MIGRATIONS OF SPINY ROCK-LOBSTERS, *JASUS LALANDII*, AT LUDERITZ: ENVIRONMENTAL CAUSES, AND EFFECTS ON THE FISHERY AND BENTHIC ECOLOGY.

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ABSTRACT

A dispute arose in the Luderitz rock-lobster, Jasus lalandii, fishery as to whether declines in CPUE were due to changes in rock-lobster migration patterns or a reduction in fishable biomass. Rock-lobster migrations were studied at two sites by estimating *in situ* density in the 10-12m and 15-20m depth zones. Water temperature and dissolved oxygen concentration profiles were obtained at several sites at approximately monthly intervals. Observations over a period of six years indicated that rock-lobster underwent seasonal in- offshore migrations and that marked interannual variation in those migration patterns did, indeed, occur. The movements and their interannual variation were directly related to the inshore presence of water with very low dissolved oxygen concentrations. CPUE was closely related to the density of legal sized rock-lobster on the fishing grounds (observed by SCUBA diving) and hence it is feasible that at least a part of the decline in CPUE at Luderitz was due to an alteration in the "normal" pattern of in-offshore migration.

The hypothesis that environmental change caused the major decline in rock-lobster catches at Luderitz was examined by time series analysis of 21 years of CPUE, wind, SST and sea-level data. Luderitz rock-lobster CPUE was found to be negatively correlated with the southerly component of summer wind stress at Diaz Point six years previously. On this basis it was hypothesised that variable settlement of puerulus larvae is an important factor driving changes in recruitment to the fishable population. The mechanism may be increased mortality of larvae as they attempt to cross the continental shelf (due to greater northward and offshore drift during periods of strong southerly wind).

The dramatic interannual changes in rock-lobster density provided an opportunity to carry out a "natural" experiment on the interaction between rock-lobsters and the associated benthic species assemblage. It was found that, although there were changes in the benthos (notably an increase and subsequent decline in whelk density), these were unrelated to variation in rock-lobster density. In addition, no relationship between *per capita* food availability and rock-lobster growth on four grounds, was apparent. As regards temporal changes in food supply and subsequent effects on rock-lobster growth rates; there was no temporal reduction in food supply at the main study site which could be related to the reduction in CPUE since 1988.

1. GENERAL INTRODUCTION

The West coast spiny rock-lobster, Jasus lalandii, supports a valuable fishery along the Southern African west coast which is of particular socio-economic importance to the Namibian town of Luderitz. J. lalandii is associated with rocky reefs along the Southern African west coast and it's biology has been thoroughly studied for many years (Gilchrist 1913 and 1918; Von Bonde and Marchand 1935; Von Bonde 1936; Paterson 1968; Heydorn 1965 and 1969; Silberbauer 1971a and 1971b; Pollock 1986). Its growth rate is slow (Pollock and Beyers 1981), and females have a relatively late age-at-maturity of between six and eight years and produce a large number of eggs (Beyers and Goosen 1987). These three factors vary along the distribution range, are interrelated (Beyers and Goosen 1987), and can display marked interannual variation (Shannon et al. 1992). The planktonic larval life may extend for at least a year and involves a trip around the entire southern Atlantic (Pollock 1986 and 1990) with associated very high larval mortality. Rock-lobsters exceeding a carapace length of about 30mm carapace length have a low natural mortality rate which (in the absence of fishing) results in very high adult densities, a size distribution skewed towards larger animals, and a considerable maximum age (Johnston 1991).

The behaviour of rock-lobster in the wild has been somewhat less well described. Their strong mandibles enable them to eat most of the abundant shellfish found on the West coast and they have been considered a major force structuring the species composition and size structure of the benthos of West coast reefs (Branch et al. 1987). One aspect of feeding that has been exhaustively studied is how mussel availability to J. lalandii depends on the size of both the mussel and the rock-lobster (Pollock 1979; Griffiths and Seiderer 1980).

It is generally thought that rock-lobster remain resident in particular areas once they reach about 30 mm carapace length. This raises the possibility that the species and size composition of the benthos will reflect the density of rock-lobsters present in a given area. An extremely marked example is the existence of two alternative stable states of the benthic community at two islands in Saldanha Bay (Barkai and Branch 1988a). These states have been demonstrated to be due to due to marked differences in rock-lobster density (Barkai and Branch 1988c; Barkai and McQuaid 1988). The generality of this scenario is challenged in this thesis and an alternative hypothesis proposed that, considering West coast reefs as a whole, benthic communities and rock-lobsters operate at different spatial scales and hence, except in a very broad sense, are independent (section 4).

The early fishery at Luderitz started at the turn of the century, but only since the 1950's have reasonably reliable catch data been available (summarised in Table 1.1).

TABLE 1.1. Estimated catch, minimum size limit (carapace length) and Total Allowable Catch (TAC) for the Luderitz rock-lobster fishery. Export refers to the fact that the TAC was enforced for exported products only and not on total landed mass. When area-based TACs were allocated they are given in brackets.

YEAR	ESTIMATED CATCH (kg)	SIZE LIMIT (mm)	T.A.C. (tonnes)
1949	9 113 676	82.6	5 448 (export)
1950	6 118 238	76.2	5 448 (export)
1951	6 700 996	63.5	5 448 (export)
1952	14 065 712	63.5	5 448 (export)
1953	10 989 018	76.2	5 448 (export)
1954	9 081 065	76.2	5 448 (export)
1955	9 188 561	76.2	5 448 (export)
1956	6 388 184	76.2	5 448 (export)
1957	7 650 861	76.2	5 448 (export)
1958	4 035 658	76.2	5 448 (export)
1959	5 230 440	76.2	5 448 (export)
1960	3 840 342	76.2	5 448 (export)
1961	5 770 393	76.2	5 448 (export)
1962	7 249 694	76.2	5 448 (export)
1963	7 276 889	76.2	5 448 (export)
1964	7 608 520	69.8	7 426.4
1965	7 999 981	69.8	7 426.4
1966	8 873 764	69.8	7 426.4
1967	5 342 672	69.8	7 426.4
1968	8 815 324	0	7 426.4
1969	6 901 918	0	7 426.4
1970	3 604 272	63.5	7 426.4
1971	2 299 422	63.5	4 082.4
1972	2 724 534	63.5	4 082.4
1973	2 825 889	63.5	4 082.4
1974	2 955 113	63.5	4 082.4
1975	1 741 432	63.5	4 082.4
1976	1 506 004	63.5	4 082.4
1977	1 803 503	63.5	4 082.4
1978	1 109 724	63.5	4 082.4
1979	1 690 770	63.5	2 100
1980	1 372 849	63.5	2 100
1981	1 198 100	65.0	2 100
1982	1 338 900	65.0	2 100
1983	1 749 719	65.0	2 100
1984	1 865 274	65.0	2 100
1985	1 819 843	65.0	2 100
1986	1 768 860	65.0	2 100
1987	1 222 761	65.0	2 100
1988	1 776 952	65.0	2 000 (600 far north)
1989	1 063 459	65.0	2 000 (600 far north)
1990	589 003	65.0	1 800 (500 south, 600 central, 200 north, 500 far north)
1991	328 983	65.0	1 704 (500 south, 504 central, 200 north, 500 far north)

Mathews (1962) and Mathews and Smit (1979) described the variation along the length of the coast in catch per unit effort (CPUE, in units of kg per trap per day), the moulting and reproductive cycles, and produced size distributions from research fishing and the fishery landings. Interestingly, Mathews (1962) was the first person to suggest that rock-lobsters could be undergoing seasonal onshore-offshore migrations in the area. The fishery grew rapidly in the 1950's and 60's as more licenses were granted. There was continual pressure from the industry to reduce the minimum size limit as catches declined. This was acceded to, and size limits were reduced from 82.6mm in 1949 to 69.8mm in 1964 (Table 1.1). Mathews and Smit (1979) warned of overfishing on the basis of decreasing mean sizes but were unable to estimate sustainable yields. An inevitable crash occurred in the 1967 as the accumulated stock was "mined" out. Dreosti (1966) argued that there was strong competition among undersize rock-lobster and that therefore the size limit should be dropped completely. This suggestion was carried out during 1968 and 1969 with an initial (predictable) increase in landings but was followed by another dramatic decline. In 1970, the effort was cut dramatically and a minimum size limit reintroduced. At this time as well, a detailed record of area based catch, effort and size distribution was started and has now been running for 22 years (Beyers and Wilke 1990; Tomalin unpubl.).

Beyers and Wilke (in press) used tagging to estimate population sizes, fishing mortality rates (F) and growth rates for most of the important areas in Namibia. Using a yield per recruit model, Beyers and Wilke (in press) concluded that a minimum size of 65 mm carapace length and an annual F of 0.3 was optimal. They (Beyers and Wilke in press) applied this F to the population size for each area and so determined area-based TACs. The sum of these TACs was 2200 tons which was imposed as a global TAC from 1979 until 1987. Although global TACs were not exceeded, calculated TACs for certain individual areas were overrun almost every year whilst other areas with a high TAC were hardly fished at all.

Blankley (1987) followed Beyers and Wilke's (in press) methods very closely (determining population size from tagging and then setting the next season's TAC at F=0.3) and introduced an area-based TAC for the 1987/88 season which was exceeded (for the area south of Mercury island). Tomalin (1988, 1989, 1990 and 1991) attempted to use other fisheries models which resulted in area-based TACs being generally reduced. Catches and CPUE dropped dramatically after 1988, in synchrony with similar declines in the Cape (see section three) and this prompted the Namibian fisheries management authorities to impose a very low TAC of 100 tonnes in 1991/92. The economic loss was compensated for by re-allocating the hake TAC from foreign trawl fleets to Namibian interests.

A recent major advance in stock assessment and management of Jasus lalandii in South Africa has been the use of a size-based matrix progression model (Bergh and Johnston 1992), but this approach has yet to be applied to the Namibian situation.

The work reported in this thesis arose out of a conflict with fishermen over the interpretation of CPUE figures: they maintained reduced CPUE was due to a change in the normal migration pattern of rock-lobsters, whereas the managers considered that CPUE declines were due to a declining stock size. Rock-lobster processors and Cape scientists have asserted that the weather (strong winds) "protected" the Luderitz rock-lobster and was responsible for the catches being lower than the global TAC (Minutes of Fisheries Advisory board meetings 1981 to 1985) i.e. catchability of Namibian rock-lobster was lower than that elsewhere. This hypothesis has never been tested. There is, in fact, a negative relationship between wind (and swell) and CPUE within a season (Tomalin unpubl.). In order to address this conflict, I documented migration patterns, their relationship to the environment and changes in CPUE over a period of six years.

Luderitz is positioned at the centre of the largest upwelling cell on the west coast (Shannon 1985). Some of the consequences are:

1. nutrient content is high and therefore during quiescent conditions, phytoplankton production can be very high (Chapman and Shannon 1985). However, in general, due to the strong southerly winds, maximum productivity is to the north of Luderitz.

2. This production cannot be totally consumed by planktonic and fish grazers (Shannon and Pillar 1986) and much of it sinks to the sea-floor where large areas of diatomaceous and often anoxic muds form between 18° S and 25° S (Bremner 1979 and 1983).

3. A bottom counter current has been proposed which causes a "tongue" of water of low oxygen content to extend southwards along the shelf (DeDecker 1970; Bailey et al. 1985) often lying just offshore of the Luderitz rock-lobster reefs.

Bailey et al. (1985) investigated the effect of this low oxygen water found off the reefs on the distribution of rock-lobster in summer and found that "crowding" occurred in the shallows, and proposed that the decline in CPUE since 1975 was due to an increase in the extent of low oxygen water. These observations, together with the fact that growth rates and size of maturity are lower at Luderitz than in the southern Cape (Beyers and Goosen 1987; Pollock and Beyers 1981), was the origin of the idea that the environment was limiting surplus production in the Namibian stock. Pollock and Shannon (1987) generalised the hypothesis to explain reductions in Northern Cape (Namaqualand) catches as well, and stated that increased volumes of low oxygen water were responsible for the simultaneous decline in catches in these two areas. They also speculated that the prime reason for the increase in volumes of low oxygen water was the collapse of pelagic fish stocks (in the late 1960's) which would previously have consumed a large proportion of the phytoplankton production. In other words, a second hypothesis for the inability of the Namibian fishery to support an apparently reasonable TAC was that although a large population was present, the productivity of this population was lower than populations elsewhere due to low dissolved oxygen conditions. This hypothesis is also essentially untested. It is hypothesised in section 2 that short-term (seasonal) onshore and offshore movements are the behavioural mechanism explaining any relationship between annual catch rates and long-term environmental changes. Hence migrations and their relationship to the environment allowed specific hypotheses relating long-term environmental indices and CPUE to be posed and tested in section three.

An obvious third hypothesis to explain the low catches at Luderitz is that the tag-return method overestimated stock size, and/or the yield-per-recruit model used to determine optimal fishing mortality was inappropriate, and/or the global TAC was not caught simply due to the fact that all the areas were not fished at the same intensity. Hence the decline in catches was primarily due to fishing (and it's spatial distribution) *per se* (Tomalin 1991 and 1992). This has been demonstrated for Namaqualand

(Barkai and Bergh 1990), but detailed examination of this hypothesis for the Namibian situation is beyond the scope of this thesis.

THESIS OUTLINE:

Section two tests the hypothesis that inter-annual changes in migration patterns occurred and were responsible for variations in CPUE. Inshore-offshore movements of Jasus lalandii over six years are documented, as well as correlations with measured environmental factors and CPUE of the fishery. Longer term trends in CPUE, and whether these could be related to the environment in any way, are examined in section three, thus partially testing the hypothesis that environmental change is driving the productivity of the Namibian rock-lobster population. Section four documents changes in benthos with time and examines whether these were related to rock-lobster density and, conversely, the possible influence of the benthos on rock-lobster growth and survival is discussed. The generality of several hypotheses relating rock-lobsters and the associated benthos are questioned.

The data collection phase became a long-term exercise due to the unexpected degree of interannual variation which was observed. It is of note that if observations had not extended through to 1992, some conclusions in sections two and four would have been completely different. In addition, this exercise became of more than academic interest when catch rates declined dramatically from 1989 onwards causing considerable conflict in the management of the fishery.

Where existing generalisations are questioned in this thesis, this should not be seen in a negative light but rather as an attempt to embrace the variability (and uncertainty) inherent in any biological system or species (Brown 1993). As Gould (1980) writes, "organisms are not billiard balls propelled by simple, measurable forces to predictable new positions on life's pool table" and according to Brown (1993), "At the ecological or ecophysiological level, virtually no statements implying universality can be expected." I have, however, attempted to be rigorous in describing that variability (Brown 1993).

2. ROCK-LOBSTER MIGRATIONS AT LUDERITZ: ENVIRONMENTAL CAUSES AND EFFECTS ON THE FISHERY.

2.1. INTRODUCTION:

Monthly and annual changes in CPUE are of profound importance to the rock-lobster fishery affecting both profitability and management of the resource. When CPUE values fluctuated dramatically between 1986 and 1991, fishermen maintained that these changes were caused mostly by varying migration patterns (W.Ghuring, Seaflower Lobster Corp.) whereas a conservative management explanation suggested that they were due to changes in the size of the legal stock. The former explanation would require no reduction in TAC as the following year might result in a normal migration, whereas the latter explanation would require a reduced TAC in order to prevent further declines of the stock size and to preserve breeding females. In addition, it had been argued for many years by both fishermen and scientists (Namibian Fisheries Advisory Board minutes 1982 to 1986) that catchability of Luderitz rock-lobster was low due to bad weather conditions i.e. the animals were present but were not entering traps, which explained why the calculated global TAC was not caught.

Rock-lobster depth distribution and the effect of the environment thereon (particularly low dissolved oxygen concentration) has been discussed by Bailey et al. (1985). Although previous authors considered that Luderitz rock-lobsters were confined to water shallower than 12m (Pollock and Beyers 1981), fishermen's observations, preliminary diving surveys at Luderitz (by the author during 1987), and research trapping for tagging purposes during the closed season all suggested that rock-lobsters migrated offshore in winter (at least to 60m) and inshore in summer. Obviously, these migrations would have a major effect on the fishery through density on the fishing ground: if rock-lobsters were massed inshore, density and CPUE would be high, whereas if they were spread offshore, density and CPUE would be low. Observations linking migrations, density and CPUE were necessary in order to resolve some of the above conflicts.

In addition, migrations could be the key to understanding the effect of environmental changes on rock-lobster population dynamics and catchability. The effect of the environment (specifically the extent of water low in dissolved oxygen) would influence migrations in the short-term (days to weeks) and, possibly, growth, survival and recruitment to the fishery in the long-term (the following year). Migrations then became the initial focus of the present study. The primary question to be addressed was, "how do changes in the environment affect the movements and density of rock-lobster at Luderitz and what effect do these migrations have on CPUE ?"

2.2. Review of lobster movements and the effect of the environment.

Knowledge of the movements of Nephropidae is confined mostly to Homarus americanus. The inshore (5-60m) population of Homarus americanus undertakes irregular small-scale offshore movements from 5-20m to 30-60m during storms (Cooper and Uzmann 1980). Ennis (1984), using diving methods similar to this study, documented small-scale seasonal movements with a mean depth of 14 m in winter and 9.5 m in summer, which were related to the breakdown of the thermocline in winter. Campbell (1986) also demonstrated seasonal movements of ovigerous females between shallow water (<20m) in summer and deep water (>200m) in winter, which apparently maximises the degree days experienced by the females and so reduces hatching time.

Baden et al. (1990) have reported Nephrops norvegicus moving inshore, from more than 24m to less than 8m water depth, in response to very low oxygen concentrations (less than 2ml/l) in the southern Kattegat between Denmark and Sweden (Baden et al. 1990). A scyllaridaen slipper lobster, Scyllarides latus, displayed high densities in spring and low densities in summer on an artificial reef in the eastern Mediterranean, presumably related to high summer temperatures in shallow water and a resultant migration of the whole population to deeper, cooler water (Spanier et al. 1988).

Several species of panulirid spiny rock-lobster exhibit seasonal migrations. In the Gulf of Mexico, Panulirus argus displays very marked mass migrations in autumn and reproductive movements in spring (summarised in Herrnkind 1980). Females move inshore in spring to mate and offshore in summer to incubate eggs and release larvae. Mass offshore migrations are apparently in response to the sudden drop in temperature caused by the first cold front of the season (Herrnkind 1980). Panulirus cygnus from western Australia exhibits a very marked offshore movement of pre-adults (Phillips 1983) and limited seasonal inshore movements of adults in winter for mating purposes, although adult movements are mostly local (Phillips et al. 1980). Panulirus ornatus which have just matured undertake a mass movement in spring from Torres Strait to the Gulf of Papua New Guinea where they spawn (Moore and MacFairlane 1984) followed by a very high mortality of adults (Dennis et al. 1992). Remaining adults stay in the Gulf, but juveniles apparently return to Torres Strait (Bell et al. 1987). In contrast, Panulirus homarus on the east coast of South Africa does not appear to undergo marked seasonal migrations, but small-scale movements on and off local reefs have been attributed to sand deposition and scouring which affects the availability of shelters (Smale 1978). Berry (1973) considered that Palinurus delagoae (which occurs in water of 180 - 320m on the east coast of South Africa) undertakes local movements related to depth which may be linked to reproduction and the onset of maturity. Juveniles are found deeper than mature individuals and dense aggregations of egg-bearing females occur in shallower water at the edge of the shelf.

Studies on other Jasus species include Jasus verreauxi in Northern New Zealand where Booth (1979) documented large-scale longshore movements of juveniles recruiting to adult populations. Annala (1983) considered that in New Zealand, Jasus edwardsii has populations which consist of migratory and non-migratory individuals. Migratory individuals move for long distances upstream against the current which carries the larvae, presumably in order to maintain population distribution. Annala and Bycroft (1984) suggested that large males move into shallow water seasonally to moult and/or mate and that there may be some exchange between deep water populations (down to 275 m) and the inshore populations. McKoy and Leachman (1982) made the observation that larger-than-average berried females form extremely dense aggregations in areas of strong tidal movement (offshore on the edges of reefs) possibly to assist rapid dispersal of newly-hatched larvae. MacDiarmid (1991) used quantitative estimates of density at different depths (by *in situ* counts along transects) in combination with underwater tagging and resighting to demonstrate a seasonal in-offshore movement on a scale of 300m. Females moved inshore in winter when they moulted (as did males in spring), moved to the edge of the reef when hatching eggs and males moved to deeper water in summer in order to feed on bivalves on the sand flats. MacDiarmid (1991) suggested that all members of the Jasus lalandii group undergo large local annual changes in density, sex ratio and size distribution with respect to depth. The exact timing and depth range would be dependent on local timing of moulting and reproduction and differences in the depth range of suitable habitat and prey species.

Movements of new recruits from inshore nursery areas to offshore reefs occur in several lobster species, but cannot be considered "migrations" as individuals do not, in general, return.

2.3 Movements of Jasus lalandii in Southern Africa

Migrations of Jasus lalandii have been commented upon since the turn of the century. Gilchrist (1913) considered that seasonal movements of J. lalandii (inferred from seasonal changes in sex ratio and catch rates) occur in response to breeding, moulting and the need for shelter from the wind in the Table Bay area (Figure 2.1 shows the position of place names mentioned in this section). He also reported on a fisherman's observation of the capture of rock-lobsters in a seine net while rock-lobsters were swimming at the water surface. I, too, have spoken with fishermen who describe "swimming" rock-lobster in the Port Nolloth area during the late 1960's.

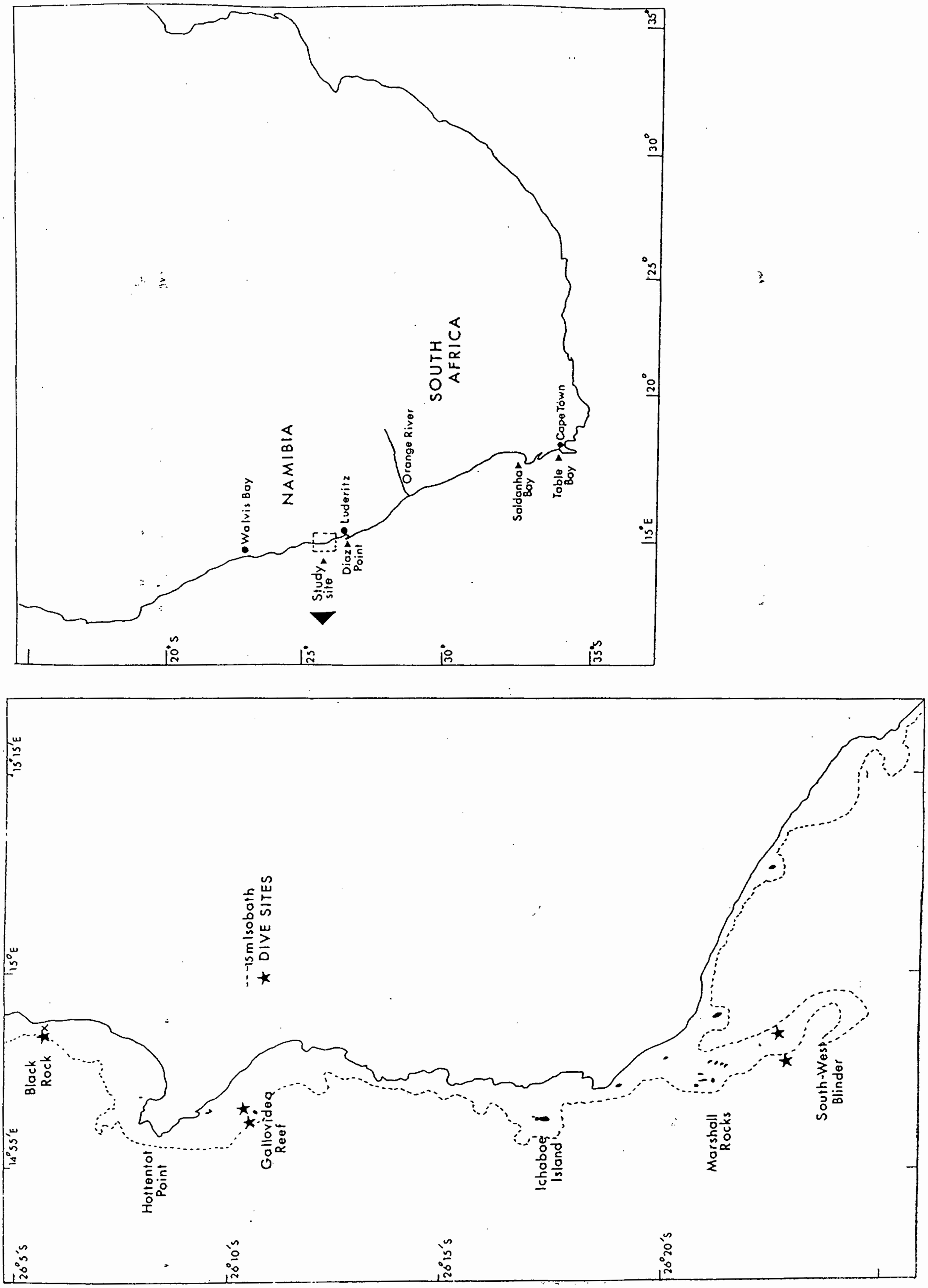

Figure 2.1 Map of place names mentioned in the text and position of the study sites.

Gilchrist (1918) demonstrated non-seasonal movements of up to 20 km from tag returns, but with no clear pattern. Since then, it has generally been accepted in the literature that Jasus lalandii does not move significant distances (more than 1 km) and variations in catch-rate and sex ratio have generally been explained as being due to seasonal changes in catchability due to different moulting seasons for males and females (e.g. Pollock and Beyers 1979). Using estimates of relative abundance (number caught per diver-hour), Heydorn (1969), found that in Table Bay (at about 10m depth, east of Robben island) abundance was lower in summer and higher in winter. Dissolved oxygen values at this site were above 3 ml/l at all depths sampled and he ascribed the seasonal movements to strong south-easterly winds in summer and north-easterly winds in winter causing rock-lobster to seek shelter on the corresponding lee of the island (cf. Gilchrist 1913). Pollock (1979), using strip counts, estimated density at 14, 20 and 27m on the West side of Robben island for 2 years. He noted that densities were greatest inshore in late spring and summer, but individuals occurred at high density in deeper water during winter. There was a marked inshore movement in October which he ascribed to males moving inshore in order to moult. Interestingly, this observation corresponds with Heydorn's (1969) and Gilchrist's (1913) hypothesis of wind-induced movement in the area. Pollock et al. (1982) found females in late-stage berry massed on top of shallow pinnacles outside St Helena Bay during January (mid summer). It was assumed that this was in association with the release of larvae as the females were found in deeper water one month later. Individuals less than 55 mm carapace length remained inshore, indicating that the offshore movement involved sexually mature individuals only.

