15

# DYNAMICS AND UTILIZATION OF SURF ZONE HABITATS BY FISH IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

by

**BARRY MALCOLM CLARK**

Thesis submitted for the degree of
Doctor of Philosophy

Zoology Department and Marine Biology Research Institute,
University of Cape Town

February 1997

*"Peruse me O Reader, if you find delight in my work, since...the perseverance to pursue it and to invent such things...is found in few people. And come, men, to see the wonders which may be discovered in nature by such studies"*

Leonardo Da Vinci, Madrid
Codex I

*To Charlotte Heijnis and my parents,*
*Mary and Brian Clark*

# DECLARATION

I declare that this thesis is my own unaided work, except where otherwise stated. It reports results of original research I carried out in the Zoology Department, University of Cape Town. This work has not been submitted for a degree at any other university.

Barry M. Clark

# ABSTRACT

The main objectives of this study were to examine, by means of beach seine netting, the composition, abundance and size structure of fish assemblages frequenting surf-zone habitats in the south-western Cape, South Africa, to investigate temporal and spatial variations in these assemblages in relation to physical environmental parameters, and to assess the importance of this habitat as a nursery and feeding ground for littoral fish. In all, 54 fish species from 29 families were recorded, with three species (*Atherina breviceps*, *Liza richardsonii* and *Rhabdosargus globiceps*) dominating numerically.

Two separate surveys were designed to provide a comprehensive assessment of the factors influencing spatial variability in the composition abundance and community structure of the surf fish assemblages in this region. In the first, surf ichthyofaunal assemblages at 11 localities, selected to encompass as wide a range of physical parameters as possible, were sampled at monthly intervals for a period of two years. Results of this study indicated that the degree of wave exposure, the presence of emergent rock on the shore and turbidity were responsible for most of the spatial variability in abundance and community structure observed. In the second survey, samples were collected at eight localities spanning an exposure gradient from highly exposed, open ocean beaches to extremely sheltered marine sandy beaches, in order to isolate and carefully examine the influences of wave exposure on surf fish assemblages. Two important trends were evident in the abundance and community structure of teleost catches in this study. Overall abundance increased markedly as wave exposure decreased, while highest species richness and diversity, and lowest dominance were recorded at intermediate levels of exposure.

Temporal variability in surf fish assemblages was also the subject of two separate investigations. Analyses of monthly seine net hauls from the first spatial variability survey revealed little seasonal variation in the catches. Seasonal fluctuations in the number of species recorded was evident at only one of the eleven sites surveyed, while no consistent seasonal variations were evident in fish abundance. Physical factors responsible for these fluctuations varied in response to differences in the physical attributes of the different sites, but water temperature, wave height, wind speed and direction and detached macrophyte abundance appeared to be the most important. When data from all sites were combined, however, a seasonal pattern was evident in the abundance of juvenile fishes in the surf and in species richness. Abundance and species richness was highest from mid-summer up to the beginning of winter, the period during which most species recruit into the surf-zone. In the second of these surveys, catches of fish in triplicate seine hauls, performed every three or four hours, were examined in conjunction with variations in physical parameters (light, wave height, surf width, wind, turbidity, tidal height and macrophyte abundance) in order to assess their influence on diurnal variations exhibited by the fish assemblages. Changes in the light environment and water clarity were responsible for most of the variability observed, with the dominant teleost species migrating into and out of the surf-zone on a daily basis. These migration patterns were moderated by variations in water clarity, which in turn were controlled by variations in wind speed and direction. When surf waters were turbid, fish moved into the breaker zone during the day in order to take advantage of the cover provided by the breaking waves, but moved offshore again after dark. When surf waters were clear, however, no increase was evident in the catches during the day, and this was thought to be because the surf waters offered few benefits under these conditions.

Finally, data on the composition, abundance and size structure of fish assemblages frequenting surf habitats from this study and others, were compared with available data on estuarine systems in the south-western Cape, in order to examine the degree of dependence displayed by littoral fish on these two habitat types. This study revealed that of the 11 species previously considered to be entirely dependent on estuaries, at least two also occur in the surf and are therefore not dependent on estuaries. However, two others species labelled as only partially dependent, appear to be completely dependent on estuaries in this area. In contrast, populations of only seven species appear to be dependent on surf habitats in the south-western Cape.

# ACKNOWLEDGEMENTS

I gratefully acknowledge financial support for this project from the Sea Fisheries Research Institute, Worldwide Fund for Nature (formerly Southern African Nature Foundation), Foundation for Research Development and the University of Cape Town. Thanks go to my supervisors Prof. Charles Griffiths and Dr Bruce Bennett for the enthusiasm and support they provided. This project would not have been possible without the intuition and foresight of Dr Bruce Bennett.

Steve Lamberth and Charlotte Heijnis accompanied me on almost all my field excursions. Steve's able bodied efforts and carefully veiled camaraderie saw us through many long days and some interminable nights hauling a recalcitrant trek net back to the beach. Charlotte was always a source of great comfort and inspiration to me and her indomitable determination ensured that I was never allowed to give up until the job was done. A special thanks also to Yves Lechanteur for his vibrance and unfailing enthusiasm even under the most miserable conditions. Also to Cameron Smith, Jon Mantel, Pierre Jansens, Kim Prochazka, Colleen Parkins, Walter Meyer, Liz Day, Bruce Bennett, Kevin Ruck, and Charles Griffiths for enduring the blazing sun, rain, hail, thundering waves and driving winds in a quest for "a few miserable fish". A succession of undergraduate student classes also became grist for my seine netting mill over the years, for which I am very grateful.

Bruce Bennett, Walter Meyer, Charles Griffiths, Steve Lamberth, Charlotte Heijnis, Kim Prochazka and Dave Glassom have all commented on rough drafts of chapters included in this thesis.

I owe a special debt of gratitude to Prof. George Branch, as without his intervention at an earlier stage, none of this would have been possible. Thanks also to all my friends and colleagues for your support, ideas and friendship. Finally I would like to thank my family for their love, tolerance and frequent financial support.

# TABLE OF CONTENTS

# GENERAL INTRODUCTION

# GENERAL INTRODUCTION

Exposed surf habitats, characterised by pounding waves and a shifting sand substratum, offer a particularly harsh environment for living organisms. Despite their prevalence world wide, the view that they are barren, physically-dominated habitats without much apparent life (Pearse *et al.* 1942, Hedgepeth 1957, Springer & Woodburn 1960) meant that they were largely ignored for many years. Early attempts to assess the abundance of fish in surf areas (Warfel & Merriman 1944, Merriman 1947, Gunter 1958, Carlisle *et al.* 1960, McFarland 1963) revealed, however, that they are frequented by a wide variety of fish species, including juveniles of many commercially important species. This realisation gave impetus to a considerable increase in the focus of sampling effort in these areas. Early efforts were confined largely to beaches in the northern hemisphere, principally those around the British Isles (Riley & Holford 1965, Macer 1967, Edwards & Steele 1968, Gibson 1973a, Lockwood 1974), Europe (Kruuk 1963, Ziljstra 1972, Kuipers 1973, Thijssen *et al.* 1974, Creutzberg *et al.* 1978) and North America (Shaefer 1967, Tyler 1971, McCleave & Fried 1975, Anderson *et al.* 1977, Hillman *et al.* 1977, Naughton & Saloman 1978). Sampling efforts intensified considerably in subsequent decades and were expanded to include some southern hemisphere localities as well, chiefly in South Africa (Lasiak 1981, 1984a, b, Bennett 1989a, Romer & McLachlan 1986, Whitfield 1989, Romer 1990, Lamberth *et al.* 1994) and Australia (Lenanton 1982, Lenanton *et al.* 1982, Robertson & Lenanton 1984, Lenanton & Caputi 1989).

A considerable volume of work has now been completed on surf fish assemblages, but the majority of studies to date have been confined to examinations of three major aspects only: community composition (species, size and age structure), temporal variations in abundance and diversity, and trophic relations. Most other aspects have received little or no attention at all. Surf habitats around the world appear to be frequented by a wide variety of species, but are usually dominated by only a small number of forms. The number of species recorded generally ranges from 20 - 80, but less than ten species usually make up >90% of the catches (Gunter 1958, McFarland 1963, Modde & Ross 1981, Lasiak 1984a, Ross *et al.* 1987, Wright 1988, Bennett 1989a). Juveniles usually make up a substantial portion of the fish collected, and the role of surf-zones as nursery areas is now widely recognised (Gibson 1973a, Modde 1980, Lasiak 1981, Lenanton 1982, Senta & Kinoshita 1985, Bennett 1989a, Wright 1989a). Juveniles often remain in the surf for a considerable period of time, and some species are thought to be highly or even entirely dependent on surf areas as nursery grounds (e.g. Florida pompano, gulf kingfish and scaled sardines - Modde 1980, McMichael & Ross 1987; evil-eye blassop, Cape gurnard, blacktail, sand steenbras and piggie - Bennett 1989a). Considering the large proportion of coastal marine habitat they occupy world wide, and the variety of fish species that utilise these areas, it is now thought that they may be at least as important as estuarine nursery areas (Lenanton 1982, Lenanton *et al.* 1982, Ross *et al.* 1987, Bennett 1989a, Potter *et al.* 1990).

Surf-zone fish assemblages exhibit a high degree of temporal variability that, despite being well documented, is rather poorly understood. Seasonal variations in composition and abundance are particularly well developed off beaches in the northern hemisphere (McFarland 1963, Lockwood 1974, Kuipers 1977, Poxton *et al.* 1982, McDermott 1983, Senta & Kinoshita 1985, Ross *et al.* 1987), but are usually less well defined or even absent off beaches in the southern hemisphere (Lasiak 1984a, Bennett 1989a, Romer 1986). Where strong seasonal variations are apparent, greatest abundance and diversity generally occur in the warmer months, with some beaches being almost devoid of fishes in winter (e.g. Warfel & Merriman 1944, Gunter 1958, McFarland 1963, Shaefer 1967, Anderson *et al.* 1977). Where seasonal variations are not well defined, however, short term variability, ascribed to variation in physical environmental variables, is thought to dominate (Lasiak 1984b, Ross *et al.* 1987). Diel variability in fish assemblages frequenting meso- and macrotidal beaches appears to be largely tidally influenced (Edwards & Steele 1968, Tyler 1971, Gibson 1973a, Kuipers 1975, Wright 1989a), whereas off microtidal beaches short term variability appears to lack any clear pattern (Lasiak 1984b, Senta & Kinoshita 1985, Romer 1986, Ross *et al.* 1987). Short term variability in these areas has been ascribed to a wide variety of factors -- including variations in wind speed and direction, turbidity, tidal height and illumination (Modde & Ross 1981, Lasiak 1984b, Ruple 1984, McMichael & Ross 1987, Ross *et al.* 1987). Few studies, including only one from southern Africa (Lamberth *et al.* 1995c), utilise data from more than one annual cycle, and thus little is known of the importance of interannual fluctuations in surf-zone fish assemblages.

Fish are thought to play an important role as consumers, predators and as energy transformers in surf habitats. Planktivorous food sources form an important, and often the major, dietary component for many surf-zone fish species, particularly in the more exposed areas (McFarland 1963, Edwards 1973, McMichael 1981, Lasiak 1982, 1986, McDermott 1983, Modde & Ross

1983, McMichael & Ross 1987). Benthic food sources appear more important off macrotidal beaches, where tidal water movements dominate. Fish enter the intertidal zone to feed as the tide floods, cropping bivalve siphons, tentacles of polychaetes and other macrofaunal organisms (Merriman 1947, Macer 1967, Edwards & Steele 1968, Tyler 1971, Thijssen *et al.* 1974). Rooted macrophytes are absent from all but the most sheltered beaches, consequently primary production within the surf-zone is accomplished largely by phytoplankton only. Herbivorous fish are thus rare in surf habitats, being limited to those straying from adjacent rocky reefs, or those able to feed directly on surf diatom accumulations (Odum 1968, Lasiak 1982, Romer & McLachlan 1986). Detached aquatic macrophytes accumulate in the surf off certain beaches, providing a major source of primary production in these areas (Zobell 1971, Cowper 1978, Lenanton *et al.* 1982, Robertson & Lenanton 1984, Hull 1987, Wright 1989b). Although few fish feed directly on the weed, these accumulations do provide rich feeding grounds, as the majority of species in these areas feed on weed-associated prey (Lenanton *et al.* 1982, Robertson & Lenanton 1984).

The present study concerns field surveys of surf-zone fish assemblages off sandy beach and mixed shore habitats in the south-western Cape, South Africa, spanning a period of five years. The primary objective of the study was to provide a better understanding of the factors and processes governing spatial, and both long and short term variations in the composition, abundance and size structure of surf-zone fish assemblages in southern Africa and to shed light on the importance of the surf-zone as a nursery and feeding ground for fish in this area. Every effort has been made to relate all findings to those made by other authors throughout the world, placing them in context both locally and internationally. The scope of this study, although limited geographically to the south-western Cape, therefore embraces the entire world. Chapters 1 and 2 deal with spatial variability in, and the influence of physical habitat variables on the composition, abundance and size structure of surf fish assemblages; Chapters 3 and 4 with long and short term temporal variations in these assemblages, respectively; and Chapter 5 with the importance of the surf-zone as a nursery and feeding ground for littoral fish.

Work for this thesis had its origins in a study commissioned by the Sea Fisheries Research Institute aimed at assessing the impact of the highly controversial beach seine fishery on fish stocks in False Bay. The results and findings of that study are not included here, however, as they form an entire volume of their own. The reader is refered to publications by Clark & Bennett (1993), Clark *et al.* (1994a, b), and Lamberth *et al.* (1994, 1995a, b, c) for details of this study.

# CHAPTER 1

# 1 SPATIAL VARIABILITY IN SURF-ZONE FISH ASSEMBLAGES IN FALSE BAY

## 1.1 INTRODUCTION

Ichthyofaunal assemblages inhabiting the surf-zones of sandy beaches around the world have been studied in some detail (e.g. Warfel & Merriman 1944, McFarland 1963, Gibson 1973a, Edwards 1973, Lenanton *et al.* 1982, Lasiak 1984a, b, Senta & Kinoshita 1985, Wright 1988). Although frequented by a wide variety of species, these habitats are typically dominated numerically by only a small number of forms: usually less than 10 species making up >90% of the catch (e.g. Gunter 1958, McFarland 1963, Modde & Ross 1981, Ross 1983, Lasiak 1984a, Bennett 1989a). The importance of these habitats as nursery areas for juvenile teleosts is well established (Warfel & Merriman 1944, Gibson 1973a, Modde 1980, Lasiak 1981, 1986, Robertson & Lenanton 1984) and is thought to rival that of estuaries in some areas (Lenanton 1982, Bennett 1989a, Potter *et al.* 1990).

Clearly, considerable progress has been made with respect to certain aspects of surf-zone fish ecology, but comparatively little attention has been paid to spatial variability in the composition and abundance of surf-zone fish assemblages. For many years, these habitats were labelled as "harsh" and "structurally homogeneous environments" and were thought to offer little in terms of habitat diversity, cover or productivity (Pearse *et al.* 1942, Hedgpeth 1957, Springer & Woodburn 1960). Recent evidence suggests, however, that fluctuations in certain physical variables such as the degree of wave exposure, sediment particle size and turbidity have a strong influence on the relative abundance of certain species and may alter the composition and species richness of surf-zone fish assemblages (Hillman *et al.* 1977, Blaber & Blaber 1980, Tallmark & Evans 1986, Romer 1990, Pihl & van der Veer 1992). The occurrence of diatom plumes, detached macrophyte accumulations, the proximity of subtidal reefs, rocky jetties, estuarine habitats and seagrass beds may all contribute significantly to spatial variability in surf-zone fish abundance and community structure (Robertson & Lenanton 1984, Romer & McLachlan 1986, Peters & Nelson 1987, Wright 1989b, Romer 1990).

Studies on juvenile flatfish distribution patterns on sandy beaches in the northern hemisphere suggest that their distribution patterns are controlled primarily by food availability, exposure and habitat structure (Lockwood 1974, Ziljstra *et al.* 1982, Poxton and Nasir 1985, Berghahn 1987, van der Veer *et al.* 1991, Pihl and van der Veer 1992). Differences in dietary preferences also result in segregation between 0+ juvenile plaice, which are concentrated in shallow (<5 m) waters, and larger 1+ individuals, which prefer deeper waters (Lockwood 1974, Ziljstra *et al.* 1982).

Few researchers have sampled more than one or two localities simultaneously, and thus most of the information available is derived from the work of different authors, often using different equipment and methodologies. Comparisons have thus largely been limited to discussions concerning dominant taxa or families only, as it is well known that comparisons made between samples collected over different time periods, using different gear, or even by different researchers are fraught with problems (Ross 1983, Lasiak 1984a, Bennett 1989a, Pierce *et al.* 1990, Gibson *et al.* 1993, Lamberth *et al.* 1995b). The aim of this part of the study was thus to compile a comprehensive data set of surf-zone fish samples collected simultaneously from a number of sites over an extended time period, using the same equipment, personnel and methodologies. Such a data base could be used to make a comprehensive assessment of the factors that influence variations in surf-zone fish abundance and community structure. This chapter documents the species composition, abundance and size structure of fish communities at 11 sandy and mixed shore sites covering a range of exposure levels in False Bay, South Africa. Data were averaged over a long period (2 years) in order to get a clearer idea of the influence of between-site variations in wave exposure, turbidity and macrophyte abundance on spatial distribution patterns of surf-zone fishes.

## 1.2 STUDY AREA

False Bay (34°04'-34°23'S, 18°26'-18°51'E), situated in the southwestern Cape (Fig. 1.1) experiences a Mediterranean-type climate (Schulze 1965) with cold wet winters and hot dry summers. It is the largest true bay in southern Africa, having a total surface area of 1 082 km$^2$ and a volume of 44.6 km$^3$ (Spargo 1991). Water depth is greatest in the mouth of the Bay (approximately 80 m), which slopes up steeply towards the western and eastern coastlines which are dominated by rocky shores, while sloping gently up to the northern coastline which consists almost entirely of sandy beach. Tidal ranges in False Bay, as with most of the southern African coastline, are relatively modest compared with other parts of the world, and show a mean spring range of 1.48 m (Spargo 1991). Mean salinities in False Bay range from approximately 35.0-35.3%, but may fall below 34.0% in the northeast corner in the winter months due to river discharge (Atkins 1970). Eleven collecting stations (Figs 1.1, 1.2), selected so as to encompass as wide a range of habitat types as possible, were established on the western, northern and northeastern shores of the Bay. These sites, encompassing both mixed shore and sandy beach environments of varying exposure levels, are described briefly below.

Sites 1 and 2 (Long Beach and Mackerel Beach, Fig. 1.2), are situated in Simon's Bay, a small enclave on the western shore of False Bay. These sites have steep intertidal profiles, narrow surf-zones and very clear waters. Located in the lee of the Simonstown Peninsula and the Simonstown harbour breakwater, Long Beach is well protected from prevailing swells and wave action was practically absent on most occasions. Intertidally, this site was made up of unbroken sand, and subtidally of sand together with a narrow kelp-covered reef running parallel to the shore on the extreme northern edge. Mackerel Beach, situated further to the north, receives considerably less protection from prevailing swells and, with its steeply shelving shore, is a moderately exposed beach, made up intertidally of isolated sandstone boulders interspersed with larger areas of sand.

Muizenberg and Sunrise (sites 3 and 4, Fig. 1.2), in the northwestern corner of False Bay are both gently sloping, moderately exposed sandy beaches with broad surf-zones. The shore in this area is made up entirely of unbroken sand terminating in rocky shoreline at the western border of the Muizenberg site. Surf phytoplankton accumulations (*Anaulis biostratis*) of varying intensity were observed on occasions at both sites.

Sites 5, 6 and 7 (Cemetery, Macassar Beach and Swartklip, Fig. 1.2) are all highly exposed beaches situated on the northern shore directly opposite the mouth of the Bay. The former two sites consist entirely of unbroken sand and have steeply sloping intertidal profiles, broad surf-zones and periodically well developed rip currents with associated dense surf phytoplankton accumulations. Swartklip, lying adjacent to the Wolfgat Cliffs, is composed of low lying, isolated rocky outcrops protruding from the sand in the moderately sloping sub- and intertidal parts of the shore.

The remaining four sites (Melkbaai, Makouvlei, Blake's Cove and Gordon's Bay, Fig. 1.2) are situated in the northeastern corner of False Bay. Protection is derived from the gently shelving bottom (Fig. 1) and rocky outcrops running approximately parallel to, and 200-500 m from the shore. These break up and dissipate incoming swells, ensuring that conditions are almost always calm. Melkbaai (site 8) is the most exposed of these four sites, but is none the less a very gently sloping, sheltered sandy beach composed of fine sand. The shore at Blake's Cove is encircled on the seaward and western boundaries by rocky bars and on the eastern boundary by a slipway and wooden jetty, making it among the most sheltered areas in the Bay. Accumulations of detached aquatic macrophytes, prevalent in this area, were frequently netted in large quantities. Rooted aquatic macrophytes and macrofaunal burrows were also in evidence in the sandy bottom. The shore at Makouvlei (site 10) is made up of irregularly laid, angular sedimentary rock outcrops, overlain in places by a layer of sand containing numerous macrofaunal burrows. Elongated sedimentary rock outcrops, directed offshore and interspersed with larger gently sloping sand (high shore) and cobble (low shore) bottom areas make up the shore at Gordon's Bay (site 11). Discharge from perennial rivers emptying into the northeastern corner of the Bay, coupled with poor water circulation in this area, ensure that high turbidities and low salinities prevail at the last four sites for much of the year.

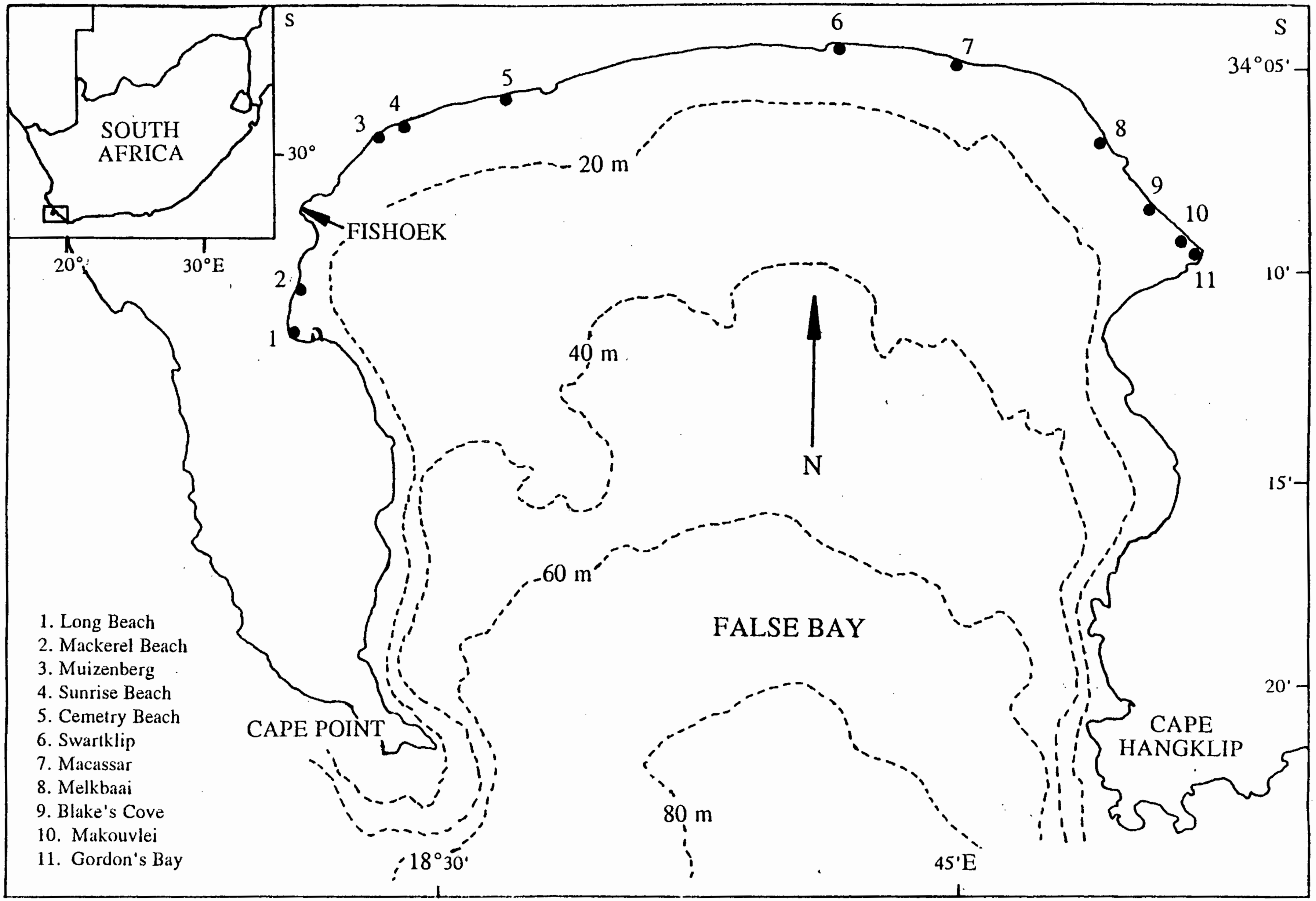
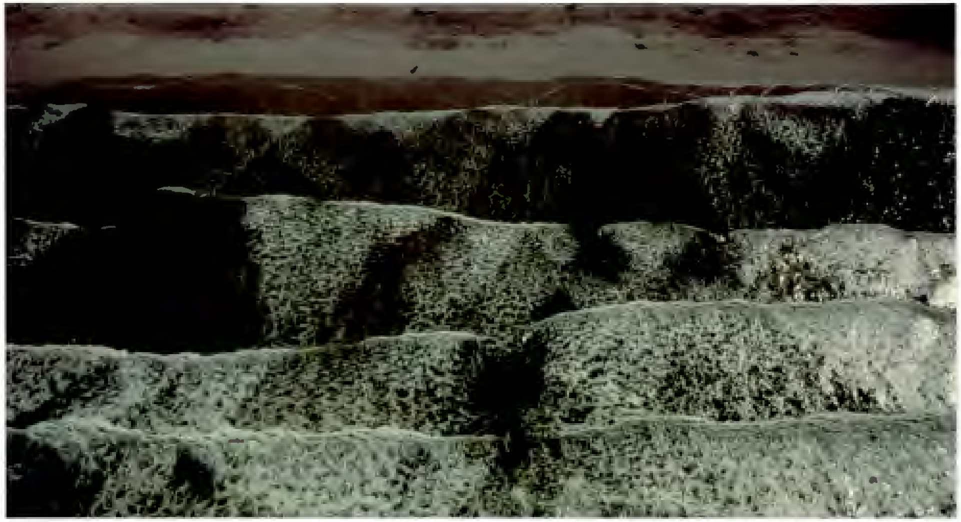


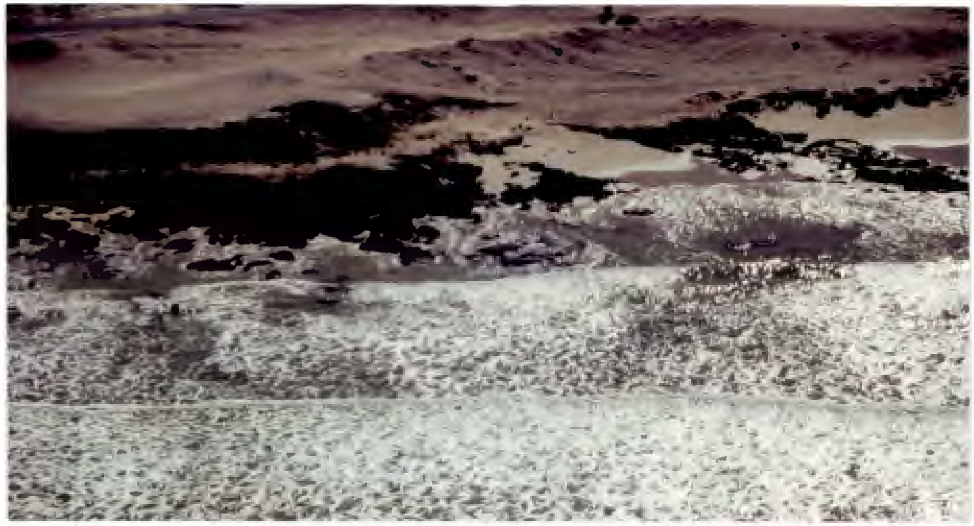
**Fig. 1.1.** Map of the southwestern Cape (inset) and False Bay, showing the location of the sampling sites and other features mentioned in the text.

Fig 1.2. Sampling stations 1-11 at which seining activities were conducted for Chapters 1 and 3.

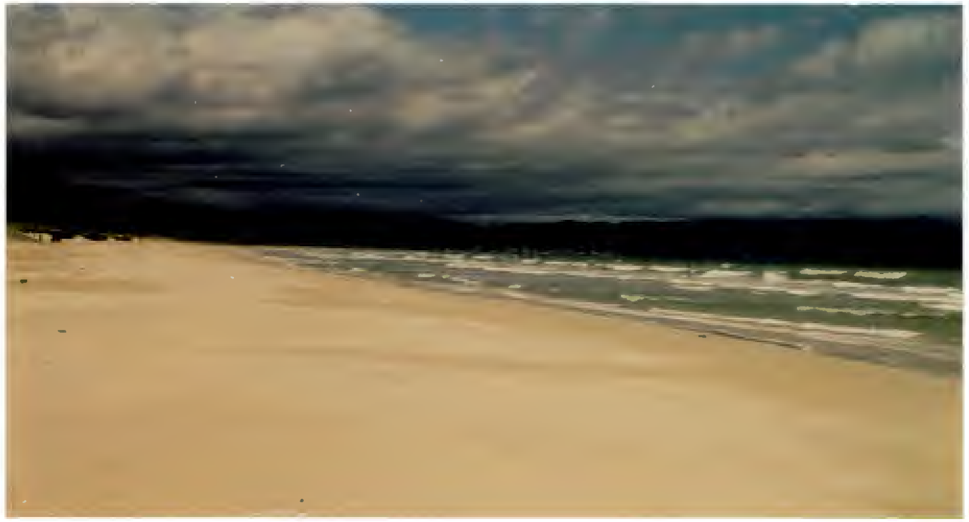
5



6



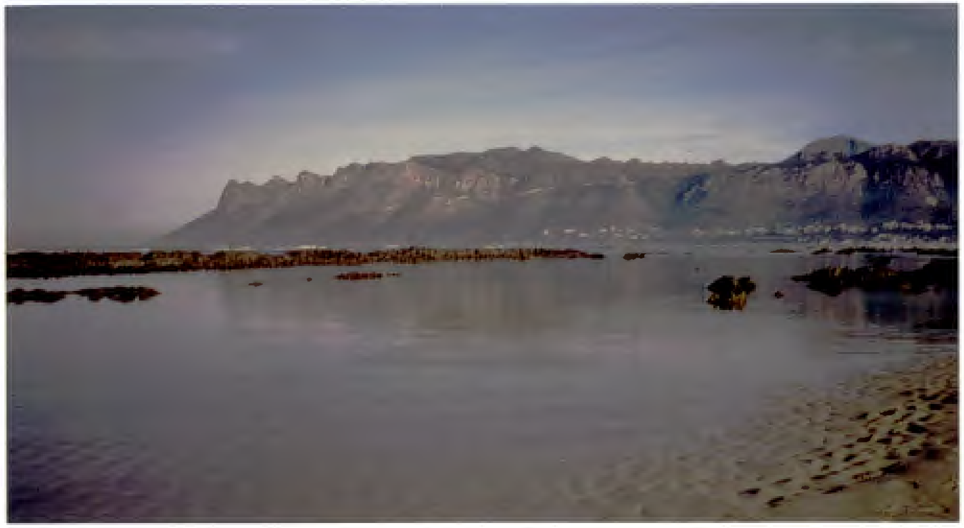
7



8

9

10



11

## 1.3 MATERIALS AND METHODS

### 1.3.1 Sampling methods

Samples were collected during daylight hours from each of the 11 sites (Fig. 1.1) around the perimeter of False Bay at approximately monthly intervals for 24 months between July 1991 and June 1993. The apparatus used was a 30 by 2 m, 12 mm stretched mesh beach-seine net fitted with a 2 m deep bag at its mid point, and a weighted foot rope, to which two 30 m long ropes were attached. The net was laid parallel to the shore in water approximately 1.5 m deep, between 10 and 60 m offshore, and was hauled by four persons, one on each end of the net and one on each rope. Total area sampled was taken as the distance the net was laid offshore multiplied by 15 m (half the length of the net).

All fish collected were identified to species and measured to the nearest 1 mm (total length), except where samples were very large, in which case measurements were restricted to a subsample of 200 individuals per species. The number of juvenile fish per species captured at each site was estimated by calculating the number of individuals below the size at 50% maturity, as reported in the literature (Table 1.3). Individuals of those species for which this information was not available, were examined visually, in order to determine their state of maturity (see Bennett 1993). Turbidity of surf-zone waters was measured in Formazin Turbidity Units (FTU) using a Hach DR/2000 spectrophotometer (where 1 FTU = 1 NTU when made with a nephelometer). Density of detached aquatic macrophytes at each site was calculated by dividing the total volume of seaweed in the net (l) by the total sampling area ($m^2$). Intertidal slope and median particle size was measured at quarterly intervals at each site and averaged over the two year sampling period. Measurements of intertidal slope were made using transect poles, using the sea horizon as a levelling device. Median particle diameter was calculated by sieving sediments through a series of sieves graded at 0.5 $\Phi$ intervals on a mechanical shaker. Maximum wave height was taken as the difference between crest and trough of the largest waves observed at the back of the surf line during each particular sampling interval. The composition of the shore at each site was rated subjectively and allocated a score (%) according to the proportion of rock on the shore within a 100 x 50 m block, with the shorter axis extending from the HWS mark seawards. These estimations were based on observations made in the field and of recent high resolution aerial photographs of the relevant sites. Approximate tidal heights were calculated for the time at which each sample was taken by extrapolation from tables of predicted hourly tidal heights published by the South African Navy Hydrographer.

### 1.3.2 Data analysis

For comparative purposes, it was necessary to transform all catch data into densities (no. fish/m$^2$) as the total area swept by the net varied considerably between samples (from 150-900 m$^2$). Data on the species composition and density of fish in the surf were compared using a variety of statistical procedures. Multivariate analyses of community structure were performed using the CLUSTER, MDS and SIMPER programs on the PRIMER software package (Plymouth Marine Laboratory, UK). Analyses were performed according to procedures recommended by Field *et al.* (1982) and Clarke (1993). Briefly, data on fish densities from each year were root-root transformed and converted into triangular matrices of similarity between all time intervals, using the Bray-Curtis similarity coefficient. Similarities between samples collected at the various time intervals were displayed in the form of a hierarchical clusters on dendrograms, using group average linking. Similarities between samples were also displayed on ordination plots, generated by a non-metric multidimensional scaling procedure. Environmental parameters providing the best predictions of the temporal variations in biotic structure in each year were selected from a suite of seven parameters using the BIOENV routine of the PRIMER package (Clarke & Ainsworth 1993). Abiotic similarity matrices were generated in the same manner as the biotic matrices by employing all possible combinations of the environmental parameters, and were compared with biotic matrices from each year, using weighted Spearman rank correlation coefficients ($\rho_w$). The suite of environmental variables yielding the highest rank correlation coefficient was considered to have the greatest predictive ability. Species principally responsible for sample grouping formed by the CLUSTER and MDS analyses were identified using Simper analysis (Clarke 1993).

Stepwise multiple regression analyses were used to determine which suite of environmental factors was most influential in controlling the observed variation in fish density between sites.

These computations were performed using the SYSTAT computer package (SYSTAT Inc., Evanston, Illinois U.S.A.), whilst adhering to protocols laid down by Zar (1984) and Wilkinson (1990). The species richness, diversity, dominance and evenness of the fish assemblages studied were calculated according to the following formulae:

| | |
|---|---|
| Richness (d) = $(S-1)/\log_e N$ | Margalef (1958) |
| Diversity (H') = $-\Sigma_i (n_i/N)\log_e(n_i/N)$ | Pielou (1969) |
| Dominance (D) = $\Sigma_i (n_i/N)$ | Simpson (1949) |
| Evenness (J) = $H'/\log_e S$ | Pielou (1969) |

where N is the number of individuals in the sample, $n_i$ the number of individuals in the ith species, and S the number of species in the sample.

## 1.4 RESULTS

### 1.4.1 Physical characteristics of the sampling sites

Table 1.1 lists important physical variables recorded at each of the 11 sites during the two year sampling period. Mean maximum wave heights recorded at Long Beach, Blake's Cove, Makouvlei and Gordon's Bay were all less than 0.3 m, with Long Beach exhibiting the lowest value (0.11 ±0.01 m). Intermediate values (0.6-0.9 m) were recorded at Melkbaai, Muizenberg, Mackerel Beach and Sunrise. Highest values (>1 m) were recorded at Swartklip, Cemetery Beach and Macassar Beach, with the highest recorded mean maximum wave height (1.26 ±0.07 m) occurring at Cemetery Beach. Mean width of the surf-zone at each of the sites ranged from 1.7-284.0 m (corresponding to Long Beach and Macassar Beach respectively). Greatest values (>195 m) were recorded along the northern shore of the Bay (Muizenberg to Macassar Beach, Fig. 1.1). Lower values (<100 m) were recorded at the sites on the western and northeastern shores of the Bay. Mean intertidal slopes ranged from a maximum of 1:8 (Long Beach) to 1:48 (Melkbaai), while median particle size ranged from 0.20 mm (Melkbaai) to 0.71 mm (Cemetery Beach). Physical and biological variables relating to wave action, sediment particle diameter, intertidal slope, depth of reduced layers and the presence or absence of macrofaunal burrows at each site were entered into a rating scheme developed by McLachlan (1980) which assesses the degree of exposure of sandy beaches on a scale of 0-20. These scores, listed in Table 1.1, ranged between 4 and 17. Lowest scores (4-7) were attributed to Blake's Cove , Makouvlei, Gordon's Bay and Long Beach, intermediate scores (13-14.5) to Muizenberg, Mackerel Beach, Sunrise and Swartklip, while Macassar Beach (16) and Cemetery Beach (17) received the highest scores. A strong positive correlation was evident between mean wave heights recorded at all sites and exposure score ($r=0.95$, $p<0.001$).

A gradient in overall mean water temperature was evident across the study sites. Mean temperatures were lowest on the western shore of the Bay (Long Beach: 16.8 ±0.7 °C, Mackerel Beach: 16.7 ±0.7 °C), but increased marginally along the northern shore (17.2-17.3 °C) to the northeastern corner of the Bay, where mean temperatures were all greater than 18 °C. Mean turbidities on the western shore of the Bay (Long Beach and Mackerel Beach) were both less than 1 FTU, with Long Beach exhibiting the lowest value (0.3 ±0.1 FTU). Surf-zone waters along most of the northern shore of the Bay (Muizenberg to Melkbaai) displayed intermediate turbidities of 2.2-5.4 FTU, while mean values at the remaining three sites (Blake's Cove - Gordon's Bay) in the northeastern corner were the highest recorded (8.6-12.7). The mean density of detached aquatic macrophytes ranged from 0.002 $l/m^2$-0.678 $l/m^2$ (Table 1.1). Lowest densities (<0.01 $l/m^2$) were recorded along the northern shore of the Bay between Muizenberg and Macassar Beach. Long Beach, Mackerel Beach, Melkbaai and Gordon's Bay exhibited intermediate densities (0.01-0.09 $l/m^2$), while the greatest concentrations were found at Makouvlei (0.150 ±0.058 $l/m^2$) and Blake's Cove (0.678 ±0.265 $l/m^2$). Macrophyte abundance was negatively correlated with both mean wave height ($r=0.54$, d.f.=9) and exposure ($r=0.68$, d.f.=9). The amount of rock on the shore at each site ranged from zero (Sunrise, Cemetery Beach, Macassar Beach and Melkbaai) up to a maximum of 69% (Makouvlei). Gordon's Bay (63%), Blake's Cove (54%), Swartklip (35%) and Mackerel Beach (27%) received high scores, while Long Beach and Muizenberg were both rated at less than 10%.

Table 1.1. Physical environmental variables recorded at sampling sites in False Bay. The variable "exposure" represents scores allocated to the sampling sites based on McLachlan's (1980) rating system, and "rock" the proportion of the shore occupied by rocky substratum. Where appropriate, values are listed as ±SE.

| | Wave height (m) | Surf zone width (m) | Intertidal slope | Median particle size (mm) | Exposure | Temperature (°C) | Turbidity (FTU) | Macrophyte abundance (l/m-2) | Rock (%) |
|---|---|---|---|---|---|---|---|---|---|
| Long Beach | 0.11 ±0.01 | 1.7 ±0.4 | 1:8 | 0.43 | 7.0 | 16.8 ±0.7 | 0.3 ±0.1 | 0.074 ±0.009 | 1 |
| Mackerel | 0.91 ±0.06 | 16.5 ±22.7 | 1:10 | 0.40 | 14.0 | 16.7 ±0.7 | 0.8 ±0.5 | 0.013 ±0.001 | 27 |
| Muizenberg | 0.87 ±0.07 | 251.3 ±50.6 | 1:31 | 0.31 | 13.0 | 17.3 ±0.7 | 2.3 ±0.5 | 0.004 ±0.002 | 8 |
| Sunrise | 0.90 ±0.06 | 232.5 ±36.3 | 1:27 | 0.36 | 13.5 | 17.2 ±0.7 | 4.6 ±1.1 | 0.006 ±0.003 | 0 |
| Cemetry | 1.26 ±0.07 | 195.0 ±35.0 | 1:13 | 0.71 | 17.0 | 17.3 ±0.7 | 5.1 ±0.9 | 0.007 ±0.002 | 0 |
| Swartklip | 1.15 ±0.07 | 207.1 ±61.1 | 1:20 | 0.31 | 14.5 | 17.3 ±0.8 | 5.2 ±2.2 | 0.008 ±0.001 | 35 |
| Macassar | 1.17 ±0.06 | 284.0 ±54.9 | 1:16 | 0.49 | 16.0 | 17.2 ±0.7 | 3.9 ±0.5 | 0.002 ±0.000 | 0 |
| Melkbaai | 0.64 ±0.07 | 96.9 ±26.5 | 1:48 | 0.20 | 9.0 | 18.0 ±0.8 | 5.4 ±0.9 | 0.013 ±0.011 | 0 |
| Blake's Cove | 0.23 ±0.04 | 8.8 ±1.9 | 1:11 | 0.28 | 4.0 | 18.2 ±0.9 | 8.6 ±1.1 | 0.678 ±0.265 | 54 |
| Makouvlei | 0.18 ±0.04 | 47.5 ±18.7 | 1:17 | 0.30 | 6.0 | 18.4 ±0.9 | 8.4 ±1.5 | 0.150 ±0.058 | 69 |
| Gordon's Bay | 0.29 ±0.06 | 66.6 ±28.0 | 1:19 | 0.24 | 6.5 | 18.1 ±0.9 | 12.7 ±2.0 | 0.082 ±0.040 | 63 |

### 1.4.2 Fish fauna

A total of 68 610 fish from 45 species representing 26 families was collected in 264 beach-seine hauls made at 11 collecting stations in False Bay during the 24 month period, July 1991-June 1993 (Table 1.2). *Atherina breviceps, Liza richardsonii* and *Rhabdosargus globiceps* were the three most abundant species at all sites, where they provided between 69 and 99% of the total numbers of fish captured. *Amblyrhynchotes honkenii* was the only other species recorded at all 11 sites. In terms of numbers, fewest fish (742) were captured at Swartklip, while the greatest number (17 436) was captured at Makouvlei. Total areas netted at each of the sampling sites differed considerably (Table 1.2), primarily as a result of differences in intertidal profile and the composition of the shore at each site.
Sampling areas ranged between 17 900 m$^2$ and 4 575 m$^2$. Total area sampled was greatest (>14 000 m$^2$) at the more sheltered, gently sloping sandy beach sites such as Melkbaai and Muizenberg, but was considerably smaller (<10 000) at the more steeply sloping sandy-mixed-shore sites such as Long Beach, Mackerel Beach and Swartklip.

Makouvlei and Swartklip contained the greatest (199.0 fish/100m$^2$) and the lowest (6.3 fish/100m$^2$) densities of fish respectively. High densities were also recorded at Blake's Cove (112.8 fish/100m$^2$) and Gordon's Bay (96.8 fish/100 m$^2$), whereas intermediate densities (26-55 fish/100 m$^2$) were recorded at the remaining seven sites. In terms of numbers of species recorded, Gordon's Bay represented the richest site with 31 species present, while Swartklip was the poorest with only 12 species. Numbers of species recorded at Blake's Cove and Makouvlei were also high (>20), while the remaining sites were represented by 13-19 species each. Community parameters (Margalef's species richness, Shannon diversity, Pielou's evenness and Simpson's dominance) associated with the fish communities sampled at each of the sites are also listed in Table 1.2. Species richness was considerably greater at Gordon's Bay (3.3) than at any of the other sites. Makouvlei, Melkbaai and Blake's Cove displayed intermediate values (2.05-2.47), while the remaining sites received low scores (1.28-1.89). Species diversity was highest at Gordon's Bay (1.55) and Blake's Cove (1.42), lowest (0.25) at Mackerel Beach and intermediate (0.61-1.15) at the remaining sites. Evenness ranged from 0.10-0.45, with greatest values at Gordon's Bay and Blake's Cove (0.45 for both) while Mackerel Beach again registered the lowest value. Greatest dominance was recorded at

Mackerel Beach (0.89), while Macassar, Long Beach, Swartklip and Makouvlei also displayed high values (0.64-0.72). Lowest levels of dominance were recorded at Gordon's Bay (0.35) and Blake's Cove (0.37). Intermediate levels (0.41-0.45) were recorded at the remaining sites. Values of species richness, diversity, evenness and dominance for catches for all sites combined were 3.95, 1.17, 0.31 and 0.42, respectively.

Numbers of juvenile fish exceeded adults at all sites, except Mackerel Beach and Gordon's Bay, where they provided 6 and 38% of the totals respectively. Overall, numbers of juvenile fish exceeded that of adult fish, making up just over half (52.9%) of the total catch, with 23 (51%) of the species being represented by immature individuals only, 18 (40%) as both adults and juvenile and only four (9%) as adults only (Table 1.3). Teleost fish (40 species), comprising 98.7-100% of the catches, far outnumbering elasmobranchs (five species, 0-1.3 % of the catches) at all sites. The majority of the fish captured were small individuals (Table 1.3), only 1.4% of which exceeded 200 mm TL. No individuals captured during this survey were greater than 1 m in length. Length frequency distributions of the 10 most abundant species are illustrated in Figure 1.3.

Faunal similarities among sites were analysed using root-root transformed density data using Cluster analysis and Multidimensional Scaling (MDS). Cluster analysis separated the 11 sampling sites into two major groups which linked at the 62% level of similarity. The first group, composed of seven sites, was made up of Swartklip, Mackerel Beach, Macassar Beach, Muizenberg, Sunrise, Cemetery Beach, and Melkbaai. The remaining four sites, Blake's Cove, Makouvlei, Gordon's Bay and Long Beach, made up the second group. At higher levels of similarity (80-90%), two closely linked groups of samples and a number of outliers was evident (Fig. 1.4). Macassar Beach, Muizenberg, Sunrise, Cemetery Beach, and Melkbaai were linked together in a group, as were Blake's Cove, Makouvlei and Gordon's Bay, while Swartklip, Mackerel Beach and Long Beach remained unattached. Separation of the sampling sites in the ordination plot derived from the MDS analysis, corresponded almost exactly to the pattern generated by the Cluster analysis. Sites linking together between the 80 and 90% levels of similarity clustered together in the MDS plot, while the three outlying samples were placed at some distance from these groups, albeit on the same side of the plot as the groups to which they were linked in the cluster analysis.

Differences in species abundance patterns across the sampling sites were examined using Cluster analysis, MDS and by examining the contributions of the more abundant species to dissimilarities between groups of sites identified earlier (Fig. 1.4) using Simper analysis. A reasonably close match was evident between sample groupings in the dendrogram and ordination plot (Fig. 1.5) despite the high stress loading (0.14) on the latter. Four groups and two outlying samples were evident in these two diagrams. From Table 1.2, it is evident that species in Groups A and B (seven and five species respectively), were captured predominantly at sites 9-11 (Blake's Cove, Makouvlei and Gordon's Bay). Species in Group C (four species) were captured in varying numbers at all sites, while those in Group D (two species), recorded in low densities at a number of sites, were recorded in by far their greatest densities at Gordon's Bay, where >90% of these individuals were captured.

Table 1.4 shows the results of breaking dissimilarities between the sites in Group 1 (Fig. 1.4; Blake's Cove, Makouvlei, Gordon's Bay) and 2 (Muizenberg, Sunrise, Cemetery Beach, Macassar Beach and Melkbaai) into the individual components provided by the top ten species. Together these species accounted for >55% of the dissimilarity between these two groups of samples. Most (seven) of these species came from Groups A and B above, while both species from Group D and one from Group C were also present.

Table 1.2. Mean density (mean monthly no. indv./100m$^2$) and community parameters associated with ichthyofaunal assemblages sampled by beach-seining at the 11 sites in False Bay.

| | Long Beach | Mackerel Beach | Muizen-berg | Sunrise Beach | Cemetry Beach | Swart-klip | Macassar Beach | Harmony Beach | Blake's Cove | Makou-vlei | Gordon's Bay | All sites | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | Density | Tot. ind. |
| *Atherina breviceps* | 0.65 | 31.28 | 15.04 | 8.39 | 10.86 | 0.39 | 4.45 | 11.24 | 30.45 | 116.20 | 43.81 | 30.89 | 37 023 |
| *Liza richardsonii* | 44.12 | 7.15 | 24.42 | 17.01 | 14.12 | 4.66 | 23.16 | 17.79 | 63.40 | 66.23 | 17.41 | 20.42 | 24 474 |
| *Rhabdosargus globiceps* | 7.58 | 0.15 | 2.72 | 2.66 | 1.60 | 0.13 | 0.32 | 2.02 | 6.36 | 1.23 | 5.57 | 2.20 | 2 641 |
| *Diplodus sargus* | 0.39 | 0.12 | 0.41 | | 0.02 | 0.23 | | 0.01 | 2.28 | 2.26 | 2.66 | 0.58 | 696 |
| *Gilchristella aestuaria* | | | 0.13 | 0.33 | 0.15 | 0.14 | 0.03 | 0.10 | 0.73 | 0.26 | 14.27 | 0.56 | 674 |
| *Psammogobius knysnaensis* | 0.27 | | 0.01 | 0.01 | 0.01 | | | 0.04 | 2.18 | 2.87 | 2.65 | 0.50 | 600 |
| *Pomatomus saltatrix* | | 0.14 | 1.82 | 0.56 | 0.06 | 0.13 | 0.60 | 0.31 | 0.57 | 8.11 | 0.17 | 0.49 | 582 |
| *Sarpa salpa* | | | | | | 0.02 | | | 0.05 | 0.01 | 5.50 | 0.41 | 488 |
| *Amblyrhynchotes honkenii* | 0.06 | 0.04 | 0.14 | 0.02 | 0.06 | 0.02 | 0.11 | 0.04 | 0.85 | 0.51 | 0.54 | 0.18 | 220 |
| *Liza tricuspidens* | | | 0.01 | | | | 0.07 | | 1.25 | 0.20 | 0.26 | 0.11 | 137 |
| *Liza dumerilii* | | | 0.02 | | | | 0.01 | 0.01 | 0.98 | 0.42 | 0.03 | 0.08 | 97 |
| *Rhinobatos annulatus* | | | 0.62 | 0.03 | | | 0.03 | 0.02 | | 0.04 | 0.16 | 0.08 | 91 |
| *Umbrina canariensis* | 0.04 | 0.02 | 0.01 | | 0.01 | 0.34 | 0.08 | 0.23 | 0.18 | 0.02 | 0.08 | 0.08 | 93 |
| *Caffrogobius nudiceps* | 0.01 | | | | | | | 0.01 | 0.43 | 0.11 | 0.56 | 0.07 | 82 |
| *Mugil cephalus* | | | | 0.01 | | | 0.03 | 0.04 | 0.05 | 0.17 | 0.32 | 0.06 | 66 |
| *Clinus superciliosus* | 0.06 | 0.02 | | | | | | | 0.41 | 0.08 | 0.18 | 0.05 | 58 |
| *Lithognathus lithognathus* | | | 0.04 | 0.03 | 0.02 | 0.09 | 0.01 | 0.08 | 0.48 | 0.04 | 0.01 | 0.05 | 62 |
| *Lichia amia* | | | | | 0.01 | | | 0.13 | 0.17 | 0.03 | 0.15 | 0.04 | 45 |
| *Heteromycterus capensis* | 0.84 | 0.02 | | | | | | 0.01 | 1.35 | 0.16 | 1.85 | 0.03 | 320 |
| *Solea bleekeri* | | | 0.01 | | 0.01 | | | 0.01 | 0.38 | | 0.03 | 0.03 | 30 |
| *Chelidonichthyes capensis* | 0.14 | 0.01 | 0.02 | 0.01 | | | | 0.04 | 0.11 | | | 0.02 | 24 |
| *Dichistius capensis* | | | 0.01 | | | 0.18 | 0.01 | | | | | 0.01 | 15 |
| *Lithognathus mormyrus* | 0.18 | 0.01 | 0.01 | | | | | | | | | 0.01 | 15 |
| *Clinus latipennis* | | 0.05 | | 0.03 | 0.01 | 0.01 | | | | | 0.04 | 0.01 | 13 |
| *Cancelloxus longior* | 0.12 | | | | | | | | | | | 0.01 | 9 |
| *Rhabdosargus holubi* | | | | | | | | | | 0.01 | 0.08 | 0.01 | 8 |
| *Myliobatis aquila* | | | 0.02 | | | | | | 0.06 | | 0.02 | 0.01 | 7 |
| *Coryphaena hippurus* | | | | 0.03 | | | | | | | | <0.005 | 3 |
| *Dasyatis crysonota* | | | | | | | | | 0.03 | | 0.01 | <0.005 | 3 |
| *Syngnathus acus* | 0.01 | 0.02 | | | | | | | | | | <0.005 | 2 |
| *Caffrogobius caffer* | | | | | | | | | | | 0.05 | <0.005 | 4 |
| *Diplodus cervinus* | | | | | | | | | 0.02 | | | <0.005 | 2 |
| *Gonorhynchus gonorhynchus* | 0.01 | | | | | | | | | | | <0.005 | 1 |
| *Trachinocephalus myops* | 0.03 | | | | | | | | | | | <0.005 | 2 |
| *Dichistius multifasciatus* | 0.01 | | | | | | | | | | | <0.005 | 1 |
| *Trachurus trachurus* | | | | | 0.01 | | | | | | | <0.005 | 1 |
| *Trachinotus botla* | | | | | | | 0.01 | | | | | <0.005 | 1 |
| *Trachinotus africanus* | | | | | | | | 0.01 | | | | <0.005 | 1 |
| *Engraulis japonicus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Heniochus acuminatus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Monodactylus falciformes* | | | | | | | | | | 0.01 | | <0.005 | 1 |
| *Haploblepharus edwarsii* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Sphyraena acutipinnis* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Triakis megalopterus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Fucominus mus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| Total density | 54.53 | 39.02 | 45.43 | 29.11 | 26.92 | 6.32 | 28.93 | 32.14 | 112.78 | 198.97 | 96.48 | 57.25 | |
| No. individuals | 4 828 | 11 765 | 5 109 | 3 073 | 2 775 | 742 | 3 126 | 3 903 | 7 255 | 17 436 | 8 903 | 68 610 | |
| Total no. species | 17 | 13 | 18 | 13 | 14 | 12 | 14 | 19 | 23 | 21 | 31 | 45 | |
| Richness | 1.89 | 1.28 | 1.99 | 1.49 | 1.64 | 1.66 | 1.62 | 2.18 | 2.47 | 2.05 | 3.30 | 3.95 | |
| Diversity | 0.64 | 0.25 | 1.15 | 1.08 | 0.95 | 0.81 | 0.61 | 1.02 | 1.42 | 0.73 | 1.55 | 1.17 | |
| Evenness | 0.22 | 0.10 | 0.40 | 0.42 | 0.36 | 0.33 | 0.23 | 0.35 | 0.45 | 0.24 | 0.45 | 0.31 | |
| Dominance | 0.71 | 0.89 | 0.41 | 0.42 | 0.45 | 0.69 | 0.72 | 0.45 | 0.37 | 0,64 | 0.35 | 0.42 | |
| Mean netting area (m$^2$) | 186 | 254 | 656 | 624 | 453 | 343 | 463 | 746 | 347 | 362 | 618 | 454 | |
| Total netting area (m$^2$) | 4 575 | 5 850 | 15 750 | 14 975 | 9 975 | 8 225 | 11 100 | 17 900 | 8 325 | 8 335 | 14 825 | 119 835 | |

**Table 1.3** Numbers of individuals, length ranges (TL) and sizes at maturity of fish captured in beach-seine hauls made at the 11 sites in False Bay.

| | | N | Size Range | Size at Maturity | % Immature |
|---|---|---|---|---|---|
| OSTEICHTHYES | | | | | |
| Atherinidae | *Atherina breviceps* | 37 023 | 16-129 | 43[a] | 14.1 |
| Carangidae | *Lichia amia* | 45 | 46-380 | 600[b] | 100.0 |
| | *Trachinotus africanus* | 1 | 98 | | 100.0 |
| | *Trachinotus botla* | 1 | 56 | | 100.0 |
| | *Trachurus trachurus* | 1 | 67 | 200[c] | 100.0 |
| | Unidentified | 8 | 22-37 | | |
| Chaetodontidae | *Heniochus acuminatus* | 1 | 42 | | 100.0 |
| Clinidae | *Cancelloxus longior* | 9 | 71-125 | | 0.0 |
| | *Clinus lattipennis* | 13 | 40-131 | 45[d] | 23.1 |
| | *Clinus superciliosus* | 58 | 38-151 | 65[e] | 13.8 |
| | *Fucomimus mus* | 1 | 95 | | |
| Clupeidae | *Gilchristella aestuaria* | 674 | 30-86 | 34[a] | 0.7 |
| Coryphaenidae | *Coryphaena hippurus* | 3 | 43-47 | | |
| Dichistiidae | *Dichistius capensis* | 15 | 33-175 | 310[f] | 100.0 |
| | *Dichistius multifasciatis* | 1 | 30 | 210[b] | 100.0 |
| Engraulidae | *Engraulis japonicus* | 1 | 95 | 90[g] | 0.0 |
| Gobiidae | *Caffrogobius caffer* | 4 | 56-93 | 55[e] | 0.0 |
| | *Caffrogobius nudiceps* | 82 | 28-108 | 65[h] | 28.7 |
| | *Psammogobius knysnaensis* | 600 | 22-71 | 37[a] | 12.7 |
| Gonorynchidae | *Gonorhynchus gonorhynchus* | 1 | 181 | | 0.0 |
| Monodactylidae | *Monodactylis falciformis* | 1 | 40 | 170[k] | 100.0 |
| Mugilidae | *Liza dumerilii* | 97 | 53-181 | 200[i] | 100.0 |
| | *Liza richardsonii* | 24 474 | 20-402 | 230[j] | 97.9 |
| | *Liza tricuspidens* | 137 | 78-290 | 400[i] | 100.0 |
| | *Mugil cephalus* | 66 | 100-420 | 450[e] | 100.0 |
| Pomatomidae | *Pomatomus saltatrix* | 582 | 73-256 | 240[l] | 99.8 |
| Sciaenidae | *Umbrina canariensis* | 93 | 27-635 | 300[d] | 75.5 |
| Soleidae | *Heteromycteris capensis* | 320 | 33-121 | 45[m] | 48.5 |
| | *Solea bleekeri* | 30 | 39-190 | 100[i] | 62.5 |
| Sparidae | *Dilpodus cervinus hottentotus* | 2 | 52-76 | 334[n] | 100.0 |
| | *Diplodus sargus capensis* | 696 | 22-220 | 180[r] | 99.7 |
| | *Lithognathus lithognathus* | 62 | 74-810 | 650[o] | 98.3 |
| | *Lithognathus mormyrus* | 15 | 42-131 | 190[p] | 100.0 |
| | *Rhabdosargus globiceps* | 2 641 | 16-172 | 260[q] | 100.0 |
| | *Rhabdosargus holubi* | 8 | 42-218 | 180[e] | 75.0 |
| | *Sarpa salpa* | 488 | 42-142 | 180[r] | 100.0 |
| Sphyraenidae | *Sphyraena acutipinnis* | 1 | 64 | | 100.0 |
| Syngnathidae | *Syngnathus acus* | 2 | 92-178 | 125[a] | 50.0 |
| Synodontidae | *Trachinocephalus myops* | 2 | 55-80 | | 100.0 |
| Tetraodontidae | *Amblyrhynchotes honkenii* | 220 | 18-178 | 80[e] | 87.9 |
| Triglidae | *Chelidonichthyes capensis* | 24 | 29-85 | 305[s] | 100.0 |
| Unidentified | | 4 | 22-37 | | |
| CHONDRICHTHYES | | | | | |
| Carcharhinidae | *Triakis megalopterus* | 1 | 440 | 1400[t] | 100.0 |
| Dasyatidae | *Dasyatis crysonota* | 3 | 225-385 | 500[u] | 100.0 |
| Myliobatidae | *Myliobatis aquila* | 7 | 290-780 | 540[v] | 71.4 |
| Rhinobatidae | *Rhinobatos annulatus* | 91 | 223-910 | 700[w] | 71.1 |
| Scyliorhinidae | *Haploblepharus edwardsii* | 1 | 240 | 410[t] | 100.0 |
| Total | | 68 610 | | | 52.9 |

a. Bennett (1989b) b. Van der Elst (1988) c. Geldenhuys (1973) d. Lamberth *et al.* 1994 e. Day *et al.* (1981) f. Bennett & Griffiths (1986) g. Armstrong & Thomas (1989) h. Whitfield (1990)[1] i. Wallace (1975) j. De Villiers (1987)[2] k. Beckley (1984a) l. Van der Elst (1976) m. Clark *et al.* 1994a n. Mann (1992)[2] o. Bennett (1993) p. Lasiak (1982)[1] q. Talbot (1955) r. Joubert (1981a)[2] s.Hecht (1977) t. Compagno (1984a) u. Cowley (1990) v. Wallace (1967a) w. Wallace (1967b)

1. Corrected from SL to TL
2. Corrected from FL to TL

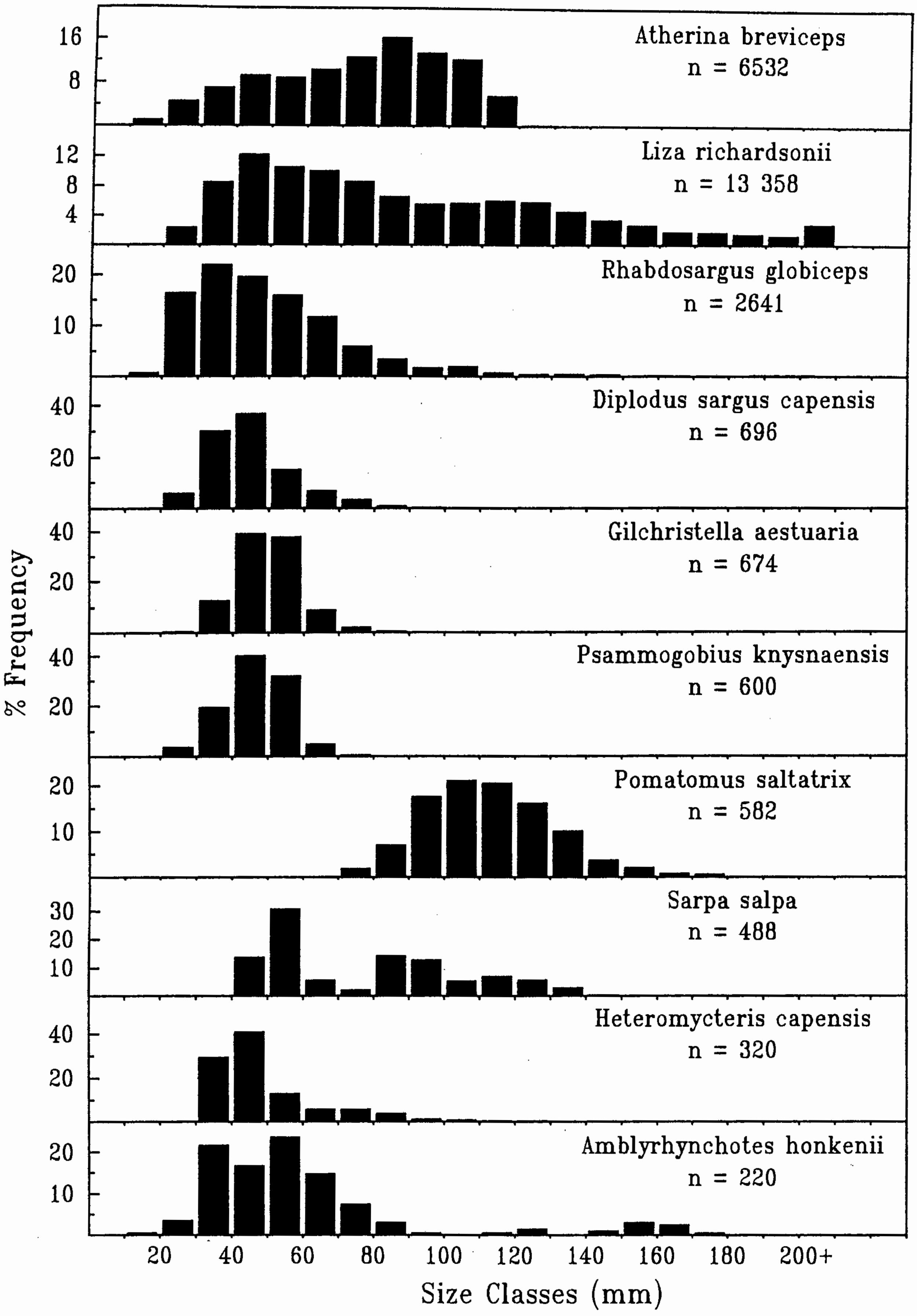


**Fig. 1.3.** Size frequency distributions of the ten most abundant fish species captured in beach-seine hauls from the False Bay surf-zone.

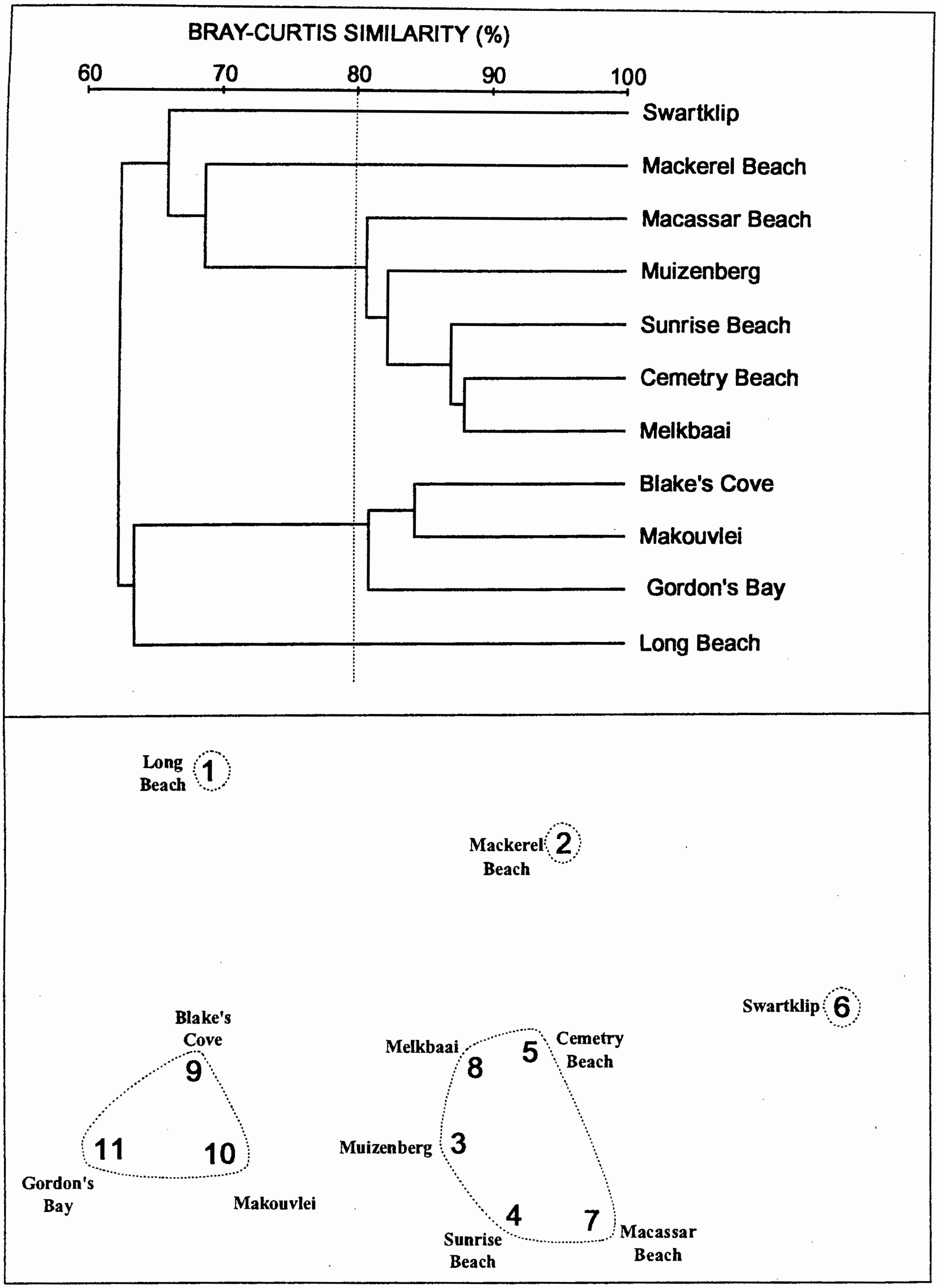


**Fig. 1.4.** Dendrogram and MDS ordination showing similarities between sites based on the composition and abundance of fish species in seine net hauls made in the surf-zone of False Bay. Groups of species delineated at the 80% level in the dendrogram are circled in the ordination plot. Stress for MDS plot = 0.07.

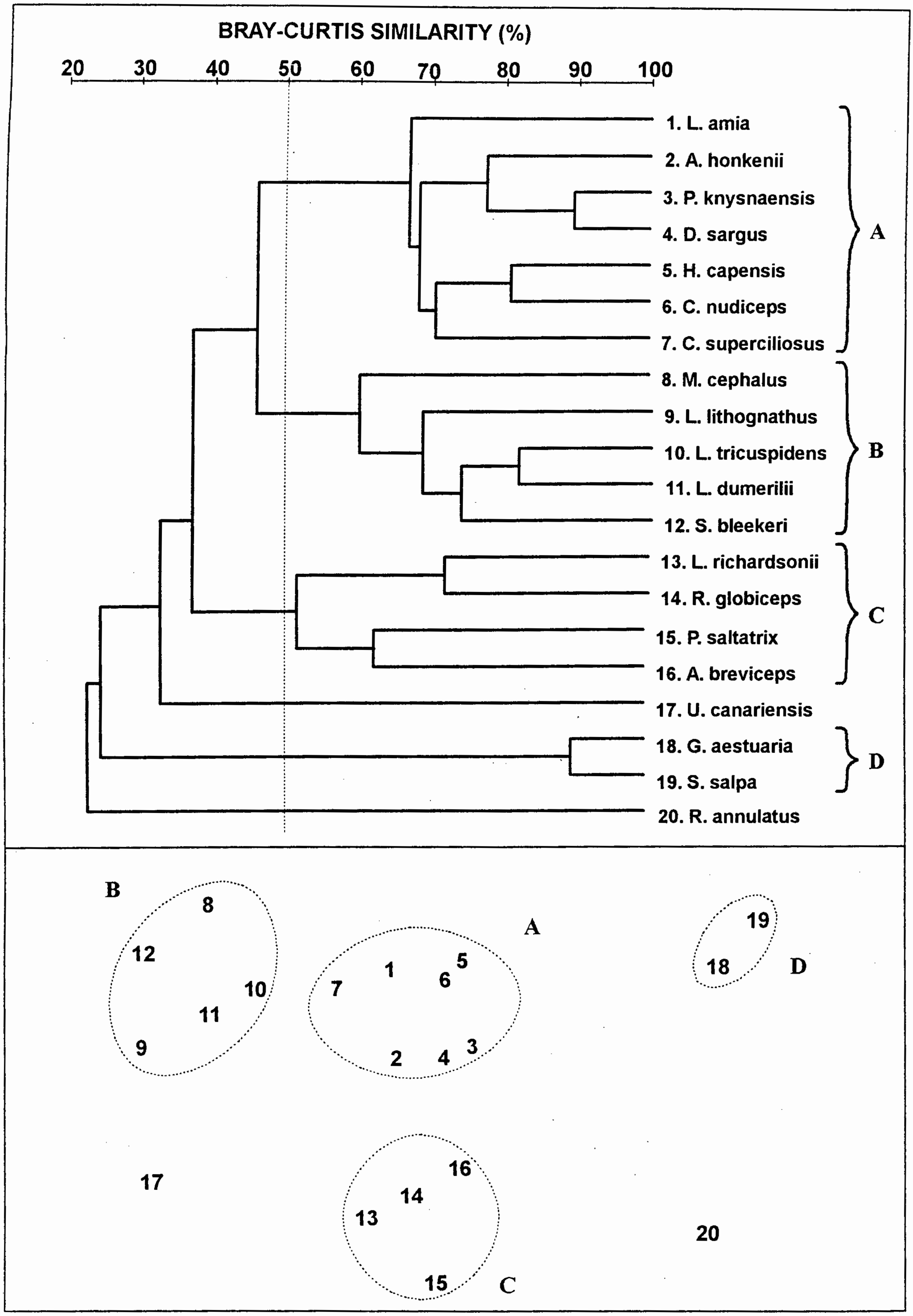


Fig. 1.5. Dendrogram and MDS ordination showing similarities between species based on their occurrence at 11 localities in the False Bay surf-zone. Groups of species delineated at the 50% level in the dendrogram are circled in the ordination plot. Stress for MDS plot = 0.13. Full genus names are given in Table 1.2.

