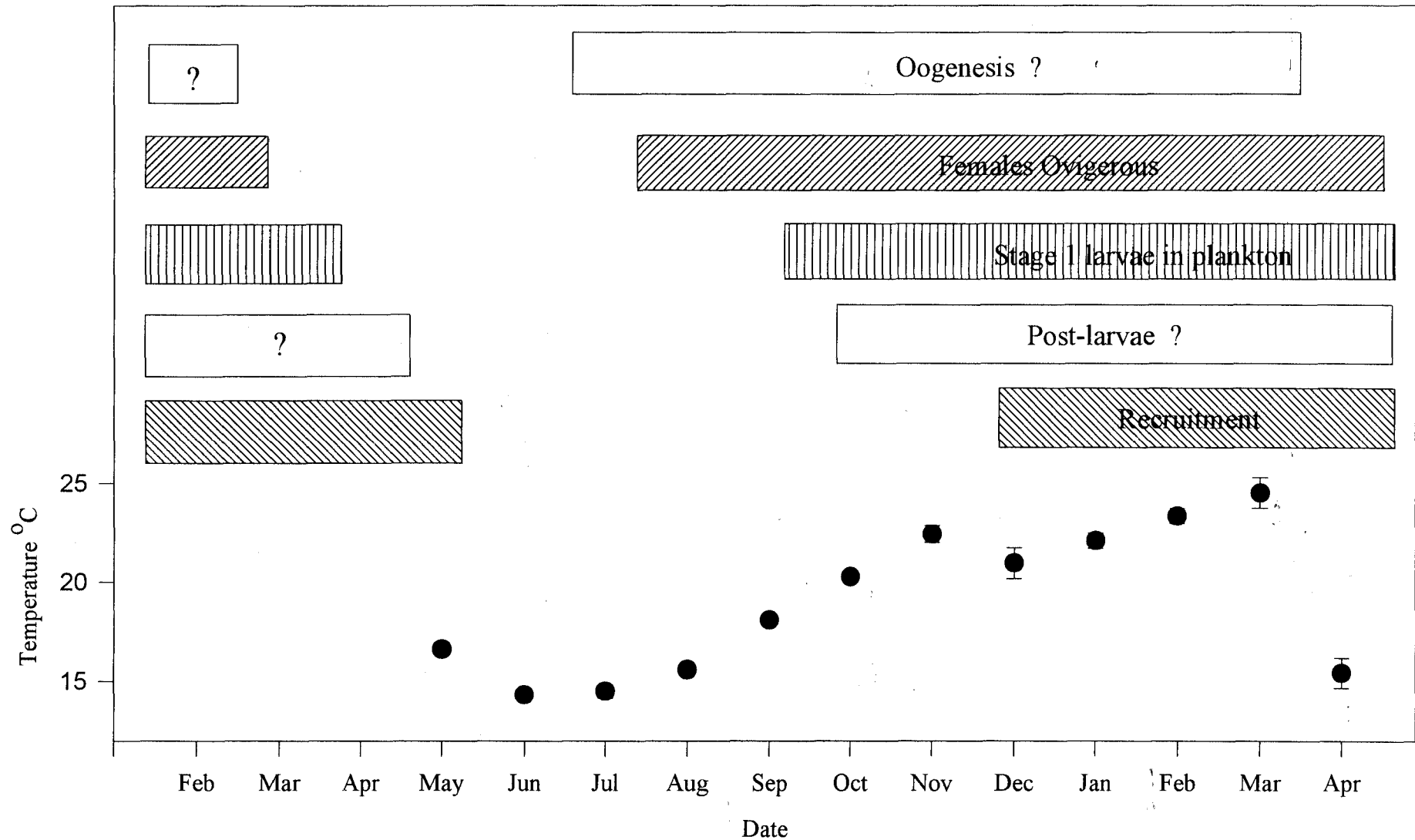


Figure 4.10. Summary of the timing of reproductive events in *U. africana* in the Knysna estuary from. Empty bars represent suggestions, these events were not sampled. Mean temperatures (of 6 sites up the estuary with standard error bars) are plotted below.

1977; Hanekom and Erasmus, 1989). The incubation period for *U. pusilla* held in the laboratory was found to range from 27 to 43 days depending on temperature (Dworschak, 1988). The duration of larval development in *U. africana* is not known. Although sampling for juveniles recruited only commenced in December, recruitment would be expected to begin from late September or October after the larvae had spent an estimated period of up to 20 days developing at sea (Loubser, 1992). The duration of larval development in *U. pusilla* is also unknown, but Dworschak (1988) suggests that a minimum period of 35 days can be assumed. The duration of the above periods is temperature dependent (Hill, 1977; Hanekom and Erasmus, 1989; Loubser, 1992).

The diel and tidal migration of the stage 1 larvae of *U. africana* in the Knysna estuary was found to be similar to the pattern described by Wooldridge (1991), Emmerson (1983) and Loubser (1992) in the Swartvlei, Swartkops and Gamtoos estuaries respectively. Stage 1 larvae were abundant in the plankton during the breeding season. As predicted from the research of Emmerson (1983) and Wooldridge (1991), no larvae of stages 2, 3 or 4 were found in the estuary. The absence of *U. africana* larvae at Red Bridge is consistent with not finding any ovigerous females at this site. The middle reaches of the estuary, e.g. Oyster Bank, have high densities and biomass of mud prawns with many individuals in the 14 mm - 20 mm CL size classes. It seems reasonable that a large proportion of the larvae to be exported would be produced in this area. At Thesens the channel narrows and the high numbers of larvae found here may represent a "funnel" of all larvae released above this point, in the middle reaches of the estuary where extensive mudflats and mud prawn populations (Fig. 4.1). The numbers caught at the Heads are taken to be representative of the number of larvae exported per cubic meter through the Heads. The number of stage 1 larvae recorded in this study reached peaks of 1500 m⁻³ in November 1995 and January 1996 on waxing quarter moons. In the estuary mouth of the Swartvlei estuary, numbers of *U. africana* stage 1 larvae peaked shortly after sunset with 692 per 100 m³ leaving the estuary,

during the remainder of the ebb the numbers varied from 162 - 300 per 100 m³ (Wooldridge, 1991). Numbers of larvae exported from the Knysna estuary are much greater than from the small, shallow Swartvlei estuary, and are comparable with numbers found leaving the Swartkops estuary, where Emmerson (1983) recorded a peak of approximately 2×10^3 m⁻³.