Newman and Pollock (1971) documented a marked inshore movement in response to the onset of low dissolved oxygen concentrations (1.4 - 1.9 mlO_2/l) at Elands Bay (just north of St Helena Bay) during summer. Catch rates (numbers per diver-hour) were highest in deeper water (21m) in winter. From detailed depth distributions of the sexes, they concluded that females were somewhat less tolerant to low dissolved oxygen concentrations than males. They also considered that males moved into Elands Bay during moulting (October) in order to seek shelter from swell action. In general they considered that females were found in more sheltered areas due to their less robust bodies (Newman and Pollock 1971). Newman and Pollock (1971) also described the stranding of thousands of rock-lobster on the beach at Elands Bay in January 1969. These were nearly all females (although males were found in very shallow water just offshore) and the stranding was ascribed to very low values of dissolved oxygen just offshore. They considered that strong south-easterly winds (prevalent in summer) caused the upwelling of offshore low oxygen water but that the extremely low values and strandings were associated with a few days of particularly calm weather. In the Lambert's Bay (just north of St Helena Bay) area Pollock (1982) found, using tag returns, that females occurred in deeper water (40-50m) in October but returned inshore by January. The lowest oxygen values at St Helena Bay were recorded during late summer and autumn. Further north at Port Nolloth, Pollock (1982) assumed that low oxygen conditions persisted throughout the year and therefore rock-lobster were confined to shallow water (<20m) all year round.

However, this has not been tested directly and Pollock (1982) also suggested that the low catches in 1977 and 1978 were due to a slightly deeper-than-usual depth distribution which would have dispersed animals, lowering densities and therefore catch rates.

It has been generally considered that as one moves north from Cape point to Namibia, Jasus lalandii is increasingly confined to shallower water due to a decrease in dissolved oxygen concentration offshore (e.g. Pollock and Beyers 1981). In addition, Pollock (1982) considered that, at least between Cape Point and Lambert's Bay, seasonal migratory behaviour increased as one moved northwards, and considered that studies in other areas would be of interest. On the basis of a research hoop-netting study in Luderitz Bay, Mathews (1962) proposed that rock-lobster in the Luderitz Bay sanctuary migrate in- and off-shore seasonally. He also showed that the sex ratio changed during the year and therefore assumed that timing of migrations were different for each sex. However, an alternative explanation is that this was due to catchability changing due to moulting (Pollock and Beyers 1979).

A photograph in Annegarn and Krut (1985) shows a stranding of rock-lobster in the Luderitz region (at a site that appears to be opposite Halifax island) in the late 1950's. This is reminiscent of strandings at Elands Bay, probably indicating that similar environmental conditions (low dissolved oxygen content) existed in the Luderitz region at least since the 1950's. The effects of low oxygen tensions on rock-lobster depth distribution at Luderitz during the late 1970's were described by Beyers and Wilke (1990) and Bailey et al. (1985). They found that dissolved oxygen concentrations of less than 2ml/l in water deeper than 20m resulted in rock-lobster becoming "crowded" into water shallower than 12m. Several other diving observations confirmed this in later years (C.J. Beyers pers. comm.). However, diving was limited to summer and so would have missed any winter movements (C.J. Beyers pers. comm.). To my knowledge the present work is the first study to systematically address migratory behaviour of rock-lobster north of Lambert's Bay.

To summarise, possible reasons proposed in various parts of the world for seasonal lobster and spiny rock-lobster migrations include:

1. Moulting and the need for shelter (from predation or water movement) during the soft shell state.
2. Mating and search for mates.
3. Release of larvae in favourable oceanographic conditions.
4. Search for optimal temperature for growth, survival or incubation of eggs.
5. Escape from effect of winter storms and swell.
6. Feeding.
7. Escape from wind-induced water movement.
8. Escape from low-oxygen conditions.

From the published literature, it is likely that the last factor (low-oxygen conditions), will be of overriding importance for Luderitz rock-lobster.

The physiological response of lobsters to low dissolved oxygen concentrations was demonstrated by Chittleborough (1975) who noted reduced growth of Panulirus cygnus at oxygen concentrations of 60% of saturation. Beyers et al. (in press) have documented the effect of lowered oxygen concentration on captive Jasus lalandii growth and mortality. Moult increment was depressed and intermoult period lengthened at saturation levels less than 30%, while mortality over the moulting period was increased. Baden et al. (1990) found under laboratory conditions that during moderate hypoxia (2.8-3.1 ml/l or 38-43% saturation) Nephrops norvegicus increased its levels of haemocyanin (Hcy), improving its capacity for oxygen uptake. When exposed to severe hypoxia (down to 12%) the lobsters initially increased Hcy and could thereby survive for some weeks. However, Hcy was eventually catabolized and the lobsters then died. At 10% saturation Hcy was not increased and death was rapid. Baden et al. (1990) concluded that Hcy (and possibly glycogen content of the hepatopancreas) would be a useful biomarker of the degree of hypoxia to which individuals have been exposed.

Luderitz is positioned in the centre of the largest upwelling cell on the west coast of Southern Africa. The consequences of this have been extensively discussed by Shannon (1985) and Chapman and Shannon (1985). Nutrient content is very high and therefore during quiescent conditions phytoplankton production can be very intense. In general, however, due to the northward drift, maximum productivity is north of Luderitz. This extremely high production results in areas of anoxic diatomaceous mud in the Walvis Bay region (see Bailey et al. 1985 and Bailey 1987 for maps of organic carbon percentages along the Southern African west coast). A "counter" current has been proposed which flows south along the bottom resulting in water of very low dissolved oxygen concentration on the inner shelf just north of Luderitz (DeDecker 1970; Bailey et al. 1985). As examples, Figure 2.2 maps offshore bottom dissolved oxygen concentrations in November 1990 (strong upwelling was present) and April 1991 (relatively quiescent conditions). Both show tongues of low oxygen water (less than 2 ml/l) extending to just south of Diaz Point. These are very similar to conditions in November 1976 and February 1977 (from Bailey et al. 1985) except that the tongue of low oxygen water extended further south in 1977 during quiescent conditions than in recent years. Both sets of observations (in 1976/77 and 1990/91) show that during active upwelling there is a greater area of oxygenated bottom water on the shelf. In contrast, during quiescent conditions, water with very low dissolved oxygen (less than 1 ml/l) occupies a larger area of the shelf.

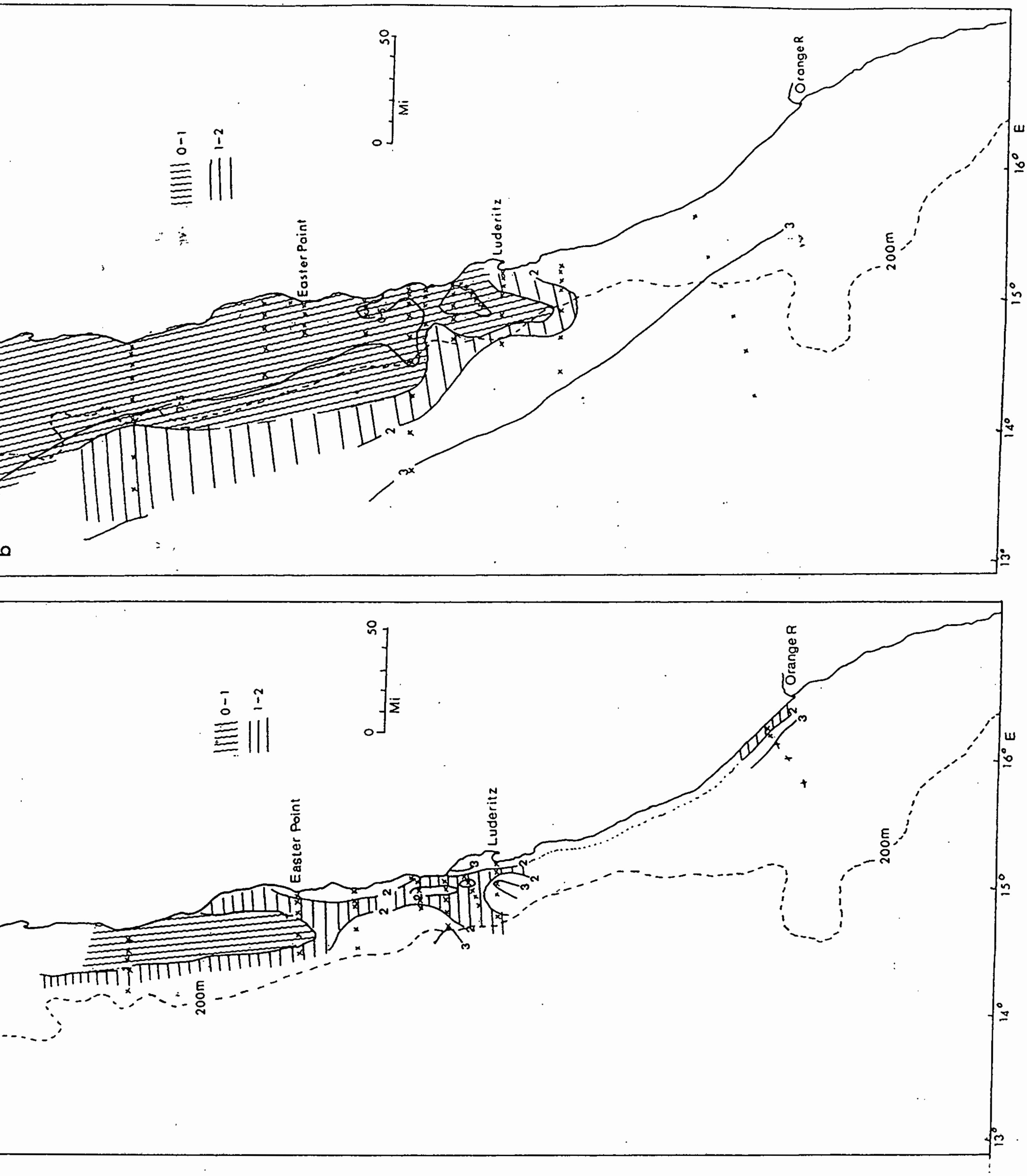

Figure 2.2 Bottom dissolved oxygen concentrations (mlO_2/l) off Southern Namibia during two research cruises on the RV Benguela. (a) November 1990, (b) April 1991.

Bailey et al. (1985) suggest that the "role of the counter current may have been overemphasised" and that upwelling is a net supplier of oxygen to the shelf area. Bailey et al. (1985) modelled the production of low dissolved oxygen water and concluded that the lower oxygen concentrations found in summer months are due to diminished upwelling, local photosynthesis, production of organic matter and subsequent decay thereof.

Against this backdrop of the importance of CPUE to fisheries management, existing knowledge of lobster movements and the specific oceanographic circumstances at Luderitz, it seemed that the major effect on CPUE on a monthly scale would be on-offshore movements caused by changes in dissolved oxygen concentrations. The present work was aimed at monitoring local rock-lobster movements and relating them to physico-chemical conditions, particularly the periodic intrusion of oxygen-deficient waters. It is apparent that, in general, tagging studies do not have the resolution to document small scale movements (up to 2 km) on an adequate seasonal time-scale. Similarly, trap catch rates are deficient because they are potentially biased due to seasonal and daily changes in catchability. Studies which use direct visual estimates of density on a regular basis (at least seasonally) for a minimum of one year can demonstrate seasonal small-scale movements but they are rare. I have found only the following in the published literature: MacDiarmid (1991) on Jasus edwardsii for 3 years, Cooper et al. (1975) on Homarus americanus for 2 years, Spanier et al. (1988) on Scyllarides latus for 3 years, Ennis (1984) on Homarus americanus for 2.5 years, Heydorn (1968) on Jasus lalandii for 3 years (east of Robben Island), Pollock (1979) on Jasus lalandii for 2 years (west of Robben Island) and Newman and Pollock (1971) on Jasus lalandii for 1 year (at Elands Bay). The present study comprised the visual estimation of density at on a regular basis for six years at one site and four years at another. Environmental data (notably bottom dissolved oxygen concentration at 20m) were collected simultaneously. Finally, to determine the effects of changes in density on the fishery, data on monthly CPUE and catch were compiled for the study areas.

2.4. METHODS:

1. Study location:

The main study site was on the southern part of Marshall Rocks reef, locally known as South West Blinder (Figure 2.1). Marshall Rocks has historically produced most of the catch landed at Luderitz. The site was chosen because of its importance to the fishing industry, its relative closeness to the harbour, generally fair underwater visibility and because it had been the focus of previous work (e.g. Beyers 1979; Mathews and Smit 1979; Bailey et al. 1985). During the course of the study, however, its contribution to landings declined dramatically. A secondary study site at Gallovidea Reef (Figure 2.1) was chosen as being moderately sheltered, contributing a fair proportion of the catch and having reasonable visibility in general. Although a site with an undisturbed (i.e. unfished population) would have been ideal, the only unfished sites available were located inside Luderitz Bay and therefore probably exposed to a different set of environmental stresses (such as siltation) from the offshore commercial fishing reefs. While the study was underway, the Ichaboe island sanctuary was re-proclaimed and the outside of this island would in the future make a good comparative site as it is now unfished. Previous tagging studies (Beyers and Wilke in press; Tomalin 1988) had indicated that SW Blinder-Marshall rocks was fairly lightly exploited (about 10-20% tag return rate) whereas Gallovidea was heavily exploited (more than 30% tag return rate in some years). Section 4 of this thesis describes the benthos at the 2 sites.

2. Physical Environment:

a. Wind speed was measured using data from Diaz Point lighthouse. Data on direction and speed, measured 3 times per day, were converted to the southerly component (responsible for upwelling) and cubed (pseudo wind-stress, Taunton-Clark and Shannon 1988). Daily and monthly averages were computed.

b. The swell size and particularly length was approximated very crudely by measuring the maximum width of the swash zone on a beach (inside Luderitz harbour) sheltered from the prevailing wind. This eliminated wind chop which has little effect underwater and measured mostly long wave-length swell which has a larger effect on the strength of bottom surge and hence, presumably, on the mobility of rock-lobster.

c. Dissolved oxygen content was measured at 20m, 15m, 10m and on the surface using the standard Winkler titration method. Measurements were made at SW Blinder at station depths of 20 and 10m throughout the period of observations (March 1988 to October 1991) and at several other sites (Diaz Point, Ichaboe Island, Gallovidea Reef, Hottentot Point and Black Rocks) somewhat less intensively.

d. Water temperature was measured (by thermometer to 0.1 °C) at the same depths and sites and standard secchi disk readings taken to an accuracy of 0.5m.

e. Two cruises were undertaken to investigate offshore dissolved oxygen conditions (Figure 2.2). These were during November 1990 and April 1991. Conductivity-temperature-depth dips were carried out to the bottom at all stations marked in Figure 2.2. In addition, water samples to determine dissolved oxygen concentration were taken at standard depths. Only results pertaining to "bottom" (between 10 and 5m off the bottom) dissolved oxygen levels are presented in Figure 2.2.

3. Rock-lobster densities:

Rock-lobster densities were determined (using SCUBA) within strips 20 m in length (marked out by a weighted rope) and 1m- or 2m-wide (depending on density). Four to eight replicates were done per sample by running out lines on the points of the compass from a central marker which was randomly chosen within a depth zone and general area (navigation was accurate to about 200 m). Attempts were made to mark the sites with bottom grids and surface buoys. However, these were lost within a few months. Compass bearings on Marshall rocks and Staple rocks were used in conjunction with depth to return to approximately the same site on South-West Blinder (see Figure 2.1). Although most samples were at approximately 10m depth, dives were also done irregularly at 15 and 20m and less than 10m (the latter in general difficult due to the exposed situation) to check whether assumed rock-lobster depth distributions were correct. Samples were more frequent during summer (more than 1/month) than during winter and spring (about every 2nd month) when conditions were more uniform. Data are available from SW Blinder from 1987 to 1992 and at Gallovidea reef from 1989 to 1992.

4. Data analysis:

The depth distribution of rock-lobster was classified as "deep" (occurring mostly in water greater than 12 m) or "shallow" (occurring only in water less than 12 m) on each occasion that diving was done. The means of various environmental variables were compared using non-parametric tests. In addition, parametric and non-parametric tests were used to compare various estimates of the correlations between environmental variables on all sampling occasions. The time series is not long enough and there are too many gaps to subject the data to formal time series analysis but inspection allowed the erection of formal hypotheses which can be tested in the future when this data base has been extended for several more years, or by using existing long-term series of environmental data (wind and sea surface temperature) and population data (see section three). In addition to the effect of the environment on rock-lobster movements, the effect of changing rock-lobster densities on catch-per-unit effort and catch was examined. The proportion of legal size animals was determined from the diver's catch and multiplied by the mean monthly density to produce an estimate of legal-sized density (male and female combined) which was regressed against that month's CPUE and catch.

2.5. RESULTS:

1. Rock-lobster movements:

Rock-lobster density in "shallow" water at 10m showed a substantial increase in all summers except 1991 (Figure 2.3). Gallovidea reef seemed to show a very similar pattern to SW Blinder.

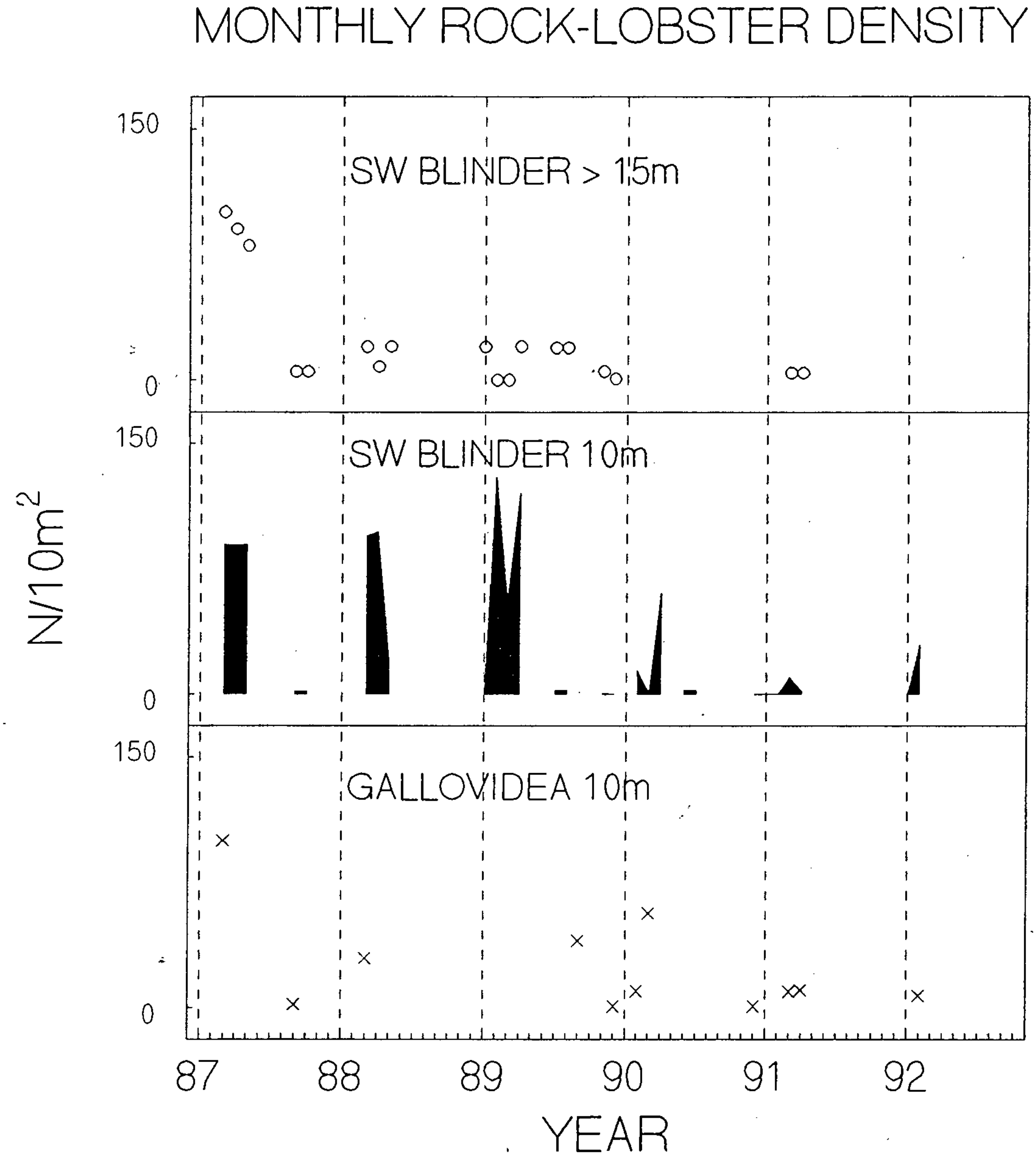

Figure 2.3 Mean monthly densities of rock-lobsters at SW Blinder > 15m, SW Blinder 10m and Gallovidea 10m. During February 1990, rock-lobsters were in water less than 10m deep.

This pattern was interpreted as a movement into shallow water (confirmed by dives at 15m and 20m). This movement was most clearly seen during December 1988 (Table 2.1) when for 2 weeks moderate densities were observed at 18-21m and no rock-lobsters occurred at 10m depth. Then on the next occasion, no rock-lobsters were seen at 20m depth. On searching they were found at about 13-15m actively walking inshore at about 1-2m per minute. A few days later rock-lobsters were only observed at 11m and less and at very high densities.

TABLE 2.1: Density (n/10m^2) and activity of rock-lobsters and dissolved oxygen concentration (mlO$_2$/l) at SW Blinder during December 1988:

Date	20m	15m	11m	Activity	O2 conc. at 20m
9/12/88	24	27	0	inactive	4.8
22/12/88	25	30	3	inactive	1.0
28/12/88	0	20	1	walking	0.4
30/12/88	0	0	33	inactive	0.5
11/1/89	0	0	130	inactive	0.8

The apparent low density at 10 m during February 1990 (Figure 2.3) was due to rock-lobsters moving even further inshore than usual into water less than 9 m deep. In general, rock-lobsters remained in shallow water until May-June when they gradually moved out and were more evenly distributed from shallow to deep water in low densities. "Deep" water is probably around 50-70m as indicated by catches from research trapping in September to October (pers obs). During "spring" (August to October) virtually no rock-lobsters were observed in water less than 20 m deep (except for August 1989 at Gallovidea reef). The inshore movement in early summer was very marked and probably took a few days. The offshore movement was however, much more gradual and probably took a few months. Of note is that there was considerable inter-annual variation. Two departures from the "normal" pattern were particularly striking: (1) Although shallow-water densities were high during summer of 1988, rock-lobsters (especially large males) continued to be found down to 18m. (2) Almost no inshore movement of rock-lobster took place during 1991 when low densities were recorded despite extensive searches in <u>all</u> depths of water (down to 22m). This resulted in very low catch rates to the fishing industry. With only three exceptions, rock-lobsters never achieved high densities (>50/10m^2) in deeper water at 15m (Figure 2.3) indicating that they become more dispersed as they move offshore into deeper water.

For each sampling occasion, the distribution of rock-lobsters was classified as "deep" or "shallow" reflecting depth distribution. The mean density at 10 m for all occasions when rock-lobster were "shallow" was 42.95/10m2 (standard deviation = 44.04 and median = 18.5) but dropped dramatically when rock-lobsters were "deep", averaging 2.04/10m2 (standard deviation = 2.85 and median = 1). The distributions of values were obviously non-normal (by inspection of density distribution graphs) therefore the Mann-Whitney U test was used to compare means. The difference between mean density at 10m when the rock-lobsters were shallow and deep was highly significant (a = 0.01, Z = 7.966).

These onshore and offshore movements appear to involve the whole population (Table 2.2) and not one particular sex. There was no significant difference between percent males (or percent above legal size) at three depth ranges (14-18m, 9-12m and <9m) at SW Blinder. On any one date and area, larger animals (and hence a higher proportion of males) were found either in deeper water (2/88 and 3/88 on SW Blinder) or shallower water (4/88, 3/89, 6/89, 3/90 on SW Blinder and 2/90 on Black rock). Unquantified observations suggested that these small-scale size related differences were due more to topography (availability of shelter) than to depth (and hence oceanographic environment) per se. Thus, if there are any endogenous migratory rhythms specific to either sex (Pollock 1979), they appear to be largely overridden by environmental constraints in the Luderitz region. The fact that males make up less than 50 % of the samples is probably mostly due to the fishery selectively removing the (larger) males.

TABLE 2.2. Summary of sex-ratios and mean sizes of diver caught rock-lobsters at various sites, depths and dates.

DATE/ AREA	DEPTH	N	% MALE	MEAN SIZE MALES	% LEGAL SIZE
SW BLINDER:					
02/87	15	56	44.6	59.1	30.4
04/87	16	65	55.4	60.0	24.6
08/87	12-14	44	25	57.4	38.6
02/88	15	44	65.9	81.8	66
02/88	10	149	42.3	55	41
03/88	16	148	47.9	69.8	38.5
03/88	6-7	141	35.4	64	30.5
04/88	17	148	31.8	64.2	27.7
04/88	9	64	32.8	60.1	41
12/88	8-16	33	52	68	40
1/89	12	75	46.7	72	62.3
2/89	11	69	34.7	66.8	34.8
3/89	11	142	26	66.1	29.6
3/89	8	65	44.6	74.6	41.5
6/89	12	57	42.1	66	47.4
6/89	18	56	16	65.1	28.6
1/90	9	75	40	73	50.1
3/90	10	151	21.7	62.2	28.5
3/90	8.5	106	16	69.2	38.7
2/91	10	58	48.3	75	44.1
1/92	8-12	124	37.9	62.2	23.4
GALLOVIDEA:					
2/87	10	242	35.1	51.2	14
8/89	12	82	26.8	52.7	29.3
10/89	11	12	25	68	58
1/90	10	75	13.3	50	14.7
2/90	10	109	22.9	59.1	25.7
2/91	11	70	37.1	54.6	14.3
1/92	9-10	40	40	70.3	27.5
BLACK ROCK:					
2/90	8-9	28	50	49	7.1
2/90	6-7	125	24	52.3	24.8
2/90	3-6	119	37.8	60.6	28.6

2. Relationship between rock-lobster densities, CPUE and catch:

Monthly CPUE indices show a high catch rate during 1988 and declining in later years (Figure 2.4). In general, CPUE is highest in January and declines thereafter.