**Table 1.4.** Breakdown of average dissimilarity between site 9-11 and sites 3-5 + 7-8 into contributions of the 10 top species, listed in order of decreasing contribution. $\delta i$ is the average contribution of the *i*th species to the dissimilarity between the two groups, $\delta i/\mathrm{SD}(\delta_i)$ the ratio between average contribution of the ith species ($\delta_i$) and the standard deviation of the $\delta$values for that species ($\mathrm{SD}\delta_i$) and Cum $\delta_i$% the cumulative contribution to the total dissimilarity, rescaled as a percentage. Also included is the average density of each of these species at the two groups of sites

| | | | | | Mean density | |
|---|---|---|---|---|---|---|
| SPECIES | $\delta i$ | $\delta i/\mathrm{SD}(\delta i)$ | $\delta i$% | Cum $\delta i$% | 9-11 | 3-5, 7-8 |
| *Atherina breviceps* | 3.09 | 1.88 | 7.21 | 7.21 | 0.63 | 0.10 |
| *Psammogobius knysnaensis* | 3.05 | 4.87 | 7.12 | 14.32 | 0.03 | 0.00 |
| *Diplodus sargus* | 2.95 | 2.87 | 6.89 | 21.21 | 0.02 | <0.005 |
| *Heteromycterus capensis* | 2.72 | 3.73 | 6.35 | 27.56 | 0.01 | <0.005 |
| *Sarpa salpa* | 2.30 | 1.53 | 5.36 | 32.92 | 0.02 | 0.00 |
| *Caffrogobius nudiceps* | 2.09 | 4.07 | 4.88 | 37.81 | 0.01 | 0.00 |
| *Clinus superciliosus* | 2.02 | 6.38 | 4.71 | 42.52 | 0.01 | 0.00 |
| *Liza tricuspidens* | 1.99 | 2.26 | 4.64 | 47.15 | 0.01 | <0.005 |
| *Gilchristella aestuaria* | 1.76 | 1.13 | 4.11 | 51.27 | 0.05 | <0.005 |
| *Liza dumerilii* | 1.73 | 1.76 | 4.03 | 55.29 | 0.01 | <0.005 |

## 1.3 MATERIALS AND METHODS

### 1.3.1 Sampling methods

Samples were collected during daylight hours from each of the 11 sites (Fig. 1.1) around the perimeter of False Bay at approximately monthly intervals for 24 months between July 1991 and June 1993. The apparatus used was a 30 by 2 m, 12 mm stretched mesh beach-seine net fitted with a 2 m deep bag at its mid point, and a weighted foot rope, to which two 30 m long ropes were attached. The net was laid parallel to the shore in water approximately 1.5 m deep, between 10 and 60 m offshore, and was hauled by four persons, one on each end of the net and one on each rope. Total area sampled was taken as the distance the net was laid offshore multiplied by 15 m (half the length of the net).

All fish collected were identified to species and measured to the nearest 1 mm (total length), except where samples were very large, in which case measurements were restricted to a subsample of 200 individuals per species. The number of juvenile fish per species captured at each site was estimated by calculating the number of individuals below the size at 50% maturity, as reported in the literature (Table 1.3). Individuals of those species for which this information was not available, were examined visually, in order to determine their state of maturity (see Bennett 1993). Turbidity of surf-zone waters was measured in Formazin Turbidity Units (FTU) using a Hach DR/2000 spectrophotometer (where 1 FTU = 1 NTU when made with a nephelometer). Density of detached aquatic macrophytes at each site was calculated by dividing the total volume of seaweed in the net (l) by the total sampling area ($m^2$). Intertidal slope and median particle size was measured at quarterly intervals at each site and averaged over the two year sampling period. Measurements of intertidal slope were made using transect poles, using the sea horizon as a levelling device. Median particle diameter was calculated by sieving sediments through a series of sieves graded at 0.5 $\Phi$ intervals on a mechanical shaker. Maximum wave height was taken as the difference between crest and trough of the largest waves observed at the back of the surf line during each particular sampling interval. The composition of the shore at each site was rated subjectively and allocated a score (%) according to the proportion of rock on the shore within a 100 x 50 m block, with the shorter axis extending from the HWS mark seawards. These estimations were based on observations made in the field and of recent high resolution aerial photographs of the relevant sites. Approximate tidal heights were calculated for the time at which each sample was taken by extrapolation from tables of predicted hourly tidal heights published by the South African Navy Hydrographer.

### 1.3.2 Data analysis

For comparative purposes, it was necessary to transform all catch data into densities (no. fish/m$^2$) as the total area swept by the net varied considerably between samples (from 150-900 m$^2$). Data on the species composition and density of fish in the surf were compared using a variety of statistical procedures. Multivariate analyses of community structure were performed using the CLUSTER, MDS and SIMPER programs on the PRIMER software package (Plymouth Marine Laboratory, UK). Analyses were performed according to procedures recommended by Field *et al.* (1982) and Clarke (1993). Briefly, data on fish densities from each year were root-root transformed and converted into triangular matrices of similarity between all time intervals, using the Bray-Curtis similarity coefficient. Similarities between samples collected at the various time intervals were displayed in the form of a hierarchical clusters on dendrograms, using group average linking. Similarities between samples were also displayed on ordination plots, generated by a non-metric multidimensional scaling procedure. Environmental parameters providing the best predictions of the temporal variations in biotic structure in each year were selected from a suite of seven parameters using the BIOENV routine of the PRIMER package (Clarke & Ainsworth 1993). Abiotic similarity matrices were generated in the same manner as the biotic matrices by employing all possible combinations of the environmental parameters, and were compared with biotic matrices from each year, using weighted Spearman rank correlation coefficients ($\rho_w$). The suite of environmental variables yielding the highest rank correlation coefficient was considered to have the greatest predictive ability. Species principally responsible for sample grouping formed by the CLUSTER and MDS analyses were identified using Simper analysis (Clarke 1993).

Stepwise multiple regression analyses were used to determine which suite of environmental factors was most influential in controlling the observed variation in fish density between sites.

These computations were performed using the SYSTAT computer package (SYSTAT Inc., Evanston, Illinois U.S.A.), whilst adhering to protocols laid down by Zar (1984) and Wilkinson (1990). The species richness, diversity, dominance and evenness of the fish assemblages studied were calculated according to the following formulae:

| | |
|---|---|
| Richness (d) = $(S-1)/\log_e N$ | Margalef (1958) |
| Diversity (H') = $-\Sigma_i(n_i/N)\log_e(n_i/N)$ | Pielou (1969) |
| Dominance (D) = $\Sigma_i(n_i/N)$ | Simpson (1949) |
| Evenness (J) = $H'/\log_e S$ | Pielou (1969) |

where N is the number of individuals in the sample, $n_i$ the number of individuals in the ith species, and S the number of species in the sample.

## 1.4 RESULTS

### 1.4.1 Physical characteristics of the sampling sites

Table 1.1 lists important physical variables recorded at each of the 11 sites during the two year sampling period. Mean maximum wave heights recorded at Long Beach, Blake's Cove, Makouvlei and Gordon's Bay were all less than 0.3 m, with Long Beach exhibiting the lowest value (0.11 ±0.01 m). Intermediate values (0.6-0.9 m) were recorded at Melkbaai, Muizenberg, Mackerel Beach and Sunrise. Highest values (>1 m) were recorded at Swartklip, Cemetery Beach and Macassar Beach, with the highest recorded mean maximum wave height (1.26 ±0.07 m) occurring at Cemetery Beach. Mean width of the surf-zone at each of the sites ranged from 1.7-284.0 m (corresponding to Long Beach and Macassar Beach respectively). Greatest values (>195 m) were recorded along the northern shore of the Bay (Muizenberg to Macassar Beach, Fig. 1.1). Lower values (<100 m) were recorded at the sites on the western and northeastern shores of the Bay. Mean intertidal slopes ranged from a maximum of 1:8 (Long Beach) to 1:48 (Melkbaai), while median particle size ranged from 0.20 mm (Melkbaai) to 0.71 mm (Cemetery Beach). Physical and biological variables relating to wave action, sediment particle diameter, intertidal slope, depth of reduced layers and the presence or absence of macrofaunal burrows at each site were entered into a rating scheme developed by McLachlan (1980) which assesses the degree of exposure of sandy beaches on a scale of 0-20. These scores, listed in Table 1.1, ranged between 4 and 17. Lowest scores (4-7) were attributed to Blake's Cove , Makouvlei, Gordon's Bay and Long Beach, intermediate scores (13-14.5) to Muizenberg, Mackerel Beach, Sunrise and Swartklip, while Macassar Beach (16) and Cemetery Beach (17) received the highest scores. A strong positive correlation was evident between mean wave heights recorded at all sites and exposure score ($r=0.95$, $p<0.001$).

A gradient in overall mean water temperature was evident across the study sites. Mean temperatures were lowest on the western shore of the Bay (Long Beach: 16.8 ±0.7 °C, Mackerel Beach: 16.7 ±0.7 °C), but increased marginally along the northern shore (17.2-17.3 °C) to the northeastern corner of the Bay, where mean temperatures were all greater than 18 °C. Mean turbidities on the western shore of the Bay (Long Beach and Mackerel Beach) were both less than 1 FTU, with Long Beach exhibiting the lowest value (0.3 ±0.1 FTU). Surf-zone waters along most of the northern shore of the Bay (Muizenberg to Melkbaai) displayed intermediate turbidities of 2.2-5.4 FTU, while mean values at the remaining three sites (Blake's Cove - Gordon's Bay) in the northeastern corner were the highest recorded (8.6-12.7). The mean density of detached aquatic macrophytes ranged from 0.002 $l/m^2$-0.678 $l/m^2$ (Table 1.1). Lowest densities (<0.01 $l/m^2$) were recorded along the northern shore of the Bay between Muizenberg and Macassar Beach. Long Beach, Mackerel Beach, Melkbaai and Gordon's Bay exhibited intermediate densities (0.01-0.09 $l/m^2$), while the greatest concentrations were found at Makouvlei (0.150 ±0.058 $l/m^2$) and Blake's Cove (0.678 ±0.265 $l/m^2$). Macrophyte abundance was negatively correlated with both mean wave height ($r=0.54$, d.f.=9) and exposure ($r=0.68$, d.f.=9). The amount of rock on the shore at each site ranged from zero (Sunrise, Cemetery Beach, Macassar Beach and Melkbaai) up to a maximum of 69% (Makouvlei). Gordon's Bay (63%), Blake's Cove (54%), Swartklip (35%) and Mackerel Beach (27%) received high scores, while Long Beach and Muizenberg were both rated at less than 10%.

**Table 1.1.** Physical environmental variables recorded at sampling sites in False Bay. The variable "exposure" represents scores allocated to the sampling sites based on McLachlan's (1980) rating system, and "rock" the proportion of the shore occupied by rocky substratum. Where appropriate, values are listed as ±SE.

| | Wave height (m) | Surf zone width (m) | Intertidal slope | Median particle size (mm) | Exposure | Temperature (°C) | Turbidity (FTU) | Macrophyte abundance (l/m-2) | Rock (%) |
|---|---|---|---|---|---|---|---|---|---|
| Long Beach | 0.11 ±0.01 | 1.7 ±0.4 | 1:8 | 0.43 | 7.0 | 16.8 ±0.7 | 0.3 ±0.1 | 0.074 ±0.009 | 1 |
| Mackerel | 0.91 ±0.06 | 16.5 ±22.7 | 1:10 | 0.40 | 14.0 | 16.7 ±0.7 | 0.8 ±0.5 | 0.013 ±0.001 | 27 |
| Muizenberg | 0.87 ±0.07 | 251.3 ±50.6 | 1:31 | 0.31 | 13.0 | 17.3 ±0.7 | 2.3 ±0.5 | 0.004 ±0.002 | 8 |
| Sunrise | 0.90 ±0.06 | 232.5 ±36.3 | 1:27 | 0.36 | 13.5 | 17.2 ±0.7 | 4.6 ±1.1 | 0.006 ±0.003 | 0 |
| Cemetry | 1.26 ±0.07 | 195.0 ±35.0 | 1:13 | 0.71 | 17.0 | 17.3 ±0.7 | 5.1 ±0.9 | 0.007 ±0.002 | 0 |
| Swartklip | 1.15 ±0.07 | 207.1 ±61.1 | 1:20 | 0.31 | 14.5 | 17.3 ±0.8 | 5.2 ±2.2 | 0.008 ±0.001 | 35 |
| Macassar | 1.17 ±0.06 | 284.0 ±54.9 | 1:16 | 0.49 | 16.0 | 17.2 ±0.7 | 3.9 ±0.5 | 0.002 ±0.000 | 0 |
| Melkbaai | 0.64 ±0.07 | 96.9 ±26.5 | 1:48 | 0.20 | 9.0 | 18.0 ±0.8 | 5.4 ±0.9 | 0.013 ±0.011 | 0 |
| Blake's Cove | 0.23 ±0.04 | 8.8 ±1.9 | 1:11 | 0.28 | 4.0 | 18.2 ±0.9 | 8.6 ±1.1 | 0.678 ±0.265 | 54 |
| Makouvlei | 0.18 ±0.04 | 47.5 ±18.7 | 1:17 | 0.30 | 6.0 | 18.4 ±0.9 | 8.4 ±1.5 | 0.150 ±0.058 | 69 |
| Gordon's Bay | 0.29 ±0.06 | 66.6 ±28.0 | 1:19 | 0.24 | 6.5 | 18.1 ±0.9 | 12.7 ±2.0 | 0.082 ±0.040 | 63 |

### 1.4.2 Fish fauna

A total of 68 610 fish from 45 species representing 26 families was collected in 264 beach-seine hauls made at 11 collecting stations in False Bay during the 24 month period, July 1991-June 1993 (Table 1.2). *Atherina breviceps, Liza richardsonii* and *Rhabdosargus globiceps* were the three most abundant species at all sites, where they provided between 69 and 99% of the total numbers of fish captured. *Amblyrhynchotes honkenii* was the only other species recorded at all 11 sites. In terms of numbers, fewest fish (742) were captured at Swartklip, while the greatest number (17 436) was captured at Makouvlei. Total areas netted at each of the sampling sites differed considerably (Table 1.2), primarily as a result of differences in intertidal profile and the composition of the shore at each site.
Sampling areas ranged between 17 900 $m^2$ and 4 575 $m^2$. Total area sampled was greatest (>14 000 $m^2$) at the more sheltered, gently sloping sandy beach sites such as Melkbaai and Muizenberg, but was considerably smaller (<10 000) at the more steeply sloping sandy-mixed-shore sites such as Long Beach, Mackerel Beach and Swartklip.

Makouvlei and Swartklip contained the greatest (199.0 fish/100$m^2$) and the lowest (6.3 fish/100$m^2$) densities of fish respectively. High densities were also recorded at Blake's Cove (112.8 fish/100$m^2$) and Gordon's Bay (96.8 fish/100 $m^2$), whereas intermediate densities (26-55 fish/100 $m^2$) were recorded at the remaining seven sites. In terms of numbers of species recorded, Gordon's Bay represented the richest site with 31 species present, while Swartklip was the poorest with only 12 species. Numbers of species recorded at Blake's Cove and Makouvlei were also high (>20), while the remaining sites were represented by 13-19 species each. Community parameters (Margalef's species richness, Shannon diversity, Pielou's evenness and Simpson's dominance) associated with the fish communities sampled at each of the sites are also listed in Table 1.2. Species richness was considerably greater at Gordon's Bay (3.3) than at any of the other sites. Makouvlei, Melkbaai and Blake's Cove displayed intermediate values (2.05-2.47), while the remaining sites received low scores (1.28-1.89). Species diversity was highest at Gordon's Bay (1.55) and Blake's Cove (1.42), lowest (0.25) at Mackerel Beach and intermediate (0.61-1.15) at the remaining sites. Evenness ranged from 0.10-0.45, with greatest values at Gordon's Bay and Blake's Cove (0.45 for both) while Mackerel Beach again registered the lowest value. Greatest dominance was recorded at

Mackerel Beach (0.89), while Macassar, Long Beach, Swartklip and Makouvlei also displayed high values (0.64-0.72). Lowest levels of dominance were recorded at Gordon's Bay (0.35) and Blake's Cove (0.37). Intermediate levels (0.41-0.45) were recorded at the remaining sites. Values of species richness, diversity, evenness and dominance for catches for all sites combined were 3.95, 1.17, 0.31 and 0.42, respectively.

Numbers of juvenile fish exceeded adults at all sites, except Mackerel Beach and Gordon's Bay, where they provided 6 and 38% of the totals respectively. Overall, numbers of juvenile fish exceeded that of adult fish, making up just over half (52.9%) of the total catch, with 23 (51%) of the species being represented by immature individuals only, 18 (40%) as both adults and juvenile and only four (9%) as adults only (Table 1.3). Teleost fish (40 species), comprising 98.7-100% of the catches, far outnumbering elasmobranchs (five species, 0-1.3 % of the catches) at all sites. The majority of the fish captured were small individuals (Table 1.3), only 1.4% of which exceeded 200 mm TL. No individuals captured during this survey were greater than 1 m in length. Length frequency distributions of the 10 most abundant species are illustrated in Figure 1.3.

Faunal similarities among sites were analysed using root-root transformed density data using Cluster analysis and Multidimensional Scaling (MDS). Cluster analysis separated the 11 sampling sites into two major groups which linked at the 62% level of similarity. The first group, composed of seven sites, was made up of Swartklip, Mackerel Beach, Macassar Beach, Muizenberg, Sunrise, Cemetery Beach, and Melkbaai. The remaining four sites, Blake's Cove, Makouvlei, Gordon's Bay and Long Beach, made up the second group. At higher levels of similarity (80-90%), two closely linked groups of samples and a number of outliers was evident (Fig. 1.4). Macassar Beach, Muizenberg, Sunrise, Cemetery Beach, and Melkbaai were linked together in a group, as were Blake's Cove, Makouvlei and Gordon's Bay, while Swartklip, Mackerel Beach and Long Beach remained unattached. Separation of the sampling sites in the ordination plot derived from the MDS analysis, corresponded almost exactly to the pattern generated by the Cluster analysis. Sites linking together between the 80 and 90% levels of similarity clustered together in the MDS plot, while the three outlying samples were placed at some distance from these groups, albeit on the same side of the plot as the groups to which they were linked in the cluster analysis.

Differences in species abundance patterns across the sampling sites were examined using Cluster analysis, MDS and by examining the contributions of the more abundant species to dissimilarities between groups of sites identified earlier (Fig. 1.4) using Simper analysis. A reasonably close match was evident between sample groupings in the dendrogram and ordination plot (Fig. 1.5) despite the high stress loading (0.14) on the latter. Four groups and two outlying samples were evident in these two diagrams. From Table 1.2, it is evident that species in Groups A and B (seven and five species respectively), were captured predominantly at sites 9-11 (Blake's Cove, Makouvlei and Gordon's Bay). Species in Group C (four species) were captured in varying numbers at all sites, while those in Group D (two species), recorded in low densities at a number of sites, were recorded in by far their greatest densities at Gordon's Bay, where >90% of these individuals were captured.

Table 1.4 shows the results of breaking dissimilarities between the sites in Group 1 (Fig. 1.4; Blake's Cove, Makouvlei, Gordon's Bay) and 2 (Muizenberg, Sunrise, Cemetery Beach, Macassar Beach and Melkbaai) into the individual components provided by the top ten species. Together these species accounted for >55% of the dissimilarity between these two groups of samples. Most (seven) of these species came from Groups A and B above, while both species from Group D and one from Group C were also present.

Table 1.2. Mean density (mean monthly no. indv./100m$^2$) and community parameters associated with ichthyofaunal assemblages sampled by beach-seining at the 11 sites in False Bay.

| | Long Beach | Mackerel Beach | Muizen-berg | Sunrise Beach | Cemetry Beach | Swart-klip | Macassar Beach | Harmony Beach | Blake's Cove | Makou-vlei | Gordon's Bay | All sites | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | Density | Tot. ind. |
| *Atherina breviceps* | 0.65 | 31.28 | 15.04 | 8.39 | 10.86 | 0.39 | 4.45 | 11.24 | 30.45 | 116.20 | 43.81 | 30.89 | 37 023 |
| *Liza richardsonii* | 44.12 | 7.15 | 24.42 | 17.01 | 14.12 | 4.66 | 23.16 | 17.79 | 63.40 | 66.23 | 17.41 | 20.42 | 24 474 |
| *Rhabdosargus globiceps* | 7.58 | 0.15 | 2.72 | 2.66 | 1.60 | 0.13 | 0.32 | 2.02 | 6.36 | 1.23 | 5.57 | 2.20 | 2 641 |
| *Diplodus sargus* | 0.39 | 0.12 | 0.41 | | 0.02 | 0.23 | | 0.01 | 2.28 | 2.26 | 2.66 | 0.58 | 696 |
| *Gilchristella aestuaria* | | | 0.13 | 0.33 | 0.15 | 0.14 | 0.03 | 0.10 | 0.73 | 0.26 | 14.27 | 0.56 | 674 |
| *Psammogobius knysnaensis* | 0.27 | | 0.01 | 0.01 | 0.01 | | | 0.04 | 2.18 | 2.87 | 2.65 | 0.50 | 600 |
| *Pomatomus saltatrix* | | 0.14 | 1.82 | 0.56 | 0.06 | 0.13 | 0.60 | 0.31 | 0.57 | 8.11 | 0.17 | 0.49 | 582 |
| *Sarpa salpa* | | | | | | 0.02 | | | 0.05 | 0.01 | 5.50 | 0.41 | 488 |
| *Amblyrhynchotes honkenii* | 0.06 | 0.04 | 0.14 | 0.02 | 0.06 | 0.02 | 0.11 | 0.04 | 0.85 | 0.51 | 0.54 | 0.18 | 220 |
| *Liza tricuspidens* | | | 0.01 | | | | 0.07 | | 1.25 | 0.20 | 0.26 | 0.11 | 137 |
| *Liza dumerilii* | | | 0.02 | | | | 0.01 | 0.01 | 0.98 | 0.42 | 0.03 | 0.08 | 97 |
| *Rhinobatos annulatus* | | | 0.62 | 0.03 | | | 0.03 | 0.02 | | 0.04 | 0.16 | 0.08 | 91 |
| *Umbrina canariensis* | 0.04 | 0.02 | 0.01 | | 0.01 | 0.34 | 0.08 | 0.23 | 0.18 | 0.02 | 0.08 | 0.08 | 93 |
| *Caffrogobius nudiceps* | 0.01 | | | | | | | 0.01 | 0.43 | 0.11 | 0.56 | 0.07 | 82 |
| *Mugil cephalus* | | | | 0.01 | | | 0.03 | 0.04 | 0.05 | 0.17 | 0.32 | 0.06 | 66 |
| *Clinus superciliosus* | 0.06 | 0.02 | | | | | | | 0.41 | 0.08 | 0.18 | 0.05 | 58 |
| *Lithognathus lithognathus* | | | 0.04 | 0.03 | 0.02 | 0.09 | 0.01 | 0.08 | 0.48 | 0.04 | 0.01 | 0.05 | 62 |
| *Lichia amia* | | | | | 0.01 | | | 0.13 | 0.17 | 0.03 | 0.15 | 0.04 | 45 |
| *Heteromycterus capensis* | 0.84 | 0.02 | | | | | | 0.01 | 1.35 | 0.16 | 1.85 | 0.03 | 320 |
| *Solea bleekeri* | | | 0.01 | | 0.01 | | | 0.01 | 0.38 | | 0.03 | 0.03 | 30 |
| *Chelidonichthyes capensis* | 0.14 | 0.01 | 0.02 | 0.01 | | | | 0.04 | 0.11 | | | 0.02 | 24 |
| *Dichistius capensis* | | | 0.01 | | | 0.18 | 0.01 | | | | | 0.01 | 15 |
| *Lithognathus mormyrus* | 0.18 | 0.01 | 0.01 | | | | | | | | | 0.01 | 15 |
| *Clinus latipennis* | | 0.05 | | 0.03 | 0.01 | 0.01 | | | | | 0.04 | 0.01 | 13 |
| *Cancelloxus longior* | 0.12 | | | | | | | | | | | 0.01 | 9 |
| *Rhabdosargus holubi* | | | | | | | | | | 0.01 | 0.08 | 0.01 | 8 |
| *Myliobatis aquila* | | | 0.02 | | | | | | 0.06 | | 0.02 | 0.01 | 7 |
| *Coryphaena hippurus* | | | | 0.03 | | | | | | | | <0.005 | 3 |
| *Dasyatis crysonota* | | | | | | | | | 0.03 | | 0.01 | <0.005 | 3 |
| *Syngnathus acus* | 0.01 | 0.02 | | | | | | | | | | <0.005 | 2 |
| *Caffrogobius caffer* | | | | | | | | | | | 0.05 | <0.005 | 4 |
| *Diplodus cervinus* | | | | | | | | | 0.02 | | | <0.005 | 2 |
| *Gonorhynchus gonorhynchus* | 0.01 | | | | | | | | | | | <0.005 | 1 |
| *Trachinocephalus myops* | 0.03 | | | | | | | | | | | <0.005 | 2 |
| *Dichistius multifasciatus* | 0.01 | | | | | | | | | | | <0.005 | 1 |
| *Trachurus trachurus* | | | | | 0.01 | | | | | | | <0.005 | 1 |
| *Trachinotus botla* | | | | | | | 0.01 | | | | | <0.005 | 1 |
| *Trachinotus africanus* | | | | | | | | 0.01 | | | | <0.005 | 1 |
| *Engraulis japonicus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Heniochus acuminatus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Monodactylus falciformes* | | | | | | | | | | 0.01 | | <0.005 | 1 |
| *Haploblepharus edwarsii* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Sphyraena acutipinnis* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Triakis megalopterus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| *Fucomimus mus* | | | | | | | | | | | 0.01 | <0.005 | 1 |
| Total density | 54.53 | 39.02 | 45.43 | 29.11 | 26.92 | 6.32 | 28.93 | 32.14 | 112.78 | 198.97 | 96.48 | 57.25 | |
| No. individuals | 4 828 | 11 765 | 5 109 | 3 073 | 2 775 | 742 | 3 126 | 3 903 | 7 255 | 17 436 | 8 903 | 68 610 | |
| Total no. species | 17 | 13 | 18 | 13 | 14 | 12 | 14 | 19 | 23 | 21 | 31 | 45 | |
| Richness | 1.89 | 1.28 | 1.99 | 1.49 | 1.64 | 1.66 | 1.62 | 2.18 | 2.47 | 2.05 | 3.30 | 3.95 | |
| Diversity | 0.64 | 0.25 | 1.15 | 1.08 | 0.95 | 0.81 | 0.61 | 1.02 | 1.42 | 0.73 | 1.55 | 1.17 | |
| Evenness | 0.22 | 0.10 | 0.40 | 0.42 | 0.36 | 0.33 | 0.23 | 0.35 | 0.45 | 0.24 | 0.45 | 0.31 | |
| Dominance | 0.71 | 0.89 | 0.41 | 0.42 | 0.45 | 0.69 | 0.72 | 0.45 | 0.37 | 0,64 | 0.35 | 0.42 | |
| Mean netting area (m$^2$) | 186 | 254 | 656 | 624 | 453 | 343 | 463 | 746 | 347 | 362 | 618 | 454 | |
| Total netting area (m$^2$) | 4 575 | 5 850 | 15 750 | 14 975 | 9 975 | 8 225 | 11 100 | 17 900 | 8 325 | 8 335 | 14 825 | 119 835 | |

**Table 1.3** Numbers of individuals, length ranges (TL) and sizes at maturity of fish captured in beach-seine hauls made at the 11 sites in False Bay.

| | | N | Size Range | Size at Maturity | % Immature |
|---|---|---|---|---|---|
| OSTEICHTHYES | | | | | |
| Atherinidae | *Atherina breviceps* | 37 023 | 16-129 | 43[a] | 14.1 |
| Carangidae | *Lichia amia* | 45 | 46-380 | 600[b] | 100.0 |
| | *Trachinotus africanus* | 1 | 98 | | 100.0 |
| | *Trachinotus botla* | 1 | 56 | | 100.0 |
| | *Trachurus trachurus* | 1 | 67 | 200[c] | 100.0 |
| | Unidentified | 8 | 22-37 | | |
| Chaetodontidae | *Heniochus acuminatus* | 1 | 42 | | 100.0 |
| Clinidae | *Cancelloxus longior* | 9 | 71-125 | | 0.0 |
| | *Clinus lattipennis* | 13 | 40-131 | 45[d] | 23.1 |
| | *Clinus superciliosus* | 58 | 38-151 | 65[e] | 13.8 |
| | *Fucomimus mus* | 1 | 95 | | |
| Clupeidae | *Gilchristella aestuaria* | 674 | 30-86 | 34[a] | 0.7 |
| Coryphaenidae | *Coryphaena hippurus* | 3 | 43-47 | | |
| Dichistiidae | *Dichistius capensis* | 15 | 33-175 | 310[f] | 100.0 |
| | *Dichistius multifasciatis* | 1 | 30 | 210[b] | 100.0 |
| Engraulidae | *Engraulis japonicus* | 1 | 95 | 90[g] | 0.0 |
| Gobiidae | *Caffrogobius caffer* | 4 | 56-93 | 55[e] | 0.0 |
| | *Caffrogobius nudiceps* | 82 | 28-108 | 65[h] | 28.7 |
| | *Psammogobius knysnaensis* | 600 | 22-71 | 37[a] | 12.7 |
| Gonorynchidae | *Gonorhynchus gonorhynchus* | 1 | 181 | | 0.0 |
| Monodactylidae | *Monodactylis falciformis* | 1 | 40 | 170[k] | 100.0 |
| Mugilidae | *Liza dumerilii* | 97 | 53-181 | 200[i] | 100.0 |
| | *Liza richardsonii* | 24 474 | 20-402 | 230[j] | 97.9 |
| | *Liza tricuspidens* | 137 | 78-290 | 400[i] | 100.0 |
| | *Mugil cephalus* | 66 | 100-420 | 450[e] | 100.0 |
| Pomatomidae | *Pomatomus saltatrix* | 582 | 73-256 | 240[l] | 99.8 |
| Sciaenidae | *Umbrina canariensis* | 93 | 27-635 | 300[d] | 75.5 |
| Soleidae | *Heteromycteris capensis* | 320 | 33-121 | 45[m] | 48.5 |
| | *Solea bleekeri* | 30 | 39-190 | 100[i] | 62.5 |
| Sparidae | *Dilpodus cervinus hottentotus* | 2 | 52-76 | 334[n] | 100.0 |
| | *Diplodus sargus capensis* | 696 | 22-220 | 180[r] | 99.7 |
| | *Lithognathus lithognathus* | 62 | 74-810 | 650[o] | 98.3 |
| | *Lithognathus mormyrus* | 15 | 42-131 | 190[p] | 100.0 |
| | *Rhabdosargus globiceps* | 2 641 | 16-172 | 260[q] | 100.0 |
| | *Rhabdosargus holubi* | 8 | 42-218 | 180[e] | 75.0 |
| | *Sarpa salpa* | 488 | 42-142 | 180[r] | 100.0 |
| Sphyraenidae | *Sphyraena acutipinnis* | 1 | 64 | | 100.0 |
| Syngnathidae | *Syngnathus acus* | 2 | 92-178 | 125[a] | 50.0 |
| Synodontidae | *Trachinocephalus myops* | 2 | 55-80 | | 100.0 |
| Tetraodontidae | *Amblyrhynchotes honkenii* | 220 | 18-178 | 80[e] | 87.9 |
| Triglidae | *Chelidonichthyes capensis* | 24 | 29-85 | 305[s] | 100.0 |
| Unidentified | | 4 | 22-37 | | |
| CHONDRICHTHYES | | | | | |
| Carcharhinidae | *Triakis megalopterus* | 1 | 440 | 1400[t] | 100.0 |
| Dasyatidae | *Dasyatis crysonota* | 3 | 225-385 | 500[u] | 100.0 |
| Myliobatidae | *Myliobatis aquila* | 7 | 290-780 | 540[v] | 71.4 |
| Rhinobatidae | *Rhinobatos annulatus* | 91 | 223-910 | 700[w] | 71.1 |
| Scyliorhinidae | *Haploblepharus edwardsii* | 1 | 240 | 410[t] | 100.0 |
| Total | | 68 610 | | | 52.9 |

a. Bennett (1989b) b. Van der Elst (1988) c. Geldenhuys (1973) d. Lamberth *et al.* 1994 e. Day *et al.* (1981) f. Bennett & Griffiths (1986) g. Armstrong & Thomas (1989) h. Whitfield (1990)[1] i. Wallace (1975) j. De Villiers (1987)[2] k. Beckley (1984a) l. Van der Elst (1976) m. Clark *et al.* 1994a n. Mann (1992)[2] o. Bennett (1993) p. Lasiak (1982)[1] q. Talbot (1955) r. Joubert (1981a)[2] s.Hecht (1977) t. Compagno (1984a) u. Cowley (1990) v. Wallace (1967a) w. Wallace (1967b)

1. Corrected from SL to TL
2. Corrected from FL to TL

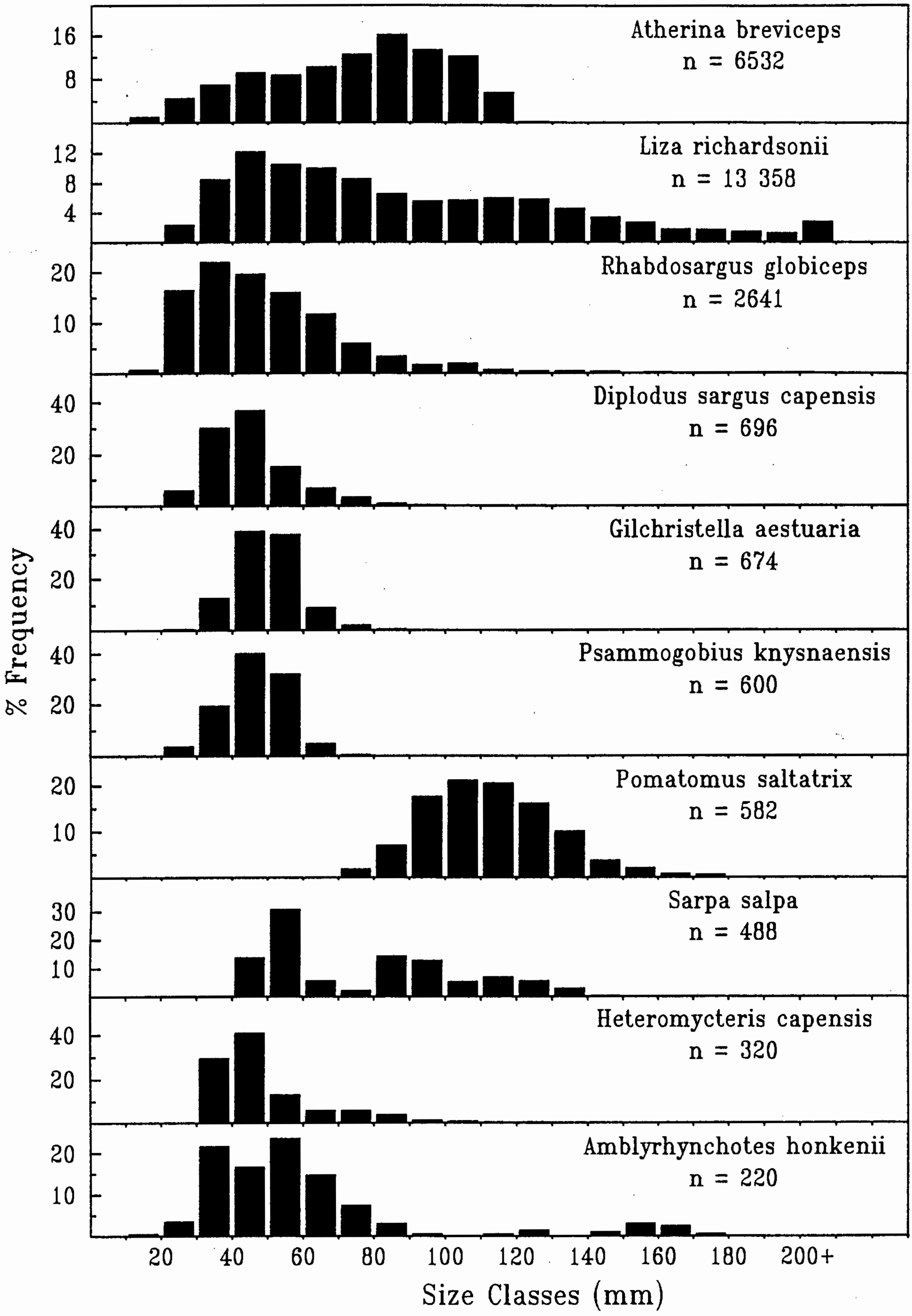


**Fig. 1.3.** Size frequency distributions of the ten most abundant fish species captured in beach-seine hauls from the False Bay surf-zone.

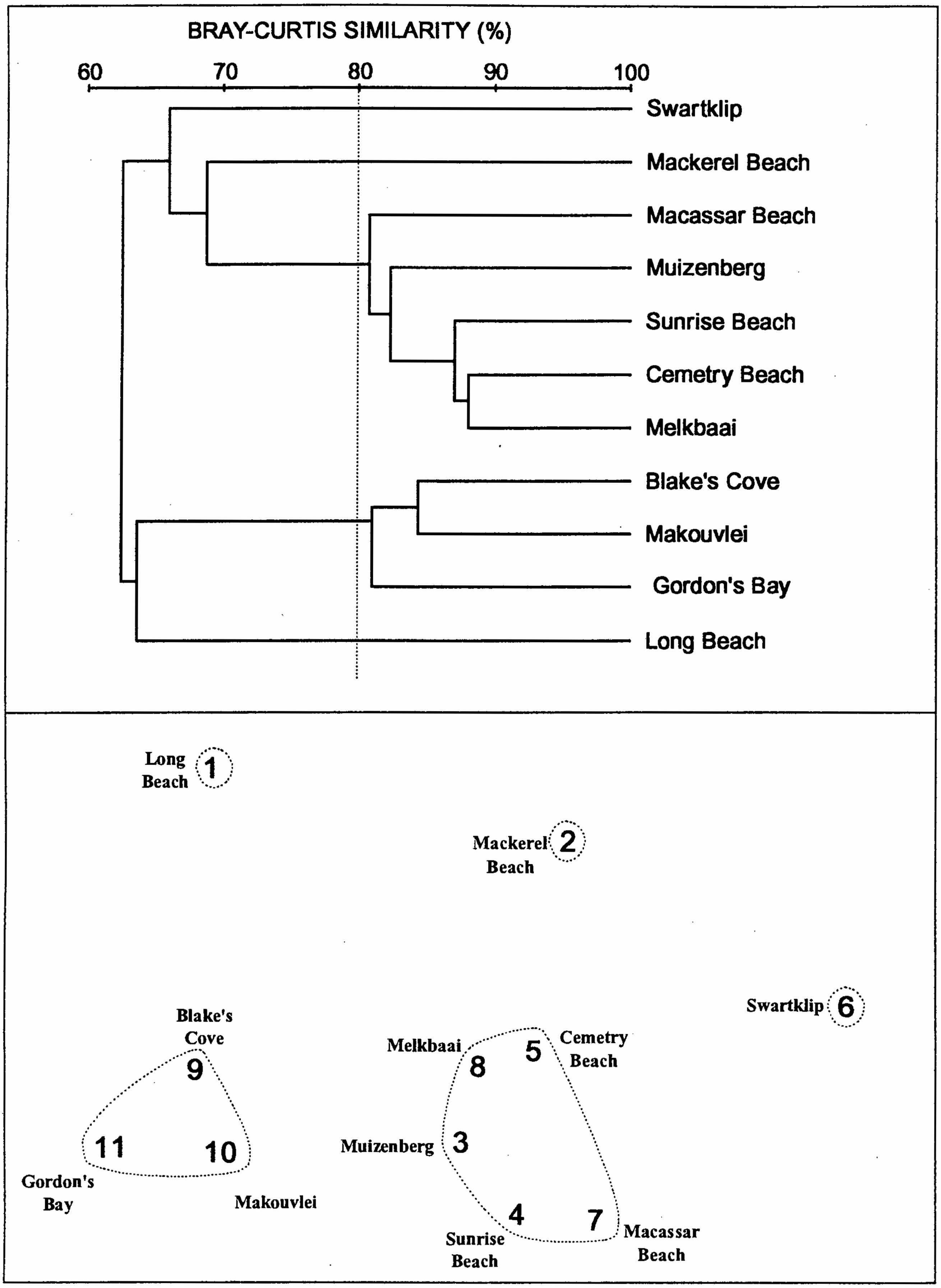


**Fig. 1.4.** Dendrogram and MDS ordination showing similarities between sites based on the composition and abundance of fish species in seine net hauls made in the surf-zone of False Bay. Groups of species delineated at the 80% level in the dendrogram are circled in the ordination plot. Stress for MDS plot = 0.07.

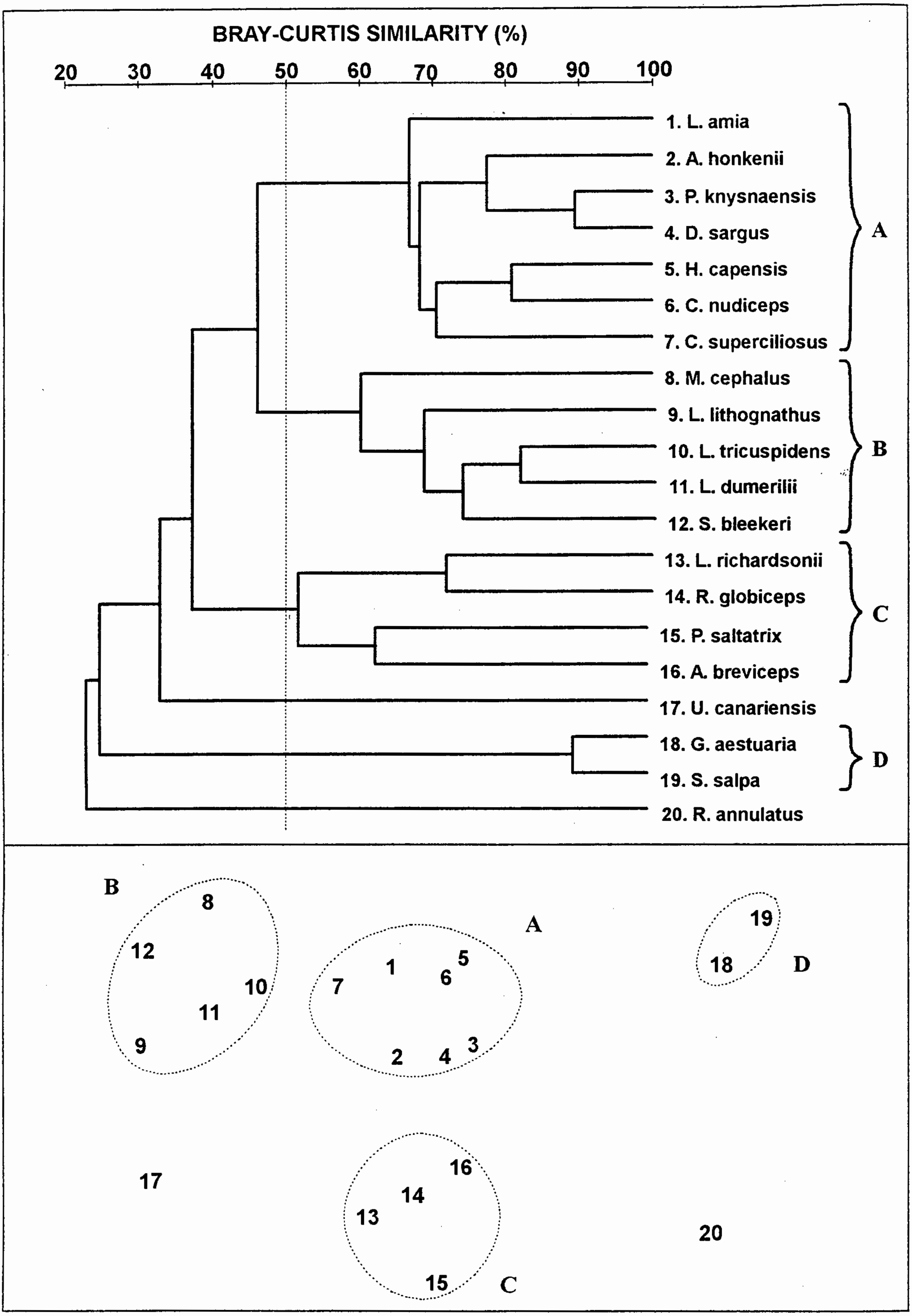


Fig. 1.5. Dendrogram and MDS ordination showing similarities between species based on their occurrence at 11 localities in the False Bay surf-zone. Groups of species delineated at the 50% level in the dendrogram are circled in the ordination plot. Stress for MDS plot = 0.13. Full genus names are given in Table 1.2.

**Table 1.4.** Breakdown of average dissimilarity between site 9-11 and sites 3-5 + 7-8 into contributions of the 10 top species, listed in order of decreasing contribution. $\delta i$ is the average contribution of the *i*th species to the dissimilarity between the two groups, $\delta i/\mathrm{SD}(\delta_i)$ the ratio between average contribution of the ith species ($\delta_i$) and the standard deviation of the $\delta$values for that species ($\mathrm{SD}\delta_i$) and Cum $\delta_i$% the cumulative contribution to the total dissimilarity, rescaled as a percentage. Also included is the average density of each of these species at the two groups of sites

| | | | | | Mean density | |
|---|---|---|---|---|---|---|
| SPECIES | $\delta i$ | $\delta i/\mathrm{SD}(\delta i)$ | $\delta i$% | Cum $\delta i$% | 9-11 | 3-5, 7-8 |
| *Atherina breviceps* | 3.09 | 1.88 | 7.21 | 7.21 | 0.63 | 0.10 |
| *Psammogobius knysnaensis* | 3.05 | 4.87 | 7.12 | 14.32 | 0.03 | 0.00 |
| *Diplodus sargus* | 2.95 | 2.87 | 6.89 | 21.21 | 0.02 | <0.005 |
| *Heteromycterus capensis* | 2.72 | 3.73 | 6.35 | 27.56 | 0.01 | <0.005 |
| *Sarpa salpa* | 2.30 | 1.53 | 5.36 | 32.92 | 0.02 | 0.00 |
| *Caffrogobius nudiceps* | 2.09 | 4.07 | 4.88 | 37.81 | 0.01 | 0.00 |
| *Clinus superciliosus* | 2.02 | 6.38 | 4.71 | 42.52 | 0.01 | 0.00 |
| *Liza tricuspidens* | 1.99 | 2.26 | 4.64 | 47.15 | 0.01 | <0.005 |
| *Gilchristella aestuaria* | 1.76 | 1.13 | 4.11 | 51.27 | 0.05 | <0.005 |
| *Liza dumerilii* | 1.73 | 1.76 | 4.03 | 55.29 | 0.01 | <0.005 |

### 1.4.3 Multivariate analyses of relations between biotic and environmental variables

A total of eight physical environmental variables: mean wave height, mean width of the surf-zone, amount of rock in the netting area (rock), water temperature, intertidal slope, median particle size, detached macrophyte abundance and turbidity, were used for multivariate analyses. These data were employed in two different ways. In the first instance, values for all eight variables (as detailed in Table 1.1), were entered directly into the multivariate models. The models were then rerun, but all variables pertaining to the relative exposure of the sites (wave height, surf-zone width, intertidal slope, and median particle size) were replaced with "exposure scores" generated using McLachlan's (1980) rating scheme, as detailed in the previous section (Table 1.1).

Results from the Bioenv procedure yielded rank correlation coefficients ($P_w$) of 0.63 and 0.52 for the full and reduced sets of environmental variables respectively. Wave height, rock and turbidity were selected as the combination of variables best able to predict spatial variations in community structure in the first instance, and the variables exposure, rock and turbidity in the second. Stepwise multiple regression analyses performed using the two sets of environmental variables, selected rock and wave height for the former and rock and exposure for the latter, as the best predictors of spatial variations in surf-zone fish density. Coefficients of determination ($r^2_{adj.}$) generated by these two models were 68.4 and 62.7% respectively.

When plots of all environmental variables, scaled according to their magnitude, were overlain on the biotic ordination of the 11 sites (Fig 1.6a), it was immediately clear why the variables incorporated in the final Bioenv models, were in fact selected (Fig 1.6b-j). The variable wave height and exposure separated not only the two groups of closely linked sites formed by the MDS analysis, but also split all sites clearly into two groups corresponding to those formed in the higher levels of the cluster diagram (Fig 1.4). Amount of rock on the shore (Fig. 1.6d) and turbidity (Fig. 1.6e) differentiated clearly between the two groups of samples formed by the MDS analysis, but not between the three outlying samples. Although it was not selected by any of the multivariate models, macrophyte abundance (Fig. 1.6f) split the samples in a similar way to wave height and exposure. Little concordance was evident between the scaling of the remaining environmental variables (surf-zone width, intertidal slope, median particle size and water temperature; Fig. 1.6g-j) and biotic similarities evident between sites (Fig. 1.6a).

## 1.5 DISCUSSION

Marked differences were evident between the fish assemblages recorded at the 11 sites studied during this survey. Mean density of fish, for example, varied by a factor of >30 between sites, while the number of species recorded at some sites was more than double that at others. Although factors such as water clarity, nature of the substratum, temperature, wave exposure and macrophyte abundance are all thought to influence the capture efficiency of beach seine nets (Hunter & Wisby 1964, Lyons 1986, Romer 1990, Pierce *et al.* 1990, Lamberth *et al.* 1995b), I believe that in the case of this study, these influences were probably minimal. Capture efficiency may have been reduced under conditions of heavy surf or low turbidity, when the net was lifted over rocky obstacles, or when large quantities of macrophytes were netted, but extra care was taken during these periods, so as to ensure that this did not happen. Problems of this nature were also minimised by adjusting the hauling area accordingly or aborting the haul if it was considered to be inefficient. Despite clear seasonal variability evident in the overall data set used for this part of the study (see Clark et al. 1996b, Chapter 3), averaging of monthly data over a two year period and using fourth root transformed density data for multivariate analyses are also likely to have increased the robustness of the data set and will, to a certain extent, have mitigated the absence of replicate samples at each site in each month. Thus, differences in the physical make-up or physical characteristics of these sites must, to a large extent, be responsible for these differences, as these sites are all located in close proximity to one another (less than 40 km apart) within False Bay.

Study sites were made up of varying combinations of physical characteristics, however, with few gradients extending uniformly across more than one or two sites, which makes it very difficult to determine which are the most important contributory factors. The influences of a selection of these variables will therefore first be discussed individually before attempting to draw general conclusions.

### 1.5.1 Exposure

Wave action, thought by many authors to be synonymous with exposure, is considered to be one of the major factors controlling physical and chemical characteristics of the surf-zone environment (Eltringham 1971, Eleftheriou & Nicholson 1975, McLachlan 1980). This variable exerts a considerable influence on the composition, community structure and zonation of benthic invertebrate assemblages (McLachlan *et al.* 1984, Morin *et al.* 1985, Dexter 1990). Blaber & Blaber (1980) found that juveniles of certain fish species inhabiting inshore waters of the Indo-Pacific occurred only in calm, non-turbulent areas, while this variable appeared to have no influence on the other species. Romer (1990) compared surf-zone fish assemblages at three localities spanning an exposure gradient in Algoa Bay, South Africa, and found that as exposure increased, fish abundance (catch rate) and diversity declined, while the degree of dominance increased.

The influence of exposure on the fish communities sampled during this study was examined using both the mean wave height at all sites and the rating system developed by McLachlan (1980), which incorporates variables such as wave height, surf-zone width, intertidal slope and median particle size. Mean wave height and exposure were greatest at sites situated along the northern shore, directly opposite the mouth of the Bay. According to Mclachlan's (1980) rating system, these sites were considered to be exposed to very exposed. Mean wave height tailed off rapidly on approaching the northeastern corner of the Bay, where all sites were rated as sheltered, but less rapidly along the western shore, due to the presence of more steeply shelving bottoms which did little to dissipate incoming waves. Abundance of fish in the surf, and community parameters showed a strong positive response to gradients in both parameters. However, these were only general trends, and the greatest density of fish was not recorded at the most sheltered sites, nor was the lowest density recorded at the most exposed site. Similarly, peaks in the numbers of species recorded, species richness, diversity and evenness did not coincide with the sites with lowest wave action or exposure, despite showing a general decline with increasing exposure. In contrast to Romer's (1990) findings, the degree of dominance recorded for the fish communities at the various sites did not increase with increasing exposure. High and low levels of dominance were recorded at both sheltered and exposed sites. When either mean wave height or exposure were entered into multivariate analyses examining the influence of all physical variables on spatial variations in community structure and fish density in the surf, these variables were both included in the final sets of variables best able to predict biotic variability. Models incorporating mean wave height had coefficients of determination that were marginally higher than those incorporating exposure in both cases. A high degree of concordance was evident between the scaling of these two variables and the biotic ordination plots upon which they were overlain (Fig. 1.6).

### 1.5.2 Rock

Despite their prevalence, shores composed of mixed rock and sand have been extremely poorly studied. Only three publications (Bally *et al.* 1984, McQuaid & Dower 1990, Brown *et al.* 1991) deal specifically with invertebrate communities inhabiting these areas in southern Africa, and studies of such communities in other areas are equally sparse (e.g. Taylor & Littler 1982, Littler *et al.* 1983). Some authors have recorded the presence of reef fishes in surf-zone habitats (e.g Anderson *et al.* 1977, Futch & Dwinell 1977), whereas others have suggested that the proximity of rocky reefs may influence the composition of assemblages under study (e.g. Romer 1990, Gibson *et al.* 1993). Hillman *et al.* (1977) sampled fish assemblages at six surf-zone localities in Long Island Sound with substrata composed of varying amounts of emergent rock, but provided little discussion on the differences between these assemblages. Differences observed between the numbers of individuals and fish species collected from surf-zone habitats immediately adjacent to rock jetties and those further (>1 km) away, led Peters and Nelson (1987) to conclude that the additional habitat diversity provided by these structures significantly enhances the species richness of fish assemblages inhabiting surf-zone environments.

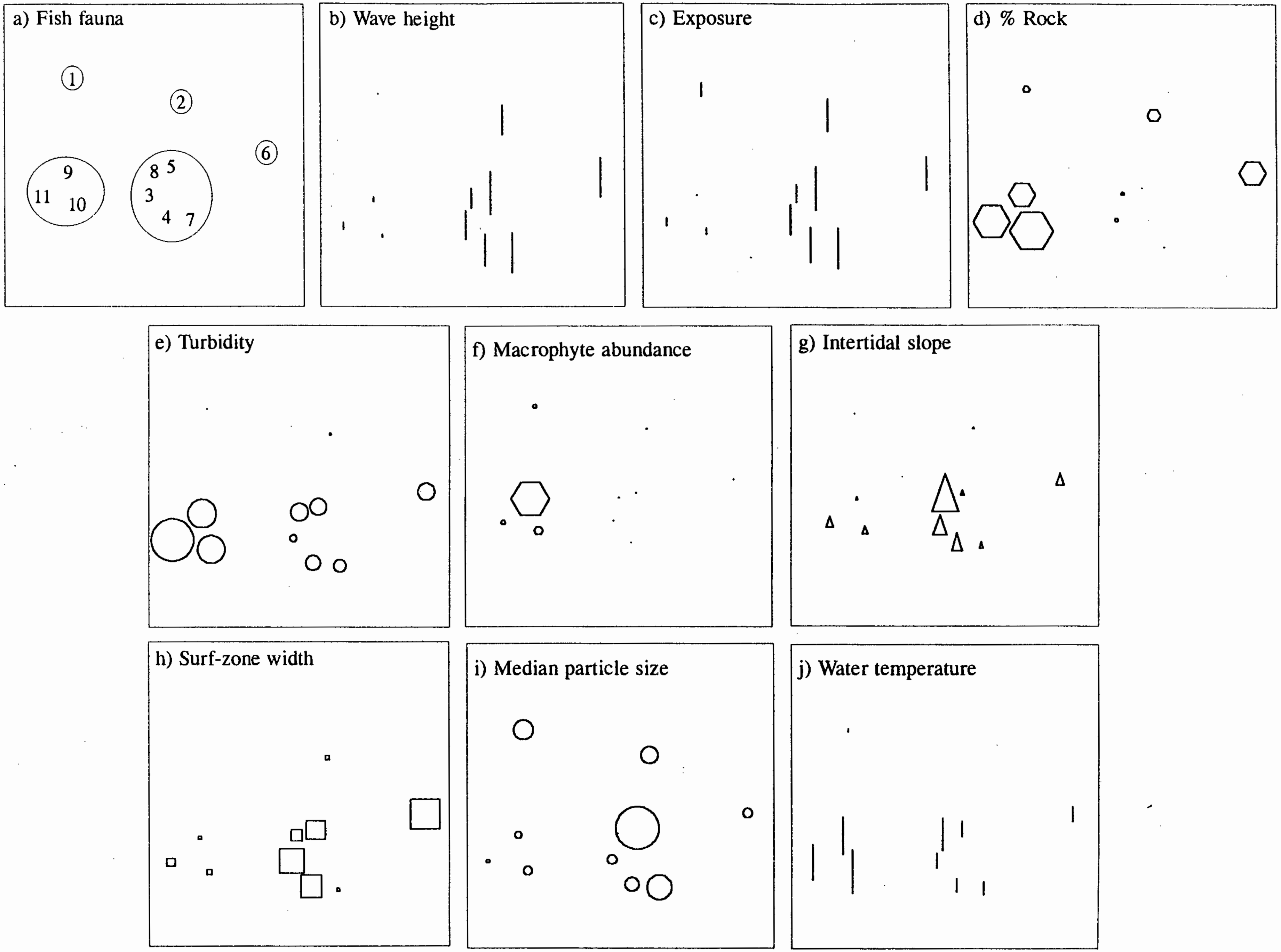


**Fig. 1.6.** Relation of site similarities based on ichthyofaunal composition (a) to a variety of environmental variables. Objects representing the environmental variables in each case were scaled according to their relative magnitudes and superimposed on the biotic plot (b-j).

The proportion of the substrata at the 11 sampling sites composed of emergent rock ranged between zero (three sites) and 69%. However, few unequivocal patterns in abundance or structure between the various fish assemblages were evident. Fish abundance and numbers of species were greatest at the three sites containing the largest proportion of rock (>50%), but little structure could be distinguished in these variables at the remaining sites, except that those sites containing no rock had intermediate to low fish densities. Considerable differences were, however, evident when comparisons were drawn between the biota at comparable sites, situated in close proximity, but with (e.g. Muizenberg) or without (Sunrise) rocky substrata. Fish abundance, number of species, species richness and diversity were all higher at Muizenberg, which lies immediately adjacent to a rocky coastline, than at Sunrise, which is bound on either side by extensive sandy beaches. Multivariate models employed to select the combination of variables best able to predict spatial variations in fish density and community structure, all contained the variable rock. When this variable was overlain on the biotic ordination (Fig. 1.6), variations in amount of rock clearly distinguished between the two groups of sites formed by the MDS analysis.

### 1.5.3 Turbidity

Much attention has been focused on the influence of turbidity on the distribution patterns of fish in inshore waters, chiefly estuarine systems in southern Africa (Cyrus 1983, Cyrus & Blaber 1982, Blaber & Cyrus 1983, Bruton 1985, Cyrus & Blaber 1987a, b, c, Cyrus & Blaber 1992) and Australia (Blaber & Blaber 1980, Blaber *et al.* 1985, Weng 1990). It is thought to be the single most important factor influencing estuarine fish distribution patterns, as it provides cover for juveniles through a reduction in light intensity, which obscures prey species from visually orientating predators such as piscivorous fish and birds (Blaber & Blaber 1980, Blaber 1981, Cyrus 1983, Cyrus & Blaber 1987a, b). Some authors have suggested that higher invertebrate densities found in turbid areas may also attract some species to turbid waters, while others believe that turbidity may act as an important environmental cue, guiding fish into estuarine habitats (Blaber & Blaber 1980, Cyrus 1983). Fewer studies concerning the influence of turbidity on fish abundance have been undertaken in the marine environment and the influence of turbidity on distribution patterns in the marine environment is less well known.

Blaber *et al.* (1985) attributed low numbers of fish recorded in mangrove and open shore habitats in Western Australia to low turbidities in this area, and Ross *et al.* (1987) found that fish abundance in a surf-zone habitat in the Gulf of Mexico was lowest during periods of clear water that occurred in conjunction with diminished wave activity. From data collected during their study of sheltered inshore marine environments in eastern Australia, Blaber & Blaber (1980) concluded that although the presence of shallow water was the only common denominator sought by juveniles of most fish species, turbidity was probably the single most important factor influencing the distribution of species within these shallow water habitats. Although all turbidities recorded during this study fell within the clear to partially turbid category (<50 NTU) of Cyrus & Blaber (1987a), this variable did appear to exert a strong influence on fish distribution patterns in False Bay.

Based on water clarity, the section of False Bay studied during this survey can be divided into three regions. Turbidities were generally low on the western side of the Bay, intermediate at sites across the northern shore and high in the northeastern corner. Discolouration of nearshore waters in the northern part of False Bay appear as milky green colour fronts to the naked eye and zones of high radiance on satellite images (Shannon *et al.* 1991). These authors found that this discolouration extends right through the water column, and divided these phenomena into four spatial categories: those prevalent in the northeastern and northwestern corners of the Bay, a narrower zone, and a tongue-like off-shore extension prevalent along the northern shore of the Bay. They found that discolouration was most prevalent in the northeastern corner of the Bay (40% of all occasions), and attributed it to a combination of high primary production from localised upwelling and nutrient cycling within a semi-permanent eddy in this sector of the Bay and the recirculation of suspended material within this eddy. They attributed the remaining three features to a process whereby winds circulate organically rich material lifted by wave action in the middle of the Bay in a westerly direction along the northern shoreline. Silt-laden freshwater discharged from four perennial estuaries emptying into the northeastern corner of the Bay probably also contributes to the high turbidities found there, while the diminished wave action, lack of estuarine input and close proximity of deep water on the western shore result in clearer waters at the two sites in this area. Once again, few general patterns are evident in the spatial distribution of fish sampled during this survey with respect to this variable. Abundance and numbers of species captured were greatest at sites in the northeastern corner of the Bay, where turbidities were highest (>8 FTU). Highest values for species richness, diversity and turbidity all coincided at Gordon's Bay, while dominance was greatest at sites where turbidity was lowest (Long Beach and Mackerel Beach), indicating that most species avoid very clear waters, as other authors (e.g. Blaber *et al.* 1985, Ross *et al.* 1987) have noted. Results of the multivariate analyses suggested that turbidity is a good predictor of spatial variations in surf-zone fish community structure as a whole, but not of abundance alone. When overlain on the biotic MDS plot of the 11 sites, it was clear that this variable played an important role in discriminating between the two major groups of sites (Fig. 1.6a, e), but not the three outlying sites.

### 1.5.4 Detached macrophyte abundance

After becoming detached from rocky substrata under the influence of storms or heavy wave action, macrophytes accumulate in the surf-zones of sandy beaches in many parts of the world (Zobell 1971, Cowper 1978, Robertson & Lenanton 1984, Hull 1987, van der Merwe and McLachlan 1987, Wright 1989b). These accumulations are thought to contribute to the quality of the surf-zone habitat for colonization by juvenile fishes through the protection they provide from piscivorous birds and fish and by the provision of additional food sources, both directly and indirectly through the detritus food chain (Lenanton *et al.* 1982, Robertson & Lenanton 1984, Lenanton & Caputi 1989, Wright 1989b). In some areas, as much as 25% of the total coastal primary production is thought to pass through the surf-zone of sandy beaches in the form of detached macrophyte detritus (Robertson & Hansen 1982).

Volumes of aquatic macrophytes recorded at most of the sampling localities in this study were negligible ($x < 0.1$ l/m$^2$), except for the four most sheltered sites (Long Beach, Gordon's Bay, Makouvlei and Blake's Cove), where average values of up to 0.7 l/m$^2$ were recorded. Maximum values recorded at these sites (0.8-8.0 l/m$^2$) correspond closely with those calculated by Robertson & Lenanton (1984) (9.58 l/m$^2$) and Lenanton and Caputi (1989) (1.73 l/m$^2$), both of which noted a positive correlation between algal volumes and numbers of fish captured. Indeed, Robertson & Lenanton (1984) found that fish abundance may be up to ten times greater in weed patches than in areas of open sand. It is surprising therefore that, despite large differences between macrophyte abundance at sites on the left and right hand sides of the biotic ordination plot (Fig. 1.6a, h), this variable did not contribute significantly to spatial variations in fish abundance or community structure. However, this variable was significantly negatively correlated with both mean wave height and exposure, thus the addition of macrophyte abundance to any of the multivariate models generated during this analysis would not have improved the fit of the models. The high degree of co-linearity that exists between macrophyte abundance, exposure and wave height results in the model selecting that variable with the highest partial correlation coefficient only (in this case wave height). Wright (1989b) found no correlation between algal volumes and fish abundance off sandy beaches in Sulaibikhat Bay, Kuwait, but maximum volumes of weed in this area were very much lower than those recorded here, and did not exceed 0.03 $l/m^2$.

### 1.5.5 Other variables

Studies on 0-group flatfish distribution patterns on European beaches have shown that fish densities are usually greatest in areas where fine to intermediately sized sands predominate and least in exposed areas where sediments are coarser (Riley & Holford 1965, Poxton & Nasir 1985, Dorel *et al.* 1991, Pihl & van der Veer 1992). This is believed to be related to the inability of the smaller fish to bury themselves in coarse sediments and hence take advantage of reduced drag forces induced by bottom currents, lower predation levels and potentially reduced metabolic rates (Riley & Holford 1965, Berghahn 1986, Gibson & Robb 1992, Pihl & van der Veer 1992, Ansell & Gibson 1993). Differences in sediment composition have also been shown to influence the distribution patterns of gobiid fish, also as a result of predator related mortalities (Evans & Tallmark 1984, 1985, Tallmark & Evans 1986). Variations in median particle size are closely linked to exposure and intertidal slope, as median particle size increases with exposure, whereas intertidal slope usually increases with increasing particle size while decreasing with increasing exposure (Davies 1972, Eleftheriou & Nicholson 1975, McLachlan 1980). Thus, although variations in particle size may influence fish distribution patterns significantly on sheltered beaches in Europe, their effects are probably limited to benthic dwelling or feeding species on the very much more exposed beaches in South Africa, as their influence is probably overshadowed for the most part by exposure itself.

Likewise, I thought that surf-zone width was unlikely to play a large role in structuring surf-zone fish assemblages, apart from influencing the amount of available cover provided by turbulence and foam generated by breaking waves. Variations in mean water temperature, on the other hand, is known to exert a strong influence on seasonal variations in surf-zone fish abundance (Gunter 1958, McFarland 1963, Anderson *et al.* 1977), and may have influenced the structure of surf-zone fish populations in this study. Although the variations in mean water temperatures were not great (<2 °C), higher temperatures prevalent at the sites in the northeastern corner of the Bay probably contributed to the greater abundance of fish in this area.

While salinity was not monitored during this survey, this may also have exerted some influence on fish distribution patterns within the surf-zone of False Bay. Salinity is considered to be one of the most important variables controlling fish distribution patterns in estuaries, as the ability to cope with fluctuations in this variable is the most essential adaptation by fish penetrating these environments (Pannikkar 1960, Whitfield *et al.* 1981). Indeed, fishes frequenting estuaries around the world are generally classified on the basis of their origin and salinity tolerances (e.g. Gunter 1945, McHugh 1967, Wallace *et al.* 1984, Claridge *et al.* 1986). Atkins (1970) noted that lowered salinities (<34 ppt) are sometimes prevalent in the northeastern corner of False Bay due to river discharge, particularly during winter. Brief observations made during this survey indicate that lowered salinities occur at the sampling sites in this area considerably more frequently than Atkins suggests, usually in conjunction with highly turbid waters. On one occasion (23/6/92) a number of live amphibian tadpoles were captured in a haul made at Gordon's Bay together with a good catch of fish. Turbidity on this occasion was 46 FTU, the highest recorded. When present, water with lowered salinity is likely to be particularly attractive to estuarine opportunistic and/or dependent species, as the energetic costs of osmoregulation are reduced in salinities below that of sea-water (Potter *et al.* 1990).

It is apparent from the foregoing discussion that many factors influence spatial variations in surf-zone fish community structure in False Bay. Although the three variables selected most frequently by multivariate analyses (exposure, presence of rock on the shore and turbidity) are probably primarily responsible for the variability observed, no factor acts in isolation and variations in some of the other physical variables (e.g. abundance of detached macrophytes, salinity and temperature) almost certainly also play a role. Some variables also interact in a complex manner. For example, the amount of rock may have a positive influence on fish abundance at sheltered or moderately exposed sites (e.g. Makouvlei or Gordon's Bay vs Long Beach and Muizenberg vs Sunrise), but not at more exposed sites (e.g. Swartklip vs Macassar Beach). By examining variations in the abundance of some of the more common species over different combinations of these abiotic variables it is also possible to identify groups of species based on habitat associations. For example, by comparing assemblages across shelter-exposure and sand-rock gradients, three groups of species can be identified. Four species (*Liza richardsonii*, *Atherina breviceps*, *Rhabdosargus globiceps* and *Pomatomus saltatrix*) were present in varying numbers under all combinations of these variables. *Psammogobius knysnaensis* and *Heteromycteris capensis* appear to be indifferent to the presence of rock on the shore, but seem to prefer sheltered areas, whereas *Sarpa salpa*, found only in association with rocky substrata, appears to be indifferent to variations in exposure. Juvenile galjoen (*Dichistius capensis*), although recorded in small numbers, were found exclusively at exposed sites composed of mixed rock and sand. Despite being one of southern Africa's premier angling species (Penrith & Loutit 1982, Bennett 1988), only three juveniles of the size range recorded during this survey (33-175 mm, Table 1.3) have previously been recorded in the marine environment (van der Lingen 1994), probably as such habitats have never been properly sampled.

Finally, it is instructive to examine the way in which the more common species were grouped based on their occurrence at the various sampling localities, using multivariate analyses (Fig. 1.5). One group (Group C) contained seemingly ubiquitous species identified earlier as being indifferent to variations in exposure and the amount of rock on the shore. Another group (Group B) contained species found almost exclusively at sites in the northeastern corner of the Bay only. These species have all been classified as entirely or largely dependent on estuaries as juveniles (Wallace *et al.* 1984), and therefore may have been attracted to the low salinities and high turbidities prevalent in this area. A third group (Group A), composed of seven species, were found predominantly at sheltered sites, and form a "calm water group". Thus species in Group C can be seen as a "core" group present at all sites, to which a variety of other species are added, depending on the particular suite of environmental conditions prevailing.

## 1.6 CONCLUSIONS

Results of this study indicate that three factors, namely; the degree of wave exposure, the presence of emergent rock on the shore and turbidity are the most important factors controlling spatial variations in surf-zone fish abundance and community structure in False Bay. Certain other variables, e.g. abundance of detached macrophytes, salinity and temperature also play a role, but are probably of secondary importance. Species-specific preferences for varying combinations of these variables result in variations in the structure and overall abundance of fish assemblages in different areas. This study clearly demonstrates the value of simultaneously studying the influence of a whole suite of environmental variables on fish community structure, as it allows the relative importance of a variety of these factors to be assessed relative to one another. Subsequently isolating and analyzing changes in surf-zone fish abundance and community structure over gradients of a single variable, allows the influence of the more important factors identified in this study to be explored in more detail.

# CHAPTER 2

# 2 VARIATION IN SURF-ZONE FISH COMMUNITY STRUCTURE ACROSS A WAVE-EXPOSURE GRADIENT

## 2.1 INTRODUCTION

The degree of wave exposure is generally considered to be one of the primary factors structuring invertebrate and fish communities frequenting sandy beach environments (McLachlan *et al.* 1984, Morin *et al.* 1985, Romer 1990, Gibson 1994, Clark *et al.* 1996a, Chapter 1). Although influences of this variable on invertebrate communities have been well studied, and are reasonably well understood (Oliver *et al.* 1980, McLachlan 1983, Morin *et al.* 1985, Dexter 1990, Brown & McLachlan 1990), much confusion still surrounds the influence of wave exposure on fish communities. Recent research suggests that increases in wave exposure are generally accompanied by decreases in fish abundance and diversity, and increases in dominance (Hillman *et al.* 1977, Romer 1990, Clark *et al.* 1994b, Clark *et al.* 1996a, Chapter 1). This cannot be held as a general rule, however, as abundance, diversity and dominance are not always greatest in the most sheltered or least turbulent areas, nor is dominance lowest at the most sheltered sites (see for example Reynolds & Thompson 1974, Berghahn 1986, Pihl & van der Veer 1992, Clark *et al.* 1996a, Chapter 1). Much of this confusion can be attributed to three sources. Firstly, many studies which have attempted to examine the influence of wave exposure on fish community structure have employed data collected using differing methodologies and/or equipment. Secondly, difficulties associated with separating the influences of other interacting variables such as macrophyte abundance, salinity and turbidity from that of wave exposure confounds many studies. Thirdly, no study of fish assemblages conducted to date encompasses data collected over a wide range of exposure levels from exposed open ocean beaches through to sandy beaches completely protected from oceanic swell.