No post larvae were caught in the plankton over the entire year. It is possible that the aperture of the net used was too small and that larger volumes of water should have been sampled for an estuary mouth of this size. The mouth of the Knysna estuary is extremely deep and wide and it is likely that this is the reason why post larvae were not found. It is interesting that not a single post larvae was recorded in any of the trawls. In spite of finding low numbers *U. africana* stage 1 larvae leaving the estuary, post-larvae entering the Swartvlei mouth were recorded in numbers of greater than 250 per 100 m³ on the nocturnal flood tide with a peak of 3580 per 100 m³ at the beginning of the flood tide and post larvae were present in the surf zone throughout the night (Wooldridge, 1991).

The mechanism by which *U. africana* larvae maintain their position in coastal waters is unknown. Korringa (1956) noted that oyster larvae settling on collectors placed in the Knysna estuary, came from parent stocks at sea. He suggested that they are carried into the estuary by a counter current flowing very close inshore, and are washed into the lagoon with the flood tide. It has been suggested that larval development in *U. africana* occurs relatively close inshore (Wooldridge, 1991). Stage 1 larvae were seldom found in the surf zone off the Swartvlei estuary mouth once the tide had turned to flood. This strategy would minimise premature re-entry into the estuary. The exact duration of larval development and the distribution of larvae off-shore is unknown, but it has been suggested that rapid metamorphosis to stage 2 and a reversal in larval taxis to a more benthic existence would reduce transportation away from the estuary and suitable adult habitat (Wooldridge, 1991). Many species of zooplankton and invertebrate larvae are known to actively

maintain their position in the water column and to show specific behavioural patterns of vertical migration (Jacobs, 1968; Sandifer, 1975; Wooldridge & Erasmus, 1980; Epifanio, 1988; McConaugha, 1988). It must be suspected that the active movement of *U. africana* larvae is a factor in determining their horizontal distribution.

The largest number of *U. africana* juveniles recruited to the Knysna estuary was recorded in December 1995. After December the percentage of females in berry and the numbers of larvae in the plankton also decreased. The decrease in the number of recruits is possibly more marked as the numbers of mud prawns surviving are likely to be greatly reduced from eggs to stage 1 larvae to those post larvae developing, settling and recruiting successfully. Numbers of recruits are significantly lower at the Oyster Bank which is situated behind the Railway Bridge, than at the Thesens site on the main channel.

Hydrodynamic processes are likely to have an effect on the recruitment of benthic species (Eckman, 1983). Few data are available on factors affecting recruitment in *U. africana*. Successful recruitment into estuaries which close periodically would be predicted to depend on the relationship between open and closed phases of the tidal inlet (Wooldridge, 1994), but in the permanently open Knysna estuary, this does not influence recruitment. Exploitation of *U. africana* populations in estuaries that close periodically, would be expected to impact on the density of the bait stock as successful reproduction and post-larval recruitment to these systems may be sporadic.

It is not known whether adult *U. africana* leave their burrows under normal circumstances, and whether adult migration may represent another form of recruitment to mud prawn populations. Exploited *Arenicola marina* populations are thought to be repopulated from immediately neighbouring areas. Other processes likely to be involved in maintaining the population are

recruitment of larvae or adults from the subtidal population, or the recruitment of larvae or adults from other areas (Blake, 1979b). It is unusual to find *U. africana* emerged from their burrows and wandering on the surface under normal circumstances. Martin (1988) noted that a small proportion (c. 1 in 11000 per low tide cycle) of mud prawns did come to the surface, and that most of these were eaten by birds. The individuals found on the surface were typically larger prawns (17 - 21 mm carapace length) which carried very heavy parasite loads (100 - 200 parasites of a variety of species). High levels of parasitism may cause this unusual behaviour (Martin, 1988). It is therefore unlikely that repopulation of exploited *U. africana* populations would occur by way of adult immigration from unexploited areas (e.g. the subtidal populations or middle banks):

Summary

1. The reproduction of *U. africana* in the Knysna estuary is seasonal and occurs in a single breeding season from late July to April. There is evidence that this breeding season is composed of two overlapping breeding cycles.
2. The largest percentage of ovigerous females is found in the middle reaches of the Knysna estuary at the Oyster Bank where the highest numbers of stage 1 larvae are released.
3. Larvae are exported from the estuary on the crepuscular ebb tide with peaks in abundance of nearly 1500 m⁻³ in November 1995 and January 1996. Larvae are nearly twice as abundant on crepuscular neap tides following a new moon (waxing quarter) than on those following a full moon (waning quarter).
4. Recruitment of juvenile *U. africana* to populations in the estuary was highest in December (45 m⁻²) and decreased over the summer. The highest numbers of recruits were found at those sites closest to the mouth or on the main channel.
5. Recruitment to the Leisure Isle and Thesens sites which are intensively exploited by bait collectors is high (20 - 32 m⁻²). Since exploitation is continuous, recruitment of juveniles may be successfully replenishing these mud prawn stocks.