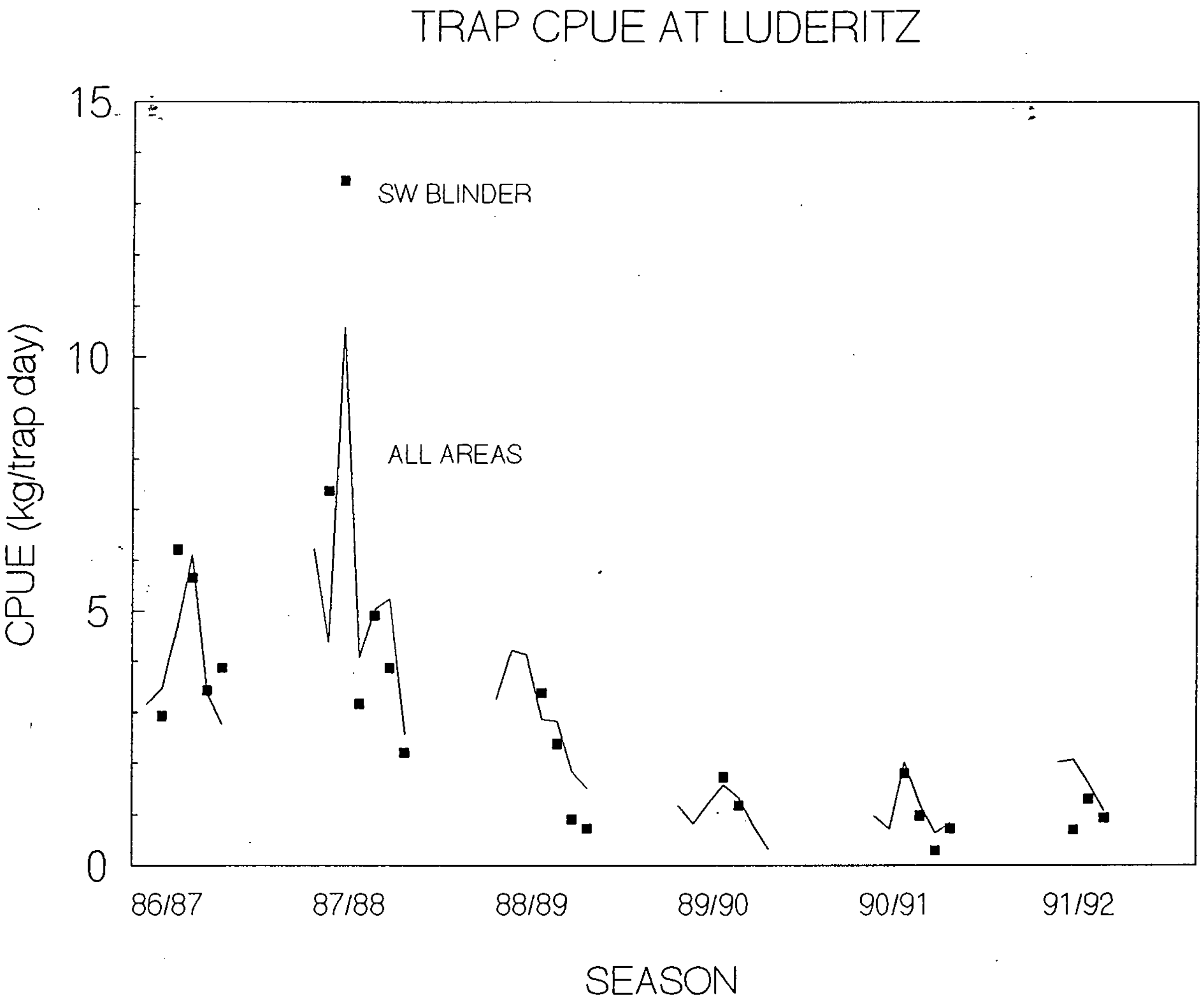

Figure 2.4 Mean monthly trap CPUE at SW Blinder and all areas combined (1991/92 unpubl. data of K. Grobler).

There was a marginally significant correlation (R^2 = 0.13, P = 0.108) between all legal-size monthly mean densities and CPUE at SW Blinder and Gallovidea. When two outlying points (January and March 1989) were removed, the significance increased (P = 0.003, R^2 = 0.41) dramatically (Figure 2.5). The relationship between density and catch was highly significant (P = 0.016, R^2 = 0.4) at SW Blinder but not at Gallovidea (Figure 2.5) due to the smaller number of data points at the latter.

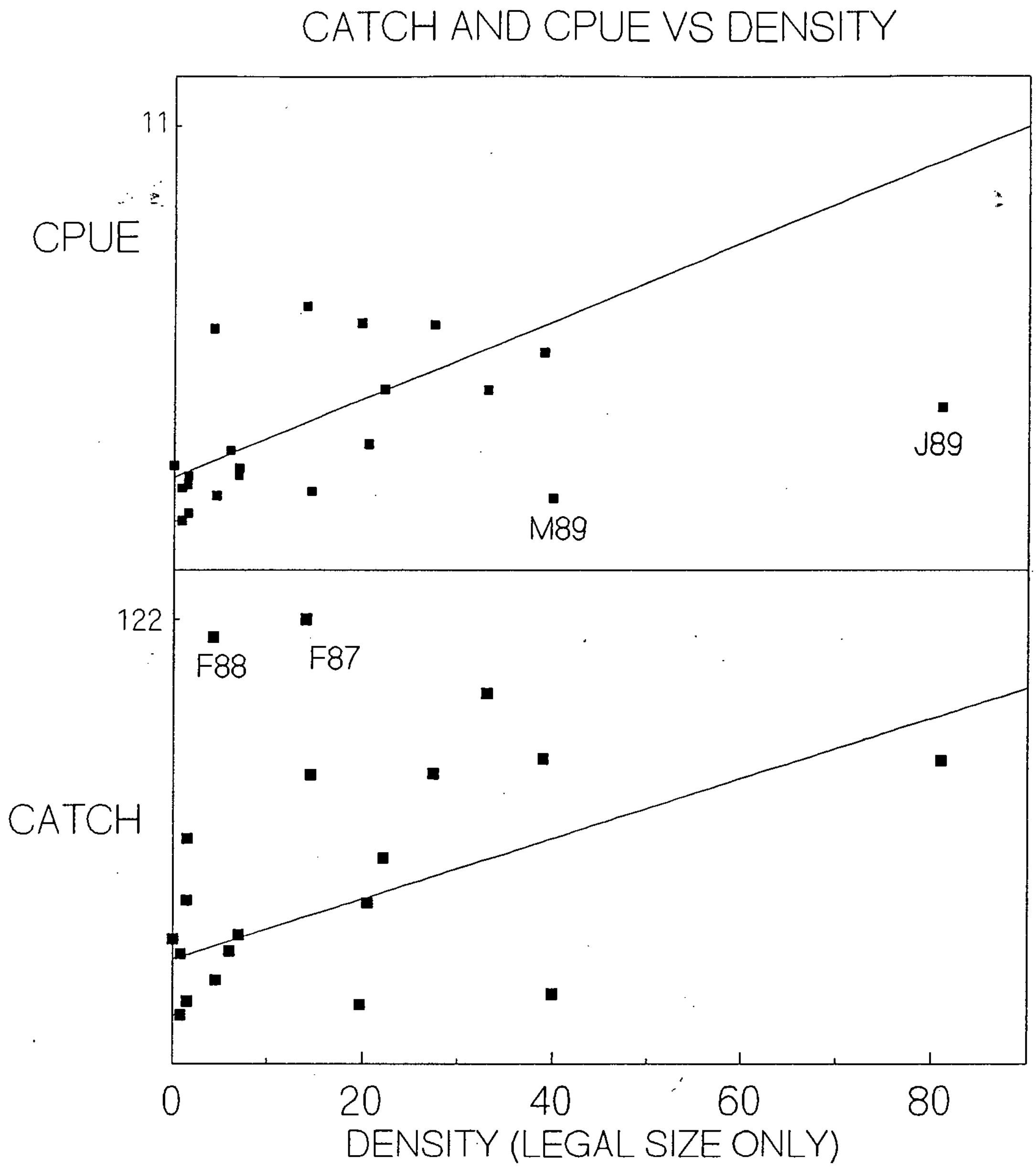

Figure 2.5 Mean monthly density of legal-sized rock-lobster (n/10m^2) vs that month's trap CPUE (kg/day) and catch (tonne) at SW Blinder and Gallovidea.

3. Physical environment:

a. Time series of oxygen, wind and water temperature:

Figure 2.6 summarises the time series of observed dissolved oxygen levels at SW Blinder, Diaz Point and Gallovidea reef on the bottom at 20 m depth. In general, all three areas show similar trends, although the values for Diaz point were often much higher than those for the other two sites. This is possibly due to it being an upwelling point (Bailey et al. 1985). The abrupt drops in summer oxygen levels which occurred in December 1988 and January 1990 are apparent. Extremely low oxygen conditions persisted thereafter, until April 1989 and May 1990 in the respective years. Of interest was a "stranding" of benthic fish (notably west coast sole), but not rock-lobster, inside Luderitz Bay during March 1989 after a period of strong upwelling. Very low dissolved oxygen concentrations were measured during this period in Luderitz Bay (Tomalin unpubl). A very short low-oxygen event occurred at SW Blinder during February 1991. January 1992 appeared to be a "normal" low oxygen event on SW Blinder.

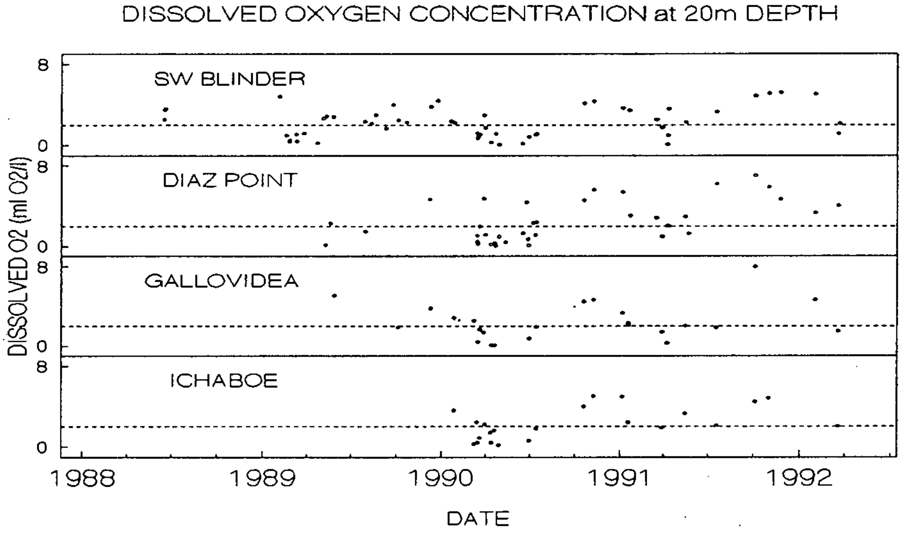

Figure 2.6 Time series of dissolved oxygen concentration at 20m at SW Blinder, Diaz Point, Gallovidea and Ichaboe Island. The "critical" level of 2ml O2/l is indicated by a dotted line.

Fig 2.7 summarises surface dissolved oxygen levels at SW Blinder, Diaz Point and Gallovidea reef. Supersaturation (above 5-6 mlO_2/l at about 12°C) indicates the presence of plankton blooms which were confirmed by secchi disk readings (Figure 2.8) and examination of water samples (high concentrations of diatoms confirmed by F. Molloy pers. comm.). Surface values only dropped below 2ml/l on one occasion (at Diaz point).

Figures 2.9 and 2.10 show water temperature at SW Blinder at 20m and the surface respectively and Figure 2.11 the southerly component of wind stress at Diaz point. A clear seasonal component is apparent - high wind stress, strong upwelling and resultant low temperatures at 20m and the surface during spring and low winds in winter. An indication of swell size from swash zone width in Luderitz harbour is given in figure 2.12. An increase in winter is apparent due to swells generated by cold fronts passing the Cape but with large day-to-day variability.

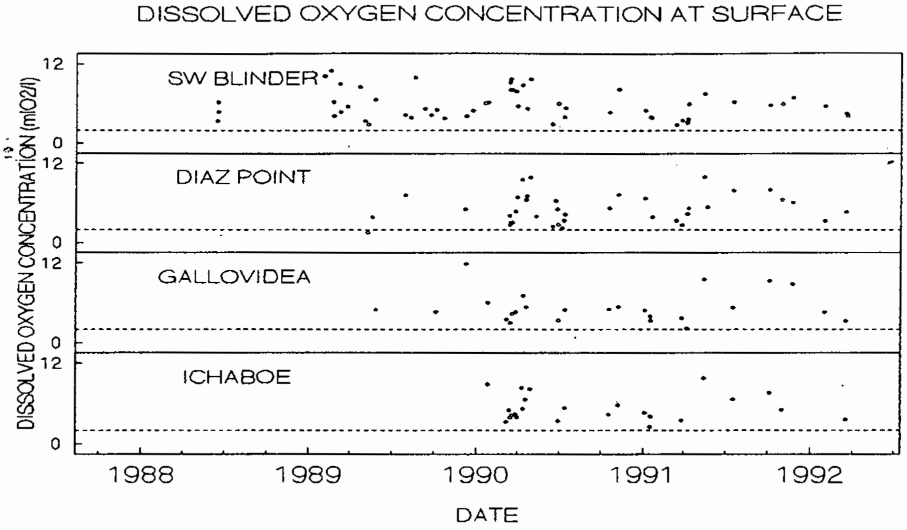

Figure 2.7 Surface dissolved oxygen concentration at SW Blinder, Diaz point, Gallovidea and Ichaboe Island.

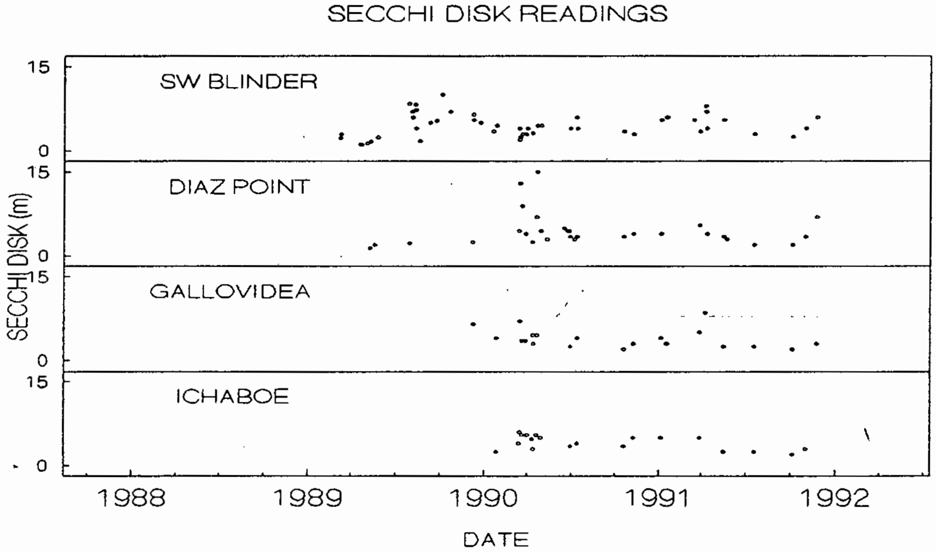

Figure 2.8 Secchi disk readings at SW Blinder, Diaz Point, Gallovidea and Ichaboe Island.

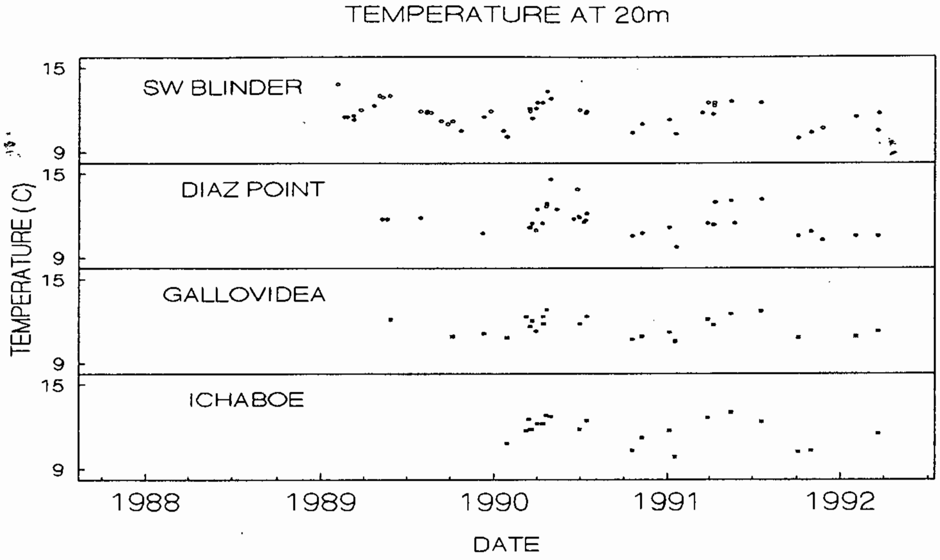

Figure 2.9 Water temperature at 20m depth at SW Blinder, Diaz Point, Gallovidea and Ichaboe Island.

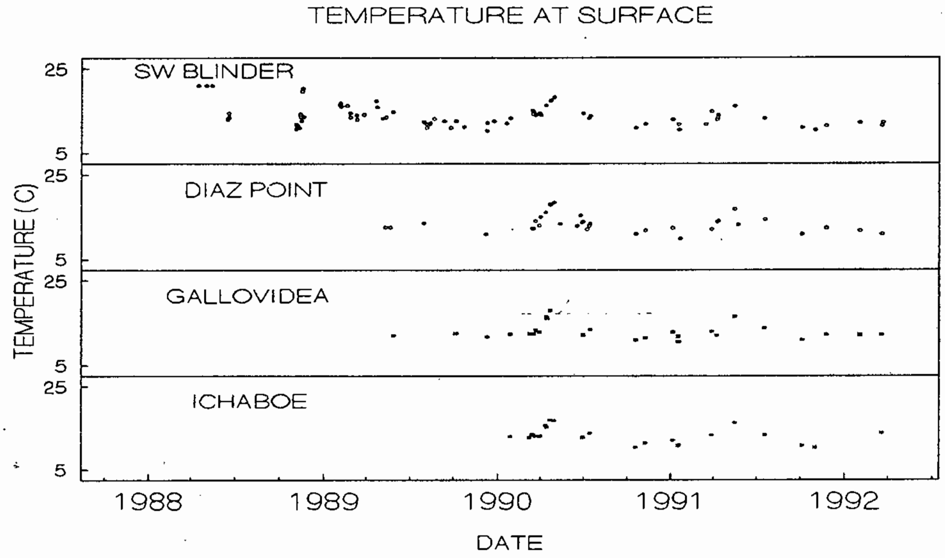

Figure 2.10 Surface water temperature at SW Blinder, Diaz Point, Gallovidea and Ichaboe Island.

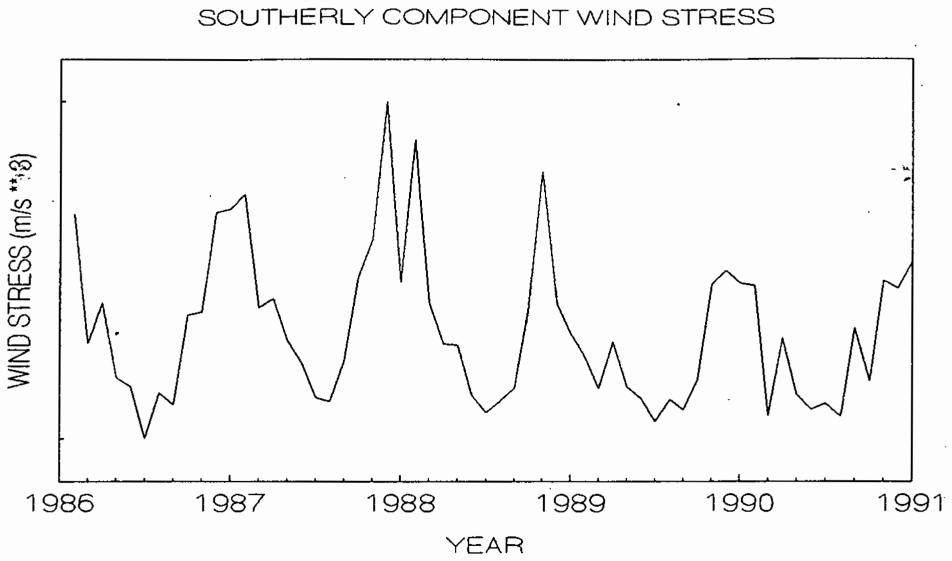

Figure 2.11 Total monthly southerly component of pseudo wind stress at Diaz Point

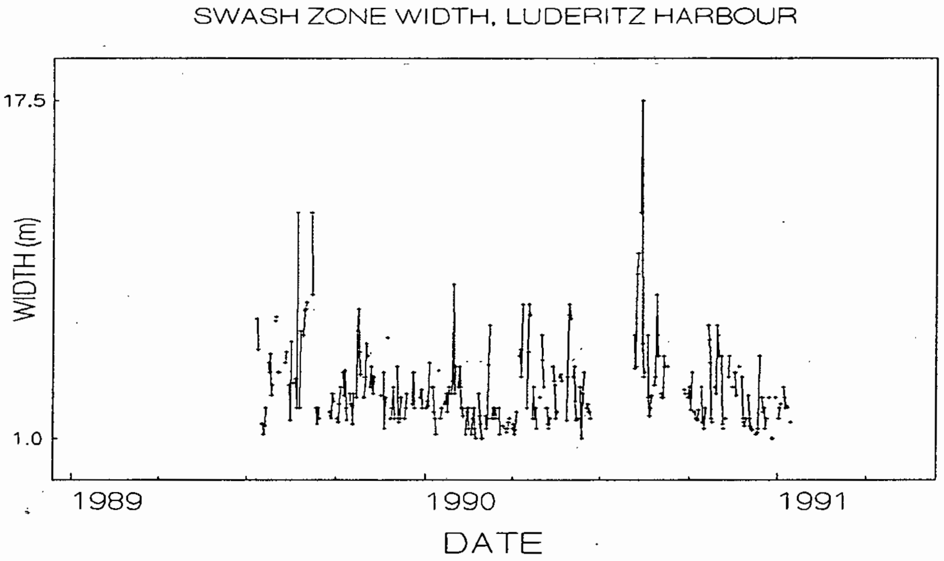

Figure 2.12 Daily width of the swash zone in Lüderitz harbour.

To summarise, three "seasons" can be distinguished at Luderitz.

a. Spring (Figure 2.13). From September to December the water is very cold, well mixed and upwelling is intense due to strong southerly winds. Oxygen levels are high over rock-lobster reefs. Swell is of moderate intensity.

b. Summer (Figure 2.14). From January to April the water is warmer and can be strongly stratified with extremely low dissolved oxygen levels below about 12m depth. "Warm events" of varying intensity can occur. Very low dissolved oxygen levels can develop suddenly and remain until about May-June but their intensity and persistence varies between years. Swell is low. This is the most variable period and the fishery lands most of it's catch in this season. Therefore sampling was concentrated in this period.

c. Autumn and Winter (Figure 2.15). From May to August there are low winds, the water is warmer, oxygen levels are higher and large swells of long wave length occur.

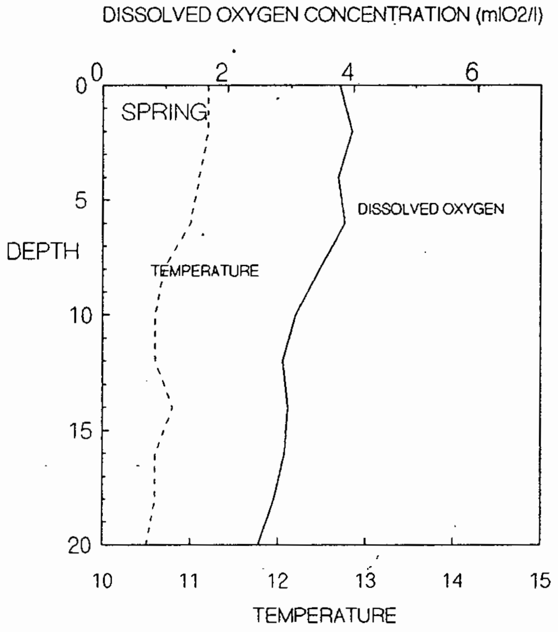

Figure 2.13 A typical "spring" (September to December) dissolved oxygen and temperature profile at SW Blinder.

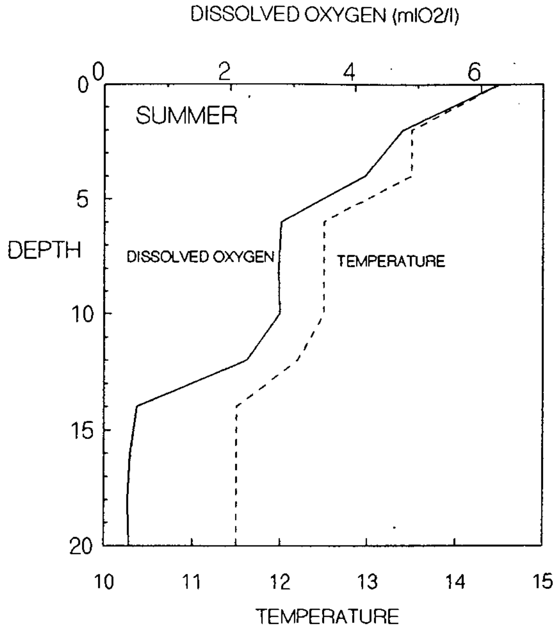

Figure 2.14 Typical "summer" (January to April) dissolved oxygen and temperature profile at SW Blinder.

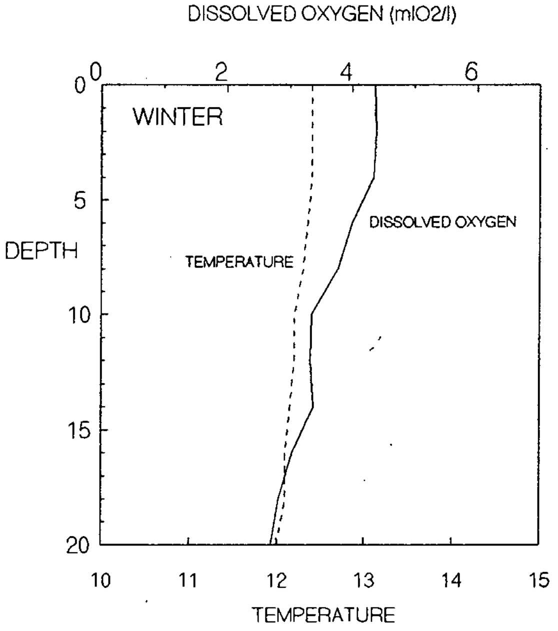

Figure 2.15 Typical "winter" (May to August) dissolved oxygen and temperature profile at SW Blinder.

Correlations between environmental variables:

Correlations were sought in an attempt to identify a few variables which could be easily and rapidly measured in the future (such as surface temperature) or which have been routinely measured in the past (such as wind) and which have a significant effect on rock-lobster movements. Correlation coefficients between various of the environmental measures were tested singly using the student t distribution and t test statistic, assuming normality of both x and y and an Ho of no correlation (see Table 2.3 for a summary of results of tests).

1. Surface dissolved oxygen vs. surface temperature:

A significant relationship ($r = 0.73$, $n = 52$, $t_o=5.17$, $a=0.01$) was found. This has relevance as higher surface temperatures imply higher surface productivity but probably more decomposition of plankton in deeper waters and resultant low oxygen conditions in deeper water.

2. Secchi disk vs. surface oxygen:

A significant negative relationship at ($a=0.01$, $r = -0.48$, $n = 42$, $t_o = 3.45$) was found. Surface oxygen is higher when there is low visibility. This was due to plankton blooms as confirmed by microscopic examination of water samples. The high (sometimes supersaturated) oxygen concentrations were due to photosynthetic activity.

3. Secchi disk vs bottom oxygen and surface oxygen concentration vs bottom oxygen showed no significant relationship indicating that surface blooms were a poor indicator of bottom oxygen levels (although it was expected that bottom oxygen values would be low during blooms).

4. Bottom temperature vs. bottom oxygen concentration:

A significant negative correlation was found ($r = -0.49$, $n=48$, $t_o = 2.04$, $a=0.025$). Colder bottom water corresponds to higher oxygen levels indicating the role of upwelling in supplying oxygen (cf Bailey et al. 1979). Alternatively, this may be a spurious relationship as dissolved oxygen concentrations were generally much higher in winter and spring when the water temperature was also higher.