The Saldanha Bay - Langebaan Lagoon complex on the west coast of South Africa provides an ideal setting in which to examine the influence of a gradient in wave exposure, which extends from exposed open ocean beaches, through a semi-exposed bay, into an extensive lagoon complex into which oceanic swell penetrates only a short distance. The aim of this study is thus to critically examine the influence of a wave exposure gradient on the composition, abundance and size structure of fish assemblages frequenting sandy beach surf-zone environments. It also provides valuable information on the composition and size structure of surf-zone ichthyofaunal assemblages along the South African west coast which, to date, have not been properly sampled or documented.

## 2.2 STUDY AREA

The Saldanha Bay-Langebaan Lagoon complex (33°S 18°E) consists of a roughly semi-circular bay with a radius of 7 km and an elongate lagoon about 15 km in length and 2 km in width extending from its southern edge (Fig. 2.1). These two bodies of water together cover an area of approximately 135 $km^2$. Sea surface temperatures on the South African west coast (outside Saldanha Bay) typically range from 10-14°C, but are slightly warmer inside the bay (14-19°C) and even warmer (up to 24°C) in Langebaan Lagoon itself (Shannon 1966, Shannon & Stander 1977). Salinity in the Lagoon (34.8-37.0‰) is more variable and usually higher than in Saldanha Bay (34.9-35.0‰) or the waters outside the Bay (34.6-34.9‰) (Shannon 1966, Shannon & Stander 1977). Winds in this area are predominantly southerly throughout the year, but northerly winds are frequent between May and August (Weather Bureau 1965, 1972).

Oceanic swell entering Saldanha Bay decreases progressively into the inner Bay as it is refracted around the inner headlands, decreasing to ca. 1/100 of the energy entering the outer Bay (Flemming 1977). Eight sampling localities (Fig. 2.1) were selected on sandy beaches covering a wave exposure gradient extending from a very exposed beach situated outside Saldanha Bay (site 1), through to highly sheltered areas situated at the southern end of Langebaan Lagoon (site 8).

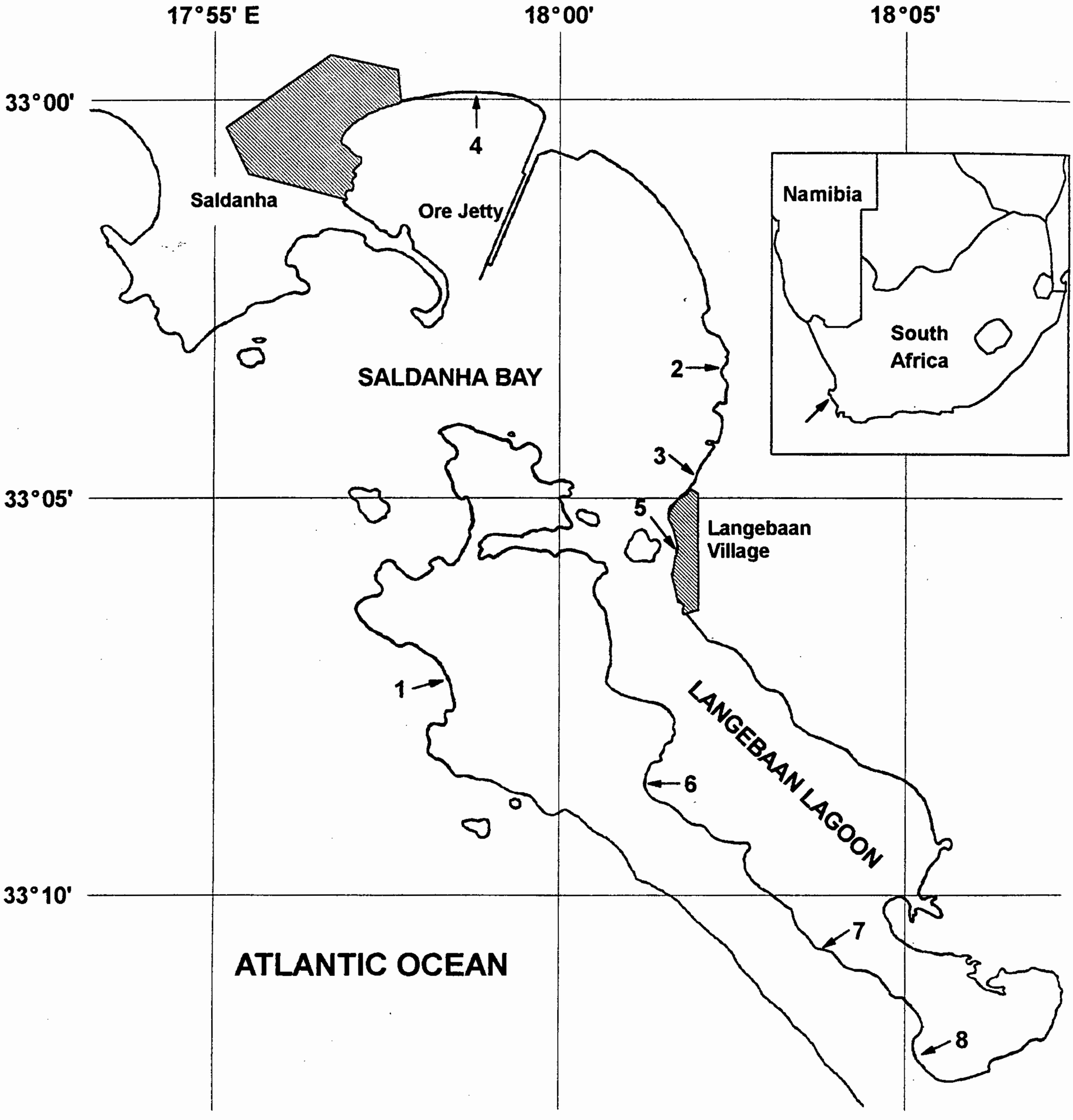


Fig. 2.1. The south-western Cape (inset) and the Saldanha Bay - Langebaan Lagoon complex, showing the location of the sampling sites and features mentioned in the text.

McLachlan (1980) highlighted the problems associated with rating sandy beaches in terms of exposure, and proposed a compound index designed to assess the hydrodynamic force experienced by intertidal sandy beaches throughout the world (see Chapter 1). Use of this index for at least three of the sites in this study appears inappropriate, however, since wave exposure (maximum wave height) clearly declined when moving from sites 1 to 8, while McLachlan's index, when applied to these sites did not (see Results). This is because exposure values at sites 5-7 were artificially inflated by the effects of tidal currents flowing in and out of the lagoon, which influence many of the parameters (e.g. intertidal slope, median particle size, depth of reduced layers) on which this index is based. Currents are strongest (up to 1 m/sec) at the entrance to the lagoon, but weaker further up the lagoon (Shannon & Stander 1977), which is consistent with the discrepancy noted between maximum wave height and exposure scores at the various sites in the lagoon (Table 2.1). Therefore, based on McLachlan's index, although some of the sites within the lagoon may appear to be more exposed than those outside, with respect to wave exposure, this is not the case. Sites 1 (outside the Bay) and 2 (inside the Bay) can thus be considered exposed, sites 3-5 of intermediate status, and sites 6-8, sheltered.

## 2.3 METHODS

Fish assemblages at the eight localities were sampled over a four day period in April 1994 using the beach-seine net described in Chapter 1. Langebaan Lagoon and parts of Saldanha Bay are situated in the West Coast National Park, declared a RAMSAR site in 1988. Sampling was therefore restricted to as short a period as possible, ensuring minimal disturbance. Five hauls, approximately 50 m apart, were made at each site during daylight hours, between 10h00 and 14h00, to ensure consistency with regard to the time of day and tidal height as far as possible. Samples were all collected on the rising tide, with tidal peaks in the sea occurring between 14h30 and 16h00 each day. The net was taken out through the surf to a depth of 1.5 m and laid from the boat at all localities except site 1, where the net was laid by hand, as the large waves precluded the use of a boat. Areas swept by the net, calculated as distance off-shore multiplied by the mean width of the haul, varied from 225-450 m$^2$. Following each haul, fish were identified to species, counted, batch weighed and measured to the nearest 1 mm. Salinity was measured using an Atago S/Mill hand refractometer and reported according to the Practical Salinity Scale, while measurements of all other physical and biological parameters were made as described in Chapter 1.

Multivariate and univariate analyses of fish community data were performed using the CLUSTER, MDS, SIMPER and DIVERSE programs on the PRIMER software package (Plymouth Marine Laboratory UK), as described in Chapter 1. Non parametric Kruskal-Wallace and Tukey multiple range tests (Zar 1984) were used to detect significant differences among the ranking of community parameters calculated for seine net hauls made at the eight stations.

## 2.4 RESULTS

### 2.4.1 Physical variables

Details of the physical data collected at the eight sampling stations are listed in Table 2.1. Water temperature was lowest (14°C) at site 1 outside Saldanha Bay, slightly warmer (16°C) at the sites within the Bay (sites 2-5), and warmest (18-19°) at the three sites (sites 6-8) in Langebaan Lagoon. Salinity remained constant at 35 ‰ across all eight sites. Maximum wave height measured decreased sharply from 2.4 m at site 1 outside Saldanha Bay to 0.3 m at the entrance of the Lagoon, from where it dropped to zero at the head of the Lagoon. Progressing from the most exposed (site 1) to the most sheltered site (site 8), the surf-zone width increased initially from 60 to 120 m (site 3), but then declined gradually to zero at the top of the Lagoon. In contrast, the steepness of the intertidal slopes initially decreased from 1:15-1:26 at the entrance to the Lagoon (site 5), from where it became very steep again, varying between 1:7 and 1:15 over the remaining four sites. Similarly, median particle size and depth of the reduced layers on the shore decreased initially over the first four sites (>100 to 45 cm), but became very variable (20 to >100 cm) from the entrance to the Lagoon (site 5) onwards. The magnitude of exposure scores, calculated according to McLachlan's (1980) rating system, displayed an unexpected trend. Values initially declined from a high of 17 at site 1 to seven at site 4, as anticipated, but then increased unexpectedly to ten over the next three sites, before dropping to two at the head of the Lagoon.

**Table 2.1.** Measurements of physical variables recorded at eight sampling sites in the Saldanha Bay-Langebaan Lagoon complex during April 1994. "Exposure scores" allocated to the sites were based on the scoring system developed by McLachlan (1980), as detailed in the text.

| | 1 Plankies-baai | 2 Lynch Point | 3 Strand-loper | 4 Blue Water Bay | 5 Langebaan Beach | 6 Kraal-baai | 7 Church-haven | 8 Geel-bek |
|---|---|---|---|---|---|---|---|---|
| Temperature (°C) | 14 | 16 | 16 | 16 | 16 | 18 | 18 | 19 |
| Salinity (‰) | 35 | 35 | 35 | 35 | 35 | 35 | 35 | 35 |
| Wave height (m) | 2.4 | 1.8 | 1.0 | 0.6 | 0.3 | 0.2 | 0.1 | 0.0 |
| Surf-zone width (m) | 60 | 100 | 120 | 75 | 40 | 20 | 10 | 0 |
| Intertidal slope | 1:15 | 1:18 | 1:24 | 1:26 | 1:14 | 1:7 | 1:10 | 1:15 |
| Median particle size (mm) | 0.51 | 0.42 | 0.19 | 0.16 | 0.21 | 0.38 | 0.44 | 0.24 |
| Depth of reduced layers (cm) | >100 | >100 | 90 | 45 | 75 | >100 | >100 | 20 |
| Exposure score | 17 | 15 | 10 | 7 | 7 | 9 | 10 | 2 |

No permanent macrofaunal burrows were evident at the two most exposed sites, while the remaining six sites all displayed varying numbers of burrows, their density increasing substantially as wave exposure decreased. Macrophytes (*Gracilaria verrucosa*) were first encountered at site 4, but as wave exposure declined their diversity increased with the addition of *Cladophora* sp. (sites 6-8), *Zostera capensis* (sites 7-8), *Sarconia perennis* and *Spartina maritima* (site 8 only).

### 2.4.2 Fish fauna

Species composition and abundance of fish in seine net hauls at the eight stations are presented in Table 2.2. A total of 25 676 fish from 24 species were captured in the 40 seine net hauls made. The numerical dominants *Atherina breviceps* (45.1%), *Liza richardsonii* (34.0%) and *Psammogobius knysnaensis* (13.6%), together accounted for nearly 80% of the total catch. Numbers of teleosts far exceeded that of elasmobranchs, which made up <1% of the catch. With regard to biomass, *L. richardsonii* (10.6%) and *A. breviceps* (3.8%) remained the most important teleost species captured, but these were far outweighed by the larger elasmobranch species, which together accounted for 82.7% of the 434 kg of fish collected (Table 2.3). Of these, *Rhinobatos annulatus* (37.0%), *Mustelus mustelus* (29.7%) and *Myliobatis aquila* (15.6%) dominated, together providing over 80% of the total mass of the catch. In terms of abundance, juvenile fish made up 46.1% of the total number of fish caught, the bulk of which (89.5%) were *L. richardsonii*.

Owing to the difference in species ranking based on numbers and biomass for most species, catch data from each station were split into teleost and elasmobranch components before trends in abundance, biomass and other community parameters were examined across sites. The trend in numbers of teleost species recorded per site displayed a clear convex profile (Fig. 2.2), with more species (11-12) being captured at the intermediately-exposed sites than at the more sheltered (2-9) or more exposed ones (4-7). However, in terms of abundance, mean teleost density displayed a general increase from the exposed to the sheltered sites. Mean density increased from <1 fish/m$^2$ at the most exposed sites up to a peak of 4.5 fish/m$^2$ at the most sheltered site (Fig. 2.2).

**Table 2.2.** Species composition, abundance and sizes of fish caught by beach-seining at eight sites in Saldanha Bay and Langebaan Lagoon. Species are divided into teleost and chondrichthyan components and listed in order of decreasing abundance.

|  | 1 Plankies-baai | 2 Lynch Point | 3 Strand-loper | 4 Blue Water Bay | 5 Langebaan Beach | 6 Kraal-baai | 7 Church-haven | 8 Geel-bek | Total catch | Maturity (mm) | Percent immature | Size range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TELEOSTEI |  |  |  |  |  |  |  |  |  |  |  |  |
| *Atherina breviceps* |  | 1 | 1 | 2944 | 2156 | 1520 | 616 | 4351 | 11589 | $43^{a}$ | 3.0 | 14-117 |
| *Liza richardsonii* | 701 | 903 | 469 | 1564 | 1254 | 1120 | 397 | 2313 | 8721 | $230^{b}$ | 99.7 | 18-290 |
| *Psammogobius knysnaensis* |  |  |  |  | 157 | 2809 | 511 | 20 | 3497 | $37^{a}$ | 45.0 | 23-75 |
| *Caffrogobius nudiceps* |  |  |  | 36 | 38 | 505 | 151 | 40 | 770 | $65^{c}$ | 95.8 | 22-113 |
| *Heteromycteris capensis* |  | 415 | 42 | 11 | 7 | 1 |  |  | 476 | $45^{d}$ | 0.4 | 40-109 |
| *Rhabdosargus globiceps* |  | 4 | 15 | 139 | 42 | 6 | 1 |  | 207 | $310^{e}$ | 100.0 | 32-100 |
| *Clinus superciliosus* |  |  |  | 18 | 48 | 8 |  |  | 74 | $65^{f}$ | 70.3 | 36-233 |
| *Chelidonichthys capensis* |  | 13 |  | 5 | 17 | 1 |  |  | 36 | $305^{g}$ | 0.0 | 21-95 |
| *Clinus latipennis* |  | 14 | 9 |  |  |  |  |  | 23 | $45^{h}$ | 21.7 | 34-91 |
| *Syngnathus acus* |  | 0 | 1 | 5 | 2 | 2 | 1 |  | 11 | $125^{a}$ | 36.4 | 89-170 |
| *Pomatomus saltatrix* |  | 3 |  | 2 |  | 1 |  |  | 6 | $240^{i}$ | 100.0 | 67-118 |
| *Diplodus sargus* |  |  |  | 5 |  |  |  |  | 5 | $180^{j}$ | 100.0 | 61-93 |
| *Solea bleekeri* |  |  |  | 0 |  |  | 3 |  | 3 | $100^{k}$ | 33.3 | 53-124 |
| *Spondyliosoma emarginatum* |  |  |  | 3 |  |  |  |  | 3 | $220^{l}$ | 100.0 | 82-87 |
| *Etrumeus terres* |  |  |  | 2 |  |  |  |  | 2 |  | 100.0 | 89-97 |
| *Cancelloxus longior* | 1 | 1 |  |  |  |  |  |  | 2 |  | 0.0 | 120-127 |
| *Lichia amia* |  |  |  |  | 2 |  |  |  | 2 | $600^{l}$ | 0.0 | 540-670 |
| *Trachurus trachurus* |  |  |  |  | 1 |  |  |  | 1 | $200^{m}$ | 100.0 | 195 |
| *Clinus agilis* |  |  |  |  |  | 1 |  |  | 1 |  | 0.0 | 68 |
| ELASMOBRANCHS |  |  |  |  |  |  |  |  |  |  |  |  |
| *Rhinobatos annulatus* | 3 | 15 | 22 | 2 | 7 | 121 | 17 |  | 187 | $700^{n}$ | 73.3 | 190-890 |
| *Myliobatis aquila* |  | 31 |  | 3 |  |  |  |  | 34 | $540^{o}$ | 100.0 | 320-540 |
| *Mustelus mustelus* |  | 8 |  | 6 |  |  |  |  | 14 | $700^{p}$ | 35.7 | 515-1650 |
| *Callorhynchus capensis* |  | 10 |  |  |  |  |  |  | 10 | $580^{q}$ | 50.0 | 400-909 |
| *Poroderma africana* |  |  |  | 2 |  |  |  |  | 2 | $580^{p}$ | 100.0 | 680-700 |
| Total catch | 705 | 1418 | 559 | 4747 | 3731 | 6095 | 1697 | 6724 | 25676 |  |  |  |
| Percent immature | 99.7 | 67.1 | 90.5 | 38.4 | 37.1 | 50.3 | 49.5 | 38.1 | 46.1 |  | 46.1 |  |
| Total area sampled | 1125 | 2250 | 2250 | 2250 | 2250 | 2250 | 1125 | 1500 | 15000 |  |  |  |

a. Bennett (1989b), b. de Villiers (1987)[1], c. Whitfield (1990), d. Clark *et al.* (1994a), e. Talbot (1955)[2], f. Day *et al.* (1981), g. Hecht (1977), h. Lamberth *et al.* (1994), i. van der Elst (1976), j. Joubert (1981a)[1], k. Wallace (1975), l. van der Elst (1988), m. Geldenhuys (1973), n. Wallace (1967a), o. Wallace (1967b), p. Compagno (1984b), q. Freer & Griffiths (1993)

Superscripts 1 and 2 indicate values were converted to total length from fork length and standard length respectively

**Table 2.3.** Biomass (g) of fish caught by beach-seining at eight sites in Saldanha Bay and Langebaan Lagoon. Species are separated into teleost and chondrichthyan components and listed in order of decreasing total mass for each.

| | 1 Plankiesbaai | 2 Lynch Point | 3 Strandloper | 4 Blue Water Bay | 5 Langebaan Beach | 6 Kraalbaai | 7 Churchhaven | 8 Geelbek | Total biomass |
|---|---|---|---|---|---|---|---|---|---|
| TELEOSTEI | | | | | | | | | |
| *Liza richardsonii* | 1520 | 4449 | 1856 | 12240 | 2589 | 618 | 2334 | 20362 | 45968 |
| *Atherina breviceps* | | 12 | 8 | 5260 | 3689 | 2584 | 630 | 4194 | 16377 |
| *Lichia amia* | | | | | 5500 | | | | 5500 |
| *Psammogobius knysnaensis* | | | | | 100 | 1700 | 255 | 59 | 2114 |
| *Rhabdosargus globiceps* | | 15 | 75 | 852 | 685 | 17 | 1 | | 1645 |
| *Heteromycteris capensis* | | 1344 | 155 | 41 | 8 | 2 | | | 1550 |
| *Caffrogobius nudiceps* | | | | 81 | 44 | 558 | 74 | 78 | 835 |
| *Clinus superciliosus* | | | | 425 | 134 | 30 | | | 589 |
| *Trachurus trachurus* | | | | | 62 | | | | 62 |
| *Clinus latipennis* | | 26 | 27 | | | | | | 53 |
| *Diplodus sargus* | | | | 51 | | | | | 51 |
| *Chelidonichthys capensis* | | 19 | | 4 | 18 | 8 | | | 49 |
| *Solea bleekeri* | | | | | | 0 | 44 | | 44 |
| *Pomatomus saltatrix* | | 29 | | 5 | | 6 | 0 | | 40 |
| *Spondyliosoma emarginatum* | | | | 25 | | | | | 25 |
| *Syngnathus acus* | | | 6 | 11 | 1 | 1 | 1 | | 20 |
| *Cancelloxus longior* | 7 | 5 | | | | | | | 12 |
| *Etrumeus terres* | | | | 11 | | | | | 11 |
| *Clinus agilis* | | | | | | 3 | | | 3 |
| ELASMOBRANCHS | | | | | | | | | |
| *Rhinobatos annulatus* | 2782 | 9146 | 14415 | 3185 | 6099 | 112202 | 12839 | | 160668 |
| *Mustelus mustelus* | | 87150 | | 19600 | | | | | 106750 |
| *Myliobatis aquila* | | 63150 | | 4400 | | | | | 67550 |
| *Callorhinchus capensis* | | 21360 | | | | | | | 21360 |
| *Poroderma africanum* | | | | 2900 | | | | | 2900 |
| TOTAL | 4309 | 186705 | 16542 | 49091 | 18929 | 117729 | 16178 | 24693 | 434176 |

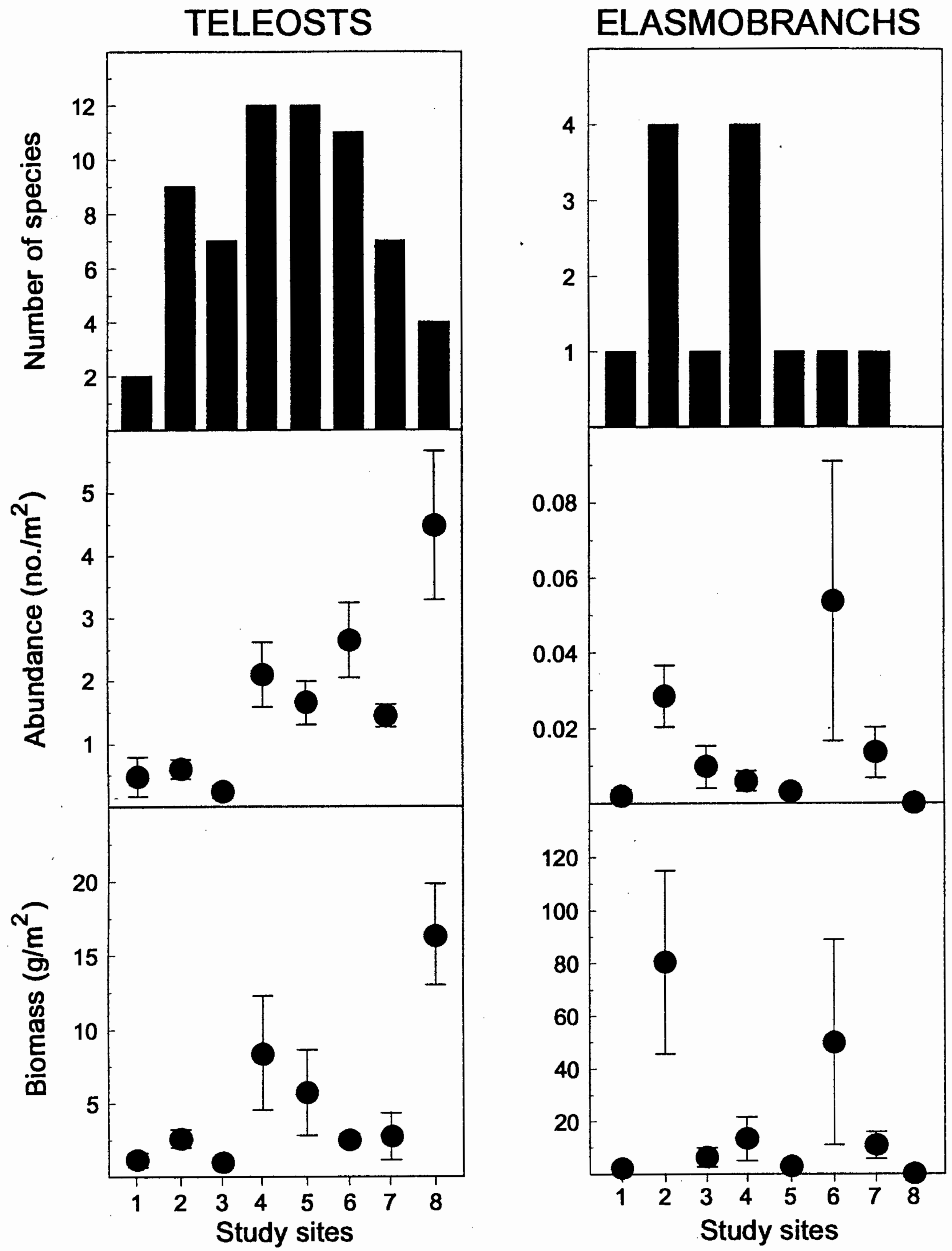


Fig. 2.2. Total numbers of species, individuals and biomass (mean ± S.E.) of teleost and elasmobranch fishes recorded in seine net hauls from eight sandy beaches in the Saldanha Bay-Langebaan Lagoon complex.

No discernible trends were evident in the mean teleost biomass which peaked at site 8 (16.5 g/m$^2$) and was lowest at site 3 (0.9 g/m$^2$). Neither were there any trends evident in the numbers of species, numbers of individuals or biomass of elasmobranchs captured at the eight stations. Peaks in the density and biomass of elasmobranchs were recorded at sites 2 (0.03 ind./m$^2$, 80.4 g/m$^2$) and 6 (0.05 ind./m$^2$, 49.9 g/m$^2$).

Figure 2.3 depicts trends in species richness, Shannon diversity and dominance of teleost catches at the eight stations sampled. Trends in species richness and diversity exhibited convex profiles across the exposure gradient, whereas the trend in dominance was roughly concave. Species richness peaked at site 4 (1.07), but dropped off rapidly to lows at the most exposed (0.06) and most sheltered sites (0.37). The trend in species diversity across the sites exhibited a right skewed convex profile, with peak diversity (1.14) occurring at the sheltered end of the exposure gradient (site 6), while tailing off toward the more sheltered and more exposed sites. Diversity was greater at the most sheltered site (0.62) than at the most exposed site (0.04). The dominance profile was also skewed to the right, with a trough occurring at site 6 (0.4) and peaks at sites 1 (0.98) and site 8 (0.82), the most exposed and most sheltered sites respectively. Figures for elasmobranch species are not displayed, as these species were captured relatively infrequently and no obvious trends in these parameters could be discerned.

Kruskal-Wallis and Tukey multiple range tests were used to detect if differences between the ranking of teleost abundance, biomass, richness, diversity and dominance, and elasmobranch abundance and biomass were significant at the 95% level. Results of these tests are presented in Table 2.4. Patterns of significance for each of these parameters varied according to the shapes of the profiles, but on the whole, closely allied sites did not differ significantly, while those further apart did. For example, in the case of teleost abundance, where the exposure vs. abundance profile was approximately linear, sites which were similar in terms of exposure did not differ significantly in terms of abundance; whereas in cases where profiles were convex or concave, sites immediately adjacent to one another tended to differ significantly, while those on opposite sides of the spectrum, did not.

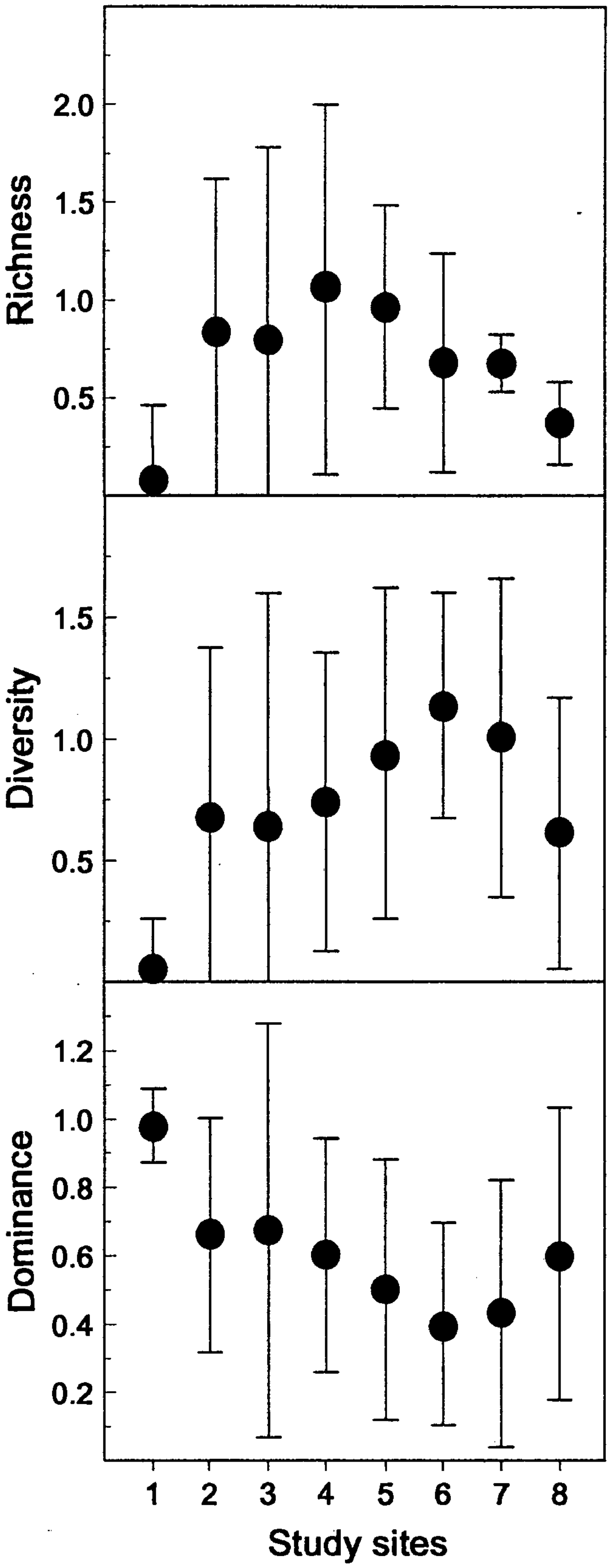


**Fig. 2.3.** Species richness, diversity and dominance (mean ± 95% confidence limits) of teleost fishes in seine net hauls from eight sandy beach stations in Saldanha Bay-Langebaan Lagoon complex.

**Table 2.4.** Results of Tukey tests performed following Kruskal-Wallis tests comparing teleost abundance, biomass, richness, diversity and dominance and elasmobranch abundance and diversity in seine net hauls made at eight localities in the Saldanha Bay-Langebaan lagoon complex. Columnwise, asterisks denote homogenous groups at the 95% level.

| | Teleost abundance | | | | | Teleost biomass | | | Elasmobranch abundance | | | | Elasmobranch biomass | | | | | | | | Teleost richness | | Teleost diversity | | | | | Teleost dominance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | * | * | | | | * | | | * | | | | * | * | | | | | | | | | | | | | | | | |
| 2 | * | | | | | | * | * | | * | | | | | * | | | | | | * | | * | * | | | | * | * | |
| 3 | | * | | | | * | | | | | * | | | * | | * | * | | | | | * | | | * | | | * | | |
| 4 | | | * | * | | | | | | | * | * | | | | * | | * | | | * | | * | | * | | | * | | |
| 5 | | | * | * | | | | * | * | | | * | * | | | | * | | * | | | | | * | | * | | | * | |
| 6 | | | * | | * | | * | | | * | | | | | * | | | * | * | * | | * | | | | * | * | | | * |
| 7 | | | | * | | | * | | | | * | | | | | * | | * | | * | | * | | | | | * | | | * |
| 8 | | | | | * | | | | * | | | | * | | | | | | | | | | | | * | | | * | | |

Variations in mean density for the six most abundant teleost species across the exposure gradient are depicted in Fig. 2.4. *L. richardsonii* was recorded at all sites, with mean density ranging from 0.21-1.54 ind./$m^2$. *A. breviceps* was recorded at all but the most exposed site, but was represented by only one individual at sites 2 and 3 (Table 2.2). Mean density at sites 4-8 ranged from 0.52-2.90 ind./$m^2$ for this species. *Psammogobius knysnaensis* and *Caffrogobius nudiceps* which were both abundant under moderately sheltered conditions, reached peak density at site 6. *C. nudiceps,* however, was distributed over a wider range of exposure levels, extending from sites 4-8, whereas *P. knysnaensis* was recorded from sites 5-8 only. *Rhabdosargus globiceps* was most abundant at the intermediately exposed sites (3-5), but was recorded at all but the most exposed and most sheltered sites. Mean density of *Heteromycteris capensis* peaked at site 2 (0.18 ind./$m^2$), and was low (<0.01 ind./$m^2$) at the more sheltered sites.

Variations in fish size with exposure were examined by comparing size frequency distributions of those species represented by >100 measurements from at least two of the eight stations. Data for four species fitting these criteria are depicted in Fig. 2.5. *L. richardsonii* was the only species represented by >100 measurements at all eight stations, but no obvious trends were evident in the position of the modal size classes at the various sites. Individuals >120 mm, were present in abundance at the more exposed sites (sites 1-3) and most sheltered sites (7-8), but notably absent from the intermediately exposed sites (4-6). *A. breviceps* displayed a consistent decrease in the modal size of individuals captured as wave exposure declined. Initially presenting a bimodal size frequency distribution, the modal size of this species declined from 80 mm (site 4) through 65 mm (sites 5 & 6) to 55 mm at sites 7 and 8. No trends were evident in the size range of individuals captured, except that the individuals of <30 mm were recorded only at the most sheltered site (site 8). *P. knysnaensis* was recorded in sufficient numbers at only three sites, but both the modal and maximum sizes decreased from the more exposed to the more sheltered sites. The modal and maximum sizes decreased from 55 and 113 mm respectively at site 5, through 45 and 76 mm at site 6 to 35 and 64 mm at site 7. No differences were evident between the modal sizes or size ranges of *C. nudiceps* at sites 6 and 7.

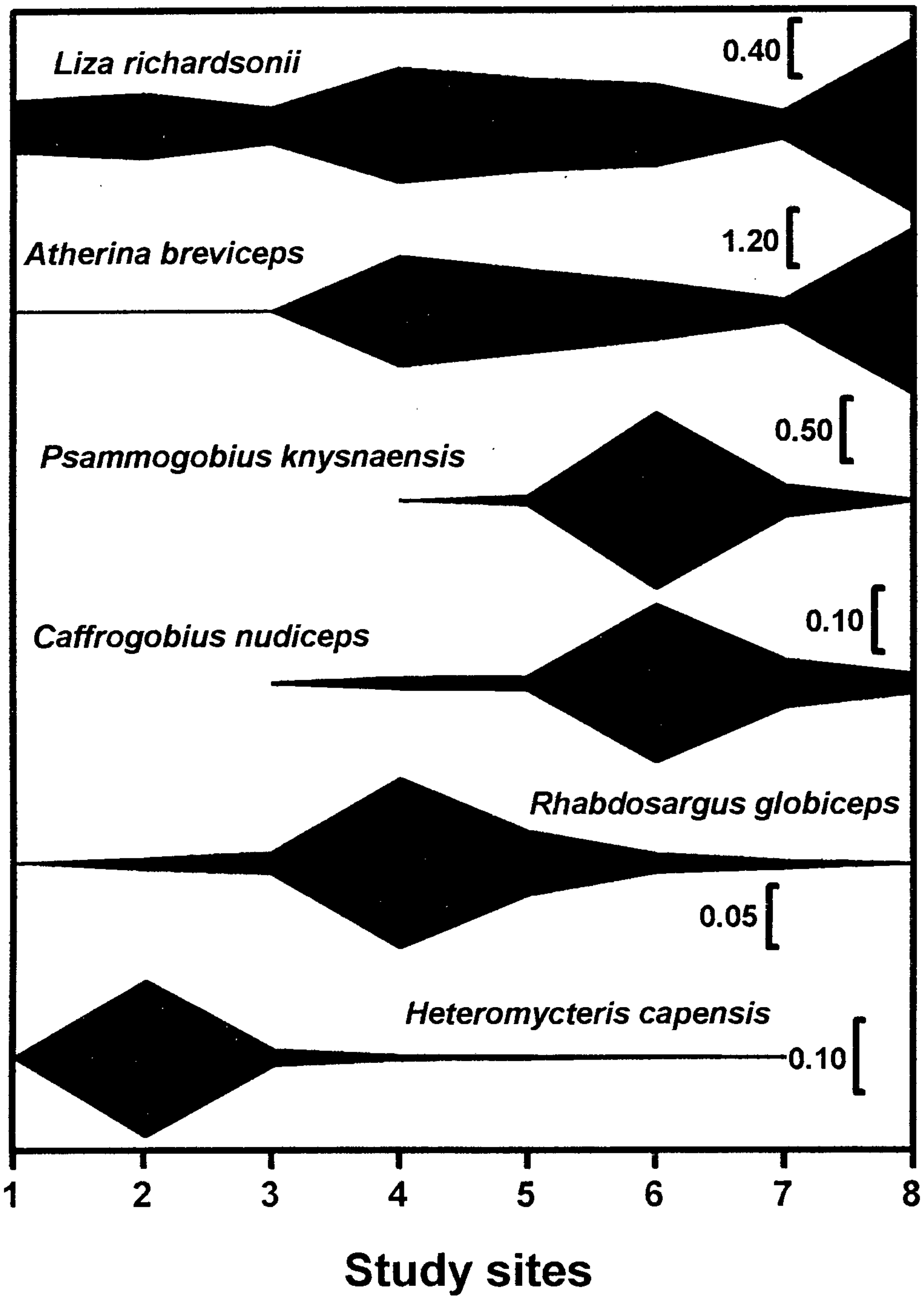


**Fig. 2.4.** Mean density (no. fish m$^2$) of six teleost species at eight sampling stations in the Saldanha Bay-Langebaan Lagoon complex. Sites are ordered from most exposed (1) to most sheltered (8).

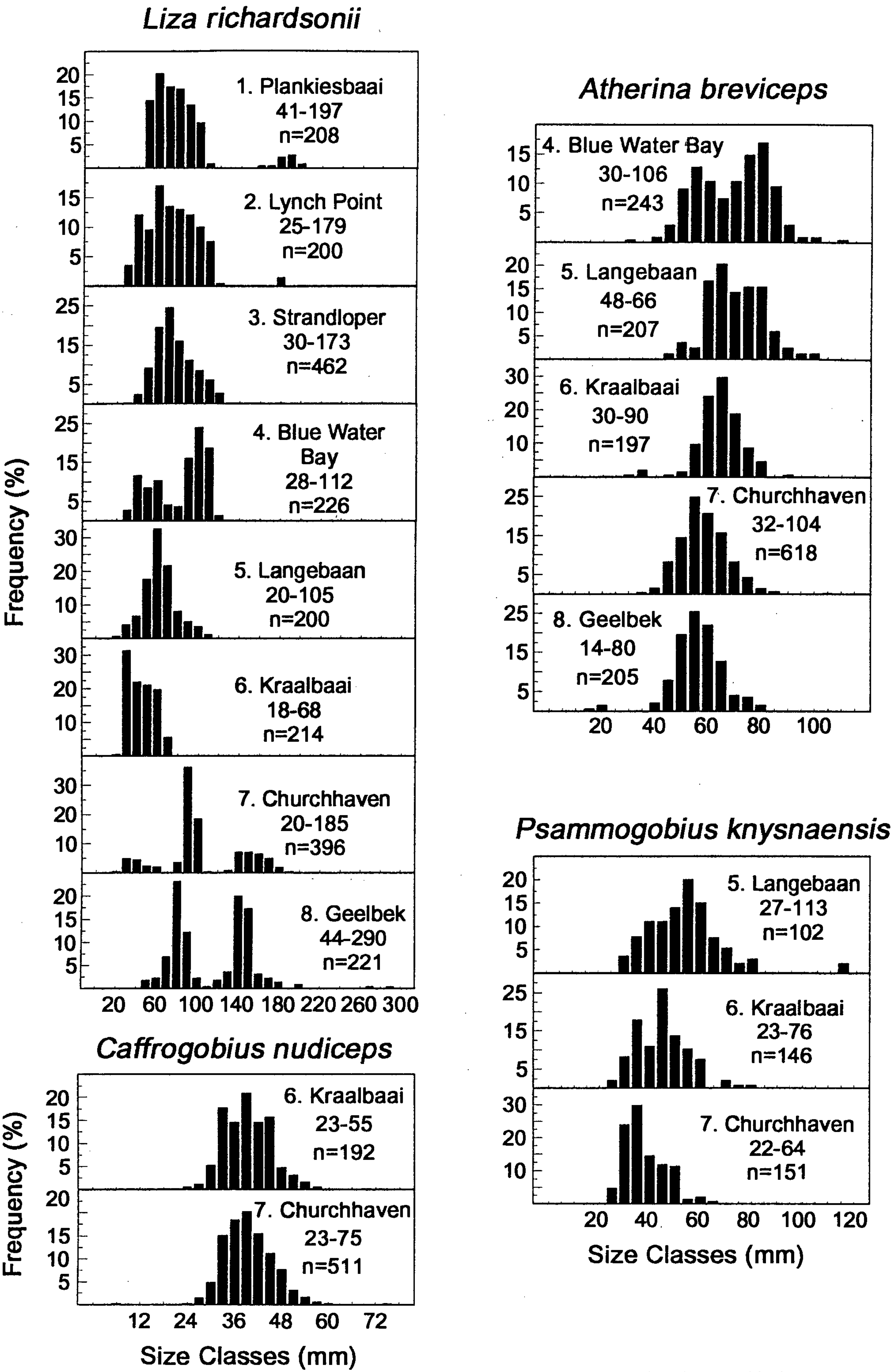


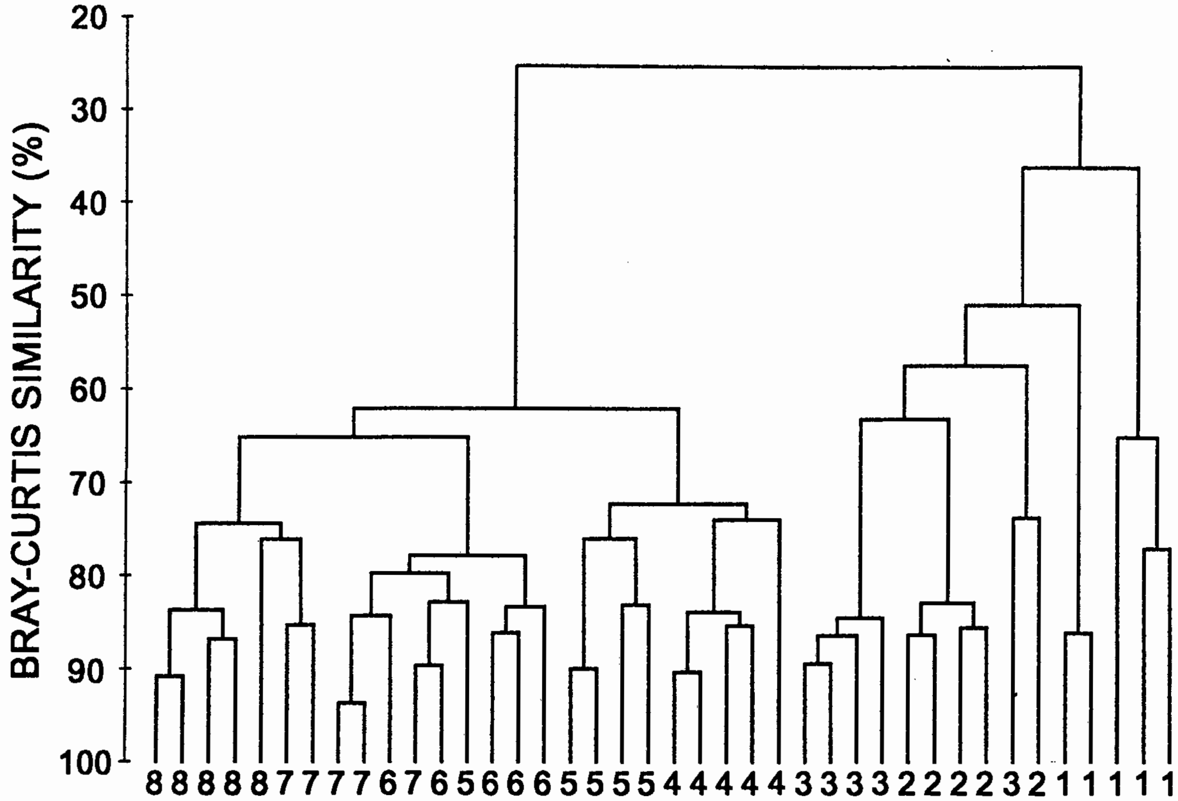
Fig. 2.5. Size frequency distributions of four teleost species at sampling stations in the Saldanha Bay-Langebaan Lagoon complex at which ≥100 individuals were captured. Sample size (n) and size ranges of fish at each station are also listed.

Faunal similarities among sites as indicated by the multivariate analyses performed are depicted in Fig. 2.6. The five hauls made at each of the sampling localities, for the most part, clustered closely together in the dendrogram and ordination plots, with samples from the eight sites forming two distinct groups in both plots. Samples from sites 1-3 formed one group, while samples from sites 4-8 formed another. Hauls from sites 4-8 showed a greater degree of similarity (>60%) than the three sites from the former group (35-90%), hence the higher clustering of sites 4-8 in the MDS plot as opposed to the more diffuse distribution of sites 1-3.. Results of the Simper analysis, (Table 2.5), indicated that *L. richardsonii* provided the greatest contribution (65.6%) to similarities between sites 1-3; *H. capensis*, *R. annulatus* and *Clinus latipennis* also made significant contributions (>5%). *A. breviceps* (36.%) and *L. richardsonii* (28.8%) were the major species responsible for similarity between sites 4-8, while *P. knysnaensis* and *C. nudiceps* each contributed >10%. Most (78%) of the dissimilarity between the two groups of sites was attributed to seven species. In order of importance these were: *A. breviceps* (26.5%), *P. knysnaensis* (14.0%), *C. nudiceps* (11.1%), *L. richardsonii* (8.1%), *H. capensis* (7.6%) and *R. annulatus* and *C. latipennis* (both 5.2%).

## 2.5 DISCUSSION

No obvious trends were evident in the abundance or biomass of elasmobranchs recorded in this study, as the total number of species captured (5) was low, and their distribution patchy, with 75% of the total number and 68% of the biomass concentrated at only two sites. However, two clear trends were evident in the composition of the teleost catches across the eight sites:

1) Overall fish abundance (mean density) increased as wave exposure decreased.
2) Highest species richness and diversity, and lowest dominance were recorded at intermediate levels of exposure.



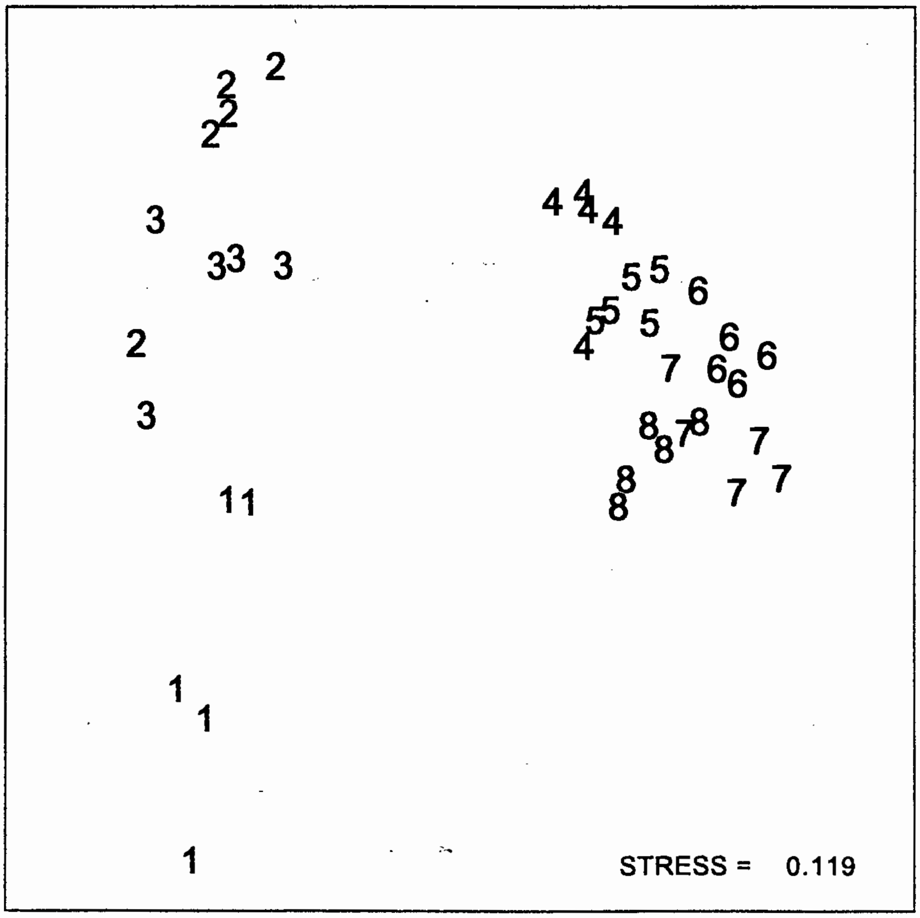


Fig. 2.6. Dendrogram and MDS plot showing similarities between replicate seine net hauls made at eight sandy beach stations in the Saldanha Bay-Langebaan Lagoon complex.

**Table 2.5.** Breakdown of species' contributions to similarities within and dissimilarities between groups of sites identified using Cluster and MDS analyses. Species are listed in order of numerical abundance, and dashes (-) indicate values <5%.

| | Similarity: Sites 1-3 | Similarity: Sites 4-8 | Dissimilarity: Sites 1-3 vs 4-8 |
|---|---|---|---|
| *Atherina breviceps* | - | 36.6 | 26.5 |
| *Liza richardsonii* | 65.6 | 28.8 | 8.1 |
| *Psammogobius knysnaensis* | - | 12.9 | 14.0 |
| *Caffrogobius nudiceps* | - | 12.0 | 11.1 |
| *Heteromycteris capensis* | 13.8 | - | 7.6 |
| *Rhabdosargus globiceps* | - | - | 5.2 |
| *Rhinobatos annulatus* | 9.5 | - | 5.2 |
| *Clinus latipennis* | 6.5 | - | - |

Fish abundance on sandy beaches around the world is generally greatest in the most sheltered areas (Gunter 1958, Hillman *et al.* 1977, Moore 1979, Poxton & Nasir 1985, Allen 1988, Romer 1990, Rogers 1992, Clark *et al.* 1994b, Clark *et al.*1996a, Chapter 1, 2). Wave exposure can affect fish directly through turbulence generated by breaking waves, by modifying sediment structure, or through its influences on food resources. Turbulence and wave action are thought to reduce food intake rates (and hence growth rates) due to the need for continual adjustment of body position and the reduction of visual fields in waters made turbid by suspended sediment (Moore & Moore 1976, Gibson 1994). However, the presence of turbid waters in estuaries is commonly considered to be advantageous for juvenile fish, as they provide cover from predators and frequently harbour higher invertebrate densities than clear waters (Blaber & Blaber 1980, Blaber 1981, Cyrus 1983, Cyrus & Blaber 1987a, b). Indeed, authors working in estuaries and marine habitats have found that fish abundance is usually higher in turbid waters (e.g. Swenson 1978, Blaber & Blaber 1980, Clark *et al.* 1996a, Chapter 1), while low catches have often been attributed to the presence of clear waters (e.g. Lasiak 1982, Blaber *et al.* 1985, Ross *et al.* 1987). The diversity and abundance of invertebrate macrofauna on sandy beaches is known to increase with decreasing wave exposure (Day 1959, Eltringham 1971, Bally 1981, McLachlan 1983). Benthic invertebrates form an important component of the diet of almost all of the more abundant species collected in this study (Table 2.6) and thus, greater food availability may indeed be responsible for greater fish densities recorded in sheltered areas during this study.

Some criticism has been levelled at comparisons involving seine net data collected under varying conditions of wave exposure (sampling efficiency is thought to decrease with increasing wave exposure: e.g. Hillman 1977, Brown & McLachlan 1990, Romer 1990). Abundance and biomass data collected during this study, however, are likely to provide a good reflection of actual abundance with little sampling bias, as the net was always laid at a constant depth behind the surf-line and hauling was facilitated by the large number of people involved.

**Table 2.6.** Diets and modes of feeding for species comprising ≥1% of the total number or biomass of fish in seine net catches made in the Saldanha Bay-Langebaan Lagoon complex during this study.

| Species | Diet | Mode of feeding | Reference |
|---|---|---|---|
| *Atherina breviceps* | planktonic & benthic invertebrates | filterfeeding & active capture | Blaber (1979), Coetzee (1982), Romer (1986), Bennett (1989c) |
| *Liza richardsonii* | detritus, microalgae & surf diatoms | filterfeeding & active capture | Blaber (1979), Coetzee (1982), Romer (1986), Lasiak (1982) |
| *Psammogobius knysnaensis* | benthic invertebrates | active capture | Hanekom & Baird (1984), Bennett (1989c) |
| *Rhabdosargus globiceps* | zooplankton, zoobenthos & macrophytic algae | active capture & algal cropping | Talbot (1955), Hanekom & Baird (1984), Lasiak (1986), Bennett (1989c), |
| *Caffrogobius nudiceps* | benthic invertebrates, & algae | active capture, algal cropping, scavenging | Jackson (1950) |
| *Clinus superciliosus* | invertebrates & fish | active capture | Jackson (1950), Bennett *et al.* (1983), Prochazka (in press) |
| *Rhinobatos annulatus* | benthic invertebrates | active capture | Rossouw (1983), Compagno *et al.* (1989), Harris *et al.* (1988) |
| *Mustelus mustelus* | benthic invertebrates & fish | active capture | Wallett (1978), Compagno (1984b), Compagno *et al.* (1989) |
| *Myliobatis aquila* | benthic invertebrates & fish | active capture | van der Elst (1988), Compagno *et al.* (1989) |
| *Callorhinchus capensis* | benthic invertebrates & fish | active capture | Compagno *et al.* (1989), Freer & Griffiths (1993) |

Fish assemblages on sandy beaches in Europe are usually dominated by juvenile flatfish, some of which are known to actively select substrata on the basis of grain size (Gibson & Robb 1992). Median particle size declines with wave exposure, and juvenile flatfish are generally more abundant on fine sediments (Riley & Holford 1965, Poxton & Nasir 1985, Rogers 1992), as most smaller flatfish are unable to bury in coarse sediments (Riley & Holford 1965, Gibson & Robb 1992). The ability to bury in the sediment is thought to afford protection from predators and drag forces as well as offering metabolic advantages (Gibson & Robb 1992, Ansell & Gibson 1993). Although macrophytes may reduce flatfish densities on European beaches (Pihl & van der Veer 1992, Wennhage & Pihl 1994), in other parts of the world the physical refuge and associated epifaunal food source they provide in protected inshore habitats are considered to be the main reasons for the occurrence of greater fish densities in vegetated areas (Kikuchi & Pérès 1977, Orth & Heck 1980, Pollard 1984). Macrophytes also tend to trap large volumes of sediment and organic detritus (Barnes 1974, Newell 1979), and thus, increases in macrophyte abundance evident with decreasing exposure in the Saldanha Bay-Langebaan Lagoon complex are likely to have contributed to the increase in the densities of invertebrate and detritus feeding fish with increasing shelter from wave action.

The influence of physical disturbance on the diversity of ecological communities has been well studied, and it is now generally recognised that greatest diversity is found at intermediate levels of disturbance (e.g. Menge & Sutherland 1976, 1987, Connell 1978, Sousa 1979, Pickett & White 1985). Classic theory dictates that diversity should be low in harsh (highly exposed) environments because of the intolerance of all but the most opportunistic and highly resistant species to such conditions. Under conditions of intermediate disturbance (moderate wave exposure) diversity should peak, because species abundances should be high, and species are removed with sufficient regularity to prevent competitive exclusion. In stable environments abiotic disturbance (wave exposure) is no longer capable of preventing competitive exclusion, and thus diversity declines. In this study, trends in species richness and diversity exhibited classic bell shaped curves, peaking at intermediate to low levels of exposure (sites 4 and 6 respectively). Dominance exhibited the reverse pattern, with the lowest value corresponding with the most diverse site. In his study of three beaches in Algoa Bay, Romer (1990) found that greatest diversity and lowest dominance were recorded at the most sheltered site (Kings Beach). This is not surprising, however, as the mean wave size (0.7 m) and exposure ranking (12.5, McLachlan 1980) at this site indicate that it is intermediately exposed in the context of this study.

A marked relationship is evident between fish size and depth on European beaches, where newly settled 0-group flatfish are found in shallow waters, while the older (larger) fish usually occur in deeper areas (Edwards & Steele 1968, Poxton *et al.* 1982, Dorel *et al.* 1991). No studies to date have demonstrated relationships between fish size and exposure, however. As median particle size is closely correlated with exposure (Davies 1972, McLachlan 1980, Brown & McLachlan 1990), and juvenile flatfish are known to actively select substrata on the basis of grain size (Tanda 1990, Gibson & Robb 1992), due in part to their increased ability to bury with size (Gibson & Robb 1992), such relationships must presumably exist. *Heteromycteris capensis*, the only flatfish species recorded in abundance in this study, was distributed over a wide range of exposure levels (sites 206), but nearly 90% of the total were found at sites 2, where median particle size was 0.42 mm. A positive relationship between fish size and exposure was demonstrated for at least two species (*Atherina breviceps* and *Caffrogobius nudiceps*) in this study. *C. nudiceps* is a benthic feeding goby and may thus be influenced by sediment structure, while *A. breviceps* feeds on zoobenthos and zooplankton (Table 2.6), and may be responding directly to the increase in wave action as well. Smaller individuals are probably unable to feed efficiently in highly turbulent waters due to their poorer swimming abilities. Further, individual sizes of macrofaunal invertebrates on sandy shores increase with exposure (Bally 1981, McLachlan 1983, Brown & McLachlan 1990), and many are thus likely to become unavailable as a food source to small fish at high levels of exposure. This may also explain why peak elasmobranch biomass was found at a relatively high level of exposure (site 2). These, predominantly large individuals, are likely to preferentially seek the larger prey items found here, as opposed to the smaller teleost species, which will target smaller prey items found in greater abundance at lower levels of exposure.

The exposure ranges over which the six most abundant species were recorded in this study appear to concur well with published distributions. *Liza richardsonii* has been recorded in moderate to high numbers in fine mesh seine net catches at 15 sites, covering a wide range of exposure levels in South Africa (Clark *et al.* 1994b, Bennett 1989a, Lasiak 1984a, b, Romer 1986, Clark *et al.*1996a, Chapter 1, 4). *A. breviceps* and *Rhabdosargus globiceps* were also recorded at all these sites, indicating that they may extend over a wider range of exposure levels. *Psammogobius knysnaensis* and *C. nudiceps* were recorded in moderate to high numbers only at the most sheltered sites sampled by earlier authors, and infrequently at some of their more exposed sites, thus matching the distribution patterns recorded during this study. *Heteromycteris capensis* was recorded less frequently than the other species, but was recorded at a number of the more sheltered sites sampled by Clark *et al.* (1996a, Chapter 1) in South Africa. Catches in this study were composed mostly of adult fish (only 0.4% immature). However, catches made by Clark (in press) included a greater proportion of juveniles (48.5%). This indicates that this species may exhibit size-dependent distribution patterns, as do *A. breviceps* and *C. nudiceps*.

McLachlan (1980) identifies four exposure categories into which sandy beaches can be placed. The multivariate analyses employed in the present analysis to examine similarities in the species composition between sites, identified two groups of sites. Group 1 contained hauls from sites 1-3, which corresponds essentially to the exposed and very exposed categories identified by McLachlan, while sites 4-8 fall within the sheltered and very sheltered categories he identified. Whether this represents a general categorisation which can be extrapolated to other systems is unknown, but it does offer some insight into concerns raised by Romer (1990) with respect to the extrapolation of interactions between invertebrate and fish predator arrays from one system to another.

# CHAPTER 3

# 3 LONG-TERM TEMPORAL VARIATIONS IN SURF-ZONE FISH ASSEMBLAGES IN FALSE BAY

## 3.1 INTRODUCTION

Temporal variations in surf-zone fish communities are well documented, but much confusion still prevails over the factors influencing or controlling these variations. These have been attributed to fluctuations in a wide variety of both biological and physical variables including the timing of spawning seasons and hence the influx (immigration/recruitment) and efflux (emigration) of individuals to and from populations (e.g. Edwards & Steele 1968, Jones 1973, Lockwood 1974, Ziljstra *et al.* 1982, Wright 1988, Gibson *et al.* 1993), food availability (Lockwood 1974, Creutzberg *et al.* 1978, Ross *et al.* 1987, Lamberth *et al.* 1995a), predation pressure (Riley & Corlett 1966, Macer 1967, Van der Veer & Bergman 1987, Pihl 1990), water temperature (e.g Warfel and Merriman 1944, Gunter 1945, Anderson *et al.* 1977), wind speed and direction (e.g. Modde & Ross 1981, Lasiak 1982, Pihl 1990, Gibson *et al.* 1993), turbidity (e.g. Blaber & Blaber 1980, Ross *et al.* 1987), salinity (e.g. Gunter 1945, Wright 1988), tidal influences (e.g. Merriman 1947, Edwards & Steele 1968, Gibson 1973a, b, Modde & Ross 1981) and time of day (e.g. Lasiak 1984b, Robertson & Lenanton 1984, Burrows *et al.* 1994).

All long-term surf-zone fish studies have been conducted in temperate and high latitudes, and most have demonstrated the existence of seasonal variations in the abundance and/or species composition of these assemblages (e.g. McFarland 1963, Modde & Ross 1981, Gibson *et al.* 1993). Many authors (e.g. Gunter 1958, McFarland 1963, Ross *et al.* 1987) consider these variations to be the primary characteristic of surf-zone fish assemblages. However, few long term studies, and only one of the southern African studies (Lamberth *et al.* 1995a) utilize data collected over a period exceeding one annual cycle. Little is thus known of the importance of interannual variations in surf-zone fish communities. Comparisons between temporal variability at different localities have also been hampered by differences in sampling gear and methodology.

In this part of the study, seasonal and interannual variations in the species composition and abundance of fish communities were examined at 11 separate localities in False Bay, covering a range of physical conditions. This paper serves to document seasonal and interannual variations in the composition, abundance and community structure of the surf-zone fish assemblage as a whole, and at different sites in the bay. Using multivariate techniques it provides a detailed analysis of the relative importance of the influence of factors such as water temperature, wind speed and direction, wave exposure and macrophyte abundance on temporal variability in surf-zone fish community structure and abundance.

## 3.2 MATERIALS AND METHODS

This paper forms a companion to Chapter 1 in that it examines temporal variability in physical and biological data collected during that part of the study. The reader is therefore referred to that work for a detailed description of the study area, study sites, sampling equipment and methodology. Briefly, data for this study were collected from approximately monthly seine net hauls made over a 24 month period between July 1991 and June 1993 at 11 surf-zone localities in False Bay (34°15'S, 18°40'E), South Africa.

Temporal variations in community structure, physical environmental factors and interactions between these variables were analysed using the CLUSTER, MDS and BIOENV programs on the PRIMER computer package, version 3.1 (Plymouth Marine Laboratory, U.K.). The influence of physical environmental factors on temporal variations in fish density were examined using multiple stepwise regression analyses (Zar 1984) using the SYSTAT computer package (SYSTAT Inc., Evanstan IL., U.S.A.). Spearman rank correlation coefficients ($p_w$) and an adjusted multiple coefficient of determination ($r^2_{adj.}$) were used as indices of predictive value for the BIOENV and Multiple stepwise regression analyses respectively.

All multivariate analyses were performed using data collected and analysed as stated in Chapter 1, except for wind speed and direction. This variable was transformed from a circular to a linear variable by taking the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore and multiplying it by the wind speed. Onshore winds were thus allocated the highest directional components (+1), offshore winds the lowest (-1) and cross-shore winds from either direction, components between +0.9 and -0.9. This was deemed to be the optimal solution as it was felt that priority should be given to the relative "on-" or "off-shoreness" of the wind, as the influence of winds blowing parallel to the shore from opposite directions were considered to be similar. As the stretch of shoreline over which the sampling sites were distributed was not linear, when biotic data were combined for all sites, wind direction data was transformed from a circular to a linear variable using the cosines of the angle the wind made on a magnetic compass rose. Using this method, winds blowing directly from the south received a score of +1.0, winds from the north -1.0, and those with easterly or westerly components, scores between +0.9 and -0.9. Species richness, diversity and evenness were estimated using Margalef's Index (d, Margalef 1958), Shannon's Diversity Index (H') and Pielou's Evenness Index (J) (Pielou 1969), respectively. For the purposes of this study, seasons were defined as follows: September-November = Spring; December-February = Summer; March-May = Autumn; June-August = Winter.

## 3.3 RESULTS

### 3.3.1 Temporal variations in physical environmental factors

Monthly variations in water temperature, wind speed and direction, wave height, surf-zone width, turbidity and detached macrophyte detrital abundance averaged over the 11 sites are illustrated in Figure 3.1. Seasonal patterns were evident in the fluctuations in water temperature, wind direction and possibly turbidity. Water temperatures were highest during the summer months, peaking (20-22°C) during December and January. Lower temperatures were recorded during the winter months, with the lowest temperatures (11-13°C) occurring in July. When data were grouped by season, the summer (mean = 21.5°C), spring (mean = 18.2°C) and autumn (mean = 17.1°C) temperatures were significantly greater than those of winter (mean = 13.2°C) (ANOVA: $p<0.05$; d.f = 23, F = 16.1). Mean temperature during the study period was 17.5°C. Winds recorded during the summer of both years, being of variable intensity (0.6-19.0 knots), were either southerly or southeasterly. Winds with a northerly component were encountered more frequently (42% of the time) during Autumn and Spring, but remained primarily of southerly origin. Mean wind speed varied from 0-10 knots during this period. Northerly and northwesterly winds reached their greatest frequency during winter where their frequency of occurrence (67%) and intensity (2.7 - 7.0 knots) was greater than that of southerly winds (17%, 3.5 knots). Turbidity of the surf-zone waters appeared to fluctuate seasonally during the first year, but not in the second. Winter readings were clearly greater than the other seasons during the first year, but although the same general trend was evident during the second year, the highest turbidity (6.9 FTU) was recorded during mid summer of that year. Mean wave height did not vary greatly, ranging between 0.4 and 1 m. Surf-zone width varied between 25 and 350 m, and correlated significantly with wave height ($r=0.63$, $p<0.01$), but displayed no seasonal trends. The total density of detached aquatic macrophytes in the sampling areas ranged from <0.001 $lm^{-2}$ (July and October 1992) to 0.5 $lm^{-2}$ (March 1992). The mean macrophyte abundance during the entire sampling period was 0.1 $lm^{-2}$ with no seasonal trends evident.

### 3.3.2 Temporal variations in fish composition and abundance

Considerable variation was evident in the density and number of fish species collected from the surf at each of the 11 sampling stations. Fluctuations in abundance at the various sites were not in phase with one another, nor did peaks in abundance correspond from the first year to the second. Similarly, no consistency was evident when the numbers of species captured per month was compared across sites, or when comparisons were made from one year to the next at the individual sites. An exception was Blake's Cove, where the number of species taken between December and June of both years (7-13) was greater than the numbers taken during the latter part of both years (4-7).

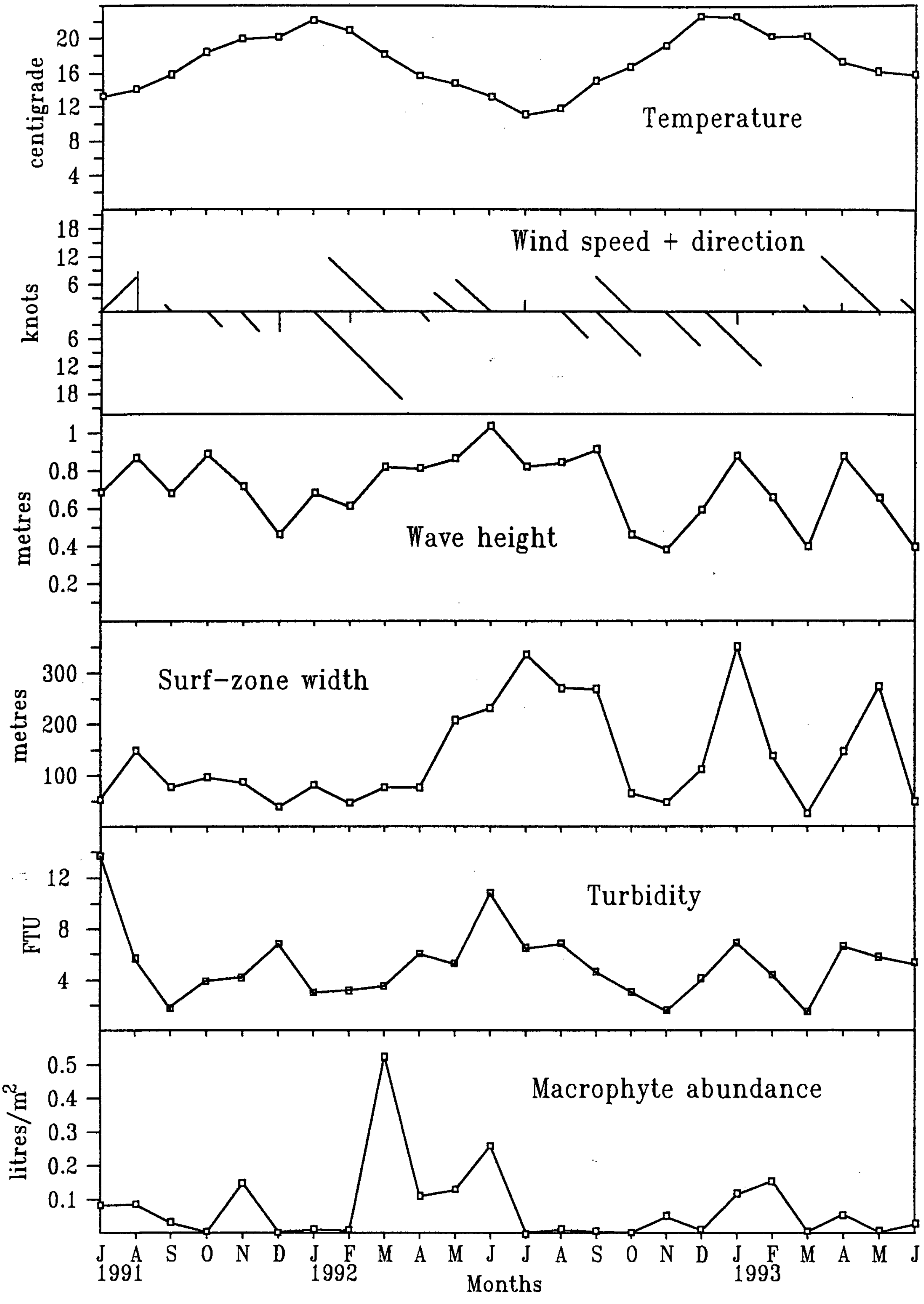


**Fig. 3.1.** Monthly variations in mean water temperature (°C), wind speed (knots) and direction, mean wave height (m), mean surf-zone width (m), mean turbidity (FTU) and total macrophyte abundance at 11 surf-zone localities in False Bay between July 1991 and June 1993.

Even when data from all sites were combined (Fig. 3.2), no seasonal patterns were evident in the total numbers of individuals captured or in the density of fish in the surf-zone. Total monthly catch varied between 707 (July 1992) and 9773 (March 1993), while density ranged between 0.15 (July 1992) and 1.76 individuals $m^{-2}$ (September 1991). Mean monthly catch and mean density of fish in the surf were 2859 and 0.64 $m^{-2}$, respectively.

A weak seasonal trend was evident in the total number of species captured per month (Fig. 3.2). Fewest species were captured between July and October 1991 (10-15) and between July and December 1992 (10-14). Numbers of species were greatest between November 1991 and June 1992 (16-20) and between January and June 1993 (16-22). Numbers peaked during May 1992 (20 species) and April-May 1993 (22 species). Fluctuations in species richness also exhibited a rough seasonal trend. Lowest values ($\leq 1.8$) were recorded between July-October 1991 and July-December 1992, while values were higher (1.9-2.3) from November 1991-June 1992 and from January-June 1993. No seasonality was evident in species diversity (H') or evenness (j) (Fig. 3.2). Diversity ranged from 0.553 (Sep 1991) to 1.615 (Jan 1993), while evenness ranged from 0.191 (Dec 1991, Feb 1992) to 0.548 (June 1993).