CHAPTER FIVE

GENERAL DISCUSSION

Bait collectors as mud prawn predators and management considerations

Physical characteristics of the environment, food availability, larval recruitment and biological interactions may all affect the composition of benthic communities (Wynberg and Branch, 1994). The influence of physical factors on the distribution, density and population structure of *Upogebia africana* has been discussed in Chapter 2. Sediment composition limits mud prawns to areas where the substratum is composed of muddy sand (Day, 1981a; McLachan and Grindley, 1974). Furthermore, *U. africana*, is limited to the intertidal and shallow subtidal areas, as tidal currents result in coarser, sandy sediments in deeper channels between banks.

The intra-estuarine variations in adult mud prawn size with distance from the estuary mouth were discussed in Chapter 2. The mean size of *U. africana* from the upper reaches of the Knysna estuary, at Red Bridge, was significantly smaller than the size of mud prawns from the lower reaches. Female *U. africana* from populations up-estuary were also found to be reproductively inactive. Another factor which may influence mud prawn densities is exploitation by bait collectors. It is estimated that 8.5 % of mud prawn stocks at popular bait collecting sites are removed by bait collectors annually (Chapter 3). The intertidal *Zostera* zone, which is most intensely exploited, shows significantly lower densities than the *Spartina* zone above it and the lower *Zostera* zone which is only exposed at spring low tides (Chapter 2).

With man's increasing population growth and effect on the environment, there is an urgent need for sustainable resource management. An understanding of population dynamics is an essential ingredient for effective resource management (Holling, 1968). By developing models and using them to determine how the organisms' strategy is expressed, one can understand and predict

population events (Holling, 1968). In the context of population ecology, man as a bait collector, can be viewed as a predator of *U. africana*. In this chapter the "behaviour" of bait collectors as predators is described.

Bait collectors are specialist predators who target a certain species of prey and show a preference for larger individual prey items. In order to understand what determines a consumer's actual diet within its wide potential range, ecologists apply the optimal foraging theory. This theory assumes that the foraging behaviour of a consumer is one which most enhances the animals fitness. High fitness is achieved by a high net rate of energy intake (Begon, Harper and Townsend , 1990). Man does not ideally fit this assumption as he does not actually consume the mud prawns and therefore does not gain energy directly from the prey. Although this study was not designed with this in mind, the theory of predator prey interactions is interesting and useful in describing the use of mud prawns by bait collectors.

The majority of anglers collect and fish with *U. africana*, although many prefer the cracker shrimp, *Alpheus crassimanus*, the pink prawn, *Callinassa kraussi*, or the bait worms, *Arenicola loveni*, *Polybrachiorhynchus dayi* and *Marphysa sanguinea* as bait. The collection of cracker shrimp, pink prawn and bloodworms requires a prawn pump and these species occur in much lower densities than *U. africana*. It is illegal to collect bait worms using a spade in the Knysna estuary so this activity is restricted to moonlit nights. *U. africana* is so much more abundant and easily gathered than the other bait organisms that it is most often used as bait.

Predators must expend energy to obtain prey, first in searching for it and then in handling it (*i.e.* pursuing, subduing and consuming it) (Begon *et al.*, 1990). Searching time for bait collectors involves locating *U. africana* burrow openings. Handling time would include the actions of placing the implement (tin can, prawn pusher or pump) over the burrow opening, forcing the prawn out, picking it up and placing it in a container.

The factors affecting predation can be classed into five groups: 1) prey density, 2) predator density, 3) environmental characteristics (*e.g.* availability of other foods), 4) characteristics of the prey (*e.g.* defense mechanisms) and 5) characteristics of the predator (*e.g.* attack methods). Prey and predator density are two inevitable variables in every predator-prey situation (Holling, 1961). The most obviously important factor to a predator is the density of its food. The relationship between a predator's consumption rate and food density is known as the consumer's functional response (Begon *et al.*, 1990).

Three basic components of a consumer's functional response to prey density have been identified: 1) the rate of successful search, 2) the time spent handling the prey and 3) the effective time that predator and prey are exposed to each other (Holling, 1968). Since the nature of this response varies, Holling (1959) has classified it into three types. In a type I functional response, consumption rate increases linearly with prey density (*i.e.* density dependently) to a maximum density, then remains at the maximum regardless of further increases (density independently). The consumption rate reaches a plateau because even if food density is increasing, the consumer is limited by handling time (*i.e.* can only "swallow" so fast).

Type II responses are more frequently observed, where the consumption rate increases with prey density (density dependent action) but gradually decelerates until a plateau is reached. The consumption rate increases as prey density increases because finding prey becomes increasingly easy. Handling a prey item still takes the same length of time and therefore the time spent handling prey takes up an increasingly large proportion of the consumer's time until it is again limited by handling time. The type III response is characterised by an initial (density dependent) accelerating phase in consumption rate at low food densities, when increasing food density leads to an increase in the consumer's searching efficiency or a decrease in handling time (as these two factors determine consumption rate). At higher food densities, the type III response shows an inversely density dependent relation, similar to a type II response (Holling, 1968; Begon *et al.*, 1990).

When the collection rates (catch per unit effort or CPUE) of bait collectors using tin cans, prawn pushers and prawn pumps are plotted against mud prawn density (Fig. 5.1), the theoretical functional responses outlined above can be applied to bait collectors as predators of mud prawns. Bait collectors using prawn pushers show the clearest response pattern (Fig. 5.1b). The type III model fits the sigmoid curve obtained, indicating that increasing prawn density ($50 - 90 \text{ m}^{-2}$) leads to an increase in searching efficiency, accelerating the collection rate. At densities above 90 m^{-2} , when the CPUE is 1, handling time limits the collection rate and the curve reaches a plateau (Fig 5.1b). The collector still has to bend and retrieve the prawns and put them into a container before continuing pushing for more.