5. Surface temperature vs. bottom oxygen concentration:

A significant negative relationship was found ($r = -0.45$, $n=50$, $t_o = 4.42$, $a=0.01$). Warmer surface water is related to lower bottom dissolved oxygen. This may just reflect the autocorrelation in the series (seasonal higher temperature and low oxygen events being in summer) but holds out some hope that a long-term series of sea surface temperature may be useful in predicting bottom oxygen concentration, given careful interpretation (see section three). Of interest is an outlier of 17° C and 4.9 mlO_2/l. This was during a "warm event" when Angolan water moved down the coast in 1988 (Roux 1988) and demonstrates the importance of recognising such events in any long-term analysis of sea surface temperature.

Spearman's rank correlation test for zero correlation confirmed all the above correlations for the non-parametric assumption.

TABLE 2.3. Summary of tests of correlation coefficients.

Factors	Normal student t		Spearman's rank correlation	
	r	P	r	P
Secchi vs surface oxygen	-0.49	0.001	-0.81	$1.8e^{-7}$
surface t vs surface oxygen	0.73	0.00001	0.44	0.002
bottom t vs bottom oxygen	-0.49	0.047	-0.31	0.03
surface t vs bottom oxygen	-0.45	0.00001	-0.51	0.0003
Secchi vs bottom oxygen		not significant		
surface oxygen vs. bottom oxygen		not significant		

4. The relationship between the physical environment and rock-lobster movements:

The role of changes in bottom dissolved oxygen concentration (at 20m) on rock-lobster migrations is apparent from the time series. Although observations were somewhat less intense in summer 1988, it appeared that oxygen concentrations were relatively high and that rock-lobsters were distributed from 9m to 16-18m depth. In contrast, in December 1988 and January 1990 there were marked and sudden drops in dissolved oxygen concentration followed by an inshore movement of rock-lobsters. In summer 1991, the drop in oxygen concentration was very brief and not very intense and the rock-lobsters did not move inshore in great numbers that year.

The mean dissolved oxygen concentration at 20m when the rock-lobsters occurred in deep water was 2.89 ml/l (variance = 1.4, median = 2.71) and when rock-lobsters were concentrated in the shallows, it was 1.35 (variance = 1.48 and median =1.00). Density distributions for oxygen were non-normal therefore a non-parametric test was used. The Mann-Whitney U test showed a significant difference at the a = 0.01 level (Z = 3.167). Using the Chi square test and dividing dissolved oxygen observations into 5 levels (0.00-0.99, 1.00-1.99, 2.00-2.99, 3.00-3.99, 4.00-4.99) and rock-lobsters into deep and shallow, the depth distribution of rock-lobsters was significantly dependent on bottom oxygen concentration at the a=0.025 level (4 d.f., chi square = 13.15).

Mean temperature at 20m when rock-lobsters were deep was 11.62°C (variance = 0.83) and when they were shallow it was 12.01°C (variance = 0.19). A Mann-Whitney U test on the difference of these means was not significant (Z = 1.79). Similar tests on surface temperature were also non-significant although again mean temperature was lower when rock-lobsters were in deep water compared to when they were in the shallows.

2.6. DISCUSSION

A "well defined seasonal pattern" of on- and off-shore migration "which is environmentally induced" very similar to that described for Elands Bay (Newman and Pollock 1971) has been demonstrated for Jasus lalandii at SW Blinder and Gallovidea reef in the Luderitz area. The strong environmental forcing by low oxygen concentrations (water temperature was not a significant factor during this study) on the inshore migration appears to override any potential endogenous rhythms in most years. The offshore migration in autumn may be due to feeding requirements (there appears to be a large supply of small mussels in deeper water, section 4), shelter from water movement (which is stronger in winter due to long period swells produced by cold fronts at the southern Cape) and/or female release of larvae. The inshore migration is so marked that more intensive confirmatory sampling such as resighting of tags, use of sonic tags or additional samples at different depths would be difficult to justify. In fact, on the basis of these six year's observations, all that is required to predict depth distribution of rock-lobster is a measure of dissolved oxygen concentration at 20m at several sites. This could be used as an index of depth distribution in the future.

CPUE and monthly catch is correlated to the monthly mean density of legal-sized animals (determined by diver counts) and there is no noticeable change in catchability during March-April when CPUE is invariably low. This implies that most of the decline in CPUE within a fishing season is due to a reduction in density of legal sized animals both because of fishing itself and the gradual offshore migration. Hence, the argument by the Namibian Fisheries Advisory board that catchability of Luderitz rock-lobster is lower than that of rock-lobster along the rest of the coast is probably wrong, i.e. the most likely reason that the global TAC could not be caught was simply that the population could not sustain that level of exploitation. This implies that the either the tag-return method upon which the TACs were based was positively biased or that the yield-per-recruit calculation which produced an F at MSY = 0.3 was inappropriate. Alternatively, the assumption of constant recruitment (inherent in yield-per-recruit models) was wrong and recruitment was, in fact, declining (Tomalin 1992; section 3).

What is, perhaps, of greater interest than the "normal" seasonal migrations, is the interannual variation in migration which has been demonstrated in this study for the first time. For example, the distribution to relatively deeper depths (16-18m) during February-March 1988 and the absence of inshore movement in 1991 contrasts with 1989 and 1990 when there were marked inshore migrations of virtually the entire rock-lobster population to shallow water (<12m). This has profound implications for the fishery and it would have been difficult to interpret CPUE data in a meaningful way without independent data on depth distribution and density. It appears therefore that changes in migration pattern (caused by variations in environmental factors) are, as proposed by the fishermen, an alternative hypothesis explaining the recent declines in CPUE. This can be corroborated in future years by analysing size-frequencies as follows. If migration patterns had changed, then fishing mortality (F) would be much lower and an increase in mean size could be expected when migrations return to normal. On the other hand, if reduced recruitment across the legal size (Shannon et al. 1992) was the cause, F would remain about the same and when recruitment returned to normal, size distributions would be approximately the same as before.

The hypothesis of changing migration patterns only applies to relatively short term events (one to three years) and does not imply that the long term decline (over decades) in CPUE is due to the same cause (see section three).

The possibility of using a time series of this type of survey as a recruitment index exists. One would first have to determine the area with bottom dissolved oxygen levels above (say) 2 ml/l and then obtain the average rock-lobster density within that area. This density could be directly measured by divers or calculated from research trap CPUE (due to direct relationship between density and CPUE demonstrated here). One could then multiply the area by the density (and the fraction per size class from samples) to obtain population estimates per size class. This has obvious fisheries implications for input to stock assessment models and would cost a fraction of similar surveys done by large trawlers on hake.

This migration is indeed a "consistent behaviour pattern involving directed active movement by the organisms ... (and is) reflective of adaptive responses to processes or conditions which regulate recruitment (i.e. net reproductive success and survival to adulthood of the progeny, at the population level). Thus it is reasonable to look at such behaviour patterns as clear indicators of the identity of the predominant processes controlling recruitment variability" (Bakun 1985; Bakun in press) and this is done below.

Two hypotheses as to the effect of the environmentally-induced migration on rock-lobster population dynamics and the fishery can be proposed on the basis of the last six years of observations. A third relates to the survival of puerulus larvae. An attempt will be made to test these hypotheses using long term data in section three.

Hypothesis 1:

The length of time that water with oxygen levels less than $2mlO_2/l$ is present offshore (at 20m) during summer is inversely proportional to growth and survival rates the following moulting season (spring) and, hence, recruitment of legal size animals to the fishery the following season (D.Pollock pers.comm.). This study shows that prolonged low dissolved oxygen levels result in an inshore movement and very high densities in the shallows. This would possibly cause a reduction in available food per capita, increased cannibalism and decreased mobility. The latter would be due to extremely high densities and increased bottom surge in shallow water compared to that experienced by rock-lobster in deeper water. All these circumstances would result in reduced food intake and hence lower growth and higher mortality during the following moult. In addition, low dissolved oxygen levels per se would inhibit growth and increase moult-related mortality (Beyers et al. in press). Interannual variation (as described in this section) in the above would result in variable recruitment across the legal size limit the following season (as described by Shannon et al. 1992).

Hypothesis 2:

(a). Catch rates should be high during coastal "warm events" (e.g. 1988). Warm water (of Angolan origin and, hence, high in oxygen and low in nutrient content) extends to relatively deep levels, the oxycline is deep and not very intense and phytoplankton blooms do not occur. Weather may exhibit extended calm periods. These warm events are remotely forced by equatorial weather (V. Shannon pers. comm.) and therefore local weather may be variable. Rock-lobsters do move inshore (therefore occur in high densities) but their summer depth range extends down to about 16-18m. They are therefore less affected by swell, less crowded and probably feed more actively than during low oxygen events. This would result in high catch rates, the likelihood of removing a high proportion of the legal size population (i.e. high fishing mortality) and probably high "discard mortality". The latter would be caused by reduced manpower available for hand-sorting the catch during periods of high CPUE (pers. obs.). Although high CPUE would be experienced that season, the high discard mortality would result in low recruitment the following season and a good season would be followed by a poor season.

(b). Conversely, catchability should be low during years with strong thermoclines, intense local phytoplankton production (which further strips oxygen from upwelled water) and shallow and intense oxyclines (e.g. 1989 and 1990). Winds consist of alternating periods of (1): southerly gales which cause upwelling of high nutrient, low oxygen water and (2): short calms resulting in local phytoplankton blooms which intensify low-oxygen conditions. Rock-lobsters are limited to very shallow water (less than 11m in 1989 and less than 9m in 1990). Low oxygen per se inhibits feeding rates. Furthermore, due to the shallow distribution of rock-lobsters, swell may restrict feeding and interfere with operation of traps and nets. Density on the fishing grounds would be high, but catchability would be low. A low proportion of the legal-size population would be removed but incentive for illegal trade in undersize rock-lobsters will be high (partly because fishermen's catch-related "bonuses" would be low). The latter, plus probable low growth and survival (hypothesis 1), would result in low recruitment into the legal size population the next season. In other words, a poor season would be followed by another poor season. (c). Catch rates would be low in years when oxygen levels remain high (perhaps due to very strong upwelling and continuous strong winds which induce mixing) because the rock-lobsters do not move inshore and density will be low (e.g. 1991). Catchability may also be reduced as the strong winds reduce effectiveness of traps. However, the rock-lobsters would exhibit higher growth and survival (hypothesis 1), a low proportion would be removed, discard mortality and illegal trade would be low and consequently, recruitment and hence availability of legal-sized animals the next season would be high. A poor season would be followed by a good season.

Hypothesis 3:
Stronger than normal southerly winds would result in increased northward drift, increased mortality of puerulus larvae as they attempt to cross the shelf and therefore decreased settlement of puerulus larvae.

Hypothesis 1 could be tested in the long term by extending this survey for several years in conjunction with growth data, and cannot be tested with the data at hand. Hypothesis 2 would require data on annual discard mortality, illegal capture of undersized animals (both currently unavailable) as well as the normal catch by size class and effort data. Although the existing data probably do not cover a long enough time period, the existence of a direct relationship between density and CPUE as demonstrated here (Figure 2.5), strongly suggests that environmental, weather and biological factors do not affect catchability (on a monthly scale) as significantly as previously thought. Therefore hypothesis 2b is probably false. Movements of rock-lobsters are, indeed, of cardinal importance to the rock-lobster fishery and if the seasonal inshore movement does not occur, catches are very poor. Both these hypotheses would result in some relationship between the environment and catch rates either in the same year or with a one year lag. In order to test hypothesis 3, one would ideally require a time series of puerulus settlement rates. However, if density-dependent effects on growth and survival are weak, variations in puerulus settlement should be detectable in recruitment across the legal size limit several years later. This hypothesis is partially tested in section three.

If hypothesis 1 is true, then the relationship between dissolved oxygen and growth and survival could be used to predict recruitment of legal-sized lobsters the following season in order to calculate TACs. If hypothesis 2 is correct, then managing the fishery by limiting or having fixed effort is irrational (as more effort will be expended for the same F when densities are low due to changes in migration pattern) and management should be by an annual TAC alone.

As regards the correlation of one or more environmental factors (such as SST, wind or sea-level) with bottom dissolved oxygen levels, none was found in this study and due to the complexity of the oceanographic mechanisms involved, none can be expected. Bailey et al. (1985) came to a similar conclusion. Therefore, no retrospective estimates of past dissolved oxygen conditions over rock-lobster reefs are possible (e.g. Pollock and Shannon 1987) and future monitoring will have to include the regular measurement of bottom dissolved oxygen concentration itself.

Maximum densities recorded here when rock-lobster were concentrated in shallow water (120/10m^{2}) were extremely high compared to other published results. For example, Pollock (1979) found a maximum of 26/10m^2 at Robben island, Barkai and Bergh (1990) found a maximum of 21/10m^2 at Malgas island (but see Barkai and Branch 1988), 31/10m^2 at Groenrivier and 21/10m^2 at Port Nolloth and MacDiarmid (1991) found a maximum of 1.6/10m^2 for Jasus edwardsii in New Zealand. An attempt will be made to address the consequences of these extremely high seasonal densities of rock-lobster for the benthos in section four.

To summarise: marked in-offshore migrations of rock-lobster occur at Luderitz in response to changes in dissolved oxygen concentration which varies dramatically both seasonally and interannually. Rock-lobster densities are directly related to monthly averaged CPUE and changes in migration pattern may have been at least partially responsible for recent declines in CPUE. If short term management decisions are to be made (such as annual Total Allowable Catches) then data on dissolved oxygen concentrations and resultant rock-lobster movements are required (in addition to conventional fisheries data) in order to properly interpret CPUE figures (e.g. Tomalin 1989, 1990 and 1991). Interannual changes in growth rates and their relationship to variations in dissolved oxygen conditions should be investigated and the possibility of carrying out meaningful annual biomass/recruitment surveys (using SCUBA diving surveys) for input into fisheries models exists.

3. LONG-TERM ENVIRONMENTAL EFFECTS ON LUDERITZ ROCK-LOBSTER FISHERY'S CATCH PER UNIT EFFORT.

3.1 INTRODUCTION

This section of the thesis will attempt to test the hypothesis that Luderitz rock-lobster catches are related in some way to changes in the marine environment (Bailey et al. 1985; Beyers and Wilke 1990; Pollock and Shannon 1987; Crawford et al. 1990). A search is made for significant correlations between CPUE at Luderitz and various environmental factors which have been measured for a sufficient period of time (wind, sea-level and sea-surface temperature).

The search for causes of variability in fin-fish stocks has focused on larval recruitment as being the "critical" life history stage (Rothschild 1986). Many authors have extracted recruitment indices from age-structured models (e.g. virtual population analyses - VPA) of fish stocks and correlated these with environmental factors (e.g. Shepherd et al. 1984). The inherent danger of this approach has been described in Walters and Collie (1988) and especially the likelihood of spurious correlations being found if errors in ageing are present (Bradford 1991). The problem is compounded in crustaceans where ageing is not possible and hence any attempt at a VPA (for example, Tomalin (1992) used size frequencies and time-invariant growth parameters) is bound to be biased (M. Bergh pers. comm.). Crustacean studies have therefore inferred recruitment from adult biomass indices with an appropriate time lag (e.g. Fogarty 1989) or, in a few cases, from direct surveys of puerulus larvae (e.g. Pearce and Phillips 1988).

Crustacean studies have been more general in their explanation of fishable stock size compared to fin-fish (where the recent emphasis is on recruitment processes) and four major mechanisms have been proposed to explain the stock size of lobsters:

(1). Environmental effects on larval survival have been proposed for Tasmanian and New Zealand rock-lobster, Jasus edwardsii (Harris et al. 1988), American lobster, Homarus americanus (Fogarty 1989), Western Australian rock-lobster, Panulirus cygnus (Phillips and Brown 1989) and Hawaiian rock-lobster, Panulirus marginatus (Pollovina and Mitchum 1992).

(2). A stock size - egg production relationship which is, in some cases modified by density-dependent effects (Fogarty and Iodine 1986; Pollock 1991; Pollock 1993).

(3). Density dependent effects on juvenile growth and survival were hypothesised to operate in Panulirus cygnus (Chittleborough 1979), Homarus americanus (Fogarty and Iodine (1986), Nephrops spp (Hill and White 1990) and Jasus lalandii (Pollock 1986). However, density dependence is difficult to demonstrate directly (Caddy 1985 and section four of this thesis).

(4). Environmental effects on juvenile and adult growth and survival (Ennis 1986; Pollock 1987; Pollock and Shannon 1987).
(5). The immediate effect of the environment on catchability has been taken into account when CPUE was used as an index of stock size (Fogarty 1989).

Pringle (1986), summarising a workshop on lobster fisheries and recruitment variability, considered that it appears that where data are available that the "life history critical stage" is usually the supply of early benthic stage puerulus larvae (Pringle 1986) i.e. the same as that for fin-fish (Rothschild 1986). No spatial or temporal data on the strength of puerulus settlement to Jasus lalandii populations have been published, but Pollock and Goosen (1991) imply that it should be highly variable due to the oceanographic environment which the larvae have to negotiate before settling.

Although hard evidence is lacking in most cases (Caddy 1986; Cobb and Caddy 1989), it appears that lobster, spiny rock-lobster and crab populations are capable of recruitment enhancement when densities are reduced by fishing. This seems to be the explanation for these populations' apparent resilience to extremely high rates of exploitation (Pollock 1993). The mechanism may be increased egg production and/or increased sub-legal growth and survival. However, under high exploitation rates when the fishery depends on only a few year classes, density-dependent effects are not strong enough to continue to damp out recruitment variation and the landings become more variable (Pollock 1993).

In the light of the above examples, it would be surprising if larval settlement was not driving Jasus lalandii catches, at least in Namibia where fishing mortality is high (Tomalin 1992) and the species is at the edge of it's range. On the other hand, Jasus lalandii is first harvested at a relatively advanced age (6-7 years), which would allow more time for density-dependent and environmental factors to affect the population via juvenile growth and mortality. However, Tasmanian spiny rock-lobster (Harris et al. 1988) and American lobster (Ennis 1986) landings have been shown to be correlated with environmental conditions about 7 years previously when they may have acted on the larvae. Another factor which may explain why the Luderitz Jasus lalandii stock could be an exception to the general rule of limitation by puerulus settlement, is that it appears that no other rock-lobster area in the world has a controlling factor as potentially variable as the low oxygen water body off the Namibian coast (section two) so that modification of puerulus settlement pulses may well occur due to later changes in sub-legal growth and survival.

Pollock and Shannon (1987) were of the opinion that environmental change was driving Jasus catches in Namibia and northern South Africa. Principally, they considered that low oxygen water had expanded since the late 1960's (due to increased phytoplankton production *per se* or reduced grazing by clupeoid fish) and that this caused the drop in catches in Namibia and the northern Cape. The implication is that environmental effects on juveniles and adults are driving the stock size. This hypothesis is essentially untestable (as comparable dissolved oxygen data are not available for different periods). However, it appears that low oxygen conditions have been observed along the Namibian coast at least since the turn of the century and rock-lobsters were stranded at Luderitz in the late 1940's probably due to an extremely low oxygen event (Annegarn and Krut 1985). It does, however, also appear that equatorward wind stress increased in the late 1970's and declined in the early 1980's (Shannon and Taunton-Clark 1989) with possible resultant effects on upwelling, productivity and, hence, low oxygen conditions (section two discusses possible pathways by which wind stress may affect dissolved oxygen concentrations). Pollock and Shannon (1987) used catch (when CPUE would have been a more sensitive indicator) but CPUE variation along the Southern African coast shows the same pattern as catch (Figure 3.1). Pollock and Shannon (1987) considered the coherence between sea surface temperature and catches and reported increased catches during generally warmer periods. They assumed that the effect would be almost immediate via increased/decreased growth rates and survival and did not appear to consider possible effects on puerulus settlement. Crawford et al. (1990) echoed this hypothesis for Namibian rock-lobster and, in addition, mentioned that restriction of rock-lobster to a narrow depth range will increase susceptibility to fishing gear and hence CPUE.

An obvious alternative hypothesis to explain long-term changes in CPUE is that they are due to a reduction in stock size caused by fishing itself. This has been demonstrated for the Namaqualand zone (Barkai and Bergh 1990). Tomalin (1992) attempted to test this hypothesis for the Namibian situation, but his methods (Virtual Population Analysis, catch curve analysis and Jones' length based VPA) were probably biased due to the assumption of constant growth and the inability to age rock-lobster (M. Bergh pers. comm.). He (Tomalin 1992) found that a decline in recruitment across the legal size was the cause of the long term decline in Luderitz CPUE and proposed several possible reasons for this (including reduction in puerulus settlement and a high discard mortality).

In summary, larval recruitment has generally been shown to be the main determinant of adult population sizes in species of lobsters and spiny rock-lobsters other than Jasus lalandii. Published literature on Jasus lalandii assumes that density-dependent and environmentally-dependent growth and mortality rates after settlement are the main causes of variation in population size. The two effects (larval recruitment and juvenile growth and mortality) would be compounded in the record of recruitment across the legal size limit, which is measured by CPUE. However, if puerulus settlement was the major factor, then correlations between environmental factors and CPUE would be lagged by 5-7 years. Conversely, if environmental effects were operating on the sub-legal or legal sizes, effects would be lagged by only a few years or be immediate.

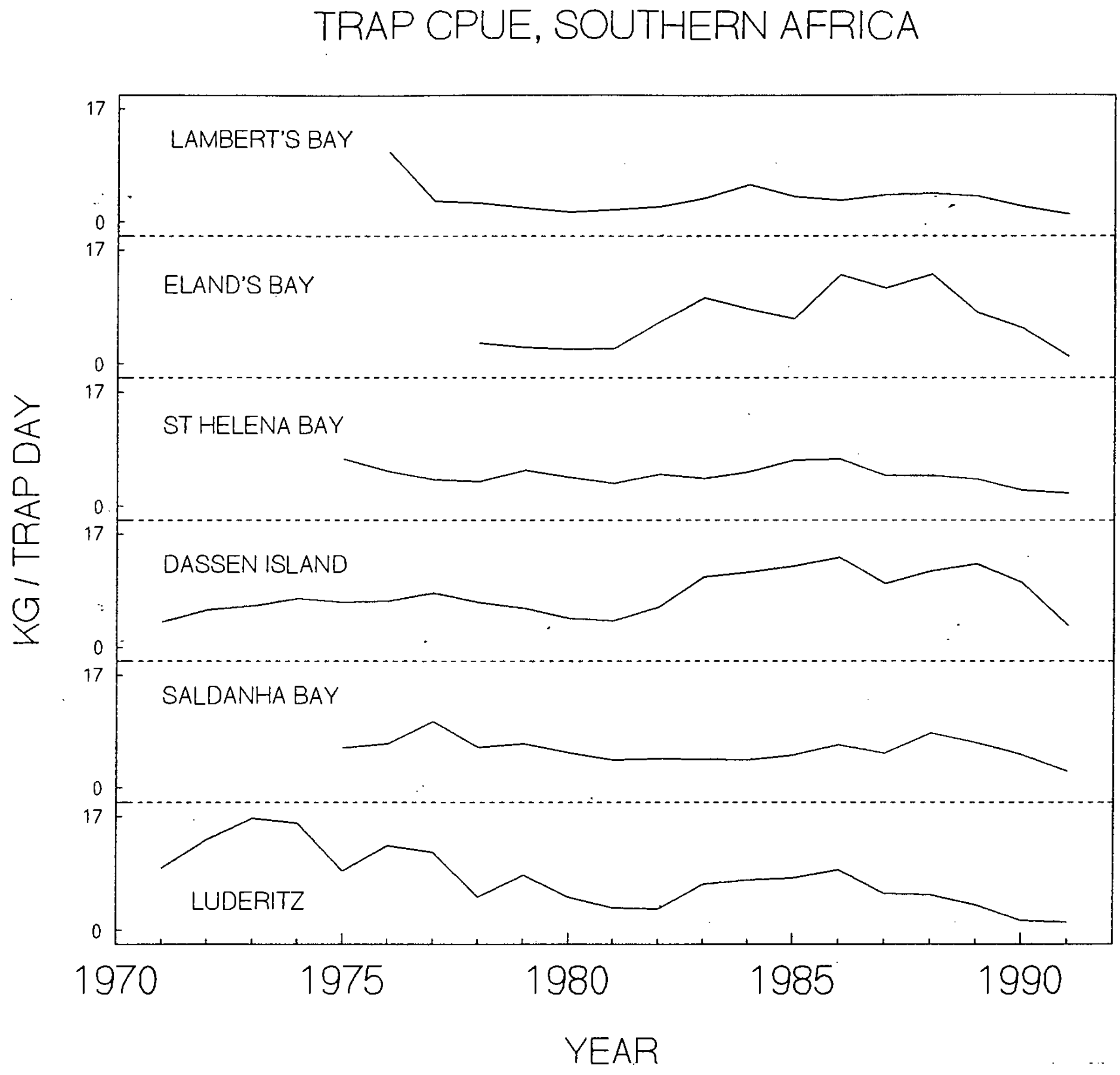

Figure 3.1 Catch per Unit effort (kg/trap day) from various areas along the Southern African coast.

This section attempts to test the hypothesis of a long-term environmental effect on Luderitz rock-lobster productivity. I use an exploratory approach (time series analysis) to determine whether there are significant cross correlations between CPUE of the Luderitz rock-lobster fishery and environmental factors and at what time lag they occur.

3.2 METHODS:

Fogarty (1989) discusses techniques of time series analysis applied to crustacean fisheries. Applying his suggestions, data were detrended and autocorrelation removed to produce "white noise" before correlations were attempted. Multiple linear regressions have to be interpreted with care; if one regresses a sufficiently large number of explanatory variables against the dependent variable, some significant correlations will be observed purely by chance. The probability of declaring a significant correlation when there is in fact no correlation (type I error) should be multiplied by the number of possible interactions (Trippel and Hubert 1990). Cross-correlations were considered significant when values were outside the range +/- 2/r*t(n) (Chatfield 1989).

Residuals were plotted against time and fitted values to check for heteroscedascity, trends and autocorrelation as well as a cumulative plot to check for normality (Draper and Smith 1981).

Catch per unit effort (from Tomalin unpubl.) was used as an index of density on the fishing ground and compared to: (a) the southerly component of pseudo wind stress; ie. wind speed squared, (Shannon and Taunton-Clark 1989), data obtained from Diaz point lighthouse; (b) offshore SST data from area 5 (Shannon and Taunton-Clark 1989), from the South African Data Centre for Oceanography (SADCO) voluntary observing ships (VOS) database; (c) sea level at Luderitz harbour (data from UCT sea level group).

Offshore SST was chosen because preliminary analysis showed a good relationship between residuals from decadal mean CPUE and residuals from offshore SST (Tomalin unpubl) using SST data from Butterworth (1988). This should give an index of whether or not a Benguela Nino or cold event (Shannon and Agenbag 1990) was occurring. Although inshore SST would be more useful for rock-lobster grounds, the VOS data for inshore SST in the region are very patchy as it is outside the shipping lanes. Luderitz harbour temperatures are available from the 1970's but were not used here as they are strongly correlated to local wind. Wind stress is an index of upwelling strength and may be related to productivity and strength of the counter current and hence dissolved oxygen levels. Sea level is a general indicator of a warm/cold event and intensity of upwelling.