When all fish were divided into adult and juvenile components (Fig. 3.3a), it was apparent that although peaks in abundance of adult fish did not correspond from one year to the next, a clear seasonal trend was evident in the abundance of juvenile fish in the surf. During the first year (Jul '91 - Jun '92), numbers of juvenile fish were greatest (1 594-3 800, mean = 2 500) from January-May, compared to the remainder of the year (935-1 744, mean = 1 246). Similarly, catches made between February and June of the second year (119-5 449, mean = 2 667) were considerably greater than during the remaining months (235-802, mean = 662). After the application of a smoothing algorithm (three month mean) to these data, seasonal trends in abundance (Fig. 3.3b) became even more clear, with peaks occurring in February 1992 and March 1993.

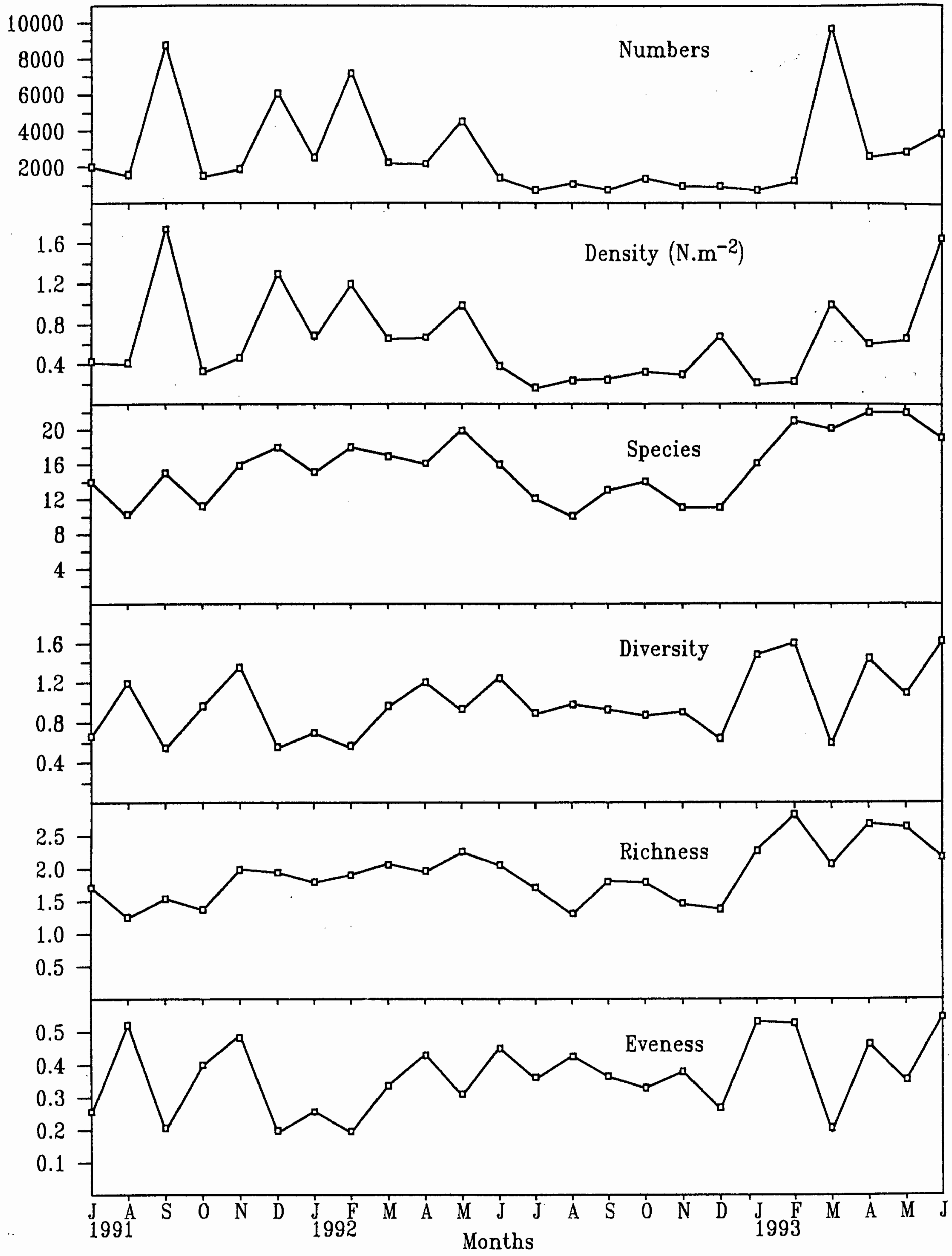


**Fig. 3.2.** Monthly variations in the number of individuals, density, number of species, diversity, richness and evenness of surf-zone fish in False Bay, between July 1991 and June 1993. Data for all sites combined.

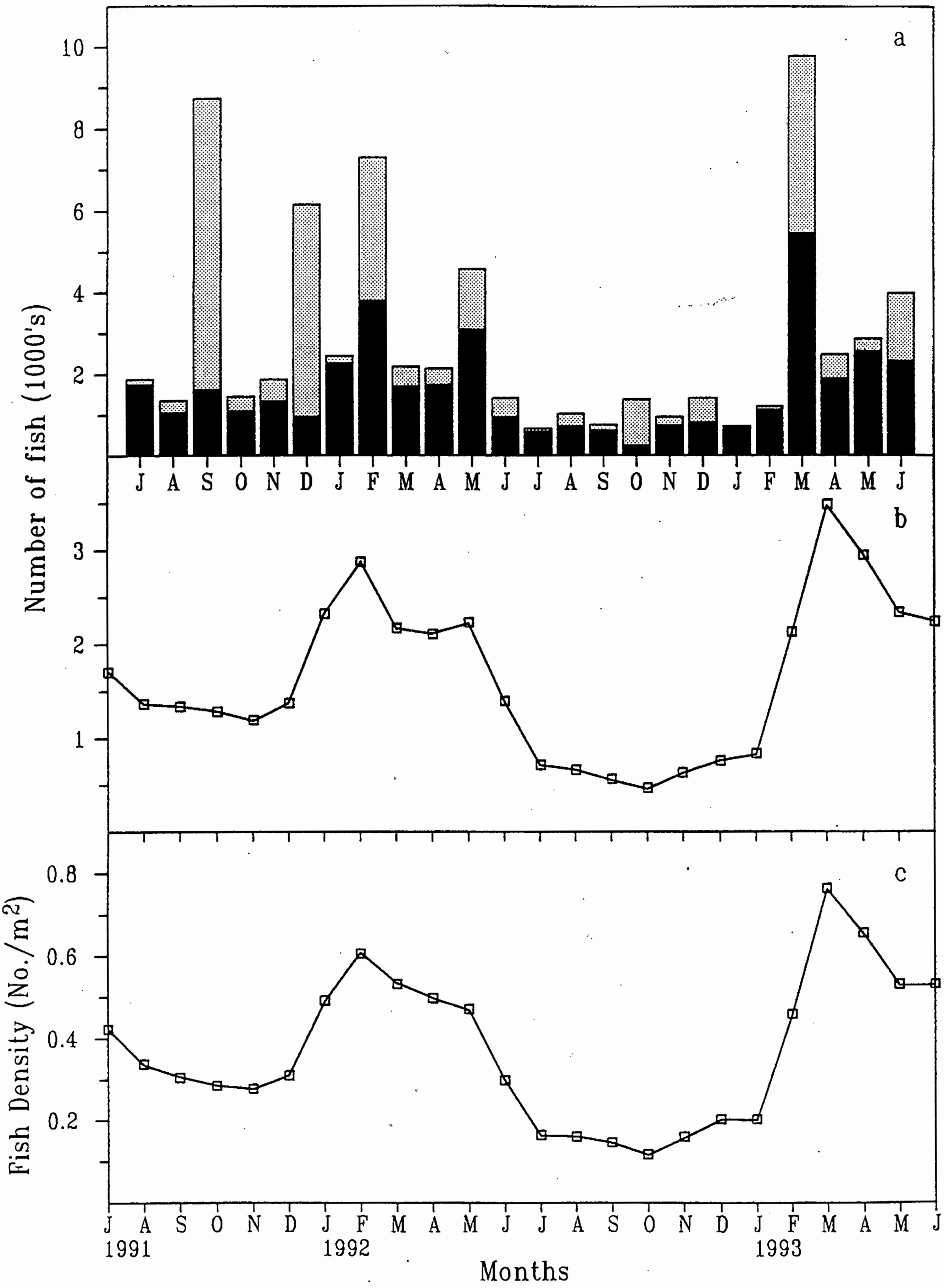


Fig. 3.3 Monthly variations in the number of juvenile (solid bars) and adult fish (stippled bars) (a) and three month mean of juvenile fish abundance (b) and density (c) in the surf-zone of False Bay from July 1991 to June 1993.

Cluster analysis of the monthly samples (combined sites) separated them into four major groups at the 70% level on the basis of similarities between species composition and abundance (Fig. 3.4). Groups formed through this analysis showed considerable similarity to the seasonal fluctuations in the number of juvenile fish in the surf, species numbers and richness. Groups 1 and 2 from the cluster analysis (composed of samples collected from July-December 1991 and from June-December 1992) corresponded to periods when juvenile density, species numbers and richness were low, while Groups 3 and 4 (composed of samples collected from January-May 1992 and from January-June 1993) corresponded to periods of high juvenile density, species numbers and richness. This categorisation was borne out by the MDS analysis which separated out the four groups of samples identified above, with Groups 1 and 2 appearing on the right, and Groups 3 and 4 appearing on the left hand sides of the ordination plot respectively (Fig. 3.4).

Temporal fluctuations in the total numbers of individuals of each species captured per month (Table 3.1), allows the separation of these species into three major groups. The first group comprises eight "Resident" species which were present in the catches more or less throughout the year. This group was made up primarily of the more abundant species, all of which were represented by more than 50 individuals. All but one of these (*Rhabdosargus globiceps*) were represented by adult and juvenile individuals. The second group of 11 "Migrant" species included some (e.g. *Lichia amia, Pomatomus saltatrix, Amblyrhynchotes honkenii*) which were most abundant during summer and autumn (Dec-May) and others (e.g. *Liza dumerilii, L. tricuspidens, Mugil cephalus*) which were most numerous during autumn and winter (Jun-Nov). Most (9) of these species were represented largely, or exclusively by juveniles. *Gilchristella aestuaria*, the last species in this category, was more abundant during winter and spring, rarely being present in catches during the rest of the year. The final group, termed "Sporadics", contained the greatest number of species (26), almost all of which (25) were represented by only a few (<25) individuals. These species were recorded as varying combinations of adult and juvenile fish.

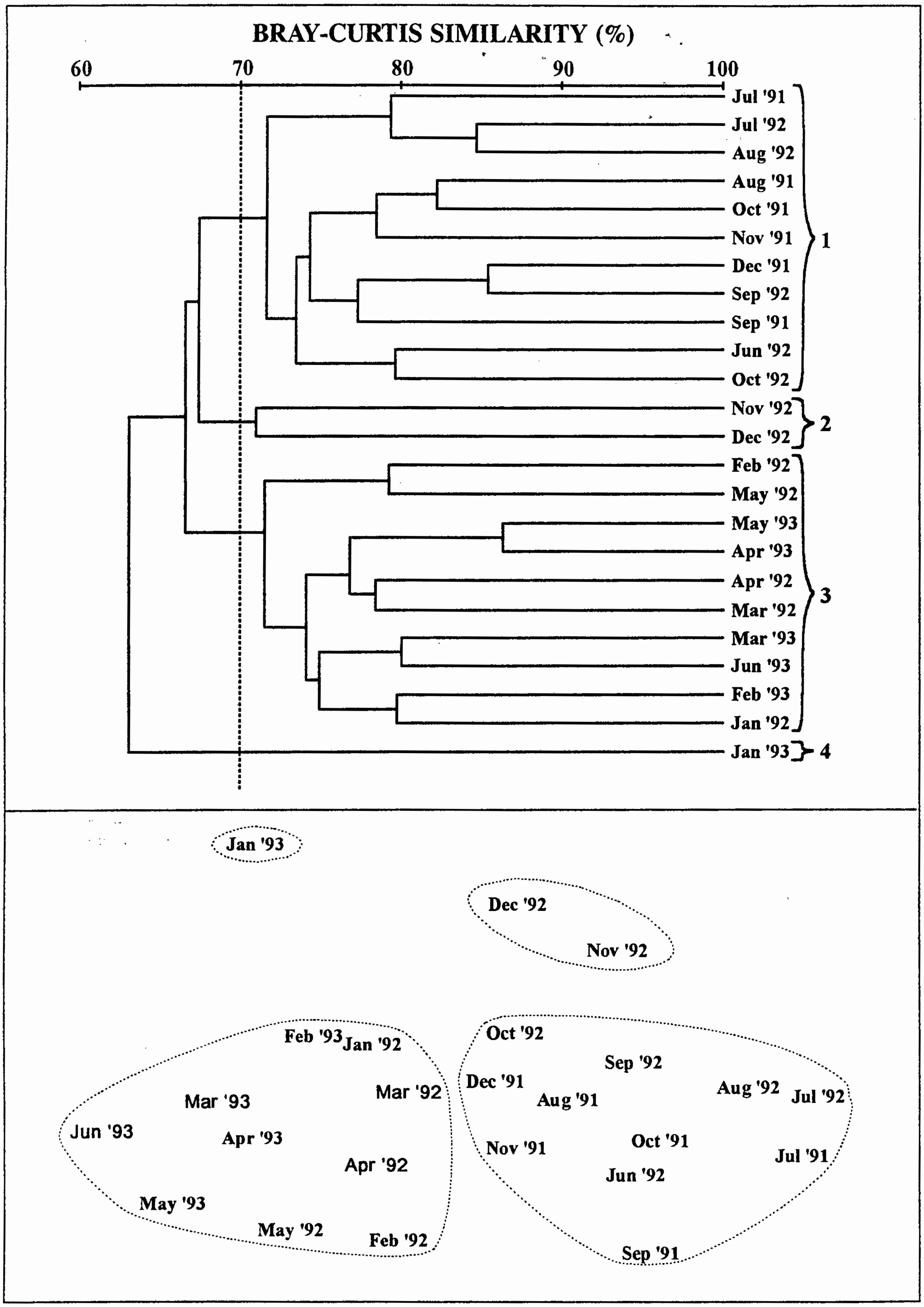


Fig. 3.4. Dendrogram and MDS ordination plot of density data from monthly seine net hauls made in the surf-zone of False Bay, between July 1991 and June 1993. Groups of species delineated at the 70% level in the dendrogram are circled in the ordination plot. Stress for the MDS ordination = 0.20.

**Table 3.1.** Composition and abundance of fish in monthly seine net hauls made in the surf at 11 sites in False Bay, South Africa between July 1991 and June 1993. Fish are classified as being Resident (R), migrant (M) or Sporadic (S) species, based on their occurrence in the catches.

| | | 1991 | | | | | | 1992 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Class. | JUL | AUG | SEP | OCT | NOV | DEC | JAN | FEB | MAR | APR | MAY | JUN |
| *Atherina breviceps* | R | 116 | 320 | 7338 | 310 | 466 | 5147 | 215 | 6269 | 1233 | 433 | 1885 | 580 |
| *Liza richardsonii* | R | 1682 | 849 | 1276 | 1006 | 933 | 869 | 2044 | 762 | 827 | 1303 | 2494 | 610 |
| *Rhabdosargus globiceps* | R | 11 | 160 | 29 | 69 | 95 | 20 | 74 | 81 | 63 | 324 | 50 | 94 |
| *Psammogobius knysnaensis* | R | 14 | 7 | 33 | 41 | 60 | 23 | 25 | 18 | 6 | 12 | 17 | 33 |
| *Rhinobatos annulatus* | R | 34 | | 3 | 1 | 6 | 2 | 1 | | 7 | 2 | 1 | 1 |
| *Caffrogobius nudiceps* | R | | 3 | | | 5 | 11 | 3 | 1 | 4 | 1 | 7 | |
| *Lithoganthus lithognathus* | R | 3 | | 1 | 1 | 11 | 8 | 5 | 2 | 2 | 6 | 7 | |
| *Clinus superciliosus* | R | 3 | 4 | | 2 | | 6 | | | 1 | | 6 | 1 |
| *Diplodus sargus* | M | 1 | | | | 2 | | | | 2 | | | 1 |
| *Pomatomus saltatrix* | M | | | | | | 11 | 38 | 20 | 20 | 1 | 3 | 4 |
| *Heteromycteris capensis* | M | | 2 | 22 | 6 | 6 | 1 | 3 | 8 | 1 | 4 | 1 | |
| *Umbrina canariensis* | M | 6 | | 2 | | | 1 | | 1 | | | 3 | 4 |
| *Lichia amia* | M | | | | | | 6 | 1 | 1 | 2 | | | |
| *Amblyrhynchotes honkenii* | M | | 1 | | | 1 | 27 | 25 | 1 | 3 | 2 | | |
| *Liza tricuspidens* | M | 1 | | | 2 | | | 1 | 69 | | 12 | | 157 |
| *Liza dumerilii* | M | 4 | 2 | | | | | | 50 | | | 20 | 7 |
| *Mugil cephalus* | M | | | | | | | | 1 | 10 | 1 | 24 | 1 |
| *Solea bleekeri* | M | | | | | | 1 | | | 1 | | 28 | |
| *Gilchristella aestuaria* | M | 105 | 160 | 40 | 26 | 5 | 1 | | 2 | | 1 | 4 | |
| *Trachinotus africanus* | S | | | | | | | | | | | | |
| *Trachinotus botla* | S | | | | | | | | | | | 1 | |
| *Heniochus acuminatus* | S | | | | | | | | | | | | |
| *Coryphaena hippurus* | S | | | | | | | 3 | | | | | |
| *Monodactylus falciformis* | S | | | | | | | | | | | | |
| *Rhabdosargus holubi* | S | | | | | | | | | 3 | | | 1 |
| *Sphyraena acutipinnis* | S | | | | | 1 | | | | | | | |
| *Trachinocephalus myops* | S | | | | | | | | | | | | |
| *Dichistius multifasciatus* | S | | | | | | | | | | 1 | | |
| *Sarpa salpa* | S | | | | | 271 | | | | | 29 | 6 | |
| *Caffrogobius caffer* | S | | | | | | | | 1 | | | | |
| *Diplodus cervinus* | S | | | | | | | | | | | | |
| *Haploblepharus edwarsii* | S | | | | | | | | | | | | |
| *Fucomimus mus* | S | | | | | | | | | | | | |
| *Gonorhynchus gonorhynchus* | S | | | | | | | | | | | | |
| *Lithoganthus mormyrus* | S | | | | | | 5 | 5 | | | | | |
| *Syngnathus acus* | S | | | | 1 | | | | | | | | |
| *Chelidonichthyes capensis* | S | 3 | | 6 | | | | | | | | | 4 |
| *Cancelloxus longior* | S | 1 | 2 | 3 | | 1 | | | | | | | |
| *Trachurus trachurus* | S | | | | | 1 | | | | | | | |
| *Engraulis japonicus* | S | | | | | | 1 | | | | | | |
| *Dichistius capensis* | S | | | 2 | | | | 2 | 3 | | 3 | 4 | 1 |
| *Clinus latipennis* | S | | | 3 | | 1 | 5 | | | 1 | | 1 | |
| *Triakis megalopterus* | S | | | | | | | | | | | | |
| *Dasyatis crysonota* | S | | | | | | | | | | | 1 | 1 |
| *Myliobatis aquila* | S | 1 | | 4 | | | | | 1 | | | | |

continued...

**Table 3.1.** (Continued)

| | 1992 | | | | | | 1993 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | JUL | AUG | SEP | OCT | NOV | DEC | JAN | FEB | MAR | APR | MAY | JUN | TOTAL |
| *Atherina breviceps* | 67 | 282 | 61 | 1078 | 142 | 23 | 13 | 51 | 8480 | 717 | 257 | 1540 | 37023 |
| *Liza richardsonii* | 546 | 690 | 563 | 93 | 692 | 815 | 387 | 652 | 763 | 1264 | 2093 | 1261 | 24474 |
| *Rhabdosargus globiceps* | 19 | 19 | 27 | 133 | 22 | 9 | 58 | 235 | 188 | 122 | 206 | 533 | 2641 |
| *Psammogobius knysnaensis* | 14 | 13 | 69 | 34 | 51 | 19 | 2 | 27 | 26 | 10 | 2 | 44 | 600 |
| *Rhinobatos annulatus* | | | | 2 | | | 10 | 30 | 56 | 242 | 139 | 210 | 696 |
| *Caffrogobius nudiceps* | 1 | 2 | | 3 | 13 | 20 | 71 | 34 | 158 | 21 | 22 | 140 | 582 |
| *Lithoganthus lithognathus* | | | 1 | | | 2 | | 35 | 40 | 3 | 36 | 147 | 324 |
| *Clinus superciliosus* | 1 | | | 2 | 1 | | 4 | 10 | 14 | 27 | 9 | 8 | 93 |
| *Diplodus sargus* | 1 | 2 | 1 | 5 | | | | 4 | | 3 | | 20 | 91 |
| *Pomatomus saltatrix* | | | 11 | 1 | 5 | 2 | 4 | 2 | 3 | 1 | | 18 | 82 |
| *Heteromycteris capensis* | 1 | 2 | | | | 4 | 2 | 1 | | 7 | | 5 | 62 |
| *Umbrina canariensis* | 2 | 1 | 1 | | 1 | | 1 | 1 | 3 | 1 | 6 | 18 | 58 |
| *Lichia amia* | | | | 1 | | 4 | 5 | 8 | 14 | 3 | | | 45 |
| *Amblyrhynchotes honkenii* | | | 1 | 9 | | 2 | 23 | 80 | 19 | 13 | 6 | 7 | 220 |
| *Liza tricuspidens* | 52 | 69 | 4 | 21 | | | | 17 | | | 9 | 5 | 674 |
| *Liza dumerilii* | 3 | | 1 | | | | | 8 | 1 | 2 | 9 | 1 | 137 |
| *Mugil cephalus* | 2 | | | | | | | | | 7 | 7 | | 97 |
| *Solea bleekeri* | | 1 | 2 | | | | | | | 5 | 18 | | 66 |
| *Gilchristella aestuaria* | | | | | 5 | | | 4 | 1 | 1 | 4 | 9 | 30 |
| *Trachinotus africanus* | | | | | | | | | 1 | | | | 1 |
| *Trachinotus botla* | | | | | | | | | | | | | 1 |
| *Heniochus acuminatus* | | | | | | | | 1 | | | | | 1 |
| *Coryphaena hippurus* | | | | | | | | | | | | | 3 |
| *Monodactylus falciformis* | | | | | | | | | | 1 | | | 1 |
| *Rhabdosargus holubi* | | | | | | | 1 | | | 2 | 1 | | 8 |
| *Sphyraena acutipinnis* | | | | | | | | | | | | | 1 |
| *Trachinocephalus myops* | | | | | | | | | 2 | | | | 2 |
| *Dichistius multifasciatus* | | | | | | | | | | | | | 1 |
| *Sarpa salpa* | | | | | | | 134 | | | 30 | 17 | | 488 |
| *Caffrogobius caffer* | | | | | | | | | | | 1 | 2 | 4 |
| *Diplodus cervinus* | | | | | | | | | | | | 2 | 2 |
| *Haploblepharus edwarsii* | | | | | | | | | | | 1 | | 1 |
| *Fucomimus mus* | | | | | | | | | | | 1 | | 1 |
| *Gonorhynchus gonorhynchus* | | | | | | | | | 1 | | | | 1 |
| *Lithoganthus mormyrus* | | | | 1 | 2 | | 1 | | 1 | | | | 15 |
| *Syngnathus acus* | | | | | | | | 1 | | | | | 2 |
| *Chelidonichthyes capensis* | | | 3 | | | | | | 1 | | 4 | 3 | 24 |
| *Cancelloxus longior* | | | | | 1 | | | | 1 | | | | 9 |
| *Trachurus trachurus* | | | | | | | | | | | | | 1 |
| *Engraulis japonicus* | | | | | | | | | | | | | 1 |
| *Dichistius capensis* | | | | | | | | | | | | | 15 |
| *Clinus latipennis* | | | | | | | | 2 | | | | | 13 |
| *Triakis megalopterus* | | | | | | | | | | | 1 | | 1 |
| *Dasyatis crysonota* | | | | 1 | | | | | | | | | 3 |
| *Myliobatis aquila* | | | | | | | | 1 | | | | | 7 |

Similarities between patterns in the abundance of the 20 most common species recorded, based on their occurrence in the 24 sampling months, were also examined using CLUSTER and MDS analysis. Species grouping evident at the 40% level in the dendrogram (Fig. 3.5) were also evident in the MDS plot, but were not clearly delineated due to the high stress loading (0.17) on the latter. Groups of species formed by this analysis showed a strong similarity to the categorisation outlined above, in that Groups 1 and 2 (6 and 2 species respectively) were composed solely of "Resident" species, Groups 2 and 4 (4 and 2 species respectively) of "Migrant" species most abundant during summer and autumn, while Group 5 (4 species) contained migrant species most abundant during autumn and winter (Fig. 3.4, Table 3.1). The two remaining species, *Sarpa salpa* and *G. aestuaria* were not included in any of these groups. The former occurred sporadically in the catches, while the latter was a migrant species most prevalent during winter.

Examination of the recruitment patterns dispayed by some of the more abundant species (Fig. 3.6) recorded during this study, indicated that most 0+ juveniles first enter the surf between summer and early winter. Recruitment was confined to a few months only for most species, either during summer (*P. saltatrix*, *A. honkenii*, *Atherina breviceps*, *R. globiceps*, *D. sargus*, and *P. knysnaensis*), or during autumn and early winter (*M. cephalus*, *L. tricuspidens*, *L. dumerilii*, *Solea bleekeri*), but some species recruited over more extended periods (*Heteromycterus capensis*: summer - early winter, *L. richardsonii*: all year round). Size at first recruitment for most species entering the surf during the summer months (<25 mm) was generally smaller than those entering entering the surf during winter (60-100 mm).

Differences were evident in overall numbers of fish and in population parameters recorded during the first and second years of the study. Both the total number of fish captured (41 769) and the mean density (0.763 fish $m^{-2}$) during the first year were considerably higher than those recorded during the second year (26 850 individuals, 0.517 fish $m^{-2}$). However, total number of species recorded during the first year (37) was lower than that recorded during the second (40), with only 30 of the 45 species being recorded in both years. Species richness (3.48), diversity (0.98) and evenness (0.27) were also lower during the first than the second year ($d = 3.82$, $H' = 1.39$, $j = 0.38$).

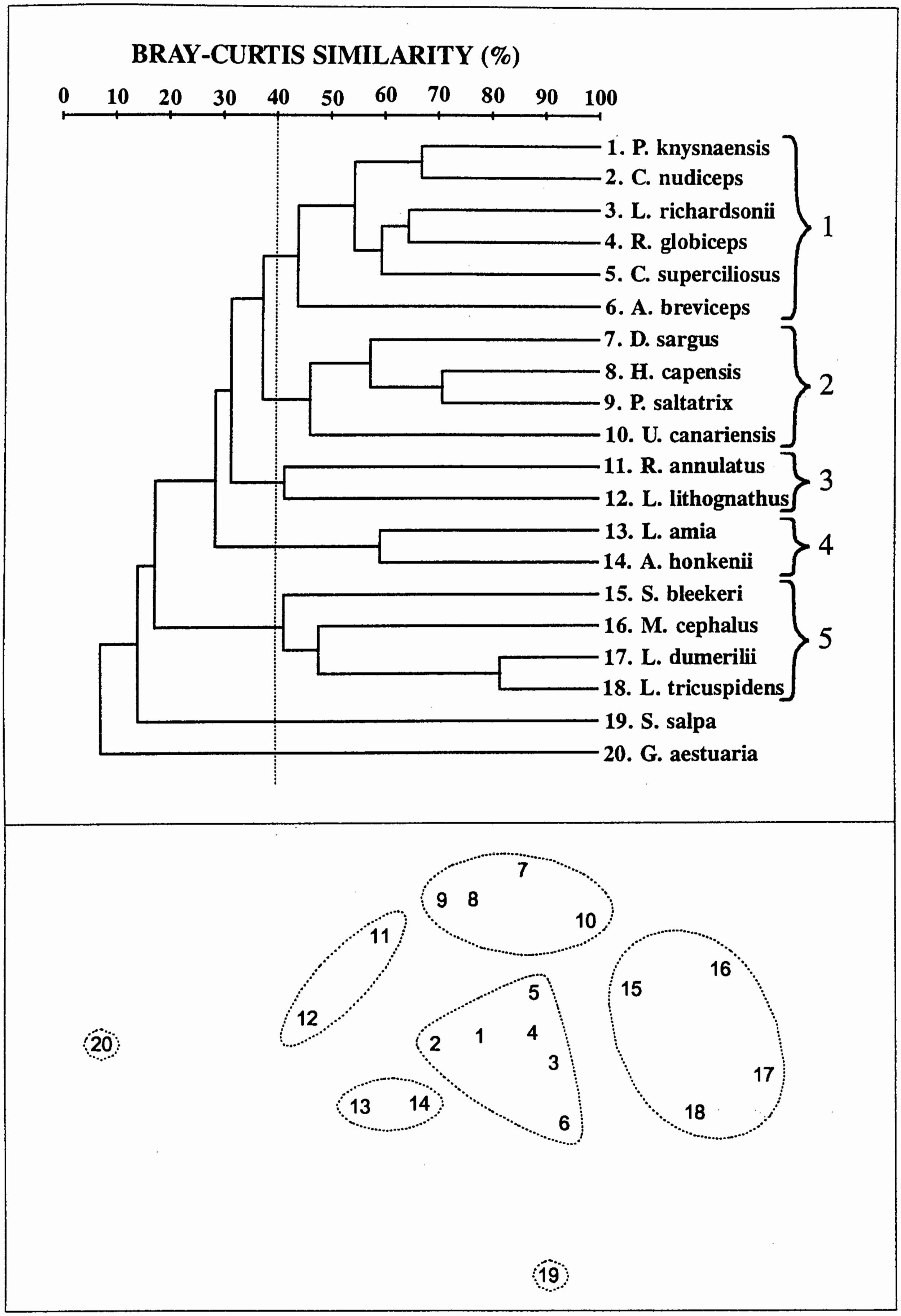


Fig. 3.5. Dendrogram and MDS ordination plot showing similarities between species based on their occurrence in the 24 sampling months. Groups of species delineated at the 40% level in the dendrogram are circled in the ordination plot. Stress for the MDS ordination = 0.17.

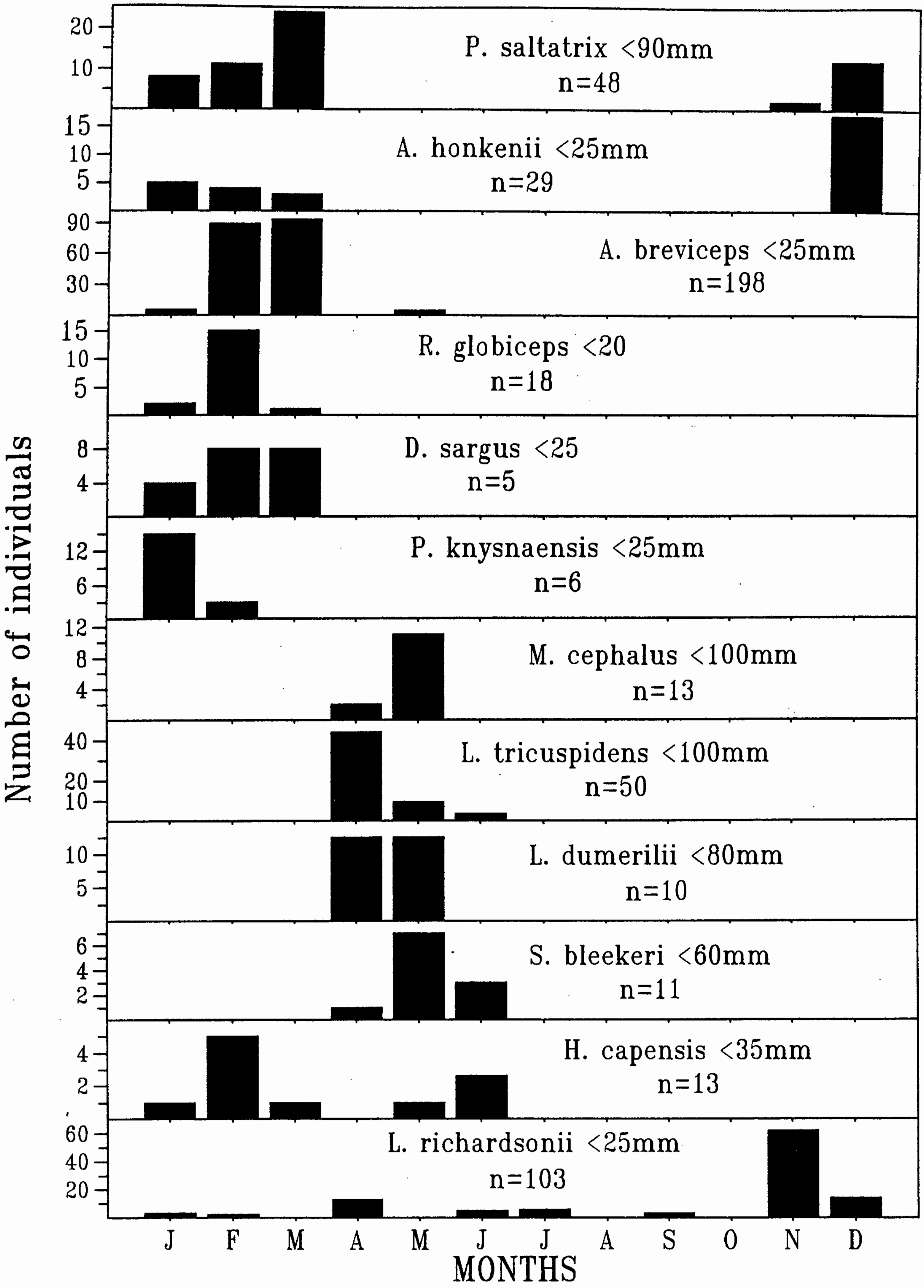


Fig. 3.6. Seasonal variation in recruitment of 0+ juveniles into the False Bay surf zone.

Decreases in the abundance of the two most common species recorded during this study (*A. breviceps* and *L. richardsonii*), by 48 and 33% respectively, were primarily responsible for the decline in overall numbers and density between the first and second years (Table 3.1). This trend was not universal, however, as many of the less numerous species (e.g. *Diplodus sargus*, *P. saltatrix*, *Heteromycterus capensis*, *R. globiceps* and *Umbrina canariensis*) showed considerable increases (up to 98 fold) in abundance from the first to the second year. Although no change was evident in the ranking of the top three species (*A. breviceps*, *L. richardsonii*, *R. globiceps*) from the first year to the second, some changes were evident in the relative positions occupied by species in the remaining top ten places. Some of these (e.g. *D. sargus*, *P. saltatrix*, *H. capensis*) increased their relative positions, while others (e.g. *L. tricuspidens*, *L. dumerilii*, *Gilchristella aestuaria*) decreased, or maintained relatively constant (e.g. *Psammogobius knysnaensis*, *A. honkenii*) positions.

### 3.3.3 Multivariate analyses of relations between biotic and environmental variables

Results of the BIOENV and stepwise multiple regression analyses performed on the species composition and the total density data from each of the individual sites are shown in Tables 3.3 and 3.4 respectively. Nine environmental variables (water temperature, wave height, surf-zone width, turbidity, wind speed, wind direction, macrophyte detrital abundance, tidal height and time at which the sample was taken) were used in these analyses. Results from the BIOENV procedure yielded rank correlation coefficients ($p_w$) of 0.08-0.35, with the number of environmental correlates for each site ranging between 1 and 6 (Table 3.2). Wave height (six sites) and water temperature (five sites) were correlated with temporal variability in community structure at a greater number of sites than any of the other variables (2-3 sites only). Results of the stepwise regression analyses indicated that the suite of environmental variables measured have little influence on temporal variations in overall density of fish at the different sites. These variables were able to predict ≥40% of the temporal variability at only three of the 11 sites, these being Cemetery Beach ($r^2_{adj.} = 0.56$), Sunrise Beach ($r^2_{adj.} = 0.51$) and Melkbaai ($r^2_{adj.} = 0.40$) (Table 3.3). Variables included in these models were wind direction (all three sites), wind speed (Sunrise and Melkbaai), time of day (Sunrise only) and temperature and tidal height (Cemetery only). Environmental variables accounted for <1% of the fluctuations in overall fish density at the other sites, except for Swartklip, where 16% of the variability was attributed to variations in surf-zone width.

Multivariate analyses involving the grouped data (monthly data from all sites combined) were performed with the same set of physical environmental variables as the above, except that the variables "time of day" and "tidal height" were omitted from the models and wind direction was coded in a slightly different manner (see methods). The BIOENV procedure indicated that of these variables, water temperature alone was responsible for the greatest part of the variability observed ($p_w = 0.18$). Stepwise multiple regression analysis suggested that <20% of the variability associated with monthly fluctuations in the density of fish in the surf could be predicted by the environmental factors measured, with surf-zone width being the only environmental variable selected by the model ($r^2_{adj.} = 0.17$).

## 3.4 DISCUSSION

Ross *et al.* (1987) advocated that temporal variations in surf-zone fish assemblages and the factors that control these variations could be visualized as a hierarchy, ranging from climatic events that influence annual variations in year class strength, through reproductive and feeding movements that result in seasonal patterns of occurrence and abundance, to short term fluctuations in physico-chemical factors such as wave height, salinity, temperature and wind speed that influence point abundance. In this study, the difference between the number of species caught in the first and second years of sampling was not great (37 and 40 species respectively). However, the overall numbers of fish caught and the mean density of fish in the surf declined by 32 and 36% respectively. Declines in the abundance of the top two species (*Atherina breviceps*, *Liza richardsonii*) were primarily responsible for this reduction (nearly 50% for the former) but no change was evident in the relative ranks occupied by the top three species. However, important changes were evident in the relative ranking and abundance of some other important species. Many of the summer migrants (e.g. *Diplodus sargus*, *Heteromycterus capensis* and *Pomatomus saltatrix*) increased in abundance and relative ranking from the first to the second year, whereas most winter migrants (e.g. *Liza tricuspidens*, *L. dumerilii*, *Gilchristella aestuaria*), decreased over the same period.

Table 3.2. Results of the BIOENV analysis of the influence of nine environmental parameters on surf-zone fish community structure at 11 sites in False Bay. Spearman rank correlation coefficients ($p_w$) are included for each combination of variables selected by the model.

| | Temperature | Wave height | Surf-zone width | Turbidity | Wind speed | Wind direction | Macrophyte abundance | Tidal height | Time of day | $p_w$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Long Beach | | | | | | | X | | | 0.34 |
| Mackerel Beach | | | | | | X | | | | 0.31 |
| Muizenberg | X | X | X | X | X | | | X | | 0.26 |
| Sunrise | X | X | | | | | | | | 0.20 |
| Cemetry Beach | | X | | | | X | | | | 0.17 |
| Swartklip | | X | | | | X | | | X | 0.08 |
| Macassar Beach | | | | X | | | | | | 0.12 |
| Melkbaai | X | X | | | | | | | | 0.12 |
| Blake's Cove | X | | X | X | | | X | X | X | 0.15 |
| Makouvlei | | | | | | | X | | | 0.15 |
| Gordon's Bay | X | | | | X | | | X | X | 0.24 |
| All sites | X | | | | | | | | | 0.18 |

Table 3.3. Results of the multiple stepwise regression analysis of the influence of nine environmental parameters on surf-zone fish abundance at 11 sites in False Bay. Correlation coefficients ($r^2_{adj}$) are included for each combination of variables selected by the model.

| | Temperature | Wave height | Surf-zone width | Turbidity | Wind speed | Wind direction | Macrophyte abundance | Tidal height | Time of day | $r^2_{adj.}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Long Beach | | | | | | | | | | <0.01 |
| Mackerel Beach | | | | | | | | | | <0.01 |
| Muizenberg | | | | | | | | | | <0.01 |
| Sunrise | | | | | X | X | | | X | 0.51 |
| Cemetry Beach | X | | | | | X | | X | | 0.56 |
| Swartklip | | | X | | | | | | | 0.16 |
| Macassar Beach | | | X | | | | | | X | 0.01 |
| Melkbaai | | | | | X | X | | | | 0.40 |
| Blake's Cove | | | | | X | | | | | <0.01 |
| Makouvlei | | | | | | | X | | | <0.01 |
| Gordon's Bay | | X | X | | X | | | | | <0.01 |
| All sites | | | X | | | | | | | 0.17 |

Sampling equipment and methodology used by Bennett (1989a) to sample the fish assemblage at Fishoek Beach (also in False Bay), during 1980-81 was similar to that employed here, and it is interesting to note that although the overall composition of the catches are relatively similar, a considerable change was evident in at least one species -- *Pomadasys olivaceum.* This was the second most abundant species recorded by Bennett (1989a), but was completely absent from the catches made here. It is possible that I simply failed to catch this species, but this is unlikely, as many of the sites sampled during this survey were situated in close proximity to Bennett's (1989a) site, and no species captured at any of the 11 sites sampled during this survey displayed such high site specificity. It is more likely that changes in recruitment success, brought about by large scale changes in climatic and hydrological factors, were responsible for these changes, as Ross *et al.* (1987) and other authors (e.g. Ziljstra & Whitte 1985, Bergman *et al.* 1988, Pihl 1990) have suggested.

False Bay, situated on the southeastern tip of Africa, is flanked by two dominant ocean current systems. The Agulhas current, flowing southwards along the east coast of southern Africa is a warm current, while the Benguela is considerably colder and flows northwards up the western side of the subcontinent. The Agulhas current tends to follow the edge of the continental shelf as it moves down the coast of southern Africa, remaining close inshore off the east coast but tending to move offshore as it passes the southern part of the subcontinent. Apon reaching a point south of Cape Point the bulk of the water is reflected eastwards forming the return Agulhas current which flows into the South Indian Ocean Gyre (Shannon *et al.* 1973). Not all water is channelled in to the return current, however, as small pockets of warm Agulhas water or larger eddies periodically break off and continue to move westward round Cape Point (Talbot & Penrith 1962, Bang 1971) or may even move into False Bay (Tajaard 1991). Timing of these warm water intrusions are likely to have profound effects on larval advection and consequent recruitment to nearshore waters of the southwestern Cape.

Seasonal changes in abundance are considered by many authors (e.g. Gunter 1958, McFarland 1963, Ross *et al.* 1987) to be the primary characteristics of surf-zone fish assemblages. Seasonality is clearly of considerable importance, as almost all studies of sufficient duration have demonstrated the existence of seasonal fluctuations in abundance and species richness in the surf (Warfel & Merriman 1944, Gunter 1945, 1958, McFarland 1963, Anderson *et al.*

1977, Lasiak 1984a - fine mesh study only, Peters & Nelson 1987, Wright 1988, 1989a, Gibson *et al.* 1993, Lamberth *et al.* 1995a), in abundance only (Modde & Ross 1981, McMichael & Ross 1987, Ross *et al.* 1987, Whitfield 1989), or at least in the number of species present (Senta & Kinoshita 1985, Bennett 1989a). Although he provided no evidence to substantiate his conclusion, Bennett (1989a) suggested that the differences in the strengths of seasonal cycles reported in the literature for surf-zone fishes merely reflected the magnitude of seasonal variations in physical factors (water temperature being the most important), and are thus governed by latitude.

Typically, it appears that in areas where the seasonal variation in water temperature are considerable (>20°C), such as beaches in the Gulf of Mexico, on the Atlantic coast of the United States and in the Persian Gulf (Warfel & Merriman 1944, Gunter 1945, 1958, McFarland 1963, Schaefer 1967, Anderson *et al.* 1977, Wright 1988, 1989a) seasonal fluctuations are very pronounced. However, seasonal fluctuations in fish communities frequenting sandy beaches in northern Europe, where water temperatures have a small range, but are very low (<8°C) for much of the year, are arguably the most pronounced of all. These communities are made up of almost entirely of flatfish species comprising primarily transient juveniles, that inhabit inshore sandy beach areas for only a few months each year (Macer 1967, Edwards & Steele 1968, Gibson 1973a, Lockwood 1974, Kuipers 1977, Poxton *et al.* 1982, Poxton & Nasir 1985, Pihl & Van der Veer 1992, Gibson *et al.* 1993). Immigration of larvae and juveniles of most species into these nursery grounds is highly synchronous and takes place over a couple of months (April-June) at the beginning of summer. After peaking during this period, numbers decline steadily as a result of natural mortality (due mainly to predation ) until autumn (September/ October) when numbers drop suddenly as practically all the survivors move into deeper waters off-shore. Similarly, researchers working on Gulf and Atlantic coast beaches in the United States have noted that fish are either completely absent or very rare in the surf during the coldest winter months (Warfel & Merriman 1944, Gunter 1958, McFarland 1963). Typically, however, this occurs for only one or two months of each year, when temperatures reach their lowest values. In contrast to this, in areas in which temperatures do not drop particularly low (≤10°C), such as California and Spain, seasonal variations in the abundance, biomass and community structure of fish communities frequenting sandy beaches are usually weak or ill defined (Allen & De Martini 1983, Reina-Hervas & Serrano 1987).

Of the seven physical variables recorded during this study, only surf-zone water temperature and (to a lesser extent) wind direction showed clear seasonal variations. Water temperature, which ranged from 11-22°C, peaked during mid-summer and was significantly greater during spring, summer and autumn than during winter. Wind direction was predominantly southerly to southeasterly, punctuated by winds with a northerly component more frequently during winter than the other seasons. Mean turbidity appeared to be seasonally greater during winter in the first year, but this pattern was not matched by data from the second year. Although neither the total number nor the overall density of fish in False Bay fluctuated seasonally, seasonal patterns were evident in the total number and density of juvenile fish in the surf-zone, and to a lesser extent in the species richness and the total number of fish species present in the catches. Peaks in these variables did not necessarily coincide exactly in both years, but all reached their greatest magnitude during summer and autumn (December-May). Cluster and MDS analysis separated the monthly samples roughly into seasonal components (summer, autumn and winter, spring), suggesting that surf-zone fish community structure also fluctuates seasonally in this area.

Abundance of juvenile fish and species richness of the whole assemblage were greatest in a broad period extending from mid-summer right through to the beginning of winter. This prolonged peak in abundance may be attributed to two overlapping waves of juveniles that recruited during this period. The first group of species (most abundant in the surf during summer and autumn) is composed of juveniles that recruit directly into the surf-zone during the summer months after being spawned in spring. The second group (most abundant in the surf during autumn and early winter) is composed of post-estuarine juveniles that enter the surf as the first rains of autumn breach the mouths of southwestern Cape estuaries in which these fish reside over the summer months. Most of these recruits do not remain in the surf for long and have been classified in this study as seasonal migrants (e.g. *L. amia*, *P. saltatrix*, *L. dumerilii*, *L. tricuspidens*), while others (e.g. *R. globiceps*) remain in the surf for most of the year, and have therefore been classified as resident species. *G. aestuaria* was the only species more abundant during winter than any other season. This species, classified as an estuarine resident by Wallace *et al.* (1984), migrates to the heads of estuaries at the onset of the rainy season (Winter 1979), and is probably only flushed into the surf after considerable rainfalls.

These results are consistent with those obtained in other South African studies. Bennett (1989a) noted that weak seasonal fluctuations were evident in the number of species present, and in the community structure of the surf-zone fish assemblage at Fishoek Beach, also in False Bay. Seine net hauls made by Bennett (1989a) yielded the greatest number of species (9-10) during the summer months and the lowest (4-5) during winter. Multivariate analyses separated Bennett's catches into "spring", "summer" and "autumn and winter" components. Lamberth *et al.* (1995a) found that variations in commercial beach-seine net catches in False Bay are strongly seasonal, with most fish (93%) being caught between late spring and early autumn. However, it is unknown how much this reflected the abundance of fish in the surf and how much was a function of variations in fishing effort. Lasiak (1984a) found that no seasonal trends were discernible in either the overall abundance or species diversity of fish in coarse-mesh beach-seine hauls made in the surf at King's Beach, in Algoa Bay. However, she did find that diversity and number of species in the fine mesh catches made in the same area, were both greater during summer than winter. Water temperatures range from 11-26°C in this area. However, little correspondence was evident between groups of species identified on the basis of seasonal variation in their abundance, and those identified on the basis of spatial variations in occurrence and abundance (Clark *et al* 1996a, Chapter 1). Migrant species most abundant during autumn and early winter (Group 5, Fig. 3.5) were all found exclusively at sites in the northeastern corner of the Bay. This supports the notion of Clark *et al.* (1996a, Chapter 1) that, shortly after being flushed from estuaries, these estuarine dependent species (*sensu* Wallace *et al.* 1984) are attracted to, and briefly congregate in the estuarine-like conditions that prevail in this part of the Bay. No other obvious similarities between spatially and temporally separated groups of species were evident.

Despite the application of some sophisticated multivariate techniques to data collected during this survey, the precise factors that control variations in fish abundance and community structure remain obscure. Although certain variables (e.g. water temperature, wave height, wind speed and direction) were implicated more frequently than others, every single one of the environmental variables used in this analysis were incorporated into models describing fluctuations in abundance or community structure in at least one of the 11 sites. Coefficients of determination ($r^2_{adj.}$ values) and rank correlation coefficients ($p_w$) were, in most cases, low or not significant. This apparent unpredictability is probably a function of a number of interacting influences. Differences in the physical attributes of different sites has a profound influence on the composition of surf-zone fish communities (Clark *et al.* 1996a, Chapter 1), which in turn is likely to influence the response of the community to any changes in these variables. Variations in the abundance of detached macrophytes, identified by Robertson & Lenanton (1984) as the primary determinant of fish abundance, has a profound influence on fish community structure at Long Beach (site 1), for example, but not at any of the other sites. The protection this material affords to benthic species at this site is important, as it is the only cover available in the exceptionally clear and calm waters prevalent there. The influence of wind (speed and/or direction) on abundance was strongly evident at some sites, and may, as Lasiak (1982) suggested, be one of the primary abiotic variable at some sites, as it has the ability to influence wave action, turbidity and localized water temperature. All biotic and environmental data were collected concurrently, and thus the influences of abiotic factors acting prior to sampling, or the duration over which these variables were active were automatically excluded. Lasiak (1984a), for example, found that the wind speed averaged over the preceding 12-48 hours had a greater influence on fish abundance than that recorded at the time of sampling, or averaged over the whole month. Also, as suggested by Clark *et al.* (1996a, Chapter 1), the influences of many of the abiotic factors measured are probably controlled or at least strongly moderated by others, while some (wave height and surf-zone width for example) are collinear with each other, or with some variables that were not even measured. Shoaling behaviour exhibited by many species results in a patchy distribution of these individuals in the surf (Lasiak 1982, Ross *et al.* 1987, Gibson *et al.* 1992), which means that all hauls made do not necessarily represent the true abundance of fish in the surf. Thus, the interaction of these factors and the influence of variations in netting efficiency (Hunter & Wisby 1964, Lyons 1986, Pierce *et al.* 1990) are likely to make long term variability highly unpredictable and difficult to explain. However, when these multivariate techniques were applied to data from all sites combined, I found that variations in overall community structure could best be attributed to water temperature alone, which does suggest that this may be the overriding factor, within which all the other variables interact. It is still not surprising that a strong correlation was not found between this variable and fish composition, however, since high numbers of one species at one time of the year, i.e. autumn, were not necessarily accompanied by high numbers in spring, when water temperatures are similar.

## 3.5 CONCLUSIONS

Results of this study suggest that although temporal variations in surf-zone fish assemblages are no greater than those evident over spatial scales (see Clark *et al.* 1996a, Chapter 1), these variations are far less predictable. Variations in point abundance appear to be least predictable of all, whereas variations in the overall structure of surf-zone fish assemblages, particularly when averaged over large spatial scales, are more consistent and predictable. Long term variations appear to be predominantly seasonal in nature and correlated with the breeding cycles of most fishes in temperate and high latitudes. Seasonal variation in water temperature appears to be the primary driving mechanism, but it is probably not the magnitude of the variation in water temperature *per se* that is important, but rather the lower limits thereof that determine the strength of seasonal cycles in fish abundance in surf-zone environments. When water temperatures fall below 5 °C, for example, they are likely to exceed the lower critical level for most species, forcing them to move elsewhere or perish. Seasonal variations in productivity are also usually very pronouced in high latitudes and will exacerbate the influence of these low water temperatures. The turbulence that characterises the surf-zone environment is likely to make it an energetically expensive habitat for fish, and thus the benefits it provides in terms of cover are probably outweighed by foraging and maintenance costs for most species, when water temperatures drop below a certain level. Nevertheless, even in areas where seasonal variations in temperature are small, these results suggest that seasonal fluctuations still predominate. The spawning periods of surf-zone fish are usually timed in order to allow both transient and resident 0+ juveniles to maximise initial growth rates while making full use of the cover provided by the surf-zone waters.

# CHAPTER 4

# 4 SHORT-TERM VARIATIONS IN SURF-ZONE FISH ASSEMBLAGES IN FALSE BAY

## 4.1 INTRODUCTION

Ichthyofaunal assemblages frequenting sandy beaches are thought to be highly dynamic, exhibiting considerable fluctuations over diurnal periods (Merriman 1947, Edwards & Steele 1968, Gibson 1973a, Lasiak 1984a, Senta & Kinoshita 1985, Romer & McLachlan 1986, Ross *et al.* 1987, Wright 1989a). These fluctuations vary considerable in magnitude, and may involve changes in the size composition of the component species as well as variations in abundance and biomass (Toole 1980, Ruple 1984, Berghahn 1987, Ross *et al.* 1987, Methven & Bajdik 1994).

Diel movements between shallow intertidal regions of sandy beaches and deeper waters offshore take place primarily in response to cyclical changes in tidal height and light-dark phases, as fish seek to maximise their use of available food resources (Edwards & Steele 1968, Gibson 1973a, Kuipers 1975, Romer & McLachlan 1986), as a predator avoidance mechanism (Toole 1980, Modde & Ross 1981, van der Veer & Bergman 1986, Wright 1989a) and so as to maximise their use of prevailing environmental conditions (Warfel & Merriman 1944, Reynolds & Thompson 1974, van der Veer & Bergman 1986, Rountree & Able 1993).

Inherent variations in the activity patterns, as well as changes in the fishes ability to detect fishing gear over diel periods influences their susceptibility to capture and hence may damp out or exaggerate natural patterns of movement (Hempel 1963, Kruuk 1963, Blaxter & Parrish 1965, Gibson 1973b, Walsh 1988, Wright 1989a). Patterns observed to date have been highly variable, exhibiting little consistency with regard to times of peak abundance and biomass.

The primary aim of this study was to determine if consistent, identifiable changes in the abundance, standing stocks or size structure could be discerned in the fish assemblages frequenting the surf-zones of temperate, microtidal beaches in South Africa. To this end, a total of five diel seine net studies were conducted in False Bay, South Africa, during which information on fish abundance, biomass and size composition and a variety of physical parameters were recorded.

## 4.2 MATERIALS AND METHODS

### 4.2.1 Sampling gear and methodology

All sampling was conducted at two sandy beach sites, Sunrise Beach (34°06'S, 18°29'E) and Fishoek Beach (34°08'S, 18°26'E) in False Bay (Fig. 4.1). The two sandy beach sites are both gently sloping, moderately exposed beaches with broad surf-zones. The reader is referred to Chapter 1 and Bennett (1989a) for more detailed descriptions of the two study sites. Fish were collected over three 24 hour periods (October 1991, March 1992, July 1993) at Sunrise Beach and over one 48 hour (July 1994) and one 24 hour period (July 1995) at Fishoek Beach. All samples were collected with a 30 by 2 m, 12 mm stretched mesh beach-seine net fitted with a bag at its mid point. During sampling, the net was laid parallel to the shore, 30-50 m from the beach, and hauled by 6-10 persons. Three samples, at least 50 m apart, were taken every four hours during each sampling period, except in 1993, when sampling was conducted every three hours. Sampling was initiated at the times indicated, and usually required approximately one hour to complete all three hauls. Predicted hourly tidal heights published by the South African Navy Hydrographer were used as an index of tidal variation, while all other physical variables were recorded as described in Chapter 1.

All fish collected were counted, batch weighed by species (nearest 0.1 g), measured (TL) to the nearest millimetre and a subsample preserved in 10% formalin for gut analyses. Gut fullness was calculated as a proportion of the total weight of the fish according to the following formula:

$$\text{GFI (Gut Fullness Index)} = \text{Gut Mass} / \text{Fish Mass} \times 100\%$$

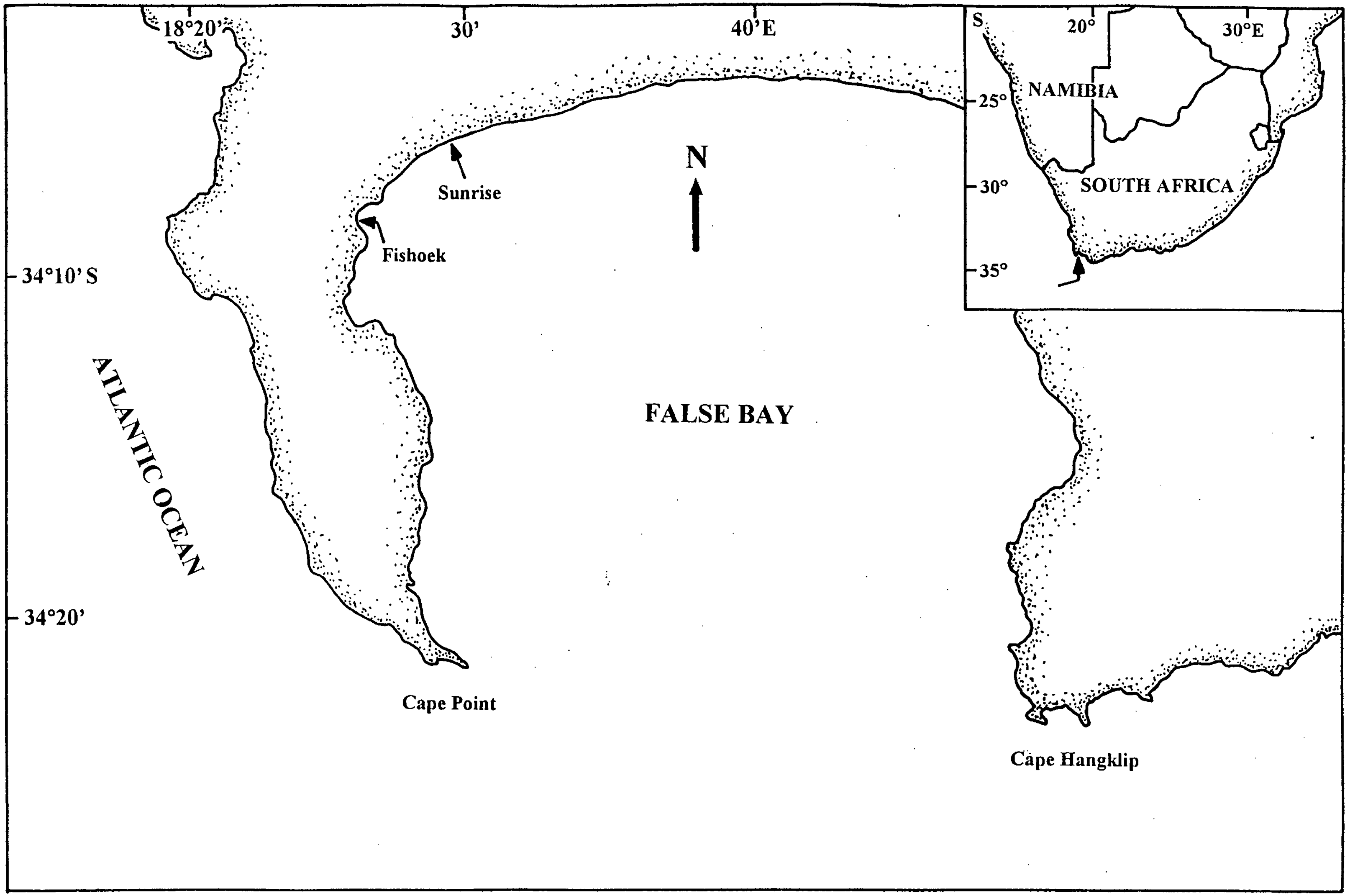


Fig. 4.1. Map of False Bay and the southwestern Cape (inset) showing the location of the sampling sites: Sunrise Beach and Fishoek Beach.

### 4.2.2 Data analysis

Multivariate analyses of community structure were performed using the CLUSTER and MDS programs on the PRIMER software package (Plymouth Marine Laboratory, UK), as detailed in Chapter 1. Stepwise multiple regression analyses were used to determine which combination of environmental parameters was most influential in controlling variations in overall fish abundance, and the abundance of the dominant species in each year. Computations were performed using the SYSTAT software package (SYSTAT Inc., Evanston, IL, USA) whilst adhering to protocols laid down by Zar (1984) and Wilkinson (1990).

Data on the wind speed and direction recorded at each time interval was transformed from a circular to a linear variable for incorporation into the statistical analyses performed for this study, in the manner described in Chapter 3. The influence of changes in day-night illumination were entered into the statistical models by allocating daytime hauls a score of +1, crepuscular hauls +2, and nocturnal hauls +3. The other five environmental parameters (wave height, surf width, turbidity, tidal height and macrophyte abundance) were entered into the statistical models without any transformation.

## 4.3 RESULTS

### 4.3.1 Composition of the catches

A total of 20 380 fish weighing 262.4 kg from 27 species were captured during the five diel sampling excursions (Tables 4.1-4.5). The greatest number of hauls (36) and the largest area sampled (15 750 m$^2$) were recorded in 1994, but catches for 1993 yielded the greatest number of species (14) and the greatest overall catch (10 565 ind., 157.4 kg). The smallest catch (1 958 ind.) was taken in 1995, the lowest biomass (11.8 kg) in 1994 and the fewest species (7) during 1992. The total area netted was lowest in 1992 (8 100 m$^2$), while 1991, 1992 and 1995 shared the fewest overall number of hauls (21).

Table 4.1. Composition, abundance, biomass (g) and length ranges (mm) of fish captured in sets of three beach-seine hauls made at four-hourly intervals at Sunrise Beach in October 1991.

|  | 06h00 | 10h00 | 14h00 | 18h00 | 22h00 | 02h00 | 06h00 | Total | Percent | Size range |
|---|---|---|---|---|---|---|---|---|---|---|
| **NUMBERS** |  |  |  |  |  |  |  |  |  |  |
| *Liza richardsonii* | 230 | 488 | 173 | 110 | 66 | 10 | 329 | 1 406 | 57.60 | 32-266 |
| *Rhabdosargus globiceps* | 41 | 201 | 241 | 231 | 167 | 62 | 8 | 951 | 38.96 | 32-122 |
| *Atherina breviceps* | 14 | 16 | 1 | 9 | 1 |  |  | 41 | 1.68 | 52-124 |
| *Gilchristella aestuaria* |  | 3 | 6 |  | 2 | 1 | 2 | 14 | 0.57 | 45-58 |
| *Rhinobatos annulatus* | 3 |  |  |  | 6 | 5 |  | 14 | 0.57 | 280-810 |
| *Chelidonichthyes capensis* |  |  |  | 1 | 2 | 1 |  | 4 | 0.16 | 42-52 |
| *Lithognathus lithognathus* |  |  |  | 2 | 1 |  |  | 3 | 0.12 | 173-179 |
| *Pomatomus saltatrix* |  |  | 1 |  | 1 |  | 1 | 3 | 0.12 | 98-112 |
| *Amblyrhynchotes honkenii* |  |  |  | 1 |  |  | 1 | 2 | 0.08 | 54-151 |
| *Callorhynchus capensis* |  |  |  |  |  | 1 |  | 1 | 0.04 | 710 |
| *Galeichthyes feliceps* |  |  |  |  | 1 |  |  | 1 | 0.04 | 278 |
| *Clinus latipennis* |  |  |  |  | 1 |  |  | 1 | 0.04 | 31 |
| Total | 288 | 708 | 422 | 354 | 248 | 80 | 341 | 2 441 |  |  |
| **BIOMASS** |  |  |  |  |  |  |  |  |  |  |
| *Liza richardsonii* | 705.4 | 2 382.7 | 885.8 | 574.1 | 2 965.6 | 93.6 | 412.6 | 8 019.7 | 39.75 |  |
| *Rhinobatos annulatus* | 3 370.5 |  |  |  | 539.5 | 906.8 |  | 4 816.8 | 23.88 |  |
| *Callorhynchus capensis* |  |  |  |  |  | 3 155.0 |  | 3 155.0 | 15.64 |  |
| *Rhabdosargus globiceps* | 84.0 | 452.9 | 497.3 | 736.3 | 780.0 | 239.1 | 9.9 | 2 799.5 | 13.88 |  |
| *Lithognathus lithognathus* |  |  |  | 482.5 | 241.7 |  |  | 724.2 | 3.59 |  |
| *Atherina breviceps* | 46.9 | 95.4 | 12.1 | 70.4 | 6.5 |  |  | 231.2 | 1.15 |  |
| *Galeichthyes feliceps* |  |  |  |  | 207.3 |  |  | 207.3 | 1.03 |  |
| *Amblyrhynchotes honkenii* |  |  |  | 80.4 |  |  | 12.3 | 92.7 | 0.46 |  |
| *Chelidonichthyes capensis* |  |  |  | 23.0 | 45.9 | 23.0 |  | 91.9 | 0.46 |  |
| *Pomatomus saltatrix* |  |  | 10.6 | 0 | 8.1 | 12.2 |  | 30.9 | 0.15 |  |
| *Gilchristella aestuaria* |  | 1.2 | 2.0 |  | 0.5 | 0.3 | 0.6 | 4.7 | 0.02 |  |
| *Clinus latipennis* |  |  |  |  | 0.2 |  |  | 0.2 | <0.005 |  |
| Total | 4 206.7 | 2 932.2 | 1 407.8 | 1 966.7 | 4 795.4 | 4 430.1 | 435.4 | 20 174.1 |  |  |
| Netting area ($m^2$) | 1 350 | 1 125 | 900 | 1 350 | 1 350 | 900 | 1 350 | 8 325 |  |  |

**Table 4.2.** Composition, abundance, biomass (g) and length ranges (mm) of fish captured in beach-seine hauls made at four-hourly intervals at Sunrise Beach in March 1992.

| | 18h00 | 22h00 | 02h00 | 06h00 | 10h00 | 14h00 | 18h00 | Total | Percent | Size range |
|---|---|---|---|---|---|---|---|---|---|---|
| **NUMBERS** | | | | | | | | | | |
| *Liza richardsonii* | 371 | 184 | 214 | 132 | 313 | 248 | 198 | 1 660 | 62.15 | 29-309 |
| *Atherina breviceps* | 142 | 7 | 1 | 118 | 157 | 260 | 205 | 890 | 33.32 | 82-125 |
| *Rhabdosargus globiceps* | 29 | 11 | 12 | 8 | 16 | 7 | 4 | 87 | 3.26 | 24-73 |
| *Pomatomus saltatrix* | 5 | | 2 | 15 | 2 | 1 | 2 | 27 | 1.01 | 32-131 |
| *Mugil cephalus* | | | | | 2 | 1 | | 3 | 0.11 | 125-173 |
| *Callorhynchus capensis* | | 2 | | | | | | 2 | 0.07 | 760-810 |
| *Rhinobatos annulatus* | | | | 1 | | 1 | | 2 | 0.07 | 235-810 |
| Total | 547 | 204 | 229 | 274 | 490 | 518 | 409 | 2 671 | | |
| **BIOMASS** | | | | | | | | | | |
| *Liza richardsonii* | 14 136.7 | 4 674.7 | 6 395.8 | 3 566.3 | 3 054.6 | 1 724.2 | 7 544.7 | 41 097.0 | 71.81 | |
| *Callorhynchus capensis* | | 7 010.0 | | | | | | 7 010.0 | 12.25 | |
| *Atherina breviceps* | 1 038.5 | 71.1 | 7.9 | 883.2 | 1 244.6 | 2 108.1 | 1 499.2 | 6 852.6 | 11.97 | |
| *Rhinobatos annulatus* | | | | 1 791.9 | | 35.5 | | 1 827.4 | 3.19 | |
| *Pomatomus saltatrix* | 27.1 | | 0.1 | 160.0 | 29.0 | 16.3 | 10.8 | 243.3 | 0.43 | |
| *Rhabdosargus globiceps* | 39.5 | 20.7 | 10.5 | 11.0 | 23.2 | 9.1 | 5.4 | 119.4 | 0.21 | |
| *Mugil cephalus* | | | | | 35.5 | 43.9 | | 79.4 | 0.14 | |
| Total | 15 241.7 | 11 776.5 | 6 414.4 | 6 412.4 | 4 386.8 | 2 626.7 | 9 060.1 | 57 229.1 | | |
| Netting area ($m^2$) | 1 350 | 1 125 | 1125 | 1 350 | 1 125 | 900 | 1125 | 8100 | | |

**Table 4.3.** Composition, abundance, biomass (g) and length ranges (mm) of fish captured in beach-seine hauls made at four-hourly intervals at Sunrise Beach in July 1993.

| | 09h00 | 12h00 | 15h00 | 18h00 | 21h00 | 24h00 | 03h00 | 06h00 | 09h00 | Total | Percent | Size range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **NUMBERS** | | | | | | | | | | | | |
| *Liza richardsonii* | 262 | 172 | 292 | 1 399 | 273 | 57 | 572 | 558 | 476 | 4 061 | 38.44 | 22-286 |
| *Rhabdosargus globiceps* | 243 | 138 | 89 | 979 | 501 | 373 | 427 | 510 | 354 | 3 614 | 34.21 | 30-103 |
| *Atherina breviceps* | 339 | 1 290 | 799 | 31 | 70 | 2 | 21 | 40 | 93 | 2 685 | 25.41 | 40-130 |
| *Gilchristella aestuaria* | 2 | 2 | 8 | 9 | 39 | | 1 | 8 | 30 | 99 | 0.94 | 35-64 |
| *Lithognathus lithognathus* | 1 | 1 | | 28 | | | 6 | 2 | | 38 | 0.36 | 185-208 |
| *Mugil cephalus* | 1 | | | 6 | 2 | | 4 | 10 | 3 | 26 | 0.25 | 118-158 |
| *Solea bleekeri* | 2 | 1 | 1 | 6 | 5 | 1 | | 1 | 2 | 19 | 0.18 | 70-84 |
| *Pomatomus saltatrix* | 5 | | | | 1 | | 2 | | | 8 | 0.08 | 118-158 |
| *Amblyrhynchotes honkenii* | | | | | 5 | | | | | 5 | 0.05 | 66-145 |
| *Liza tricuspidens* | 2 | 1 | | | | | | | | 3 | 0.03 | 41-180 |
| *Rhabdosargus holubi* | | | | 1 | 1 | | | | 1 | 3 | 0.03 | 60-76 |
| *Rhinobatos annulatus* | | | | | | | 1 | | 1 | 2 | 0.02 | 314-650 |
| *Clinus latipennis* | | | | | | 1 | | | | 1 | 0.01 | 103 |
| *Synaptura marginata* | | | | | | 1 | | | | 1 | 0.01 | 283 |
| Total | 857 | 1 605 | 1 189 | 2 459 | 897 | 435 | 1 034 | 1 129 | 960 | 10 565 | | |
| **BIOMASS** | | | | | | | | | | | | |
| *Liza richardsonii* | 1 954.5 | 1 208.4 | 3 188.2 | 62 053.3 | 8 313.6 | 659.1 | 26 077.4 | 15 476.5 | 2 334.0 | 121 264.9 | 77.03 | |
| *Atherina breviceps* | 1 236.9 | 6 964.5 | 2 601.9 | 20.3 | 55.5 | 1.4 | | | | 10 880.6 | 6.91 | |
| *Lithognathus lithognathus* | 252.4 | 254.9 | | 7 038.7 | | | 1 489.3 | 498.2 | | 9 533.5 | 6.06 | |
| *Rhabdosargus globiceps* | 457.4 | 255.7 | 151.6 | 2 621.2 | 1 360.8 | 898.8 | 909.1 | 1 251.9 | 866.3 | 8 772.8 | 5.57 | |
| *Mugil cephalus* | 18.5 | | | 86.1 | 417.6 | | 523.3 | 1 745.8 | 2 062.8 | 4 854.1 | 3.08 | |
| *Rhinobatos annulatus* | | | | | | | 88.9 | | 892.0 | 980.8 | 0.62 | |
| *Amblyrhynchotes honkenii* | | | | | 489.2 | | | | | 489.1 | 0.31 | |
| *Synaptura marginata* | | | | | | 248.7 | | | | 248.7 | 0.16 | |
| *Pomatomus saltatrix* | 106.3 | | | | 14.4 | | 20.3 | | | 141.0 | 0.09 | |
| *Solea bleekeri* | 12.8 | 5.6 | 5.8 | 18.6 | 30.6 | | | 5.4 | 9.5 | 88.4 | 0.06 | |
| *Liza tricuspidens* | 77.4 | 0.4 | | | | | | | | 77.8 | 0.05 | |
| *Gilchristella aestuaria* | 0.7 | 1.7 | 6.0 | 6.1 | 22.4 | | 0.9 | 4.6 | 17.3 | 59.7 | 0.04 | |
| *Rhabdosargus holubi* | | | | 5.6 | 2.6 | | | | 5.6 | 13.7 | 0.01 | |
| *Clinus latipennis* | | | | | | 13.4 | | | | 13.4 | 0.01 | |
| Total | 4 117.0 | 8 691.2 | 5 953.5 | 71 849.9 | 10 706.7 | 1 821.4 | 29 109.2 | 18 982.4 | 6 187.4 | 157 418.7 | | |
| Netting area ($m^2$) | 1 350 | 900 | 1 125 | 1 350 | 1 350 | 900 | 1 350 | 1 350 | 900 | 10 575 | | |

**Table 4.4.** Composition, abundance, biomass (g) and length ranges (mm) of fish captured in beach-seine hauls made at four-hourly intervals at Fishoek Beach in July 1994.

| | 10h00 | 14h00 | 18h00 | 22h00 | 02h00 | 06h00 | 10h00 | 14h00 | 18h00 | 22h00 | 02h00 | 06h00 | Total | Percent | Size range |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **NUMBERS** | | | | | | | | | | | | | | | |
| *Liza richardsonii* | 139 | 443 | 534 | 98 | 228 | 101 | 102 | 8 | 157 | 77 | 9 | 165 | 2 061 | 75.08 | 19-270 |
| *Rhabdosargus globiceps* | 1 | 1 | 95 | 42 | 79 | 4 | | | 49 | 53 | 50 | 58 | 432 | 15.74 | 35-95 |
| *Clinus latipennis* | 5 | 1 | 49 | 8 | 18 | 5 | 13 | 1 | | | | | 100 | 3.64 | 34-150 |
| *Trachurus trachurus* | | | 13 | 6 | 1 | | | | 1 | 27 | 21 | | 69 | 2.51 | 120-167 |
| *Chelidonichthyes capensis* | 10 | 7 | | | 1 | | 1 | 12 | 6 | 19 | 6 | | 62 | 2.26 | 21-87 |
| *Atherina breviceps* | | | 1 | 1 | | 1 | | 1 | | 3 | 8 | | 15 | 0.55 | 78-115 |
| *Lithognathus mormyrus* | | | | | | | | | 2 | | | | 2 | 0.07 | 125-134 |
| *Engraulis japonicus* | | 1 | | | | | | | | | | 1 | 2 | 0.07 | 90-96 |
| *Clinus superciliosus* | | | 1 | | | | | | | | | | 1 | 0.04 | 71 |
| *Psammogobius knysnaensis* | | | | | | | | 1 | | | | | 1 | 0.04 | 35 |
| Total | 155 | 453 | 693 | 155 | 327 | 111 | 116 | 23 | 215 | 179 | 94 | 224 | 2745 | | |
| **BIOMASS** | | | | | | | | | | | | | | | |
| *Liza richardsonii* | 143.8 | 1 564.4 | 4 675.8 | 108.5 | 155.7 | 88.6 | 322.4 | 10.2 | 161.7 | 47.2 | 4.2 | 158.6 | 7 441.1 | 62.96 | |
| *Trachurus trachurus* | | | 313.5 | 137.3 | 19.3 | | | | 20.9 | 585.0 | 475.2 | | 1 551.2 | 13.12 | |
| *Rhabdosargus globiceps* | 1.5 | 0.8 | 310.3 | 145.7 | 283.2 | 7.4 | | | 124.9 | 165.6 | 175.0 | 202.7 | 1 417.1 | 11.99 | |
| *Clinus latipennis* | 27.4 | 23.7 | 690.0 | 71.2 | 188.8 | 36.7 | 159.0 | 17.1 | | | | | 1 213.9 | 10.27 | |
| *Atherina breviceps* | | | 10.6 | 10.6 | | 10.6 | | 8.8 | | 27.5 | 78.8 | | 146.9 | 1.24 | |
| *Lithognathus mormyrus* | | | | | | | | | 48.8 | | | | 48.8 | 0.41 | |
| *Chelidonichthyes capensis* | 7.4 | 2.6 | | | 6.6 | | 0.2 | 4.5 | 2.5 | 12.1 | 6.3 | | 42.2 | 0.36 | |
| *Engraulis japonicus* | | 6.1 | | | | | | | | | | 4.2 | 10.3 | 0.09 | |
| *Clinus superciliosus* | | | 5.8 | | | | | | | | | | 5.8 | 0.05 | |
| *Psammogobius knysnaensis* | | | | | | | | 0.2 | | | | | 0.2 | <0.005 | |
| Total number | 172.7 | 1 588.9 | 6 000.2 | 473.3 | 647.0 | 143.3 | 481.4 | 36.1 | 356.3 | 825.3 | 733.2 | 361.3 | 11 819.0 | | |
| Netting area (m²) | 1 350 | 1 350 | 1 350 | 1 350 | 1 350 | 900 | 1 350 | 1 350 | 1 350 | 1 350 | 1 350 | 1 350 | 15 750 | | |

Table 4.5. Composition, abundance, biomass (g) and length ranges (mm) of fish captured in beach-seine hauls made at four-hourly intervals at Fishoek Beach in July 1995.

| | 10h00 | 14h00 | 18h00 | 22h00 | 02h00 | 06h00 | 10h00 | Total | Percent | Size range |
|---|---|---|---|---|---|---|---|---|---|---|
| **NUMBERS** | | | | | | | | | | |
| *Liza richardsonii* | 375 | 117 | 71 | 50 | 65 | 113 | 66 | 857 | 43.77 | 27-345 |
| *Rhabdosargus globiceps* | | 1 | 194 | 93 | 191 | 224 | 3 | 706 | 36.06 | 23-105 |
| *Lithognathus mormyrus* | | | 19 | 23 | 70 | 46 | | 158 | 8.07 | 31-77 |
| *Chelidonichthyes capensis* | 5 | 22 | 12 | 51 | 17 | 31 | 18 | 156 | 7.97 | 20-80 |
| *Clinus latipennis* | 12 | 4 | 12 | 16 | 6 | | 1 | 51 | 2.60 | 17-170 |
| *Atherina breviceps* | 8 | | | | 1 | 1 | | 10 | 0.51 | 60-115 |
| *Psammogobius knysnaensis* | 2 | 2 | 2 | | 3 | | | 9 | 0.46 | 37-60 |
| *Sardinops sagax* | | | | | 6 | | | 6 | 0.31 | 210-258 |
| *Dichistius capensis* | | | 1 | 2 | | | | 3 | 0.15 | 41-47 |
| *Cancelloxus longior* | | | 1 | | | | | 1 | 0.05 | 133 |
| *Solea bleekeri* | | | | | 1 | | | 1 | 0.05 | 220 |
| Total | 402 | 146 | 312 | 235 | 360 | 415 | 88 | 1 958 | | |
| **BIOMASS** | | | | | | | | | | |
| *Liza richardsonii* | 1 879.1 | 266.7 | 3 782.6 | 733.2 | 2 868.2 | 1 033.3 | 1 505.1 | 12 068.2 | 76.65 | |
| *Rhabdosargus globiceps* | | 1.6 | 535.1 | 210.2 | 637.2 | 752.1 | 2.4 | 2 138.6 | 13.58 | |
| *Sardinops sagax* | | | | | 497.2 | | | 497.2 | 3.16 | |
| *Clinus latipennis* | 57.5 | 18.9 | 131.2 | 88.9 | 58.4 | | 0.4 | 355.3 | 2.26 | |
| *Lithognathus mormyrus* | | | 50.9 | 52.2 | 141.5 | 82.3 | | 326.9 | 2.08 | |
| *Solea bleekeri* | | | | | 150.1 | | | 150.1 | 0.95 | |
| *Chelidonichthyes capensis* | 4.0 | 11.0 | 9.4 | 49.6 | 8.2 | 25.7 | 9.4 | 117.3 | 0.75 | |
| *Atherina breviceps* | 56.8 | | | | 10.8 | 1.1 | | 68.7 | 0.44 | |
| *Psammogobius knysnaensis* | 0.8 | 2.0 | 1.8 | | 2.5 | | | 7.1 | 0.05 | |
| *Cancelloxus longior* | | | 6.4 | | | | | 6.4 | 0.04 | |
| *Dichistius capensis* | | | 1.1 | 2.3 | | | | 3.4 | 0.02 | |
| Total | 1 998.2 | 300.2 | 4 518.3 | 1 146.3 | 4 369.3 | 1 894.5 | 1 517.2 | 15 744.0 | | |
| Netting area ($m^2$) | 1 350 | 1 350 | 1 350 | 1 350 | 1 350 | 1 350 | 1 350 | 9 450 | | |

*Liza richardsonii* and *Rhabdosargus globiceps* dominated the catches during 1991 (Table 4.1), providing 57.6 and 40.0 % of the total number of fish captured. *L. richardsonii* provided the greatest contribution to the biomass during this year (39.8%), while *Rhinobatos annulatus*, *Callorhynchus capensis* and *R. globiceps* all contributed >10%. *L. richardsonii* (62.2%) and *Atherina breviceps* (33.3%) were the most numerous species recorded during 1992 (Table 4.2), while three species, *L. richardsonii* (71.8%), *C. capensis* (12.3 %) and *A. breviceps* (12.0%) each provided >10% of the biomass. In 1993 (Table 4.3), *L. richardsonii* (38.4%), *R. globiceps* (34.2%) and *A. breviceps* (25.4%) dominated numerically, while *L. richardsonii* (77.0%) was the only species to contribute >10% of the biomass. *L. richardsonii* (75.1%) and *R. globiceps* (15.7%) were the most abundant species recorded during 1994, while *L. richardsonii* (63.0%) once again dominated the biomass, with *Trachurus trachurus*, *R. globiceps* and *Clinus latipennis* each contributing >10% (Table 4.4). In 1995 (Table 4.5), *L. richardsonii* and *R. globiceps* were the only species to contribute more than 10% of the total numbers or biomass of fish captured. *L. richardsonii* provided 43.8% of the numbers and 76.7% of the biomass, while *R. globiceps* provided 36.1% of the numbers and 13.6% of the biomass.