Bait collectors using tin cans appear to show a type II response. Their collection rate increases with increasing prawn density ($10 - 90 \text{ m}^{-2}$) as finding prawn holes becomes easier. At densities above 90 prawns m^{-2} , it is unclear whether the curve reaches a plateau or whether collection rate continues to increase (Fig 5.1a). If the collection rate is assumed to continue increasing, it may reach a plateau at a higher CPUE. If the curve is assumed to reach a plateau at a CPUE of 0.3 (*i.e.* a prawn is caught every third attempt), then this indicates that prawn pushers are more effective than tin cans for collecting *U. africana*.

Insufficient data were available to determine the type of functional response of collectors using prawn pumps. The distribution of the points in Figure 5.1c do however indicate that bait collectors do not attempt to collect prawns where densities are below 70 m^{-2} and that a plateau may be reached at a much lower CPUE (0.12) than in the other two curves. This implies that prawn pumps are much less efficient implements than tin cans or pushers for collecting mud prawns. This can be explained by the differences in area covered with each attempt by the various implements. A prawn pump has a diameter of 60 mm, the most frequently used tin cans are 75 mm in diameter (*per. obs.*) and the diameter of prawn pushers varies from 150 - 200 mm. At prawn

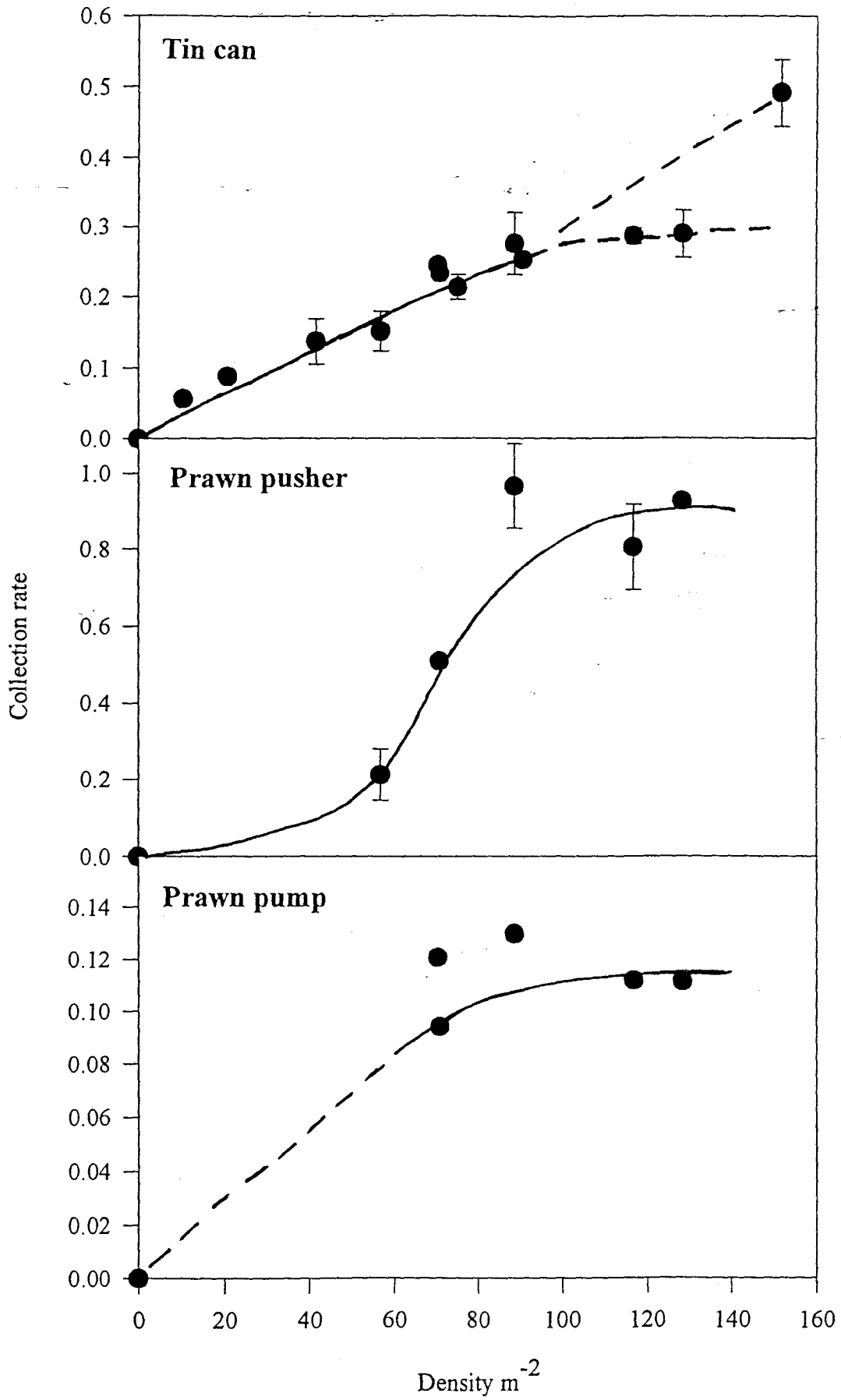


Figure 5.1. Mean collection rate (or catch per unit effort) (with standard error bars) of bait collectors using tin cans, prawn pushers and prawn pumps.

densities of 50 - 90 m⁻². A bait collector using a pusher does not have to search for and cover a specific individual prawn hole precisely. The pusher is large enough to cover numerous holes per attempt and bait collectors with large pushers have been observed to obtain up to 4 mud prawns with each attempt. This would account for the increase in searching efficiency which led to the acceleration in the collection rate observed in Figure 5.1b.

The consequences of the functional responses of the three "types" of predator (those with tin cans, pushers and pumps), have varying effects on the population dynamics of the bait organism and the bait collectors (Begon *et al.*, 1990). If the rise in consumption rate decelerates as food density increases (type I response as the plateau is reached, type II responses and type III response at higher densities), then mud prawns in high density populations will have less chance of being affected than prey in low density populations. This relationship is inversely density dependent and will have a destabilizing effect on the population dynamics. If the rise in consumption rate accelerates as food densities increase (type III at low densities, *e.g.* bait collectors with prawn pushers; Fig. 5.1), then individuals at low densities have less chance of being affected than those at high densities. This density dependent effect will have a stabilizing effect on the population dynamics of the interaction (Begon *et al.*, 1990).