Each time series (including recruitment and catchability) was detrended and monthly environmental indices deseasonalised using the DETREND and seasonal decomposition (difference from moving averages) routines in the STATSGRAPHICS package (vers 3.0). This is considered essential before any time-series analysis is carried out (Fogarty 1989) for obviously if two time series have trends (as most do), they will be significantly correlated. In addition, Box and Jenkins autocorrelation models were applied to the input (environmental) series and the same model applied to the output (CPUE) series (Fogarty 1989). Cross correlations between each environmental index and between environment and CPUE were sought using the cross correlation routine in STATGRAPHICS.

Finally, the residuals after detrending and applying an autoregression 1 model (i.e. "white noise") were used in multiple linear regression in the STATSGRAPHICS stepwise multiple linear regression routine with CPUE as the dependent variable and the following as explanatory variables:

A. First multiple regression (using wind only):
On the basis of chapter 1 four time-lags of wind stress were considered:
1. The same summer (January to March) for direct catchability effects.
2. The previous "spring" (September-December) for direct effects during male moulting season (growth and survival) or indirect effects on dissolved oxygen levels in following summer.
3. The previous summer (January to March) for direct effects on male nutrition (with consequences for the following moult increment and mortality and, hence, following season's recruitment) and indirect effects on following summer's dissolved oxygen levels.
4. The summer six years previously (suggested by cross-correlation results) for effects on settlement of puerulus larvae (possibly due to wind-induced drift affecting puerulus survival as they attempt to cross the shelf).

B. Second multiple regression:
A second multiple regression was carried out using wind, SST and sea-level for summer and spring but with only 0 and 1 year time lags.

3.3 RESULTS

A. Trends, seasonality and auto-correlation within variables:

a. Luderitz sea-level. The raw data for sea-level exhibits 6 outlying points in 1965 and 1966 which were removed. There was then an overall increase in sea level (Figure 3.2). However most of the increase was during the 1960's. There was a highly significant seasonal signal with higher levels in summer months compared to winter. After detrending and deseasonalisation (Figure 3.2), there remained significant autocorrelations and partial autocorrelations at time lags of 1 and 3-6 months. An autoregressive 1 and moving average 5 model removed these, but the original residuals were used in further analysis. When the mean summer values were used, the autocorrelation (now between years) disappeared.
b. Diaz point southerly component of wind stress. There was a very slight trend of increase with time and a strong seasonal component with high winds in November-December and low winds in winter (Figure 3.3). The residuals (after detrending and deseasonalisation) were normally distributed (significant at 0.01, CHI squ test) but showed significant autocorrelation at 1 and 3-5 months lag with significant partial autocorrelations at 1 and 3-6 months lag. A marginally significant lag at 12 months for both

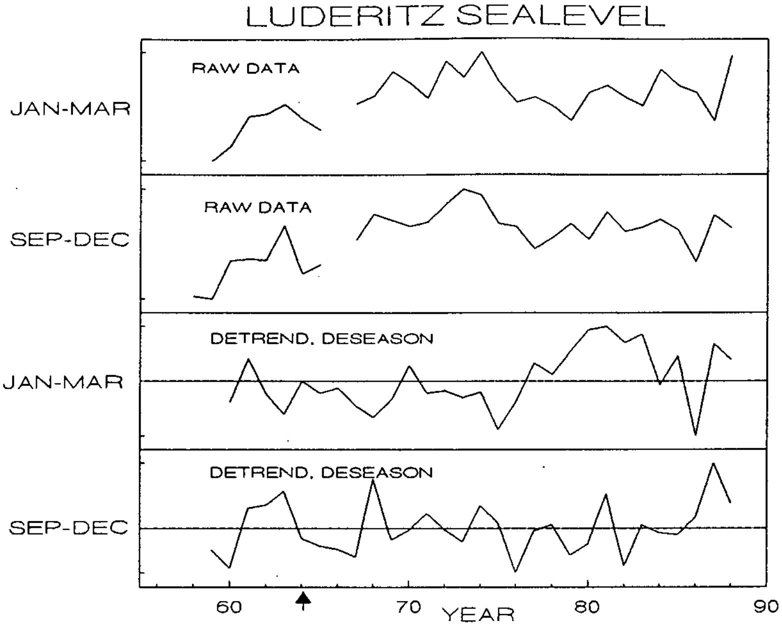

Figure 3.2 Time series of sea-level at Luderitz harbour, raw data and detrended and deseasonalised for "spring" and "summer" (see text). The arrow indicates a break in the data and possible shift in the datum point (data from UCT sea-level group).

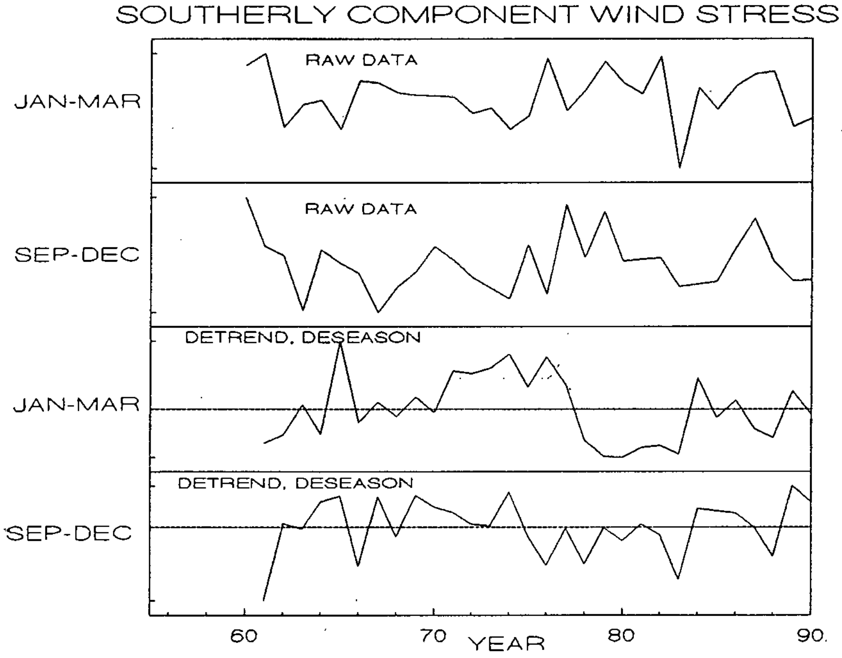

Figure 3.3 Time series of southerly component of "pseudo" wind stress (m/sec^3) from Diaz Point lighthouse. Raw data and detrended and deseasonalised for "spring" and "summer" (see text).

suggests that the seasonality may not have been completely removed. This pattern suggests that a windy month is likely to be followed by another windy month. The summer means were still autocorrelated (i.e. windy summers would be followed more often than expected by another windy summer the next year) and this was removed using an AR1 model.

c. Offshore SST. Strong seasonality was present with highest temperatures in February-March and lowest in August-October (range about 5° C, Figure 3.4). After seasonality was removed a positive trend remained from around 19.4° C in 1960 to 19.9° C in 1989 with large scatter around those values. Residuals are normally distributed (sig. level = 0.077, CHI squ test). Again, residuals are significantly autocorrelated and partially autocorrelated at 1 and 3-6 months lags. The same argument applies as for the wind. Summer means were not autocorrelated.

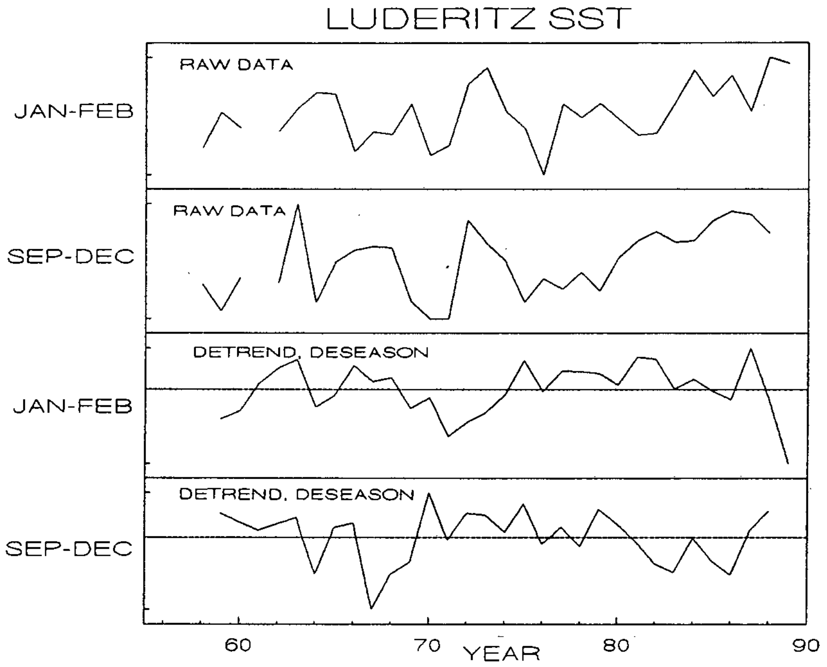

Figure 3.4 Time series of sea-surface temperature from an area offshore from Luderitz. Raw data and detrended and deseasonalised for "spring" and "summer" (see text). V.O.S. data from S.A.D.C.O.

Cross-correlations between SST and wind residuals indicated strongest negative relationships at lags of 0 and 1 months suggesting stronger winds result in lower SST offshore, as one would expect in this upwelling area. On regressing SST against wind there is indeed a significant negative slope but this explains only 7 % of the variance in SST suggesting that warm and cold "events" are remotely forced by events in the tropical Atlantic (Shannon and Aggenbach 1990).

d. CPUE.

There was a significant declining trend in Luderitz CPUE and a significant autocorrelation at a one year lag (Figure 3.1). These were removed.

B. Cross correlations between CPUE and wind.

Detrended and AR1 residuals from the wind and CPUE time series showed the cross correlations below:

LAG	CORRELATION
0	0.4
1	0.11
2	-0.12
3	0.09
4	-0.09
5	-0.1
6	-0.32
7	0.14
8	0.07

A large positive correlation was observed at 0 lag and a negative one at 6 years. However, these were not significant (ie. < 0.44). Nevertheless, the results are consistent with an immediate catchability effect and an effect on puerulus recruitment (the age to recruitment to the fishery at 65mm carapace length is probably 6-7 years, Tomalin 1992).

C. Multiple linear correlations:

1. A stepwise multiple linear correlation between CPUE (dependent variable) and summer and spring wind-stress at 3 time lags (0,1 and 6 years) resulted in one significant variable being chosen - summer wind 6 years previously ($R^2 = 0.25$, $P = 0.014$). If the type I error probability is adjusted for the number of possible correlations (6) the following is obtained:

$$P = 0.014*6 = 0.084$$

i.e. the result is significant only at the 0.1 level. Residuals are normally distributed, do not demonstrate significant "runs" and are heteroscedastic (Figures 3.5 and 3.6)

2. If all the summer and spring environmental factors at two time lags (0 and 1 years) are regressed against CPUE (12 interactions), then only summer wind of that year is significant ($R^2 = 0.38$, $P = 0.0048$). Again adjusting for number of possible correlations, the real probability of a type I error is:

$$P = 0.0048*12 = 0.058$$ Again, this is marginally significant.

To summarise, it appears that, although correlations are not highly significant, marginal correlations exist between environmental factors and CPUE both in the same year and six years previously. However, the present year effect is not significant in the presence of the six year lag indicating that most of the effect is due to the latter.

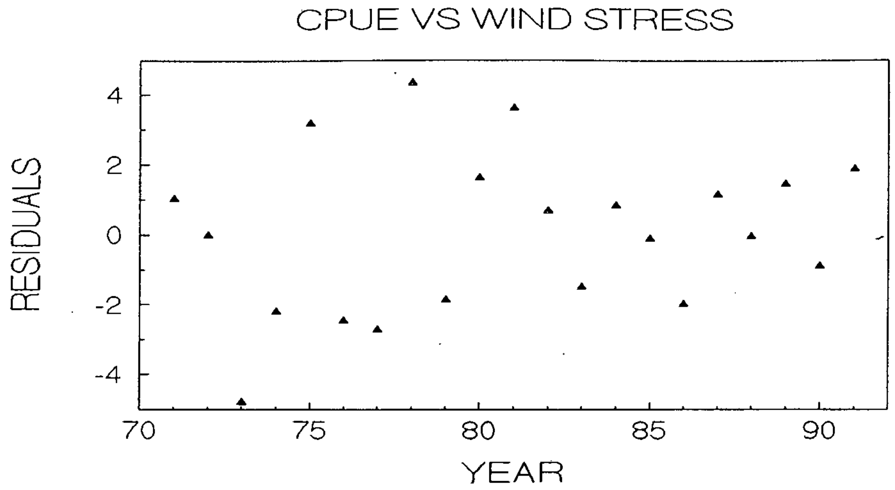

Figure 3.5 Residuals of CPUE vs wind stress lagged by six years (both series detrended and AR1 model applied) plotted against time.

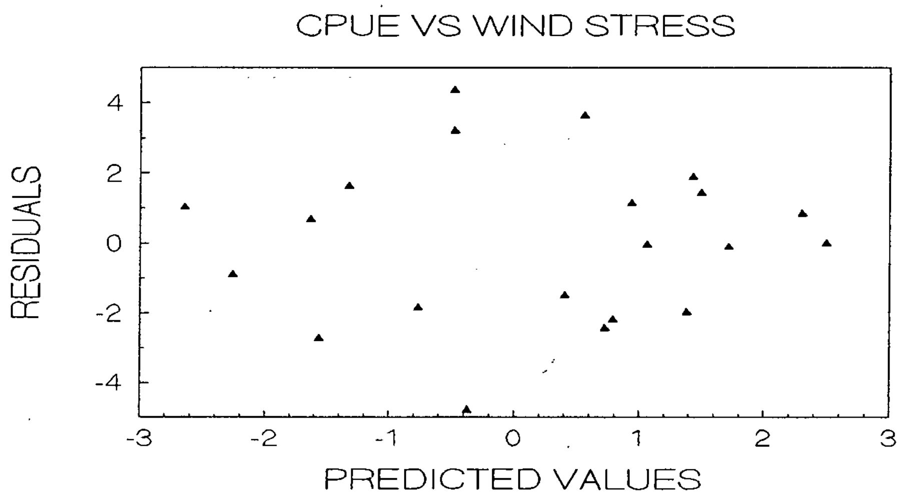

Figure 3.6 Residuals of CPUE vs wind stress lagged by six years (both series detrended and an AR1 applied) plotted against the predicted value.

3.4 DISCUSSION:

The marginally significant negative correlation between CPUE and an environmental variable (wind stress) 6 years previously (corresponding to estimated age at legal size) indicates that this may be due to a reduced settlement of puerulus larvae during years with strong summer winds. Is this a spurious correlation?

Walters and Collie (1988) point out how easy it is to find spurious correlations when numerous potential correlations are screened (as in stepwise multiple linear regression) and/or such data are autocorrelated. Fogarty (1988) recommends that trends and autocorrelations be removed before analysis and that the same models be applied to input and output data and this was done. Walters and Collie (1988) recommend that, in reporting the outcome of multiple correlations, the number of possible correlations be reported, that post hoc rationalisation be avoided unless independent data are available, and that evidence about whether the correlation holds for the same species in other areas should be reported (or other species in the same area). Box and Jenkins (1970) state that at least 50 (and preferably 100 !) observations should be available. Hence the present results (and most other efforts of this nature) are obviously preliminary. The only real test is whether the correlation will remain after a number of further data points have been collected at a rate of one per year (Walters and Collie 1988). When additional tests of this nature have been done, preliminary correlations often break down (e.g. Drinkwater and Myers 1987; Mann 1993). Probabilities were adjusted for the number of possible correlations using the method of Trippel and Hubert (1990) although Walters and Collie (1988) state that full compensation is not possible even with the common technique of splitting the data set into model estimation and model testing sections.

Using Walters and Collie's (1988) other criterion (i.e. using comparisons with other species or between areas), there is strong evidence from other lobster fisheries that larval settlement is linked to catches several years later (Fogarty 1989, Phillips and Brown 1989, Polovina and Mitchum 1992, Harris et al. 1988). In addition, this seems a plausible hypothesis to explain the observed synchrony in catch rates for Jasus lalandii along the whole Southern African coast, although a similar time series analysis should be done for each area separately. Although *post hoc* rationalization should be avoided, the mechanism of increased mortality of puerulus larvae when southerly winds are strong is a convincing one.

Arguments against the larval recruitment hypothesis are:

(1) CPUE (and hence recruitment across the legal size) shows no particular decline from 1971 to 1989 in southern Cape areas (Figure 3.1) whereas it does in Namibia. However this may be due to other processes such as a high and increasing discard and fishing mortality in Namibia (Tomalin 1992).

(2) The recent (1990 - 1992) reduction in CPUE has been shown to be due to reduced growth (and hence recruitment across the size limit) in all areas in the Cape, implying that Luderitz should be the same (Shannon et al. 1992). The implication is that previous declines and increases were also due to variations in growth and not larval settlement. However, section two advances the alternative hypothesis that the reduction in CPUE at Luderitz was, at least partly, due to a change in migration patterns and section four shows that no reduction in food supply was apparent at Luderitz during the recent declines in CPUE. Reduction in food supply has been proposed as a possible cause of reduced growth in the Cape (Shannon et al. 1992).

(3) Barkai and Bergh (1990 and 1992), using a size-based population model, concluded that most of the variation in CPUE was due to variations in catch, both in Namaqualand and at Dassen Island. This implies that environmental effects are unimportant (at least up until 1990) and that variations are due to the population's response to fishing pressure. However, does this explain the synchrony in rise and fall of catches along the whole Southern African coastline?

The techniques used here of seeking correlations between environmental indices at various time lags and CPUE should be seen as merely an exploratory approach (Drinkwater and Myers 1987) with the aim of detecting whether there are obvious environmental effects on CPUE and, if there are, at what stage of the life cycle those effects are operating. These insights can then be incorporated into a more "structured" (Fogarty 1989) model of rock-lobster populations to decide whether this knowledge should affect management or monitoring strategies (Walters and Collie 1988). For example, the effect of environmentally-induced decreased growth of Jasus lalandii has been simulated using a size-based matrix progression model and a risk assessment approach (Barkai and Bergh 1992). Pre-season growth rates have been monitored in the Cape for several years and research is now taking place to attempt to predict these approximately six months in advance of the season (A. Cockcroft pers.comm.). However, pre-recruit density has not been monitored even though this would potentially provide a longer warning period and would not be dependent on knowledge of any environmental forcing mechanisms.

Interannual trends in West coast environmental indices have been extensively discussed (Walker 1987; Shannon et al. 1990; Taunton-Clark and Shannon 1988) and Siegfried et al. (1990) attempted to predict effects of global warming on West coast fisheries. Considering the rock-lobster fishery, Siegfried et al (1990) were uncertain as to whether the extent of low oxygen water would increase or decrease with global warming, but a phase of increased winds favouring upwelling would probably be followed by a reduction in such winds. Empirical results from this section imply that that would result in a decline in puerulus settlement followed by an increase, with resultant effects on the fishery six years later. Mann (1993) concludes that although evidence is mainly correlational, there is "strong circumstantial evidence that large-scale oceanographic processes have a major influence on the rise and fall of fish stocks world-wide". He considers that "implications for management of the stocks is profound, calling for little less than a revolution in the approach to the problem". Caddy (1985), referring to commercially highly valuable crustaceans, argues that fishing mortality is invariably very high (and next to impossible to reduce) and, hence, knowledge of recruitment and the stock-recruitment relationship is vital. He argues that stock size, area of juvenile habitat, density of predators or competitors and environmental factors affect recruitment to a greater or lesser extent and discusses a suite of possible models to account for them. Other practitioners of fisheries stock assessment disagree, arguing that "benefits to be gained in fish yield from considering environmental factors are... not worth the cost of data collection" (Hilborn 1992). They maintain that a good feedback control system which is robust to uncertainty (including environmental effects) is all that is required (Butterworth et al. 1992; Hilborn 1992).

In conclusion: although statistical evidence is weak, there are indications that, at least at Luderitz, environmental conditions during the fishing season affect CPUE but that the major environmental effect is on puerulus settlement several years before recruitment of rock-lobster to the fishery. Circumstantial evidence from other lobster fisheries strongly supports this statement.

4. THE RELATIONSHIP BETWEEN ROCK-LOBSTERS AND BENTHIC SPECIES DENSITIES.

This section of the thesis deals with interactions between rock-lobsters and the benthic species assemblage found in association with them. Three specific interactions are considered:

(a) The effects of variation in rock-lobster predation on benthic species densities and size distributions.

(b) The question of whether variation in "prey" species densities affects rock-lobster growth at Luderitz.

(c) Whether temporal variation in densities of the whelk, Burnupena papyracea, affects the distribution of rock-lobster.

The introduction surveys world-wide knowledge of interactions between the benthos and lobsters and spiny rock-lobsters and then concentrates on the Southern African situation. Two alternative hypotheses will be proposed to explain the observations made at Luderitz during this study and predictions arising from each hypothesis are tested.

4.1. REVIEW OF LOBSTER - BENTHOS INTERACTIONS:

A. Lobsters, urchins and sea-weed.

There is an enormous published literature on the relationship between mobile predators (fish, crabs and Homarus americanus), sea-urchins and sea-weed in Nova Scotia. This system was initially modelled as an energy-flow diagram (Miller et al. 1971) and later as the product of "strong interactions" (summarised in Mann 1982). Mann's (1982) hypothesis (based on "very strong" circumstantial evidence in both time and space) was that reduction of lobster densities due to fishing diminished predation on urchins. Urchin densities increased and formed dense feeding aggregations that consumed the kelp forests, which were replaced by "barrens" consisting of coralline algae. The resulting decrease in productivity and cover for lobster caused further declines in lobster stocks (Mann 1982). Others argued against the "strong interaction" hypothesis and suggested that recruitment rates of planktonic larvae (Hart and Scheibling 1988) and disease outbreaks (Miller 1985) were driving the sea-urchin population size. Turning the issue around to the effect of the benthos on lobster, no evidence was found for a relation between increased kelp biomass and increased lobster survival or growth although there was an unexplained direct relation between relative kelp abundance and lobster landings in the same year (Miller 1985). Elner and Campbell (1987) found very similar diets for lobsters from barren areas and those from kelp grounds, with mussels being the most important constituents. They concluded that food availability did not affect growth. In contrast, Ennis (1973), found mostly crab remains in lobster stomachs.

Elner and Vadas (1990) summarised research and analysis of the sea-urchin problem and contended that the procedures used consisted primarily of "weak inference" and retained the keystone "paradigm" for Homarus americanus by *ad hoc* revisions instead of experimentation and refutation of clear alternative hypotheses. They concluded that ecological research had been inadequate to expose the mechanisms behind the observations because changes in proposed scenarios were largely due to the force of natural events (reduction in urchin density due to disease and subsequent recovery of kelps).

Tegner and Levin (1983) contend that reduction of spiny lobster (Panulirus interruptus) density by fishing resulted in the release of sea-urchin populations in southern Californian kelp beds and subsequent destruction of those kelp beds in the 1950's (i.e. spiny lobster were the keystone species). They asserted that a reduction in numbers of sea-otters could not be responsible for the increase in sea-urchins as they became locally extinct 130 years previously (Tegner and Levin 1983). Experimental work has been done in the Gulf of Maine where increasing the abundance of a suit of large, mobile predators (fish, crabs and Homarus americanus) by providing artificial shelter reduced the abundance of small benthic species (especially urchins) in the vicinity of such shelters (Ojeda and Dearborn 1991).

Andrew and MacDiarmid (1991) found no evidence for a relationship between New Zealand spiny rock-lobsters, Jasus edwardsii and the local sea-urchin. It had been suggested that Southern African sea-urchins (Parechinus angulosus) may a play a similar role to North American ones and Fricke (1979) showed that P. angulosus has a significant effect on kelp recruitment in Southern Africa. However, P. angulosus appeared incapable of affecting existing kelp beds, possibly due to their inability to sever holdfasts (Fricke 1979), their susceptibility to the extreme wave action prevalent in the Cape and the fact that they do not form "feeding fronts" (Fricke 1980).

In summary, it appears that, world-wide, the effect of sea-urchins on algae is undisputed whereas the role of predation (including that by commercially exploited lobsters and spiny-lobsters) in controlling sea-urchins is controversial.

B. Spiny lobsters, feeding and the benthos.

Spiny lobster feeding is summarised in Joll and Phillips (1984) quoting references stating that among spiny lobsters, Jasus lalandii, Panulirus homarus and Jasus novaehollandiae consume primarily molluscan prey whilst Panulirus argus and P. interruptus consumed algae. Studying Panulirus cygnus diet, Joll and Phillips (1984) found a high proportion of molluscs were consumed in an area of high rock-lobster growth but mostly coralline algae was consumed in a low-growth area. Joll and Phillips (1984) found no support for Chittleborough's (1975) hypothesis that under moderate food shortage, growth of smaller lobsters and females would be more retarded than larger and male animals. In addition, Joll and Phillips (1984) found no relationship between density, mortality and diet (between years), further questioning whether food supply was a limiting factor. However, their argument is weakened by the fact that they did not measure mortality at the low-growth site. Jernakoff et al. (1987), using evidence of much larger nocturnal foraging ranges than previously estimated also rejected Chittleborough's (1975) hypothesis that limited food supply affects growth and survival of juvenile Panulirus cygnus. A separate line of evidence suggesting only a limited role for density-dependent growth and survival is the close relationship between indices of puerulus settlement and catches four years later in Panulirus cygnus (Phillips and Brown 1989). Joll and Phillips (1984) did, however, turn the argument around and hypothesised that, due to their high densities, P. cygnus should control the shallow reef communities of Western Australia. This assertion does not appear to have been tested or explored further.

The effect of Jasus edwardsii on the benthos in New Zealand has not been documented, but MacDiarmid et al. (1991) considered that it would be limited to a small range around shelter due to this lobster's small foraging range. In contrast, P. cygnus forages widely on sea-grass beds distant from it's daytime shelter (Jernakoff 1987). Jasus edwardsii is similar to the Cape rock-lobster, Jasus lalandii, in this respect. However, J. edwardsii occurs at much lower densities than J. lalandii (Macdiarmid et al. 1991). Thus, it is, perhaps, not surprising that no strong effects on the benthos have been noted for J. edwardsii. The inverse effect, that of food availability on growth and mortality does not appear to have been described for Jasus edwardsii.

C. Jasus lalandii and it's interactions with the benthos.

The relationship between Jasus lalandii and its associated benthos in Southern African waters has been particularly well studied (summarised in Branch and Griffiths 1988) compared to lobster-benthos relationships in other parts of the world (apart from the North American lobster-sea-urchin-kelp interaction discussed above). Five generalisations or hypotheses have been proposed at various times for interactions between Jasus lalandii and the benthos. The first three relate to the effect of the benthos on rock-lobster and the last two to the effect of rock-lobster on the benthos.

(1). A positive relationship exists between rock-lobster densities and those of the ribbed mussel, Aulacomya ater (Newman and Pollock 1977). Newman and Pollock's (1977) original observation compared Cape Peninsula and Dassen island whilst another example of a clear correlation is apparent from data in Field et al. (1980) from seven sites extending around Cape Point. The latter observations crossed the limit of distribution of both Aulacomya and Jasus and should therefore be treated with some caution whilst the former compared only two sites. Barkai (unpubl) found no significant linear relationships between rock-lobster densities and benthic species in a study ranging from Port Nolloth to Cape Point. Hence this generalisation is not generally true.