### 4.3.2 Diel variation in physio-chemical parameters

Fluctuations in all physio-chemical parameters recorded, fish abundance and biomass for the diel sampling excursions are depicted in Figs. 4.2-4.6. In 1991 (Fig. 4.2), sampling was conducted in October, commencing at 06h00 and continuing until 06h00 the following day. The sun rose shortly after sampling commenced (06h19), and set at 18h51, to rise again at 06h18 the following morning. Conditions were windless until 14h00, when a 10 knot offshore breeze was recorded. It continued to blow at 5-10 knots throughout the night, but had abated by 06h00 the following morning. Maximum wave height rose from 0.6 m at the start of sampling to 2.0 m at 18h00, but subsequently dropped to 0.6 m at the time of the last sample. Tidal peaks occurred at 13h31 and 01h56, and troughs at 07h21 and 19h53. The width of the surf-zone and turbidity varied little over this sampling cycle, with surf-zone width ranging from 50-100 m and turbidity from 6-8 FTU. Detached macrophytes were scarce (<5 l haul$^{-1}$)

during this period, and variation in their abundance is not displayed. The moon was in its 'new moon' phase at the time of sampling.

Sampling in 1992 (Fig. 4.3) commenced at 18h00, shortly before sunset (18h48) on the 27th of March, continued through sunrise the following morning (06h55) and was halted (18h00) shortly before sunset that evening. No wind was recorded during this excursion, apart from a light (5 knot) onshore breeze at 14h00. Maximum wave height was relatively small until 06h00 (1.0-1.3 m) but rose to 1.6 m thereafter. Similarly, surf-zone width was relatively narrow (100-150 m) at the start of sampling, but increased to 300 m at 14h00, concurrently with maximum wave height. Sampling began immediately after low tide (17h22) and continued until low tide the following evening. Tidal peaks occurred at 23h43 and 12h07, with the moon being approximately half full. Surf-zone waters were initially turbid (6-7 FTU), and became even more so (7-8 FTU) from 10h00 onwards. No macrophytes were netted.

Sampling in 1993 was conducted in July, and ran for 24 h from 09h00. Sunset occurred at 17h54 and sunrise at 07h49. Winds were very variable, initially being light offshore (1-2 knots NW), but turning onshore by 15h00 of the first day (10 knots SE), and remaining so for most of the night, before abating completely prior to the 06h00 sample on day 2. Maximum wave height oscillated between 0.6 and 1.0 m, while the width of the surf-zone ranged between 100-500 m. High tide occurred shortly after sampling commenced (11h30) and again at 23h46, while low tides were recorded at 17h34 and 06h15. Turbidity was initially moderately high (6 FTU), dropped somewhat (3 FTU), then rose to very high levels (7-10 FTU) for the remainder of this session. The moon was approximately 1/3 full and no macrophytes were netted.

The 1994 sampling excursion was run at Fishoek Beach in July, from 10h00 on day 1 to 06h00 on day 3. Sunset occurred at around 17h53 and sunrise around 07h50. Winds were initially onshore (1-4 knots SE), dropped completely at the start of the second day, then from 10h00 blew with variable intensity in an offshore direction (2-15 knots NW). Wave height oscillated between 0.6 and 1.0 m, periodically dropping to 0.3 m or rising to 1.1 m, while the surf-zone remained relatively narrow (20-50 m width). Peaks in tidal height occurred in the evenings (18h19, 19h07) and in the morning (06h42), and low tide at around midday (12h00, 12h45) and midnight (00h39). Surf-zone waters were initially mildly turbid (3-4 FTU), but became clearer (<2 FTU) as the wind dropped and began to blow offshore. Macrophyte abundance started off very low (0.1 $lm^{-2}$), rose to the highest recorded level at sunset (0.9 $lm^{-2}$), then dropped again to moderate to low levels (0.1-0.5) until 14h00 the following day before returning to low levels again for the rest of the time. The moon was approximately half full.

The final sampling excursion was conducted over two days at Fishoek Beach in July 1995. Sampling began at 10h00 approximately two hours after sunrise and continued until the same time the following morning. Sunset occurred at 17h57 and sunrise at 07h47. Winds blew offshore for the entire study period, ranging primarily between 2-5 knots NW, but swung to the west (5 knots) for a short period at 18h00. Macrophyte abundance was low (<0.03 $lm^{-2}$) until 14h00, but rose rapidly thereafter to a peak (0.30 $lm^{-2}$) at 22h00, but dropped again to 0.03 $lm^{-2}$ at 10h00. Maximum wave height was initially large (1.6 m), but dropped gradually over the entire sampling cycle to 1.0 m. The surf-zone width remained at 50 m for most of this session, except for 06h00 when it dropped briefly to 40 m width. The moon was half full, with low tide troughs appearing at 14h19 and 03h23 and tidal peaks at 20h51 and 09h28. Turbidity was initially relatively high (5 FTU) but dropped progressively to 1.5 FTU at 10h00.

### 4.3.3 Diel variation in fish abundance and standing stock

Diel variation in the abundance (no. ind. $m^{-2}$) and standing stock ($gm^{-2}$) were analysed for the community as a whole, and separately for those species contributing >10% of the total numbers in each of the five diel sampling sessions (Figs. 4.2-4.6).

In 1991 (Fig. 4.2), overall fish abundance was greatest during the daylight hours, peaking at 0.63 ind. $m^{-2}$ at 10h00. Fewest fish were captured at 02h00 (0.18 ind. $m^{-2}$). Abundance of *Liza richardsonii* tracked overall fish abundance almost exactly, peaking at 10h00 (0.43 ind. $m^{-2}$) and 06h00 (0.24 ind. $m^{-2}$). Abundance of this species was lowest (0.01 ind. $m^{-2}$) at 02h00. Peak *Rhabdosargus globiceps* abundance (0.27 ind. $m^{-2}$) was recorded at 10h00, while lowest values were recorded at the start (06h00 - 0.03 ind. $m^{-2}$) and at the end (0.01 ind. $m^{-2}$) of this sampling excursion. On the whole, biomass in the nocturnal samples was greater than the daylight ones, with peaks in overall standing stocks evident at 06h00 (1 402.2 $gm^{-2}$) and 22h00 (1 598.5 $gm^{-2}$) (Fig. 4.2). Lowest overall standing stock was recorded at 14h00 (469.3 $gm^{-2}$) and 06h00 (145.1 $gm^{-2}$). Standing stocks of *L. richardsonii* peaked at 10h00 (794.3 $gm^{-2}$) and 22h00 (988.5 $gm^{-2}$), but were lowest at 02h00 (31.2 $gm^{-2}$). Standing stocks of *R. globiceps* were lowest at the start and end of this sampling excursion (<30 $gm^{-2}$), but peaked at 22h00 (260.0 $gm^{-2}$).

In terms of abundance, overall catch rates in 1992 (Fig. 4.3) were initially high (0.41 fish $m^{-2}$), dropped rapidly after sunset to a minimum at 22h00 (0.18 fish $m^{-2}$), and then remained low for most of the night, before rising to a peak of 0.57 fish $m^{-2}$ at 14h00 the following afternoon. Fluctuations in the abundance of *L. richardsonii* and *Atherina breviceps* displayed similar patterns, exhibiting peaks at 18h00 (0.27 and 0.11 ind. $m^{-2}$ respectively) on the first day and 14h00 (0.27 and 0.28 ind. $m^{-2}$ respectively) on the second. *L. richardsonii* catches were lowest at 06h00 (0.10 ind $m^{-2}$) whereas those of *A. breviceps* reached a minimum at 02h00 (0.01 ind $m^{-2}$). Standing stocks of all species were greatest in the evenings, displaying peaks (10.5 and 8.1 $gm^{-2}$) at 18h00 each day. Biomass was lowest at 10h00 (3.9 $gm^{-2}$). *L. richardsonii* displayed a similar trend, peaking at 18h00 both days, while *A. breviceps* peaked at 18h00 and 14h00 on days 1 and 2, respectively.

Considerable variations in fish abundance were evident in 1993, but on the whole, catches were generally greatest during the day (Fig. 4.4). Peaks in abundance were recorded at 12h00 (1.78 fish $m^{-2}$), 18h00 (1.82 fish $m^{-2}$) and 09h00 (1.01 fish $m^{-2}$). Lowest abundance values were recorded at the start of the sampling program (09h00 - 0.63 fish $m^{-2}$) and at midnight (0.48 fish $m^{-2}$). Examination of the variation in the density of the component species, revealed that *A. breviceps* was primarily responsible for the 12h00 peak in overall abundance, *L. richardsonii* and *R. globiceps* for the 18h00 peak, and all three species to the final peak at 18h00. Standing stocks were on the whole greater during the nocturnal samples, with peaks appearing in the evening (18h00 - 53.2 $gm^{-2}$), early morning (03h00 - 21.6 $gm^{-2}$), to a lesser extent at midday (9.7 $gm^{-2}$). *L. richardsonii* was almost solely responsible for the biomass peaks at 18h00 (46.0 $gm^{-2}$) and 03h00 (19.3 $gm^{-2}$), while *A. breviceps* provided the greatest portion of the biomass in the small peak at midday (7.7 $gm^{-2}$).

Fluctuations in abundance and biomass over the 44 hour sampling period in 1994 are depicted in Fig. 4.5. Over the first 24 hours, daylight catches were, on the whole, greater than the night-time catches. Following this, the pattern was reversed, with lower catches being taken during the day than at night. Greatest abundance was recorded at the end of the first day (18h00 - 0.51 fish m $^{-2}$), but smaller peaks occurred at 02h00 on the first night (0.24 fish m$^{-2}$), at the end of the second day (18h00 - 0.16 fish m $^{-2}$) and on the morning of the third day (06h00 - 0.17 fish m $^{-2}$). Lowest overall abundance (0.02 fish m $^{-2}$) was recorded at 14h00 on the second day. Catches of *L. richardsonii* followed the trend in overall abundance very closely, with peaks and troughs occurring at the same time for both. *R. globiceps* was caught almost exclusively in nocturnal hauls, with only two of the 432 individuals captured after dark. Overall standing stocks at Fishoek Beach in 1994 were initially low, but rapidly rose in the afternoon of the first day to a high of 4.4 gm $^{-2}$. Standing stocks dropped rapidly thereafter, however, and remained at relatively low levels during the remainder of the first night and second day (<0.5 gm $^{-2}$). Standing stocks peaked again during the second night (22h00 - 0.6 gm $^{-2}$) before declining again towards daybreak. *L. richardsonii* biomass followed a similar pattern initially, providing the bulk of the biomass, but dropped off after the evening of the second day, contributing little to the final peak in overall standing stock. Biomass of *R. globiceps* was greatest in the evening, nocturnal and early morning catches, with peaks appearing at 18h00, 02h00 (0.2 gm$^{-2}$ for both) and 06h00 (0.1 gm$^{-2}$).

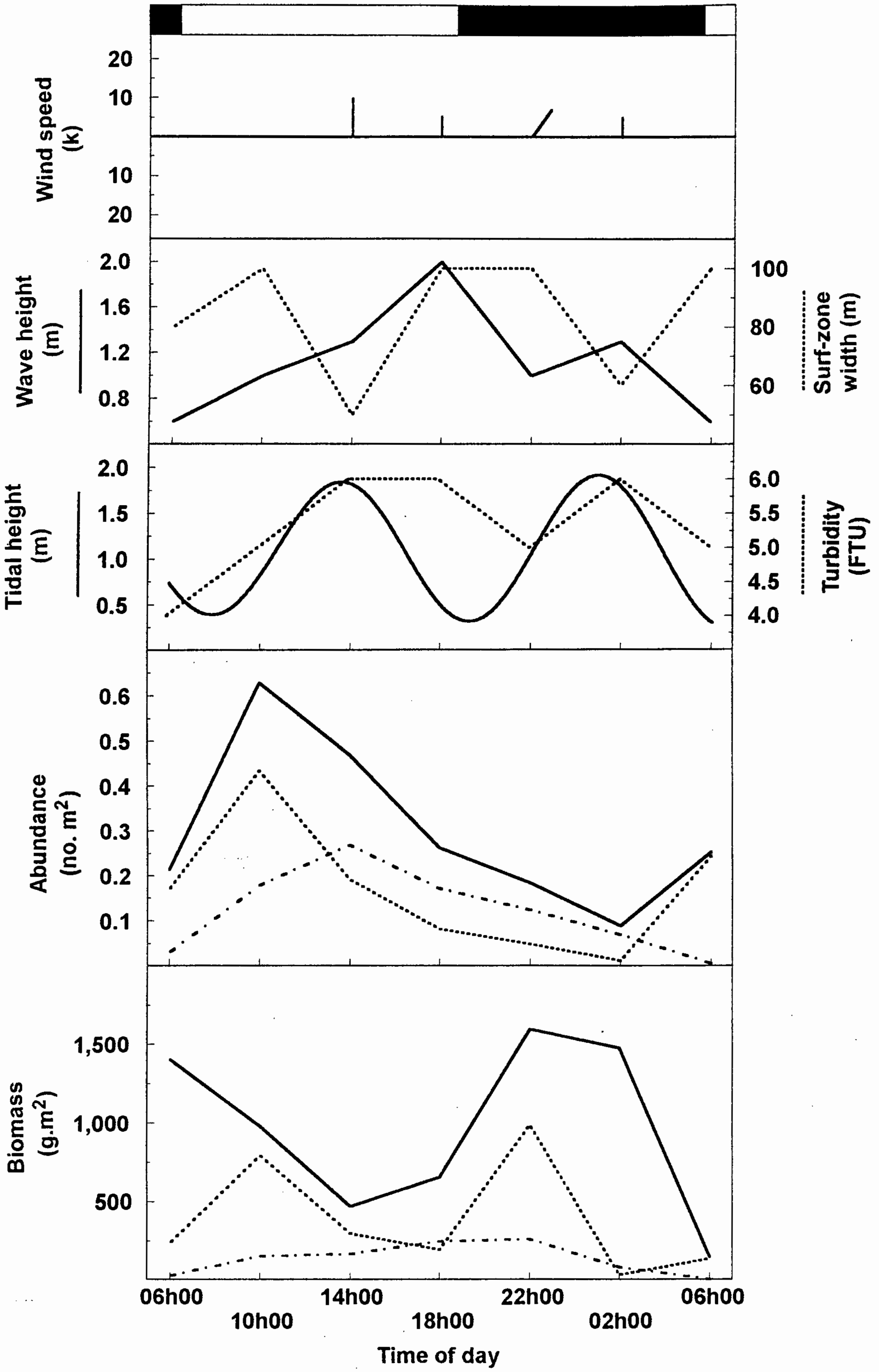


Fig. 4.2. Diel variation in physical parameters (wind speed & direction, wave height, surf-zone width, tidal height, and turbidity) and total abundance and biomass of fish (all species combined:——— , *Liza richardsonii*:- - - - and *Rhabdosargus globiceps*: — - — ) recorded in seine net hauls made at four-hourly intervals at Sunrise Beach in 1991.

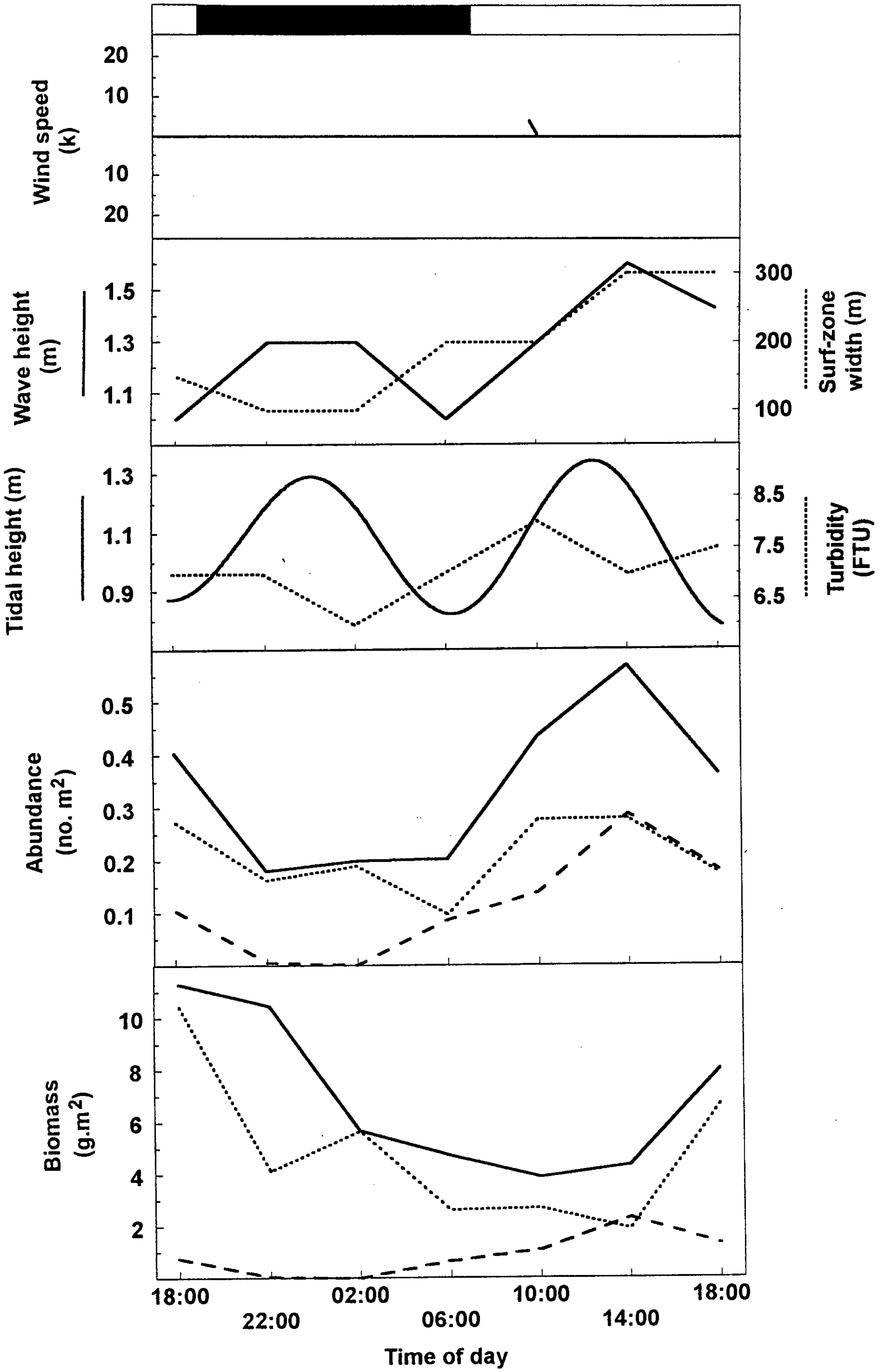


**Fig. 4.3.** Diel variation in physical parameters (wind speed & direction, wave height, surf-zone width, tidal height, and turbidity) and total abundance and biomass of fish (all species combined: ——— , *Liza richardsonii*: - - - - and *Atherina breviceps*: — — ) recorded in seine net hauls made at four-hourly intervals at Sunrise Beach in 1992.

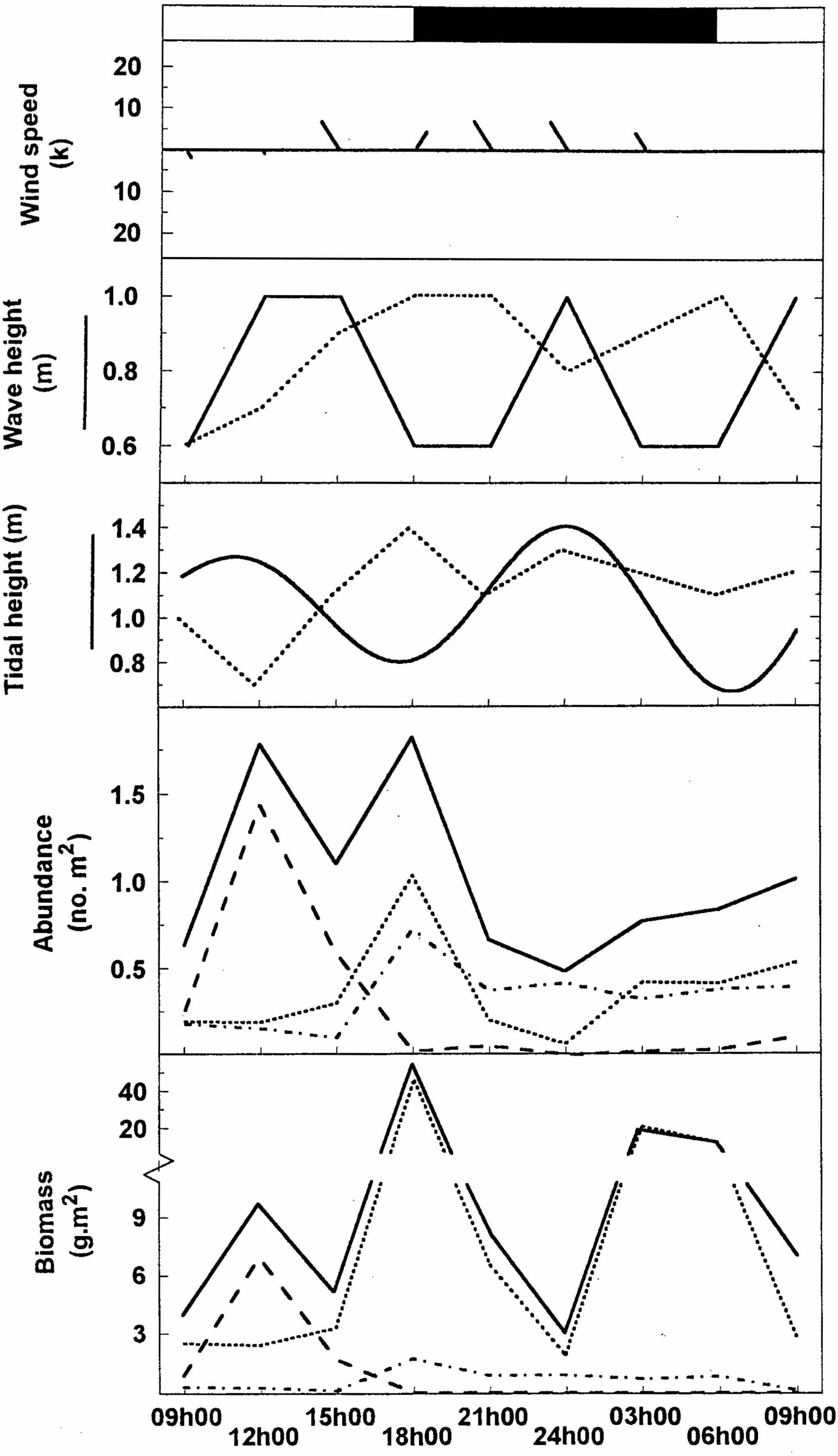


Fig. 4.4. Diel variation in physical parameters (wind speed & direction, wave height, surf-zone width, tidal height, and turbidity) and total abundance and biomass of fish (all species combined: ——— , *Liza richardsonii*: - - - - - , *Rhabdosargus globiceps*: — · — and *Atherina breviceps*: — — —) recorded in seine net hauls made at three-hourly intervals at Sunrise Beach in 1993.

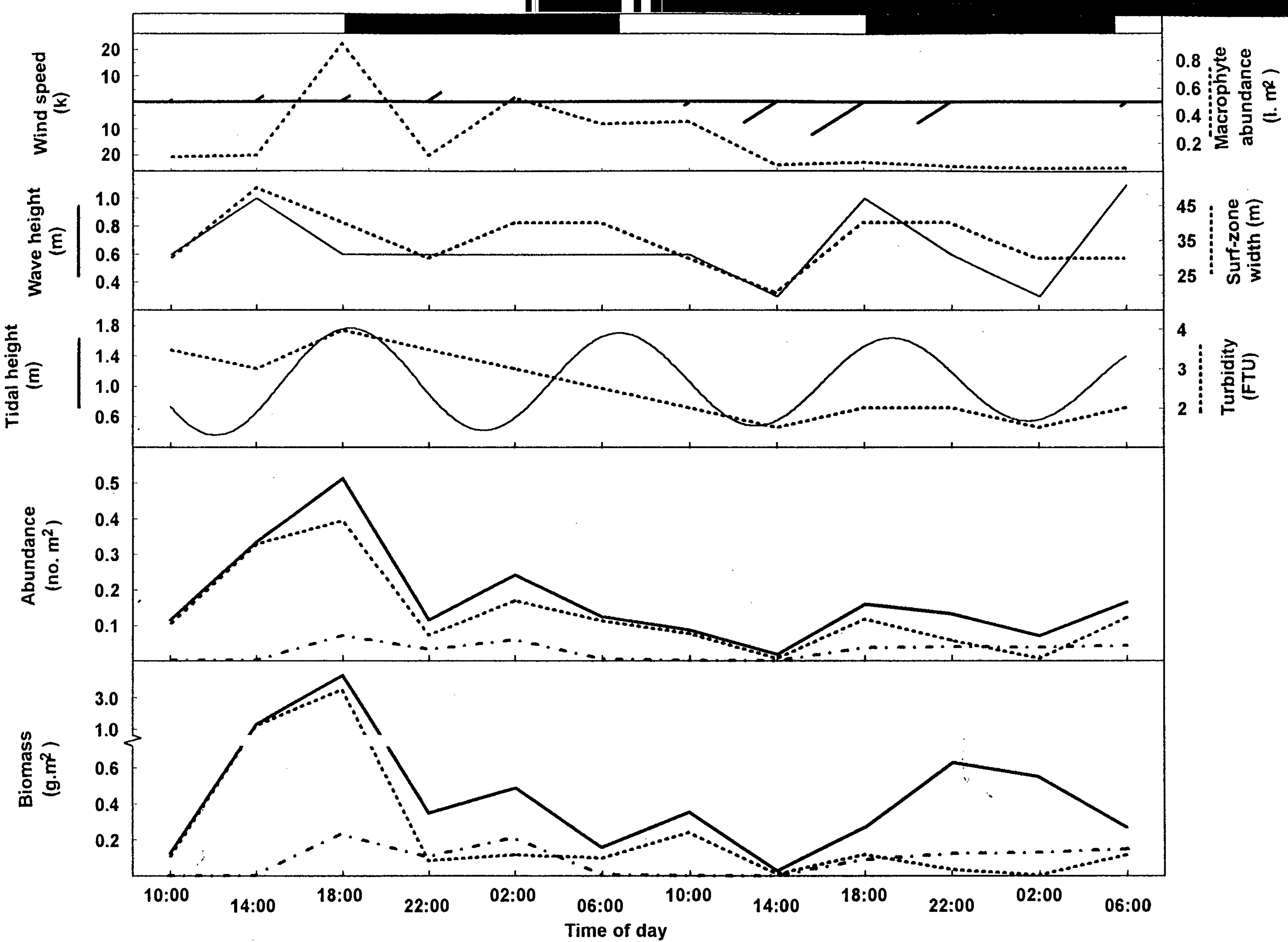


Fig. 4.5. Diel variation in physical parameters (wind speed & direction, wave height, surf-zone width, tidal height, and turbidity) and total abundance and biomass of fish (all species combined: ———, *Liza richardsonii* · · · · · , *Rhabdosargus globiceps:* — · — ) recorded in seine net hauls made at four-hourly intervals at Fishoek Beach in 1994.

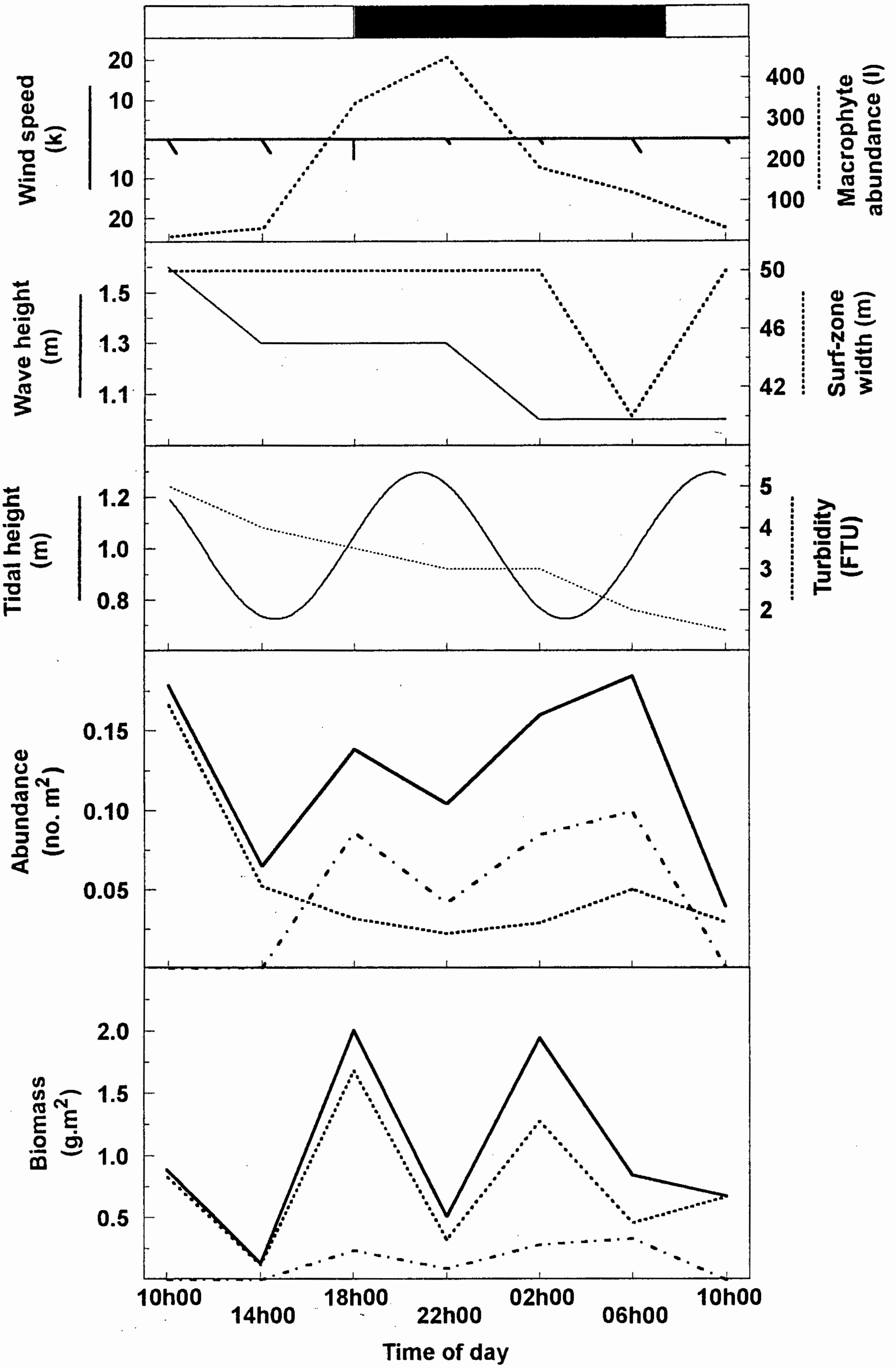


Fig. 4.6. Diel variation in physical parameters (wind speed & direction, wave height, surf-zone width, tidal height, and turbidity) and total abundance and biomass of fish (all species combined: ———, *Liza richardsonii*: - - - - , *Rhabdosargus globiceps*:— - — -) recorded in seine net hauls made at four-hourly intervals at Fishoek Beach in 1995.

Overall fish abundance in 1995 was highly variable (Fig. 4.6) with peaks evident at the start (10h00 - 0.18 ind. m $^{-2}$), at sunset (18h00 - 1.40 ind. m $^{-2}$) and sunrise (06h00 - 0.18 ind. m $^{-2}$). Lowest overall abundance was recorded in the final sample (10h00 - 0.04 ind. m $^{-2}$). *L. richardsonii* (0.17 ind. m $^{-2}$) was largely responsible for the abundance peak recorded at the start of this sampling session, but contributed little to the rest of the samples, except for a small contribution (0.05 ind. m $^{-2}$)to the peak at 06h00. Catches of *R. globiceps* were considerably greater at night than during the day, with peaks in abundance appearing in the evening (18h00 - 0.09 ind. m $^{-2)}$ and morning (06h00 - 0.10 ind. m $^{-2}$). Only four individuals of this species were captured in the daylight hauls (Table 4.5). Peaks in overall standing stocks were largely a function of variations in the abundance of *L. richardsonii*, with biomass peaks for both evident at 10h00, 18h00 and at 02h00. Biomass of *R. globiceps* peaked at sunset (18h00) and at sunrise (06h00).

### 4.3.4 Relations between biotic and environmental parameters

Results of the CLUSTER and MDS analyses in which faunal similarities between samples collected during the five diel sampling periods were examined, are displayed in Fig. 4.7. Samples from 1991 form two distinct groups at the 60% level of similarity in the dendrogram, with nocturnal samples (22h00 and 02h00) and crepuscular and diurnal samples (06h00 x 2, 18h00, 10h00 and 14h00) grouping separately. Similarly, the 1992 samples also separated into a nocturnal and a crepuscular-daytime group, but in this case at an even higher level of similarity (75%). At this level in the 1993 dendrogram, while all diurnal samples except the second 09h00 sample form a single group, all the nocturnal and crepuscular samples, save the 24h00 sample, form a second group together with the second 09h00 sample. The 24h00 sample was an outlyer in this instance. In the 1994 dendrogram, all nocturnal and crepuscular samples formed a single group, and all daylight samples except the outlying 14h00 sample, form a second group at the 60% level of similarity. Samples collected in 1995 form two distinct groups, at the 65% level, with daytime samples forming one group and crepuscular and nocturnal samples, another. Samples grouping in the ordination plots matched those in the dendrograms closely in all years, except where stress levels on the ordination plots were high (>0.1), as was the case in 1994.

Results of the BIOENV and multiple stepwise regression (MSR) procedures used to examine the influence of seven environmental parameters on diel variability in fish community structure (BIOENV), and on total fish abundance and the abundance of dominant species (MSR) are detailed in Table 4.6. Judging from these results, changes in light levels between day and night appeared to be the dominant variable influencing overall fish community structure, as well as the abundance of the more important species. This variable was incorporated into all models generated by the BIOENV procedure, which yielded rank correlation coefficients ranging from 0.26-0.58. Turbidity was included in BIOENV models for three of the five sampling sessions (1993-1995), while the other five variables appeared in predictive models for no more than two sessions. Changes in light levels had an important influence on *Rhabdosargus globiceps* abundance in all years in which it was tested, on *Liza richardsonii* in all but one (1992) and on *Atherina breviceps* in one of the two years in which this species was prominent (1992).

Correlation coefficients ranged from 0.95-0.26 for models in which at least one variable was incorporated. Variations in macrophyte abundance had an important influence on the abundance of *L. richardsonii* and *R. globiceps* for both years (1994 and 1995) in which substantial volumes of material were recorded. The remaining variables were incorporated only sporadically into the various models (Table 4.6), but in not more than one instance for any particular species. Light levels were found to have an important influence on the abundance of all species combined in 1991 and 1992, whereas the MSR model for 1994 contained the variable surf width and macrophyte abundance only, and the 1993 and 1995 models included none of the available variables.

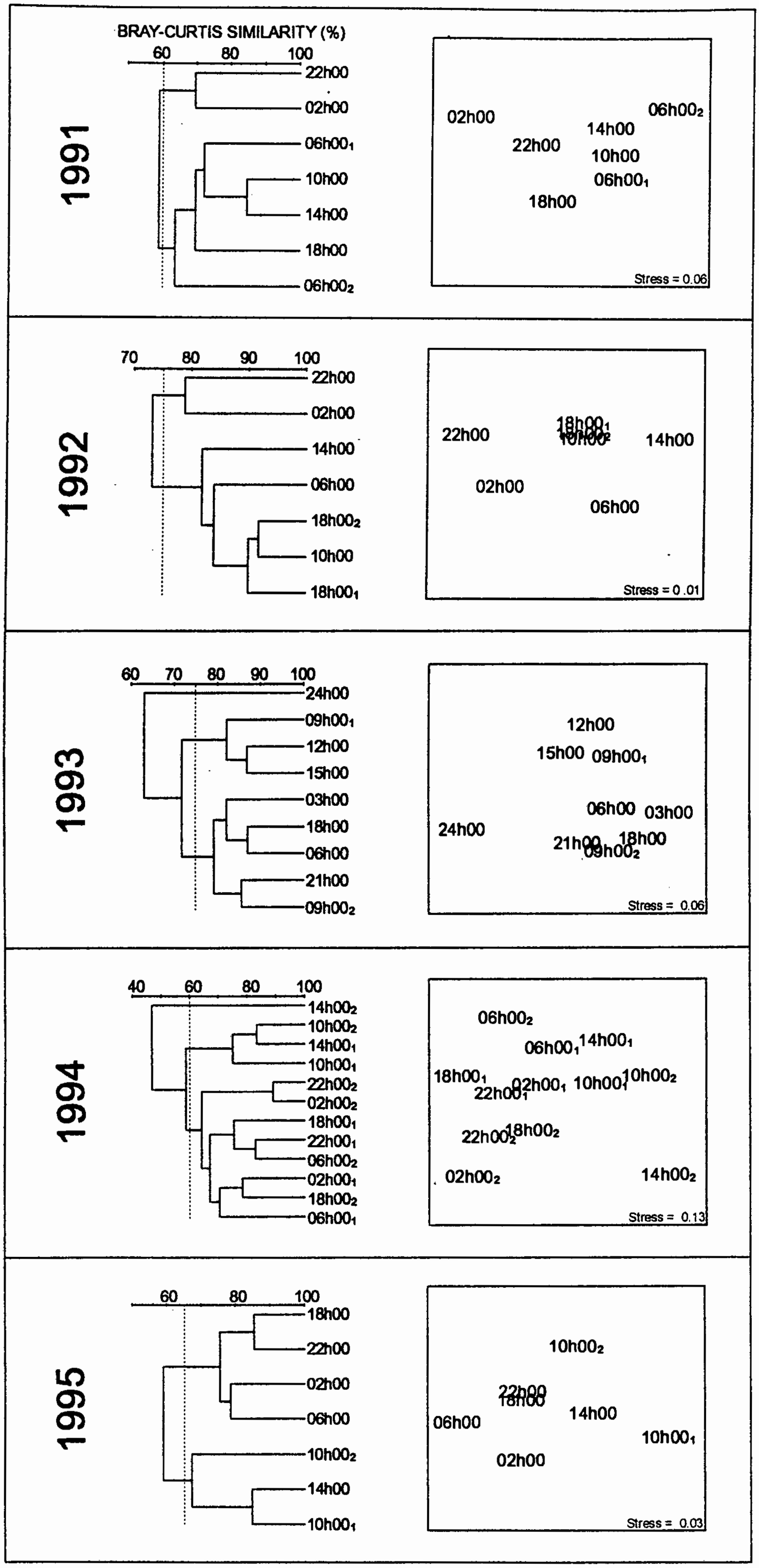


**Fig. 4.7.** Dendrograms and MDS plots showing similarities between seine net samples collected at regular intervals during 5 diel sampling sessions conducted in consecutive years from 1991 to 1995.

**Table 4.6.** Results of the BIOENV and Multiple Stepwise Regression (MSR) analyses of the influence of seven environmental parameters on surf-zone fish community structure (BIOENV) and total fish abundance and the abundance of dominant species (MSR) captured in beach seine net hauls made during five diel sampling programs, conducted in consecutive years from 1991-1995. Correlation coefficients $\rho_w$ and $r^2_{adj.}$ are included for each combination of variables selected by the BIOENV and MSR models, respectively.

| | Light/ Dark | Wave Height | Surf width | Wind | Turbidity | Tidal height | Macrophyte* abundance | |
|---|---|---|---|---|---|---|---|---|
| **BIOENV** | | | | | | | | $\rho_w$ |
| 1991 | X | | | | | | | 0.26 |
| 1992 | X | | | | | X | | 0.55 |
| 1993 | X | X | | | X | X | | 0.46 |
| 1994 | X | | | X | X | | | 0.50 |
| 1995 | X | X | | | X | | X | 0.58 |
| **MULTIPLE REGRESSION** | | | | | | | | $r^2_{adj.}$ |
| **1991** | | | | | | | | |
| *L. richardsonii* | X | | | X | | | | 0.78 |
| *R. globiceps* | X | | | X | | | | 0.77 |
| All species | X | | | | | | | 0.79 |
| **1992** | | | | | | | | |
| *L. richardsonii* | | | | | | | | - |
| *A. breviceps* | X | | X | X | | | | 0.95 |
| All species | X | | | | | | | 0.70 |
| **1993** | | | | | | | | |
| *L. richardsonii* | | | | | | X | | 0.26 |
| *R. globiceps* | X | | | | | | | 0.33 |
| *A. breviceps* | | X | | | X | | | 0.76 |
| All species | | | | | | | | - |
| **1994** | | | | | | | | |
| *L. richardsonii* | X | | | | X | | X | 0.71 |
| *R. globiceps* | X | | | | | | X | 0.63 |
| All species | | | X | | | | X | 0.69 |
| **1995** | | | | | | | | |
| *L. richardsonii* | X | | | | | | X | 0.72 |
| *R. globiceps* | X | | | | | | X | 0.58 |
| All species | | | | | X | | | - |

* This parameter was included in statistical models for 1994 and 1995 only

### 4.3.5 Diel variation in size composition

Size frequency distributions of the dominant species at each sampling interval for the five diurnal sampling excursions are depicted in Figs. 4.8-4.12. *Liza richardsonii* individuals captured in 1991 ranged from 32-266 mm (Table 4.1), but the majority (>97%) were smaller than 200 mm in all sampling intervals except for the 22h00 sample (Fig. 4.8a). This sample was composed of equal portions of individuals greater than and less than 200 mm. Evening (18h00) and nocturnal (22h00 and 02h00) catches of *Rhabdosargus globiceps* in this year also contained a greater proportion (20-35%) of individuals >70 mm than catches made during the daylight hours (0-6%) (Fig. 4.8b). Overall, individuals of this species ranged from 32-122 mm in length (Table 4.1). The change in the relative proportions of large and small individuals for both species in the transition from day to night was a result of both an increase in the number of large individuals in the catches, and a reduction in the number of small individuals captured after dark (Fig. 4.8a & b).

*L. richardsonii* collected during 1992 ranged in size from 29-309 mm (Table 4.2), with samples from most time intervals displaying bimodal size frequency distributions, with peaks evident in the region of 60-80 mm and 140-180 mm (Fig. 4.9a). Individuals making up the larger peak were, however, scarce in the two samples collected during the daytime (10h00 and 14h00). Individuals >120 mm made up only a small proportion (<16%) of these two samples, while providing a much larger proportion (48-70 %) of the nocturnal and crepuscular samples. Absolute numbers of small individuals (<120 mm) in the daylight catches were larger than the nocturnal or crepuscular catches, while the opposite was true for the larger individuals. Size frequency distributions for *Atherina breviceps* in 1992 were unimodal (Fig. 4.9b) with individuals ranging in size from 82-125 mm (Table 4.2). Frequency distributions for crepuscular and daytime samples for this species were superficially similar, while the number of individuals captured in the nocturnal samples was not high enough to allow reasonable comparisons to be drawn.

*L. richardsonii* >100 mm in length provided a considerably larger proportion (44-94%) of nocturnal and crepuscular samples in 1993 (Fig. 4.10a) than in the daylight samples (27-36% of the total). Hauls made during the daytime contained few large individuals and many small ones, whereas nocturnal and crepuscular samples contained few small but many large individuals. The overall length range for this species was 22-286 mm (Table 4.3). *R. globiceps* individuals captured in these hauls ranged from 30-103 mm (Table 4.3), but most (>97%) were less than 80 mm. No obvious changes in the size composition over time were evident for this species (Fig. 4.10b). Size frequency distributions of *A. breviceps* in 1993 (Fig. 4.10c) were bimodal during the day (09h00 - 15h00), with peaks evident in the ranges 40-60 mm and 80-90 mm. Crepuscular and nocturnal catches contained few large individuals and were mostly unimodal, centred around the 40-50 mm range. The magnitude of these catches were very much smaller than the daytime catches, and it is difficult to draw an accurate comparison. Overall, *A. breviceps* individuals captured ranged in size from 40-130 mm.

The size range of *L. richardsonii* collected in 1994 was very restricted, as no individuals >120 mm were taken in the day or night-time samples (Fig. 4.11a). The evening samples, however, contained individuals up to 270 mm in length. *R. globiceps* collected in 1994 ranged in size from 35-95 mm (Table 4.4). Crepuscular and nocturnal samples were similar in terms of their size composition (Fig. 4.11b). The paucity of individuals in the daytime catches precluded comparisons with these samples, however.

The length range of *L. richardsonii* in daylight samples collected in 1995 (10h00 and 14h00) was, once again, very restricted in comparison to that of the nocturnal and crepuscular catches (Fig. 4.12a). No individuals >140 mm were captured during the day, whereas individuals greater than this size provided up to 30% of the crepuscular and nocturnal samples, with individuals up to 345 mm appearing in the catches. The smallest individual captured in 1995 measured 27 mm (Table 4.5). *R. globiceps* displayed no obvious differences with respect to the size composition of individuals captured during nocturnal and crepuscular periods (Fig. 4.12b), and too few individuals were captured in the daylight hauls for comparative purposes. The overall length range of individuals captured in 1995 was 23-105 mm (Table 4.5).

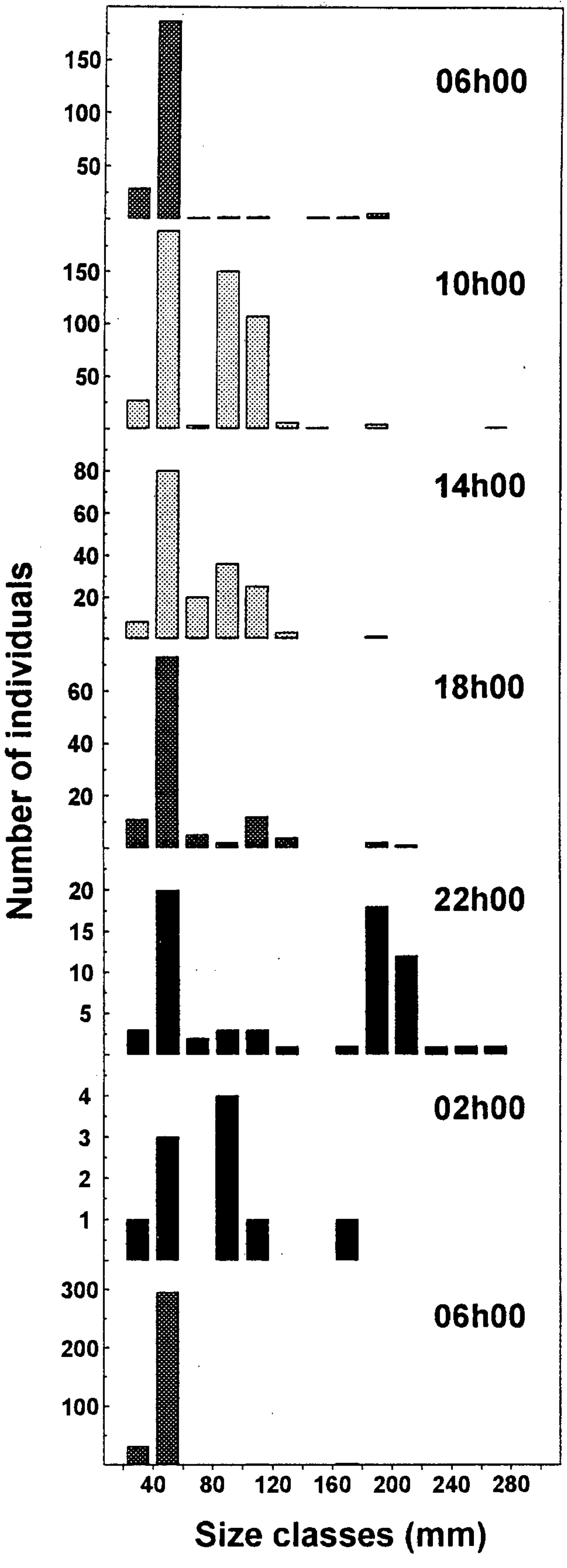


**Fig. 4.8a.** Size frequency distributions of *Liza richardsonii* collected in beach seine hauls made at four-hourly intervals in 1991. Shading indicates daytime, crepuscular and nightime samples (as for Figs. 4.8 - 4.12)

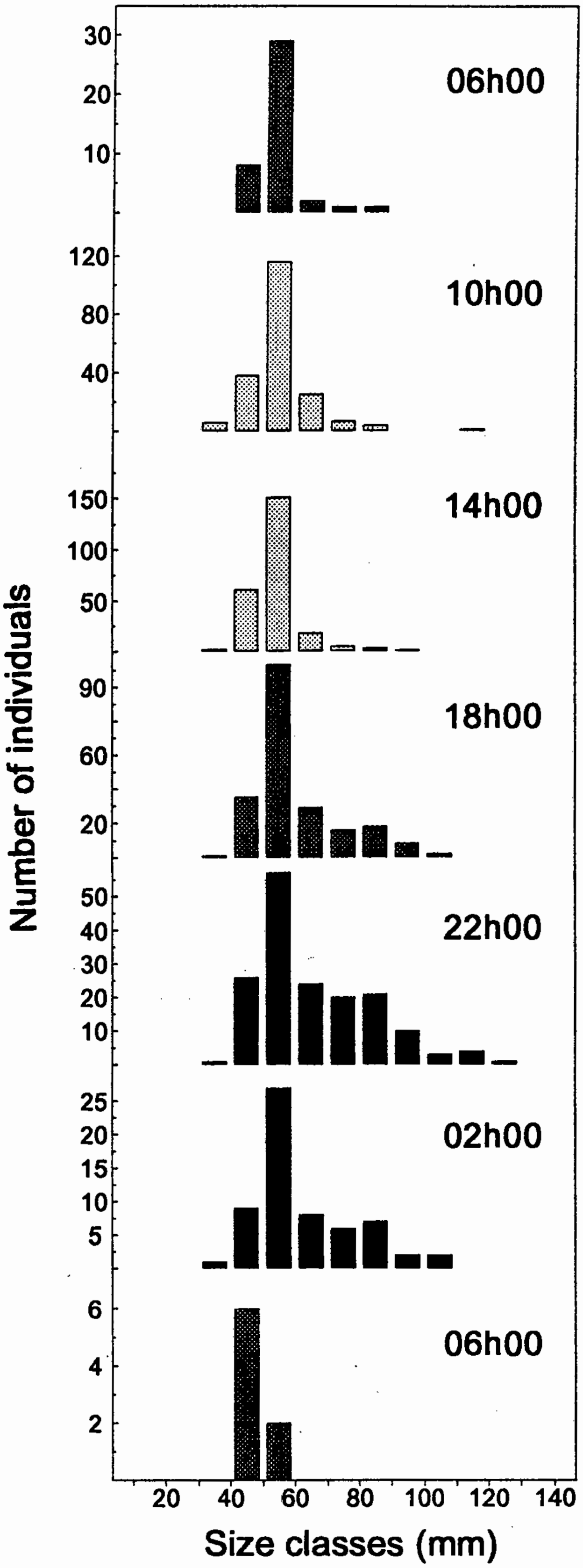


**Fig. 4.8b.** Size frequency distributions of *Rhabdosargus globiceps* collected in beach seine hauls made at four-hourly intervals in 1991.

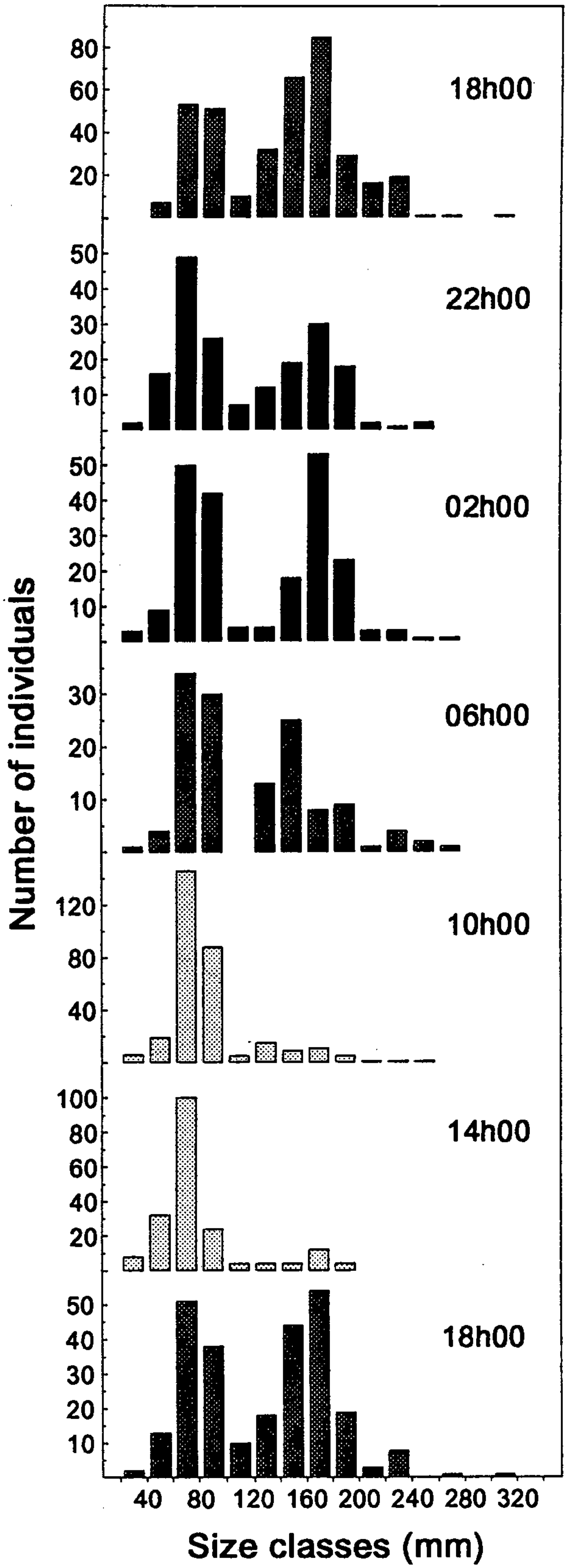


**Fig. 4.9a.** Size frequency distributions of *Liza richardsonii* collected in beach seine hauls made at four-hourly intervals in 1992.

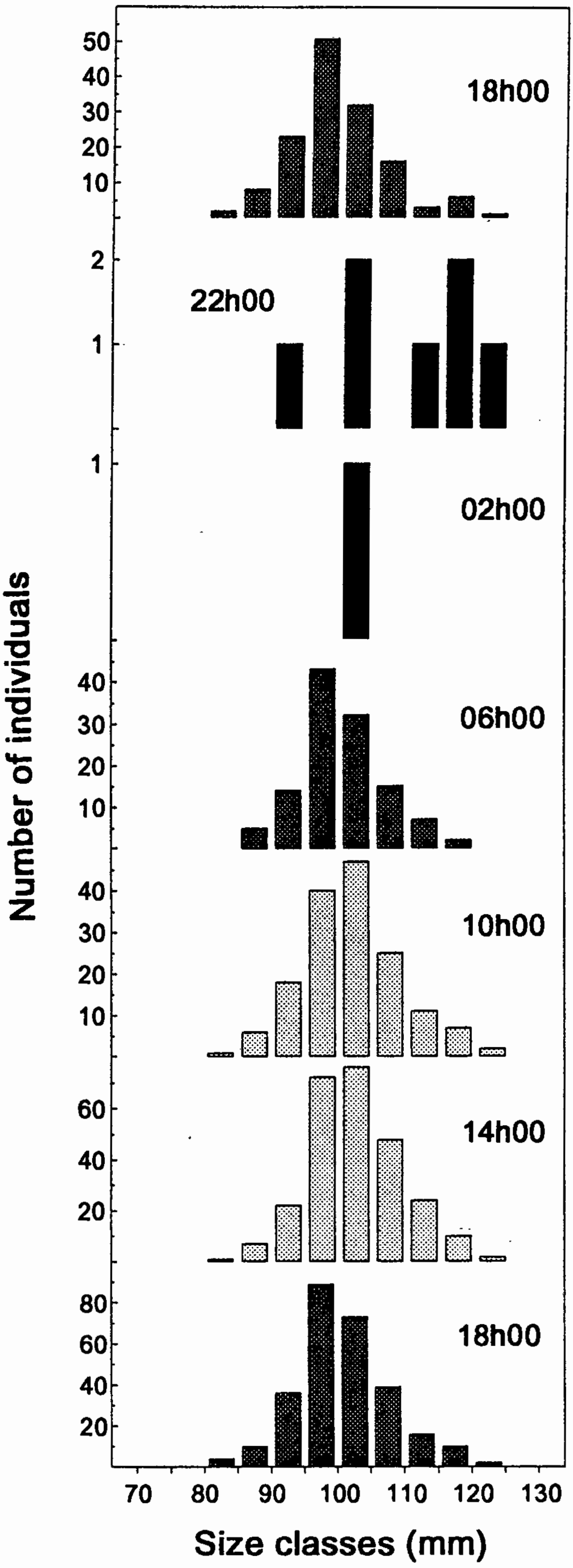


**Fig. 4.9b.** Size frequency distributions of *Atherina breviceps* collected in beach seine hauls made at four-hourly intervals in 1992.

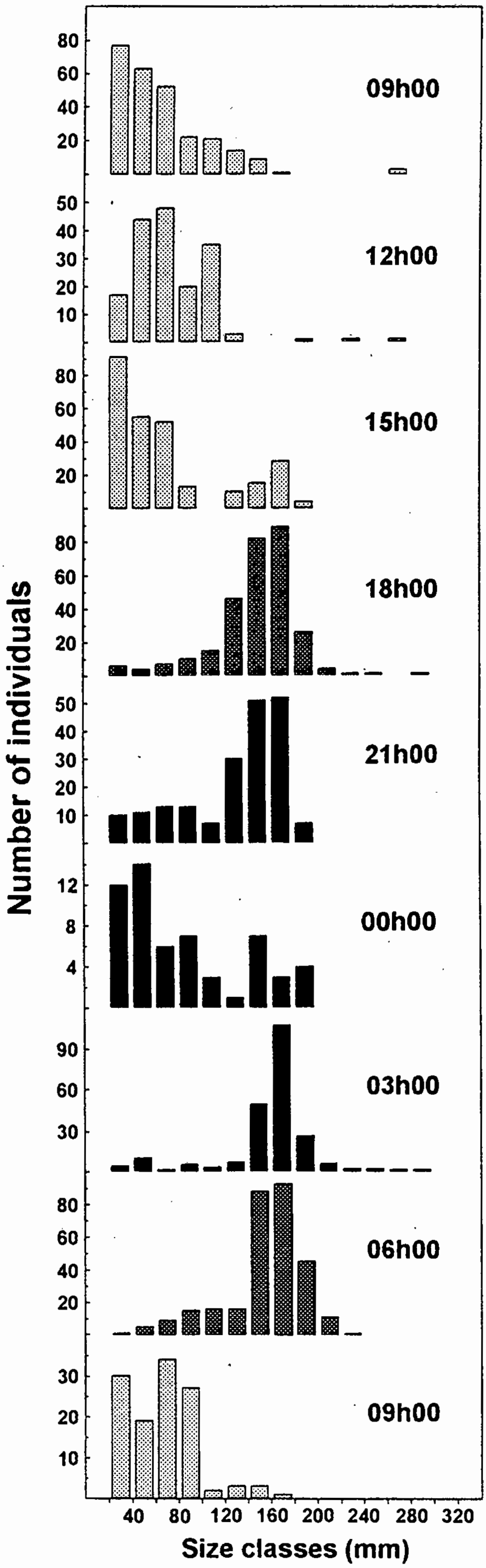


Fig. 4.10a. Size frequency distributions of *Liza richardsonii* collected in beach seine hauls made at four-hourly intervals in 1993.

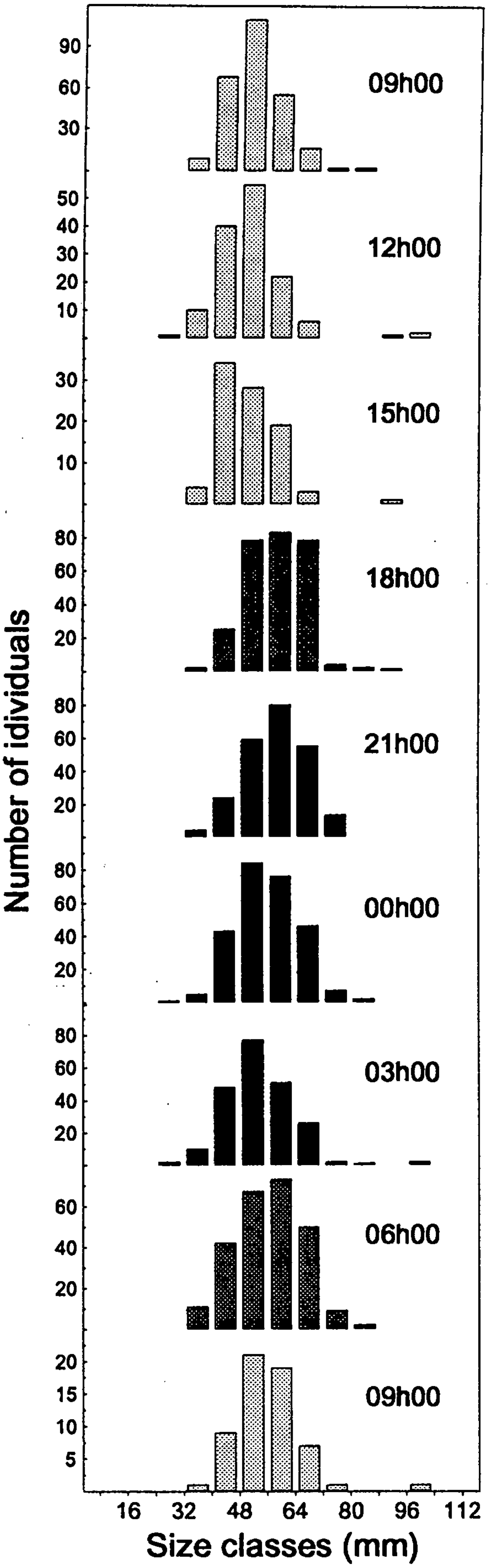


**Fig. 4.10b.** Size frequency distributions of *Rhabdosargus globiceps* collected in beach seine hauls made at four-hourly intervals in 1993.

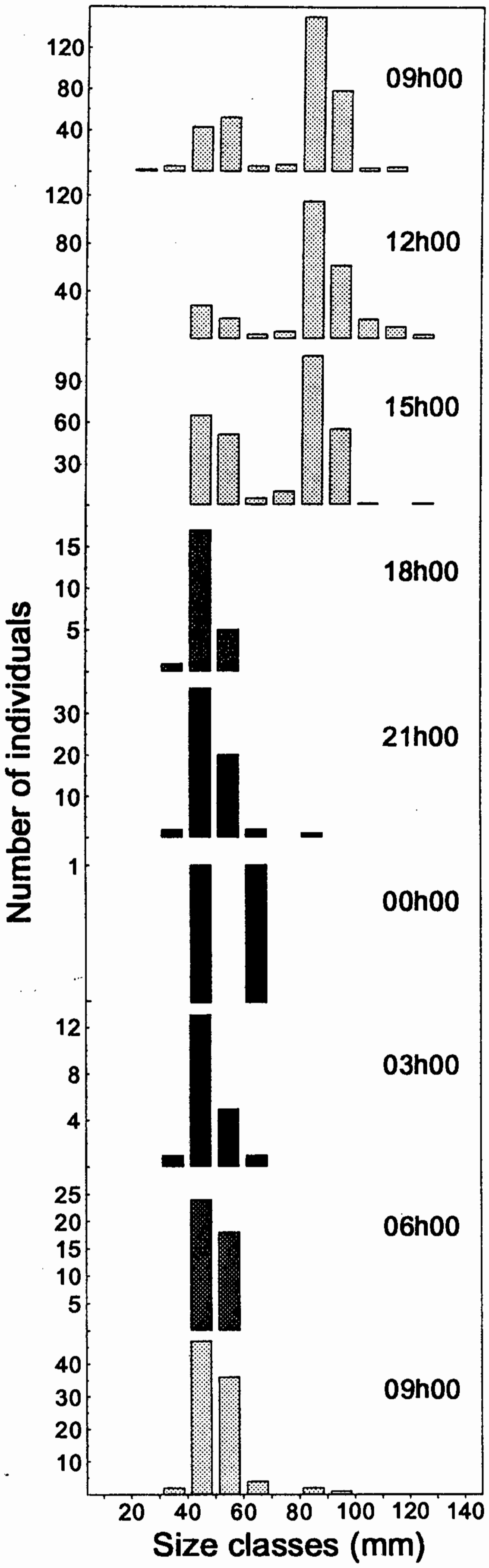


**Fig. 4.10c.** Size frequency distributions of *Atherina breviceps* collected in beach seine hauls made at four-hourly intervals in 1993.