Partial refuges can stabilize the population dynamics of a predator-prey interaction. If a number of prey remain unattacked even at high predator densities, this buffers the prey population from the most drastic effects of its predator. This is a by-product of the consumer's preference for high profitability patches (Begon *et al.*, 1990). Bait collectors show a preference for such high profitability "patches". They collect mud prawns in areas where the densities are highest (*e.g.* in the *Zostera* zones as opposed to the higher marsh) and where it is easiest to collect bait (*e.g.* in the exposed areas of the intertidal, as opposed to the subtidal and on mud banks which are easily accessible and close to good fishing spots).

The Oyster Bank has been identified (in Chapter 2) as a refuge for *U. africana*. This mud bank (and other "middle banks") is inaccessible to most bait collectors and it supports high mud prawn densities. The spawning stock of *U. africana* is not threatened by the present level of exploitation. The length of time for which the prey population is immersed and exposed to bait collectors is limited by the state of the tide. A proportion of the population will escape predation as bait collectors are not 100 % efficient. It is unlikely that the bait collecting process damages the prawns which are not removed, and "popping" prawns appears to cause minimal disturbance of sediment. Prawns which are not selected and emerge from their burrows following disturbance by bait collectors are likely to fall prey to birds. Kelp gulls in particular are quick to take advantage of any prawns left on the surface and *U. africana* makes up 58 % of this bird's diet (Martin, 1988).

Although recruitment to *U. africana* populations requires a more thorough study the preliminary data gathered in this study (see Chapter 4) invites speculation as to whether recruitment is sufficient to balance the exploitation of bait stocks. The mean rate of larval recruitment to populations in the estuary is estimated to be 20 - 32 recruits m^{-2} per month, and 240 - 384 m^{-2} per year. If the numbers of mud prawns taken as bait annually from the popular bait collecting sites is 1.85×10^6 (see Chapter 3), then the mean numbers of *U. africana* taken annually per square meter at these sites is 4.9 m^{-2} . Recruitment therefore is at least four times exploitation, the juvenile recruitment rate should be sufficiently high to replenish exploited mud prawn populations. In addition, it is unknown whether or not adult *U. africana* leave their burrows and if immigration occurs. Daily bait collection must result in some burrows being left vacant and available for habitation by other *U. africana*.

It must be borne in mind that these simple theoretical components operate in complex systems. Man is not the only predator of *U. africana*. Many bird and fish species rely on the mud prawn for food and the contribution made to the detrital food webs of estuaries by mud prawn

populations through exuvial loss is considerable (Hanekom and Baird, 1992). Conservation of the estuarine environment is as important as effective management of bait resources. The concept of tidal flats serving as an "ecological turntable" (Reise, 1985) between land and sea provides a warning of the potential risks involved in destroying large areas of mud flats through bait collecting (Wynberg and Branch, 1994).

In the establishing of the Invertebrate Reserve area in the Knysna estuary, the eastern marshes were identified as requiring specific conservation measures (Grindley and Cooper, 1979). The reserve area is protected against the taking of bait and from other human activities. Although this area does not support high densities of bait organisms, it was recognised that intertidal saltmarshes are primary producers and contribute substantially to the generation of organic detritus which supports much of the life in estuaries. Grindley and Cooper (1979) suggested that the conservation of such areas is of fundamental importance for the survival of the lagoon ecosystem and that the area between Leisure Island and Ashmead be rigidly protected with no exploitation of any form being allowed. Specific measures to protect estuarine bait organisms were established in 1965. It is illegal to remove estuarine bait organisms for angling in the sea, a quota was stipulated for each bait species and methods of collection were prescribed (making the use of spades or forks illegal). It is also illegal to remove or destroy aquatic vegetation while collecting bait and it is deemed illegal to buy or sell bait organisms (Gaigher, 1987).

These measures restricting the methods of bait collecting would successfully limit sediment disturbance caused by legal bait collecting methods in the Knysna estuary. Since sediment disturbance, and not the removal of prawns *per se*, is reported to be the factor responsible for most of the repercussions on the associated fauna (Wynberg and Branch, 1994) this would limit the potential damage caused by bait collecting. Meiofauna are known to recolonise disturbed sediments rapidly (Sherman and Coull, 1980), while the rates of macrofaunal recolonisation are

documented to be markedly slower (Woodin, 1981; Bell and Devlin, 1983; Wynberg and Branch, 1994). This can be attributed to the shorter generation times of meiofauna (McIntyre, 1969) and the greater rapidity with which meiofauna can recolonise sediments (Savidge and Taghon, 1988).

The stipulation of a quota or bag limit of bait allowed per person per day (50 *U. africana* in the Knysna estuary) is not easily enforced. In the Knysna estuary, subsistence and supplementary anglers, who rely on bait collection and fishing to different degrees for a living, on average take 101 mud prawns per day (and as many as 470 per person). Whereas the 87.1 % of leisure fishermen interviewed responded that the allowed bag limit of 50 *U. africana* was sufficient or even in excess of their needs, 71.7 % of the local anglers replied that this quota is insufficient. Management of natural resources must involve at least two aspects. Management of the resource to ensure that the exploited populations survive as part of the estuarine ecosystem and socio-ecological management which must ensure that the available resources are available to local communities for sustainable exploitation.