(2). Rock-lobster productivity decreases to the north of the Southern African west coast due to increasing incidence of low oxygen water, which leads to "overcrowding" and density-dependent effects on growth and mortality in the shallows (Pollock and Beyers 1981). Pollock and Beyers (1981) compared growth rates between areas ignoring the known variation within "grounds" and using Marshall rocks as typical of Namibia. Later work by Beyers and Wilke (in press) showed that other areas of Namibia had growth rates only slightly lower than those in the Cape. In general, variation in growth rate seems to be larger within "grounds" (on a scale of kilometres) than between areas (tens to hundreds of kilometres) and therefore demands explanation on a local scale (see hypothesis 3). Natural mortality has not been determined on an area-by-area basis, but Pollock (1987) explicitly modelled the effects of density dependent growth rates at Robben island and Port Nolloth and adjusted natural mortality rates to "explain" observed size distributions. However, Barkai and Bergh (1990) explained these same size distributions in terms of low growth, a uniform natural mortality (between areas) and an overwhelming effect of fishing. Sustainable yields per unit area have not been estimated for all regions,hence this generalisation awaits rigorous testing.

(3). Rock-lobsters are food limited at least in some parts of their range (Newman and Pollock 1974; Pollock and Beyers 1981). This applies even in areas of high mussel biomass if mussels exceed the critical consumable size for the size of rock-lobster present (Pollock 1979; Griffiths and Seiderer 1980). A corollary is that growth and mortality should be density-dependent, and fishing (by reducing density) should result in higher growth and survival of the survivors, thus maintaining stable yields (Chittleborough 1979; Seiderer et al. 1982). Naturally, this has considerable fishery management implications and was one of the arguments (Dreosti 1966) which led to the abandonment of a legal size-limit in the Namibian fishery during 1968 and 1969. The consequences of size-dependent availability of mussels to rock-lobster were modelled by Wickens and Field (1988) in the context of harvesting strategies, but no statement could be made on food limitation in the field.

The hypothesis of food limitation was originally based on a relation between biomass of available benthos and growth rates at various scales (Newman and Pollock 1977). Densities of rock-lobsters (as measured by trap CPUE) were approximately equal between areas of different growth rates within Dassen island (Newman and Pollock 1974) but Aulacomya was more common in the high growth area. In contrast, CPUE was double in areas of high growth rate compared to areas of low growth rate in the Saldanha-Columbine region (Pollock et al. 1982) and densities and growth rates were higher at Dassen island than the Cape Peninsula (Newman and Pollock 1977). In both these areas, more Aulacomya were present in areas of high growth although the per capita availability of Aulacomya to rock-lobsters was not calculated. Griffiths and Seiderer (1980) calculated that annual available energy provided by mussels at Robben island (taking into account the maximum size which rock-lobster can open) was only 32% of that consumed by rock-lobster in the laboratory. In order to test the basis of the food limitation hypothesis thoroughly, a compilation of available food biomass per m^2 (calculated from size distribution of mussels and rock-lobster), corresponding densities of rock-lobster, and growth rates needs to be done for the whole geographic range of Jasus lalandii and at various spatial scales. No study has been published on temporal variability in food availability, but a reduction in available food has been stated as the reason for the recent declines in rock-lobster growth rates and subsequent yield to the South African fishery (Shannon et al. 1992).

Barkai and Branch (1988b) called into question the whole basis of the food limitation hypothesis by showing that rock-lobster can feed (and apparently grow normally) using "unorthodox" food sources (e.g. barnacle recruits and planktonic mysids) which are not detected in normal benthic surveys. Later work on the direct effect of low oxygen water (Beyers et al. in press) showed that a reduction in growth rate may be caused by low oxygen conditions *per se*. Hence, an appeal to "overcrowding" and food limitation to the north of Jasus lalandii's range to explain reduced yields was, perhaps, unnecessary. As in the case of Palinurus cygnus, it appears that the evidence to support density-dependent growth and mortality due to food limitation is limited and that an experimental approach (manipulation of food supply) is required in order to test the hypothesis.

It appears that the above three generalizations are based on limited data and may not survive close scrutiny. In order to avoid sterile paths of research, it is important that ecological patterns are properly quantified before predictive hypotheses to explain them are proposed and experimentally tested (Andrew and Mapstone 1987). This is one of the aims of this section.

The following two hypotheses, while not necessarily incompatible with food-limitation, consider the effect of rock-lobsters on the benthos.

(4). Rock-lobster are keystone species and regulate the species abundance and size composition of shallow subtidal benthos on hard substrata (Barkai and Branch 1988a; Branch et al. 1987; Branch and Griffiths 1988). At high densities, rock-lobsters consume all Choromytilus recruits and most Aulacomya, leaving an algal-dominated benthos. In the absence of rock-lobster predation, Choromytilus outcompetes Aulacomya and urchins eliminate algae, resulting in a multilayered Choromytilus bed (with many associated species). A prediction of this scenario would be that mussel densities (particularly Choromytilus) are inversely proportional to rock-lobster densities (assuming equivalent predation rates between areas). Intermediate levels of rock-lobster predation could favour Aulacomya (by reducing the competitive dominant, Choromytilus) and result in a positive relationship between rock-lobster density and Aulacomya biomass (i.e. the same prediction as scenario 1 outlined above). The experiments reported in Branch et al. (1987) could also be used to argue that the whelk Burnupena papyracea is a keystone species since, at sufficiently high densities, it has been shown to exclude rock-lobsters in a particular area. In addition to the effect of rock-lobster predation on benthic species densities, Pollock (1979) explained the bi-modal size distribution of Aulacomya at Robben and Dassen islands in terms of rock-lobster predation. Barkai (unpubl.) similarly described bi-modal size distributions for most Burnupena spp, Choromytilus and Aulacomya in areas where rock-lobsters are dense. Size distributions for these species were all unimodal in areas where rock-lobster densities are low, and those for Burnupena papyracea (which is protected from rock-lobster predation by a commensal bryozoan) are unimodal in all areas irrespective of rock-lobster densities (Barkai unpubl).

(5). Benthic communities can exist in two extreme stable states: (a) an algal-dominated state associated with high rock-lobster densities and (b) a Choromytilus/whelk-dominated state associated with very low rock-lobster densities (Barkai and Branch 1988a and 1988b). The whelk, Burnupena papyracea, reaches very high densities in the latter state and excludes rock-lobster by reversing the normal predator-prey interaction between the two species (Barkai and McQuaid 1988), thus causing that state to be stable. The stability of the first state appears to rest on the continued high density of rock-lobster which survive on mussel and barnacle recruits and unconventional prey (Barkai and Branch 1988c). This hypothesis and it's predictions have been very well tested in the series of papers quoted above, but only at two sites (Marcus and Malgas Islands) within one area (Saldanha Bay). It is unclear as to whether the states are to be considered "attractors" (Peterman et al. 1979) in the sense that an assemblage of benthic species in an intermediate state would tend to move towards one or other of the two extreme states. If they are, and the mechanism is general, one would expect a large collection of samples of benthic species assemblages from the Southern African region to be classified into one or other of the two states. It appears however, that most benthic communities are intermediate between these two extremes. Therefore, either the two states are not attractors but are stable if some event causes the benthos to fall into one of the extremes, or the hypothesis is not generally applicable for the whole west coast. G.Branch (pers. comm.) has suggested that stability is maintained at the two islands where the original study was done because they are isolated from other rocky areas by extensive areas of sand flats (which Jasus lalandii does not cross) which may make them unique on the West coast. Most off-shore reefs where commercial fishing takes place consist of much larger areas of rocky bottom.

Two key questions apply to this scenario: (1) can the alternative states alternate in a given area and (2) what might be the cause of such a change (Branch et al. 1987)? This has management implications for the fishery: if fishing, by decreasing density of large rock-lobster, causes the density of whelks to increase, the system may move into a stable whelk-dominated state of low rock-lobster density. The above two hypotheses have been well tested experimentally but were designed to answer a specific question: why does the benthos of Marcus and Malgas islands differ? For this reason their generality for the Southern African west coast as a whole is in question.

All the above scenarios operate within a larger "paradigm": that either the benthos affects rock-lobster and/or vice versa. Branch et al. (1987) assert that sub-tidal communities are stable due to the long-lived nature of the species involved (rock-lobster and mussels) and therefore they should show strong species interactions. In general, benthic populations at a particular site, may not always be particularly stable in time (due to variation in recruitment of sessile species and the intensity of rock-lobster predation, for example). This may make testable predictions (such as correlations between rock-lobster and mussels) very difficult. Logically, an alternative to the "strong interaction" paradigm is that interactions are weak and that benthos and rock-lobster vary independently. This may be due to a "supply-side" ecology (Underwood and Fairweather 1989), or to variations in density due to local migrations of rock-lobster, etc. It is interesting that the "supply-side" paradigm (recruitment of puerulus larvae) seems to be the current explanation for variation in Panulirus cygnus population sizes (Philips and Brown 1989) whereas food limitation and density-dependence were originally proposed (Chittleborough 1979).

Recent theoretical work on interspecific interactions includes the concept of a "metapopulation" made up of more or less isolated "local populations" and considers rates of predation and competition within local populations, rates of dispersal between local populations and disturbance on various scales (Caswell and Cohen 1991). The model therefore includes all the above scenarios and hypotheses and it appears that almost all the observed patterns can be generated by adjusting the different rates of interaction between scales. Mussels, whelks and algae could be considered to be local populations (interacting on a scale of tens of metres) with rock-lobster as one of a number of more-or-less random disturbance factors. Perhaps this is a more suitable framework in which to place future research on rock-lobster - benthos interactions in order to address the whole west coast?

In summary, there seems to be a general (world-wide) consensus that mussels can out-compete other benthic species such as barnacles (Menge 1976; Paine 1974) or algae (Dayton 1975) but are, in turn, often controlled by predators such as gastropods (Menge 1976), sea-stars (Dayton 1975; Paine 1976) or spiny rock-lobster (Barkai and Branch 1988c; Joll and Phillips 1984; Ojeda and Dearborn 1991; Pollock 1979). The early studies all ignored "unobservables" such as planktonic recruitment and other mobile predators (Edwards et al. 1982) and so failed to test all alternative hypotheses. The hypothesis that mussels compete strongly for space, but are, in general kept at a low density by a "keystone" predator (hypothesis 4) can be considered to have been strongly corroborated (in the sense of Popper 1980) for Choromytilus and Jasus lalandii under specific circumstances. However, it is also apparent that Popperian science has not been applied consistently to the alternative hypotheses relating to interactions between South African rock-lobsters and the benthos.

4.2. INTRODUCTION.

This section of the thesis addresses the potential role that rock-lobster play in modifying the benthos of Luderitz reefs and is the first to document temporal changes in rock-lobsters, benthic species and the physical environment in a single area for a reasonable length of time in Southern Africa. The benthic species assemblage monitored was intermediate between the two extremes described by Barkai and Branch (1988a) and may throw some light on the question of transition between, and the temporal stability of, those extreme states (Branch et al. 1987) and the generality of the alternative stable state hypothesis for west coast reefs. The study is similar to that undertaken by Barkai (unpubl.) on the Cape west coast except that the emphasis is on temporal rather than spatial variations.

The approach taken can be classified as a "natural experiment" (sensu Diamond 1986) or "mensurative experiment" (Hurlbert 1984) because rock-lobster density was not under the control of the experimenter. This type of experiment can only yield "tentative conclusions and patterns for further testing" (Elner and Vadas 1990) and is less powerful than experimental manipulation for hypothesis testing, but it does have the merit of being able to examine relatively large-scale patterns over long periods (Andrew and Mapstone 1987).

The central question to be addressed in this section is: what is the effect of the dramatic seasonal and interannual changes in rock-lobster density on benthic species density and size structure? To answer this, three steps were taken: (1) determination of what rock-lobster in the Luderitz region eat and how their diet is related to available benthos, (2) ascertain whether there were significant differences in the prey spp. between sample dates (using ANOVA) and (3) a determination of whether these differences were related to corresponding differences in rock-lobster densities or physical factors (using regression analysis). A related question arises: are there significant differences in benthic species assemblages (species densities and size compositions) between areas within the Luderitz region and are these related to mean differences in rock-lobster density?

Two alternative hypotheses and associated mutually exclusive predictions will be tested:

(1). Benthic species densities are driven by fluctuations in recruitment and rock-lobster predation has little effect on benthic communities. Predictions of this are that:

a. Benthic species densities should be uncorrelated with rock-lobster densities both in time and space.

b. Irrespective of rock-lobster densities, Choromytilus should be more common than Aulacomya in all areas due to its superior ability to compete for space (Barkai and Branch 1988c).

c. If recruitment is sufficiently discrete through time, one should be able to follow a progression of modes in the size-frequency distribution of potential prey species through time and their overall size frequencies should be unimodal.

(2). Rock-lobster predation controls benthic species and new recruits of prey species are rapidly consumed. Predictions are:

a. Prey species densities should be negatively correlated with rock-lobster densities through space and time.

b. Due to their thicker shell and greater resistance to predation (Griffiths and Seiderer 1980), Aulacomya should be relatively more dense than Choromytilus when rock-lobster are present at high densities.

c. In areas where rock-lobster are abundant, size frequencies of mussel prey species (Choromytilus and Aulacomya) should be bi-modal due to size selectivity of rock-lobster predation. Although this may also be true of whelks (Barkai unpubl., but see Juanes 1992), whelks are not examined here because size selective predation by rock-lobster on whelks has not been adequately described experimentally.

There may or may not be selectivity for certain species under both hypotheses so selectivity cannot be used to test between them. Similarly, rock-lobster might eat resources normally undetected in benthic surveys (e.g. barnacle recruits) under both hypotheses and mean size of prey may be either less (only new recruits survive) or greater (refuge is found in size) under the predation hypothesis, therefore these criteria cannot be used to distinguish between the two competing hypotheses.

This section will attempt to demonstrate that whilst the hypotheses of alternative stable states and rock-lobster as keystone predators explain certain extreme situations in Southern Africa, the more common intermediate states are probably controlled by other factors.

The converse issue - whether the benthos influences rock-lobsters - is explored in terms of two interactions:

(1) Whether variations in the density of Burnupena papyracea have any effect on rock-lobster densities.

(2) Although the effect of benthos (food supply) on rock-lobster growth and mortality was not explicitly examined during the period of the study, available data on growth rates will be examined to see whether they bear any obvious relationship with benthic standing stocks. In addition, the issue of the relationship of temporal variation in rock-lobster food supply to the recent reduction in landings will be briefly discussed.

4.3. METHODS

A. Benthos.

Benthic macrofaunal densities were estimated *in situ* during dives when rock-lobster densities were measured (see section two). Sampling was conducted by counting numbers per 1/4 m^2 (whelks and urchins) or estimating percent cover (mussels, sponges, brittle-stars, algae) in 4 to 10 quadrats (1/4 m^2) randomly chosen 2m apart along a 20m weighted bottom line. Initially, on SW Blinder, the above samples were conducted within a 10 m^2 strip marked by a chain and a surface buoy. Four such marked strips 200-300 m apart were done between June and August 1989, two in October 1989 and a further four in early 1990. Unfortunately, this sampling procedure could not be maintained for longer periods as marker buoys were lost within 4 months and bottom chains were overgrown by benthos. Thereafter, only single, unmarked 20m^2 strips were sampled for benthos on each occasion and in each area. Size-frequencies for the mussel and whelk species were obtained from random samples in the same area. The rock-lobster densities were the means of between four and eight 20m^2 belt counts (section two). Two 45-minute dives were usually required for one diver to complete the above tasks. Physical factors measured were: mean swell height for the previous week (from swash zone width at Luderitz harbour), dissolved oxygen concentration at 20m, temperature at 20m and Secchi disk reading (see section two for details of methods). The measurements were carried out at the following sites: SW Blinder less than 15m deep (SW BL <15m), SW Blinder more than 15m deep (SW BL >15m), Gallovidea reef less than 15m deep (GALLO <15m), Gallovidea more than 15m deep (GALLO >15m), Black rock less than 15m, Hottentot Point less than 15m (HOTT) and islands in Luderitz bay less than 15m (BAY ISL). Table 4.1 gives the number of sampling occasions, total number of quadrats sampled for benthos, total number of rock-lobster counts and number of stomachs analyzed.

TABLE 4.1. Sampling intensity by area.

AREA	NUMBER SAMPLE DATES	TOTAL NUMBER QUADRATS	TOTAL NO. R/L COUNTS	TOTAL NUMBER STOMACH
BAY ISLES	8	38	20	105
SW BL < 15m	15	90	85	220
SW BL > 15m	8	31	32	48
GALLO < 15m	8	19	32	117
GALLO > 15m	2	6	4	0
HOTTENTOT	1	4	4	0
BLACK ROCK	2	0	12	50

B. Stomach contents.

On most sampling occasions (when rock-lobsters were present in sufficient numbers), between 10 and 30 rock-lobsters (from 55 to 80mm carapace length) were caught by hand within an area approximately 4 * 20m in the same area that the benthos was sampled. Each foregut was dissected out and its contents were examined under a low power microscope and identified to the lowest taxonomic level possible (whelks and mussels to species level). The usual bias towards species with hard parts was thus introduced. The percentage frequency of each species group consumed, the fullness of the foregut (on a scale of 0 to 10) and size and sex of rock-lobster were recorded. For each individual, the fullness was multiplied by the percent frequency of each group to obtain an importance value by group. For each occasion, the overall importance value of each benthic species group was calculated as the sum of importance values by group for each individual rock-lobster sampled. Sexes and all size classes were combined into one value per benthic species group per sample date.

Correlation coefficients between the importance values of species groups in stomachs and their density in the benthos were examined for significance. An index of selectivity (such as ODD's ratio, Gabriel 1978) could not be used as there was no available uniform index of importance among species in the benthos (some were measured as percent cover and others as density).

C. Statistical considerations.

For logistical reasons only one "experimental unit" (i.e. approximately 20 m^2 of substratum) was sampled per date, in general, and this unit varied in position by about 200m between sample dates. Consequently the use of inferential statistics using all quadrats within those "experimental units" as replicates would be committing "simple pseudoreplication" (Hurlbert 1984) if hypotheses were posed at the scale of an area ("fishing ground"). The approach taken was to use the mean of the samples for each date and area as a single data point as recommended by Hurlburt (1984) who pointed out that using nested ANOVA would not be any more powerful. These single sample dates were then used as replicates within an area (e.g. SW Blinder) and therefore each area was repeatedly sampled through time on a sufficiently large scale to compare between areas. It was not valid to compare between sample dates within one area as this would be committing temporal pseudoreplication. However, regarding individual sample dates as replicates within a year was valid and therefore I could compare between years in the two areas (SW Blinder and Gallovidea) where sufficient sampling had been done. The significance of differences was tested using ANOVA. If this was significant, means were compared using 95 % ranges (Day and Quinn (1989) discuss more sophisticated comparisons of treatments after ANOVA). In general, data were not transformed as ANOVA is robust to violations of the normal distribution requirement (Underwood 1981). All tests were done using the ANOVA, LINEAR REGRESSION and MULTIPLE CORRELATION ANALYSIS routines in the STATGRAPHICS package (vers 3.0).

D. Hypothesis testing.

Predictions 1a and 2a of the two hypotheses proposed in the introduction were tested using the data on densities of benthos and rock-lobster. Differences in mean densities of benthic species were related to mean rock-lobster densities both through time on SW Blinder and between areas. Predictions 1b and 2b were tested by calculating the ratio of Aulacomya to Choromytilus for each sample date and area and regressing the ratios against rock-lobster density. Predictions 1c and 2c were tested by applying a bi-modal size distribution (using the Battacharya method) to the observed combined size distributions of mussel species. The separation index between the two modes was noted (a meaningful separation requires the index to be >2) and the significance of the resultant distribution was tested using a chi square test (using the ELEFAN package, vers 3.01). Differences in the separation index could then be related to rock-lobster densities. In addition, multiple linear regression was carried out using all physical factors and species densities, and correlations tested for significance.

4.4. RESULTS:

A. Descriptive patterns.

Figure 4.1 compares benthic species densities between areas. Hottentot was anomalous in being dominated by hydroids. Gallovidea was dominated by algae and a few *Aulacomya*, whilst the Bay islands were dominated by *Aulacomya* and ophiuroids which occur in dense patches and apparently filter-feed. SW Blinder deeper than 15m was dominated by *Choromytilus* whilst *Aulacomya* was more common on SW Blinder < 15m together with some algae. Only Gallovidea and SW Blinder < 15m had high *mean* densities of rock-lobsters. No quantitative benthic surveys were done at Black rock, but observations suggested benthos very similar to Gallovidea.

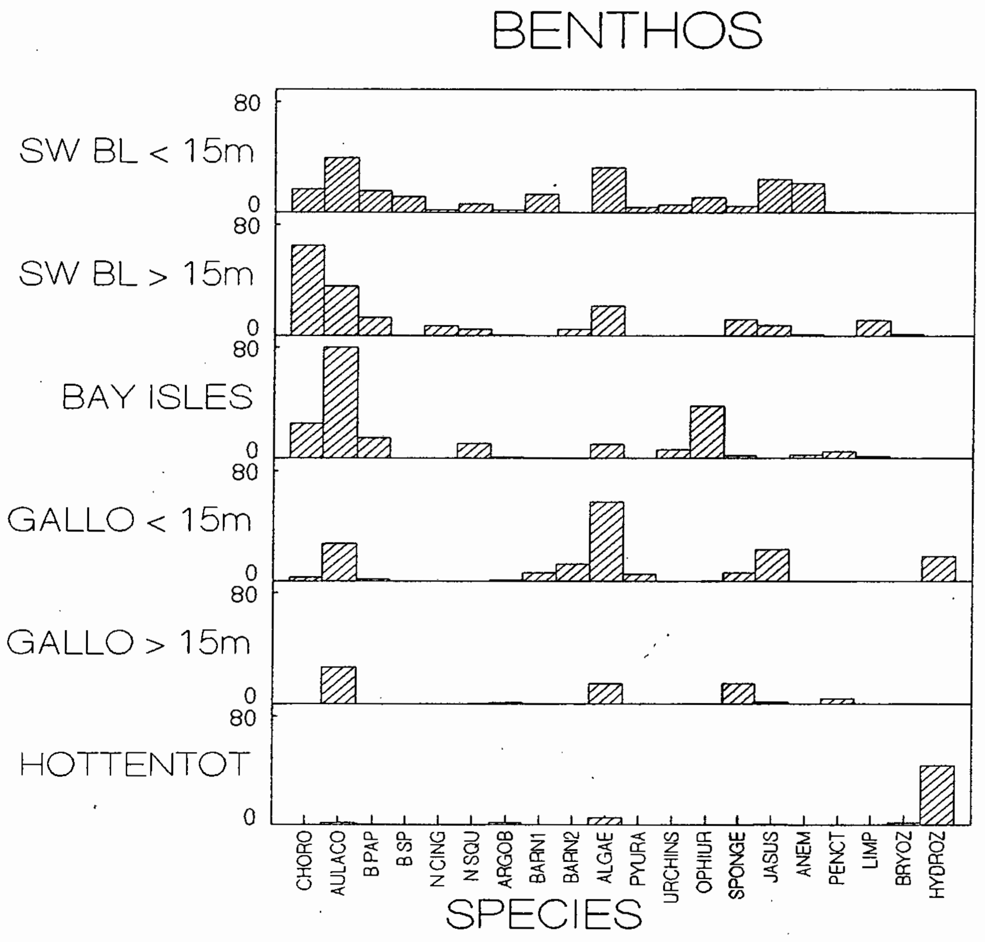

Figure 4.1 Benthic species densities at four Luderitz reefs, mean of all sample dates. Mussels, barnacles, algae, sponge, bryozoa and hydrozoa as percent cover, all others as numbers/m^2.

CHORO = *Choromytilus meridionalis*
AULACO = *Aulacomya ater*
B PAP = *Burnupena payracea* .
B SP = *Burnupena* spp
N CING = *Nucella cingulata*
N SQUAM = *Nucella squamosa*
ARGOB = *Argobuccinum argus*
BARN1, BARN2 = 2 spp. of barnacles

ECHIN = Echinoids
OPHIUR = Ophiuroids
ANEM = Anemones
PENCT = *Pentacta doliolum*
LIMP = Unidentified limpet
BRYOZ = Bryozoa
HYDROZ = Hydrozoans
REDALG = red algal species.

Stomach contents seemed to reflect densities of species present (Figure 4.2) except that gut contents from animals sampled at Black rock and Gallovidea had significant amounts of barnacles which were not noted in surveys.

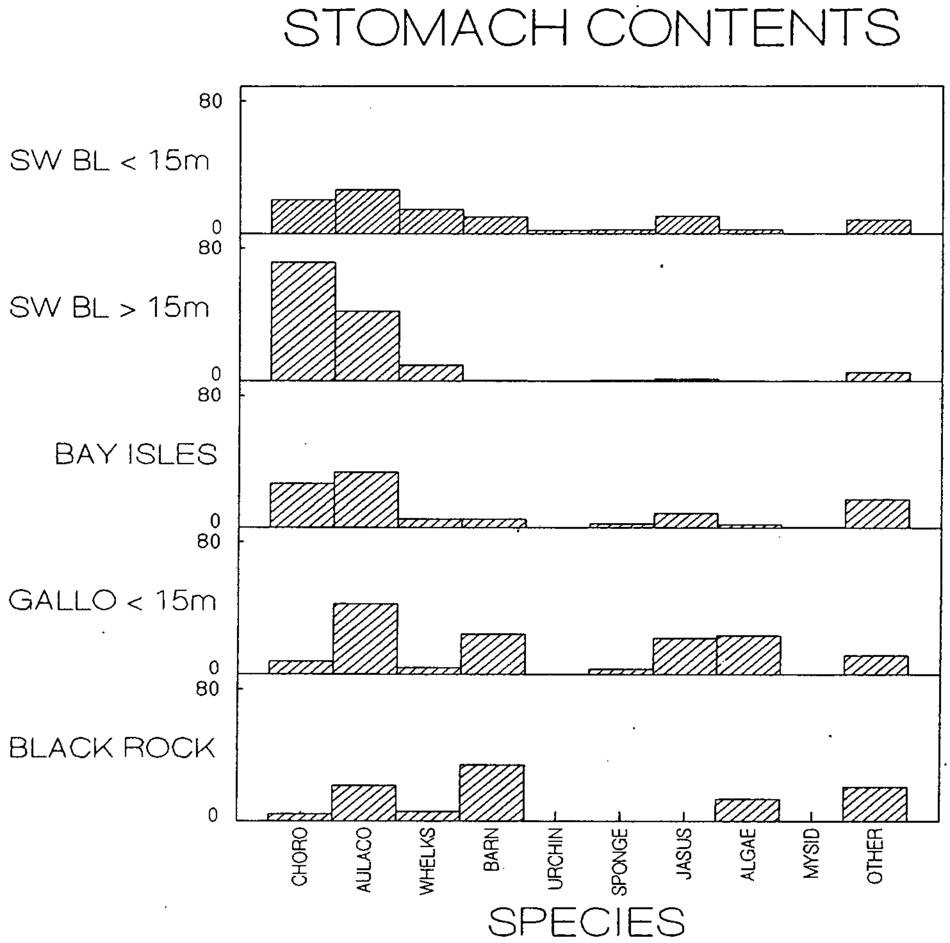

Figure 4.2 Importance values (percent) of species from Jasus lalandii stomach contents at various areas.