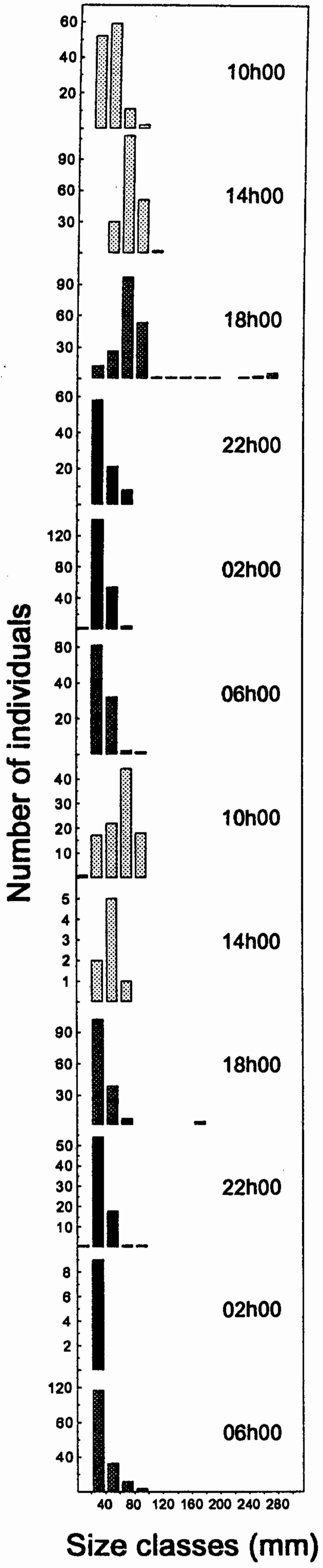


**Fig. 4.11a.** Size frequency distributions of *Liza richardsonii* collected in beach seine hauls made at four-hourly intervals in 1994.

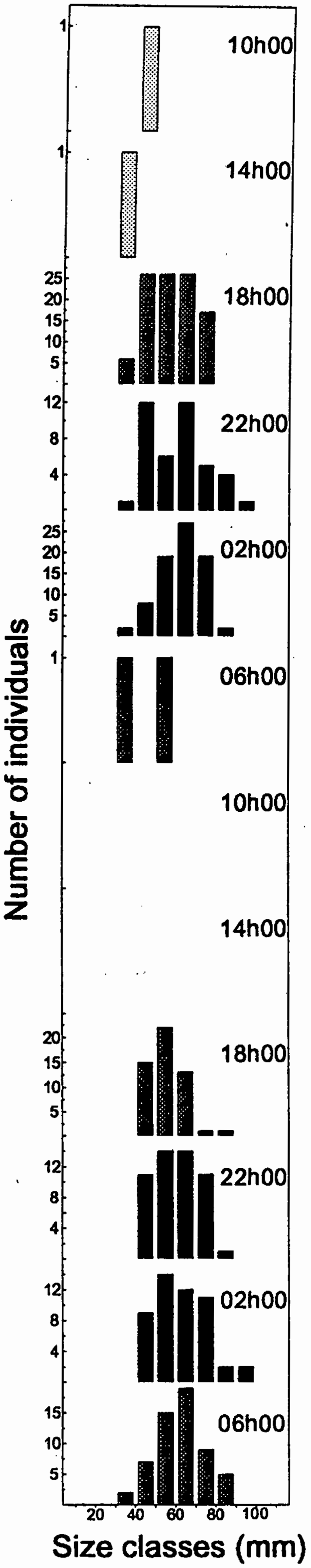


**Fig. 4.11b.** Size frequency distributions of *Rhabdosargus globiceps* collected in beach seine hauls made at four-hourly intervals in 1994.

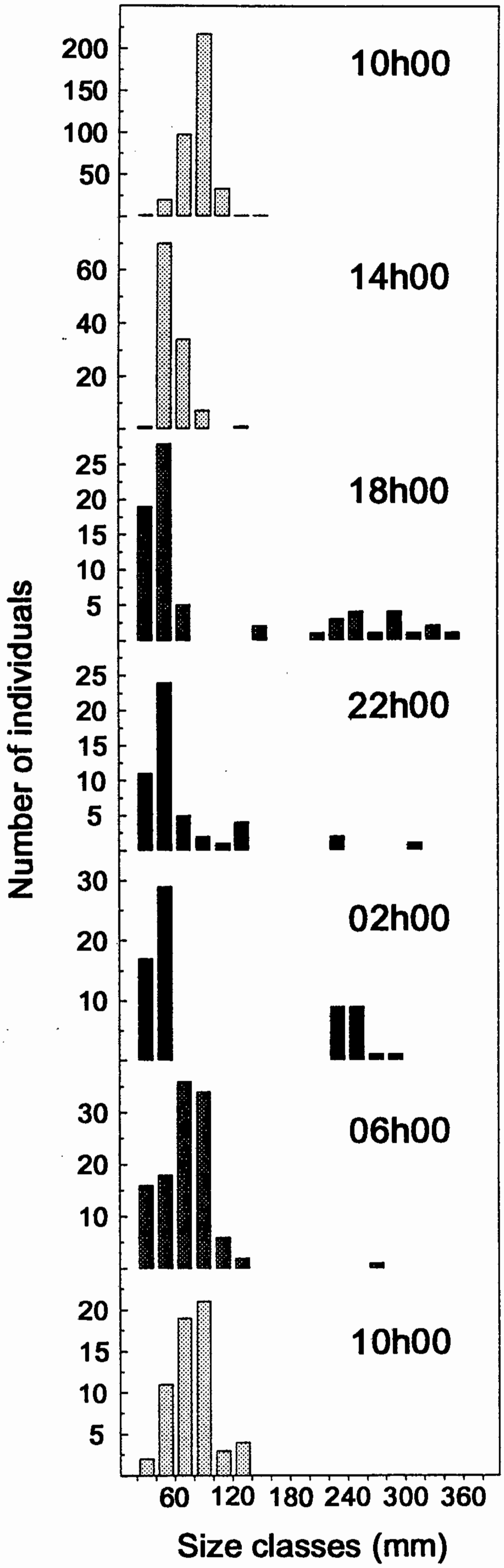


**Fig. 4.12a.** Size frequency distributions of *Liza richardsonii* collected in beach seine hauls made at four-hourly intervals in 1995.

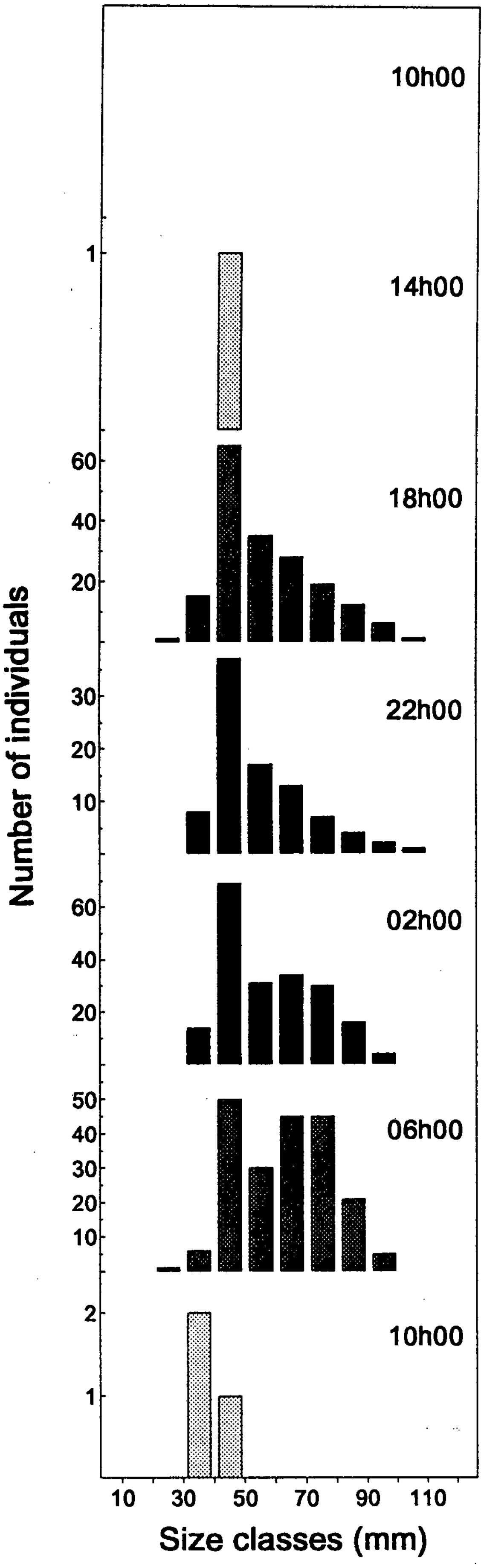


**Fig. 4.12b.** Size frequency distributions of *Rhabdosargus globiceps* collected in beach seine hauls made at four-hourly intervals in 1995.

Species other than those dominating catches in each year also displayed a marked shift in size structure between day and night. The mean size of fish taken in daytime hauls was smaller than for crepuscular or nocturnal hauls for all five sampling excursions (Table 4.7). The maximum size of fish captured was smaller in daytime catches in all cases except 1993, while the minimum sizes were similar for all three time periods, across the entire study.

### 4.3.6 Diel feeding periodicity

Examination of diel variations in gut fullness were undertaken for *Liza richardsonii* and *Rhabdosargus globiceps* during the 1994 and 1995 study periods only. In 1994, the mean gut fullness index for *L. richardsonii* (Fig. 4.13) was low (0.5%) at the time of the mid-morning sample (10h00), rose to a peak of 2.6% at 14h00 and subsequently dropped gradually through the evening to a low of 0.9% at 06h00 the following morning. A small rise to 1.2% was evident again at daybreak the following morning. In 1995, mean gut fullness for this species began at its highest level (3.6%) at 10h00, dropped marginally to 3.1% towards the afternoon, then fell more steeply through the night to a minimum of 1.22% at 02h00. Gut fullness rose again at sunrise, and continued to climb up to 2.2% at 10h00 the following morning.

**Table 4.7.** Mean, minimum and maximum sizes of all fish other than dominant species captured in diurnal, crepuscular and nocturnal seine net hauls made during diel sampling excursions in False Bay from 1991-1995.

| | Day | Crepuscular | Night |
|---|---|---|---|
| **1991** | | | |
| Mean | 82.2 | 141.3 | 239.3 |
| Min | 44.0 | 49.0 | 31.0 |
| Max | 117.0 | 810.0 | 710.0 |
| **1992** | | | |
| Mean | 70.0 | 75.7 | 102.3 |
| Min | 24.0 | 25.0 | 25.0 |
| Max | 235.0 | 810.0 | 810.0 |
| **1993** | | | |
| Mean | 83.7 | 139.7 | 92.0 |
| Min | 35.0 | 41.0 | 36.0 |
| Max | 463.0 | 366.0 | 344.0 |
| **1994** | | | |
| Mean | 60.6 | 103.1 | 103.7 |
| Min | 21.0 | 30.0 | 28.0 |
| Max | 144.0 | 167.0 | 166.0 |
| **1995** | | | |
| Mean | 51.8 | 53.2 | 55.7 |
| Min | 21.0 | 22.0 | 17.0 |
| Max | 122.0 | 152.0 | 258.0 |

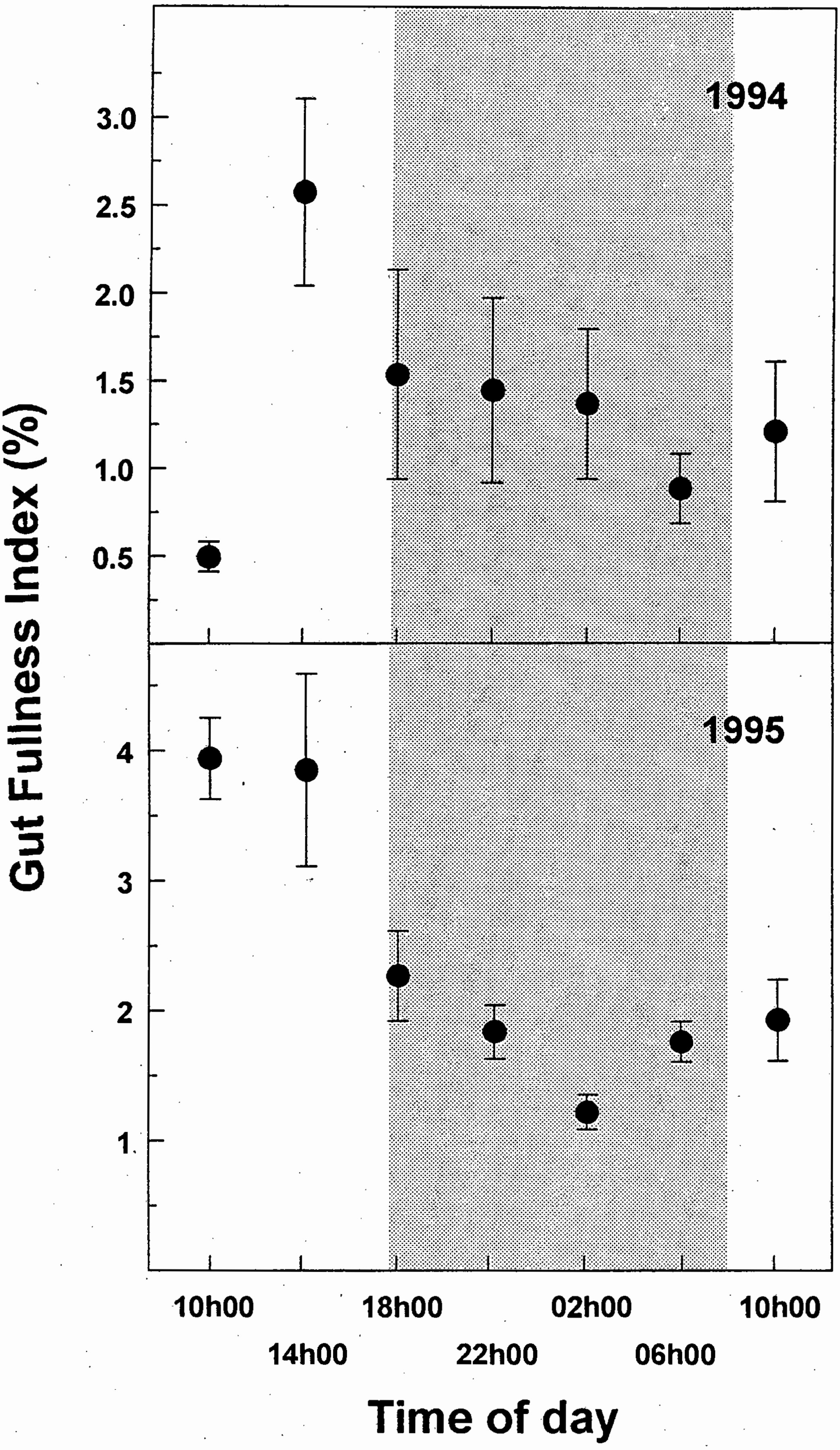


**Fig. 4.13.** Diel variation in the Gut Fullness Index of *Liza richardsonii* (mean ± S.E.) collected in seine net hauls at Fishoek Beach in 1994 and 1995.

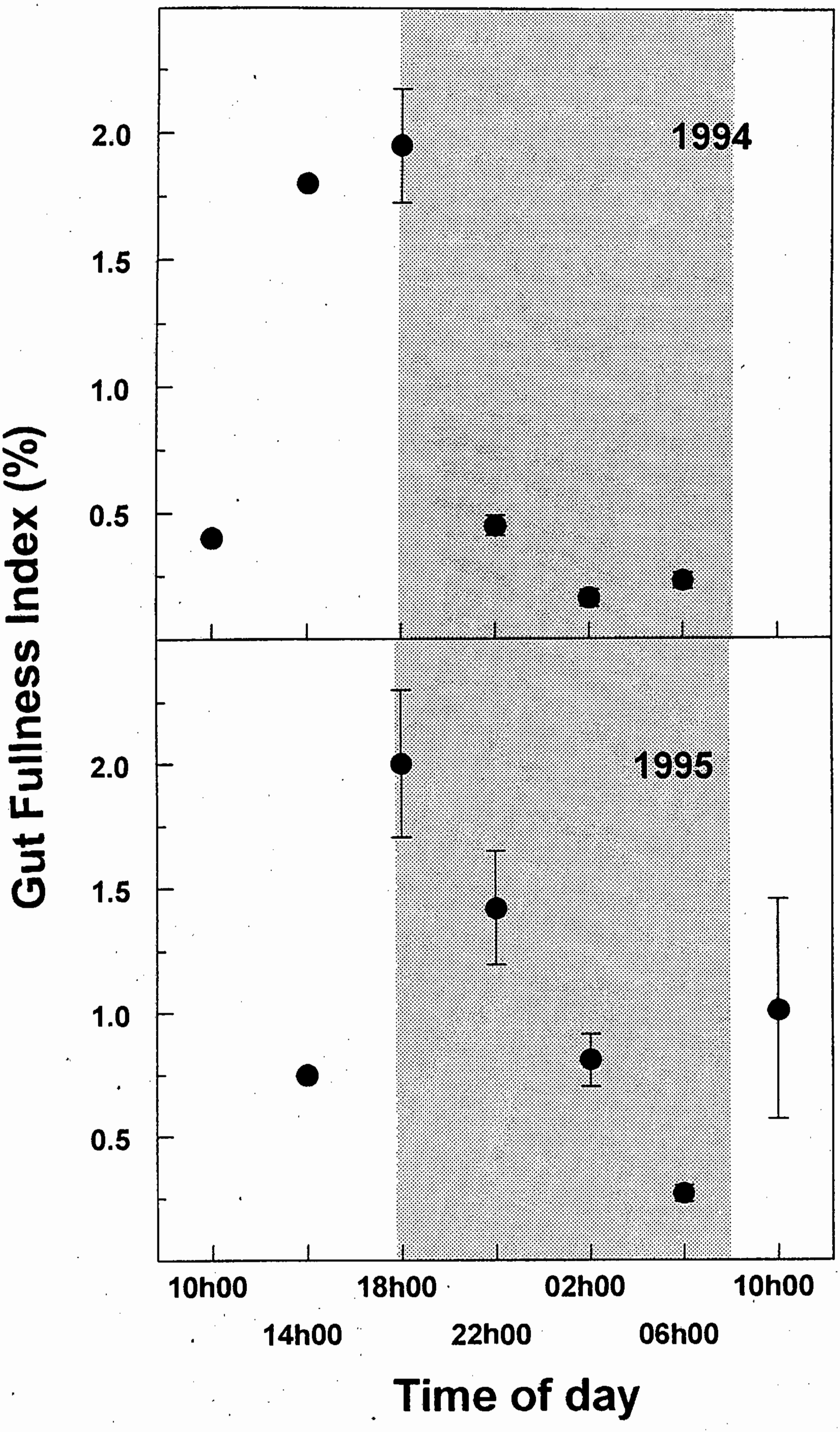


**Fig. 4.14.** Diel variation in the Gut Fullness Index of *Rhabdosargus globiceps* (mean ± S.E.) collected in seine net hauls at Fishoek Beach in 1994 and 1995.

Trends for *R. globiceps* (Fig. 4.14) were less clear due to the paucity of individuals in the daytime samples in 1994 and 1995, but data suggested a similar feeding pattern as for *L. richardsonii*. Peak and lowest gut fullness were recorded in the late afternoon and early morning for both periods, respectively.

## 4.4 DISCUSSION

As is the case in most other studies around the world (Ross 1983, Lasiak 1984a, b, Robertson & Lenanton 1984, Wright 1989a, b, Gibson *et al.* 1993), catches made during all five diel sampling excursions were dominated by very few species; 2-3 species made up ≥80% of the total catch in each case. *Liza richardsonii* provided the greatest numerical contribution in all cases, *Rhabdosargus globiceps* was second in all but one, and *Atherina breviceps* second or third in three of the five studies. Other studies examining surf-zone fish assemblages in False Bay (e.g. Bennett 1989a, Lamberth *et al.* 1994, Clark *et al.* 1994a, b, 1996a, Chapter 1) have also found these three species to be among the most abundant in this area. All important short-term temporal changes in the fish assemblages frequenting this area are thus likely to be functions of changes in the abundance or distribution of these species.

The abundance and composition of surf-zone fish assemblages is thought to vary considerably as a result of the movements of fish into and out of nearshore waters in response to diel changes in the physiochemical characteristics of the surf-zone environment. By far the bulk of the studies examining short-term variability in fish abundance and biomass on sandy beaches have been conducted in meso- and macrotidal areas* . Consequently, the ebb and flow of the tide is thought to be the most important parameter controlling the movements of sandy beach fish. The vast majority of fish frequenting meso- and macrotidal beaches are flatfish species, almost all of which migrate up and down the shore with the tides, during the day and night (Edwards & Steele 1968, Tyler 1971, Gibson 1973a, Kuipers 1973, van der Veer & Bergman 1986, Berghahn 1987). Reasons advocated for the movement patterns observed are varied, but generally fall into three categories, of which feeding is probably the most popular. Fish are thought to migrate into the intertidal with incoming tide in order to maximise feeding and

---

* tidal range of 2-4 m = mesotidal, >6 m = macrotidal; sensu Davies (1964)

growth. This is particularly important in areas where food is scarce in the subtidal (Smidt 1951, Kuipers 1973, Berghahn 1987, Raffaelli *et al.* 1990), but may also function to reduce competition where food is abundant both subtidally and intertidally (Macer 1967, Poxton *et al.* 1983, Berghahn 1987, Ansell & Gibson 1990), and allows fish to take advantage of food (e.g. bivalve siphons) not available during low tide periods (Merriman 1947, Edwards & Steele 1968, Tyler 1971, Wells *et al.* 1973). Tidal migration has also been advocated as being an important predator avoidance mechanism. Large piscivorous fish are thought to favour deeper water, and thus by migrating up the shore, prey species are able to avoid predators that move into the lower intertidal levels as the tide rises (Edwards & Steele 1968, Gibson 1973a, van der Veer & Bergman 1986, Burrows *et al.* 1994). It has also been proposed that by migrating with the tide, fish are able to track physiologically optimal conditions. By migrating offshore at low tide, they are able to escape unfavourable conditions such as high (potentially lethal) temperatures during the day and low oxygen saturation at night, which are likely to occur in the intertidal at low water (van der Veer & Bergman 1986, Raffaelli *et al.* 1990, Rountree & Able 1993, Nash *et al.* 1994).

In comparison to their meso- and macrotidal counterparts, microtidal beaches around the world are rather poorly studied, and processes controlling short-term variations in fish composition and abundance in such areas are consequently poorly understood. Studies conducted to date seem to indicate, however, that the daily cycle of light and darkness replaces the tidal cycle as the primary factor influencing these fish assemblages. Almost all authors who have examined fish assemblages on microtidal beaches have noted the effects of day-night changes on at least some portion of their fish community (Modde & Ross 1981, Allen & DeMartini 1983, Lasiak 1984b, Ruple 1984, Senta & Kinoshita 1985, Romer & McLachlan 1986, Ross *et al.* 1987, Whitfield 1989, McMichael & Ross 1987). Very few (Modde & Ross 1981, Whitfield 1989) have identified any consistent changes with regard to fluctuations in tidal height, however. Modde & Ross (1981) pronounced tide level to be one of the dominant factors affecting the abundance of fishes in the surf off Horne Island, Mississippi, but the analyses performed by these authors were limited to samples collected during the daytime only, and did not include time of day as one of the variables. Whitfield (1989) found that larval fish densities peaked at low tide, and were generally low at higher tide levels in his 24 hour sampling study at Swartvlei Bay in South Africa. By his own admission, however, he acknowledged that increased wave action at high tide may have reduced gear efficiency at these times.

Despite what seems to be a general consensus over the predominating influence of day-night changes on the fish fauna of microtidal beaches, much confusion still prevails over exactly how fish respond to these changes. Some authors report taking greater catches of some or all species during the day (Modde & Ross 1981, Senta & Kinoshita 1985, McMichael & Ross 1987, Whitfield 1989), some have recorded greater catches at night (e.g. Ruple 1984, Ross *et al.* 1987) and others report increases in abundance during crepuscular periods only (e.g. Modde & Ross 1981, Lasiak 1984b, McMichael & Ross 1987). Most authors have shied away from providing explanations for the patterns observed, but a few interpretations have been forthcoming. Romer & McLachlan (1986) found that daytime catches of mullet (*L. richardsonii*) were considerably greater than nocturnal catches, and attributed this to the diurnal feeding habits of these fish. They proposed that mullet moved into the surf-zone during the morning in order to feed off surf diatoms that accumulate at the water surface during the day only, and moved offshore after dark, when the diatom population sank from the surface and became less concentrated and hence less available to the fish. Crepuscular and daytime peaks in the abundance of various kingfish species were interpreted by McMichael & Ross (1987) as being anti-predator and/or reproductive responses and crepuscular peaks in the density of clupeoid species recorded by Modde & Ross (1981) were also simply interpreted to be a predator avoidance strategy. Nocturnal increases in the abundance of fish in the surf-zone of microtidal beaches has, in some cases, been attributed to gear avoidance by some of the component species (especially the larger ones) during daylight (e.g. Ruple 1984), or to the movement of larger individuals into shallow waters after dark (e.g. Ross *et al.* 1987). At first glance, variations in fish abundance in this study seem to be just as confusing as those reported in the literature. Peaks in overall fish abundance appear at all times of the day and night: at sunrise (1991, 1995), mid-morning (1991, 1994), noon (1993), mid-afternoon (1992), evening (1992, 1993, 1994 & 1995) and even at night (1994), and variations in standing stocks are equally variable.

When variations in overall community structure or fluctuations in the abundance of dominant species are examined separately, however, some interesting patterns emerge. Multivariate analyses used to examine similarities between samples collected during each diel sampling excursion, indicate that time of day was the primary determinant of similarities between samples. Almost without exception, day and night-time samples formed separate groups in each sampling session, with crepuscular samples grouping with the diurnal samples during the summer excursions (1991 & 1992) and with the night-time samples during the winter sessions (1993-1995). Seasonal fluctuations in community structure of fish assemblages in False Bay are very weak (Clark *et al.* 1996b, Chapter 3), and are thus unlikely to be responsible for this switchover. It is more likely that seasonal changes in the times of sunrise and sunset are the important variable. Sampling during crepuscular periods was always initiated at 06h00 and 18h00 respectively, during all years. Evening samples in summer were usually completed by sunset, whereas sampling in winter was only initiated at around this time. Similarly, sunrise occurs before 06h00 in mid summer, but only around 07h30 in winter.

Multivariate and multiple regression analyses also selected changes in light levels as being the dominant variable influencing temporal changes in community structure and the abundance of the most important species in each year, respectively. All multivariate models dealing with overall community structure and all but a few of the multiple regression models dealing with variations in the abundance of *L. richardsonii*, *R. globiceps* and *A. breviceps* incorporated this variable. However, before attempting to explain how changes in the light environment of the surf-zone may influence the movements of fish into and out of these areas, it is necessary to consider how some of the more important characteristics of this environment may influence these fish.

The first researchers to study exposed surf-zone habitats, dismissed them as being very harsh or extreme physically dominated habitats, which had very little to offer in terms of environmental diversity (e.g. Hedgepeth 1957, Springer and Woodburn 1960). However, subsequent research has shown that many organisms including small juvenile fish abound in these habitats. This has led many authors to reconsider these old ideas, and it is now generally accepted that the surf-zones of sandy beaches act as important nursery areas for the juveniles of many fish species (McFarland 1963, Gibson 1973a, Modde & Ross 1981, Lenanton 1982, Lasiak 1986, Robertson & Lenanton 1984). Water movement and general turbulence generated by waves in the breaker zone must, however, make surf-zone waters an energetically expensive habitat within which to reside -- certainly more so than the calmer, less turbulent deeper waters off shore.

It has been argued that by scouring the substratum, wave action exposes infaunal prey items, thereby increasing their availability to fish (Lasiak 1986), but water movement is also likely to hinder and disrupt feeding, and is even thought to reduce growth rates of fish in some areas (Berghahn 1987). Further, the density of macrofaunal invertebrates on microtidal beaches in South Africa and abroad, generally seem to be lower in the surf-zone than in the deeper waters further offshore (Field 1971, Massé 1972, Christie 1976, Fleischack & de Frietas 1989).

Some evidence is available to suggest that when residing in the surf-zone, planktonic organisms may replace benthic food sources as the major dietary component of many species that also occur in estuarine and offshore areas. According to Marais (1980) mullet residing in estuaries and coastal areas in South Africa have a diet consisting primarily of decaying plant detritus and epiphytic and benthic microalgae. When studying the diet of *L. richardsonii* collected from the surf, however, Romer & McLachlan (1986) found that this species was a planktonic carnivore as a juvenile, and exhibited a change to a diet consisting almost entirely of surf diatoms at a larger size. Lasiak (1986) found that when in the surf-zone, planktonic crustaceans formed the bulk (>50%) of the diet of *R. globiceps*. Individuals of this species residing in estuaries or offshore areas, consume primarily benthic invertebrates and algae (Talbot 1955, Buxton & Kok 1983, Bennett 1989c). Similarly, *A. breviceps* generally feeds on benthic and planktonic organisms in estuarine areas (Blaber 1979, Coetzee 1982, Bennett 1989c), but only seems to feed on planktonic organisms while in the surf-zone (Romer 1986). Studies by McLachlan (1983) and Wooldridge (1983) have shown that the abundance and biomass of zooplankton is generally greater in the surf-zone than offshore. This, together with the surf diatom accumulations which occur in high densities in certain areas (McLachlan & Lewin 1981, Lewin & Shaefer 1983), clearly provides a suitable alternative food resource for fish frequenting surf-zone habitats. Surf phytoplankton blooms themselves are thought to enhance the abundance of certain zooplankton species, as they are found in significantly higher densities in phytoplankton blooms than outside (Romer 1986).

Many of these planktonic food resources are only likely to be available to fish during daylight hours, however. Surf diatoms undergo diel vertical migration patterns within the surf-zones of sandy beaches, accumulating at the surface during the daytime and remaining buried in the sediments during the night (McLachlan & Lewin 1981, Sloff *et al.* 1984, Talbot *et al.* 1990). Diatoms are thought to acquire positive buoyancy by adhering to air bubbles during the day, rising up from the sediment to the surface, where they can become concentrated in dense blooms. During the late afternoon, the diatom cells switch adherence from air bubbles to sand particles and return to the sediment. In contrast to the situation in estuarine and other coastal areas, the stomachs of *L. richardsonii* collected from the surf contain very few sand particles, indicating that they feed on the diatom accumulations only when they occur in dense blooms at the surface (Romer & McLachlan 1986). Diatom blooms are thus really only available as a food resource for fish (and most likely zooplankton) during daylight hours. *R. globiceps* and *A. breviceps* in the surf feed preferentially on single prey species, which they take in a disproportionate percentage to that in the water column (Lasiak 1986, Romer 1986). They are thus likely to be visual feeders, feeding during the daytime only. Food resources in the surf-zone therefore, only seem to be available to fish during the daytime. Examination of the diel feeding periodicity of *L. richardsonii* and *R. globiceps* in this study, and elsewhere, seems to suggest that this is indeed the case.

Peaks in gut fullness for *L. richardsonii* and *R. globiceps* in this study occurred, for the most part, between late morning and early afternoon. As feeding periods are likely to occur when the stomachs are filling, i.e. immediately prior to peak fullness, feeding for these species must take place between early morning and noon,. Similarly, Romer & McLachlan (1986) recorded peak stomach fullness for *L. richardsonii* in the Eastern Cape just before sunset (18h30), which indicates that peak feeding occurred between noon and mid-afternoon. Of the few individuals captured by these authors after dark, almost all had empty stomachs.

Another important benefit afforded by surf-zone habitats throughout the world, is the cover they provide, which serves as a refuge from predation for numerous small fish. Innumerable examples exist in the literature detailing how diel movement patterns of animals have been modified by predation risk (see review by Lima & Dill 1990, for example). Prey species are often forced to trade off foraging profitability for predation risk. The presence of foam on the surface of the water, and the continual suspension of sand, detritus and air bubbles in the water column are all likely to make the surf-zone an ideal habitat in which to seek refuge, as most piscivores (birds and fish) use vision to locate and attack their prey (Hobson 1979). Foam is likely to act in a similar way that turbidity does, by providing a protective cover for prey species, enabling them to evade detection or capture by predators (Bruton 1979, 1985, Blaber & Blaber 1980, Gradall & Swenson 1982, Cyrus & Blaber 1987b, Gregory 1993).

As mentioned previously, studies throughout the world have shown that catches of fish from surf-zone habitats are dominated by small, mostly juvenile fishes. Large piscivorous species are generally rare in the catches, a fact which has led many authors (e.g. Lasiak 1986, Bennett 1989a) to suggests that coastal waters are relatively predator free. Indeed, the abundance of large piscivores is generally thought to be very low in almost all shallow water habitats (Reynolds & Thompson 1974, Whitfield & Blaber 1978, Blaber & Blaber 1980, Lasiak 1986, Wright 1989a, Ponomerenko 1994). However, as Lenanton (1982) pointed out, the premise that surf-zone waters are generally predator free, assumes that the small, fine meshed beach seine nets typically used to sample these habitats, adequately samples the largest individuals present. Trawl and line-fish catches indicate that large piscivorous fish, such as *Pomatomus saltatrix* and *Argyrosomus hololepidotus,* known to feed on species frequenting surf-zone habitats, occur in considerable numbers in the shallow waters immediately beyond the surf-zone in South Africa (Smale 1984, Smale & Bruton 1985, Smale & Badenhorst 1991, pers. obs.). These and other species (e.g. *Lichia amia* and *Seriola lalandi*) seem to penetrate the surf-zone on occasion, as they have been recorded, sometimes in considerable numbers, when larger (particularly commercial) beach seine nets are operated in the surf (e.g. Biden 1930, van der Elst 1976, Penney 1991, Lamberth *et al.* 1994). Furthermore, many large piscivorous species are caught by recreational anglers fishing in the surf off sandy beaches throughout the country, and frequently dominate their catches (Horne 1955, van der Elst 1976, Schoeman 1978, Joubert 1981b, Bennett 1991). Thus, it appears that piscivorous predators do occur in reasonable numbers in surf-zone waters, and that they are likely to play a significant role in structuring the behavioural characteristics of fish species present in these areas.

From the foregoing we can surmise that, although residing in the surf-zone may be energetically more expensive for fish than living in deeper waters offshore, it does offer fairly extensive food resources (to planktivores at least) and provides small fish with a certain amount of protection from predation. Cover provided by the surf action is, however, unlikely to be of any value when ambient light levels are very low anyway. In addition, some evidence has been presented that suggests that the abundance of large piscivorous fish may increase substantially in shallow waters after dark, as a result of inshore movements. Abundance of cod and other gadoids have been shown to increase after dark in a variety of shallow marine areas (Pihl 1982, Keats 1990, Clark & Green 1990, Methven & Bajdik 1994, Gibson *et al.* 1996), including surf-zones of sandy beaches. No direct evidence of this nature is available for surf-zone waters in South Africa (or the southern hemisphere for that matter), but some indirect evidence does suggest that this may be true here as well. Popular angling lore in South Africa holds that large fish move into shallow waters off beaches at night, and that catches of piscivorous species such as *A. hololepidotus* are usually much greater after dark (Horne 1961, Schoeman 1978, Whibley & Garrat 1989). Based on its presence in her seine net catches after dark, Lasiak (1982) classified this species (among others) as nocturnal.

Catches of the three dominant species in this study were made up mostly of relatively small individuals (<200 mm total length). Surf-zone waters offer few (if any) advantages to these individuals after dark, and we can predict therefore, that in order to take greatest advantage of the surf waters, when these fish move or stray into the surf after sunrise, they are likely to remain within the breaker zone throughout the day. They should, however, move offshore again at around sunset. Patterns of abundance for *L. richardsonii* and *R. globiceps* in 1991, *L. richardsonii* and *A. breviceps* in 1992 and *A. breviceps* in 1993 seem to follow this prediction perfectly, displaying peaks in abundance between 10h00 and 14h00 in all cases. This was not the case, however, for *L. richardsonii* or *R. globiceps* in 1993, 1994 or 1995. For the most part, these species displayed peaks in abundance in the evening or morning; abundance often being higher in nocturnal as opposed to daytime hauls.

An examination of the remaining physical variables indicates that the influence of wind direction, coupled with turbidity, on food availability and netting efficiency, could offer an explanation for deviations from the predicated trend. Changes in ambient light intensity, particularly between day and night, can affect susceptibility to capture by fishing nets, as fish are better able to see, and thus avoid (or escape from within) approaching gear under daylight as opposed to night-time conditions (Blaxter *et al.* 1964, Parish *et al.* 1964, Gibson & Ezzi 1978, Walsh 1988, Whitfield 1989, Wright 1989a, Ledgerwood *et al.* 1991, Rountree & Able 1993). However, escapement is usually only significant in reasonably clear waters (Hunter and Wisby 1964, Allen & De Martini 1983, Ross *et al.* 1987).

Turbidity was moderately high (>6 FTU) for the whole of the 1991 and 1992 sampling periods, and for the latter part (15h00 onwards) of the 1993 sampling excursions. During the early part of the 1993 survey and during 1994 and 1995, however, turbidity did not exceed 6 FTU at any stage. The presence of turbid waters in this study generally occurred in conjunction with onshore winds; while waters were usually clear when offshore winds prevailed. On occasions when winds swung from offshore to onshore during a sampling period (e.g. 1991 or 1992), an associated increase in turbidity was always evident. On the other hand, on occasions when the wind swung from onshore to offshore (e.g. 1994) or blew in an offshore direction for a sustained period (e.g. 1995), turbidity always decreased. This phenomenon has been documented and is associated with coastal upwelling (Frank & Leggett 1981a, b, 1982, Taggart & Leggett 1987, Taggart & Frank 1987). Offshore winds have the effect of reducing turbidity in inshore waters, as they are thought to drive surface waters out to sea, which are then replaced by cold clear subsurface waters. They also tend to rapidly dissipate any foam generated by the breaking waves offshore (pers. obs.), thus ridding the surf-zone of any form of surface cover as well. Onshore winds, on the other hand, in addition to bringing surface waters inshore, have the effect of generating wave action that disturbs beach sediments (Frank & Leggett 1981a), which increases turbidity in inshore waters.

Thus, the surf-zone is only likely to function effectively as a predation refuge when winds blow onshore, i.e. when surf waters are significantly more turbid that those immediately offshore. When surf waters are clear, fish moving or straying into the breaker zone are unlikely to remain there for extended periods, with the result that daytime catches are likely to be lower than, or equal to nocturnal densities. In all likelihood, increased net avoidance during the day is likely to reduce daytime catches relative to night-time catches in all studies, even when surf waters are moderately turbid.

Wind direction and strength also have an important influence on the intensity and abundance of phytoplankton blooms in the surf-zone. Blooms are reported to be more dense and to occur more frequently in conjunction with onshore winds (Becking *et al.* 1927, Rapson 1954, Gianuca 1983, Lewin & Schaefer 1983, Eagle & Hennig 1984), while strong offshore winds have the effect of blowing diatoms out to sea (Rapson 1954, Lewin & Schaefer 1983). Romer (1986) demonstrated a positive relationship between onshore winds and phytoplankton blooms at Sundays River Beach in South Africa, while Lewin *et al.* (1975) found that diatom blooms usually disappear during upwelling.

Thus, it appears that my original prediction (that the abundance of the dominant species should be greatest in the surf-zone during daylight hours), is only likely to hold when cover and food resources are provided by the surf-zone are sufficiently high so as to outweigh the negative influences of turbulent wave action. During periods of onshore winds, when surf-zone waters are clear (non-turbid) and/or food resources low, we would expect few fish to, move into, or remain within the breaker zone, as it holds few benefits for them. Fish abundance may appear to peak during crepuscular periods, as capture efficiency is likely to peak at this time, with the result that large catches are made as fish move inshore at daybreak and/or before they move offshore at night.

Variations in abundance in 1993-1995, when turbidity was low (<5 FTU) for at least part of the sampling period, seem to bear out these predictions. In 1993, turbidity was low during the daytime samples (3-5 FTU) and abundance of *L. richardsonii* and *R. globiceps* were consequently low during the day. They peaked at sunset, but dropped sharply thereafter and remained, for the most part, at a higher level than that observed during the day. Abundance increased again for the last sample taken at dawn the following day. Turbidity was low (<4.0 FTU) for the entire period in 1994 and fish abundance seemed to follow the pattern predicted. Abundance of *L. richardsonii* and *R. globiceps* in the seine catches was on the whole greater at night than during the day, with peaks in abundance appearing in the evening on both days, and at dawn on the third day. Turbidity declined steadily across the entire sampling period in 1995, and abundance of *L. richardsonii* started off reasonably high at the start (10h00) when turbidity levels were highest (5 FTU), but dropped by almost an order of magnitude by 14h00, remaining low throughout the night, before displaying a small peak again at dawn the following day. *R. globiceps* was considerably more abundant in the catches during the night than by day for this session, predictably displaying peaks at dusk and dawn.

A wide variety of other factors have been implicated in influencing the capture efficiency of fishing nets, but it is unlikely that they influenced catches significantly during this study. These include wave action, macrophyte abundance and changes in lunar period. It is thought that the sampling efficiency of beach seine nets operated in the surf decreases with increasing wave exposure as a result of gear malfunction in heavy swells (Whitfield 1989, Romer 1990). Fluctuations in maximum wave height recorded during this study were not great (maximum range = 0.6-2.0 m), with no waves exceeding the overall height of the net. Thus, any reduction in netting efficiency in times of greater wave exposure would probably have been countered by a decrease in the visibility of the net resulting from an increase in the suspension of sand particle and air bubbles in the water column, and the increased proliferation of foam on the surface. Changes in lunar phase have also been suggested as a potential factor influencing netting efficiency, due to the effects of illumination on net avoidance (Quinn & Kojis 1981). This is unlikely to have been important in this study either, as the moon was no more than half full during any of the sampling excursions. Pierce *et al.* (1990) reported that dense macrophyte growths can cause seine nets to roll up off the bottom, hence reducing capture efficiency. No comments have been published regarding the influence of detached macrophyte accumulations on netting efficiency, however. When netted in large quantities, macrophyte detritus tended to slow down the hauling speed, but the manner in which the fish became trapped in amongst the weed is likely to have offset any potential reductions in capture efficiency.

At first glance, variations in the biomass of fish over the five diel cycles seemed rather confusing, with neither overall trends, nor those of the dominant species, displaying consistent patterns. However, when examined in conjunction with trends in abundance, some interesting patterns are evident. When surf-zone waters were turbid, fish abundance peaked during the day (e.g. 1991 and 1992), while variation in biomass produced almost a mirror image of abundance. When surf waters were clear, however, fish abundance peaked during crepuscular periods, and variations in biomass seemed to follow those of abundance reasonably closely.

The reversal in these patterns seems to be a function of the variations in the size composition of the fish caught over the various diel cycles.

On the whole, fish in the nocturnal and crepuscular catches were larger than those in the diurnal catches. *L. richardsonii* in the catches ranged in size from 22-345 mm, but few individuals >140 mm were taken in daylight hauls. Individuals of this size usually made up >50% of the nocturnal and crepuscular catches, however. The length range of *R. globiceps* collected (23-122 mm), was smaller than that of *L. richardsonii*, and only displayed a clear diurnal variation in size during 1991. Individuals > 70 mm provided less than 6% of the daytime hauls in this year, whereas they provided 20-35% of the evening and nocturnal hauls. No variation in size was evident for this species in 1993, but very few of the individuals (<3%), exceeded 80 mm in length. Individuals captured in 1994 and 1995 were also small (maximum size of 95 and 105 mm respectively), and too few individuals were taken in the daylight hauls for comparative purposes. Numbers of *A. breviceps* taken during nocturnal hauls in 1992 and 1993, when this species was prominent, were also too low for comparative purposes and the largest individual recorded was only 130 mm in size. The average size of the remaining less common species was also smaller in the daytime than in the crepuscular or nocturnal hauls, for all five sessions.

A number of researchers (e.g. Ruple 1984, Ross *et al.* 1987, Gibson *et al.* 1996) sampling shallow nearshore habitats have noted a similar increase in the size of fish captured after dark. Some (e.g. Parish *et al.* 1964, Ross *et al.* 1987, Rountree & Able 1993, Gibson *et al.* 1996) have attributed this phenomenon to a nocturnal inshore movement of larger fish, while others have suggested that this may be a function of larger fish being better able to avoid their nets during the daytime (De Martini & Allen 1984, Ruple 1984, Methven & Bajdik 1994). Larger fish, on the whole, have higher maximum swimming speeds than small individuals (Brainbridge 1958, Blaxter 1967) and are thus better able to escape during periods when the net was visible. Although we cannot rule out the possibility that larger individuals (>140 mm) of the dominant species tended to move into the surf-zone after dark, it seems more likely that the nocturnal increase in the size of individuals captured was simply a function of increased net avoidance during the day. Thus, even when fish were more abundant in the catches during the day, peaks in biomass were still recorded during crepuscular or nocturnal periods because of the larger size of the fish in these catches.

In summary therefore, it appears that species dominating catches in this study exhibit extensive migration patterns between surf-zone and deeper waters beyond the breaker zone. Migration patterns are modified by water clarity and food availability, which in turn are moderated by prevailing winds. During periods when water clarity is low, fish move into the surf-zone in the morning to take advantage of the cover provided by the breaking waves, remain there throughout the day and move offshore again at night. When surf waters are clear, however, fish moving or straying into the breaker zone are unlikely to remain there, with the result that reduced netting efficiencies make daytime densities equal to or lower than those recorded at night. Peak densities are then often recorded during crepuscular periods, as netting efficiencies are likely to remain high during these intermediately lit periods.

# CHAPTER 5

# 5 RELATIVE UTILIZATION OF SURF-ZONE AND ESTUARINE NURSERY HABITATS BY FISH IN THE SOUTH-WESTERN CAPE

## 5.1 INTRODUCTION

Certain characteristics typically found in estuarine environments make them particularly suitable for colonization by marine fish species. They are considered to be among the most highly productive systems in the world, offering rich feeding grounds and providing excellent conditions for growth (Schelske & Odum 1961, Woodwell *et al.* 1973, Haedrich 1983). Spring and summer temperatures are high relative to the sea when peak juvenile recruitment occurs (Miller *et al.* 1985), and lowered salinities are advantageous as they reduce the osmotic differential between body fluids and their environment (Farmer & Beamish 1969, Lutz 1975). Lower incidence of piscivorous fish relative to the marine environment and high turbidity of estuarine waters are also thought to reduce the likelihood of predation (Blaber & Blaber 1980, Day *et al.* 1981, Haedrich 1983).

It is hardly surprising therefore, that fish form the dominant component of the nekton of estuaries throughout the world (McHugh 1967, Day & Yáñez-Aranciabia 1985, De Sylva 1975, 1985). The abundance of juvenile fish in estuaries, together with their apparent absence from other areas, led to suggestions that they might be "estuarine dependent" (see for example Cronin & Mansueti 1971, Pollard 1976, Day *et al.* 1981, Wallace *et al.* 1984a). Much criticism has been leveled at the use of this term, however, since juveniles of many of the marine species originally termed "estuarine dependent" have subsequently been found in protected inshore marine areas in various parts of the world, particularly where no permanent estuaries exist (Gordon & De Silva 1980, Gordon 1981, Hedgpeth 1982, Claridge *et al.* 1986, Lenanton & Potter 1987, Potter *et al.* 1990). These authors contest that given time, all marine species originally classified as being "estuarine dependent" will eventually be found in the marine environment, and that any species making extensive use of estuaries would be better termed "estuarine-opportunists" than "estuarine dependent".

Estuaries in southern Africa are considered to play a particularly important role in their capacity as nursery and feeding grounds for adult and juvenile fish as they contain much of the sheltered habitat in this area, due to the highly exposed, almost linear nature of the coastline (Beckley 1984a, Field and Griffiths 1991, Potter *et al.* 1990). In a series of studies in which both estuaries and a wide range of other potentially suitable alternative nursery areas -- such as surf-zone habitats, intertidal rock pools, shallow bays and reefs -- were examined, Wallace *et al.* (1984a, b), Beckley (1984b) and Smale (1984) revealed that eight fish species require estuarine conditions during their entire life-cycles, 22 species as migratory routes or during the juvenile stages of their life cycles and a further 47 depend largely, or at least partially on estuaries as juveniles. More recently, Whitfield (1994) developed a revised estuary-association classification system for fishes in southern African estuaries, listing 37 taxa that are completely dependent on estuaries and a further 68 that are at least partially dependent on estuaries in this region.

Surf-zone habitats around the world are widely used as alternative nursery habitats (Gunter 1958, McFarland 1963, Lasiak 1981, Modde & Ross 1981, Lenanton 1982, Lenanton *et al.* 1982, Senta & Kinoshita 1985, Wright 1989a, b, Bennett 1989a), but until relatively recently, have been poorly studied in southern Africa, especially the south-western Cape. Thus, although a good deal of information was available on the composition and abundance of fish species frequenting estuaries and inshore marine areas in southern Africa, data on the occurrence of fish in surf-zone habitats were sparse. Almost all of what was available (Wallace 1975a, Lasiak 1981, 1982, 1983, 1984 a, b, c 1986, Roussouw 1983, 1984, Romer 1986, 1990, Romer & McLachlan 1986, Whitfield 1989) came from south and east coast localities, with little information available on the utilization of surf-zone and other inshore marine areas in the south-western Cape. In the last few years, however, a host of studies have examined the composition, abundance and size structure of fish populations frequenting sandy and mixed shore surf-zone habitats in the south-western Cape (Clark *et al.* 1994a, b, 1996a, b, *in press*, Clark *in press*, Lamberth *et al.* 1994, 1995a, b, c).

The aim of this study is to draw together all available information on the ichthyofauna frequenting estuarine and surf-zone environments in the south-western Cape, to assess the utilization of these habitats by the relevant species during various life history stages and to examine the validity of the terms "estuarine dependent" and "estuarine opportunist" as they apply to the south-western Cape ichthyofauna.

## 5.2 ESTUARIES OF THE SOUTH-WESTERN CAPE

### 5.2.1 Physical characteristics

The south-western Cape coast stretches from the Olifants River mouth in the north (34°42′S, 18°11′E) to the mouth of the Breë River (34°24′S, 20°51′E) in the east, corresponding roughly to the Fynbos Bioregion (Eekhout *et al.* In prep). It is characterized by a Mediterranean-type climate with predominantly winter rainfall and oligotrophic rivers with waters that are often peat stained and acid.

Forty-four river mouths open to the sea along the south-western Cape coast (Fig. 5.1), but only fourteen of these (Olifants, Berg, Diep, Zand, Eerste, Lourens, Rooiels, Palmiet, Kleinmont, Bot, Klein, Uilkraals, Heuningnes and Breë) possess true estuaries *sensu* Day (1981)*. The remaining 30 river mouths opening to the sea along the south-western Cape coast possess few if any estuarine characteristics, and are unlikely to harbour conditions suitable for marine fish over extended time periods.

---

* Day's (1981) definition is an adaptation of Prichard's (1967) classic definition, and reads as follows: "An estuary is a semi-enclosed coastal body of water which is either permanently or periodically open to the sea and in which there is a measurable variation of salinity due to the mixture of sea water with freshwater derived from land drainage". This definition incorporates the numerous "blind" estuaries" typically found in arid regions such as southern-Africa that are periodically closed by sand bars for variable periods periodically becoming hypersaline, that are excluded by Pritchard's (1967) definition.

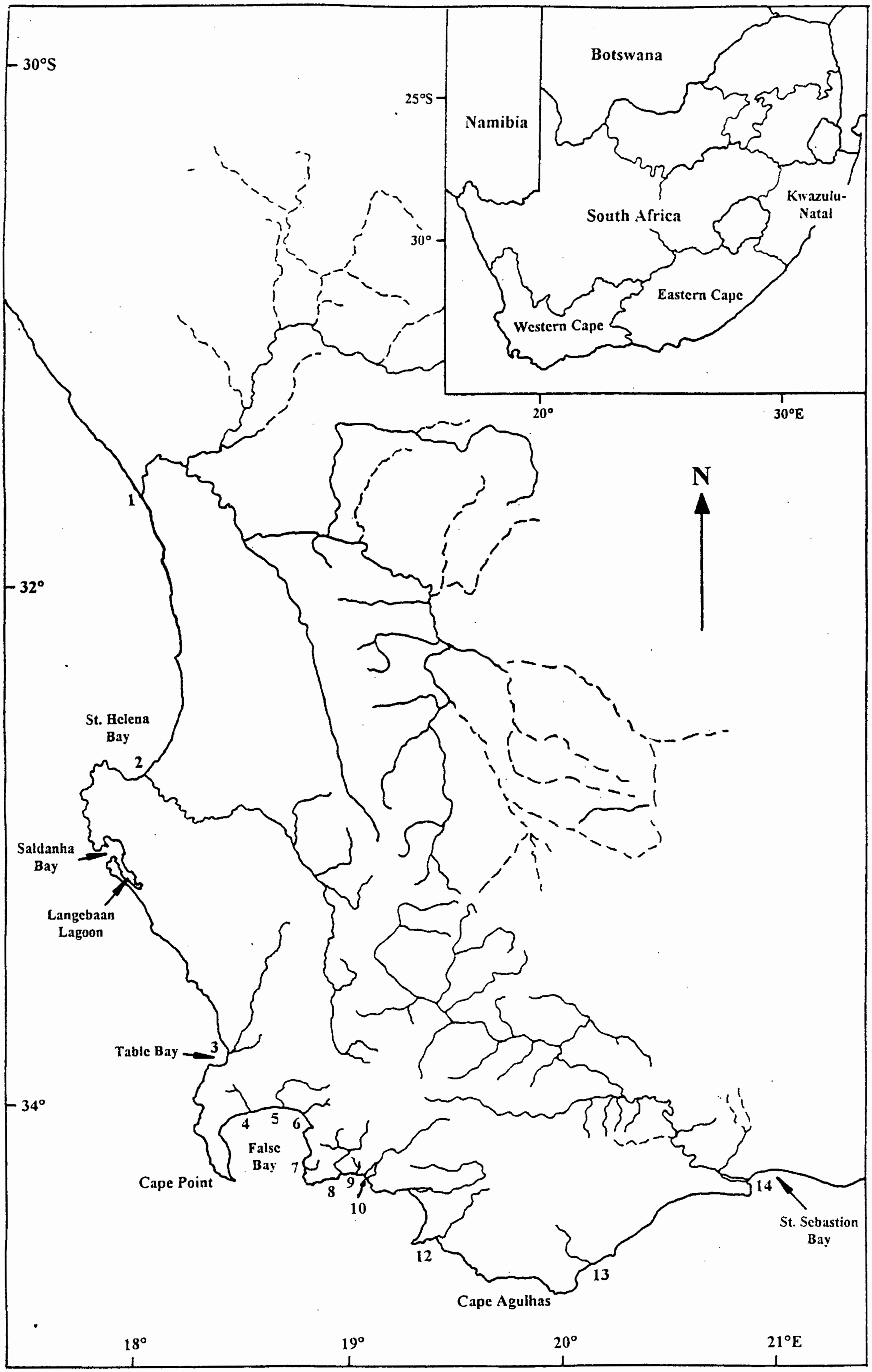


Fig. 5.1. Southern Africa (inset) and the south-western Cape showing estuaries and surf-zone localities mentioned in the text.

Various attempts have been made to categorize southern African estuaries on a biogeographic basis, as has been done for the marine littoral. This has proved to be very difficult, since the composition of South African estuarine fauna appears to be more dependent on the physical characteristics of the respective estuaries (e.g. depth, salinity regime, turbidity) than on its geographic position (Day 1964). Brown and Jarman (1978) recognize only two geographically distinct categories of estuaries - mangrove estuaries on the east coast as far south as the Mngazana (31°42′S; 29°25′E) and those on the south and west coasts where mangroves do not occur. Day (1981) divides southern Africa estuaries into three biogeographic groups: subtropical (Morrumbene 23°44′S; 35°24′E - Great Kei 32°40′S; 28°23′E), warm temperate (Keiskamma 33°17′S; 27°29′E - Zand 34°54′S; 18°28′E) and cold temperate (Black* 33°54′S; 18°28′E - Orange 28°39′; 16°29′E). In their study of southern African estuaries, Potter *et al.* (1990) adopted the littoral biogeographic divisions of Brown & Jarman (1978) and Field & Griffiths (1991), labeling estuaries north of Cape Point (34°S; 18°E) as far as central Namibia (23°S; 14°E) as cold temperate, those east and north of Cape Point to latitude 31°S on the east coast as warm temperate, and those northwards to 26°S as subtropical. Whitfield (1994) accepted the classification of Potter *et al.* (1990), but modified it by changing "cold temperate" to "cool temperate" as he considered the latter term inappropriate considering water temperatures in west coast estuaries never drops below 10°C. He also moved the point of separation between subtropical and warm temperate estuaries to the Mbashe mouth (32°17′S; 28°54′E) which lies between that proposed by Day (1981) and Potter *et al.* (1990). Estuaries of the south-western Cape appear to straddle two biogeographic regions therefore, the cool/cold temperate west coast and the warm temperate south coast.

Most of the 14 estuarine systems in the south-western Cape have been studied in detail, and the major physical characteristics of each are detailed in Table 5.1. The total surface area of water available to fish in each estuary ranges from 1 ha in the Rooiels estuary to 1 490 ha in the Bot (Duvenage 1983). All 14 estuaries together provide a total available estuarine surface area of 6 277 ha on the south-western Cape coast. Presently, only eight south-western Cape estuaries are open to the sea throughout the year, the remainder being periodically closed by

---

* The estuary of the Black River has been omitted from this study as it is grossly polluted and its water toxic, with the result that it effectively no longer functions as an estuary.

sand bars which form across their mouths during periods of reduced freshwater inflow and are open either on a seasonal basis (3) or only intermittently (3) (Table 5.1). Surface water temperatures vary seasonally, generally in the region of 12-24 °C, but extend as low as 10 °C and as high as 27 °C in some cases (Table 5.1).

### 5.2.2 Biological status

Disruption of the natural functioning of estuarine systems is a widespread problem throughout the world, from which southern Africa is not immune. Extensive damming and the abstraction of water from the catchment areas of the systems in the south-western Cape means that many of the estuary mouths (e.g. Diep, Zand and Klein) have to be breached artificially, either to maintain estuarine conditions within the systems, or simply to prevent damage to properties situated on the flood plains. Dams, weirs or bridges obstruct the river channel in or immediately above all but one (the Breë) of the 14 estuaries in this area. The lower reaches of most of these systems have also been stabilized, moved, dredged or modified in some manner. Almost all systems are polluted by agricultural runoff (fertilizers and pesticides), while runoff into at least six (Berg, Diep, Zand, Eerste, Lourens, Klein) is supplemented by storm water, industrial and/or sewerage effluent.

Assessments of the health of estuaries in the south-western Cape indicates that the biological status of these systems is generally very poor (Table 5.1). Heydorn (1986) considered only one system (the Palmiet) to be in good biological condition; nine (Olifants, Berg, Rooiels and Kleinmont - Breë) to be in fair condition; and the remaining four in poor condition. The situation has undoubtedly deteriorated since that time, which is reflected in the results obtained by Harrison *et al.* (1994, 1995). Rating all South African estuaries on a scale of 1-10, they allocated scores above 5 to only four (Olifants, Berg, Zand and Breë) of the fourteen south-western Cape systems, the maximum score being 6.6 (for the Breë). Half of the remaining systems received scores between 3 and 5, while the rest all received scores of <3.

**Table 5.1.** Summary of the physical characteristics: location, total surface area (including area covered by emergent macrophytes), catchment size, mouth characteristics (defined as being permanently open = PO, seasonally open = SO or intermittently open = IO) and and mean minimum and maximum surface water temperatures of 11 estuaries in the south-western Cape, with evaluations of their biological status as defined by Heydorn (1986) and Harrison *et al.* (1984, 1985).

| Estuary | Location | Total surface area (ha)[1] | Catchment size ($km^2$)[2,3] | Mouth characteristics[4-19] | Biological health Heydorn (1986)[a] | Biological health Harrison *et al.* (1994, 1995)[b] | Surface water[4, 6-21] temperature (°C) Min | Surface water[4, 6-21] temperature (°C) Max |
|---|---|---|---|---|---|---|---|---|
| Olifants | 31°42′S, 18°11′E | 648 | 46 220 | PO | 2 | 6.0 | 10 | 21 |
| Berg | 32°46′S, 18°09′E | 789 | 7 715 | PO | 2 | 5.3 | 12 | 27 |
| Diep | 33°53′S, 18°28′E | 428 | 1 495 | SO | 3 | 4.0 | 11 | 27 |
| Zand | 34°06′S, 19°29′E | 121 | 83 | IO | 3 | 6.0 | 11 | 24 |
| Eerste | 34°05′S, 18°46′E | 15 | 710 | PO | 3 | 3.3 | 10 | 26 |
| Lourens | 34°06′S, 18°49′E | 4 | 140 | PO | 3 | 2.7 | 12 | 27 |
| Rooiels | 34°18′S, 18°49′E | 1 | 21 | SO | 2 | 2.7 | 15 | 21 |
| Palmiet | 34°21′S, 19°00′E | 18 | 535 | PO | 1 | 1.7 | 13 | 20 |
| Kleinmont | 34°21′S, 19°04′E | - | - | SO | 2 | 1.2 | | |
| Bot[c] | 34°21′S, 19°06′E | 1490 | 920 | IO | 2 | 3.2 | 12 | 24 |
| Klein | 34°25′S, 19°18′E | 1280 | 906 | IO | 2 | 4.8 | 12 | 25 |
| Uilkraals | 34°36′S, 19°25′E | 260 | 390 | PO | 2 | 1.7 | | |
| Heuningnes | 34°43′S, 20°07′E | 110 | 1 400 | PO | 2 | 3.6 | 12 | 24 |
| Breë | 34°24′S, 20°51′E | 1 113 | 12 384 | PO | 2 | 6.6 | 13 | 24 |

a. Individual estuaries were rated as good (1), fair (2) or poor (3) based on the deliberations of the SANCOR Estuaries Programme working groups in 1984/85.

b. Biological Health Index (0-10) developed by Harrison *et al.* (1994, 1995) based on comparison between fish species in each system to an 'expected' list of species in the absence of, or prior to degradation.

c. Estimates of total surface area and catchment size for the Bot estuary includes that of the Kleinmont estuary.

1. Duvenage (1983) 2. CSIR (1987) 3. CSIR (1988) 4. Morant (1984) 5. Slinger & Taljaard (1994) 6. Morant & Grindley (1982) 7. Grindley & Dudley (1988) 8. Grindley (1982) 9. Clark *et al.* (1994b) 10. Cliff & Grindley (1982) 11. Heinecken (1982) 12. Clarke (1989) 13. Koop (1982) 14. Bennett (1989b) 15. Branch & Day (1985) 16. De Decker (1989) 17. Heydorn & Bickerton (1982) 18. Bickerton (1984) 19. Carter (1983) 20. Day *et al.* (1981) 21. Mehl (1973)

### 5.2.3 Ichthyofaunal composition and estuarine dependence

A number of assessments have been made of the relative estuarine-dependence of fish frequenting South African estuaries (Day 1951, Day *et al.* 1981, Wallace & van der Elst 1975, Wallace *et al.* 1984a, Whitfield 1994). According to Whitfield's assessment, all fish species identified from south-western Cape estuaries (Table 5.2), can be split into five groups based on their breeding habits and utilization of estuarine environments. "Estuarine species" are able to spawn and successfully complete their entire life-cycles in the estuarine environment. Most have not been recorded spawning in marine or freshwater environments and are considered to be completely dependent on estuaries for their survival. A few species in this category do have marine or freshwater breeding populations, however, and are hence only partially dependent on estuaries. "Estuary dependent marine species" are unable to breed in estuaries and must return to the marine environment to do so. This group consists primarily of juveniles that show varying degrees of dependence on estuaries, from complete dependence to species that utilize estuaries on an opportunistic basis only. "Marine species" and "Freshwater species" include adults and juveniles of euryhaline species able to tolerate varying degrees of salinity, that occasionally stray into estuaries from marine or riverine environments, respectively. Species in these two categories show no dependence on estuaries, and are usually confined to the lower reaches where salinities approximate those of the sea (in the case of marine species), or to the upper reaches where salinities do not exceed 10‰ (in the case of freshwater species). Finally, obligate diadromous species use estuaries as a transit route between marine and freshwater environments and thus depend on estuaries as access routes.

Based on their dependence on estuarine systems, Whitfield (1989) subdivides fish species frequenting south-western Cape estuaries into a further three groups (Categories I-III, Table 5.2). Firstly, "Estuarine dependent" or Category I species, that are entirely dependent on estuaries for their survival, including all diadromous species, most estuarine species and some estuary dependent marine species. Secondly, "Marine estuarine opportunists" or Category II species, that are partially dependent on estuaries, that includes mostly estuary dependent marine species but also some true estuarine species. The last group, Category III includes all those that show no dependence on estuaries.

A total of 67 fish species have been recorded from south-western Cape estuaries (Table 5.2), but many, particularly the marine species, have been recorded in very low numbers, and are of little interest here. Only 30 of the 67 species constitute ≥1% of the fauna in any one estuary. For the purposes of this study, these have been labeled as common (1-10% numerical abundance) or abundant (>10% numerical abundance). Estuarine dependent marine species (15) and estuarine species (8) make up the greatest portion of the common and abundant ichthyofauna of south-western Cape estuaries (50% and 17% respectively). Marine (3% - 1 species) and freshwater species (17% - 5 species) provide much smaller contributions (Table 5.2). Only one catadramous species (*Anguilla mossambica*) has been recorded from south-western Cape estuaries in the past (Thompson 1913), but not in recent years. No anadromous species have ever been recorded from southwestern Capoe estuaries. In total, 11 species (3 estuarine, 8 marine) are considered to be entirely dependent on estuaries (Category I), 13 to be partially dependent on estuaries (Category II) and 6 to show no dependence on estuaries (Category III). One species, *Argyrosomus hololepidotus,* labeled by Whitfield (1994) as an estuarine dependent marine species, has since been reclassified as two species (*A. japonicus* and *A. inodorus*) by Griffiths & Heemstra (1995). Both are marine species, but the former (*A. japonicus*) is considered to be truly estuarine dependent (Category I), frequenting estuaries between Cape Agulhas (35°S; 20°E) and northern Natal (28°S; 32°E), while the latter shows no dependence on estuaries (Category III) and occurs from Namibia (29°S;16°E) southwards and eastwards up to the Kei River (33°S28°E). *Argyrosomus* sp. recorded in estuaries from the Olifants-Zand (Table 5.2) are likely to be *A. inodorus,* while those recorded from the Kleinmont-Breë are probably mostly *A. japonicus.*

In summary therefore, based on the findings of this study and those of Whitfield (1994), a total of 30 species of fish make extensive use of southern African estuaries, 11 of which completely dependent and 12 partially dependent on these habitats as nursery/feeding grounds.

Table 5.2. A list of all positively identified fish species recorded from 11 south-western Cape estuaries. Species are split into four groups according to their breeding habits and their utilization of estuarine environments (estuarine species, estuarine dependent marine species, marine species and freshwater species) and according to their dependence on these habitats (I = entirely dependent on estuaries, II = partially dependent on estuaries, III = marine or freshwater species showing no dependence on estuaries) after Whitfield (1994). ◆ denotes ≥10% numerical contribution, ♦ 1-10% contribution and • <1% contribution. Species contributing <1% of the total in any of the 14 estuaries are included as a footnote only.

| | Olifants | Berg | Diep | Zand | Eerste | Lourens | Rooi-els | Palmiet | Kleinmond | Bot | Klein | Uilkraals | Heuningnes | Breë | Dependence category |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Estuarine species** | | | | | | | | | | | | | | | |
| *Atherina breviceps* | ◆ 1,3,4 | ◆ 1,3,5,6 | ◆ 3,7,8 | ◆ 1,9,10,11 | • 1,9 | ◆ 14 | ◆ 15 | ◆ 16,17 | ◆ 2,16,18 | ◆ 2,16,18 | ◆ 2,3,19,20 | ◆ 2 | ◆ 3,22 | ◆ 23 | II |
| *Caffrogobius multifasciatus* | | • 5 | | • 9 | | | | ♦ 16,17 | ♦ 16,18 | ♦ 16,18 | ♦ 2 | | ♦ 22 | ♦ 23 | II |
| *Caffrogobius nudiceps* | ◆ 4 | ◆ 1,5, 6 | ◆ 1,7,8 | • 1,11 | | | | | | | • 19,20 | ◆ 21 | | | II |
| *Clinus spatulus* | | | | | | | | | • 16 | ♦ 2,16 | • 2 | | | | I |
| *Clinus superciliosus* | • 4 | ♦ 5 | • 3,7,8 | • 11 | | | | | | | • 2,3,19,20 | | | • 3 | II |
| *Gilchistella aestuaria* | ◆ 1,3,4 | ◆ 1,3,5,6 | ◆ 3,7,8 | ◆ 1,9,10,11 | ◆ 9 | ◆ 1 | ◆ 1 | ◆ 16,17 | ♦ 16,18 | ◆ 2,16,18 | ◆ 2,3,19,20 | | ◆ 3,22 | ◆ 3,23 | I |
| *Psammogobius knysnaensis* | ◆ 1,4 | ◆ 1,3,5,6 | ◆ 3,7,8 | ◆ 1,9,10,11 | ◆ 1,9,13 | ◆ 1,14 | ◆ 1, 15 | ◆ 2,16,17 | ◆ 2,16,18 | ◆ 2,16,18 | ◆ 2,3,19,20 | ♦ 2,21 | ◆ 22 | ◆ 3,23 | I |
| *Syngnathus acus* | ♦ 1,3,4 | ♦ 1,3,5,6 | ♦ 1 | • 11 | | | | • 18 | • 16,18 | ◆ 2,16,18 | ♦ 2,3,19,20 | | ♦ 22 | • 3 | II |
| **Estuarine dependent marine species** | | | | | | | | | | | | | | | |
| *Galeichthyes feliceps* | • 1,4 | • 1,5,6 | | | | • 14 | | • 2,17 | • 16 | • 2,18 | • 2,3,19,20 | | • 22 | ◆ 3,23 | II |
| *Heteromycterus capensis* | ♦ 4 | | ♦ 1,7,8 | • 1,10,11 | ♦ 9,13 | | • 1,15 | | | | • 19,20 | | ♦ 22 | ♦ 3,23 | II |
| *Lichia amia* | ♦ 4 | ♦ 3,5,6 | | ♦ 1,10,11,12 | • 13 | • 14 | | ♦ 16,17 | ♦ 16,18 | • 16,18 | ♦ 3,19,20 | | ♦ 3,22 | ♦ 3,23 | I |
| *Lithognathus lithognathus* | • 3,4 | • 3,6 | ♦ 3,7,8 | ♦ 9,11,12 | | ♦ 14 | ♦ 15 | ◆ 16,17 | ◆ 16,18 | ♦ 16,18 | ♦ 3,19,20 | ◆ 21 | ♦ 3,22 | ♦ 3,23 | I |
| *Liza dumerilii* | | | | • 1 | ♦ 9 | | | ♦ 16,17 | | | | | | • 3,23 | II |
| *Liza richardsonii* | ◆ 1,3,4 | ◆ 1,3,5,6 | ◆ 1,3,7,8 | ◆ 1,9,10,11,12 | ◆ 1,9,13 | ◆ 1,14 | ◆ 1 | ◆ 2,16,17 | ◆ 2,16,18 | ◆ 2,16,18 | ◆ 2,3,20 | ◆ 2 | ◆ 3,22 | ◆ 3,23 | II |
| *Liza tricuspidens* | | | | | ♦ 9 | | | • 16,17 | • 17 | | | | | • 23 | II |
| *Monodactylus falciformis* | | • 3 | | • 11 | | | | • 16 | | | | | ♦ 22 | ♦ 3,23 | I |
| *Mugil cephalus* | ♦ 1,4 | ♦ 3,5,6 | ♦ 1,3,7,8 | ♦ 1,9,10,11,12 | ♦ 1,9 | ♦ 1 | | ♦ 2,16,17 | ♦ 16,18 | ♦ 2,16,18 | ♦ 2,19,20 | ◆ 2 | ♦ 3,22 | ♦ 3,23 | I |
| *Myxus capensis* | | | | | | | | ◆ 16,17 | • 17 | | | | | • 3 | I |
| *Pomadasys commersonni* | | | | | | | | | | | • 3 | | ♦ 3,22 | ♦ 3,23 | I |
| *Pomatomus saltatrix* | ♦ 1,4 | ♦ 1,3,5,6 | • 3,7,8 | • 9,10,11,12 | • 9 | • 14 | | ♦ 16,17 | • 16, 18 | • 18 | • 2,3,19,20 | | • 22 | ♦ 3,23 | II |
| *Rhabdosargus globiceps* | • 4 | • 3,5,6 | ♦ 3,7,8 | ♦ 1,9,10,11,12 | ♦ 1,9 | • 14 | | ♦ 16,17 | ♦ 16,18 | • 18 | ♦ 3,19,20 | | ♦ 3,22 | ♦ 3,23 | II |
| *Rhabdosargus holubi* | | • 5 | • 3,7,8 | • 10 | | | | ♦ 16,17 | ♦ 16 | • 16 | ♦ 2,3,19,20 | | | ♦ 3 | I |

continued...

Table 5.2. Continued.

| | Olifants | Berg | Diep | Zand | Eerste | Lou-rens | Rooi-els | Pal-miet | Klein-mond | Bot | Klein | Uil-kraals | Heuning-nes | Breë | Dependence category |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Estuarine dependent marine species cont.** | | | | | | | | | | | | | | | |
| *Solea bleekeri* | ◆[4] | ◆[5,6] | | ◆[9,10] | ◆[9] | | | ◆[16,17] | | | ◆[3,19,20] | | ◆[22] | ◆[3,23] | II |
| *Argyrosomus* sp. | ♦[1,4] | ♦[5] | | ♦[12] | | | | | ♦[18] | ♦[18] | ♦[,20] | | ♦[3,22] | ◆[3,23] | I/III |
| **Marine species** | | | | | | | | | | | | | | | |
| *Rhinobatos annulatus* | | ◆[5] | ♦[8] | | | | | | | | ♦[19,20] | | | | III |
| **Freshwater species** | | | | | | | | | | | | | | | |
| *Cyprinus carpio* | | ◆[1,5,6] | | ◆[9,10,11,12] | ◆[9] | | | | ♦[18] | ◆[2,16,18] | | | ◆[22] | | III |
| *Lepomus macrochirus* | ◆[4] | ◆[5] | | | | | | | | | | | ♦[22] | | III |
| *Micropterus dolimieu* | ◆[4] | ◆[5,6] | | | | | | | | | | | | | III |
| *Oreochromis mossambicus* | ◆[4] | ◆[1,5,6] | ◆[8] | ◆[9,10,11,12] | | | | | ◆[16,18] | ◆[16,18] | | | | | III |
| *Tilapia sparrmanii* | | | | ◆[9] | | | | | | | | | | | III |

*Amblyrhynchotes honkenii*[1,3,4,5,11,19,23], *Atractoscion aequidens*[19,20,23], *Barbus serra*[3], *Caffrogobius caffer*[3], *Caffrogobius saldanha*[8], *Chaetodon marlei*[6], *Chelidonichthyes capensis*[1,4,5,8,18,19,20], *Clarias gariepinus*[9,10], *Dichistius capensis*[22], *Diplodus cervinus*[18,19,22], *Diplodus sargus*[12,16,18,3,19,20,22], *Elops machnata*[3], *Engraulis japonicus*[18], *Etrumeus whiteheadi*[1], *Galaxias zebratus*[4,5,8,11,20,22], *Gambusia affinis*[5,6,10], *Haploblepharus pictus*[1,4], *Hemiramphus far*[23], *Hippocampus capensis*[22], *Hyporhamphus capensis*[16,18,19,23], *Iso natalensis*[11], *Lithognathus mormyrus*[9,15,19], *Liza macrolepis*[23], *Micropterus punctulatus*[20,22], *Microperus salmoides*[11,18,20,22], *Monodactylus argenteus*[3], *Oncorhynchus mykiss*[1], *Ophisurus serpens*[5,8,18,20], *Otolithes ruber*[3], *Pomadasys olivaceum*[3,19,23], *Salmo trutta*[13], *Sandelia capensis*[11,20,22], *Sarpa salpa*[16,18,19,22,23], *Seriola lanlandi*[3], *Therapon jarbua*[17].

1. Harrison *et al.* (1994) 2. Harrison *et al.* (1995) 3. Day *et al.* (1981) 4. Lamberth unpubl. 5. Bennett (1994) 6. Lamberth (Unpubl. data) 7. Millard & Scott (1954) 8. Grindley & Dudley (1988) 9. Clark *et al.* (1994b) 10. Quick & Bennett (1989) 11. Begg (1976) 12. Gaigher & Thorne (1979) 13. Grindley (1982) 14. Cliff & Grindley (1982) 15. Heinecken (1982) 16. Bennet (1989b) 17. Branch & Day (1984) 18. Koop (1982) 19. Talbot (1955) 20. Scott *et al.* (1952) 21. Heydorn & Bickerton (1982) 22. Bickerton (1984) 23. Carter (1983).

## 5.3 SURF-ZONE HABITATS OF THE SOUTH-WESTERN CAPE

### 5.3.1 Physical characteristics

Shores composed of sand and mixed sand and rock (mixed shores) provide the bulk of the coastal marine habitat in the south-western Cape. Hockey *et al.* (1983) calculated that sandy shores account for some 68% of the marine littoral in southern Africa, and roughly 66% in the south-western Cape. Bally *et al.* (1984) calculated that approximately 42% of the southern African coastline comprises open sandy beaches and 31% mixed shore habitats, with mixed shores accounting for no less than 26% of the marine littoral in the south-western Cape. If we take Bally *et al.*'s estimate for both habitat types (73%), an average surf-zone width of 137 m (after Clark *et al.* 1994a) and the total length of coastline (excluding river mouths) as 917.3 km (CSIR 1987, 1988) the total surf-zone area available off sandy and mixed shores in the south-western Cape is in the region of 91.7 $km^2$ or 9 174 ha. This is roughly 1.5 x the corresponding surface area of water available in estuaries in the south-western Cape.

Mean annual sea surface temperatures differ markedly between the west and south coast in the south-western Cape. This is due largely to the influence of the different current systems on each of these coasts, the Benguela current on the west coast and the Agulhas current on the south coast. The Benguela current originates from water upwelled from subsurface layers along the west coast, while the Agulhas current is the western boundary current of the Indian Ocean and has its origin in the south equatorial current of the Indian Ocean. Although this current flows some distance offshore in the region of the south-western Cape, it still exerts a strong influence on coastal water temperatures in the region. Inshore surface temperatures on the west coast typically range from 10-14 °C in summer and 12-14 °C in winter (Shannon 1966). Inshore temperatures on the south coast increase progressively eastward due to the influence of the Agulhas current, with those west of Cape Agulhas (summer: 15-20 °C; winter 14-16 °C) being only marginally higher than those on the west coast, while those to the east of this point (summer: 17-20 °C; winter: 15-17 °C) are considerably greater.

Apart from high productivity and the reduced incidence of piscivores (Day 1951, 1959, Blaber 1974, 1981, Blaber & Whitfield 1977), the presence of calm waters in estuaries is considered to be one of the main features that attract fish to these environments. The southern African coastline, however, is considered to be very exposed due to its almost linear nature, with very little available shelter (Beckley 1984a, Wallace *et al.* 1984a, Field & Griffiths 1991). It is for the most part, considered unsuitable as a nursery area for juvenile fish (Blaber 1981, Potter *et al.* 1990). However, the south-western Cape coastline incorporates a number of features that significantly enhance the amount of shelter available in this area. The Saldanha Bay/Langebaan Lagoon complex and False Bay constitute two of only four large bay systems in southern Africa considered deep enough to provide significant shelter from wave action (Field & Griffiths 1991). In addition, the south-western Cape coast incorporates three large half-heart shaped bays (St. Helena Bay, Table Bay and St. Sebastion Bay), a number of smaller similarly shaped bays (e.g. Yzerfontein, Struisbaai, and Markusbaai) and a series of small embayments and pocket beaches (e.g. Doringbaai, Jackobsbaai, Hout Bay on the west coast; Maasbaai, Betty's Bay, Sandbaai on the south coast) that provide a more limited amount of protection from wave action.

Surface temperatures of waters in these enclosed bays are generally higher than those in the surrounding coastal waters, while those in the protected embayments within these systems are higher still. In Saldanha Bay on the west coast, for example, characteristic surface temperatures are in the region of 14-19 °C (Shannon & Stander 1977), while those in the southern offshoot, Langebaan Lagoon, typically range from 17-20 °C, but are known to exceed 24 °C on occasion. Similarly, even in a relatively large bay such as False Bay, temperatures are generally 1-2 °C higher than those outside (Atkins 1970), while those in the nearshore waters are known to exceed 23°C (pers. obs.).

Detached macrophytes that accumulate in surf-zone areas in various parts of the world (Zobell 1971, Lenanton *et al.* 1982, Robertson & Hansen 1982, Robertson & Lenanton 1984, Hull 1987, Lenanton & Caputi 1989, Wright 1989b) are also thought to enhance their suitability as nursery areas by providing protection from predators and an abundant food source. Such accumulations also occur off beaches in various parts of southern Africa (Lasiak 1986, van der Merwe & McLachlan 1987) including the south-western Cape (Bennett 1989a, Lamberth *et al.* 1995c, Clark *in press*, Clark *et al.* 1996 a, b, in press). Densities and volumes of macrophytes in surf-zone areas in the south-western Cape are comparable to those in western

Australia (Clark *et al.* 1996a) where fish abundance has been positively correlated with algal volume (Robertson & Lenanton 1984, Lenanton & Caputi 1989).

### 5.3.2 Ichthyofaunal composition

A total of 101 species have been recorded from surf-zone habitats in the south-western Cape (Table 5.3), but only 39 of these can be considered to be common (1-10% numerical abundance) or abundant (≥10% numerical abundance) at at least one site. Size frequency distributions of these species (Figs 5.2a-e) indicate that not all species are present in the surf throughout their life-cycles and that some variation is evident in terms of their utilization of sheltered and exposed areas of the surf-zone*. Roughly half (56%) of the species are common in both sheltered and exposed areas (species 1-22, Figs 5.2a-c), roughly one third (28%) frequent sheltered areas only (species 23-33, Fig. 5.2d), while the remaining 15% frequent exposed areas only (species 34-39, Fig. 5.2e).

Among those species common in both sheltered and exposed areas, almost all are represented by both adult and juvenile individuals (at least 10% of the numbers sampled in each case, Figs 5.2a-c) except two species (*Gilchristella aestuaria* and *Seriola lalandi*) which were both represented almost exclusively by adults only. Among those species recorded in sheltered areas only (Fig. 5.2d), a much smaller proportion (36% - species 23-26) were represented by both adults and juveniles. The largest portion in this case (55%, species 27-32), were represented by juveniles only. Only one species in this subset (*Decapterus macrosoma*, Fig 5.2d) was represented by adults only. Most species recorded from the exposed surf areas only (species 34-39, Fig. 5.2e) were represented by both adults and juveniles (4 species), with only one (*Carcharhinus brachyurus*) by juveniles and one (*Sardinops sagax*) by adults only.

In some cases, further separation is also evident among adult and juveniles of the same species, between sheltered and exposed areas. A total of 20 species, represented by both adults and juveniles, have been recorded from both sheltered and exposed areas (Figs 5.2a-c).

---

* For the purposes of this study, sheltered areas were defined as those receiving only a small amount of wave action (mean wave height ≤0.8 m), corresponding to an exposure score of ≤12 (after McLachlan 1980).

Adults and juveniles of 30% of these (species 1-7, Fig. 5.2a) are equitably distributed across both sheltered and exposed areas, while the remainder show some sort of segregation between the different life history stages. Approximately 40% (species 8-15, Fig. 5.2b) are represented by both adults and juveniles in exposed areas but by juveniles only in the sheltered areas; 15% (species 16-18, Fig. 5.2c) are represented by both juveniles and adults in sheltered areas, but by adults only in the exposed surf areas; while the remaining two species show completely different patterns, with either the adults and juveniles both prevalent in the exposed areas and adults alone in the sheltered areas (species 20, Fig. 5.2c) or a complete separation of adult and juveniles with juveniles prevalent in sheltered areas and adults in exposed areas only (species 19, Fig. 5.2c).

In summary, a total of 39 species make extensive use of surf-zone habitats in the south-western Cape; 75% (29 species) are represented by adults and juveniles, 15% (6 species) by juveniles only, and 10% (4 species) by adults only. This habitat therefore acts as an important nursery area for at least 35 species of fish, 54% (19 species) of which utilize both sheltered and exposed areas, 31% (11 species) which use sheltered areas only, and 17% (6 species) which use exposed areas only.

**Table 5.3.** Abundance of all positively identified fish species from sheltered and exposed surf-zone habitats in the south-western Cape. ◆ denotes >10% contribution, ⬥ 1-10% contribution and ⬩ <0.5% contribution. Species contributing < 1% in all five areas are listed as a footnote.

| | SHELTERED | | | EXPOSED | |
|---|---|---|---|---|---|
| | Saldanha[1-3] Bay | Langebaan[1, 2-5] Lagoon | False[3, 6-10] Bay | Saldanha[3] Bay | False[7-10, 11] Bay |
| *Amblyrhynchotes honkenii* | | | ⬥ | | ⬥ |
| *Argyrosomus inodorus* | | | ⬩ | | ⬥ |
| *Atherina breviceps* | ◆ | ◆ | ◆ | ⬩ | ◆ |
| *Caffrogobius nudiceps* | ◆ | ◆ | ◆ | | |
| *Callorhynchus capensis* | ⬩ | | ⬥ | | ⬥ |
| *Carcharhinus brachyurus* | | | | | ⬥ |
| *Chelidonichthyes capensis* | ⬥ | ⬩ | ⬥ | ⬩ | ⬩ |
| *Clinus lattipennis* | ⬥ | | ⬥ | ⬥ | ⬥ |
| *Clinus superciliosus* | ◆ | ⬥ | ⬥ | | |
| *Dasyatis crysonota* | ⬩ | | ⬩ | ⬩ | ⬥ |
| *Decapterus macrosoma* | | | ⬥ | | |
| *Dichistius capensis* | | | ⬩ | | ⬥ |
| *Diplodus sargus* | ⬥ | ⬥ | ◆ | | ⬥ |
| *Engraulis japonicus* | | | ⬥ | | ⬩ |
| *Galeichthyes feliceps* | | | | | ⬥ |
| *Gilchristella aestuaria* | | | ⬥ | | ⬥ |
| *Heteromycteris capensis* | ◆ | ⬥ | ◆ | ◆ | ⬥ |
| *Lichia amia* | ⬩ | ⬩ | ⬥ | | ⬥ |
| *Lithognathus lithognathus* | | ⬩ | ⬥ | | ⬥ |
| *Lithognathus mormyrus* | | | ⬥ | | ⬩ |
| *Liza dumerilii* | | | ⬥ | | |
| *Liza richardsonii* | ◆ | ◆ | ◆ | ◆ | ◆ |
| *Liza tricuspidens* | | | ⬥ | | |
| *Mugil cephalus* | | ⬩ | ⬥ | | ⬥ |
| *Mustelus mustelus* | | ⬥ | | ⬥ | ⬥ |
| *Myliobatis aquila* | ⬥ | ⬩ | ⬥ | ⬥ | ⬥ |
| *Pomatomus saltatrix* | ⬥ | ⬩ | ◆ | ⬥ | ◆ |
| *Psammogobius knysnaensis* | ◆ | ◆ | ◆ | | ⬩ |
| *Raja clavata* | | | ⬥ | | |
| *Rhabdosargus globiceps* | ◆ | ⬥ | ◆ | ⬥ | ◆ |
| *Rhinobatos annulatus* | ⬥ | ⬥ | ⬥ | ⬥ | ⬥ |
| *Sardinops sagax* | | | ⬩ | | ⬥ |
| *Sarpa salpa* | | ⬩ | ⬥ | | ⬥ |
| *Seriola lalandi* | | | ⬥ | | ⬥ |
| *Solea bleekeri* | ⬩ | ⬩ | ⬥ | | ⬩ |
| *Spondyliosoma emarginatum* | ⬩ | | ⬥ | | |
| *Syngnathus acus* | ⬩ | ⬥ | ⬥ | | |
| *Trachurus trachurus* | ⬩ | | ⬥ | | ⬥ |
| *Umbrina canariensis* | | | ⬥ | | ⬥ |

*Alectis ciliaris*[9], *Aluterus monoceros*[8-9], *Apletodon knysnaensis*[2], *Arothron stellatus*[7], *Atratoscion aequidens*[8], *Austroglossus microlepis*[8], *Caffrogobius caffer*[1-2], *Caffrogobius saldanha*[1], *Cancelloxus longior*[3, 10], *Cantherines pardalis*[8], *Carcharias taurus*[8], *Carcharodon carcharias*[8], *Cheimerius nufar*[9], *Chorisochismus dentex*[1], *Clinus agilis*[1, 8], *Coryphaena hippurus*[7, 10], *Cynoglossus capensis*[8-9], *Dactyloptena peterseni*[9], *Dasyatis brevicaudata*[8], *Dichistius multifasciatis*[10], *Dilpodus cervinus*[10], *Draculo celetus*[9], *Elops machnata*[8], *Etrumeus whiteadi*[3, 12], *Fucomimus mus*[10], *Gonorhynchus gonorhynchus*[10], *Gymnura natalensis*[8], *Halaelurus natalensis*[8], *Haploblepharus edwarsii*[8-10], *Haploblepharus pictus*[9], *Heniochus acuminatus*[10], *Kuhlia mugil*[8], *Lophodiodon calori*[8], *Mustelus nigropunctatus*[1]; *Mustelus palumbes*[1], *Narke capensis*[8], *Ostracion* sp.[9], *Pagellus bellottii natalensis*[9], *Parablennius cornutus*[7], *Parapunecens rubescens*[9, 11], *Parascorpis typus*[8], *Pelagocephalus marki*[9], *Pomadasys commersonni*[8], *Pomadasys olivaceum*[6], *Poroderma africanum*[3, 8], *Pterogymnus laniarius*[8], *Pteromylias bovinus*[8], *Raja alba*[8], *Raja miraletus*[8], *Rhabdosargus holubi*[6, 9, 10], *Scomber japonicus*[8], *Solea fulvomarginata*[8], *Sphyraena acutipinnis*[8,9,10], *Stephanolepis auratus*[8-9], *Stromateus fiatola*[8], *Synaptura marginata*[3, 9], *Torpedo fuscomaculata*[1, 8], *Trachinocephalus myops*[9-10,11], *Trachinotus africanus*[10], *Trachinotus botla*[10,11], *Triakis megalopterus*[8, 10],

1. Day (1959) 2. Clark (1990) 3. Clark (*in press*) 4. Day *et al.* 1981 5. Whitfield (1989) 6. Bennett (1989a) 7. Clark *et al.* (1994a) 8. Lamberth *et al.* (1994) 9. Lamberth *et al.* (1995a) 10. Clark *et al.* (1996a) 11. Clark *et al.* (In prep.)

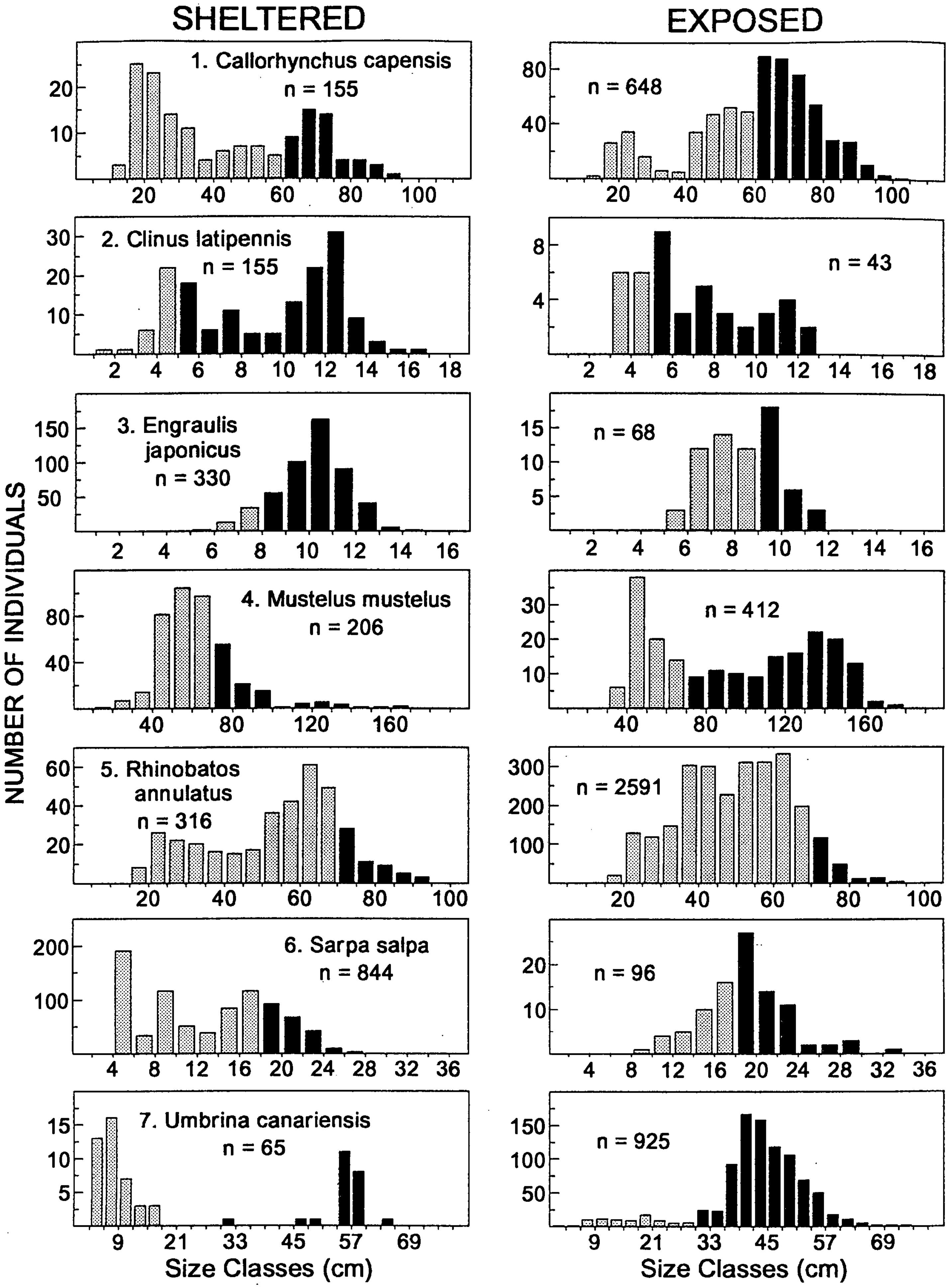


Fig. 5.2a. Size composition of fish species collected from sheltered and exposed surf habitats in the south-western Cape. Stippled bars represent juvenile fish and solid bars adult individuals. Data sources: Bennett (1989), Clark (in press), Clark *et al.* 1994, Clark *et al.* (1996), Clark *et al.* (in prep.), Lamberth *et al.* (1994, 1995b).

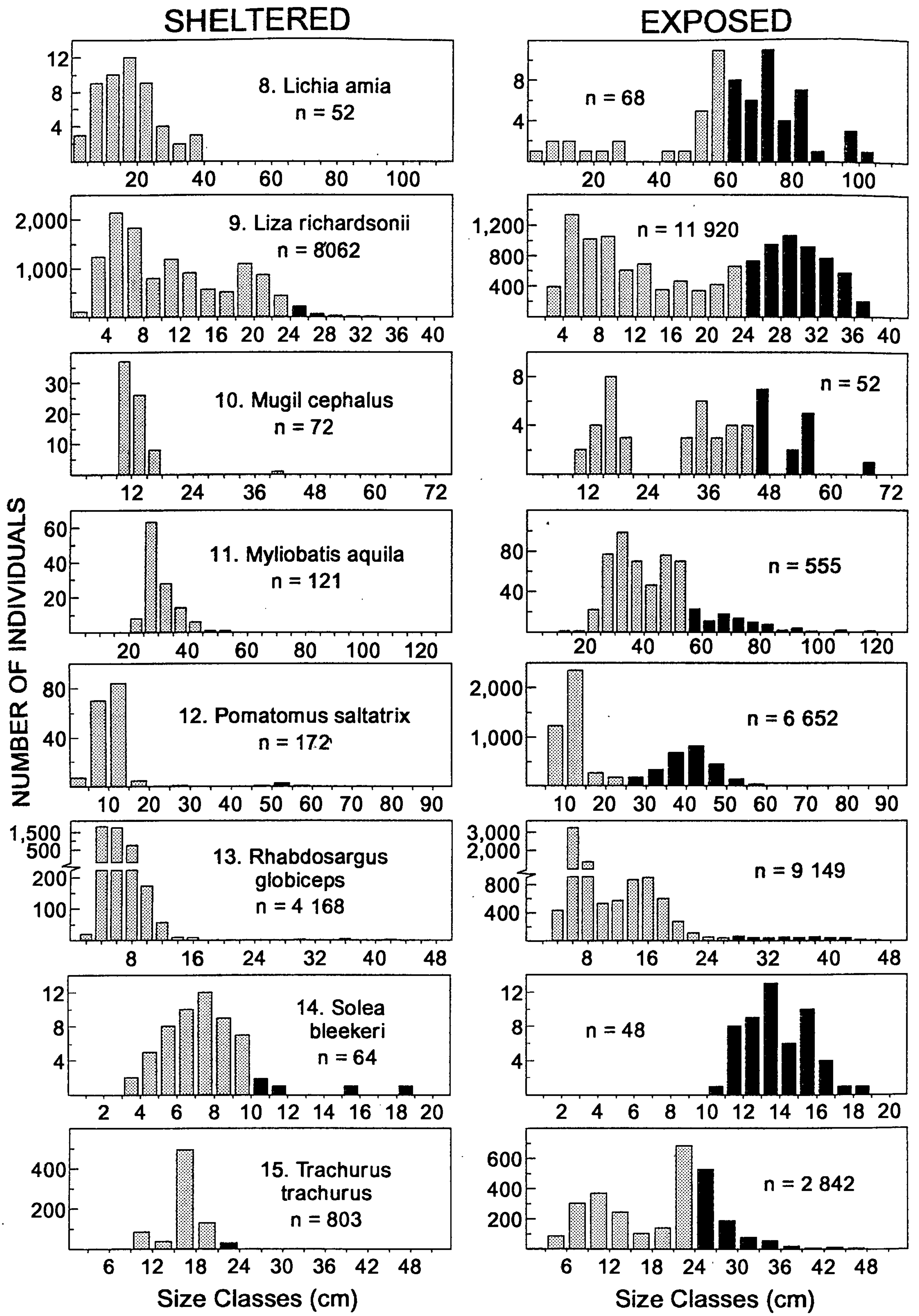


Fig. 5.2b. Legend as for Fig. 5.2a

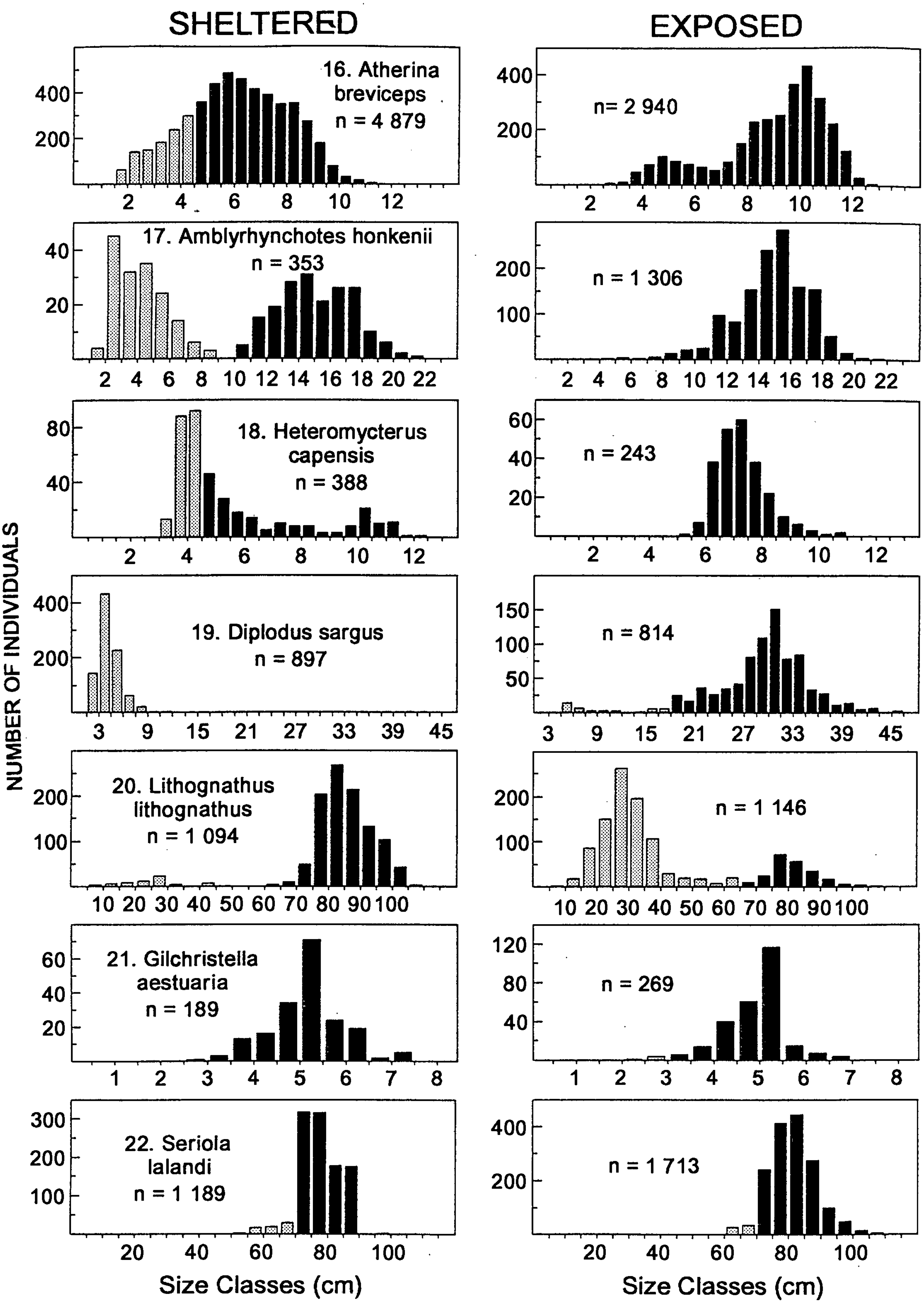


Fig. 5.2c. Legend as for Fig. 5.2a

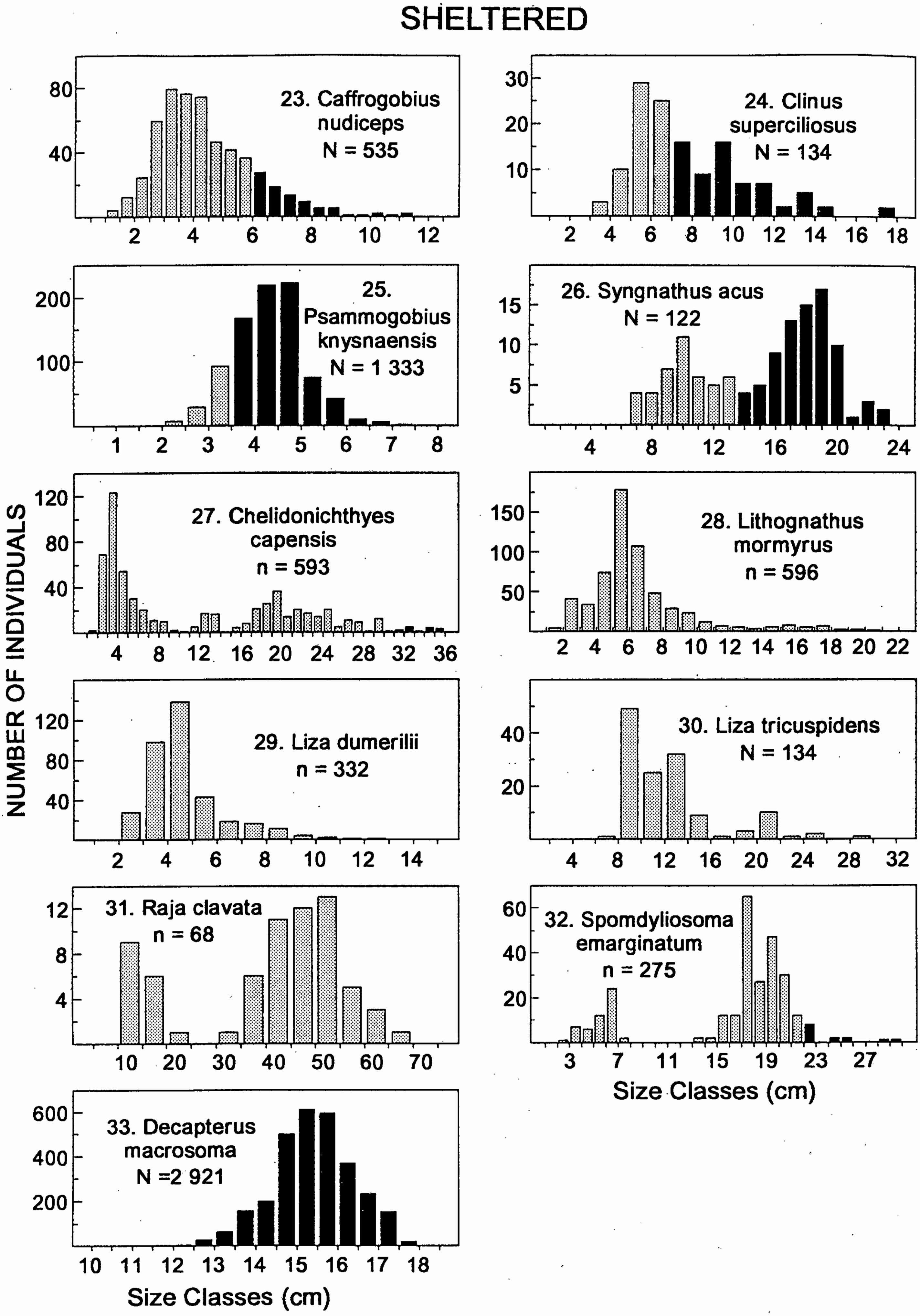


Fig. 5.2d. Legend as for Fig. 5.2a

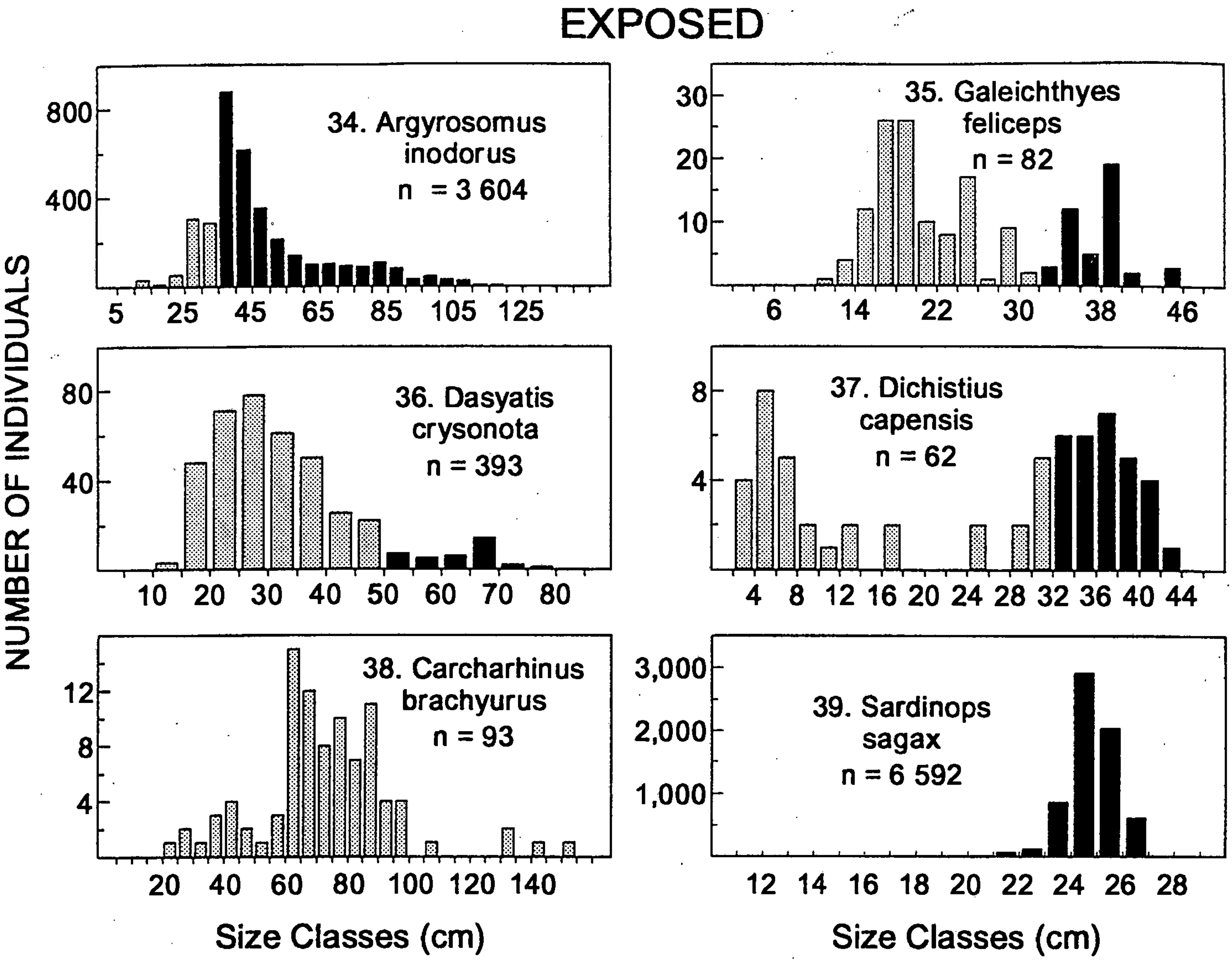


Fig. 5.2e. Legend as for Fig. 5.2a

### 5.3.3 Occurrence of estuarine dependent species in the surf

Among the ten species identified as estuarine dependent (Category I) by Whitfield (1994) from southwestern Cape estuaries, it appears that at least five are also common in surf-zone habitats in this area. These are *Gilchristella aestuaria, Psammogobius knysnaensis, Lichia amia, Lithognathus lithognathus* and *Mugil cephalus*. *G. aestuaria* and *P. knysnaensis* are listed as true estuarine species not having been recorded spawning in the marine or freshwater environments (Wallace *et al.* 1984a, Whitfield 1994), while *L. amia, L. lithognathus* and *M. cephalus* are all marine species thought to be dependent on estuaries during the juvenile stages of their life cycles (Wallace *et al.* 1984a, Whitfield 1994).

Almost all *G. aestuaria* recorded from the surf were adult individuals (<2% immature, Fig. 5.2c). Clark *et al.* (1996 a, b) noted that these individuals typically occur in the immediate vicinity of river mouths only, usually during winter. This species does not occur in surf-zone habitats distant from estuary mouths, even in the most sheltered areas (Bennett 1989a, Clark *in press*). It is thought to spawn in the upper reaches of estuaries and extend downstream only as they grow larger (Melville-Smith & Baird 1980, Winter 1979). Thus, it appears that adult individuals are flushed out of estuaries into the surf by the winter rains, and probably do not survive in the sea for long.

*P. knysnaensis* is present in the surf throughout its entire size range, albeit in sheltered areas only (Fig. 5.2d). The size range of individuals in the surf (22-75 mm, Clark *in press*, Clark *et al.* 1996a) is at least as broad as that of estuarine populations (18-70 mm - Clark *et al.* 1994b, Bennett unpubl.) and the proportion of juveniles in surf catches (18% - Clark *in press*, Clark *et al.* 1996a) is similar to, if not greater than, that of estuarine catches taken with the same equipment (13-14% juveniles - Clark *et al.* 1994b). In contrast to *G. aestuaria*, this species occurs in abundance in Langebaan Lagoon (Clark *in press*), an enclosed lagoonal system situated in excess of 120 km from the nearest viable estuarine system. It appears that *G. aestuaria* is indeed dependent on estuaries during its entire life cycle, but that *P. knysnaensis* is not. It seems likely that *P. knysnaensis* has marine as well as estuarine breeding populations in the south-western Cape, and is thus only partially dependent on estuaries for its survival.

Adults and juveniles of this species seem to require calm water, not estuaries *per se*, for their survival.

Bennett (1993) made a detailed study of the biology and life history of *L. lithognathus* and concluded that juveniles are dependent on estuaries for at least the first year of life (50-150 mm), but thereafter become semi-resident in the surf until they mature (150-650 mm). Data from this study appears to support these ideas. *L. lithognathus* from south-western Cape estuaries range from 18-390 mm (Mehl 1973, Bennett 1989b, Clark *et al.* 1994b), but the majority (78%) are < 250 mm in length. Individuals from the surf range from 74 mm upwards (Clark *et al.* 1996a), but those <150 mm make up no more than 2% of the population (Fig. 5.2c). Juveniles appear to favour the more exposed areas, while the adults have been caught in greatest numbers off sheltered sandy beaches.

*M. cephalus* is a cosmopolitan mullet species commonly found in seas, estuaries and freshwater between latitudes 42°S and 42°N (Thompson 1963). Adults spawn at sea, but are thought to reside in estuaries for most of their lives, while juveniles (<100 mm) were until recently thought to be entirely dependent on estuaries throughout their range (Wallace & van der Elst 1975, De Sylva & Sylva 1979, Chubb *et al.* 1981, Wallace *et al.* 1984a, Whitfield 1994). However, juveniles of this species have been shown to use protected marine embayments as a nursery area in parts of south-western Australia, where no permanent estuaries exist (Potter *et al.* 1990). The same does not appear to be true in the south-western Cape, however, as no juveniles <98 mm have been recorded outside of estuaries here. Juvenile *M. cephalus* occur in both exposed and sheltered surf habitats in the south-western Cape, ranging in size from 98 mm upwards (Fig 5.2b), whereas those in estuaries range from 20 mm upwards (Bennett 1989b, Clark *et al.* 1994b).

*L. amia* is thought to spawn off the east coast of southern Africa during spring. Larvae and juveniles are carried southwards by coastal currents and enter estuaries on the eastern, southern and south-western Cape coasts (van der Elst 1988). Juveniles are abundant in estuaries of the eastern and southern Cape (Blaber 1974, Wallace & van der Elst 1975, Winter 1979, Smale & Kok 1983), but are less common in Natal (Wallace and van der Elst 1975, Blaber & Cyrus 1983) and the south-western Cape (Table 5.2). A few juveniles of this species have been reported from the surf in the Eastern Cape (Lasiak 1982, 1984a, Romer 1986, 1990), but it is nonetheless regarded as being entirely dependent on estuaries during the early part of its life history (Wallace *et al.* 1984a, Whitfield 1994). Juveniles from 46 mm upwards have, however, been recorded from surf-zone habitats in the south-western Cape, the smallest individuals (<300 mm) being most abundant in sheltered areas (Fig. 5.2b, Clark *et al.* 1996a, Bennett 1989a, Lamberth *et al.* 1994). Although numbers in the surf in the south-western Cape are low, they appear to be similar to those in estuaries in this area (Tables 1 & 2). Bennett (1989a) and Clark *et al.* (1996a) recorded 13 and 45 individuals in 26 and 264 hauls respectively, from surf-zone habitats in the south-western Cape, while Bennett (1989b) recorded 49 in roughly 182 hauls in the Bot, Kleinmont and Palmiet estuaries. Branch & Day (1984) recorded 5 in 29 hauls in the Palmiet estuary, Millard & Scott (1954) and Clark *et al* (1994b) reported none from the Milnerton, Zand or Eerste estuaries respectively, and Harrison *et al.* (1994, 1995) reported *L. amia* from only 2 of the 11 estuaries they sampled. These results suggest that *L. amia* is probably only partially dependent on estuaries in the south-western Cape, with sheltered surf habitats being at least as important as estuarine nursery areas.

Whitfield (1994) identifies 12 species common or abundant in the south-western Cape estuaries as being at least partially dependent on estuaries as nursery areas (Table 5.2). These are *Atherina breviceps*, *Caffrogobius multifasciatus*, *C. nudiceps*, *Clinus superciliosus*, *Syngnathus acus*, *Galeichthyes feliceps*, *Heteromycterus capensis*, *Liza dumerilii*, *L. richardsonii*, *L. tricuspidens*, *Pomatomus saltatrix* and *Rhabdosargus globiceps*. All but one of these species (*C. multifasciatus*) are also common in surf-zone habitats in the south-western Cape. *C. multifasciatus* does not appear to occur in other nearshore marine habitats (intertidal rock pools, inshore sandy or reef areas) either, and it seems likely that unless viable breeding populations exist in freshwater habitats, stocks of this species in the south-western Cape are entirely dependent on estuaries for their survival. Most of the remaining species labeled as partially dependent on estuaries (*A. breviceps*, *H. capensis*, *L. dumerilii*, *L. tricuspidens*, *S. bleekeri* - Figs 5.2b-d) appear to be confined to sheltered areas during the juvenile phase of their life cycles, or in some cases (*C. nudiceps*, *C. superciliosus*, and *S. acus* - Fig. 5.2d), during their entire life-cycles. However, juveniles of some species in this group occur in exposed and sheltered areas (*L. richardsonii*, *P. saltatrix*, *R. globiceps* - Fig. 5.2b), and at least one (*G. feliceps* - Fig. 5.2e) occurs only in exposed areas.

At least two of these partially estuarine dependent species (*L. dumerilii* and *L. tricuspidens*) only appear in the surf-zone as fairly well developed juveniles. *L. dumerilii* has been recorded from 53 mm upwards in surf-zone catches (Clark *et al.* 1996a), but individuals <80 mm are rare (<8% abundance - Fig. 5.2d). *L. tricuspidens* occurs in the surf from 78 mm upwards (Clark *et al.* 1996a), but once again individuals <80 mm are very rare (<1% abundance - Fig. 5.2d). These two species are present in south-western Cape estuaries in the range 40 mm upwards (Clark *et al.* 1994b) and at an even smaller size (10 mm upwards) in estuaries further east (Hanekom & Baird 1984, Hall *et al.* 1987, Whitfield & Kok 1992). Assuming a similar growth rate to those of other mullet species, these two species enter the surf at an age of approximately one year (Thompson 1951, 1966, Ratte 1977, De Sylva & Sylva 1979, Chubb *et al.* 1981). The absence of the younger (smaller) fish in the surf catches strongly suggests that, in the south-western Cape at least, juveniles of these two species are dependent on estuaries as nursery areas during their first year of life. Adults and juveniles of both species are abundant in eastern Cape estuaries (Beckley 1984a, Hanekom & Baird 1984, Kok & Whitfield 1986, Hall *et al.* 1987, Termorshuizen & Whitfield 1994) with *L. dumerilii* still reasonably common in estuaries in Kwazulu-Natal (Day & Morgans 1956, Bruton & Appleton 1975, Blaber & Blaber 1976, Blaber 1977). Spawning by both species is thought to take place in the marine environment, usually in the vicinity of estuaries (Wallace 1975b, van der Horst & Erasmus 1978, 1981, Day *et al.* 1981). Comparatively few adults or juveniles have been recorded from the surf or other inshore marine habitats in the eastern Cape or Natal, Romer (1986) being the only author actually having reported the presence of juveniles in the surf (*L. tricuspidens*: 29 mm SL upwards, *L. dumerilii*: 95 mm SL upwards). These species are both nonetheless regarded as being only partially dependent on estuaries as juveniles (Wallace & van der Elst 1975, Whitfield 1994). It appears as though populations of both species are most likely entirely dependent on estuaries for their first year of life in the south-western Cape and potentially in the rest of southern Africa as well.

### 5.3.4 Occurrence of surf-zone dependent species

The abundance of adult and juveniles of species found to be common or abundant in the surf-zone was examined in a variety of other nearshore habitats in the south-western Cape for which data were available (estuaries, intertidal rock pools, and shallow sandy and reef areas) in order to assess their dependence on the surf-zone (Table 5.4). A total of seven species appear to be present in low numbers only, outside of surf habitats during some portion of their life-cycles. *Amblyrhynchotes honkenii* and *Clinus latipennis* are largely confined to surf-zone habitats as adults and juveniles, *Heteromycterus capensis*, *Solea bleekeri* and *Liza richardsonii* are confined to the surf-zone as adults only, while *Lithognathus lithognathus* and *Dichistius capensis* appear to be confined to surf-zone habitats during a portion of the juvenile stage of their life cycles.

Juvenile *H. capensis* and *S. bleekeri* are common in both estuaries and surf-zone habitats as juveniles, but mature individuals are rare in estuaries and seem to be confined to surf areas only (Table 5.4). It has already been stated that results from this study support the ideas of Wallace *et al.* (1984a), Bennett (1993) and Whitfield (1994) that *L. lithognathus* is entirely dependent on estuaries during the first year of life. However, they also suggest that subadults of this species are rare outside of the surf-zone, thus supporting Bennett's (1993) hypothesis that this species is largely dependent on the surf-zone as a post-estuarine nursery area. *L. richardsonii* is found in abundance in surf and estuarine environments in the south-western Cape and is also common off rocky intertidal and subtidal reef areas during the juvenile stage of its life-cycle (Table 5.4). However, this species appears to be confined largely to surf-zone habitats as an adult. Romer & McLachlan's (1986) study of the diet of *L. richardsonii* off a high energy beach in the Eastern Cape, South Africa, suggested that adult and sub-adult individuals fed exclusively on surf diatoms (*Anaulis biostratus*). Surf diatoms are thought to have a high nutritional value, and these authors suggested that because they form such a richly concentrated and reliable food source, they are likely to be considerably better than a "normal" diet of decaying plant material, sediment and associated microbenthos. Surf diatom accumulations occur off most exposed beaches in southern Africa (Romer 1986, McLachlan & Lewin 1981, McLachlan & Erasmus 1983, CSIR 1984, Romer 1986).

**Table 5.4.** Relative abundance of fish species in estuarine, surf-zone, rocky intertidal, shallow sandy habitats(<100 m) and subtidal reef habitats (<50 m) in the south-western Cape. ◆ denotes >10% numerical contribution, ♦ 1-10 % and ⬩ <1%.

| | JUVENILES | | | | | | ADULTS | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estuaries | Sheltered Surf | Exposed Surf | Rocky$^{1-5}$ Intertidal | Inshore$^{6-7}$ Sandy | Inshore$^{7-9}$ Reef | Estuaries | Sheltered Surf | Exposed Surf | Rocky$^{1-5}$ Intertidal | Inshore$^{6-7}$ Sandy | Inshore$^{7-9}$ Reef |
| *Amblyrhynchotes honkenii* | ⬩ | ♦ | ⬩ | | ⬩ | | ⬩ | ♦ | ♦ | | ⬩ | ⬩ |
| *Argyrosomus inodorus* | | | ⬩ | | ♦ | | | ⬩ | ♦ | | ♦ | |
| *Argyrosomus japonicus* | ♦ | | | | | | | | ⬩ | | | |
| *Atherina breviceps* | ◆ | ◆ | ⬩ | | | | ◆ | ◆ | | | ♦ | ♦ |
| *Caffrogobius multifasciatus* | ♦ | ⬩ | | | | | ♦ | | | | | |
| *Caffrogobius nudiceps* | ◆ | ◆ | | ⬩ | | | ◆ | ◆ | | | ⬩ | |
| *Callorhynchus capensis* | | ♦ | ♦ | | ♦ | | | ⬩ | ♦ | | ♦ | ⬩ |
| *Carcharhinus brachyurus* | | | ♦ | | ⬩ | ♦ | | | ⬩ | | | |
| *Chelidonichthyes capensis* | ⬩ | ♦ | | | ♦ | | | ⬩ | | | ♦ | |
| *Clinus lattipennis* | | ♦ | | | | | | ♦ | | | | |
| *Clinus superciliosus* | ♦ | ♦ | | ◆ | | ◆ | ♦ | ♦ | | ◆ | | |
| *Dasyatis crysonota* | | ⬩ | ♦ | | ♦ | | | | ⬩ | | ⬩ | |
| *Decapterus macrosoma* | | | | | | | | ♦ | | | | ♦ |
| *Dichistius capensis* | ⬩ | ⬩ | ♦ | ⬩ | | ♦ | | | ♦ | | ⬩ | ♦ |
| *Diplodus sargus* | ⬩ | ◆ | ♦ | ♦ | | ◆ | | ♦ | ♦ | | | ♦ |
| *Engraulis japonicus* | ⬩ | ⬩ | ♦ | | | | ⬩ | ⬩ | ♦ | | | ⬩ |
| *Galeichthyes feliceps* | ♦ | | ♦ | | | | ⬩ | | ♦ | | ♦ | |
| *Gilchristella aestuaria* | ◆ | ⬩ | ⬩ | | | | ◆ | ♦ | ♦ | | | |
| *Heteromycteris capensis* | ♦ | ◆ | | | ♦ | | ⬩ | ♦ | ♦ | | | |
| *Lichia amia* | ♦ | ♦ | ♦ | | ⬩ | | ♦ | ⬩ | ♦ | | ⬩ | ⬩ |
| *Lithognathus lithognathus* | ♦ | ⬩ | ♦ | | | ⬩ | ⬩ | ♦ | ♦ | | ♦ | ⬩ |
| *Lithognathus mormyrus* | ⬩ | ♦ | ⬩ | | ♦ | | | ⬩ | | | ♦ | |
| *Liza dumerilii* | ♦ | ♦ | ⬩ | | | | | | | | | |
| *Liza richardsonii* | ◆ | ◆ | ◆ | ♦ | | ♦ | ⬩ | ⬩ | | | | ⬩ |
| *Liza tricuspidens* | ♦ | ♦ | ⬩ | | | ⬩ | | ⬩ | | | | |
| *Mugil cephalus* | ♦ | ♦ | ♦ | | | ⬩ | ♦ | | ⬩ | | | |
| *Mustelus mustelus* | | ♦ | ♦ | | ♦ | ♦ | | ♦ | ♦ | | ♦ | ♦ |
| *Myliobatis aquila* | | ♦ | ♦ | | ♦ | ⬩ | | ⬩ | ⬩ | | ♦ | |
| *Pomatomus saltatrix* | ♦ | ◆ | ◆ | | ♦ | | | ⬩ | ◆ | | ♦ | |
| *Psammogobius knysnaensis* | ◆ | ◆ | | ⬩ | | ⬩ | ◆ | ◆ | | | ⬩ | ⬩ |
| *Raja clavata* | | ♦ | | | ♦ | ⬩ | | | | | ♦ | ⬩ |
| *Rhabdosargus globiceps* | ♦ | ◆ | ◆ | | ♦ | ⬩ | | ⬩ | ♦ | | ♦ | |

Continued...

**Table 4. Cont.**

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rhinobatos annulatus* | ♦ | ◆ | ◆ | | ◆ | | ◆ | ◆ | ◆ | | ◆ | |
| *Sardinops sagax* | ♦ | ♦ | | | ♦ | | | ♦ | ◆ | | ♦ | ◆ |
| *Sarpa salpa* | ♦ | ◆ | ◆ | ◆ | | ◆ | | ◆ | ◆ | | | ◆ |
| *Seriola lalandi* | | ◆ | ♦ | | | ♦ | | ◆ | ◆ | | | ◆ |
| *Solea bleekeri* | ◆ | ◆ | | | | | ♦ | ♦ | ◆ | | ♦ | |
| *Spondyliosoma emarginatum* | | ◆ | ◆ | | ◆ | ◆ | | ♦ | | | ◆ | ◆ |
| *Syngnathus acus* | ◆ | ◆ | | | ◆ | ♦ | ◆ | ◆ | | | ◆ | |
| *Trachurus trachurus* | ♦ | ◆ | ◆ | | ◆ | ♦ | | ♦ | ◆ | | ◆ | ♦ |
| *Umbrina canariensis* | | ◆ | ◆ | | ◆ | ♦ | | ◆ | ◆ | | ◆ | ♦ |

1. Jackson (1950) 2. Bennett & Griffiths (1984) 3. Bennett (1987) 4. Prochazka & Griffiths (1992) 5. Prochazka (1996) 6. SFRI demersal data base 7. Pers. obs 8. Fowler (1994) 9. Lechanteur *in prep.*

Juvenile *Dichistius capensis* frequent subtidal rocky reefs in moderate numbers (Table 5.4), but only from a size of approximately 25 cm upwards (Lechanteur in prep.). Small juveniles (3-18 cm) are found almost exclusively in exposed surf-zone areas, particularly off shores composed of mixed rock and sand (Clark *et al.* 1996a).

A number of other species (*Decapterus macrosoma*, *Engraulis japonicus*, *Sardinops sagax* and *Seriola lalandi*) were recorded as common, or even abundant in the surf-zone, but not in any other nearshore habitats examined (Table 5.4). These are by no means dependent on the surf-zone, however. Individuals recorded from the surf represent only a small part of the large stocks that occur in pelagic zones offshore (van der Elst 1988, Smith & Heemstra 1991) many of which form the target of directed purse-seine and line fisheries (Penney *et al.* 1989, Crawford *et al.* 1978, van der Elst 1988).

Bennett (1989a) is the only other author to have examined the degree to which fish species depend on the surf-zone. He considered only the nursery function of this habitat, however, and his observations were based on comparisons between the fish fauna of Fishoek Beach, South Africa and a suite of other nearshore habitats in the south-western Cape. He identified five species whose juveniles he considered to be entirely, and a further three species to be largely dependent on the surf-zone as a nursery area. Data available at the time suggested that juveniles of the former group (*A. honkenii*, *Chelidonichthyes capensis*, *Diplodus sargus*, *Lithognathus mormyrus* and *Pomadasys olivaceum*) were common or abundant in the surf-zone and rare or absent from other nearshore habitats. Increased coverage and sampling of the nearshore zone in recent years, now indicates that of these, only *A. honkenii* is confined to surf-zone habitats. Juvenile *Chelidonichthyes capensis and L. mormyrus* are common in shallow water sandy areas as well as in surf-zones habitats, while *D. sargus* is abundant off shallow water reefs as well as surf areas. Despite intensive sampling of a range of surf-zone habitats in the south-western Cape (including Fishoek Beach) over a period of five years (1991-1995; Clark *et al.* 1994a, 1996a, Clark *in press*, Lamberth *et al.* 1994, 1995a, b), not a single *P. olivaceum* has been recorded, following Bennett's (1989a) work. It is, however, one of the most abundant species in surf-zone and shallow water sandy areas in the Eastern Cape, as well as being very common off shallow water reefs in this area and Natal (Joubert & Hanekom 1980, Zoutendyk 1982). It seems likely that it is a warm temperate species that briefly extended its range into south-western Cape waters at the time of Bennett's (1989b) survey, and has not done so since. Contrary to Bennett's suggestion therefore, it seems unlikely that it shows any dependence on surf-zone habitats in the south-western Cape.

Bennett (1989a) also identified a group of species that he considered to be largely dependent on the surf-zone as a nursery area (*Lichia amia*, *Liza richardsonii* and *Rhabdosargus globiceps*). He found that juveniles of these species were abundant in the surf-zone, but were also prevalent in other nearshore habitats in lower numbers. *L. amia* was previously thought to be entirely dependent on estuaries by many authors, but results of this study (see above) support those of Bennett (1989a) that in the south-western Cape, juveniles appear to utilize both estuarine and surf-zone habitats as a nursery area. Results of this study also indicate that juvenile *R. globiceps* are more abundant in the surf than in the other nearshore habitats in which they occur (estuaries and shallow water sandy areas - Table 5.4) and thus support the ideas of Bennett (1989a). Juvenile *L. richardsonii*, however, occur over a wide range of nearshore habitats in the south-western Cape (estuaries, surf-zone, rocky intertidal and shallow water reefs) and appear to be no more numerous in surf waters than estuarine habitats. They can thus be considered no more than partially dependent on the surf-zone as a nursery area. Juvenile *H. capensis* occur only in estuarine and surf-zone areas in the south-western Cape (Table 5.4), however, and appear to be more abundant in the latter. They can thus also be considered to be largely dependent on this habitat as a nursery area.

## 5.4 ESTUARINE DEPENDENCE AND THE ROLE OF ALTERNATIVE NURSERY HABITATS IN THE SOUTH-WESTERN CAPE

It is clear from the results of this study and others, that conditions considered to make estuaries ideal areas for temporary colonization by juvenile marine fishes are also prevalent in other inshore marine areas. Nearshore surface water temperatures in protected bays (certainly in the south-western Cape) in spring and summer are at least as high as those in estuaries, and probably do not display the extreme fluctuations often found in the latter. Detached aquatic macrophytes abound in certain surf-zone areas, contributing significantly to the quality of these areas by providing both protection and an abundant food source for a variety of fish species (Lenanton *et al.* 1982, Robertson & Lenanton 1984, Lenanton & Caputi 1989, Wright 1989b). The abundance of zooplankton and dense phytoplankton blooms that prevail in certain areas, further enhance food supplies in the surf-zone (McLachlan 1983, Wooldridge 1983, McLachlan & Lewin 1981, Lewin & Shaefer 1983). The use of alternative planktivorous food sources and variations in diel migratory habitats exhibited by dominant fish species in the surf (Lasiak 1981, 1986, Romer & McLachlan 1986, Clark *et al.* in press), ensures that food sources available in these areas are more than adequate, while at the same time, allowing fish to take maximum advantage of the cover provided by turbulent wave action.

It is also clear, however, that a number of fish species are dependent on estuarine conditions for their survival in certain parts of the world, whether they be geographically restricted areas (e.g. the south-western Cape) or entire regions (e.g. southern Africa). The lack of suitable alternative nursery/feeding areas implies that if the current rate at which estuaries are being degraded is not severely curtailed, we are likely to see considerable reductions in the abundance and/or geographical ranges occupied by certain species. In the south-western Cape, at least 23 fish species show some sort of dependence on estuaries, with eleven (*Argyrosomus japonicus*, *Clinus spatulus*, *Gilchistella aestuaria*, *Lithognathus lithognathus*, *Liza dumerilii*, *L. tricuspidens*, *Mugil cephalus*, *Monodactylus falciformes*, *Myxus capensis*, *Pomadasys commersonii* and *Rhabdosargus holubi*) probably entirely dependent on estuaries for their survival.

Surf-zone areas are available as an alternative for a great many species, and account for a considerable proportion of coastal marine habitats world wide. However, if we assume that suitable available habitat is restricted to the breaker zone, the amount of area available relative to that in estuaries may not be as large as has previously been suggested (see for example Bennett 1989a, Ross *et al.* 1987). Total available surf-zone habitat in the south-western Cape, for example, amounts to only 1.5 x that available in estuaries. Much of this comprises highly exposed beaches, not suitable for colonization by many species. Only 20% of the species making extensive use of surf-zone habitats in the south-western Cape are able to utilize both sheltered and exposed areas through their lives, the remainder being restricted to sheltered (54%) or exposed areas only at some period in their life histories. Estuary-associated species are particularly vulnerable from this point of view, as most juveniles and many adults of species able to utilize surf habitats are confined to sheltered areas only. A total of seven species (*Amblyrhynchotes honkenii, Clinus latipennis, Dichistius capensis, Heteromycterus capensis, Lithognathus lithognathus, Liza richardsonii* and *Solea bleekeri*) depend on surf habitats in the south-western Cape at some stage in their life histories.

Unlike their estuarine counterparts, surf-zone areas in the south-western Cape are reasonably unpolluted and relatively healthy from a biological point of view. Circulation patterns within the surf-zone often form closed cells, however, that although being advantageous in that they increase the residence time of nutrients and plankton within the breaker zone (McLachlan 1981, McLachlan *et al.* 1981, Winter 1983), are also likely to do the same for pollutants. Sheltered sections of coastline, particularly those within sheltered bays, are likely to face the greatest threat, considering the reduced water movement within these areas and their popularity as harbour sites and centres for recreational activity.

# OVERVIEW

# AND

# SYNTHESIS

# OVERVIEW AND SYNTHESIS

This study addressed four major questions regarding the dynamics and utilisation of surf-zone habitats by fish in the south-western Cape. Chapters 1 and 2 examined spatial variations in composition, abundance and community structure of fish assemblages across a variety of physical environmental gradients. Chapter 3 and 4 examined temporal variations in a similar set of biological parameters over long and short term temporal scales, respectively, while Chapter 5 addressed questions regarding the utilisation of surf habitats in the south-western Cape as nursery and feeding grounds

## Species composition, abundance and biomass

Surf habitats in the south-western Cape are frequented by a large number of fish species. A total of 101 species have been recorded from this area, 54 of which were recorded during the course of this study. Surf habitats in other parts of the world are similarly frequented by large numbers of species, typically between 26 and 71 (Brown & McLachlan 1990). Numbers of species in the surf seem to exceed those recorded from other intensively studied nearshore habitats in the south-western Cape, such as estuaries (67 species - Chapter 5) and intertidal rock pools (38 species - Bennett *et al.* 1983, Bennett & Griffiths 1984, Bennett 1987, Prochazka & Griffiths 1992, Fowler 1994, Prochazka 1996). This is most likely a function of the large proportion of the coastal marine habitats they occupy ( 73% - Chapter 5) and their open access to the ocean.

The number of species able to tolerate conditions within the surf-zone for long periods, however, appears to be low. Assemblages both here and abroad are generally dominated by few species, usually <10 making up greater than 90% of the catches (Gunter 1958, McFarland 1963, Modde & Ross 1981, Lasiak 1984a, Ross *et al.* 1987, Wright 1988, Bennett 1989a). Four species, *Atherina breviceps*, *Liza richardsonii*, *Rhabdosargus globiceps* and *Psammogobius knysnaensis*) numerically dominated catches in this study, typically providing 90-95% of the total number of fish caught. A further six species (D*iplodus sargus*, *Pomatomus saltatrix*, *Gilchristella aestuaria*, *Sarpa salpa*, *Heteromycterus capensis* and *Caffrogobius nudiceps*) provided substantial contributions on occasion, while the remaining species were generally recorded infrequently. Important families in this area thus include the Atherinidae, Mugilidae, Sparidae, Gobiidae, Clupeidae, Pomatomidae and Soleidae. Other South African studies (e.g. Lasiak 1984a, b, Romer 1986, Romer 1990) indicate a high degree of uniformity among surf fish assemblages. They also highlighted the importance of the Atherinidae, Sparidae, Carangidae and Mugilidae as dominant families, as well as the Haemulidae and Scianidae. Studies conducted abroad have highlighted the importance of the Pleuronectidae (European beaches - Edwards & Steele 1968, Ziljstra 1982, Gibson 1973a, Poxton *et al.* 1982), the Engraulidae, Clupeidae, Carangidae and Scianidae (Gulf of Mexico - McFarland 1963, Gunter 1958, Modde & Ross 1981, Ross *et al.* 1987) and the Atherinidae, Clupeidae, Terapontidae, Sillaginidae and Mugilidae (Western Australia - Lenanton 1982, Lenanton *et al.* 1982, Robertson & Lenanton 1984). All collections made as part of this study were completed with a small, relatively fine meshed beach seine net, and are thus likely to have been biased somewhat toward smaller individuals and species. Comparisons with collections made using larger, coarser meshed nets, however, indicates that this was not really the case. The study of Lamberth *et al.* (1994) on commercial beach seine net catches in False Bay highlighted *Liza richardsonii* as being by far the most numerous species (87% of the total), while *P. saltatrix*, *Trachurus trachurus*, *R. globiceps* and *S. salpa* were the only other species contributing more than 1% of the total. The only additional family of importance not highlighted during the course of this study, were the Carangidae therefore.

Numerical contributions by elasmobranch fishes to surf-zone fish abundance is typically low, with contributions to catches in this study (typically <1%) being similar to seine net studies conducted locally (Lasiak 1984a, Romer 1986, Bennett 1989, Clark *et al.* 1994a, 1995a) and abroad (Gunter 1958, Modde & Ross 1981, Robertson & Lenanton 1984, Ross *et al.* 1987, Gibson *et al.* 1993). Elasmobranch contributions to total biomass, however, is usually considerably higher, often providing over 50% of the total catch (Chapter 2,4, Lasiak 1982, 1984a, Romer 1986, Ross *et al.* 1987).

## Spatial variability

Up until the start of this work, few studies had examined the influence of physical factors on the spatial distribution of fish within surf-zone habitats. The importance of factors such as exposure, sediment particle size, turbidity, detached macrophyte abundance and the proximity of rocky reefs had been highlighted by a number of authors (Hillman *et al.* 1977, Blaber & Blaber 1980, Robertson & Lenanton 1984, Tallmark & Evans 1986, Peters & Nelson 1987, Romer 1990, Pihl & van der Veer 1992), but a comprehensive assessment of all these factors had yet to be completed. An examination of fish assemblages at 11 sites in False Bay, covering as wide a range of physical gradients as possible, was completed during this study. Multivariate analyses indicated that the degree of wave exposure, the presence of emergent rock on the shore and turbidity were responsible for most of the variability in abundance and community structure observed. It was clear, however, that none of the factors acted in isolation, all combining to produce a unique set of conditions at each site. Certain species were able to tolerate a wide variety of conditions, being present at all sites, while others complemented this core group of species depending on the particular suite of environmental conditions prevalent at each site.

The influence of wave exposure on surf fish assemblages was also examined as part of a separate study (Chapter 2), in order to isolate the influences of this variable from the others. The Saldanha Bay - Langebaan Lagoon complex provided an ideal setting in which to complete this study, with an exposure gradient extending across eight sites from high exposed, open ocean beaches through to extremely sheltered ones. The distribution of elasmobranchs was patchy at the sites was patchy, showing no clear patterns, but teleost catches revealed two important trends. Overall teleost abundance increased markedly in response to a decreasing exposure gradient, a result similar to that found in Chapter 1 and by other authors (e.g. Gunter 1958, Poxton & Nasir 1985, Romer 1990); while highest species richness and diversity, and lowest dominance were recorded at intermediate levels of exposure. The latter result conforms to ideas incorporated within the intermediate disturbance hypothesis (Menge & Sutherland 1976, 1987, Connell 1978) which suggests that diversity should be low under very harsh or benign conditions, due to a high rate of species removal under the effects of environmental disturbance and competitive exclusion, respectively. Peak diversity is usually recorded at intermediate levels of disturbance, where the effects of competition and predation interact to maintain high species numbers.

## Temporal variability

Fish assemblages frequenting surf-zone habitats are highly dynamic, exhibiting considerable fluctuations over all time scales. Seasonal changes in abundance, composition and or biomass are often very marked, and are considered by many authors to be the primary characteristic of these communities (e.g. Gunter 1958, McFarland 1963, Ross *et al.* 1987). Off beaches where considerable variation in water temperature is evident (typically in the higher latitudes) greatest abundance and diversity of fishes generally occurs in the warmer months, with some beaches being almost devoid of fish in winter (Warfel & Merriman 1944, Macer 1967, Shaefer 1967, Edwards & Steele 1968, Lockwood 1974, Anderson *et al.* 1977, Gibson *et al.* 1993). However, in areas where seasonal variations in water temperature are of a lower magnitude, as with this study, corresponding fluctuations in the fish assemblages are generally weak or ill defined. Seasonal fluctuations in fish abundance and numbers of species captured were absent, except at one site, where numbers of species recorded varied seasonally. Physical factors responsible for these fluctuations varied in response to differences in the physical attributes of the different sites, but water temperature, wave height, wind speed and direction and macrophyte abundance seem to be the most important. When data from all sites were combined, however, seasonal variations were evident in the abundance of juvenile fish in the surf, and to a lesser extent in the species richness and total number of species captured. Abundance and species richness was highest from mid-summer up to the beginning of winter, the period during which most species recruit into the surf-zone. Thus, even when seasonal variations in physical variables such as water temperature are not great, spawning periods of surf-zone fish are nevertheless timed to allow most resident and transient 0+ juveniles to optimise their use of this habitat.

Short term (diel) variations in composition, abundance and/or biomass are typically very well developed in surf fish assemblages, but up until now, factors controlling this variability were poorly understood. Much of the variability was attributed to stochastic fluctuations resulting from the complex interactions between alongshore, onshore and offshore migrations necessitated by a rapidly changing physiochemical environment. Increased water temperatures, food availability and abundant cover generally found in surf-zone areas offer numerous advantages to fish, but must be weighed up against the energetic costs of living in a constantly moving, often turbulent environment. Off meso- and macrotidal beaches, water movements are dominated by the ebb and flow of the tide, and fish frequenting these areas generally move up and down the shore with the tide, during the day and night (Edwards & Steele 1968, Tyler 1971, Gibson 1973a, Kuipers 1973, van der Veer & Bergman 1986, Berghahn 1987, Raffaelli *et al.* 1990). This enables fish to exploit abundant food resources that occur in the intertidal zone, that are otherwise unavailable, as well allowing for the avoidance of piscivorous fish that move into the lower tidal levels as the tide rises, and enabling them to avoid physiologically unfavourable conditions that are likely to occur in the intertidal at low water.

Off microtidal beaches, wave and wind generated turbulence predominates over tidal movements, and there is a general consensus concerning the overriding influence of day-night changes (Modde & Ross 1981, Allen & DeMartini 1983, Lasiak 1984b, Ruple 1984, Senta & Kinoshita 1985, Romer & McLachlan 1986, Ross *et al.* 1987, Whitfield 1989, McMichael & Ross 1987). Earlier authors have not, however, been able to provide satisfactory explanations as to precisely how the composition and abundance of the fish faunal assemblages vary in response to these changes. Results of this study suggest that fish frequenting surf habitats migrate into and out of the surf-zone on a daily basis. Their movement patterns are modified by variations in water clarity and food availability, however, which are in turn moderated by prevailing wind conditions. When prevailing winds blow onshore, surf waters are generally turbid and fish move into the surf-zone in order to take advantage of the available food resources and cover, but move offshore again at night in order to conserve energy. When surf waters are clear, however (typically associated with offshore winds), fish do not move inshore as surf waters offer few benefits under these conditions. These patterns are often complicated still further by variations in netting efficiency, with the result that peak abundance is often recorded during crepuscular periods.