The collection of bait by the fishermen should be regarded as part of the estuarine angling experience and it is not recommended that bait organisms in general be commercially exploited by private individuals. A form of controlled collection and sale of specific bait species does, however, have merit under certain circumstances. If the activities of subsistence bait collectors could be organised and effectively controlled, there is potential for a restricted number of people to operate as professional bait collectors and sell bait. There is an obvious opening for private enterprise in the bait market, where the buying and selling of mud-prawns is illegal at present. It is possible that conservation authorities could initiate an improvement of the standard of living of those members of the local community who physically live beside the water and have no means of income besides from the estuary. As an example, the bait industry could be managed by issuing or "selling" a limited number of permits to interested local people. A set of rules

governing the areas and bait species which may be exploited and a regulated outlet for the sale of bait could be provided. The authorities would hold the right to revoke the permit of an operator who violated the rules and the permit could then be purchased by another person in need of employment. The control measures should, however, be based on a sound understanding of the ecology and population dynamics of the specific bait organism in question.

The conclusion reached from this study is that the present levels of exploitation of *U. africana* in the Knysna estuary are not having a detrimental effect on the mud prawn populations. Populations of *U. africana* do not appear to have declined over the last 30 years of bait collecting and the density and population structure of mud prawns in heavily exploited areas is comparable to that of less intensely exploited and unexploited sites. Anglers tend to return to the same area to collect bait, often on a daily basis, and experience no trouble collecting sufficient mud prawns. Unlike the destructive methods used in Langebaan Lagoon, legal bait collecting methods used in the Knysna estuary are not detrimental to the mud banks and associated fauna and flora.

Bait stocks of the Knysna estuary are not over-exploited and appear to be “naturally regulated”, as the recruitment of juvenile mud prawns is sufficiently high to sustain present levels of exploitation and the spawning stocks of *U. africana* are not threatened. A possible management consideration is that sampling of the population structure and density of the mud prawn populations be continued. This study has provided the base-line data and it would be useful to monitor bait stocks annually over a five or ten year period to assess the robustness of the conclusions reached in this study.

In addition to having a scientifically researched, sound knowledge of the bait species in order to ensure their conservation, it is especially important to ensure the conservation of the estuarine environment. Bait collecting and other practices which result in damage to aquatic vegetation or the disturbance of sediments, must be prohibited.

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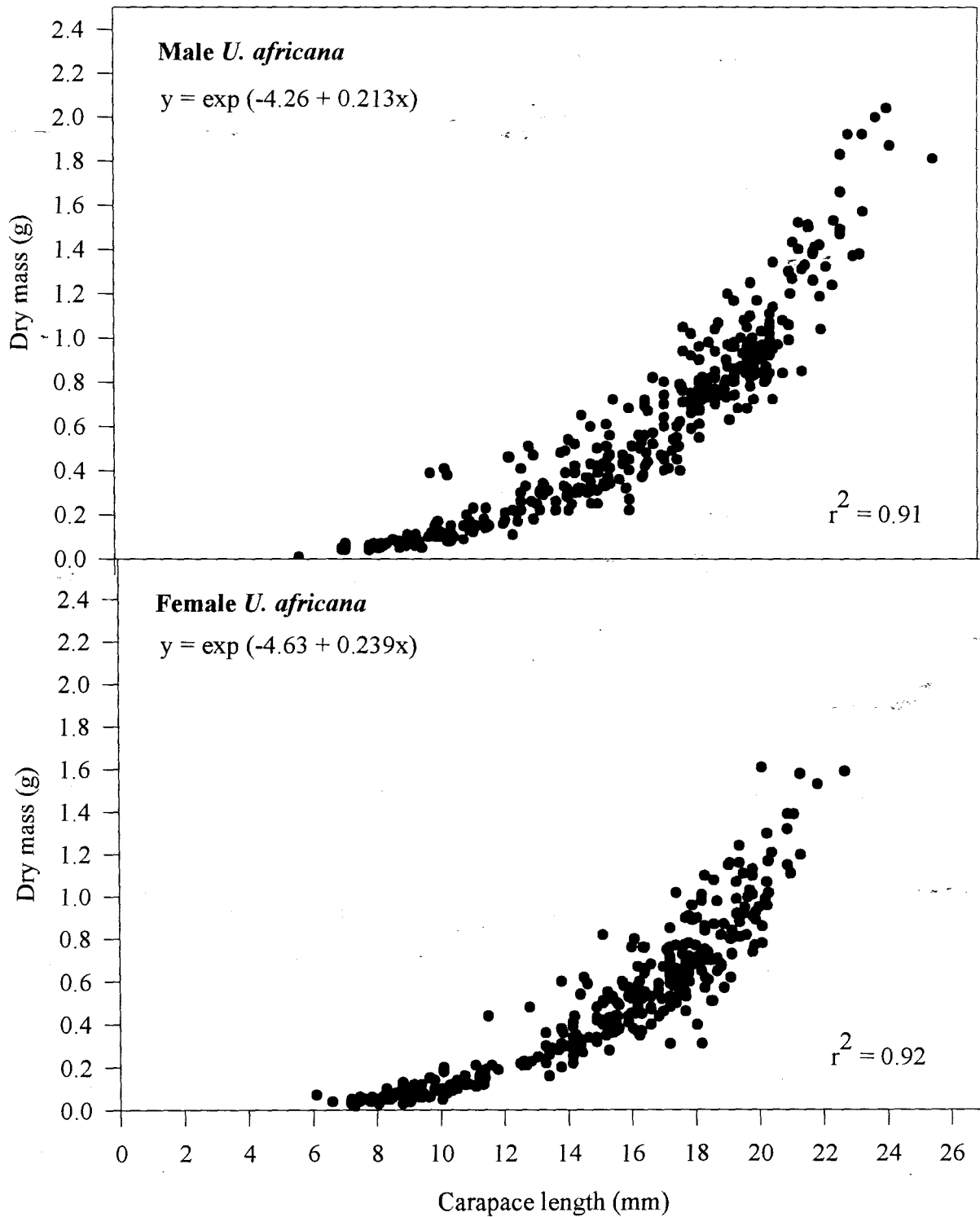
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Appendix I. Exponential regressions of the dry mass (g) of male and female *U. africana* against carapace length (mm), used to convert mud prawn lengths into biomass.