CHORO = Choromytilus meridionalis	URCHINS = Echinoids
AULACO = Aulacomya ater	JASUS = Jasus lalandii
WHELKS = various whelk species	ALGAE = red and brown algae
BARN = 2 spp. of barnacles	MYSIDS = unid. planktonic mysids

OTHER = includes sand, unid. animal parts and various rare spp. (see text)

Although no measure of selectivity could be calculated, table 4.2 compares the ratio of Choromytilus to Aulacomya in the benthos and that in the stomachs. In three of the areas, the ratio of Choromytilus to Aulacomya is double in stomachs compared to that in the benthos, indicating some degree of selectivity for Choromytilus.

TABLE 4.2. Ratio of Choromytilus to Aulacomya in the benthos and stomachs.

AREA	BENTHOS	STOMACHS
SW BL < 15m	0.43	0.78
SW BL > 15m	1.82	1.71
BAY ISLE	0.31	0.79
GALLO < 15m	0.09	0.18

Of note is a significant level of cannibalism, particularly at Gallovidea < 15m. Species lumped under "others" included polychaete jaws, holothurian spicules, sponge spicules, ophiuroid and echinoid shell fragments. No remains of hydroids or anemones were ever found.

Size compositions of Choromytilus (Figure 4.3) were apparently bimodal and the mussels were smaller in deeper water. Aulacomya was less obviously bimodal, possibly due to it's slower growth rate (Griffiths and King 1979), and again deeper water tended to contain smaller mussels (Figure 4.4). Burnupena papyracea and Argobuccinum size distributions were unimodal with the possible exception of SW Bl < 15m (Figures 4.5 and 4.6) whilst that of Nucella squamosa was bimodal at the Bay isles (Figure 4.7).

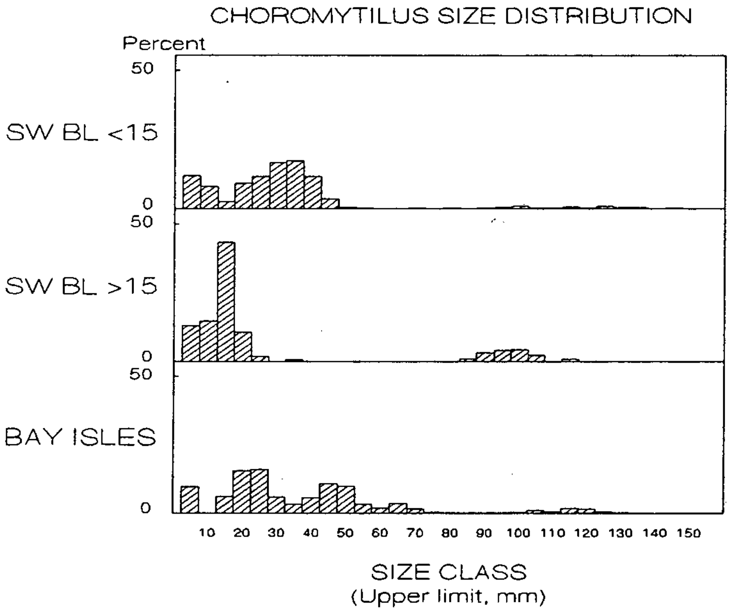

Figure 4.3 Size composition of Choromytilus meridionalis at three sites from diver surveys. Percent of total numbers combined from all occasions.

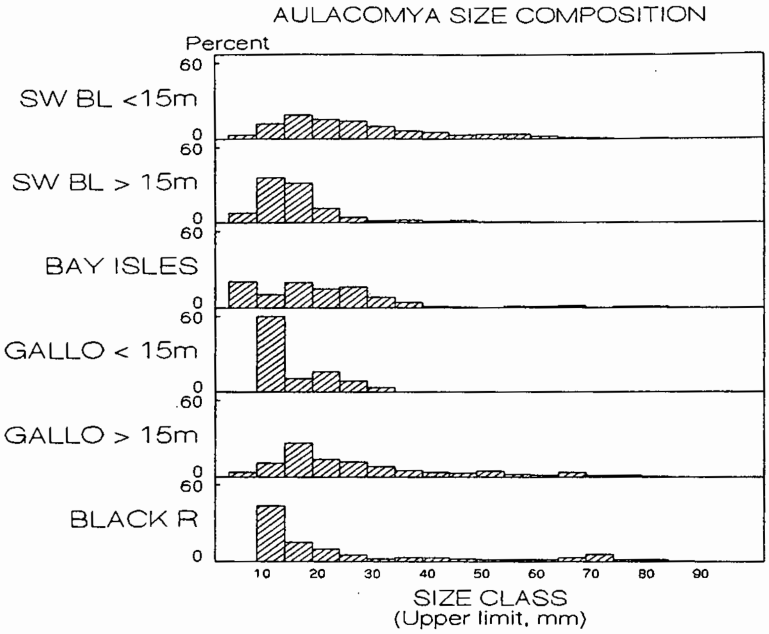

Figure 3.4 Size composition of Aulacomya ater from six sites by diver surveys. Percent of total numbers combined for all occasions.

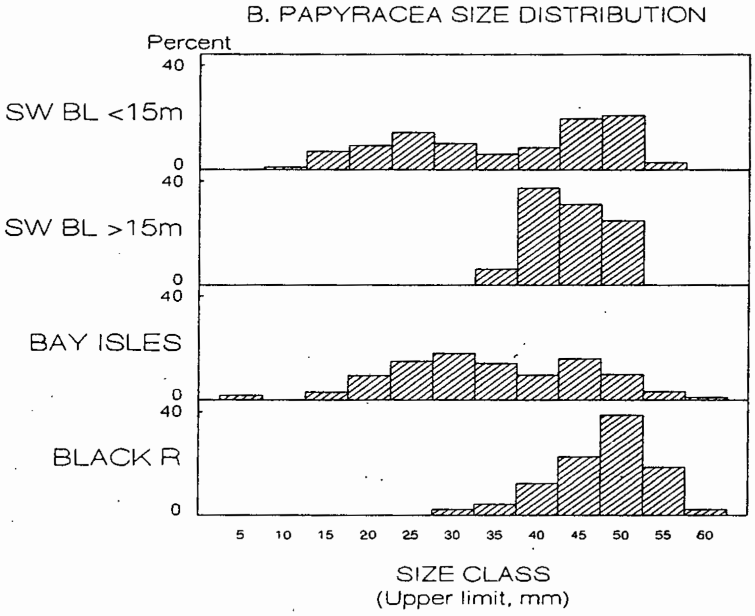

Figure 4.5 Size composition of Burnupena papyracea from 4 sites by diver surveys. Percent of total numbers collected all samples combined.

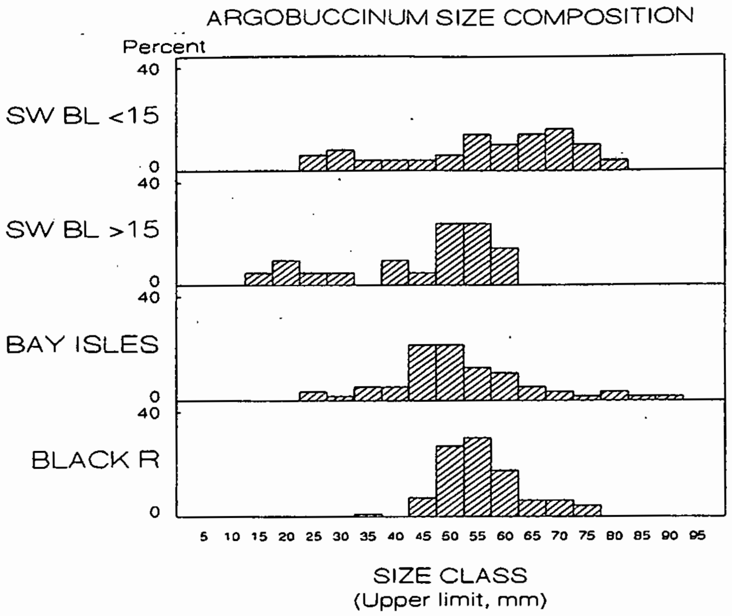

Figure 4.6 Size composition of Argobuccinum argus from diver surveys at four sites. Percent of total numbers collected from all occasions.

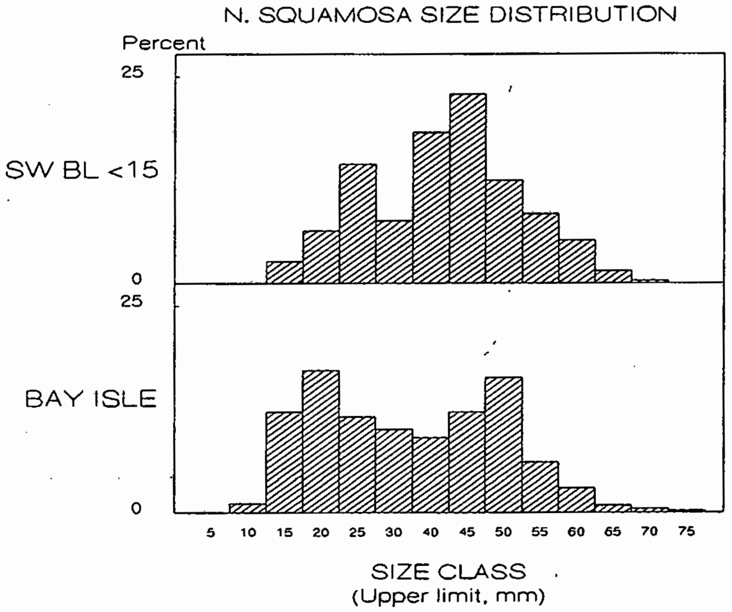

Figure 4.7 Size composition of Nucella squamosa from diver surveys. Percent of total numbers combined from all samples.

Time series of mussel size distributions (Figures 4.8 and 4.9) on SW Blinder serve to illustrate that, on most dates, the majority of mussels did not exceed the "critical" size for a rock-lobster of 75mm carapace length (the average from section 2). These critical sizes are 65 mm for Choromytilus and 55 mm for Aulacomya (Griffiths and Seiderer 1980). In other words, the majority of the mussels of both species were "available" to most of the rock-lobsters on almost all occasions. In addition, modes appeared to be stationary with time and could not be "followed". However, the irregular nature of the sampling may have masked such progressions. The time series of Burnupena papyracea size distributions (Figure 4.10) indicated possible recruitment in March 1990 and February/March 1991 but by January 1992, only large individuals remained.

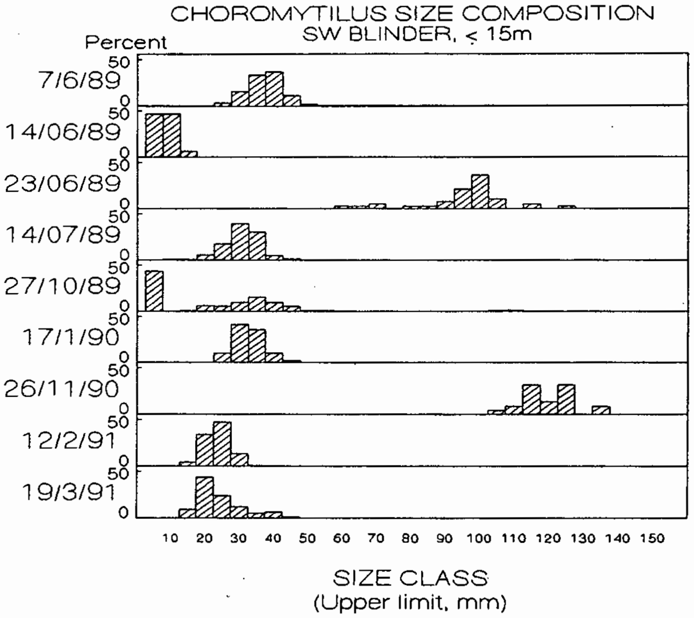

Figure 4.8 Time series of Choromytilus size composition at SW Blinder less than 15m deep. Percent total numbers for those dates when black mussels were present at high densities.

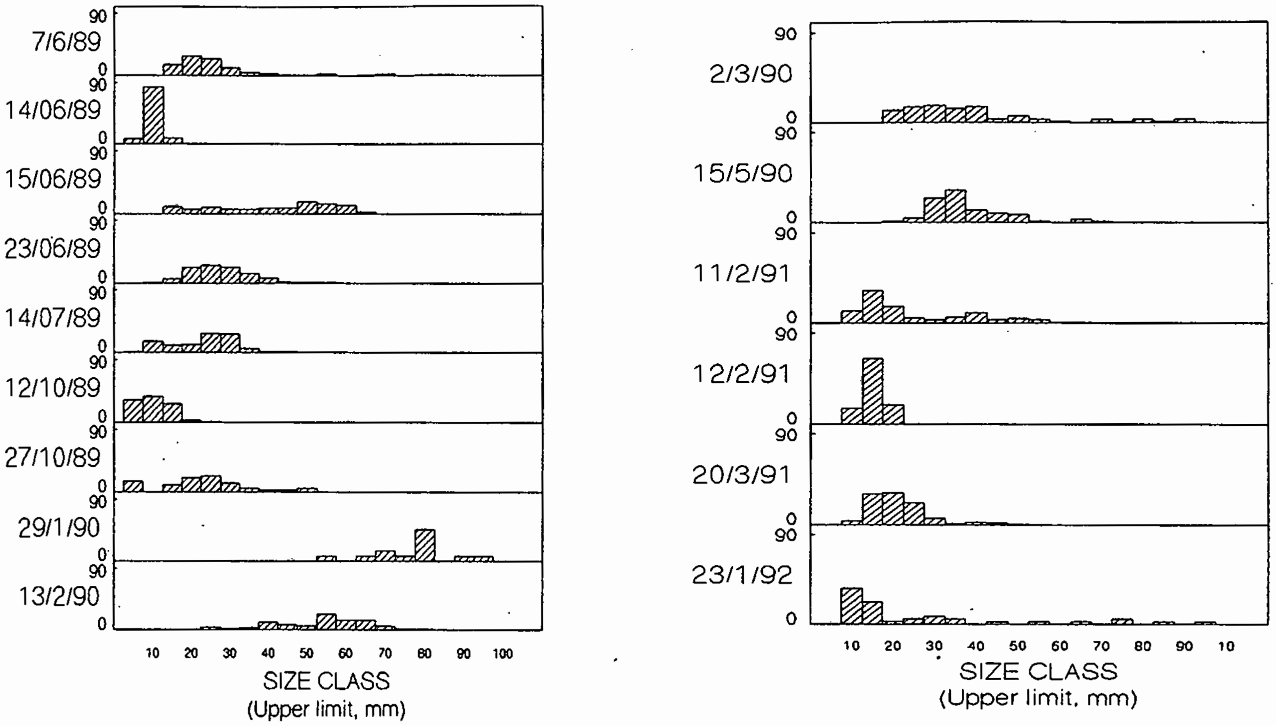

Figure 4.9 Time series of Aulacomya ater size composition at SW Blinder less than 15m deep. Percent numbers for dates when present in sufficient density to sample.

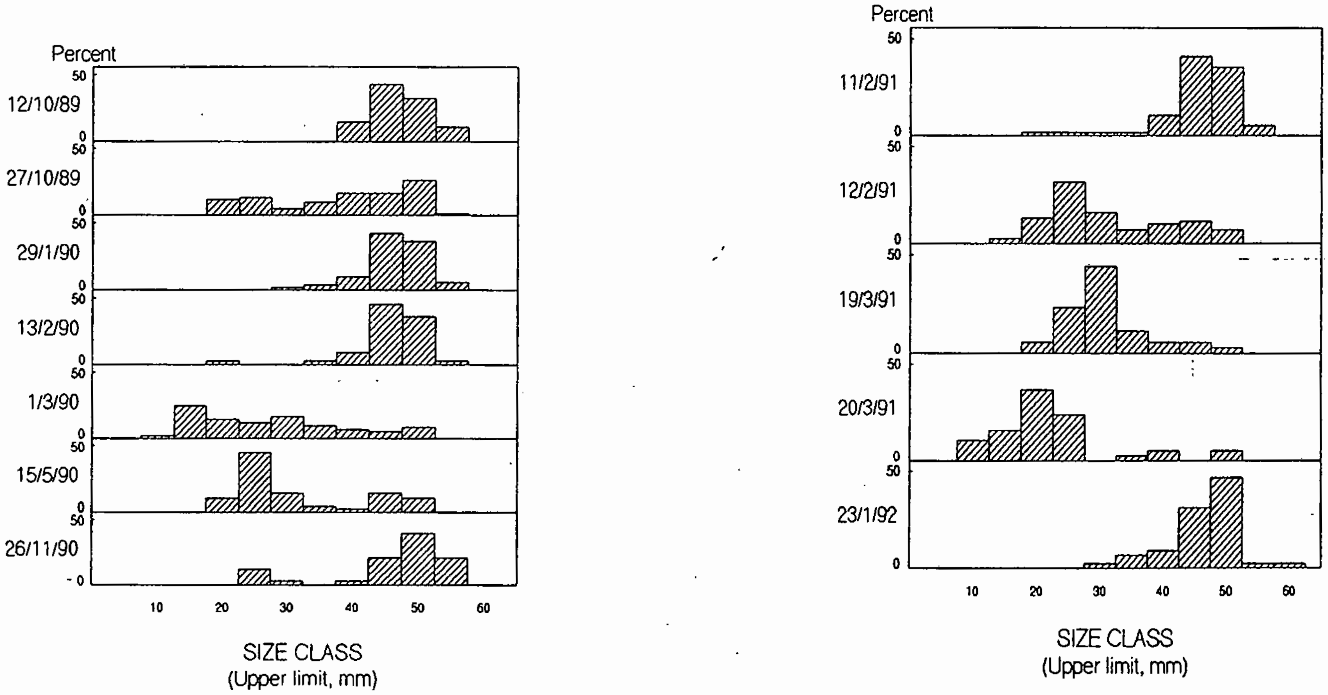

Figure 4.10 Time series of Burnupena papyracea size composition at SW Blinder less than 15m depth.

If recruits are defined as individuals less than 20mm in length and recruitment calculated as proportion less than 20mm multiplied by density, then Choromytilus seemed to exhibit one major recruitment episode in March 1991 (Figure 4.11). Aulacomya recruits appeared through the second half of 1989 and strong recruitment occurred again during early 1991 and 1992 (Figure 4.11). Recruitment is inherently far more variable with time than density and the sampling in this study was certainly not regular enough to reliably detect recruitment episodes in benthic species.

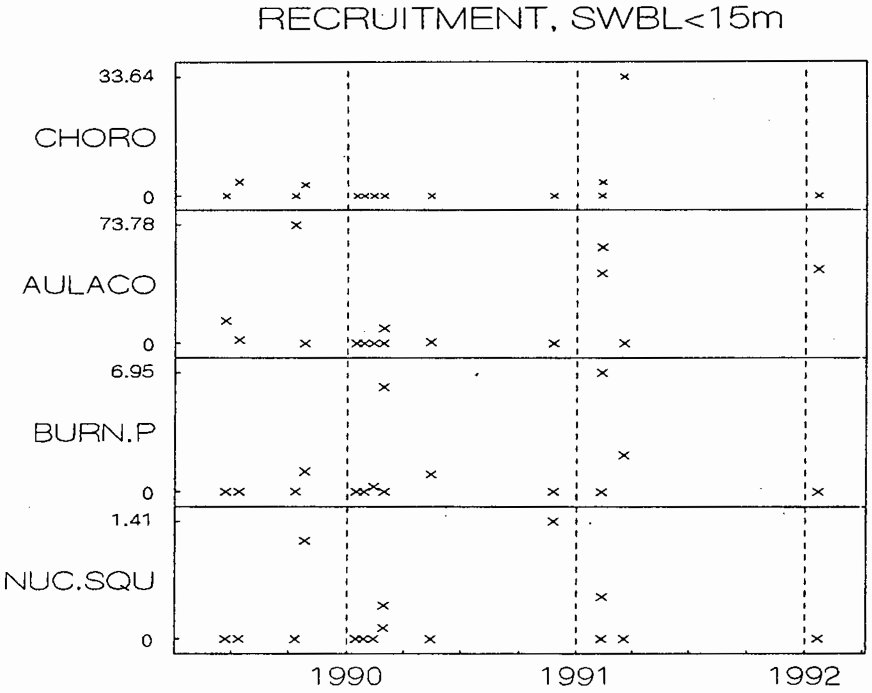

Figure 4.11 Time series of recruitment for benthic species on SW Blinder less than 15m. Recruits defined as number of individuals < 20mm in length (percent cover for mussels and n/m^2 for whelks).

High densities of rock-lobsters occurred on SW Blinder <15m in early 1989 (see section 2) and 1990 with much lower densities in 1991 and 1992 (Figure 4.12). The significance of apparent changes in density through time of various benthic species (Figure 4.12) and rock-lobster stomach contents (Figure 4.13) with time will be tested below.

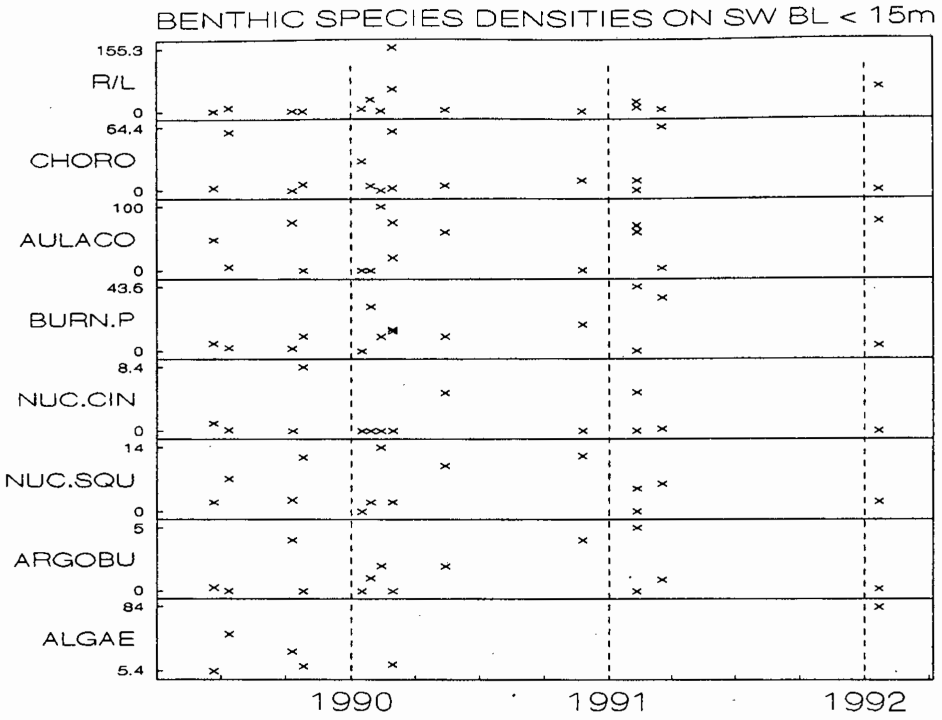

Figure 4.12 Benthic species densities at SW Blinder less than 15m deep through time. See section2 for rock-lobster densities between 1987 and 1989.

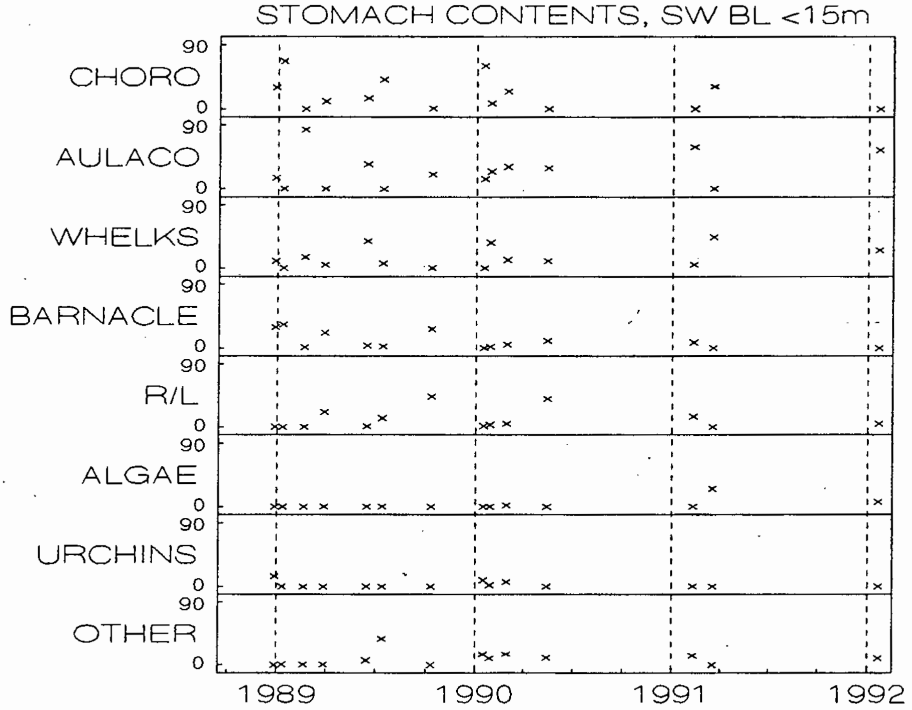

Figure 4.13 Time series of rock-lobster stomach contents (percent importance value) at SW Blinder less than 15m deep. Refer to Figure 4.2 for species names, R/L = rock-lobster.

B. STATISTICAL TESTS

(1). Comparing grounds:

(a). ANOVA, using means of sample dates as replicates:

Twenty seven samples distributed among five areas were tested. ANOVA comparisons based on untransformed data between areas for Choromytilus, Aulacomya, Burnupena papyracea, Nucella cingulata, Argobuccinum and Jasus was not significant at the 90 % level. Nucella squamosa showed a marginally significant difference between areas (P = 0.085). When the data for N. squamosa were square root transformed ($\sqrt{x+1}$)the significance level rose to 0.0065. The Bay islands and SW Blinder < 15m had significantly higher mean densities of N. squamosa than Gallovidea (both depths), Hottentot and SW Blinder deeper than 15m.

(b). ANOVA using all available quadrats:

145 individual 0.25 m^2 quadrats were sampled at 4 areas (Gallovidea < 15m and > 15m and SW Blinder < 15m and > 15m). One way ANOVA was done on all species and revealed more significant differences between areas than were detected using single means, as would be expected from the increased number of replicates. Significant results are summarised in Table 4.3.

TABLE 4.3. Significant results of one-way ANOVA between grounds using all quadrats as replicates and for each benthic species.

SPECIES	P	DIFFERENCES
CHOROMYTILUS	0.0001	SW BL>15m higher than GALLO<15m and GALLO>15m
B. PAPYRACEA	0.0043	SW BL<15m higher than GALLO>15, GALLO<15 and SW BL>15m
N. SQUAMOSA	0.0039	SW BL<15m higher than GALLO>15, GALLO<15 and SW BL>15m
ALGAE	0.0009	GALLO<15m higher than GALLO>15m, SW BL<15 and SWBL>15
SEA-URCHINS	0.0018	SW BL<15m higher than GALLO<15, GALLO>15 and SW BL>15m

All other species, including rock-lobsters showed no significant differences between areas.