Modde & Ross (1981) observed that studies on surf-zone fish assemblages seldom exceed one annual cycle, with the result that knowledge regarding long term (interannual) variations is very poor. Although this study spanned a period of two years, it does little to advance knowledge in this area. Declines in the abundance of the top two species (*A. breviceps* and *L. richardsonii*) resulted in an overall reduction in the abundance of fish in the surf from the first year to the second. Some changes were also evident in the relative rankings of some of the other important species between years and relative to an earlier study. It is likely that these changes were a result of variations in the recruitment success brought about by large scale changes in climatic and hydrological factors, but this was not confirmed.

**Estuarine and surf-zone dependence**

Numerous fish species frequent southern African estuaries, and many have been thought to depend on estuaries at some stage of their life cycles. Discoveries of species previously considered estuary-dependent in the marine environment during critical stages of their life histories (e.g. Gordon & DeSylva 1980, Claridge *et al.* 1986, Lenanton & Potter 1987), however, had brought accepted ideas on estuarine dependence into question. Data on the composition, abundance and size structure of fish assemblages sampled during the present study were drawn together with that from earlier studies so as to compile a comprehensive database on fish species frequenting surf habitats in the south-western Cape. These were compared with available data from estuarine and other inshore marine habitats in the same area, in order to examine the validity of the terms "estuarine dependent" and "surf dependent" as they apply in the south-western Cape. A number of earlier assessments of this nature have been completed for southern African ichthyofauna, but available data on the occurrence of fish in surf-zone habitats at the time, particularly those in the south-western Cape, were sparse.

Of the 11 species previously considered to be entirely dependent on south-western Cape estuaries, two species were also found in the surf during the course of this study. Two other species previously considered to be only partially dependent on estuaries, however, do not appear to occur outside of these habitats in the south-western Cape. It is clear therefore, that although many of the conditions considered to make estuaries ideal areas for colonisation by juvenile marine fish species (e.g. warm waters, shelter and abundant food) are also available in surf habitats, certain species remain dependent on estuaries for their survival. The lack of suitable alternatives and the current rate at which estuaries are being degraded, implies that we are likely to see further reductions in the abundance and/or ranges occupied by these species.

This study also revealed a group of seven species that appear to depend on surf habitats at some stage of their life cycles. These species are not as severely threatened as their estuarine counterparts, however, as surf habitats are largely unimpacted relative to estuaries in the south-western Cape. Although sandy and mixed shore habitats account for a considerable proportion of coastline in the south-western Cape, the total area within the surf-zone is not particularly large (<1 000 ha, roughly 1.5x that available estuarine area). Much of this area comprises highly exposed beaches not suitable for colonisation by many species. Only 20% of the species making extensive use of surf habitats are able to utilise both exposed and sheltered areas throughout their life cycles. Sheltered sections of coastline also happen to be favoured sites for harbour and marina developments, as well as being popular centres for recreational activity, which further increases their vulnerability.

# REFERENCES

# REFERENCES

Allen, L.G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthyes californicus*) in the vicinity of Alamitos Bay-Long Beach Harbour, California, 1983-1985. *Bull. S. Calif. Acad. Sci.* 87: 19-30.

Allen, L.G. & E.E. DeMartini. 1983. Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre-Oceanside, California. *Fish. Bull.* 81: 569-586.

Anderson, W.D. Jr., J.K. Dias, R.K. Dias, D.M. Cupka & N.A. Chamberlain. 1977. The macrofauna of the surf zone off Folly Beach, South Carolina. *NOAA Tech. Rep. NMFS SSRF*-704, 23 pp.

Ansell, A.D. & R.N. Gibson. 1990. Patterns of feeding and movement of juvenile flatfishes on an open sandy beach. In: M. Barnes & R.N. Gibson (eds.) *Trophic Relationships in the Marine Environment*, Proc. 24th Europ. Mar. Biol. Symp., Aberdeen University Press, pp. 191-207

Ansell, A.D. & R.N. Gibson. 1993. The effect of sand and light on predation of juvenile plaice (*Pleuronectes platessa*) by fishes and crustaceans. *J. Fish Biol.* 43: 837-845.

Armstrong, M.J. & R.M. Thomas. 1989. Clupeoids. In: A.I.L. Payne & R.J.M. Crawford (eds.) *Oceans of Life Off Southern Africa.* Vlaeberg, Cape Town pp. 105-121.

Atkins, G.R. 1970. Thermal structure and salinity of False Bay. *Trans. Roy. Soc. S. Afr.* 34: 11-128.

Bally, R. 1981. *The Ecology of Three Sandy Beaches on the West Coast of South Africa.* Unpubl. Ph.D. Thesis, University of Cape Town, South Africa, 404 pp.

Bally, R., C.D. McQuaid & A.C. Brown. 1984. Shores of mixed sand and rock: an unexplored marine ecosystem. *S. Afr. J. Sci.* 80: 500-503.

Bang, N.D. 1971. The southern Benguela Current region in February, 1966. Part II. Bathythermography and air-sea interactions. *Deep Sea Res.* 18: 209-224.

Barnes, R.S.K. 1974 *Estuarine Biology.* Edward Arnold, London.

Becking, L.B., C.F. Tolman, H.C. McMillin, J. Field & T. Hashimoto. 1927. Preliminary statement regarding the diatom "epidemics" at Copalis Beach, Washington, and an analysis of diatom oil. *Econ. Geol.* 22: 356-368.

Beckley, L.E. 1984a. The ichthyofauna of the Sundays estuary, South Africa, with particular reference to the juvenile marine component. *Estuaries* 7: 248-258.

Beckley, L.E. 1984b. Shallow water trawling off the Swartkops estuary, Algoa Bay. *S. Afr. J. Zool.* 19: 248-250.

Begg, G.W. 1976. Some notes on the Sandvlei fish fauna. *Piscator* 96: 4-14.

Bennett, B.A. 1987. The rock-pool fish community of Koppie Alleen and an assessment of the importance of Cape rock-pools as nurseries for juvenile fish. *S. Afr. J. Zool.* 22: 25-32.

Bennett, B.A. 1988. Some considerations for the management in South Africa of the galjoen *Coracinus capensis* (Cuvier), an important shore angling species off the southwestern Cape. *S. Afr. J. mar. Sci.* 6: 133-142.

Bennett, B.A. 1989a. The fish community of a moderately exposed beach on the southwestern Cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Est. cstl Shelf Sci.* 28: 293-305.

Bennett, B.A. 1989b. A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the southwestern Cape, South Africa. *S. Afr. J. mar. Sci.* 8: 43-55.

Bennett, B.A. 1989c. The diets of fish in three south-western Cape estuarine systems. *S. Afr. J. Zool.* 24: 163-177.

Bennett, B.A. 1991. Long-term trends in the catches by shore anglers in False Bay. *Trans. Roy. Soc. S. Afr.* 47: 683-690.

Bennett, B.A. 1993. Aspects of the biology and life history of white steenbras *Lithognathus lithognathus* in southern Africa. *S. Afr. J. mar. Sci.* 13: 83-96.

Bennett, B.A. 1994. The fish community of the Berg River estuary with an assessment of the likely effects of reduced freshwater inflows. *S. Afr. J. Zool.* 29: 118-125.

Bennett, B.A. & C.L. Griffiths. 1984. Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa. *S. Afr. J. Zool.* 19: 97-104.

Bennett, B.A. & C.L. Griffiths. 1986. Aspects of the biology of galjoen *Coracinus capensis* (Cuvier) off the south-western Cape, South Africa. *S. Afr. J. mar. Sci.* 4: 153-162.

Bennett, B.A., C.L. Griffiths & M.-L. Penrith. 1983. The diets of littoral fish from the Cape peninsula. *S. Afr. J. Zool.* 18: 343-352.

Berghahn, R. 1986 Determining abundance, distribution and mortality of 0-group plaice (*Pleuronectes platessa* L) in the Wadden Sea. *J. Appl. Ichthyol.* 2: 11-22.

Berghahn, R. 1987. The Wadden Sea as a nursery for fish and crustacean species. pp. 69-85. In: S. Tougard & S. Asbirk (eds.) Proc. 5th Int. Wadden Sea Symp. National Forest and Nature Agency and the Museum of Fishery and Shipping, Esbjerg, Denmark.

Bergman, M.J.N., H.W. van der Veer & J.J. Ziljstra. 1988. Plaice nurseries: effects on recruitment. Proc. 17th EBSA Sympos. Fish in Estuaries. *J. Fish Biol.* 33 (Suppl. A): 201-218.

Bickerton, I.B. 1984. Estuaries of the Cape. Part II. Report No. 25. Heuningnes (CSW 19). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 424: 63 pp.

Biden, C.L. 1930. *Sea-Angling Fishes of the Cape*. Juta, Cape Town, 303 pp.

Blaber, S.J.M. 1974. The population structure and growth of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae) in a closed estuary. *J. Fish Biol.* 6: 455-460.

Blaber, S.J.M. 1977. The feeding ecology of mullet (Mugilidae) in Natal and Pondoland estuaries. *Biol. J. Linn. Soc.* 9: 259-275.

Blaber, S.J.M. 1979. The biology of filter feeding teleosts in Lake St Lucia, Zululand. *J. Fish Biol.* 15: 37-59.

Blaber, S.J.M. 1981. The zoogeographic affinities of estuarine fishes in south-east Africa. *S. Afr. J. Sci.* 77: 305-307.

Blaber, S.J.M. & T.G. Blaber. 1976. The food and feeding ecology of Mugilidae in the St. Lucia lake system. *Biol. J. Linn. Soc.* 8: 267-277.

Blaber, S.J.M. & T.G. Blaber. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *J. Fish Biol.* 17: 143-162.

Blaber, S.J.M. & D.P. Cyrus. 1983. The biology of Carangidae (Teleostei) in Natal estuaries. *J. Fish Biol.* 22: 173-188.

Blaber, S.J.M. & A.K. Whitfield. 1977. The feeding ecology of juvenile mullet (Mugilidae) in south-east African estuaries. *Biol. J. Linn. Soc.* 9: 277-284.

Blaber, S.J.M., Young, J.W. & Dunning, M.C. 1985 Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of north-western Australia. *Aust. J. Mar. Freshw. Res.* 36: 247-266.

Blaxter, J.H.S. 1967. Swimming speeds of fish. *FAO Fish. Rep.* 62: 60-100.

Blaxter, J.H.S. & B.B. Parrish. 1965. The importance of light in shoaling, avoidance of nets and vertical migration by herring. *J. Cons. int. Explor. Mer.* 30: 40-57.

Blaxter, J.H.S., B.B. Parish & W. Dickson. 1964. The importance of vision in the reaction of fish to drift nets and trawls. pp. 529-536. In: H. Kristjonsson (ed.), *Modern Fishing Gear of the World*, Vol. 2. Fishing News, London.

Brainbridge, R. 1958. The speed of swimming of fish as related to size and the frequency and amplitude of the tail beat. *Exp. Biol.* 35: 109-133.

Branch, G.M. & J.H. Day. 1984. Ecology of southern African estuaries: Part XIII. The Palmiet River estuary in the south-western Cape. *S. Afr. J. Zool.* 19: 63-77.

Brown, A.C. & N. Jarman. 1978. Coastal marine habitats. In: M.J.A. Werger (ed.) *Biogeography and Ecology of Southern Africa*. Junk, The Hague, pp. 1241-1277..

Brown, A.C. & A. McLachlan. 1990 *Ecology of Sandy Shores*. Elsevier, Amsterdam, 328 pp.

Brown, A.C., R.P. Wynberg & S.A. Harris. 1991. Ecology of shores of mixed rock and sand in False Bay. *Trans. Roy. Soc. S. Afr.* 47: 563-574.

Bruton, M.N. 1979. The fishes of Lake Sibaya. In: B.R. Allanson (ed.) *Lake Sibaya*. W. Junk, The Hague, pp. 162-245.

Bruton, M.N. 1985. The effects of suspensoids on fish. *Hydrobiol.* 125: 221-241.

Bruton, M.N. & C.C. Appleton. 1975. Survey of the Mgobenzeleni Lake-system in Zululand, with a note on the effect of a bridge on the mangrove swamp. *Trans. Roy. Soc. S. Afr.* 41: 283-295.

Burrows, M.T., R.N. Gibson, L. Robb & C.A. Comely. 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *J. Exp. Mar. Biol. Ecol.* 177: 251-268.

Buxton, C.D. & H.M. Kok. 1983. Notes on the diet of *Rhabdosargus holubi* (Steindachner) and *Rhabdosargus globiceps* (Cuvier) in the marine environment. *S. Afr. J. Zool.* 18: 406-408.

Carlisle Jr, J.G., J.W. Schott & N.J. Abrahamson. 1960. The barred surf-perch in southern California. *Calif. Dept. Fish Game Fish. Bull.* 109.

Carter, R.A. 1983. Estuaries of the Cape. Part II. Report No. 21. Breë (CSW 22). Heydorn, A.E.F. & Grindley, J.R. (eds.) CSIR Research Report 420: 58 pp.

Christie, N.D. 1976. A numerical analysis of the distribution of a shallow sublittoral sand macrofauna along a transect at Lamberts Bay, South Africa. *Trans. Roy. Soc. S. Afr.* 42: 149-172.

Chubb, C.F., I.C. Potter, C.J. Grant, R.C.J. Lenanton & J. Wallace. 1981. Age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon river system, Western Australia. *Aust. J. Mar. Freshw. Res.* 32: 605-628.

Claridge, P.N., I.C. Potter & M.W. Hardisky. 1986. Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn estuary. *J. Mar. Biol. Ass. U. K.* 66: 229-258.

Clark, B.M. 1990. The impact of fish predation on the cultured mussel, *Mytilus galloprovincialis* in the Seafarm dam, Saldanha. Unpubl. B.Sc. Hons. Thesis, University of Cape Town, Cape Town. 39 pp.

Clark, B.M. 1996. Variation in surf zone fish community structure across a wave exposure gradient. *Est. cstl. Shelf Sci.* In press.

Clark, B.M. & B.A. Bennett. 1993. Are juvenile fish an issue in the trek net controversy? *Fish, fishers and fisheries, Proc. 2nd Mar. Recreational Angling Symp., Durban, October 1992.* Beckley, L.E. & R.P. van der Elst (eds.) *Spec. Publ. oceanogr. Res. Inst. S. Afr.* 2: 157-159.

Clark, B.M., B.A. Bennett & S.J. Lamberth. 1994a. Assessment of the impact of commercial beach-seine netting on juvenile teleost populations in the surf zone of False Bay, South Africa. *S. Afr. J. mar. Sci.* 14: 255-262.

Clark, B.M., B.A. Bennett & S.J. Lamberth. 1994b. A comparison of the ichthyofauna of two estuaries and their adjacent surf-zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. *S. Afr. J. mar. Sci.* 14: 121-131.

Clark, B.M., B.A. Bennett & S.J. Lamberth. 1996a. Factors affecting spatial variability in seine net catches of fish in the surf zone of False Bay, South Africa. *Mar. Ecol. Prog. Ser.* 131: 17-34.

Clark, B.M., B.A. Bennett & S.J. Lamberth. 1996b. Temporal variations in the composition and abundance of fishes in the surf-zone of False Bay, South Africa. *Mar. Ecol. Prog. Ser.* 131: 35-47.

Clark, D.S. & J.M. Green. 1990. Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua* L., in cold environments. *Can. J. Zool.* 68: 1434-1442.

Clarke, B.C. 1989. Estuaries of the Cape. Part II. Report No. 37. Palmiet (CSW 12). Heydorn, A.E.F. & P.D. Morant (eds.) CSIR Research Report 436: 82 pp.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.* 18: 117-143.

Clarke, K.R. & M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.* 92: 205-219.

Cliff, S. & J.R. Grindley. 1982. Estuaries of the Cape. Part II. Report No. 17. Lourens (CSW 7). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 416: 39 pp.

Coetzee, D.J. 1982. Stomach content analysis of *Gilchristella aestuaria* and *Hepsetia breviceps* from the Swartvlei system and Groenvlei, southern Cape. *S. Afr. J. Zool.* 17: 59-66.

Compagno, L.J.V. 1984a. FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. *FAO Fisheries Synopsis* (125) 4: 251-655.

Compagno, L.J.V. 1984b. FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis* (125) 4: 1-249.

Compagno, L.J.V., D.A. Ebert & M.J. Smale. 1989. *Guide to the sharks and rays of southern Africa.* Struik Publishers, Cape Town, 160 pp.

Connell, J.H. 1978 Diversity in tropical rain forests and coral reefs. *Science* (Wash., D.C.) ***199***: 1302-1310.

Cowley, P.D. 1990. The taxonomy and life history of the blue stingray *Dasyatis marmorata capensis* (Batoidea: Dasyatidae) from southern Africa. MSc Thesis, Rhodes University, Grahamstown.

Cowper, S.W. 1978. The drift algae communities of seagrass beds in Redfish Bay, Texas. *Contr. mar. Sci.* 21: 125-132.

Crawford, R.J.M., O.M. Centurier-Harris, G.H.L. Wingate & B.D. Kriedemann. 1978. Revision of species and age composition of landings in the South African purse-seine fishery, 1950 to 1976. *Fish. Bull. S. Afr.* 10: 69-88.

Creutzberg, F., A. TH. G. W. Eltink & G.J. van Noort. Migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea . In: D.S. McLusky & A.J. Berry (eds.) *Physiology and Behaviour of Marine Organisms.* Proceedings of the 12th European Symposium on Marine Biology, Stirling, Scotland, 1977. Pergamon Press, Oxford, pp. 243-251.

Cronin, L.E. & A.J. Mansueti. 1971. The biology of the estuary. In: P.A. Douglas & R.H. Stroud (eds.) *A Symposium on the Biological Significance of Estuaries.* Sport Fishing Institute, Washington D.C., pp. 24-39.

CSIR 1984. Surf zone phytoplankton blooms in False Bay. A summary of available information. CSIR Report C/SEA, Stellenbosch, South Africa. pp. 1-27.

CSIR 1987. Basic Physical Geography/Hydro data for "estuaries" of the western cape (CSW 1-26). NRIO Data Report D8705, Stellenbosch, South Africa. 17 pp.

CSIR 1988. Basic Physical Geography/Hydro data for "estuaries" of the south-western cape (CW 1-32). NRIO Data Report D8802, Stellenbosch, South Africa. 18 pp.

Cyrus, D.P. 1983 *The Influence of Turbidity on Fish Distribution in Natal Estuaries.* Unpubl. Ph.D. Thesis, University of Natal, Pietermaritzburg.

Cyrus, D.P. & S.J.M. Blaber. 1982. Species identification, distribution and abundance of Gerreidae (Teleostei) Bleeker, 1859 in the estuaries of Natal. *S. Afr. J. Zool.* 17: 105-116.

Cyrus, D.P. & S.J.M. Blaber. 1987a. The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies in Lake St. Lucia on the southeastern coast of Africa. *J. Exp. Mar. Biol. Ecol.* 109: 53-70.

Cyrus, D.P. & S.J.M. Blaber. 1987b. The influence of turbidity on juvenile marine fishes in estuaries. Part 2. Laboratory studies, comparisons with field data and conclusions. *J. Exp. Mar. Biol. Ecol.* 109: 71-91.

Cyrus, D.P. & S.J.M. Blaber. 1987c. The influence of turbidity on juvenile marine fishes in estuaries of Natal, South Africa. *Cont. Shelf Sci.* 7: 1411-1416.

Cyrus, D.P. & S.J.M. Blaber. 1992. Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Est. cstl. Shelf Sci.* 35: 545-563.

Davies, J.L. 1964. A morphogenic approach to world shorelines. *Zeitschrift für Geomorphology.* 8: 127-142.

Davies, J.L. 1972 *Geographical Variation in Coastal Development*. Oliver & Boyd, Edinburgh.

Day, J.H. 1951. The ecology of South African estuaries. Part 1. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Afr.* 33: 53-91.

Day, J.H. 1959. The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. *Trans. Roy. Soc. S. Afr.* 35: 475-547.

Day, J.H. 1964. The origin and distribution of estuarine animals in South Africa. In: D.H.S Davis (ed.) *Ecological Studies in southern Africa*. Junk, The Hague, pp. 159-173

Day, J. H. 1981. The nature, origin and classification of estuaries. In: J.H. Day (ed.) *Estuarine Ecology with particular reference to southern Africa*, A.A.Balkema, Cape Town, pp. 1-6.

Day, J.H., S.J.M. Blaber & J.H. Wallace. 1981. Estuarine fishes. In: J.H. Day (ed.) *Estuarine Ecology with particular reference to southern Africa*, Balkema, Cape Town. pp. 197-221.

Day, J.H., N.A.H. Millard & A.D. Harrison. 1952. The ecology of South African estuaries. Part III. Knysna: A clear open estuary. *Trans. Roy. Soc. S. Afr.* 33: 1-414.

Day, J.H., & J.F.C. Morgans. 1956. The ecology of South African estuaries. Part 7. The biology of Durban Bay. *Ann. Natal Mus.* 13: 259-312.

Day, J.W. Jr. & A. Yáñez-Aranciabia. 1985. Coastal lagoons and estuaries as an environment for nekton. In: A. Yáñez-Aranciabia(ed.) *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration*. DR (R) UNAM Press, Mexico, pp. 17-34.

De Decker, H.P. 1989. Estuaries of the Cape. Part II. Report No. 40. Klein (CSW 16). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 439: 89 pp.

De Sylva, D.P. 1975. Nektonic food webs in estuaries. In: *Estuarine Research, Vol. 1. Chemistry, Biology and the Estuarine System*. Academic Press, New York, pp. 420-447.

De Sylva, D.P. 1985. Nektonic food webs in estuaries. In: A. Yanez-Arancibia (ed.) *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration*. DR (R) UNAM Press, Mexico, Mexico. pp. 233-246.

De Silva, S.S. & E.I.L. Silva. 1979. Biology of young grey mullet, *Mugil cephalus* L., populations in a coastal lagoon in Sri Lanka. *J. Fish Biol.* 15: 9-20.

De Villiers, G. 1987. Harvesting harders *Liza richardsoni* in the Benguela upwelling region. *S. Afr. J. mar. Sci.* 5: 852-862.

DeMartini, E.E. & L.G. Allen. 1984. Diel variation in catch parameters for fishes sampled by a 7.6-m otter trawl in southern California coastal waters. *Calif. Coop. Oceanic Fish. Invest. Rep.* 24: 194-201.

Dexter, D.M. 1990 The effect of exposure and seasonality on sandy beach community structure in Portugal. *Cienc Biol Ecol Syst* (Portugal) 10: 31-50.

Dorel D, C. Koutsikopoulos, Y. Desaunay & J. Marchand. 1991. Seasonal distribution of young sole (*Solea solea* (L)) in the nursery ground of the Bay of Vilaine (northern Bay of Biscay). *Neth. J. Sea Res.* 27: 297-306.

Du Plessis, A. & J.G. Glass. 1991. The geology of False Bay. *Trans. Roy. Soc. S. Afr.* 47: 495-517.

Duvenage, I.R. 1983. Getyrivieroppervlaktes van somige getyriviere aan die Kaapse Kus. Eenheid vir Getyrivier- en Kusnavorsing, Nationale Navorsingsinstituut vir oseanologie wetenskaplike en Nywerheidsnavorsinsraad, Stellenbosch. 89 pp.

Eagle, G.A. & H.F-K.O. Hennig. 1984. Surf zone phytoplankton blooms in False Bay: a summary of available information. CSIR Report C/SEA 8420, CSIR, Stellenbosch, South Africa.

Edwards, R.R.C. 1973. Production ecology of two Caribbean marine ecosystems. I. Physical environment and fauna. *Est. cstl Mar. Sci.* 1: 303-318.

Edwards, R. & J.H. Steele. 1968. The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. *J. Exp. Mar. Biol. Ecol.* 2: 215-238.

Eekhout, S., J.M. King, & A.W. Wackernagel. (in prep.). A biogeographic classification of the rivers of South Africa. Final report to Department of Environment Affairs and Tourism.

Eleftheriou, A. & M.D. Nicholson. 1975. The effects of exposure on beach fauna. *Cah. Biol. Mar.* 16: 695-710.

Eltringham, S.K. 1971 *Life in Mud and Sand.* English Universities Press, London, 218 pp.

Evans, S. & B. Tallmark. 1984. Seasonal dynamics of small vagile predators on marine shallow soft bottom *Holarct. Ecol.* 7: 138-148.

Evans, S. & B. Tallmark. 1985. Niche separation within the mobile predator guild on marine shallow soft bottoms. *Mar. Ecol. Prog. Ser.* 23: 279-286.

Farmer, G.J. & F.W. Beamish. 1969. Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. *J. Fish. Res. Bd Can.* 26: 2807-2821.

Field, J.G. 1971. A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. *J. Exp. Mar. Biol. Ecol.* 7: 215-253.

Field, J.G., K.R. Clarke & R.M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8: 37-52.

Field, J.G. & C.L. Griffiths. 1991. Littoral and sublittoral ecosystems of southern Africa. In: P.H. Niehuis & A.C. Mathieson (eds.) *Intertidal and Littoral Ecosystems*, Elsevier, Amsterdam. pp. 323-346.

Fleischack, P.C. & A.J. de Freitas. 1989. Physical parameters influencing the zonation of surf zone benthos. *Est. cstl Shelf Sci.* 28: 517-530.

Flemming, B.W. 1977. Distribution of recent sediments in Saldanha Bay and Langebaan Lagoon. *Trans. Roy. Soc. S. Afr.* 42: 317-340.

Fowler, J.L. 1994. Patterns of recolonisation by resident intertidal rock pool fish on the Cape west coast. Unpubl. B.Sc. Hons. Thesis, University of Cape Town, Cape Town, 32 pp.

Frank, K.T. & W.C. Leggett. 1981a. Wind regulation of emergence times and early survival in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 38: 215-223.

Frank, K.T. & W.C. Leggett. 1981b. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. *Can. J. Fish. Aquat. Sci.* 38: 1327-1338.

Frank, K.T. & W.C. Leggett. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 39: 991-1003.

Freer, D.W.L. & C.L. Griffiths. 1993. The fishery for, and the general biology of, the St. Josef *Callorhinchus capensis* (Dumeril) off the south-western Cape, South Africa. *S. Afr. J. mar. Sci.* 13: 63-74.

Futch, C.R. & S.E. Dwinell. 1977. Nearshore marine ecology at Hutchins Island, Florida: 1971-1974. IV. Lancelets and fishes. *Fla. Mar. Res. Publ.* 24: 23 pp.

Gaigher, I.G. & S.C. Thorne. 1979. Report on two gill-net surveys of the Sandvlei estuarine lake, Muizenburg, western Cape. Internal Report, Dept. Nature and Environmental Conservation, Cape Provincial Administration.

Geldenhuys ND 1973 Growth of the South African maasbanker *Trachurus trachurus* Linnaeus and age composition of the catches, 1950-1971. *Investl. Rep. Sea Fish. Brch S. Afr.* 101: 1-24.

Gianuca, N.M. 1983. A preliminary account of the ecology of sandy beaches in southern Brazil.. In: A. McLachlan & T Erasmus (eds.) *Sandy beaches as Ecosystems.* W. Junk, The Hague, pp. 65-75

Gibson, R.N. 1973a. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L). *J. Exp. Mar. Biol. Ecol.* 12: 79-102.

Gibson, R.N. 1973b. Tidal and circadian activity rhythms in juvenile plaice, *Pleuronectes platessa. Mar. Biol.* 22: 370-386.

Gibson, R.N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Neth. J. Sea Res.* 32: 191-206.

Gibson, R.N., A.D. Ansell & L. Robb. 1993. Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. *Mar. Ecol. Prog. Ser.* 98: 89-105.

Gibson, R.N. & I.A. Ezzi. 1978. The biology of a Scottish population of Fries goby, *Lesueurigobius friesii. J. Fish Biol.* 12: 371-389.

Gibson, R.N. & L. Robb. 1992 The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. *J. Fish Biol.* 40: 771-778.

Gibson, R.N., L. Robb, M.T. Burrows & A.D. Ansell. 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. *Mar. Ecol. Prog. Ser.* 130: 1-17.

Gordon, J.D.M. 1981. The fish population of the west coast of Scotland shelf. Part II. *Ann. Rev. Oceanog. Mar. Biol.* 19: 405-441.

Gordon, J.D.M. & S.S. De Silva, 1980. The fish population of the west coast of Scotland shelf. Part I. *Ann. Rev. Oceanog. Mar. Biol.* 18: 317-366.

Gradall, K.S. & W.A. Swenson. 1982. Responses of brook trout and creek chubs to turbidity. *Trans. Am. Fish. Soc.* 111: 392-395.

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 50: 241-246.

Griffiths, M.H. & P.C. Heemstra. 1995. A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Scianidae), with descriptions of two new species from southern Africa. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.* 65: 40 pp.

Grindley, J.R. 1982. Estuaries of the Cape. Part II. Report No. 16. Eerste (CSW 6). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 415: 51 pp.

Grindley, J.R. & S. Dudley. 1988. Estuaries of the Cape. Part II. Report No. 28. Rietvlei (CSW 24) and Diep Estuary (CW 25). Heydorn, A.E.F. & P.D. Morant. (eds.) CSIR Research Report 427: 90 pp.

Gründlingh, M.L. & J.L. Largier. 1991. Physical oceanography of False Bay: a review. *Trans. Roy. Soc. S. Afr.* 47: 387-400.

Gunter, G. 1945. Studies on the marine fishes of Texas. *Publ. Inst. Mar. Sci. Univ. Texas* 1: 1-190.

Gunter, G. 1958. Populations studies of the shallow water fishes of an outer beach in southern Texas. *Publ. Inst. Mar. Sci. Univ. Texas* 5: 186-193.

Haedrich, R.L. 1983. Estuarine fishes. In: B.H. Ketchum (ed.) *Ecosystems of the World.* Elsevier, Amsterdam, pp. 183-207.

Hall, C.M., A.K. Whitfield & B.R. Allanson. 1987. Recruitment, diversity and the influence of constrictions on the distribution of fishes in the Wilderness lakes system, South Africa. *S. Afr. J. Zool.* 22: 163-169.

Hanekom, N., & D. Baird. 1984. Fish community structures in *Zostera* and non-*Zostera* regions of the Kromme estuary, St. Francis Bay. *S. Afr. J. Zool* 19: 295-301.

Harris, S.A., B.A. Bennett & G.M. Branch. 1988. An assessment of the role of the sand shark *Rhinobatos annulatus* as a predator in Langebaan Lagoon. *S. Afr.J. mar. Sci.* 7: 153-159.

Harrison, T.D., J.A.G. Cooper, A.E.L. Ramm & R.A. Singh. 1994. Health of South African estuaries, Orange River - Buffels (Oos). Executive report. Prepared for the Department of Environmental affairs by the Catchment and Coastal Environmental Programme, CSIR, Congela, South Africa.

Harrison, T.D., J.A.G. Cooper, A.E.L. Ramm & R.A. Singh. 1995. Health of South African estuaries, Palmiet - Sout. Executive report. Prepared for the Department of Environmental affairs by the Catchment and Coastal Environmental Programme, CSIR, Congela, South Africa.

Hecht, T. 1977. Contributions to the biology of the Cape gurnard, *Trigla capensis* (Pisces: Triglidae): age, growth and reproduction. *Zool. Afr.* 12: 373-382.

Hedgpeth, J.W. 1957. Sandy beaches. In: J.H.W. Hedgepeth (ed.) *Treatise on Marine Ecology and Palaeociology. Geol. Soc. America Mem.* 67: 587-608.

Hedgpeth, J.W. 1982. Estuarine dependence and colonization. Proceedings of International Symposium on Utilization of Coastal ecosystems: Planning, Pollution and Productivity, 22-27 November, 1982, Rio Grande, Brazil, pp. 57-58.

Heinecken, T.J.E. 1982. Estuaries of the Cape. Part II. Report No. 8. Rooiels (CSW 10). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 407: 35 pp.

Hemple, G. 1963. Diurnal variations in catch, feeding and swimming activity of plaice (*Pleuronectes platessa* L.). *Rapp. Cons. Explor. Mer.* 155: 58-64.

Heydorn, A.E.F. & Bickerton, I.B. 1982. Estuaries of the Cape. Part II. Report No. 9. Uilkraals (CSW 17). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 408: 37 pp.

Heydorn, A.E.F. 1986. An assessment of the state of the estuaries of the Cape and Natal in 1985/86. *S. Afr. Nat. Sci. Progr. Rep.* No. 130, 39 pp.

Hillman, R.E., N.W. Davis & J. Wennemer. 1977. Abundance, diversity and stability in shore-zone fish communities in an area of Long Island Sound affected by discharge of a nuclear power station. *Est. cstl Shelf Sci.* 5: 355-381.

Hobson, E.S. 1979. Interactions between piscivorous fishes and their prey. In: R.H. Stroud & H. Clepper (eds.) *Predator-Prey Systems in Fishery Management.* Sport Fishing Institute, Washington, DC., pp. 231-242.

Hockey, P.A.R., W.R. Sirgfried & A.A. Crowe. 1983. Ecological structure and energy requirements of the sandy beach avifauna of southern Africa. In: A. McLachlan. & T. Erasmus (eds.) *Sandy Beaches as Ecosystems.* Junk, The Hague, pp. 507-521

Horne, C. 1955. *Fisherman's Eldorado.* Howard Timmins, Cape Town. 218 pp.

Horne, C. 1961. *Salt Water Fishing in Southern Africa.* Howard Timmins, Cape Town. 156 pp.

Hull, S.C. 1987. Macroalgal mats and species abundance: a field experiment. *Est. cstl Shelf Sci.* 25: 519-532.

Hunter, J.R. & W.J. Wisby. 1964. Net avoidance behaviour of carp and other species of fish. *J. Fish. Res. Bd. Can.* 21: 613-633.

Jackson, P.B.N. 1950. *The Fishes of the Intertidal Zone of the Cape Peninsula*. Unpubl. Msc. Thesis, University of Cape Town, Cape Town, 21 pp.

Jones, A. 1973 The ecology of young turbot, Scophthalmus maximus (L.), at Borth, Cardiganshire, Wales. *J. Fish Biol.* 5: 367-383.

Joubert, C.S.W. 1981a Aspects of the biology of five species of inshore reef fishes on the Natal coast, South Africa. *Investl Rep oceanogr Res Inst S Afr* 52: 1-16.

Joubert, C.S.W. 1981b. A survey of shore anglers' catches at selected sites on the Natal Coast, South Africa. *Investl. Rep. oceanogr. Res. Inst. S. Afr.* 51: 1-16.

Joubert, C.S.W & P.B. Hanekom. 1980. A study of feeding in some inshore reef fish of the Natal coast, South Africa. *S. Afr. J. Zool* 15: 262-274.

Jury, M. 1991. The weather of False Bay. *Trans. Roy. Soc. S. Afr.* 47: 401-417.

Keats, D.W. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. *J. exp. mar. Biol. Ecol.* 139: 167-173.

Kikuchi, T. & J.M. Pérès. 1977. Animal communities in seagrass beds: a review. In: McRoy, C.P. & C. Helfferich (eds.) *Seagrass Ecosystems: A Scientific Perspective* N.Y., pp. 147-193.

Kok, H.M., & A.K. Whitfield. 1986. The influence of open and closed mouth phases on the marine fish fauna of the Swartvlei estuary. *S. Afr. J. Zool.* 21: 309-315.

Koop, K. 1982. Estuaries of the Cape. Part II. Report No. 18. Bot/Kleinmont System (CSW 13). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 417: 62 pp.

Kruuk, H. 1963. Diurnal periodicity in the activity of the common sole, *Solea vulgaris* Quensel. *Neth. J. Sea Res.* 2: 1-28.

Kuipers, B. 1973. On the tidal migration of young plaice (*Pleuronectes platessa*) in the Wadden Sea. *Neth. J. Sea Res.* 6: 376-388.

Kuipers, B. 1975. Experiments and field observations on the daily food intake of juvenile plaice, *Pleuronectes platessa* L. Proc. 9th Europ. Mar. Biol. Symp. H. Barnes, (ed.). Aberdeen University Press, pp. 1-12

Kuipers, B.R. 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. *Neth. J. Sea Res.* 11: 56-91.

Lamberth, S.J., B.A. Bennett & B.M. Clark. 1994. Catch composition of the commercial beach-seine fishery in False Bay, South Africa. *S. Afr. J. mar. Sci.* 14: 69-78.

Lamberth, S.J., B.A. Bennett & B.M. Clark 1995a. The impact of beach-seine netting on the benthic fauna and flora of False Bay, South Africa. *S. Afr. J. mar. Sci.* 15: 115-122

Lamberth, S.J., B.A. Bennett & B.M. Clark 1995b. The vulnerability of fish to capture by commercial beach-seine nets in False Bay, South Africa. S. *Afr. J. mar. Sci.* 15: 25-31.

Lamberth, S.J., B.M. Clark & B.A. Bennett. 1995c. Seasonality of beach-seine catches in False Bay, South Africa, and implications for management. *S. Afr. J. mar. Sci.* 15: 157-167.

Lasiak, T.A. 1981. Nursery grounds of juvenile teleosts: evidence from surf zone of King's beach, Port Elizabeth. *S. Afr. J. Sci.* 77: 388-390.

Lasiak, T.A. 1982. *Structural and functional aspects of the surf-zone fish community in the Eastern Cape*. Unpubl. Ph.D. Thesis, University of Port Elizabeth, Port Elizabeth, 459 pp.

Lasiak, T.A. 1983. Recruitment and growth patterns of juvenile marine teleosts caught at King's Beach, Algoa Bay. *S. Afr. J. Zool* 18: 25-30.

Lasiak, T.A. 1984a. Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: long-term fluctuations. *Est. cstl Shelf Sci.* 18: 459-483.

Lasiak, T.A. 1984b. Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: short term fluctuations. *Estr. cstl. Shelf. Sci.* 18: 347-360.

Lasiak, T.A. 1984c. Aspects of the biology of three benthic-feeding teleosts from King's Beach, Algoa Bay. *S. Afr. J. Zool* 19: 51-56.

Lasiak, T.A. 1986. Juveniles, food and the surf-zone habitat: implications for teleost nursery areas. *S. Afr. J. Zool.* 21: 51-56.

Lechanteur, Y.A.R.G. (In prep.). Composition and seasonality of suprabenthic reef fish assembalges in False Bay, South Africa.

Ledgerwood, R.D., F.P. Thrower & E.M. Dawley. 1991. Diel sampling of migratory juvenile salmonids in the Columbia River estuary. *Fish. Bull. US.* 89: 69-78.

Lenanton, R.C.J. 1982. Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Aust. J. Mar. Freshw. Res.* 33: 881-900.

Lenanton, R.C.J. & N. Caputi. 1989. The roles of food supply and shelter in the relationship between fishes, in particular *Cnidoglanis macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. *J. Exp. Mar. Biol. Ecol.* 128: 165-176.

Lenanton, R.C.J. & I.C. Potter. 1987. Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. *Estuaries* 10: 28-35.

Lenanton, R.C.J., A.I. Robertson, & J.A. Hansen. 1982. Nearshore accumulations of detached macrophytes as nursery areas for fish. *Mar. Ecol. Prog. Ser.* 9: 51-57.

Lewin, J., T. Hruby & D. Mackas. 1975. Blooms of surf-zone diatoms along the coast of the Olympic Peninsula, Washington. V. Environmental conditions associated with the blooms (1971 and 1972). *Est. coast. Shelf Sci.* 3: 229-241.

Lewin, J. & C.T. Schaefer. 1983. The role of phytoplankton in surf ecosystems. In: A. McLachlan and T. Erasmus (ed.) *Sandy Beaches as Ecosystems*. Junk, The Hague, pp. 381-389.

Lima, S.L. & L.M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619-640.

Littler, M.M., D.R. Martz & D.S. Littler. 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Mar. Ecol. Prog. Ser.* 11: 129-139.

Lockwood, S.J. 1974. The settlement, distribution and movements of 0-group plaice *Pleuronectes platessa* (L) in Filey Bay, Yorkshire. *J. Fish Biol.* 6: 465-477.

Lutz, P.L. 1975. Adaptive and evolutionary aspects of the ionic content of fishes. *Copeia* 2: 369-373.

Lyons, J. 1986. Capture efficiency of a beach-seine for seven freshwater fishes in a north-temperate lake. *N. Am. J. Fish. Manage.* 6: 288-289.

Macer, C.T. 1967. The food web in Red Wharf Bay (N. Wales) with particular reference to young plaice. *Helg. wiss. Meeres.* 15: 560-573.

Mann, B.Q. 1992. *Aspects of the biology of two inshore sparid fishes (*Diplodus sargus capensis *and* Diplodus cervinus hottentotus*) off the south-east coast of South Africa.* Unbul. M.Sc. Thesis, Rhodes University, Grahamstown.

Marais, J.F.K. 1980. Aspects of the food intake, food selection, and alimentary canal morphology of *Mugil cephalus* (Linnaeus, 1958), *Liza tricuspidens* (Smith, 1935), *L. richardsoni* (Smith, 1846), and *L. dumerili* (Steindachner, 1869). *J. exp. Mar. Biol. Ecol.* 44: 193-209.

Margalef, R. 1958. Information theory in ecology. *Gen. Syst.* 3: 36-71.

Massé, H. 1972. Quantitative investigations of sand-bottom macrofauna along the Mediterranean north-west coast. *Mar. Biol.* 15: 209-220.

McCleave, J.D. & S.M. Fried. Nighttime catchs of fishes in a tidal cove in Montsweag Bay near Wiscasset, Maine. *Trans. Am. Fish. Soc.* 104: 30-34.

McDermott, J.J. 1983. Food web in the surf zone of an exposed sandy beach along the mid-atlantic coast of the United States. In: A. McLachlan. & T. Erasmus (eds.) *Sandy Beaches as Ecosystems*. Junk, The Hague, pp. 529-538.

McFarland, W.N. 1963. Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. *Publ. Inst. Mar. Sci. Univ. Texas* 9: 91-105.

McHugh, J.L. 1967. Estuarine nekton. In: G. Lauff (ed) *Estuaries*. Am Assoc Adv Sci, Washington, pp. 581-620

McLachlan, A. 1980. The definition of sandy beaches in relation to exposure: a simple rating system. *S. Afr. J. Sci.* 76: 137-138.

McLachlan, A. 1981. Exposed sandy beaches as semi-closed ecosystems. *Mar. Env. Res.* 4: 59-63.

McLachlan, A. 1983 Sandy beach ecology - a review. In: A. McLachlan. & T. Erasmus (eds.) *Sandy Beaches as Ecosystems*. Junk, The Hague, pp. 321-380.

McLachlan, A., A.C. Cockcroft & D.E .Malan. 1984. Benthic faunal response to a high energy gradient. *Mar. Ecol. Prog. Ser.* 16: 51-63.

McLachlan, A. & T. Erasmus. 1983. Preliminary investigation of surf zone phytoplankton blooms occurring off the Sundays river beach in Algoa Bay. In: A. McLachlan & T. Erasmus (eds.) *Sandy Beaches as Ecosystems*. Junk, The Hague, p. 750.

McLachlan, A., T. Erasmus, A.H. Dye, T. Wooldridge, G. van der Horst, G. Rossouw, T.A. Lasiak & L. McGwynne. 1981. Sandy beach energetics: an ecosystem approach to a high energy interface. *Est. cstl Shelf Sci.* 13: 11-25.

McLachlan, A. & J. Lewin. 1981. Observations on surf phytoplankton blooms along the coasts of South Africa. *Bot. Mar.* 24: 553-557.

McMichael, R.H. 1981 Utilization of the surf zone of a northern Gulf Coast barrier island by the *Menticirrhus* complex (Pisces: Scianidae). Unpubl. MSc Thesis, Univ. Southern Miss., Hattiesburg, 86 pp.

McMichael, R.H. & S.T. Ross. 1987. The relative abundance and feeding habits of juvenile kingfish (Scianidae: *Menticirrhus*) in a Gulf of Mexico surf zone. *NE Gulf Sci.* 9: 109-123.

McQuaid, C.D. & K.M. Dower. 1990. Enhancement of habitat heterogeneity and species richness on rocky shore inundated by sand. *Oceologia* 84: 142-144.

Mehl, J.A.P. 1973. Ecology, osmoregulation and reproductive biology of the white steenbras, *Lithognathus lithognathus* (Teleostei: Sparidae). *Zool. Afr.* 8: 157-230.

Melville-Smith, R. & D. Baird. 1980. Abundance, distribution and species composition of fish larvae in the Swartkops estuary. *S. Afr. J. Zool* 15: 72-78.

Menge, A.B. & Sutherland, J.P. 1976 Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110: 351-369.

Menge, A.B. & Sutherland, J.P. 1987 Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130: 730-757.

Merriman, D. 1947. Notes on the midsummer ichthyofauna of a Connecticut beach at different tide levels. *Copeia* 4: 281-286.

Methven, D.A. & C. Bajdik. 1994. Temporal variation in the size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. *Can. J. Fish. Aquat. Sci.* 51: 78-90.

Millard, N.A.H. & K.M.F. Scott. 1954. The ecology of South African estuaries. Part VI: Milnerton estuary and the Diep River, Cape. *Trans. Roy. Soc. S. Afr.* 34: 279-324.

Miller, J.M., L.B. Crowder & M.L. Moser. 1985. Migration and utilization of estuarine of estuarine nurseries by juveniles fishes: an evolutionary perspective. *Contrib. Mar. Sci.* 27 (Suppl.): 338-352.

Modde, T. 1980. Growth and residency of juvenile fishes within a surf zone habitat in the Gulf of Mexico. *Gulf Res. Rep.* 6: 377-385.

Modde, T. & S.T. Ross. 1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. *Fish. Bull.* 78: 911-922.

Modde, T. & S.T. Ross. 1983. Trophic relationships of fishes occurring within a surf zone habitat in the northern Gulf of Mexico. *NE Gulf Sci.* 6: 31-42.

Moore, C.G. 1979 The distribution and ecology of psammolittoral meiofauna around the Isle of Man. *Cah. Biol. Mar.* 20: 383-415.

Moore, J.W. & I.A. Moore. 1976 The basis of food selection in flounders, *Platichthys flesus* (L.), in the Severn Estuary. *J. Fish Biol.* 9: 139-156.

Morant, P.D. 1984. Estuaries of the Cape. Part II. Report No. 26. Olifants (CW 10). Heydorn, A.E.F. & Grindley, J.R. (eds.) CSIR Research Report 425: 54 pp.

Morant, P.D. & Grindley, J.R. 1982. Estuaries of the Cape. Part II. Report No. 14. Sand (CSW 4). Heydorn, A.E.F. & J.R. Grindley (eds.) CSIR Research Report 413: 70.

Morin, J.G., J.E. Kastendiek, A. Harrington & N. Davis. 1985. Organization and patterns of interaction in a subtidal sand community on an open coast. *Mar. Ecol. Prog. Ser.* 27: 163-185.

Nash, R.D.M., R.S. Santos, A.J. Geffen, G. Hughes & T.R. Ellis. 1994. Diel variability in catch rate of juvenile flatfish on two small nursery grounds (Port Erin Bay, Isle of Man and Porto Pim Bay, Faial, Azores). *J. Fish. Biol.* 44: 35-45.

Naughton, S.P. & C.H. Saloman. Fishes of the nearshore zone of St. Andrew Bay, Florida, and adjacent coast. *NE Gulf Sci.* 2: 43-55.

Newell, R.C. 1979. *The Biology of Intertidal Animals*. Logos Press, London, 781 pp.

Odum, W.E. 1968. Mullet grazing on a dinoflagellate bloom. *Chesapeake Sci.* 9: 2020-204.

Oliver, J.S., P.N. Slatterly, L.W. Hulberg & J.W. Nybakken., 1980. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. *Fish. Bull.* 78: 437-454.

Orth, R.J. & K.L. Heck. 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay. *Estuaries* 3: 278-288.

Panikkar, N.K. 1960. Physiological aspects of adaptation to estuarine conditions. *Aust. Fish. Coun. Proc.* 32: 168-175.

Parish, B.B., J.H.S. Blaxter & W.B. Hall. 1964. Diurnal variations in the size and composition of trawl catches. Rap*p. P. -v. Réun. Cons. Int. Explor. Mer.* 155: 27-34.

Pearse, A.S., H.J. Humm & G.W. Wharton. 1942. Ecology of sandy beaches at Beaufort, NC. *Ecol. Monog.* 12: 135-190.

Penney, A. 1991. The interactions between net and line-fisheries in False Bay, South Africa. *Trans. Roy. Soc. S. Afr.* 47: 663-681.

Penney, A.J., C.D. Buxton, P.A. Garrat & M.J. Smale. 1989. The commercial marine linefishery. In: A.I.L. Payne & R.J.M. Crawford *Oceans of Life Off Southern Africa*. Vlaeberg, Cape Town, pp. 214-229.

Penrith, M.J. & R. Loutit. 1982. Coastal anglers' catches at Terrace Bay during 1980. *Madoqua* 13: 35-43.

Peters, D.J. & W.G. Nelson. 1987. The seasonality and spatial patterns of juvenile surf zone fishes of the Florida east coast. *Fla. Sci.* 50: 85-99.

Pickett, S.T.A. & P.W. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, 235 pp.

Pielou, E.C. 1969. The measurement of diversity in different types of biological collections. *J. Theoretical Biol.* 13: 131-144.

Pierce, C.L., J.B. Rasmussen & W.C. Leggett. 1990. Sampling littoral fish with a seine: corrections for variable capture efficiency. *Can. J. Fish. Aquat. Sci.* 47: 1004-1010.

Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. *Neth. J. Sea Res.* 15: 419-432.

Pihl, L. 1990. Year-class strenght regulation in plaice (Pleuronectes platessa L.) on the Swedish west coast. *Hydropbiol.* 195: 79-88.

Pihl, L. & H.W. van der Veer. 1992. Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L, in coastal nursery areas. *Neth. J. Sea Res.* 29: 145-152.

Pollard, D.A. 1976. Estuaries must be protected. *Aust. Fish.* 35: 6-10.

Pollard, D.A. 1984. A review of ecological studies on seagrass fish communities, with particular reference to recent studies in Australia. *Aquatic Bot.* 18: 3-42.

Ponomarenko, V.P. 1994. On the cod migrations to the inshore waters of Novaya Zemlya. *Oceanology* 34: 87-93.

Potter, I.C., L.E. Beckley, A.K. Whitfield & R.C.J. Lenanton. 1990. Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and southern Africa. *Env. Biol. Fishes* 28: 143-178.

Poxton, M.G. & N.A. Nasir. 1985. The distribution and population dynamics of 0-group plaice (*Pleuronectes platessa* L) on nursery grounds in the Firth of Forth. *Est. cstl Shelf Sci.* 21: 845-857.

Poxton, M.G., A. Eleftheriou & A.D. McIntyre. 1982. The population dynamics of 0-group flatfish on nursery grounds in the Clyde Sea area. *Est. cstl Shelf Sci.* 14: 265-282.

Poxton, M.G., A. Eleftheriou & A.D. McIntyre. 1983. The food and growth of 0-group flatfish on nursery grounds in the Clyde Sea area. *Estuar. cstl Shelf Sci.* 17: 319-337.

Pritchard, D.W. 1967. What is an estuary, physical viewpoint. In: G. Lauff (ed.), *Estuaries*. Am. Assoc. Adv. Sci., Washington.

Prochazka, K. 1996. Seasonal patterns in a temperate intertidal fish community on the west coast of South Africa. *Env. Biol. Fish.* 45: 133-140.

Prochazka, K. In press Spatial and trophic partitioning in cryptic fish communities of shallow subtidal reefs in False Bay, South Africa. *Env. Biol. Fish.*

Prochazka, K. & C.L. Griffiths. 1992. The intertidal fish fauna of the west coast of South Africa - species, community and biogeographic patterns *S. Afr. J. Zool.* 27: 115-120.

Quick, A.J.R. & B.A. Bennett. 1989. Preliminary investigation into the role of Zandvlei as an estuarine fish nursery. Report prepared for the Cape Town City Council by the Freshwater Research Unit, Zoology Department, University of Cape Town, 17 pp.

Quinn, N.J. & B.L. Kojis. 1981. The lack of changes in nocturnal estuarine fish assemblages between new and full moon phases in Serpentine Creek, Queensland. *Env. Biol. Fish.* 6: 213-218.

Raffaelli, D., H. Richner, R. Summers & S. Northcott. 1990. Tidal migration in the flounder (*Platichthys flesus*). *Mar. Behav. Physiol.* 16: 249-260.

Rapson, A.M. 1954. Feeding and control of toheroa (Gray)(Eulamellibranchiata) populations in New Zealand. *Aust. J. Mar. Freshw. Res.* 5: 486-512.

Ratte, T.W. 1977. Age and growth of the mullet *Liza richardsoni* (Smith) in the Berg River estuary. Cape Department of Nature and Environmental Conservation, Research Report 1978: 105-135.

Reina-Hervas, J.A. & P. Serrano. 1987. Structural and seasonal variations of inshore fish populations in Malaga Bay, southeastern Spain. *Mar. Biol.* 95: 501-508.

Reynolds, W.W. & D.A. Thompson. 1974. Response of young Gulf grunion, *Leuresthes sardina*, to gradients of temperature, light, turbulence and oxygen. *Copeia* 3: 746-758.

Riley, J.D. & J. Corlett. 1966. The numbers of O-group plaice in Port Erin Bay 1964-1966. *Rep. Mar. Biol. Sta. Port Erin* 78: 51-56.

Riley, J.D. & B.H. Holford. 1965. A sublittoral survey of Port Erin Bay, particularly as an environment for young plaice. *Rep. Mar. Biol. Stn Port Erin* 77: 49-53.

Robertson, A.I. & J.A. Hansen. 1982. Decomposing seaweed: a nuisance or a vital link in coastal food chains?: *CSIRO Marine Laboratories*, 1982.

Robertson, A.I. & R.C.J. Lenanton. 1984. Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. *J. Exp. Mar. Biol. Ecol.* 84: 265-283.

Rogers, S.I. 1992 Environmental factors affecting the distribution of sole (*Solea solea* (L.)) within a nursery area. *Neth. J. Sea Res.* 29: 153-161.

Romer, G.S. 1986. *Faunal Assemblages and Food Chains Associated with Surf Zone Phytoplankton Blooms.* Unpubl. MSc Thesis, University of Port Elizabeth, South Africa. 194 pp.

Romer, G.S. 1990. Surf zone fish community and species response to a wave energy gradient. *J. Fish Biol.* 36: 279-287.

Romer, G.S., & A. McLachlan. 1986. Mullet grazing on surf diatom accumulations. *J. Fish Biol.* 28: 93-104.

Ross, S.T. 1983. A review of surf-zone ichthyofaunas in the Gulf of Mexico. pp. 25-34. In: S.V. Shabica, N.B. Cofer & E.W. Cake, Jr. (eds.). Proceedings of the northern Gulf of Mexico estuaries and barrier islands research conference. US. Dept. Int. Nat. Park. Ser., Southeast Regional Office, Atlanta, GA.

Ross, S.T., R.H. McMichael. & D.L. Ruple. 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf-zone. *Est. Cstl Shelf Sci.* 25: 391-412.

Rossouw, G.J. 1983. The importance of non-teleost fishes (elasmobranchs) in the surf zone with special reference to *Rhinobatos annulatus.* In: A. McLachlan & T. Erasmus (eds.) *Sandy Beaches as Ecosystems,* Junk, The Hague. p. 749.

Rossouw, G.J. 1984. Age and growth of the sand shark, *Rhinobatos annulatus*, in Algoa Bay, South Africa. *J. Fish Biol.* 25: 213-222.

Rountree, R.A. & K.W. Able. 1993. Diel variation in decapod crustacean and fish assemblages in New Jersey polyhaline marsh creeks. *Estuar. cstl. Shelf Sci.* 37: 181-201.

Ruple, D.L. 1984. Occurrence of larval fishes in the surf zone of a northern Gulf of Mexico Barrier Island. *Estuar. cstl. Shelf Sci.* 18: 191-208.

Schaefer, R.H. 1967. Species composition, size and seasonal abundance of fish in the surf waters of Long Island. *N. Y. Fish Game J.* 14: 1-46.

Schelske, E.H. & E.P. Odum. 1961. Mechanisms maintaining high productivity in Georgia estuaries. *Proc. Gulf and Carib. Fish. Inst.* 14: 75-80.

Schoeman, S. 1978. *Strike! A Handbook of Angling in South African Coastal Waters*. A.A. Balkema, Cape Town, 338 pp.

Schulze, B.R. 1965. Climate of South Africa, Part 8, General Survey. Weather Bureau Publ. 28, Pretoria.

Scott, K.M.F., A.D. Harrison, & W. Macnae. 1952. The ecology of South African estuaries. *Trans. Roy. Soc. S. Afr.* 33: 283-331.

Senta, T. & I. Kinoshita. 1985. Larval and juvenile fishes occuring in surf zones of western Japan. *Trans. Am. Fish. Soc.* 114: 609-618.

Shannon, L.V. 1966. Hydrology of the south and west coasts of South Africa. *Investl Rep. Sea Fish. Res. Inst. S. Afr.* 58: 1-62.

Shannon, L.V., H.F.-K.O. Hennig, F.A. Shillington, A. Bartels & D.H. Swart. 1991. Colour fronts in False Bay: origin, development and implications. *Trans. Roy. Soc. S. Afr.* 47: 447-469.

Shannon, L.V. & G.H. Stander. 1977. Physical and chemical characteristics of water in Saldanha Bay and Langebaan Lagoon. *Trans. Roy. Soc. S. Afr.* 42: 441-459.

Shannon, L.V., Stander G.H. & Cambell J.A. 1973. Oceanic circulation deduced from plastic drift cards. *Div. Sea Fish. S. Afr. Investl Rep.* 108.

Shulze, B.R. 1965. Climate of South Africa. Part 8. General Survey. Pretoria. *Weather Bureau Publ.* 28.

Simpson, E.H. 1949. Measurement of diversity. *Nature* 163: 688.

Slinger, J.H. & S. Taljaart. 1994. Preliminary investigation of seasonality in the Great Berg estuary. *Water SA* 20: 270-288.

Sloff, D.S., A. McLachlan & G.C. Bate. 1984. Spatial distribution and diel periodicity of *Anaulis biostratus* Grunow in the surf zone of a sandy beach in Algoa Bay, South Africa. *Bot. Mar.* 27: 461-465.

Smale, M.J. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 3. The occurrence and feeding of *Argyrosomus hololepidotus* , *Pomatomus saltatrix* and *Merluccius capensis*. *S. Afr. J. Zool.* 19: 170-179.

Smale, M.J. & A. Badenhorst. 1991. The distribution and abundance of secondary trawl fish on the Cape south coast of South Africa, 1986-1990. *S. Afr. J. mar. Sci.* 11: 395-407.

Smale, M.J. & Bruton, M.N. 1985. Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in south-eastern Cape waters of South Africa. *S. Afr. J. Zool.* 20: 97-108.

Smale, M.J., & H.M. Kok. 1983. The occurrence and feeding of *Pomatomus saltatrix* (elf) and *Lichia amia* (leervis) juveniles in two Cape south coast estuaries *S. Afr. J. Zool.* 18: 337-342.

Smidt, E.L.B. 1951. Animal production in the Danish Wadden Sea. *Medd. Komm. Dan. Fisk. Havunders. Ser. Fisk.* 11: 1-51.

Smith, M. & Heemstra, P.C. (eds.). 1991. *Smiths' Sea Fishes*. 1st Edition. Southern Book Publishers, Johannesburg, 1048 pp., 144 pls.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225-1239.

Spargo, P.E. 1991. False Bay South Africa - an historic and scientific overview. *Trans. Roy. Soc. S. Afr.* 47: 363-375.

Springer, V.G. & K.D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. *Fla. St. Bd. Cons. Mar. Lab. Proc. Paper. Serial.* 1.

Swenson, W.A. 1978. Influence of turbidity on fish abundance in western Lake Superior. *Research Report of the U.S. Environmental Protection Agency, Duluth, 22 pp.*.

Taggart, C.T. & K.T. Frank. 1987. Coastal upwelling and *Oikopleura* occurrence ("Slub"): a model and potential application to inshore fisheries. *Can. J. Fish. Aquat. Sci.* 44: 1729-1736.

Taggart, C.T. & W.C. Leggett. 1987. Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time-series analysis of physical--biological data. *Can. J. Fish. Aquat. Sci.* 44: 438-451.

Talbot, F.H. 1955. Notes on the biology of the white stumpnose, *Rhabdosargus globiceps* (Cuvier), and on the fish fauna of the Klein River estuary. *Trans. Roy. Soc. S. Afr.* 34: 387-407.

Talbot, M.M.B., G.C. Bate & E.E. Cambell. 1990. A review of the ecology of surf-zone diatoms, with special reference to *Anaulis australis*. *Oceanogr. Mar. Biol. Ann. Rev.* 26: 155-175.

Talbot, F.H. & Penrith, M.J. 1962. Tunnies and marlins of South Africa. *Nature* 193: 558-559.

Tallmark B & S. Evans. 1986. Substrate-related differences in antipredator behaviour in two gobiid fish species and the brown shrimp, and their adaptive value. *Mar. Ecol. Prog. Ser.* 29: 217-222.

Taljaard, S. 1991. The origin and distribution of dissolved nutrients in False Bay. Trans. Roy. Soc. S. Afr. 483-493.

Tanda, M. 1990. Studies on burying ability in sand and selection to the grain size for hatchery-reared marbled sole and Japanese flounder. *Nippon Suisan Gakkaishi* 56: 1543-1548.

Taylor, P.R. & M.M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. *Ecology* 63: 135-146.

Termorshuizen, L.D. & Whitfield, A.K. 1994. The distribution of littoral fish associated with eelgrass *Zostera capensis* beds in the Kariega estuary, a southern African estuarine system with a reversed salinity gradient. *S. Afr. J. mar. Sci.* 14: 95-105.

Thijssen, R., A.J. Lever & J. Lever. Food composition and feeding periodicity of o-group plaice (*Pleuronectes platessa*) in the tidal area of a sandy beach. *Neth. J. Sea Res.* 8: 369-377.

Thompson, J.M. 1951. Growth and habits of the sea mullet, *Mugil dobula* Gunther , in Western Australia. *Austr. J. mar. Freshw. Res.* 2: 193-225.

Thompson, J.M. 1963. Synopsis of biological data on the grey mullet *Mugil cephalus* Linn., 1978. *Commonw. Sci. Ind. Res. Org.* , Melbourne, Australia.

Thompson, J.M. 1966. The grey mullets. *Oceanogr. Mar. Biol. Assoc. Rev.* 4: 301-335.

Thompson, W.W. 1913. *The Sea Fisheries of the Cape Colony, From Van Riebeeck's Days to the Eve of the Union.* Maskew Miller, Cape Town, 163 pp.

Toole, C.L. 1980. Intertidal recruitment and feeding in relation to optimal utilisation of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). *Env. Biol. Fish.* 5: 383-390.

Tyler, A.V. 1971. Surges of winter flounder, *Pseudopleuronectes americanus*, into the intertidal zone. *J. Fish. Res. Bd. Can.* 28: 1727-1732.

van der Elst, R. 1976. Game fish of the east coast of southern Africa. I. The biology of the elf, *Pomatomus saltatrix* (Linnaeus), in the coastal waters of Natal. *Investl. Rep. Oceanogr. Res. Inst. S. Afr.* 44: 59 pp.

van der Elst, R.P. 1988 *A Guide to the Common Sea Fishes of Southern Africa.* Struik, Cape Town, 398 pp.

van der Horst, G. & T. Erasmus. 1978. The breeding cycle of male *Liza dumerili* (Teleostei: Mugilidae) in the mouth of the Swartkops estuary. *Zool. Afr.* 13: 259-273.

van der Horst, G. & T. Erasmus. 1981. Spawning time and spawning grounds of mullet with special reference to *Liza dumerili* (Steindachner, 1869). *S. Afr. J. Sci.* 77: 73-77.

van der Lingen, C.D. 1994. Aspects of the early life history of the galjoen *Dichistius capensis. S. Afr. J. mar. Sci.* 14: 37-46.

van der Merwe, D. & A. McLachlan. 1987. Significance of free-floating macrophytes in the ecology of a sandy beach surf zone. *Mar. Ecol. Prog. Ser.* 38: 53-63.

van der Veer, H.W. & M.J.N. Bergman. 1986. Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* 31: 121-129.

van Der Veer, H.W. & M.J.N. Bergman. 1987. Predation by crustaceans on a newly settled O-group plaice Pleuronectes platessa population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* 35: 203-215.

van der Veer, H.W., M.J.N. Bergman, R. Dapper & J.I.J. Whitte. 1991. Population dynamics of an 0-group flounder *Platichthyes flesus* population in the western Wadden Sea. *Mar. Ecol. Prog. Ser.* 73: 141-148.

Wallace, J.H. 1967a. The batoid fishes of the east coast of southern Africa. Part I: sawfishes and guitar fishes. *Invest. Rep. oceanogr. Res. Inst. S. Afr.* 15: 1-32.

Wallace, J.H. 1967b. The batoid fishes of the east coast of southern Africa. Part II: Manta, eagle, duckbill, cownose, butterfly and stingrays. *Invesl Rep. oceanogr. Res. Inst. S. Afr.* 16: 1-56.

Wallace, J.H. 1975. The estuarine fishes of the east coast of South Africa. I. Species composition and length distribution in the estuarine and marine environments. II: Seasonal abundance and migrations. *Investl Rep. oceanogr. Res. Inst. S. Afr.* 40: 1-72.

Wallace, J.H. 1975. The estuarine fishes of the east coast of South Africa. III. Reproduction. *Invest. Rep. oceanogr. Res. Inst. S. Afr* 41: 51 pp.

Wallace, J.H., H.M. Kok & L.E. Beckley. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 2. Occurrence of estuarine-associated fishes. *S. Afr. J. Zool* 19: 165-169.

Wallace, J.H., H.M. Kok, L.E. Beckley, B.A. Bennett, S.J.M. Blaber & A.K. Whitfield. 1984. South African estuaries and their importance to fishes. *S. Afr. J. Sci.* 80: 203-207.

Wallace, J.H., H.M. Kok, C.D. Buxton & B.A. Bennett. 1984. Inshore small-mesh trawling survey on the Cape south coast. Part 1. Introduction, methods, stations and catches. *S. Afr. J. Zool.* 19: 154-164.

Wallace, J.H. & R.P. van der Elst. 1975. The estuarine fishes of the east coast of South Africa. IV. Occurrence of juveniles in estuaries. V. Ecology, estuarine dependence and stautus. *Investl. Rep. oceanogr. Res. Inst. S. Afr.* 42: 63 pp.

Wallett, T. 1978 *Shark Attack and Treatment of Victims in Southern African Waters*. Purnell, Cape Town, 176 pp.

Walsh, S.J. 1988. Diel variability in trawl catches of juvenile and adult yellowtail flounder on the Grand Banks and the effect on resource assessment. *N. Am. J. Fish. Manage.* 8: 373-381.

Warfel, H.E. & D. Merriman. 1944. Studies on the marine resources of southern New England. 1. An analysis of the fish populations of the shore zone. *Bull. Bingham Oceanogr. Coll.* 9: 1-91.

Weather Bureau. 1965. *Climate of South Africa. Part 8. General Survey.* W.B. 28. Goverment Printer, Pretoria.

Weather Bureau. 1972 *Report on the Meterological Data of the Year 1970*. Government Printer, Pretoria.

Wells, B., Steele, D.H. & Tyler, A.V. 1973. Intertidal feeding of winter flounders (Pseudopleuronectes americanus) in the Bay of Fundy. *Fish. Res. Bd. Can.* 30: 1374-1378.

Weng HT (1990) Fish in shallow areas in Moreton Bay, Queensland and factors affecting their distribution. *Est cstl Shelf Sci* 30: 569-578.

Wennhage, H. & Pihl, L. 1994 Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous macroalgae. *Neth. J. Sea Res.* 32: 343-351.

Whibley, I. & P. Garrat. 1989. *The South African Fisherman*. Struik Timmins, Cape Town, 220 pp.

Whitfield, A.K. 1989. Ichthyoplankton in a southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? *Est. cstl Shelf Sci.* 29: 533-547.

Whitfield, A.K. 1990. Life history styles of fishes in South African estuaries. *Env. Biol. Fish.* 28: 295-308.

Whitfield, A.K. 1994. Fish species diversity in southern African estuarine systems: an evolutionary perspective. *Env. Biol. Fish.* 40: 37-48.

Whitfield, A.K. & S.J.M. Blaber. 1978. Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. *J. Fish Biol.* 13: 675-691.

Whitfield, A.K., S.J.M. Blaber & D.P. Cyrus. 1981. Salinity ranges of some southern African fish species occurring in estuaries. *S. Afr. J. Zool.* 16: 151-155.

Whitfield, A.K. & H.M. Kok. 1992. Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.* 57: 1-39.

Wilkinson, L. 1990. SYSTAT: The system for statistical evaluation. IL: SYSTAT, Inc.

Winter, D.F. 1983. A theoretical model of surf zone circulation and diatom growth. In: A. McLachlan & T. Erasmus (eds.) *Sandy Beaches as Ecosystems.* Junk, The Hague, pp. 157-167.

Winter, P.E.D. 1979. *Studies on the distribution, seasonal abundance and diversity of the Swartkops estuary ichthyofauna.* Unpubl. M.Sc. Thesis, University of Port Elizabeth, Port Elizabeth, 132 pp.

Woodwell, G.M., P.H. Rich & C.A.S. Hall. 1973. Carbon in estuaries. In: G.M. Woodwell & E.V. Pecan (eds.) *Carbon and the Biosphere*, Vol. 25. Brookhaven Symp. Biol. (AEC-CONF-720510), pp. 221-240.

Wooldridge, T.H. 1983. Ecology of beach and surf-zone mysid shrimps in the eastern Cape, South Africa.. In: A. McLachlan & T. Erasmus (eds.). *Sandy Beaches as Ecosystems.* Junk, The Hague, pp. 449-460

Wright, J.M. 1988. Recruitment patterns and trophic relationships of fish in Sulaibikhat Bay, Kuwait. *J. Fish Biol.* 33: 671-687.

Wright, J.M. 1989a. Diel variation and seasonal consistency in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. *Mar. Biol.* 102: 135-142.

Wright, J.M. 1989b. Detached chlorophytes as nursery areas for fish in Sulaibikhat Bay, Kuwait. *Est. cstl Shelf Sci.* 28: 185-193.

Zar, J.H. 1984 *Biostatistical Analysis.* Prentice Hall, Englewood Cliffs, N.J., 718 pp.

Ziljstra, J.J. 1972. On the importance of the Wadden Sea as a nursery area in relation to the conservation of the southern North Sea fishery resources. *Symp. zool. Soc. Lond.* 29: 233-258.

Ziljstra, J.J. & J.I.J. Whitte. 1985. On the recruitment of O-group plaice in the North Sea. *Neth. J. Sea Res.* 15: 250-272.

Ziljstra, J.J., R. Dapper & J.I.J. Whitte. 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. *Neth. J. Sea Res.* 15: 250-272.

Zobell, C.E. 1971. Drift seaweeds on San Diego county beaches. In: W.J. North (ed.*) The Biology of Giant Kelp Beds (*Macrocystis*) in California. Nova Hedwigia* 32 (Suppl): 269-314.

Zoutendyk, P. 1982. Agulhas Bank studies. Report No. 9. A diving survey of two reefs in Plettenberg Bay. NRIO Memorandum 8233, Stellenbosch, South Africa. 9 pp.

*I must go down to the*
*seas again, for the call of*
*the running tide,*
*Is a wild call and a clear*
*call that may not be*
*denied*

"Sea-Fever"
John Mansfield

*Pomatomus saltatrix*, *Gilchristella aestuaria*, *Sarpa salpa*, *Heteromycterus capensis* and *Caffrogobius nudiceps*) provided substantial contributions on occasion, while the remaining species were generally recorded infrequently. Important families in this area thus include the Atherinidae, Mugilidae, Sparidae, Gobiidae, Clupeidae, Pomatomidae and Soleidae. Other South African studies (e.g. Lasiak 1984a, b, Romer 1986, Romer 1990) indicate a high degree of uniformity among surf fish assemblages. They also highlighted the importance of the Atherinidae, Sparidae, Carangidae and Mugilidae as dominant families, as well as the Haemulidae and Scianidae. Studies conducted abroad have highlighted the importance of the Pleuronectidae (European beaches - Edwards & Steele 1968, Ziljstra 1982, Gibson 1973a, Poxton *et al.* 1982), the Engraulidae, Clupeidae, Carangidae and Scianidae (Gulf of Mexico - McFarland 1963, Gunter 1958, Modde & Ross 1981, Ross *et al.* 1987) and the Atherinidae, Clupeidae, Terapontidae, Sillaginidae and Mugilidae (Western Australia - Lenanton 1982, Lenanton *et al.* 1982, Robertson & Lenanton 1984). All collections made as part of this study were completed with a small, relatively fine meshed beach seine net, and are thus likely to have been biased somewhat toward smaller individuals and species. Comparisons with collections made using larger, coarser meshed nets, however, indicates that this was not really the case. The study of Lamberth *et al.* (1994) on commercial beach seine net catches in False Bay highlighted *Liza richardsonii* as being by far the most numerous species (87% of the total), while *P. saltatrix*, *Trachurus trachurus*, *R. globiceps* and *S. salpa* were the only other species contributing more than 1% of the total. The only additional family of importance not highlighted during the course of this study, were the Carangidae therefore.

Numerical contributions by elasmobranch fishes to surf-zone fish abundance is typically low, with contributions to catches in this study (typically <1%) being similar to seine net studies conducted locally (Lasiak 1984a, Romer 1986, Bennett 1989, Clark *et al.* 1994a, 1995a) and abroad (Gunter 1958, Modde & Ross 1981, Robertson & Lenanton 1984, Ross *et al.* 1987, Gibson *et al.* 1993). Elasmobranch contributions to total biomass, however, is usually considerably higher, often providing over 50% of the total catch (Chapter 2,4, Lasiak 1982, 1984a, Romer 1986, Ross *et al.* 1987).