QUESTIONNAIRE FOR SURVEY OF BAIT COLLECTORS AND FISHERMEN.

Population group: 1) Black
 2) Coloured
 3) Asian
 4) White

1

Sex: 1) Male
 2) Female

2

Age group: 1) Elderly (>55)
 2) Adult
 3) Youth (<21)

3

Collecting: 1) Mudprawns
 2) Skietkappers
 3) Pinkprawns
 4) Lint/Tapeworms
 5) Polychaete worms
 6) Bloodworm
 7) Other

4

Implement: 1) Tin Can
 2) Pusher
 3) Pump
 4) Trampling
 5) Fork
 6) Spade

5

LOCALS:

1) Are you from Knysna?
 1) yes
 2) no (go to question 45...)

6

2) Where do you live?
 1) Concordia
 2) Nekkie
 3) Noetzie
 4) Hornlee
 5) Dam se Bos
 6) Next to the lagoon (.....)
 7) Bongani
 8) Town
 9) Other (.....)

7

3) Do you have a job?
 1) yes
 2) no
 3) sometimes

8

4) if yes, what do you do?

(.....)

5) How many days a week do you work?

- 1) one 2) two etc.
- 8) less than one day per week

10

6) Is fishing or baitcollecting a source of income / do you fish for a living?

- 1) yes
- 2) no
- 3) partly

11

7) Is fishing or bait collecting your only means of subsistence?

- 1) yes
- 2) no
- if no, then what else? (.....)

12

8) How many days a week do you fish?

- 1) one 2) two etc.
- 8) less than one day per week

13

9) Do you have a favourite/regular fishing/bait collecting spot?

- 1) yes
- 2) no

14

10) Where do you fish most often?

- 1) Boat
- 2) Railway Bridge
- 3) Thesens Jetty
- 4) Belvedere
- 5) Lorie Park
- 6) Ashmead
- 7) Leisure Isle
- 8) KADA
- 9) Point
- 10) Other (.....)

15
16

11) How do you get to your fishing/bait collecting spot?

- 1) Walk
- 2) Cycle
- 3) Drive
- 4) Boat
- 5) Taxi

17

12) Do you make use of a boat?

- 1) yes
- 2) no
- 3) sometimes

18

13) What do you fish for?

(.....)

- 14) And how long do you spend fishing per outing? 20
 1) 5 - 30 minutes
 2) 30 - 60 minutes
 3) 1 - 2 hours
 4) 2 - 4 hours
 5) more (.....)
 6) all day
- 15) What fishing method do you use? 21
 1) Hand line / "tol"
 2) Planted lines
 3) Rod
 4) Other (.....)
- 16) If planted lines are used, how many lines? 22
 1) one
 2) two
 3) etc
- 17) how many hooks per line? 23
 1) one
 2) two
 3) etc.
- 18) how many prawns per hook? 24
 1) one
 2) two
 3) etc.
- 19) What do you do with your catch? 25
 1) eat only
 2) sell
 3) eat little ones and sell occasional big one
- 20) and how much money do you make per fish? 26
 1) less than R10
 2) R10 - R20
 3) R20 - R30
 4) R30 - R40
 5) more (.....)
- 21) Do you catch anything that you don't use? 27
 1) yes
 2) no
 3) sometimes
- 22) What? (.....)
- 23) What do you do with them? 29
 1) Throw them back
 2) Leave them on the bank
 3) Eat them
 4) Use as bait
 5) Other

24) How long do you spend getting bait per outing? 30

- 1) 5 - 15 minutes
- 2) 15 - 30 minutes
- 3) 30 - 60 minutes
- 4) 1 - 2 hours
- 5) more
- 6) a couple of minutes as you fish and need bait
- 7) the whole low tide

25) What bait do you use most often? 31

- 1) Mud prawns
- 2) Skietkappers
- 3) Bloodworm
- 4) Redbait
- 5) Other worms
- 6) Pink prawns
- 7) Pencilbait
- 8) Other (.....)

26) What is the best bait / your favorite? 32

- 1) Mud prawns
- 2) Skietkappers
- 3) Bloodworm
- 4) Redbait
- 5) Other worms
- 6) Pink prawns
- 7) Pencilbait
- 8) Other (.....)

27) Where do you collect bait? 33

- 1) Leisure Isle
- 2) Loerie Park
- 3) Ashmead
- 4) Thesens
- 6) KADA
- 7) Railway Bridge
- 8) Middle banks
- 9) Other (.....)
- 10) Where ever fishing
- 11) Where ever is closest or on the way from home or work

28) What do you do with left over bait? 35

- 1) Don't have left overs
- 2) Throw it away
- 3) Put back in water
- 4) Put back in holes
- 5) Sell
- 6) Keep for following trip
- 7) Give away
- 8) Other (.....)

29) Are you aware that there is a restriction on the amount of bait collected? 36

- 1) yes
- 2) no

- 30) Is the allowed amount of bait
 1) enough
 2) not enough
 3) too much 37
- 31) Why do you say so?
 (.....)
- 32) Do you think it is reasonable to restrict the amount of bait collected?
 1) yes
 2) no
 3) don't know 39
- 33) What do you think the limit per person per day should be?
 1) less than 50
 2) 50
 3) 100
 4) 150
 5) 200
 6) 300
 7) don't know 40
- 34) Why do you think there are restrictions on your collecting?
 1) Don't know
 2) Protect prawns
 3) So that everyone can have
 4) Prevent wastage
 5) Protect the environment
 6) Don't want us to make money from bait sales
 7) Other (.....) 41
- 35) Do you think that the National Parks Board
 1) are necessary
 2) are unnecessary
 3) don't know 42
- 36) Do you sell bait?
 1) yes
 2) no
 3) sometimes 43
- 37) if so, what do you sell?
 1) Prawns
 2) Tape and Lint worms
 3) Bloodworm
 4) Skietkappers
 5) Other (.....) 44
- 38) How much do you make per 50 prawns?
 1) R5 or less
 2) R5 - R10
 3) R10 - R15
 4) More (.....) 45

39) How much do you make per lint worm?