(c). Linear regression analysis between means of all samples:

No significant correlations between benthic species densities among areas were found except for the following:

TABLE 4.4. Significant results of multiple linear regression between all benthic species (using means of samples as replicates).

SPECIES 1	SPECIES 2	SIGN	R^2	P
Aulacomya	N. squamosa	+ ve	0.83	0.01
Aulacomya	B. papyracea	+ ve	0.55	0.09
Choromytilus	N. cingulata	+ ve	0.87	0.007

There was no relation between any benthic species and rock-lobster densities nor an inverse relation between Aulacomya and Choromytilus.

The above correlations suggest that if the effect of Aulacomya density on B. papyracea was taken into account, the remaining variation might be significantly different between areas. Therefore an ANCOVA was carried out on B. papyracea using Aulacomya as a covariate. However, there were still no significant differences between areas. Similarly, ANCOVA was done on Choromytilus densities using Aulacomya as a covariate (see 3 below), resulting in a significant difference between sites (P = 0.038). The density of Choromytilus at Gallovidea reef less than 15m was significantly less than SW Blinder more than 15m, but other sites were not significantly different. A similar analysis for Aulacomya using Choromytilus as a covariate did not produce a significant result.

An analysis of the power of the comparison between Choromytilus density at less than 15m vs greater than 15m at SW Blinder revealed that the power was low at 0.42 (i.e. Beta = 0.58 when H0 = 38.8, HA = 17, sigma = 39, n = 10, 2 way test, Alpha = 0.05), i.e. there was a relatively high probability of a type II error (finding no significant difference at the 5% level when there was, in fact, a difference). This is probably representative of most of the significance tests carried out in this section due to high variability and low number of sample dates in some areas.

(2). Comparing sample dates within SW Blinder <15m.

(a). Lumping data by years for SW Blinder <15m, using means of sample dates as replicates:

No significant differences in whelk densities were found between years using single factor (year) ANOVA on both untransformed and transformed data (RT(1+x) for counts and LN(1+x) for percentages). This is probably because there was only a single sample date in 1992. Examination of Figure 4.11 suggests that whelk densities were higher when rock-lobsters were less dense (e.g. early 1991). However, linear regressions between whelk and rock-lobster densities were not significant as whelk densities were high in 1991 and low in 1992 when rock-lobster were at low densities.

(b). Comparing dates on SW Blinder < 15m by ANOVA (using all available quadrats):

Analysing differences between months showed significant differences for several species, as summarised in Table 4.5.

TABLE 4.5. Significant results of one-way ANOVA between dates on SW BL < 15m, using all quadrats as replicates for all species.

SPECIES	P	DIFFERENCE
B. papyracea	0.0001	Febr 1991 higher than rest
Urchins	<0.0001	Feb 1991 higher than rest
Algae	<0.0001	Jan 1992 higher than rest
Choromytilus	<0.0001	Jul 89 higher than rest except Mar 90 and Mar91
Aulacomya	<0.0001	Feb 90 higher than rest except Jan 92

(c). Regression analysis using means of sample dates as replicates:

Fifteen dates were sampled over four years. Using single and multiple linear regressions and comparing all species densities and environmental parameters, only the relationship between Aulacomya and Choromytilus was significant (- ve slope, $R^2 = 0.34$, $P = 0.02$). There was no significant relation between mussels and the previous week's swell, any other physical parameter, rock-lobster density or whelk densities, indicating that changes in benthic species densities with time could not be explained by any of these physical or biological variables.

(3). Comparing sites within SW Blinder < 15m using marked sites between June 89 and October 1989:

Fifty individual quadrats were sampled within 6 sites (separated by 200 - 300m) within SW Blinder < 15m over a period of four months. This allowed the analysis of spatial variation within one area without the confounding effect of time. The following taxa showed significant differences (using one-way ANOVA) among sites: Choromytilus ($P<0.0001$), Aulacomya ($P<0.0001$), Burnupena papyracea ($P = 0.005$), other Burnupena spp. ($P=0.08$), Nucella cingulata ($P<0.0001$) and algae ($P<0.0001$). None of the other taxa, including rock-lobsters, showed significant differences between sites.

This implies that the distribution of the above taxa is patchy on the scale of 200-300m and that sampling within only one $20*1m^2$ unit would not provide an adequate estimate of mean density over the whole area. Therefore, the results outlined in 2(b) above should be interpreted with caution (but 2a and 2c remain valid).

No consistent differences between sites were noted in terms of depth (sites varied from 9 to 13m) or relief. Multiple correlation analysis was done between species densities using all quadrats in order to test for interactions. Aulacomya was negatively correlated with Burnupena papyracea (P=0.015), Nucella squamosa (P=0.04) and Choromytilus (P=0.08) whilst B. papyracea was positively correlated to N. squamosa (P=0.005) and N. cingulata (0.002) and N. cingulata was positively correlated to N. squamosa (P=0.0003). The positive correlations between the whelk species appeared to be due to "sucking" whelks (B. papyracea) scavenging mussels already weakened by "drilling" whelks (Nucella spp.).

(4). Comparing stomach contents between areas:

(a). ANOVA using all dates as replicates:

All components of stomachs (group importance values) were compared between areas. The following differences were significant:

TABLE 4.6. Significant results of one-way ANOVA between areas using stomach importance values for each sample as replicates.

SPECIES	P	DIFFERENCES
Choromytilus	0.006	SW BL <15m higher than all others
Barnacles	0.047	Black R and Gallo<15m higher than all others
Algae	0.024	Gallo <15m higher than rest

(b). Comparing stomach contents and available benthic species between grounds by regression analysis:

Correlations between mean stomach contents and mean benthic species densities for 4 areas (SWBL< 15m, SWBL>15m, Gallo<15m and Bay isles) were sought. The whelks in the stomachs were lumped and benthic whelk densities were combined for the "edible" whelks (Barkai and McQuaid 1988) i.e. Nucella squamosa, N. cingulata, and all Burnupena spp. excluding B. papyracea. The following were significant:

TABLE 4.7. Significant results of correlation analysis between species in benthos and in stomachs (means of all samples).

SPECIES	SIGN	R^2	P
Choromytilus	+ ve	0.99	0.003
Algae	+ ve	0.83	0.088

No other species showed significant correlations between stomach contents and benthos including rock-lobsters (i.e. cannibalism did not increase with increasing density).

(5). Comparing stomach contents and available benthos between dates at SWBL < 15m by regression analysis:

Relations with time were examined only at SWBL<15m, for which adequate samples existed. The mean of each date was used as one data point. Correlations between the importance value of a species group in the gut contents and it's mean density at the time of sampling were sought. The following were significant:

TABLE 4.8. Significant results of correlation analysis between species in stomachs and in benthos within SW BL <15m at each sample date.

STOMACH SP	BENTHIC SP	SLOPE	R^2	P
Choromytilus	Choromytilus	+VE	0.50	0.023
Aulacomya	Aulacomya	+VE	0.53	0.018
Whelks	B. Papyracea	+VE	0.53	0.018
Choromytilus	Aulacomya	-VE	0.62	0.007
Aulacomya	Choromytilus	-VE	0.47	0.03

Whelks in stomachs were not significantly correlated to edible whelks in benthos. Whelks could not always be identified to species level in stomachs and therefore it was impossible to test for a correlation between Burnupena papyracea in stomachs and in the benthos. The relation between stomach whelks and benthic B. papyracea was surprising as it implies that most of the whelks in the stomach were B. papyracea (which are reportedly inedible for rock-lobster, Barkai and McQuaid 1988). There was no positive relationship between edible whelks and B. papyracea within the benthos, therefore the correlation is not a secondary effect. Conceivably the rock-lobsters were feeding on juvenile B.

papyracea which had not had time to develop the protective covering of the bryozoan Alcyonidium that renders B. papyracea inedible to rock-lobsters (G. Branch pers. comm.).

The significant inverse relation between Aulacomya in stomachs and Choromytilus in the benthos and vice versa was due to the inverse relation between the 2 mussel species in the benthos (see 2(a)) and was therefore a secondary effect. All other correlations were not significant including that for rock-lobsters, indicating that cannibalism did not increase during periods of high density.

(6). Correlation between the ratio of Aulacomya to Choromytilus in the benthos and rock-lobster densities:

There were no significant differences between areas and no significant correlation with rock-lobster densities through time or space.

(7). Significance of bi-modal frequency distribution for Aulacomya and Choromytilus:

Table 4.9 gives the results of fitting a bi-modal frequency distribution using the Battacharya method and compares the separation index (SI) and significance of the resultant expected frequency (CHI^2 test) to mean rock-lobster densities at the site.

TABLE 4.9. Separation index and results of CHI SQUARE test after fitting a bimodal distribution to two mussel species; corresponding rock-lobster densities are also given.

	CHOROMYTILUS:		AULACOMYA:		LOBSTER:
SITE	SI	CHI	SI	CHI	N/M^2
SWBL<15	4.5	N/S	2.9	N/S	23.8
SWBL>15	15.4	N/S	2.7	**	7.1
GALLO<15			2.3	N/S	22.9
GALLO>15			4.3	N/S	1.5
BAY ISLES	4.2	**	5.9	**	0
BLACK ROCK			8.9	N/S	

** = significant at 95% level (ie. observed distribution fits bimodal distribution)
N/S = not significant (does not fit bimodal distribution)

A significant separation index (more than 2) was found between two modes for all areas, but the resultant distribution was significant only at the Bay isles and SW Blinder >15m for Aulacomya and at Bay islands for Choromytilus. Both these areas had low densities of rock-lobster, i.e. bimodality or lack thereof seems unrelated to rock-lobster densities.

C. SUMMARY OF STATISTICALLY SIGNIFICANT RESULTS.

(1). Stomach Contents:

Between areas:

Rock-lobster at SW BL <15m consumed significantly more Choromytilus, those at Black rock ate more barnacles and those at Gallo <15m more algae and barnacles than rock-lobster in all other areas. There were significant positive correlations between the amounts of Choromytilus and algae in the stomachs and their abundance in the benthos.

Between dates:

There were significant positive correlations between the quantities of Aulacomya and Choromytilus in the stomachs and their abundance in the benthos on SW BL <15m. In addition there was a positive correlation between whelks in the stomachs and B. papyracea (but not "edible" whelks) in the benthos. No indication was found of cannibalism being related to rock-lobster density.

Although no quantitative measure of selectivity was possible, it appeared that selectivity for Choromytilus over Aulacomya occurred, and that where obvious benthic "food" (such as mussels) was almost absent (at Black rock and Gallovidea), rock-lobster were eating barnacle recruits and algae. In contrast to Barkai and Branch (1988b), only a few planktonic mysids were found in stomachs although they were commonly observed in the water column over the reefs.

(2). Benthos:

Between grounds:
ANOVA between grounds revealed that SW Bl <15m had more N. squamosa than the rest whilst SW BL >15m had more Choromytilus than Gallo <15m (ANCOVA using Aulacomya as a covariate). If the possibility of pseudoreplication is ignored SW BL < 15m had more B. papyracea, N. squamosa and sea-urchins than Gallovidea (all depths) and SW Bl > 15m whilst Gallovidea <15m has more algae than Gallo >15m and SW Blinder (both depths). Positive and significant correlations were found between Aulacomya and N. squamosa, Aulacomya and B. papyracea and Choromytilus and N. cingulata among sites.

Between dates:
No significant differences between years were detectable using sample means. It was shown that within SW Blinder <15m, most species (but not rock-lobster) varied significantly on a scale larger than that which was sampled for most of the period. Therefore the results using all quadrats should be treated with circumspection (due to temporal pseudoreplication). Using sample date means, Aulacomya and Choromytilus were significantly negatively correlated through time. Over a small scale within SW Blinder <15m, there was a positive correlation between Burnupena papyracea and Nucella spp.

None of the measured physical factors nor rock-lobster densities had any significant power in explaining densities of benthic species either spatially or temporally.

(3). Benthic species size compositions:

Modes in size distribution could not be followed through time (it is not possible to test this assertion statistically) and although separation indices between two modes in mussel size distributions were significant, suggesting bi-modality, the resultant predicted size distribution was only statistically valid for two areas where rock-lobster occurred in low densities. Therefore bimodal size distributions were not linked to high levels of rock-lobster predation.

4.5. DISCUSSION:

A. Community structure of the two reefs examined in most detail:

Gallovidea reef contained a species assemblage and size structure of benthic species conforming to that normally expected under high rock-lobster densities (Barkai and Branch 1988a). In general, densities of mussels were low and the few mussels present were all Aulacomya. Whelks were also rare, but algal cover was extremely high. In these respects, it is very similar to Malgas Island in Saldanha Bay where rock-lobsters control the community by consuming recruits of several benthic species (Barkai and Branch 1988c).

In contrast to that, the community structure on SW Blinder was dominated by mussels (Aulacomya in shallower water and Choromytilus deeper). In addition, whelks of all species were far more common than on Gallovidea. Parts of SW Blinder appear similar to Marcus Island, where rock-lobsters are scarce (Barkai and Branch 1988a), but overall there were lower densities of holothuroids, urchins, ophiuroids and whelks at SW Blinder than Marcus Island. Aulacomya was more abundant and Choromytilus was smaller than on Marcus Island and Choromytilus did not form multiple layers as it does at Marcus Island (Barkai and Branch 1988a). The whelk species which were vulnerable to predation by rock-lobsters, i.e. B. cincta and B. limbosa (Barkai and McQuaid 1988), were absent, but Nucella spp. were present in high densities.

Just as the enormous difference between Marcus and Malgas Islands in Saldanha Bay demanded explanation (Barkai and Branch 1988a), so does the (lesser) difference between Gallovidea and SW Blinder at Luderitz. The explanation for the Marcus-Malgas extreme was found in different levels of rock-lobster predation and the alternative stable state hypothesis (Barkai and Branch 1988c). It might be expected that the benthic community at SW Blinder would similarly be due to a lower level of rock-lobster predation. Stomach contents indicated that rock-lobsters certainly consumed the benthic species observed in surveys, and more or less in proportion to their densities. The first and most powerful prediction of the rock-lobster predation hypothesis was that benthic species densities would be correlated with rock-lobster densities. However, mean rock-lobster densities on SW Blinder and Gallovidea were almost identical. On both reefs, rock-lobsters move offshore in winter and inshore in summer (section 2) and interannual differences were similar (high densities in 1989 and 1990 and low in 1991 and 1992). None of the statistical tests reported upon in the results (including sites additional to SW Blinder and Gallovidea) showed any effect of rock-lobster density upon the benthos at any spatial scale. In addition, the physical environment (dissolved oxygen concentration, water temperatures, Secchi disk readings and swell) appeared to be very similar between sites.

B. Differences through time on SW Blinder:

Rock-lobster densities were much higher on SW Blinder in 1988, 1989 and 1990 compared to 1991 and 1992 (section 2). This fact allowed a test of the alternative stable state hypothesis. If rock-lobsters disappeared from an area (for whatever reason), that area should become mussel and whelk dominated and whelks might then prevent the return of rock-lobsters to that area (Barkai and McQuaid 1988). There should then, be a correlation between rock-lobster densities and benthic species densities through time. Indeed, whelks at SW Blinder did appear to increase during the period when rock-lobsters were present in low numbers. On the other hand, no such increase in whelks was observed on Gallovidea although rock-lobster densities declined there as well. However, high whelk densities on SW Blinder did not appear to prohibit the return of rock-lobsters and the whelks eventually returned to a low density for reasons apparently unconnected with movements of rock-lobsters. None of the statistical tests reported upon in the results indicated any correlation between benthic species composition and rock-lobster densities through time.

C. The effect of rock-lobsters on the benthos:

On both the temporal and spatial scales, the first prediction of the predation hypotheses posed in the introduction, that benthos densities should be correlated to rock-lobster densities was shown to be wrong, so weakening the predation hypothesis.

The second prediction of the predation hypothesis (that the ratio of Aulacomya to Choromytilus would be positively correlated to rock-lobster densities) was similarly shown to be incorrect. There was, however, a negative correlation between the two mussel species both on a small scale within SW Blinder and with time on SW Blinder suggesting that a competitive interaction (Barkai and Branch 1988c) was indeed, present. However, rock-lobsters had no effect on the outcome of this interaction thus calling into question their "keystone" role (Barkai and Branch 1988c) in this area.

The third (and weakest) prediction of the predation hypothesis viz. that mussel species would display bi-modal size distributions in areas where rock-lobsters are abundant, was also tested. Results were somewhat equivocal and the validity of the tests could be questioned. Although two modes could be meaningfully separated, when statistically significant bi-modal size distributions were present these were not related to the presence of high densities of rock-lobster. The recruitment hypothesis suggests as a prediction that it should be possible to follow modes in size distribution through time. In addition, species densities should be correlated to recruitment with some time lag. Unfortunately, samples were not obtained regularly enough to test these predictions in this study.

Table 4.10 summarises results of testing the predictions of the two alternative hypotheses proposed in the introduction.

TABLE 4.10. Results of comparing predictions of two alternative hypotheses to explain variations observed in benthic communities. Numbers refer to predictions outlined in the introduction.

TEST	RECRUITMENT DRIVEN	PREDATION DRIVEN
BENTHOS CORRELATES TO ROCK-LOBSTER	1a ACCEPT	2a REJECT
AULACOMYA:CHOROMYTILUS RATIO	1b ACCEPT	2b REJECT
BI-MODAL SIZE FREQUENCIES	1c ACCEPT ?	2c REJECT ?

The predation hypothesis was strongly rejected by two of the three predictions and more weakly rejected by the third one.

Several reasons could be advanced for the rejection of the keystone species role for rock-lobsters in this study:

(1) The sampling design was inadequate (too few replicates at a large enough scale) to demonstrate an effect. At least three sites 200 - 300 m apart should have been sampled per occasion and more regular sampling should have been carried out. For logistic reasons this was not possible.

(2) The scale of the hypothesis was incorrect. That is the answer to the question posed was mu (neither yes nor no, Pirsig 1974), i.e the question was inappropriate. The questions were posed on the scale of a whole reef, but interactions may have occurred on the scale of several metres which would have required returning to fixed sites on this scale or perhaps hundreds of metres (the scale at which Barkai and Branch's (1988c) hypothesis was made). This seems unreasonable given the large scale of physical forcing (low oxygen water) and resultant large-scale movements of rock-lobsters in the Luderitz region (see section 2). However, rock-lobster predation on large reefs could be considered as a random

disturbance factor on a tightly-knit small-scale community of interacting mussel and whelk species. This could be modelled using the "metapopulation" model of Caswell and Cohen (1991). Supporting this approach are observations made during this study suggesting that B. papyracea (and occasionally Argobuccinum argus) scavenged mussels that had been initially drilled by Nucella squamosa and N. cingulata and the significant positive correlation between the whelk species on a small scale within SW Blinder. Several authors have documented interactions between mussels and whelks (Barkai and Branch 1989; Day et al. 1991; Griffiths 1981; Wickens and Griffiths 1985). In addition, this study demonstrated positive correlations between mussels and whelks and negative correlations between the two mussel species, suggesting that mussel and whelk species form an interacting community independently of a wide range of rock-lobster densities.

(3) The predation effect may, in reality, not have been as strong as expected. This could be due to variations in benthic recruitment with time and space over-riding the effect of predation, or because the pronounced migrations of rock-lobsters obscure their effects due to time-lags.

It could be argued that having only one alternative to the predation hypothesis was simplistic and many more explanations could be sought. For example, apart from variable recruitment, mortality rates of benthos may be related to some unmeasured factor. Regressions in the results demonstrate that this factor was none of the measured physical variables (temperature, dissolved oxygen concentration or swell size), nor whelk densities. Long term monitoring observations on the SW Blinder and Gallovidea areas as well as sampling at all scales (e.g. Barkai unpubl.) may generate effective and testable alternative hypotheses to the predation hypothesis. It appears that existing hypotheses based on field manipulations (Barkai and Branch 1988c) do not provide answers to the whole range and variability of benthic species assemblages associated with a range of rock-lobster densities. Long-term, large-scale and adequately replicated experimental field manipulations are required (Elner and Vadas 1990) in areas of intermediate and fluctuating rock-lobster densities. These would need to separate the effects of rock-lobster predation from variable benthic recruitment and other causes of benthic species mortality. These manipulations may answer the question posed by Branch et al. (1987) as to whether the Marcus - Malgas alternative states can alternate and what pathway exists between them.

To summarise: most of the species assemblages monitored were intermediate between the two alternative states of Barkai and Branch (1988a,b,c) and displayed fluctuations which were unrelated to dramatic changes in rock-lobster density.

D. The effect of the benthos on rock-lobsters:

Two issues are of interest here, firstly the effect of benthic food availability on rock-lobster growth and mortality, and secondly, the potential effect of whelk densities on rock-lobster distribution patterns and survival.

1. Whelks and rock-lobsters.

This relationship is of interest because Burnupena papyracea has been documented as a rock-lobster predator at Marcus island where it reaches densities of 200/m^2 (Barkai and McQuaid 1988). The implication is that if a rock-lobster fishery decreases the density of rock-lobsters below a critical level, whelks may increase and maintain a state of low rock-lobster density, preventing the recovery of the fishery. A dramatic increase in density of whelks was observed on SW Blinder in 1990 and 1991 (up to 180/m$^{2)}$. This increase raised the possibility that SW Blinder may have been moving toward a Marcus island-type stable state, dominated by whelks, and was an input to management of the rock-lobster fishery (Tomalin 1991) leading to encouragement of a whelk fishery to attempt to restore the "balance" between whelks and rock-lobster. A market was even secured for processed whelks (W. Breytenbach, Manager of Gendev, pers. comm.). However, it appeared, from direct observation, that whelks did not predate on rock-lobsters at SW Blinder even at a density of 180/m2, although they did so at a density of 200/m^2 at Marcus island (Barkai and McQuaid 1988). There were no correlations between rock-lobster and whelk densities either temporally or at various spatial scales and the whelks had disappeared by January 1992 due to unknown causes before the fishery had caught significant amounts of whelks. No such increase in whelks was observed on Gallovidea Reef although there were changes in rock-lobster density similar to those on SW Blinder. To summarise, in this study there seemed to be no significant relationship between whelks and rock-lobsters in either direction. The density and circumstances under which B. papyracea becomes a rock-lobster predator needs to be experimentally determined as existing hypotheses do not seem to be generally applicable.

2. Food availability and rock-lobster growth.

The question of availability of food to rock-lobsters and it's corresponding effect on growth rates is of central interest to the management of the resource, due to the issue of density dependence of growth and mortality. This question was not directly addressed in this study but the following table summarises available data from the Namibian region.

TABLE 4.11. Growth rates (carapace length, mm per year) for males between 70 and 79 mm carapace length, mean trap CPUE (kg per trap day) for 1986/87 to 1990/91, mean rock-lobster density/10m^2, mean mussel cover (Aulacomya plus Choromytilus) and mean mussel wet biomass (g/m^2):

AREA	ROCK-LOB GROWTH	CPUE	ROCK-LOB DENSITY	MUSSEL COVER	MUSSEL BIOMASS
SW BLINDER	3.20*	3.15	24	57 %	8919**
GALLOVIDEA	4.71*	2.53	23	29 %	4111*
ICHABOE	6.84*	3.43			4111*
EASTER CLIFFS	4.3*	4.13			7393*

* - from Beyers and Wilke (in press).
** - from Beyers (1979).
unmarked data - this study.

The studies by Beyers (1979) and Beyers and Wilke (in press) appear to confirm observations reported here that mussels are more common at SW Blinder than the Gallovidea to Ichaboe area (Beyers and Wilke (in press) lumped the Hottentot to Ichaboe area into one). This also implies that this situation has existed for at least a decade and possibly longer (Beyers (1979) and Beyers and Wilke (in press) did their work in 1974 and 1981). Beyers and Wilke (in press) calculated the percent of the mussel biomass available to different sizes of rock-lobster at Gallovidea, SW Blinder and Easter Cliffs. They found that 32.5 and 41.5% of the biomass of Aulacomya was available to a rock-lobster of 72mm carapace length at Gallovidea and SW Blinder respectively and 100% of the Perna perna biomass at Easter Cliffs. This finding does not change the relative availability in the table above. Densities and CPUE of rock-lobsters are very similar between sites, hence the per capita food availability follows the same pattern as the total biomass (Table 4.12).

TABLE 4.12. Relative mussel availability per individual rock-lobster using mussel's size-based availability to a 72mm rock-lobster and rock-lobster density (both directly measured and using CPUE as a relative measure).

AREA	MUSSELS/CAPITA - CPUE	MUSSELS/CAPITA - DENSITY	GROWTH
SW BLINDER	1175	154	3.2
GALLOVIDEA	528	59	4.71
ICHABOE	390		6.84
EASTER CLIFFS	1790		4.3*

* - assume growth rates in Beyers and Wilke (in press) refer to two moults.

Despite the availability of mussels per rock-lobster at SW Blinder being at least double that at Gallovidea and Ichaboe, growth is higher at Gallovidea and markedly higher at Ichaboe compared to SW Blinder. In addition, growth at Easter Cliffs is lower than both Gallovidea and Ichaboe although Easter Cliffs has a very high available mussel biomass (in this case mostly Perna perna) per rock-lobster.

In addition to spatial aspects, some comments on the effects of temporal changes in food supply are possible. Catches and CPUE in both Namibia and the Cape declined dramatically since 1989 (see section 3). It has been shown that, in the Cape, this was primarily due to a reduction in growth rate, which reduced recruitment of legal-size animals and the numbers available to the fishery (Shannon et al. 1992). Although no data on growth of rock-lobsters at Luderitz are available for the period, it is suspected that growth was reduced there as well (Shannon et al. 1992). Furthermore, it has been postulated that this lower growth was due to reduced availability of food (Aulacomya ater and Choromytilus meridionalis) in the Cape in recent years (Shannon et al. 1992). This study indicates that a reduction in food supply did not occur in the Luderitz region and that if, in fact, growth was reduced in Namibian waters, the explanation should be sought elsewhere. The hypothesis of food-limited growth in recent years can, perhaps, not be unequivocally rejected because the time series is too short and covers a period when growth may already have been lower. As this is an issue of crucial management importance, the monitoring of rock-lobster movements and benthic species densities should continue at Luderitz and, in addition, be linked to annual estimates of growth rates.

To summarise, in the Luderitz area, rock-lobster growth rate is not related to the amount of "food" present, but is influenced by other factors (such as oxygen content of water, section 2). These data do not support the assertion that Jasus lalandii experiences density-dependent growth rates due to food limitation (Pollock and Beyers 1981; Pollock 1986; Pollock 1993). More direct measures of individual nutritional states (Dall 1974 and 1975) may throw further light on the issue.

This study does not support any of the current hypotheses linking benthos and rock-lobster. In particular, the hypothesis that rock-lobster predation controls benthic species densities is rejected for the Luderitz region where Jasus lalandii undergoes marked seasonal migrations. It is proposed that, in general, benthic species such as whelks and mussels form an interacting community on a small scale which experiences rock-lobster predation as one of a number of essentially random disturbance factors. Rock-lobster, in turn, experience the benthos as a mosaic of patches of varying food (and shelter) type, have a catholic generalist diet, and do not generally display food-limited growth rates in the highly productive upwelling environment of the Namibian west coast.

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