- 1) R1
- 2) R2
- 3) etc.

46

40) How many tins of bait do you sell per week?

- 1) one or two
- 2) two - five
- 3) five - ten
- 4) more (.....

47

41) Do you think that your activities have a effect on the mudbanks/lagoon?

- 1) positive
- 2) no
- 3) negative

48

42) How do you think bait collecting or fishing can have a negative effect on the lagoon?

- 1) Pushing prawns
- 2) Tramping for skietkappers
- 3) Digging for worms
- 4) Littering on the mudbanks
- 5) Damaging vegetation
- 6) Other (.....
- 7) Don't know

49

43) How long have you been fishing in the Knysna lagoon for?

- 1) one year
- 2) 2 years
- 3) etc.

50
51

44) Have you noticed any changes over this time?

- 1) yes
- 2) no

52

Your comments:

if TOURIST then:

45) How long are you visiting Knysna for?

- 1) 1 week
 - 2) 2 weeks
 - 3) 3 weeks
 - 4) 4 weeks
 - 5) 5 weeks
 - 6) 6 weeks
 - 7) more (.....)
- 53

46) Where are you from?

- 1) Southern cape
 - 2) Eastern cape
 - 3) Western cape
 - 4) Gauteng
 - 5) KwaZulu-Natal
 - 6) Overseas
 - 7) Other (.....)
- 54

47) How often do you fish on holiday?

- 1) Everyday
 - 2) Every other day
 - 3) Twice weekly
 - 4) Weekly
 - 5) Fortnightly
 - 6) Monthly
 - 7) Less frequently (.....)
- 55

48) Why do you fish?

- 1) Relaxation
 - 2) Fun
 - 3) Teach kids
 - 4) Sport
 - 5) Other (.....)
- 56

49) How much money would you say you would spend on fishing this holiday (incl. gear, transport etc.)?

- 1) R10 and less
 - 2) R10 - R20
 - 3) R20 - R50
 - 4) R50 - R100
 - 5) R100 - R200
 - 6) More than R200 (.....)
 - 7) Don't know
- 57

50) Where do you fish most often?

- 1) Boat
 - 2) Railway bridge
 - 3) Thesens
 - 4) Belvedere
 - 5) Loerie park
 - 6) Ashmead
 - 7) Leisure Isle
 - 8) Point
 - 9) Heads
 - 10) Other (.....)
- 58
- 59

51) How do you get to your fishing/bait collecting spot?

- 1) Walk
- 2) Cycle
- 3) Drive
- 4) Boat

60

52) Do you make use of a boat?

- 1) yes
- 2) no
- 3) sometimes

61

53) Do you have a favourite/regular fishing/bait collecting spot?

- 1) yes
- 2) no

62

54) What do you fish for?

(.....)

56) And how long do you spend fishing per outing?

- 1) 5 - 30 minutes
- 2) 30 - 60 minutes
- 3) 1 - 2 hours
- 4) 2 - 4 hours
- 5) More (.....)

64

57) Do you catch anything that you don't use?

- 1) yes
- 2) no
- 3) sometimes

65

58) What?

(.....)

59) What do you do with them?

- 1) Throw them back
- 2) Leave them on the bank
- 3) Kill them
- 4) Eat them
- 5) Use as bait

67

60) How long do you spend getting bait per outing?

- 1) 5 - 15 minutes
- 2) 15 - 30 minutes
- 3) 30 - 60 minutes
- 4) 1 - 2 hours
- 5) 2 - 4 hours
- 6) More (.....)
- 7) the whole low tide

68

61) What bait do you use most often? 69
1) Mud prawns
2) Skietkappers
3) Bloodworm
4) Redbait
5) Other worms
6) Pink prawns
7) Pencilbait
8) Other (.....)

62) Do you 70
1) collect your own bait
2) or do you buy bait?

63) If you buy bait what do you buy?
(.....)

64) Where do you buy bait?
(.....)

65) If you collect - Where do you collect bait? 73
1) Leisure Isle 74
2) Loerie Park
3) Ashmead
5) Thesens
6) KADA
7) Railway Bridge
8) Middle banks
9) Other (.....)
10) Where ever fishing
11) Where ever is closest or on the way from home or work

66) What do you do with left over bait? 75
1) Don't have left overs
2) Throw it away
3) Put back in water
4) Put back in holes
5) Sell
6) Keep for following trip
7) Give away
8) Other (.....)

67) Are you aware that there is a restriction on the amount of bait collected? 76
1) yes
2) no

68) Is the allowed amount of bait 77
1) enough
2) not enough
3) too much

69) Do you think it is reasonable to restrict the amount of bait collected? 78
1) yes
2) no

70) What do you think the limit should be? 79
1) less than 50
2) 50 prawns
3) 100 prawns
4) 150 prawns
5) 200 prawns
6) more (.....)

71) Why do you think there are restrictions on your collecting? 80
1) don't know
2) protect prawns
3) so that everyone can have
4) prevent wastage
5) protect the environment
6) other (.....)

72) Do you think that the National Parks Board 81
1) are necessary
2) are necessary?

73) Do you think that your activities have a ... effect on the mudbanks/lagoon? 82
1) positive
2) no
3) negative

74) How do you think that bait collecting or fishing can have an effect on the lagoon? 83
1) pushing prawns
2) trampling for skietkappers
3) digging for worms
4) littering on the mudbanks/water
5) damaging vegetation
6) other (.....)

Your comments: