

PUERULUS AND EARLY JUVENILE RECRUITMENT
OF THE ROCK LOBSTER *JASUS LALANDII* IN
RELATION TO THE ENVIRONMENT AT LÜDERITZ
BAY, NAMIBIA

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

by

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February 2005

ABSTRACT

A global decline in the lobster fishery has necessitated the growout of wild-caught post-larvae (pueruli) on farms to meet the worlds lobster demand. A limited knowledge on puerulus settlement in the West Coast rock lobster (*Jasus lalandii*) constitutes a major barrier for *J. lalandii* culture development in Southern Africa. As an extension of an existing long-term puerulus monitoring program of the Ministry of Fisheries and Marine Resources of Namibia, the present study monitored puerulus recruitment (supply), puerulus condition and juvenile growth of *J. lalandii* and their relationship with environmental variables on an oyster farm at Lüderitz Bay, Namibia. Implications for lobster aquaculture and fisheries management are discussed.

Oyster bags, crates and collectors were sampled daily, weekly and bimonthly, for pueruli and juveniles, respectively, between August 2001 and July 2003 to establish spatial-temporal patterns in their distribution. Animals were transported to the laboratory for morphometric analyses where they were staged as puerulus (Pt = transparent; Pp = pigmented) and juvenile lobsters. The carapace lengths (0.1mm CL) and wet weights (0.01gram) of animals were recorded. Carapace length frequencies were subjected to Modal Progression analysis to identify early juvenile cohorts and calculate their growths. The weight-length ratios calculated and percentage fat content were used as indices of nutritional condition. Seasonal peaks in puerulus and juvenile abundance were estimated using Periodic Regression analysis. The relationships of puerulus and juvenile abundance

with respect to sea surface temperature (SST), wind speed-direction, moon phase, swell and tidal range were established using time lag analysis (ADL).

Transparent pueruli were randomly distributed on oyster bags and crates, and also between collector sites, suggesting that they have no particular settlement preference for certain areas on these structures ($p > 0.05$; $n = 150$). Pigmented puerulus ($p < 0.05$; $n = 566$) and juveniles ($p < 0.05$; $n = 3528$) preferred structurally complex structures that provided better shelter such as crates, which were more sheltered from sea swells, compared to oyster bags. Among oyster rafts, pigmented puerulus and juveniles preferred occupying the sheltered and centred raft areas, which provided better protection from wave action, compared to exposed raft areas, which were exposed to the incoming swell. Puerulus and juvenile lobster appeared to recolonise adjacent bags and crates, and possibly migrate to the substrate and off the farm due to the disturbance of the habitat during harvesting. The booth crevice collector was more efficient in collecting puerulus possibly due to the high structurally complex habitat and the better shelter they provided compared to the hogshair collector. The occupation of structurally complex habitats by early benthic stages may be related to morphological changes associated with metamorphosis.

Puerulus settlement peaked during early spring (August-September) and was related to low sea surface temperatures (12.3°C), strong south winds, and moderate swells in the week preceding settlement. These conditions are synonymous with the “spring upwelling” season of the Lüderitz upwelling cell in the central Benguela current region. Puerulus nutritional condition peaked during this period possibly due to high levels of

planktonic food (due to high nutrients from upwelling) that was available to the late stage phyllosoma larvae further offshore. A “good” puerulus settlement year during 2000 was associated with lower than average SST (11.6°C) and strong south winds and was followed by “poor” puerulus settlement years during 2001 and 2002 when higher than average SST were experienced with below average wind speeds experienced during 2001 only. Puerulus of *J. lalandii* recruited in high numbers into Lüderitz Bay during the new moon, full moon and last quarter moon phases by making use of the increased tides during these phases of the lunar cycle.

Peak juvenile abundance during early summer (November-December) lagged by 8 weeks was significantly correlated with peak puerulus abundance. Puerulus size was similar (8.5–9.7mm CL) over the study period. Juvenile cohorts, 9.9-20.6mm CL in size recruited in 2 distinct waves in August 2001-June 2002 and July 2002-February 2003. The 2001/2002 recruits had higher monthly growth increments and better nutritional condition compared to 2002/2003 recruits. Peak frequencies of 2nd moult juveniles (9.9-10.8mm CL) occurred in September of both recruitment events with nutritional condition being poorest during the 2002/2003 event. The nutritional condition of the settling puerulus did not appear to be related to the subsequent growth of juvenile lobster.

These preliminary results suggest that pueruli recruit once a year mainly during late winter/ early spring under conditions typical of coastal upwelling in the Benguela current near Lüderitz. It appears that puerulus settlement is driven by favourable shoreward currents, which help in transporting puerulus to their settlement grounds. Puerulus supply

is highly variable between years, which appears to be consistent with a highly variable Benguela environment.

The oyster farm supported a substantial standing stock averaging 123 800 lobster per day (range: 22 600-325 300 lobster per day) of which 26 600 were puerulus and 97 200 were juveniles, that may have been harvested once off on any given day during the sample period. Monthly harvesting of the total lobster standing stock during the one and a half year sampling period was just over 2 million lobsters (505 700 pueruli and 1.85 million juveniles) and would potentially have been sufficient seed for a 200 ton lobster production in puerulus lobster growout facilities. In the light of high inter-annual variation in puerulus settlement observed at Lüderitz, the seed supply at the Lüderitz oyster farm is clearly limited and therefore it is prudent that other sites of high puerulus settlement is established before large commercial scale lobster growout can commence.

The migration of lobster off the farm suggested that these lobsters potentially recruit to the fishery and therefore harvesting the entire standing stock on the farm may have adverse negative effects on the wild fishery. A policy decision will be required as to whether more efficient harvesting of lobster from the farm should be allowed. If puerulus removal in *J. lalandii* for aquaculture is allowed in the near future, it should be conducted on an experimental scale or small commercial scale until the potential effects on recruitment into the fishery are clearer.

TABLE OF CONTENTS

	PAGE
Abstract	i
Acknowledgements	vi
Chapter 1 – General Introduction	1
Chapter 2 – Materials and Methods	19
Chapter 3 – Results	40
3.1 Temporal variation in puerulus and juvenile abundance	40
3.2 Environmental correlations	49
3.3 Cohort identification, growth and nutritional condition	61
3.4 Spatial variation in puerulus and juvenile abundance	77
Chapter 4 – General Discussion	83
4.1 Seasonal and annual puerulus recruitment patterns and the environment	83
4.2 Factors affecting juvenile abundance and growth	91
4.3 Spatial variation in puerulus settlement and juvenile abundance: habitat requirements	96
4.4 Implications for lobster fisheries management and aquaculture development	100
References	109
Appendices	125

ACKNOWLEDGEMENTS

Thank you to the Department of Agriculture: Western Cape, South Africa for the ever-reliable financial support without which this project would not have been a success. To my supervisor Prof. Pete Britz, there are not enough words to express my immense gratitude. Thank you for the guidance, support and patience along this long journey that has finally brought us to this point where we can be proud of what we have achieved as a team. The professional and life skills you taught me apparently did not go to waste. I am extremely thankful to the Young Professional Program of the Department of Agriculture: Western Cape for presenting me with this once-in-a-life-time opportunity to develop myself as a “Young Professional Person”. The program added immense quality to my life in terms of the invaluable professional and life skills I’ve learned.

Dr. Andy Cockcroft of the Marine and Coastal Management branch (Department of Environmental Affairs and Tourism), your kind gesture of allowing me to make use of the booth collectors from your research unit (despite the great risk) is much appreciated. My special thanks and gratitude go to the staff members and students at the following institutions for their technical support and for allowing me to be part of their “teams”:

1. Department of Ichthyology and Fisheries Science, Rhodes University, South Africa
2. Department of Agriculture: Western Cape, South Africa (Animal Production Section and the Young Professional Persons Programme)
3. Ministry of Fisheries and Marine Resources of Namibia (Lüderitz and Windhoek Head Offices)
4. Lüderitz Mariculture, Namibia

The Rhodes University staff at the Departments of Statistics (Prof. S. Radloff, Mr. J. Baxter, Mr. R. Sypkens and Mr. L. Njovani), Economics (Dr. D. Mather and Ms M.

Wilson) and Ichthyology and Fisheries Science (Prof. T. Booth, Dr. H. Kaiser, Dr. O. Weyl and W. Sauer) deserves a special acknowledgement for their invaluable assistance with statistical analyses and various modelling.

Although I would like to thank everyone that contributed to this project by name, even in the smallest way, it is not possible. To Kollette, Hilikka, Alex, Tommy, Reinhold and Tangeni (C.A.F Grobler, H.O.N. Ndjaula, A. Hendricks, T. Kleophas, R. Amutenya), thanks for being my support through the good, bad and worst experiences.

To all my friends and fellow students (at DIFS, Geology and SAIAB), you all have made the life of thesis writing a lot easier by just being the great friends and obviously wonderful people that you are. Thanks guys! Martin Davies, thank you for believing in my abilities, though I sometimes didn't. To my extended family, thank you for your enthusiasm and encouragement, it is much appreciated. Much love to Heinrich and Ian, you are my heroes. Thank you for always fixing my problems, whether they are technical or spiritual. Eduardo, you have been most understanding and patient throughout this long journey, *muito obrigado*.

Lastly, I have to go back to where it all began, my Ma and Dad. Thank you for all the sacrifices, your constant support and encouragement since my infancy. The discipline and sincerity you instilled in me helped me through the most difficult times. There are no words to express my appreciation for your unconditional love, which I hold dear to my heart, always.

Die Here is my Herder, niks sal my ontbreek nie! Thank you Lord for blessing me with the ability and spirit to achieve my purpose up to this point.

CHAPTER 1: Introduction

Wild fisheries in Australia, New Zealand, South Africa, Cuba, Brazil, Mexico and America are the main producers of *Panulirus* and *Jasus* rock lobster supplying almost all of the 123 000 metric tons (mt) to the world's major lobster markets in Japan, Taiwan, Hong Kong and China (Jeffs and Hooker, 2000). The supply from lobster fisheries has however decreased over the past 50 years and many fisheries are unstable.

Although the west coast lobster, *Jasus lalandii*, fishery in South Africa and Namibia supplies only 2.4% of the world's export market, it is an important component of the commercial fisheries of these two countries earning approximately R227 million per year (Anon, 2001; FAO, 2003). Catches of the South African west coast lobster, *Jasus lalandii* declined from 13100 tons in the mid-1960's to 1614 tons in 2001 (FAO, 2003) as a result of over fishing and reduced growth rates (Cruywagen, 1999). In the face of declining lobster catches, more effective management of lobster fisheries (to increase natural lobster biomass) (Caputi *et al.*, 1997) and the development of lobster aquaculture (increasing lobster production) (Chittleborough, 1974a; Jeffs and Hooker, 2000) are seen as possible methods of increasing the world's rock lobster supply.

Aquaculture of *Jasus* species is however still dependent on the harvest of wild pueruli and juveniles as it is not yet practical or cost effective to breed these lobsters in captivity. In South Africa our limited knowledge of puerulus settlement dynamics and sites is the greatest barrier for both predictive fisheries management and aquaculture development. This thesis contributed to a wider study to evaluate the potential for on-growing wild lobster puerulus of *J. lalandii* under intensive aquaculture conditions. The main aim of this thesis was to gain an insight into puerulus recruitment and abundance in Lüderitz Bay, Namibia, with a view to determining whether a reliable supply of early juvenile lobster can be harvested for commercial aquaculture. Lüderitz Bay was chosen as the

study site as it is the only known location where large numbers of *J. lalandii* pueruli settle regularly.

In the following sections an overview of lobster resource management, recruitment dynamics and aquaculture is presented in order to contextualise the project and motivate the research objectives.

Lobster resource management

The declining abundance of the lobster resource is the major problem for fisheries managers in the majority of lobster producing countries. Conventional methods used in the management of lobster fisheries avoid further declines in lobster biomass include the regulation of the Total Allowable Catch (TAC), legal size limits, fishing gear and area restrictions, and limited fishing seasons (Hilborn and Walters, 1992). The fisheries for *J. lalandii* in South Africa and Namibia are managed using a combination of these strategies (Grobler and Noli-Pearl, 1997; Cockcroft and Payne, 1999). The management decisions made to reduce fishing pressure usually involve a large component of uncertainty with little indication of how these reductions in lobster harvesting will affect future catches. Australia, New Zealand and Tasmania have developed a more effective method of reducing further declines in the lobster fisheries through predictive stock management (Phillips *et al.*, 1994; Phillips *et al.*, 2003b; Melville-Smith *et al.*, 2004). This method incorporates juvenile and puerulus lobster abundance into models that act as an early warning of catch declines, and allows for the prediction of catch in the long term (Caputi *et al.*, 1995a; Addison, 1997; Caputi *et al.*, 1997; Gardener *et al.*, 2001; Melville-Smith *et al.*, 2004).

It has been shown that for some fisheries there is a close relationship between the recruitment of early life history stages and future recruitment of legal sized lobsters into the fishery (see review, Caputi *et al.*, 2003; Melville-Smith *et al.*, 2004). Predictive methods for the management of these fisheries are thus based on understanding the recruitment patterns of early stage lobsters, which are used as an early indicator of recruitment into the fishery. Understanding the life history stages preceding the stage at which lobster recruit into the fishery reduces the uncertainty incorporated in catch prediction models, especially modelling error due to slow growth of most lobster species. This predictive method of fisheries management involves monitoring the recruitment of early life history stages of lobster. The recruitment and abundance of early stage lobster are incorporated into stock assessment models, which serve as an early predictor of “good” and “poor” years of lobster catches. Thus the TACs can be determined accordingly to avoid further declines in the stock and ensure that the fishery is managed effectively.

The harvesting of early stage lobster for aquaculture could have significant implications for lobster populations and the management of the fishery. In order to predict the effect that puerulus harvesting would have on the lobster population, an understanding of lobster population dynamics is required. An understanding of the recruitment patterns of the early life history stages and their relation to the environment would enable fisheries managers to make more accurate estimations of the level of puerulus that could be removed without compromising the future stability of the resource and the wild fishery (see review, Caputi *et al.*, 2003). Fisheries managers could then allocate the total allowable puerulus catch based on low, medium and high puerulus settlement seasons so that owners of puerulus on-growing facilities could plan their production schedules accordingly (Jeffs and Hooker, 2000). The effect of puerulus removal on the future catch of the Western rock lobster, *Panulirus cygnus*, wild fishery in Western Australia was estimated to be slightly low (Phillips *et al.*, 2003b). The removal of 20 million puerulus (3.3%) during a year when puerulus settlement was 600 million was calculated to result in a 0.62% decrease in the future catch of *P. cygnus*. As part of the fishery management

strategy to ensure biological neutrality and to secure future catch of adult lobster, the Ministry of Fisheries in New Zealand invented a quota trade-off system (Jeffs, 2003). One metric tonne of the TAC of adult lobster is traded off in exchanged for the harvesting of 20 000 pueruli for the commercial grow out in land-based aquaculture systems. These improved risk management strategies will prove important to the economic viability of the lobster export market and puerulus-dependent lobster aquaculture by allowing improved financial planning by lobster farmers, especially farmers of long lived lobster species.

The Ministry of Fisheries and Marine Resources (MFMR) in Namibia launched a long-term *J. lalandii* puerulus monitoring program in November 1999 after high numbers of pueruli were observed settling on an oyster farm a few years earlier. The aim of the monitoring program was to obtain a long-term data set, which could hopefully be used as an indicator of future recruitment into the fishery. High puerulus settlement at this site presented the opportunity to investigate the harvest of puerulus for aquaculture. The Ministry was under pressure to provide estimates of the number of puerulus that can be collected for aquaculture due to demands from industry to develop commercial lobster aquaculture. In addition the MFMR needed to consider the impact that puerulus removal may have on the wild fishery before commercial-farming rights can be issued which requires long-term puerulus settlement data and an understanding of the factors driving settlement. The present study was therefore implemented as an extension of the MFMR's long-term puerulus monitoring program for predicting future lobster recruitment and to assess the Lüderitz Bay's potential supply of pueruli for aquaculture.

Larval, puerulus and juvenile monitoring and predictive catch modelling

Monitoring early lobster life stages is difficult due to the long, complicated life cycles of many lobster species (Booth and Kittaka, 1994). Lobster males and females of most species of the *Jasus*, *Palinurus* and *Panulirus* genera migrate offshore to mate in waters 100m deep, where the females spawn their eggs which hatch into phyllosoma planktonic larvae (Booth and Kittaka, 1994). The phyllosoma larvae are transported by offshore currents into oceanic circulating systems up to 1500km offshore for periods of 6-24 months, which makes monitoring of their abundance problematic. After circulating in offshore oceanic waters, larvae are transported to the continental shelf break where they metamorphose into the post larval phase called the puerulus. The puerulus is a transitional stage between the planktonic larval and the benthic juvenile stages. Pueruli swim, with the help of cross shelf currents, to the inshore zone where they settle among the benthos and later metamorphose into juveniles. Finding suitable habitat is important for the survival of settling pueruli (Booth, 1979; Herrnkind and Butler, 1986; Pollock, 1987; Phillips and Booth, 1994; Lipcius and Eggleston, 2000).

Various methods of monitoring the recruitment of early life history stages of spiny lobster have been developed over the past 50 years (Booth, 1979; Pearce and Phillips, 1994; Phillips and Booth, 1994). A series of plankton trawls were first used to collect phyllosoma larvae and puerulus in deep waters (Lazarus, 1967; Heydorn, 1969; Pollock, 1973; Booth, 1979, Jeffs *et al.*, 2001) as part of larval recruitment studies. Plankton trawls are still used today to study patterns in phyllosoma larval movement patterns in offshore waters (Dennis *et al.*, 2001; Ioue and Sekiguchi, 2001). The progressive movement of puerulus inshore is also traced using plankton trawls (Yeung *et al.*, 2001). Plankton trawl data yield insights into puerulus recruitment patterns but provide incomplete information on puerulus settlement in coastal waters. After observing large numbers of puerulus lobster settling on lobster fishing gear (pot traps/ lines), harbour walls, rock pools and under stones on beaches (e.g. *Jasus edwardsii*, previously known as *Jasus novaehollandiae*), *J. lalandii*, *Panulirus homarus rubellus*, *Panulirus ornatus*, *Panulirus polyphagus*), researchers started investigating puerulus settlement patterns

(Heydorn, 1969; Pollock, 1973; Booth, 1979; Phillips and Booth, 1994). It was however difficult to quantify settlement on these various substrates. Puerulus collectors were designed to serve as a more consistent method of measuring settlement (see reviews, Booth, 1979; Phillips and Booth, 1994). The designs were based on the association each species pueruli had with their preferred settlement substrates and the habitat where juveniles predominantly occur. Most collectors (booth crevice, witham, and hogshair collectors) were moored in coastal waters less than 15m deep since juveniles of most species (e.g. *J. edwardsii*, *P. cygnus*, Australia and New Zealand; *Panulirus argus*, Caribbean) inhabit shallow waters in this depth range (Phillips and Booth, 1994).

Sites with particularly high puerulus settlement were identified and used for long-term monitoring of *J. edwardsii* in New Zealand (Booth *et al.*, 2001a; Booth *et al.*, 2001b) and Tasmania (Gardner *et al.*, 2001) and *P. cygnus* in Australia (Caputi *et al.*, 1997). Long-term data sets were established and seasonal cycles in settlement were determined to establish the time of year when settlement is at its peak. Establishing the main settlement season enabled researchers to come up with indices of puerulus and juvenile abundance, which are numerical values calculated from the average abundance during the peak abundance seasons. Later on, patterns of puerulus settlement were correlated with patterns in environmental parameters such as Sea Surface Temperature (SST), wind stress and currents, to understand their relationship and thus establish factors that most likely explain patterns of puerulus settlement (Caputi and Brown, 1993; Caputi *et al.*, 1995a, 1995b, 2003). Puerulus settlement has also been correlated with the abundance of subsequent stages (juveniles, sub-adults) of the life cycle and with commercial and recreational landings. These relationships have been successfully used to predict future catches (Cruz *et al.*, 1995; Phillips *et al.*, 1994; Guzmán-Del Próo *et al.*, 1996; Addison, 1997; Caputi *et al.*, 1997, Booth *et al.*, 1999, 2001; Cruz *et al.*, 2001; Gardener *et al.*, 2001; Yeung *et al.*, 2001; Phillips *et al.*, 2003a, b); Melville-Smith *et al.*, 2004). Indices of puerulus recruitment may also serve as an indicator of declines in the biomass of spawning populations (Hilborn and Walters, 1992). A long-term settlement data set of at least 5 to 7 years is however required to predict future “good” and “poor” years of catch

and declines in spawning biomass of commercial lobster species (Booth and Kittaka, 1994; Phillips *et al.*, 2000a, 2000b; Gardener *et al.*, 2001). Juvenile recruitment indices are used to predict catch 2-3 years prior to the recruitment of young adult lobster into the fishery (Caputi and Brown, 1993; Caputi *et al.*, 1995a, 1995b, 2003).

Restocking pueruli and juveniles caught in the wild back to nursery areas is used as a method of rebuilding/enhancing lobster stocks for species such as *Panulirus japonicus* in Japan (Nonaka *et al.*, 2000) and *J. edwardsii* in New Zealand (Illingworth and McDermott, 1997). Pueruli collected during settlement programs are used for restocking juvenile nursery areas that have particularly low juvenile abundance. Artificial reefs and structures such as wooden platforms called "casitas" and "pesqueros", and concrete blocks (Cruz and Phillips, 2000) were deployed to enhance puerulus settlement and juvenile lobster abundance of the spiny lobster, *Panulirus argus*, in Cuba in areas where natural habitat was destroyed (Cruz *et al.*, 1995) and in the Caribbean to enhance recruitment into the fishery (Butler and Herrnkind, 1997; Herrnkind *et al.*, 1997; Butler *et al.*, 2001). In Japan artificial structures in the form of concrete blocks were used to enhance puerulus settlement and juvenile abundance of *P. japonicus* to improve coastal lobster fisheries (Nonaka *et al.*, 2000). In the above-mentioned cases lobster populations were enhanced through increased juvenile survival due to the structures providing cover to small juveniles from most natural predators. In addition, artificial structures are used to estimate mortality during the juvenile stage (Eggleson *et al.*, 1997; Phillips *et al.*, 2003a), which is incorporated into recruitment predictive models to give more accurate estimates of future recruitment into the fishery (Cruz *et al.*, 1995).

In summary it appears that to increase lobster production through more effective fishery management a long-term predictive management strategy is required which should include the following elements:

- A long-term puerulus settlement and juvenile abundance data set of at least 6-7 years
- Good long-term puerulus monitoring sites
- Consideration of a juvenile stock enhancement program

Conventional and long-term catch prediction management methods are limited in increasing lobster production in that they only help to avoid further declines and to recover natural fish stocks after several years. The benefits of such operations are only visible after a few years due to the long time lobster take to grow and the long-term nature of the puerulus settlement data sets (5-7 years) required for predictive stock assessment modelling. With the reduction of TAC, and shorter fishing seasons implemented in the face of drastic lobster catch declines, comes the liability or problem of unemployment, low incomes, and an under supply to the lobster export market. Alternative methods of boosting production such as aquaculture or stock enhancement are therefore attracting increasing attention.

Increased lobster production through on-growing and aquaculture

Various laboratory and field studies have provided a better understanding of puerulus and juvenile recruitment and settlement, and stimulated interest in the possibility of lobster aquaculture (Butler and Herrnkind, 2000). The puerulus monitoring studies that aimed at collecting long-term puerulus settlement and juvenile abundance data used in predictive fisheries management (Booth, 1979; Cruz *et al.*, 1995; Phillips *et al.*, 1994; Guzmán-Del Prío *et al.*, 1996; Addison, 1997; Caputi *et al.*, 1997, 2001; Cruz *et al.*, 2001; Gardener *et al.*, 2001; Yeung *et al.*, 2001; Phillips *et al.*, 2003b; Melville-Smith *et al.*, 2004), created the advantage of providing pueruli that could be utilised for research on basic puerulus and juvenile biology, ecology in the field and laboratory (Butler and Herrnkind, 2000). As part of the field experiments researching juvenile habitat requirements, mortality and stock enhancement, pueruli were reared to juveniles in the laboratory and then introduced into habitat areas where juveniles occur naturally (Eggleston *et al.*, 1990; Balchen, 1993; Cobb *et al.*, 1998; MacDiarmid, 2000; Nonaka *et al.*, 2000; Beal *et al.*, 2002). The natural biomass of spiny lobster *P. argus* was enhanced and thus increased the production from wild fisheries. Laboratory studies investigated juvenile lobster growth (Chittleborough, 1974a, 1974b; Crear, 2000), survival (Lellis and Russell, 1990), feeding biology (Lellis, 1992) and the effect of environmental factors (Chittleborough, 1975) on the above studied factors to understand the relationship among these factors. Information from laboratory and field studies created a better understanding of puerulus and juvenile recruitment and settlement, and stimulated interest in the possibility of lobster aquaculture.

Growing out wild-caught puerulus lobster to marketable size appears to be a potential method of increasing lobster supply to the market. The high number of pueruli collected almost annually from puerulus research collection sites and the successful growth and survival laboratory studies led researchers to investigate the viability of rearing pueruli to marketable size on a commercial scale (Chittleborough 1974b; 1975; Booth and Kittaka, 1994; Gardner *et al.*, 2000). To date *Panulirus homarus* from India and Taiwan, *Panulirus orinatus*, *Panulirus polyphagus* (India, Singapore) and *Panulirus versicolor*

(India) are the only species farmed commercially by growing out wild caught puerulus and juvenile lobster to marketable size (Rahman and Srikrishnadhas, 1994; Wickens and Lee, 2002). Taiwan was the first country to produce commercial quantities of market size lobster from wild-caught pueruli and juveniles. In 1987 there were about 20 lobster farms in Taiwan producing 400 000 lobsters (Chen, 1990). The largest farm had about 1.3 ha of water and has the capacity to produce about 150 000 marketable lobsters a year (Chen, 1990). Taiwan's lobster production from the culture of wild caught juveniles did not satisfy market demand and therefore there was a mass importation of market size lobsters from different parts of the world. Tropical species *P. orinatus* and *P. polyphagus* were commercially produced in floating fish farm cages in Singapore. The production output was around 24mt per year (Lovatelli, 1990). The on-growing of puerulus and juveniles of *Homarus gammarus*, in Florida, USA and *P. orinatus* in India has proved successful in supplying market sized and smaller sized lobster to export markets in Asia, Europe and America. These species were cultured from puerulus to the market size of 200g (Asian market) in 2years and 300g in 3 years with some species reaching these sizes in 1-2 years (Booth and Kittaka, 2000). Market supply of lobster from puerulus culture is not seasonal, but may supply lobster throughout the year, thus providing a stable or consistent supply of lobster to the export market. Suppliers of cultured lobster are not limited by legal size limits imposed on wild lobster fisheries, allowing them to supply smaller sized lobster to export markets like the Asian market where small lobsters are in greater demand. The socio-economic benefits of lobster culture operations have been identified as a source of employment all year round (puerulus harvesting, grow-out and processing and packaging) providing a stable income to communities.

Chittleborough (1974a) was the first researcher to investigate rearing commercial quantities of spiny lobster pueruli when he successfully grew out the western rock lobster, *Panulirus longipes cygnus*, from puerulus to maturity in the laboratory. Over the following 30 years advances in techniques of growing out pueruli and juveniles of spiny lobsters *Panulirus longipes cygnus* (Chittleborough, 1974a, 1974b, 1975), *J. edwardsii* (James, 1998; Jeffs and James, 2000), *Jasus verreauxi* (Crear *et al.*, 2000), *P. argus*

(Lellis and Russell, 1990; Lozano-Alvares, 1996), *P. polyphagus* (Lee and Wickens, 1992), *P. homarus*, *P. versicolor*, and *P. ornatus* (Chen, 1990; Rahman and Srikrishnadhas, 1994) were made through various studies. These other species were cultured from wild-caught puerulus to maturity on an experimental basis. However the collection of commercial quantities of puerulus has not been permitted due to concerns about the effect of removing puerulus on future catches of the wild fisheries (e.g. *P. japonicus* in Japan, *J. verreauxi* in Tasmania). Commercial rights to harvest small quantities of pueruli of *J. edwardsii* for sea-cage farming (Booth, 1992) in New Zealand were implemented in 1996 (Jeffs and Hooker, 2000), which was recently extended to larger enterprises collecting thousands of pueruli for shore-based culture (Booth and Kittaka, 2000). This large-scale collection of puerulus is exchanged for commercial quota to ensure that the operation is biologically neutral (Crear, 2000; Booth *et al.*, 1999; Phillips *et al.*, 2003a). For some species (e.g. *P. argus* from South America and *J. lalandii* from South Africa and Namibia) lobster aquaculture based on wild seed is not yet possible since most of the main criteria required for feasible commercial grow out is lacking. These criteria are summarised below:

- Working knowledge of puerulus recruitment patterns
- Collection Sites with high puerulus settlement
- Method of collecting pueruli
- Consistent seed supply
- Technology of feeding and grow-out systems
- Economic viability of commercial scale culture

The main obstacle for lobster culture using wild-caught puerulus and juvenile lobster is the high interannual variability in puerulus settlement, making puerulus supply inconsistent (Booth and Kittaka, 2000; Jeffs and Hooker, 2000).

Larval supply through hatchery rearing

Rearing lobster larvae in the hatchery was seen as an alternative source of pueruli for commercial lobster grow-out but is still in the experimental phase due to a lack of suitable commercial production techniques. The system design for large-scale production and feed formulation required for phyllosoma still needs to be perfected for commercial scale production of hatchery reared puerulus to succeed (see historical review, Kittaka, 2000). The reproductive biology of adult lobster is well studied in all species of spiny lobster. The successful mating, spawning and egg hatching in captive breeding programs and experiments of various species of spiny lobster in Australia, New Zealand, Japan, USA, South Africa and India urged researchers and managers to investigate advances into larval rearing (Chittleborough, 1976; Tong, 1993; Kittaka, 1988, 2000; MacDiarmid and Kittaka, 2000). The main challenges of lobster larval culture are the prolonged larval cycle, unusual larval morphology, lack of information on larval diet and feeding habits, and system design (Mikami *et al.*, 1994). Japanese researchers were the first to rear *Palinurus* from the egg to puerulus stage (see historical summary, Kittaka, 2000). Species that have been successfully cultured are the warm temperate species *P. japonicus*, cultured at 25°C (304-391 days) cool water (20°C) species *J. lalandii* (306 days); *J. novaehollandiae* (319 days); *J. verreauxi* (189-359 days); *J. edwardsii* (212-319 days) and *Palinurus elephas* (64- 132days). Few cultured phyllosoma larvae survived to the puerulus stage. Phyllosoma of *Thenus* genus are easier to rear because the larval cycle has four instars and one nisto stage and the cycle is completed in 40 days (Mikami *et al.*, 1994). Among the *Panulirus* tropical and subtropical species the larval culture of *Panulirus japonicus* is the best studied. Phyllosoma culture trials of *P. japonicus* were conducted over the past 50 years by prefectural fisheries experimental stations along the Pacific coast in Japan. In his pioneering study during 1986/87, Kittaka (1988) attempted to rear other important genera such as *Palinurus* and *Jasus* for phyllosoma culture. Kittaka selected species from these cool temperate genera aiming at culturing phyllosoma through all stages. He introduced *Palinurus elephas* from Ireland and France, *Jasus lalandii* from South Africa, *Jasus edwardsii* and *J. verreauxii* (both) from New Zealand and Australia for phyllosoma culture experiments at Sanriku northern Japan, where the

ambient water temperature was suitable for cool temperate species. *Jasus lalandii* was the first palinurid species cultured through its entire larval development (from the egg stage through to the puerulus stage) by Kittaka (1988). After 306 days the only remaining final staged phyllosoma larva metamorphosed into a puerulus and died after 31 days due to system failure. The major factor that contributed to the majority of larvae dying before the puerulus stage was high mortality during the first seven stages of the larval cycle. Kittaka (1988) identified feeding and nutritional requirements of phyllosoma larvae as the factor limiting the success of larval rearing of lobster for 4 cool water species. High mortality during the phyllosoma stage was probably due to bacterial infections. Phyllosoma density and the amount and type of feed are the most important factors in the spread of pathogenic infections. Many advances in research on nutritional requirements, feed formulation (Kittaka, 2000; Ritar, 2000), digestive system (Mikami, 2000), tank/system design (Kittaka, 2000; Matsuda, 2000), photoperiod and temperature requirements (Bermudes, 2000; Ritar, 2000; Tong and Moss, 2000) have been made since the pioneering study by Kittaka (1988). These recent studies on phyllosoma larval rearing technology were aimed at developing systems, feeds and understanding phyllosoma biology to increase survival and growth, and possibly shorten the larval cycle under intense culture conditions. Larvae were cultured in 40-100L conical bottom vessels in upwelling seawater (Kittaka, 2000) with a flow-through system, water purified by filtration and ultraviolet light (irradiation). Other systems used re-circulation with algae added. In Japan for example, micro-algae *Nannochloropsis* at a density of $1-2 \times 10^6$ cells per ml were used to control bacteria and maintain water quality. Renewing water every 13-14 days resulted in the best phyllosoma survival (Shioda *et al.*, 1997). At high larval densities the long appendages of phyllosoma becomes entangled with debris suspended in the water (cast shells, filamentous bacteria and algae) and therefore high levels of maintenance are needed. Japanese research efforts that involved lengthy larval phases (>300 days) suggest that it is difficult to maintain hygienic culture conditions for long periods of time in a commercial hatchery. For commercial scale rearing it is important to have a large exchange of good quality water throughout the culture period (Shioda *et al.*, 1997; Igarashi and Kittaka, 2000).

The successful culture of palinurid species through their entire larval development depends on finding the correct food required by the phyllosoma phase larvae. Mikami (2000) investigated the phyllosoma digestive system to understand the food requirements for larval grow out. Various diets were tested (Ritar, 2000; Kittaka, 2000) and newly hatched brine shrimp *Artemia sp* and arrow or glass worm, *Sagitta sp*, various fish larvae, and mussel flesh proved to be the best diets. A food combination of micro-alga *Nannochloropsis oculata* and mussel gonad of *Mytilus edulis* worked best for *J. lalandii* and *P. japonicus* phyllosoma larvae. The larvae of *J. edwardsii* and *J. verreauxii* from New Zealand were successfully reared on brine shrimp (Tong and Moss, 2000). *J. edwardsii* and *P. elephas* larvae were reared more successfully on fish larvae (*Arctoscopus japonicus*) compared to *Artemia* due to its higher level of fatty acids (Kittaka and Abrunhosa, 1997). *J. edwardsii* larvae is attracted to and prey on jelly fish which are rich in HUFA's with a similar amino acid composition of lobster larvae (Kittaka, 1997). A major concern is that the use of mussel, *Artemia* and fish larvae as feed for rearing the larvae of lobster will be difficult on a large or commercial scale. Despite the above-mentioned advances in larval rearing technology, survival to the puerulus stage is still not optimal for the success of lobster culture on a commercial scale (Jeffs and Hooker, 2000; Kittaka and Booth, 2000). Therefore, in the short to medium term the most viable approach to develop aquaculture of any lobster species is the on-growing of wild-caught puerulus and juveniles.

Puerulus supply and prospects of *Jasus lalandii* culture in Southern Africa

On growing puerulus of *Jasus lalandii* in South Africa and Namibia appears to be the only economically feasible method at present to increase production, particularly after the initial failure to produce large or significant quantities of puerulus through larval rearing (Kittaka, 1988).

However, knowledge of *J. lalandii* puerulus recruitment and settlement patterns, suitable collection sites; and collection methods on the West Coast of southern Africa, is very limited. Puerulus recruitment in *J. lalandii* on the South African southwest coast first received attention when Pollock (1973) investigated the growth rate of puerulus and post-*puerulus* lobster. Records of blanket net catches during the years 1959 to 1967 revealed that there was a seasonal pattern in the occurrence of *J. lalandii* pueruli in three areas off the South African southwest coast, namely Table Bay, Saldanha Bay and St. Helena Bay (Pollock 1973). Additional plankton net hauls were made off the breakwater at Cape Town and Hout Bay during March and April 1970. Peak puerulus abundance occurred during summer at Saldanha and St. Helena Bays. Puerulus abundance peaked later during autumn in the Table Bay area but still within the approximated time of peak plankton catches, which occur from December-April. Heydorn (1969) found pueruli in offshore waters off the South African coast during a lobster egg survey. Periods of maximum puerulus occurrence in Pollock (1973) agree well with the findings of Lazarus (1967) who found phyllosoma larvae of *J. lalandii* off the southwest coast of South Africa a few weeks prior to puerulus occurrence along the coast. In the 1990's high numbers of pueruli were observed at the water inlets of several marine farms situated on the Southwest Cape coast of South Africa (Cockcroft, MCM, *pers. comm.*, 2001).

In an attempt to boost aquaculture initiatives in South Africa, in 1999 the Animal Production Division of the Chief Directorate of Agriculture (DA) at Elsenburg initiated a program to investigate the feasibility of farming lobsters by on-growing wild caught seed from the puerulus stage. An initial workshop at Elsenburg in December 1999 called together various lobster experts and members of a number of mariculture initiatives in South Africa, in an attempt to draw up a plan of action. A Rock Lobster Steering Committee of South Africa chaired by the Department of Agriculture and comprising representatives from Marine and Coastal Management (MCM), industry and Universities of Cape Town, Stellenbosch and Rhodes was formed. The committee's role has been to guide and promote research and development of lobster farming in South Africa. The current project formed one of two MSc research projects sponsored through this initiative.

Over the following two years some abalone farmers in the south-western Cape mariculture operations were granted permits to collect puerulus lobsters and experiment with their husbandry and growth. However, initial attempts to collect pueruli, firstly from mussel ropes in Saldanha Bay, South Africa and then from man-made structures such as harbour walls, were unsuccessful. In 2000, a MSc research study was initiated to investigate puerulus settlement and collection of *J. lalandii* at various locations around the Cape Peninsula (A. Hazel, *UWC, *pers. comm.* 2001). Booth crevice collectors were utilised but captured almost no pueruli. The one-year puerulus settlement project from 2000 yielded insufficient data to perform statistical analyses, but concluded that this type of collector did not work for capturing *J. lalandii* pueruli in the locations selected.

An oyster farm at Lüderitz Bay, Namibia emerged as a promising site for puerulus collection, as good puerulus settlement was regularly observed on oyster crates and bags. Exceptionally high puerulus settlement was observed in September 1999 (Grobler, MFMR, *pers. comm.*, 2001). In October that year the MFMR launched a long-term

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program monitoring puerulus settlement on oyster crates weekly (Grobler and Ndjaula, 2001), with the aim of understanding the dynamics of puerulus recruitment in this species and determining whether puerulus settlement on the oyster farm could serve as indicator for future recruitment into the Lüderitz-based lobster fishery. Grobler and Ndjaula (2001) described the recruitment of newly settled pueruli and early juveniles in *J. lalandii* from the initial data collected. In 2000 the MFMR's 1-year data set was however limited in that it was not a long enough data set to draw conclusions of the temporal patterns in puerulus settlement and the site's ability to provide pueruli for lobster culture. As part of the rock lobster aquaculture initiative by the South African Department of Agriculture in the Western Cape Province, the present study was launched in 2001 in collaboration with MFMR as an extension of the long-term puerulus monitoring program at Lüderitz oyster farm. In addition to oyster bags and crates on the farm, the efficiency of booth and hogshair collectors in collecting *Jasus lalandii* pueruli was tested at various locations in the bay. Correlating puerulus settlement with environmental factors such as sea surface temperature, wind stress and lunar cycles would add significant value to understanding the puerulus recruitment process at Lüderitz Bay. Grobler and Ndjaula (2001) described the morphometric dimensions and size distribution of pueruli and juveniles of *J. lalandii* at Lüderitz Bay based on 3 months of data. The data was insufficient to draw any conclusions on the growth of pueruli and juveniles in the wild. The size of pueruli and juveniles was therefore recorded during the present study to estimate the growth rate of early benthic *J. lalandii* lobster at Lüderitz Bay.

Aims and Objectives

The aims of this study were therefore to describe puerulus recruitment patterns and to quantify puerulus settlement on the oyster farm in Lüderitz Bay. The specific objectives were to:

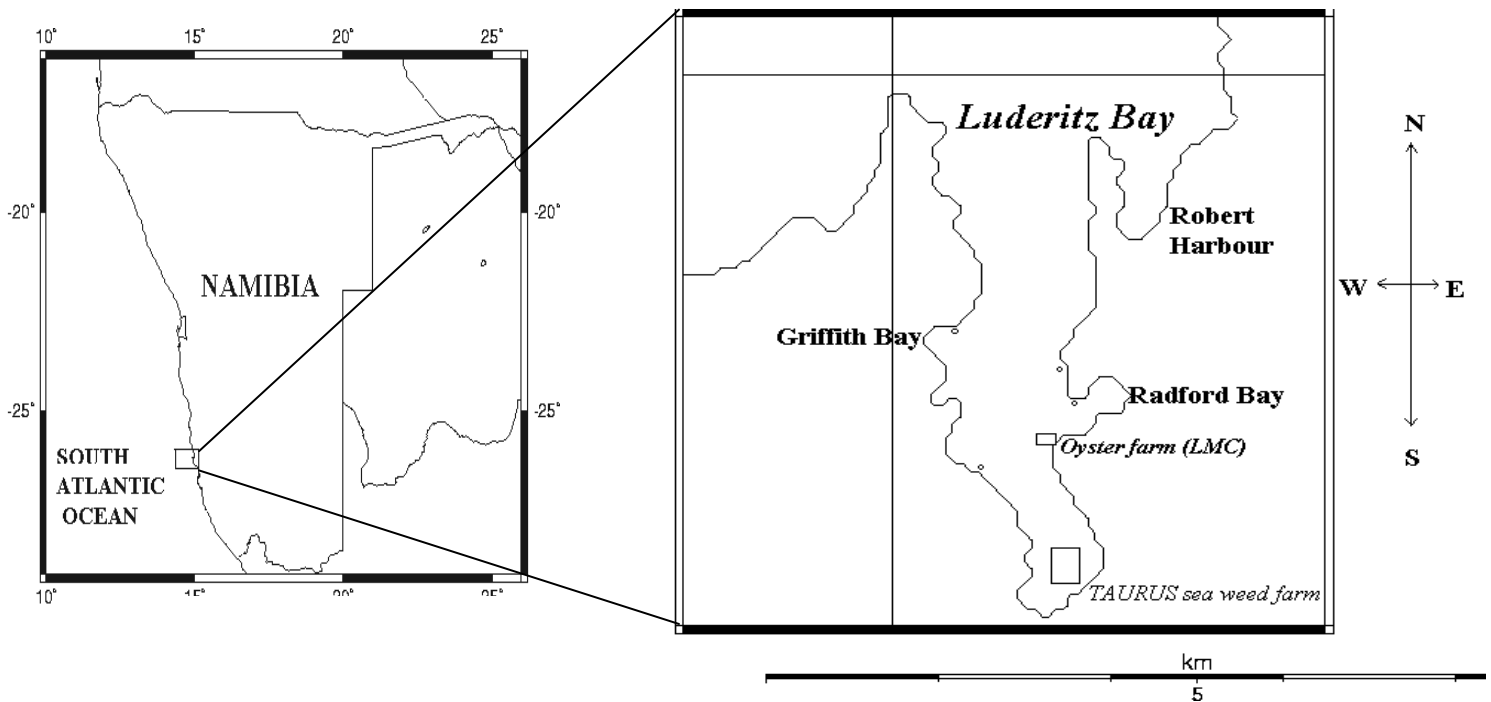
1. Describe the spatial-temporal distribution of puerulus on mariculture structures and collectors.
2. Evaluate the efficiency of two types of collectors for collecting pueruli and to reflect settlement patterns in the greater bay area.
3. Evaluate the nutritional status and growth patterns in puerulus and juvenile lobster.
4. Identify possible correlations between environmental factors and puerulus settlement on mariculture structures and at collector sites.
5. Assess the study site's potential to supply pueruli and juveniles for lobster culture.

Puerulus settlement and puerulus and juvenile recruitment patterns in relation to patterns in environmental factors in the Benguela current ecosystem and Lüderitz Bay are discussed. The implications of puerulus and juvenile recruitment patterns at Lüderitz Bay in terms of the site's potential to supply puerulus and juveniles for *J. lalandii* lobster culture are evaluated.

CHAPTER 2: Materials and Methods

2.1 Study Area

The study was conducted at Lüderitz Bay, a large bay situated at $26^{\circ}36' \text{ S}$, $15^{\circ} 08' \text{ E}$, on the southern coast of Namibia (Map 1). The coastline is influenced periodically by the cold Benguela current and its associated oceanographic features. Lüderitz Bay has several subsidiary bays (Radford Bay and Griffith Bay) and shallow lagoon areas, namely, first- and second lagoon (Penrith and Kensley 1970). Radford Bay is characterised as shallow, sandy with a lagoon on its seaward boundary. Growth on the sea bottom consists mainly of the gelatinous red algae, *Gracilaria* spp.



Map 1 The location of the study area at Lüderitz Bay on the south coast of Namibia. The enlarged map shows the main bay at Lüderitz with the subsidiary bays (Griffith and Radford Bays) and mariculture sites.

2.1.1 Important oceanographic features associated with coastal upwelling at Lüderitz

The upwelling off Lüderitz is more intense than any other area along the Namibian coast (Bailey, 1979; Shannon, 1985; Hardman-Mountford *et al.*, 2003; Campillo-Cambell and Gordoa, 2004). The features contributing to this unique upwelling environment at Lüderitz are the limited/ short coastal plain/ landscape, bathymetry (narrow continental shelf 75km wide), hydrography (permanent high pressure anticyclone offshore and low over the subcontinent) and the oceanography (Benguela current, anticyclonic eddy to the north, intrusion of oceanic waters into the inshore region, cold water filaments extending up to 214km offshore). The high-pressure cell existing over the southeast Atlantic off southern West Africa is responsible for strong southerly winds caused by atmospheric forcing along the stretch of coast. The coastal plain landscape at Lüderitz acts as a thermal barrier preventing equator-ward-southerly winds from blowing over the subcontinent thus increasing the intensity of these southerly winds. These strong southerly winds transport surface waters north and along the coast. With equator-ward flow of surface waters coming into contact with the narrow continental shelf at Lüderitz the speed at which surface waters are transported northward, increases. Geostrophic flow (Coriolis force) resulting from the earth's rotation diverts the flow of surface water offshore through Ekman transport. Surface water transported/displaced offshore is replaced with deep bottom water that is welled up to the surface layers. The upwelling of cold nutrient rich bottom water results in the formation of circulation patterns over and adjacent to the continental shelf (Shannon and O'Toole, 1998) creating a well mixed water column with high oxygen concentration and high level of nutrients over the continental shelf. Despite the high level of nutrients in upwelled water, productivity at Lüderitz is low due to the permanent wind mixing of the water column that displaces phytoplankton cells out of the euphotic zone. The poleward undercurrent distributes nutrient rich water further south where the continental shelf is wider and wind mixing is much less. This allows for the stratification of the water column, which enables phytoplankton to surface into the surface water layer where there is sufficient light for photosynthesis. Chlorophyll levels are high over the shelf between Lüderitz and the

Orange River, which results in high abundance of the prey items of fish and crustacean larvae over this shelf region. The width of the Lüderitz upwelling cell at its southern boundary is constrained close to shore by the intrusion of oceanic water thought to be an anticyclonic meander (Campillo-Cambell and Gordo 2004). This meander created the diversion of the Benguela Ocean Current (BOC) slightly offshore and a resulting cross-shelf current shoreward.

2.1.2 The Oyster farm

Within Radford bay is a commercial oyster farm growing *Crassostrea gigas* (Grobler and Ndjaula, 2001) (Fig. 2.1). At the more exposed side of the bay a set of 22 rafts are used to suspend 409 polypropylene mesh bags in which the oysters are grown. On the landward sheltered side of the bay, 17 long lines are used to suspend 450 plastic crates within which oysters are cultured. These crates (housing “spat” oyster seed) and bags (housing larger oysters) make up the production units of the oyster farm (Fig. 2.2) and are harvested daily during which production units are cleaned with pressure powered hoses. Oyster spat (seed) are grown in oyster crates with larger sized oysters stocked in bags. The oysters cultured on the rafts are submerged at a depth of 2 metres from the surface, while those on longlines are submerged at a water depth of 1 metre.



Figure 2.1 Lüderitz oyster farm within Radford Bay showing the rafts and longlines on which oysters are cultured. The oyster processing shed and service jetty are visible on shoreline (Photo: Q. Snethlage).

Lobster sampling on oyster farm structures

On the oyster farm puerulus and juvenile abundance was monitored daily on the oyster culture bags (Fig. 2.2a). Oyster bags were made of polyethylene with mesh size varying between 9mm and 23mm (depending on the size of oysters) and a length-width dimension of 1m x 2m. Bags are vertically suspended in the water from the oyster rafts by two pieces of 5-mm polythene rope attached to the corners of the bags. These culture bags were stocked with an average of 114 to 144 oysters per bag, which were harvested every 3 months (time taken for oysters to reach cocktail market size). The diverse community of seaweed, sponges and invertebrates (bio-fouling) in combination with the holes of bags provide a structurally complex habitat on the in- and outside of bags, which is utilised by puerulus and juvenile lobsters. Three bags were collected from a particular raft daily, one from the exposed, middle and sheltered side of the raft. Bags were sampled by first enclosing them with a shade cloth net bag (larger than oyster bags) while still in the water to prevent lobsters from escaping. Then the ropes of the bags were detached from the rafts from which they were suspended from, so that bags were transported to shore for samples to be sorted and seaweed cover, fish and invertebrate abundance were recorded. Onshore, lobsters collected from the oyster bags were transferred into fresh seawater in 2-litre sample bottles for further analysis in the laboratory.

As a continuation of the existing long-term monitoring program of the MFMR, puerulus and juvenile abundance was monitored weekly on crates during which, three crates were sampled weekly from the MFMR's experimental oyster crate line. Oyster crates are constructed of a square wooden or polyethylene pipe frames (50cm length x 100cm width) covered with a 9mm mesh size plastic sheeting (Fig. 2.2b, top) which, houses oyster spat. These crates are moored horizontally at 1m below the water surface. Oyster spat are translocated to bags three months after initial stocking, when they reach a minimum size of 9-mm shell length. Crates were attached with pieces of fencing wire at each corner onto long-lines floated with empty plastic water drums (Fig. 2.1). Puerulus and juvenile lobster were mostly attached to the bottom surface of crates. During sampling the fencing wires were carefully detached from the long-lines and crates were

turned bottom-side-up and hauled on board the boat. On board the boat lobsters were transferred into seawater in 2-litre sample bottles to be analysed in the laboratory. Percentage seaweed cover, fish and invertebrate abundance (Fig. 2.2 bottom) were also recorded.

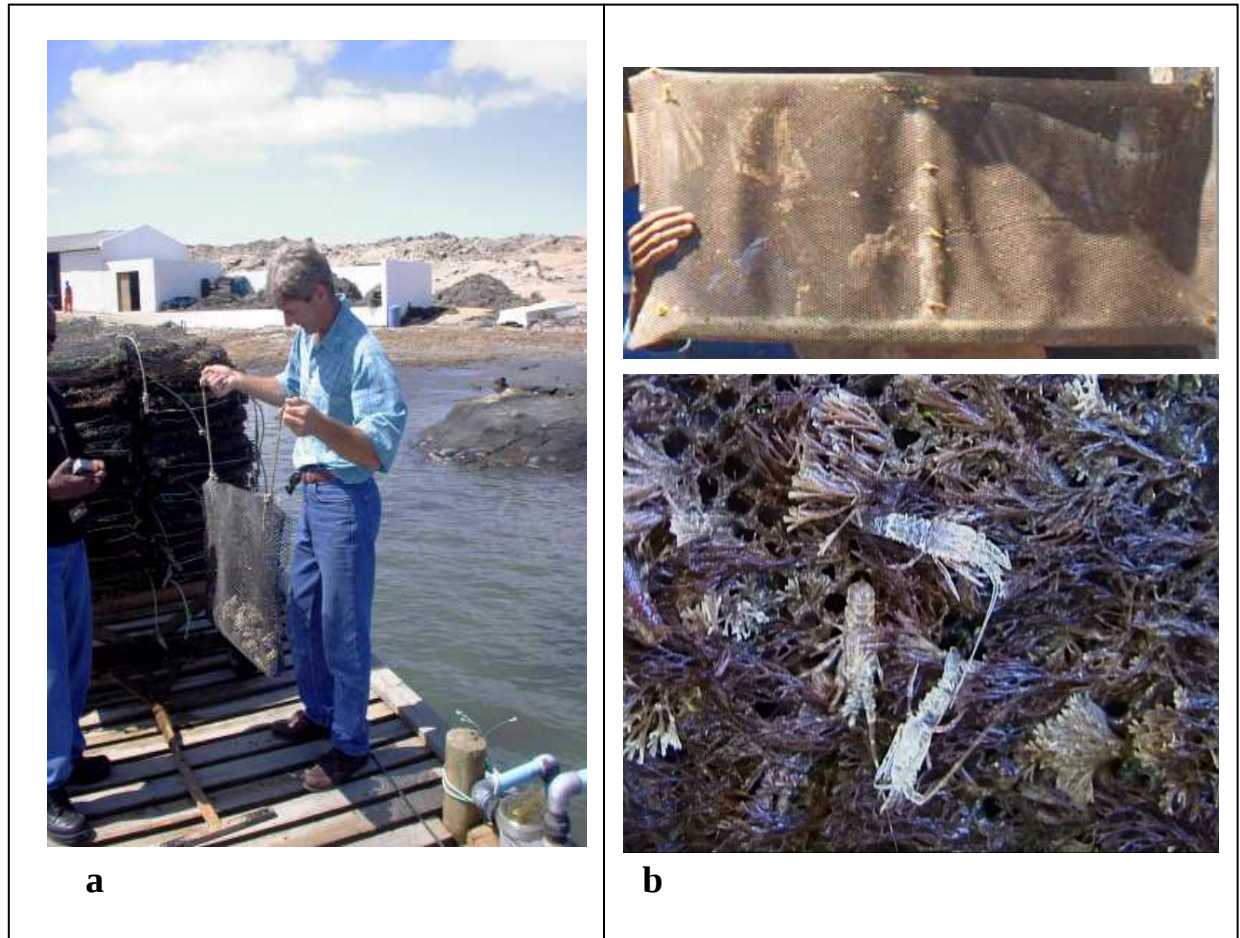


Figure 2.2 (a) Oyster bags, housing cleaned and sorted oysters ready to be returned to wooden rafts in the water (Photo: P. Britz) and (b) (top) unconditioned oyster crate; (bottom) oyster crate collected from the MFMR's experimental line showing seaweed growth, puerulus and juvenile lobster.

2.1.3 Collector site selection and mooring

Four collector sites were selected at First- and Second lagoon, Nest Hotel and Griffith Bay within the lagoon (Fig. 2.3) and three satellite points on the periphery of the oyster rafts. A small number of collector sites were selected since this project was an exploratory study to see how well booth and hogshair collectors would work at different locations in Lüderitz Lagoon. Due to logistical constraints such as the close proximity of sites, the labour intensity involved in sampling collectors (which required at least 2 divers) and sampling frequency, it was only possible to use one collector per site.

Sites were selected based on the degree of shelter, accessibility, water depth and benthic structure. The active swimming pueruli of *Jasus lalandii* settle inshore along the rocky coast in kelp beds and amongst benthic organisms such as sponges, mussels and various red algae species (Pollock, 1987), therefore these characteristics of the benthic substrate were considered in selecting the collector sites. The benthic profile or structure of Lüderitz lagoon consists of a rocky shoreline with some sandy areas. Griffith Bay was the only deepwater site (5-9m) and had a benthic structure consisting of rocky outcrops with 2 small reefs. The benthic community comprised sponges, soft corals (*ascidians*), mussels, starfish, octopus and brown, red and green seaweed (Kelp, *gracilaria* and green *ulva* etc.). The sea floor of the shallow water sites (1-3m depth) at the Nest Hotel, 1st and 2nd lagoon consisted of sulphurous black mud combined with sand. Pueruli and juveniles of *Jasus lalandii* appear to avoid the muddy bottom; therefore mid-water booth crevice collectors, floated with buoys, (see Phillips and Booth, 1994 for design) were selected for this study. This prevented collectors from sinking to the muddy bottom and enhanced seaweed and soft coral growth on the collectors. Due to the fact that puerulus and juvenile *J. lalandii* occur among kelp it was presumed that kelp played an important role in the settlement of puerulus. It is suspected that puerulus swimming inshore settle once they come into contact with kelp. The hogshair collector was therefore selected since it is suspended in mid-water and consists of sheets of multi-filament fishing net, which simulate the fronds of kelp. Hogshair collectors were therefore moored in mid-water at a depth of 2m at shallow water sites and 3m at deep-water sites.

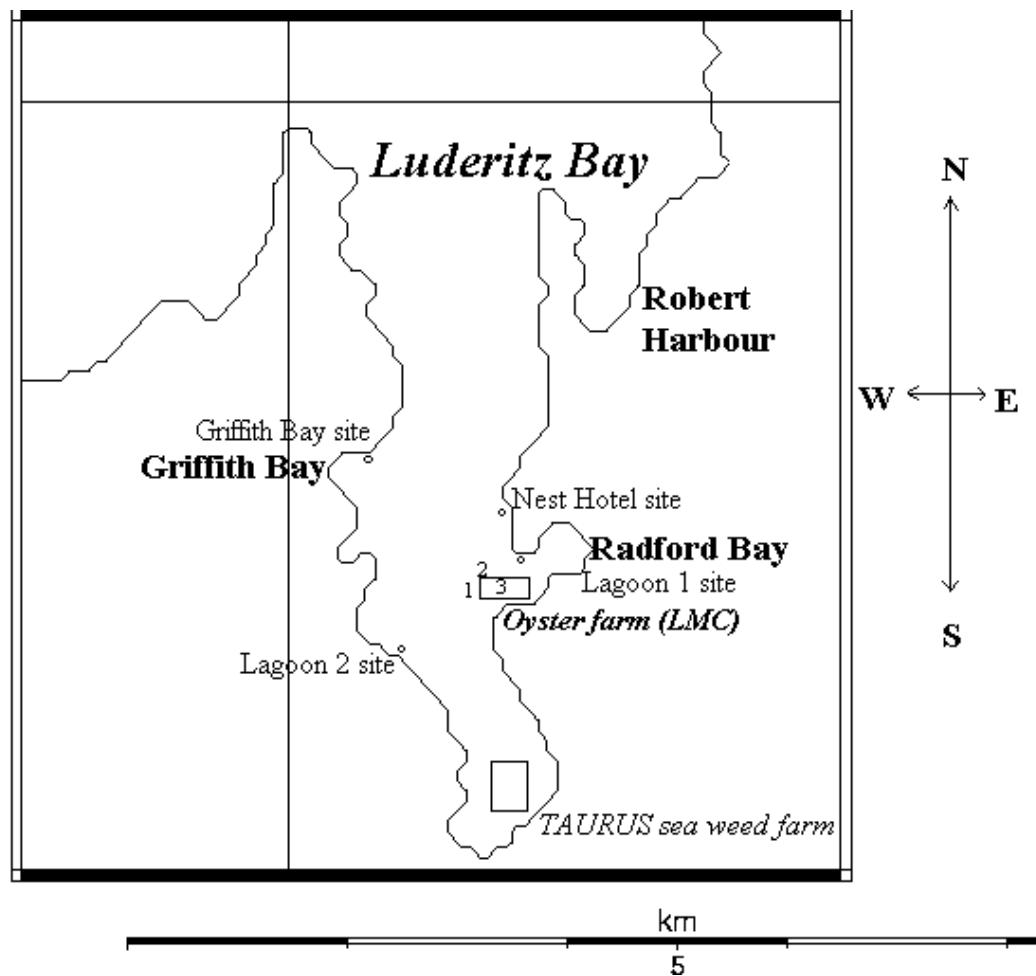


Figure 2.3 Diagram of Lüderitz Bay showing subsidiary bays, mariculture farms (squares) and collector sites (circles). The numbers 1, 2 and 3 indicates the satellite sites 1 to 3 situated on the oyster farm.

Booth crevice and hogshair collector mooring designs and sampling

Booth crevice puerulus collectors were moored at sites along the lagoon and off the oyster rafts to evaluate their efficiency in catching puerulus and juveniles. The collectors in the lagoon were moored according to the mid-water mooring designs for Booth crevice collectors (Fig. 2.4) and hogshair collectors (Fig. 2.6) described in Phillips and Booth (1994). The hogshair collector has been adapted in our study to reduce construction costs and to improve durability by replacing the air-conditioning filter material with sheets of multi-filament anchovy net. The mooring design remained almost identical to the original design (Fig. 2.6) though, with additional ropes attached on the right-hand side of the collector frame which, were attached to a similar 50kg concrete block used in mooring

the Booth crevice collector. A marker buoy was attached to another rope moored at the centre of the hogshair collector. Collectors were sampled every second week at new and full moon phases. Lagoon collectors were sampled by means of SCUBA diving and snorkelling depending on the water depth at the sites. A diver enclosed the collector in a shade cloth net bag to prevent animals from escaping. Then a marker buoy was attached to the mooring block to fix the position of the collector. The collector was then detached from the mooring block and hauled on-board the boat (Fig. 2.5). On-board the percentage seaweed, sponge and soft coral cover and various vertebrate and invertebrate abundance were estimated and recorded. The collector was scrapped using the blunt side of a hacksaw blade and washed several times to retrieve any lobster from the crevices of the collector. Lobsters were put in one-litre sample bottles with seawater to be transported to the laboratory for morphometric analyses. The collector was then returned to the site by mooring it back onto the concrete block.

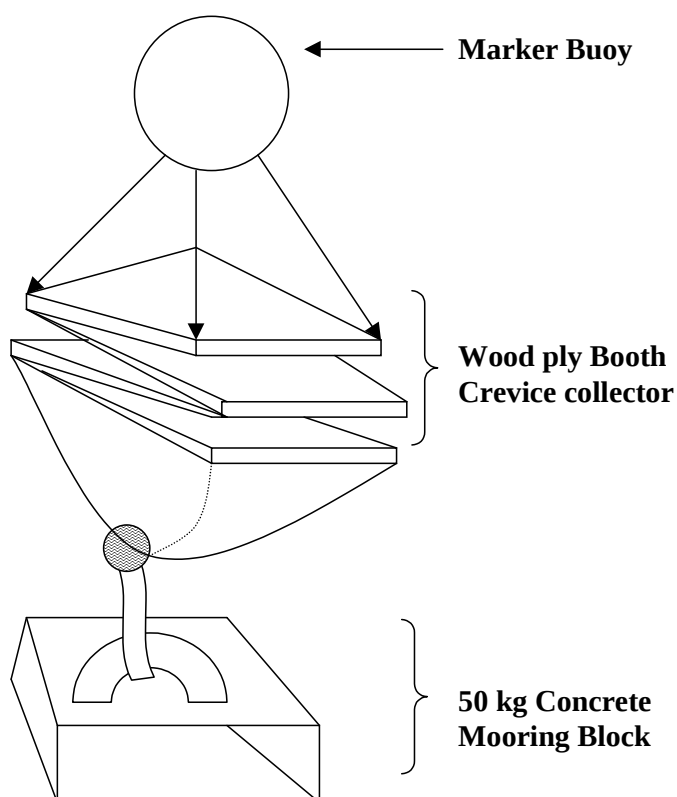


Figure 2.4 Booth crevice collector mooring designed for catching pueruli in the middle of water column. The design is suitable for mooring on uneven or unstable bottom surfaces, for example, muddy areas where the original steel stand design would fail to keep the collector suspended in water column.



Figure 2.5 Conditioned booth collector showing seaweed growth, sponge, hard and soft coral fouling.

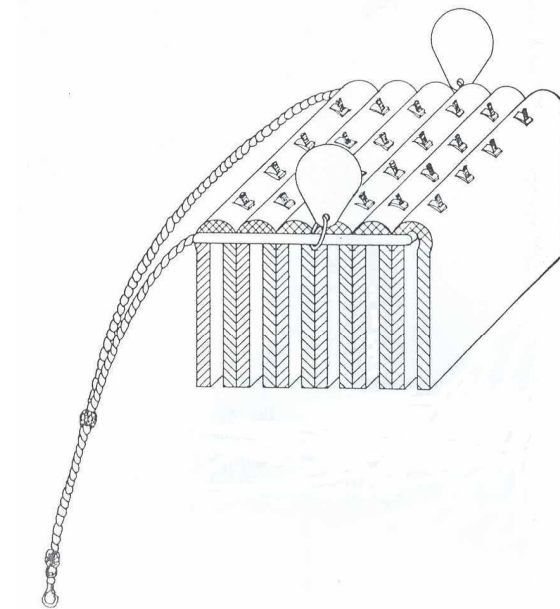


Figure 2.6 Original design of the Hunt hogshair collector (without additional mooring rope and marker buoy adaptations) used for catching puerulus of *P. argus* in the Caribbean (Figure from Phillips and Booth, 1994).

Booth crevice and hogshair collectors were first moored for conditioning (Fig. 2.5 and 2.6) end of January 2002 and settlement was first observed in June 2002 after which sampling commenced. The hogshair collector attracted no pueruli but only larger juveniles of greater than 20mm in carapace length. Structurally the hogshair collector was not suitable for the physical conditions at Lüderitz Bay with all collectors being destroyed by moderate wave action within a period of 2 months. The hogshair collectors could not be repaired and was therefore replaced with new ones. The destruction and loss of collectors after every 2 months rendered the exercise costly and unsuccessful and therefore sampling was discontinued.

2.2 Environmental monitoring

Sea surface temperature (SST) was continuously monitored with temperature data loggers on the oyster farm. Additional SST data was obtained from the Namibian Ministry of Fisheries and Marine Resources (MFMR) records of daily harbour temperatures measured with a hand-held thermometer. Wind speed and direction data was obtained from the Diaz point weather station at Lüderitz. The average swell height (in meters) per day was obtained from estimates taken three times a day at Ichaboe Island situated close to shore just north of Lüderitz. Tidal and lunar information was obtained from the South African naval tide tables. Sea surface temperature, wind speed and direction, moon phase and tidal range were correlated with average number and size of pueruli and juveniles collected on the oyster farm and Booth collectors

2.3 Morphometric Analyses

All samples were transported to the laboratory live in seawater for sorting into puerulus and early juvenile stages, after which they were subjected to morphometric analyses. Both puerulus and juveniles resemble adult lobsters with differences in size, shape and the presence of certain morphological characters. The puerulus differs from juvenile stage lobsters in that pueruli have feather-like structures called “swimming hairs” on the ventral side of the tail and they are dorso-ventrally flattened with a smooth carapace. The puerulus stages were separated according to their variation in colour ranging from transparent (recently settled pueruli) to slightly pigmented to fully pigmented (Fig. 2.7). Fully pigmented pueruli are almost identical to juveniles but display a more flattened shape and have a smooth carapace. In the laboratory all animals were staged either as transparent puerulus (Pt), pigmented puerulus (Pp) or juvenile (Fig. 2.7). The body length of each puerulus was measured as the carapace length (CL) recorded to the nearest 0.1 mm using callipers. The carapace length (CL) of all lobsters was measured dorsally from the antennal platform to the posterior edge of the carapace. Excess water was removed from all animals by placing them on absorbent paper for (period of time) before their wet weights were recorded. The wet weight of animals was recorded to the nearest 0.01gram using a Mettler balance.



Figure 2.7 Different stages of post-larval lobsters collected from Lüderitz oyster farm (Pt=transparent puerulus, Sp=slightly pigmented puerulus, Fp=fully pigmented puerulus, and J=juvenile) (Photos by J. Keulder).

2.4 Cohort Analysis and Growth

2.4.1 Cohort Analysis Methods

Carapace length measurements of 4770 early juveniles collected from the oyster bags between August 2001 and February 2003 revealed that juvenile size ranged between 7.9 and 46.3mm CL. As a result 7.0mm CL was chosen as the lower limit of the smallest size class and 50mm CL as the upper limit of the largest size class. The interval between size classes was set at 0.4mm CL. The length frequencies per 0.4mm CL interval between 7.0mm CL (minimum size class) and 50mm CL (maximum size class) was calculated for each month. The length frequency distributions were plotted as histograms using the Microsoft® Excel 97 data analysis tool. Length frequency distribution graphs were visually inspected for clear groupings of animals that possibly belong to the same cohorts. The monthly length frequency data calculated in Excel was imported into Fisheries Stock Assessment Tools II version 1.0.0 for windows (FISAT II version 1.0.0) as a grouped length frequency file under the Bhattacharya's Modal Progression Analysis Package (<http://www.fao.org/fi/statist/fisoft/fisat/index.htm>). With the aid of visually inspected graphs, groups of animals that possibly belong to the same cohort were selected for each month, respectively. The Bhattacharya program plotted the expected distribution that best describes the distribution of the selected group (Bhattacharya, 1967). The mean CL (Central tendency or average size of selected group), standard deviation (spread of distribution), R-squared value (significance of correlation between observed size distribution and fitted expected distribution), Population size (P expected population in distribution) and the Separation Index (SI, degree of separation between selected group and other group distributions over lapping that of selected group) of the expected distributions of each selected group were calculated. The output data from Bhattacharya's package were imported into the NORMSEP analysis module, which generated better estimates of the population parameters, (Mean carapace length (CL), standard deviation (SD), proportion of population size (P), separation index (SI), expected population size (N)) using a maximum likelihood algorithm.

The expected distributions for the selected groups for each month were plotted in Microsoft® Excel 97 using the Gaussian Normal Distribution function (Bhattacharya, 1967):

$$(1) y = a * \exp \{ - [(x-b) ^ 2] / [2 * c ^ 2] \}$$

Where: **a** = frequency at mean CL; **b** = mean CL; **c** = std.dev.

However the frequency at the mean CL, **a**, was not known and thus **a₁** was set as equal to 1 to obtain **y**, the total population size. Knowing the sample size **n** given by Bhattacharya's, the frequency at mean CL (**a₂**) for the expected population size **N** was calculated by solving for **a₂** as follows:

$$(2) a_2 = a_1 * N / n$$

The expected population size **N** was then calculated for identified groups for each month using **a₂** as the frequency at mean CL in equation (1). The expected population sizes calculated above were then plotted against the observed length frequencies (LF Obs) for each month to give the cohort graphs. These graphs represent the groups/ cohorts chosen in FISAT's Bhattacharya package. Additional groups identified through visual inspection and those that were biologically expected, were chosen. The mean carapace lengths of some of the groups given by Bhattacharya's did not appear to be accurate according the central tendency of the distributions. These mean carapace lengths were therefore adjusted so that the expected distribution curve best fitted the sample's distribution. The standard deviation of these groups however, was not altered. Based on information from field and laboratory studies on the growth of *J. lalandii* in the same size range, and the shape of the distributions, groups that possibly belong to the same cohorts were visually identified and followed through from month to month. The distribution curves of groups that were designated to a particular cohort were coded with the same alphabetical letter.

Animals belonging to cohort A were presumed to be the oldest and those belonging to Z, the youngest.

2.4.2 Growth Modelling

The final mean CL estimates of groups belonging to the same cohort were regressed over time in months using the linking of means method in FISAT II. The linking of means method calculated the growth increment for each cohort for each consecutive month. Only cohorts whose growth increments were traceable over several months were used in the final growth estimation. The growth increments (mm CL per month) of such cohorts were regressed against their mean carapace lengths to give the overall growth increment of all early stage juvenile lobster less than 20 mm CL in size. The average monthly growth increments for the five size classes (3 mm- size- interval) were also calculated for juveniles less than 20 mm CL.

2.5 Nutritional Condition Indices

2.5.1 Factor K as an indicator/ index of nutritional condition

Weight and length data of individual pueruli and juveniles were used to calculate the nutritional condition factor K, which is a weight- length ratio index represented in the following equation:

$$K = \text{weight (g)} / \text{carapace length (mm)}$$

The K condition factor of pueruli and juveniles was compared between months and between the peak puerulus and juvenile abundance seasons of various years for similar sized animals to indicate the months (seasons) and years during which different sized animals had the best nutritional condition, by means of Kruskal-Wallis ANOVA and Kolmogorov-Smirnoff pair-wise tests.

2.5.2 Total crude fat: Internal energy reserves as an indicator of nutritional condition.

Percentage total fat of puerulus and juvenile lobster was used as a second index of nutritional condition. Puerulus and juveniles (with the appendages removed) were frozen at 5°C following morphometric analysis. Animals were freeze-dried at a constant mass and then ground to a fine powder. Percentage crude fat content for weekly-pooled samples was determined gravimetrically using the TECATOR SOXTEC HT-6 fat extraction method using diethyl ether and petroleum ether solvents. Weekly and monthly variation in lipid content was established by plotting % fat per gram of dry weight over time. Percentage fat was compared between months and seasons for similar sized animals to indicate the season during which different sized animals had the best nutritional condition. The K and % crude fat indices were standardised by calculating their scores as follows:

$$\text{Score} = (\text{Observed value} - \text{sample average}) / \text{Sample standard deviation}$$

The scores of K and % crude fat were compared by means of a linear regression model to establish the relationship between these indices.

2.6 Data and Statistical Analysis

2.6.1 Abundance calculations

Puerulus settlement and juvenile abundance data collected from crates for the MFMR's puerulus monitoring program (November 1999-July 2003) and data collected from bags (August 2001-February 2003) were averaged as the number of lobster per bag per day, and the number of lobsters per crate per week. These abundance indices were also averaged per month.

2.6.2 Statistical analysis

Puerulus settlement and juvenile abundance data recorded on oyster bags, crates and collectors during the study were tested for normality using the Shapiro-Wilks test. The Levene's test of homogeneity of variance was used to test for equal variance between samples. The Shapiro-Wilks and Levene's test revealed that all abundance data was not normally distributed and variances between samples were unequal. Square root ($\sqrt{\cdot}$), box-cox, log linear and lognormal transformations of the data proved unsuccessful in obtaining normality. Therefore non-parametric tests were used for comparative analyses.

Spatial variation

Puerulus settlement and juvenile abundance on the oyster farm, *Gracilaria* farm and collector sites, were compared statistically by means of a Kruskal-Wallis non-parametric Analysis of Variance (ANOVA) in the Statistica 6.1 package. Scheffe's and Tukey's HSD multiple range tests were conducted to reveal the components that differed between areas throughout Lüderitz Bay.

Puerulus and juvenile abundance was compared between exposed, centre and sheltered areas on the oyster rafts using a Kruskal-Wallis ANOVA. Scheffe's test was conducted to reveal which stages differed between the raft areas.

Puerulus and juvenile abundance were compared between oyster rafts and crates using Kruskal-Wallis ANOVA and Scheffe's and Tukey's multiple range tests were

performed to reveal which stages' abundance differed between crates and bags ($p < 0.05$). Similarly, puerulus and juvenile abundance on collector sites in the lagoon was compared with that on satellite collectors suspended from oyster rafts using Kruskal-Wallis ANOVA. Scheffe's multiple range test was performed to reveal sites with significantly different puerulus and juvenile abundance.

Temporal variation in abundance (Seasonality and time lag analysis)

Puerulus and juvenile abundance data from oyster bags, oyster crates and Booth crevice collectors was analysed separately for temporal variation by means of periodic regression analysis (circular statistics) and multiple range analysis. Separate analyses for transparent and pigmented puerulus abundance on oyster bags and crates were carried out. Puerulus abundance data from crevice collectors was however pooled for the two puerulus stages due to the low number of observations. Seasonal patterns in puerulus and juvenile abundance were compared between oyster bags, crates and collectors. Seasonal peaks in puerulus and juvenile abundance were compared between years using the Kruskal-Wallis ANOVA and Tukey's multiple range tests to establish significant differences.

Periodic Regression analysis

The cycle in puerulus settlement and juvenile abundance on oyster bags and crates was tested for seasonality by means of a periodic regression analysis. Periodic regression is useful in:

- (i) describing cyclical patterns in data;
- (ii) obtaining a robust mean value where variation is cyclic with limited observations;
- (iii) modelling cyclic and linear (or categorical) parameters together, where the linear parameter is of principal interest but not obscured by the cycles and
- (iv) de-trending or removing cyclic components from data to reveal anomalies or values de-correlated from the underlying cycles (Bell, 2000).

Observed puerulus settlement and juvenile abundance data was regressed against an x-axis transformed into angular data with sine and cosine functions based on the sample dates (day of the year; DOY) to determine the seasonal pattern in puerulus recruitment and juvenile abundance. For periodic cycle to be prevalent in a data set, the R^2 -value from the multiple regressions of abundance and the angular (sine and cosine) transformed x-variable (time) need to be less than 0.25 at a significance level of $p < 0.05$. Once a significant R^2 -value for periodic regression is prevalent, the periodic component in abundance can be calculated by:

$$Y = M + B_1 \sin(R'DOY) + B_2 \cos(R'DOY)$$

$$Y = M + A \cos(R'DOY - \partial)$$

Where M , B_1 and B_2 are coefficients obtained from the multiple regression above. The peak time of recruitment and abundance were calculated by:

$$P = t_0 + \partial$$

Where: $\partial = \arctan(B_1 / B_2) + QC$

t_0 = the nominal zero of the cycle

The seasonal cycle of the puerulus and juvenile abundance was expressed by the following polynomial and linear regression models, respectively:

$$Y = M + B_1 \sin(R'X) + B_2 \cos(R'X)$$

Where: y = abundance

B_1 = multiple regression coefficient of $\sin(R'DOY)$

B_2 = multiple regression coefficient of $\cos(R'X)$

$R'X$ = time (Day of the Year (DOY) for bags and crates & Month of the Year (MOY) for collectors) in Radians

M = Mesor (multiple regression coefficient of the intercept)

$$Y = M + A \cos(R'X - \hat{\phi})$$

Where: M = the mesor

A = the amplitude

$R'X$ = time (DOY or MOY) in radians

$$\hat{\phi} = \arctan (B_1 / B_2) + QC$$

where QC = quadrant correction factor (See Bell, 2000)

The seasonal cycle in puerulus and juvenile abundance was removed by subtracting the predicted periodic component from the observed abundance to reveal the deviations from the expected cycle, termed “anomalies” (residuals) in abundance, thus giving the de-trended abundance values. Similarly, environmental parameters (temperature, wind speed and direction, moon phases and tidal range) were tested for seasonality. Environmental parameters showing a seasonal pattern were de-trended using the procedure described above. The relationship between environmental factors and abundance was established by correlating the environmental parameters with the de-trended (anomalies) puerulus and juvenile abundance values for the lobster stages that showed seasonality, and with observed puerulus and juvenile abundance values for lobster stages that showed no significant seasonal cycle. Non- seasonal (de-trended) environmental parameters were correlated with abundance by using the observed environmental parameter values. Multiple regression analysis was used to establish the relationship between transparent puerulus, pigmented puerulus and juvenile abundance. Puerulus and juvenile abundance was also correlated with sea surface temperature, wind speed, tidal range and swell height. Puerulus settlement and juvenile abundance were compared between north and south wind directions and moon phases using Kruskal-

Wallis ANOVA, and Tukey's HSD multiple range tests revealed factors that differed significantly ($p < 0.05$).

Autodistributed lag analysis

Time lag analysis was performed in cases where there was no significant correlation in the abundance between the puerulus and juvenile lobster stages, and lobster abundance with environmental factors at the time of the study. The relationships and time lags between puerulus abundance, juvenile abundance and environmental factors were established using the AUTODISTRIBUTED LAG (ADL) REGRESSION model in the EVIEWS 3.1 econometric analysis program. In this analysis all components were tested for stationarity using the Augmented Dickey-Fuller least squares unit root test (Johnston and DiNardo, 1997) at a significance level of $p < 0.05$. Only stationary components with a Durbin-Watson statistic close to 2, which is the non-significant level of autocorrelation (i.e. variation in the model that is explained by the unknown or error term), were included in the ADL analysis model. Similarly, environmental factors (temperature, wind speed and tidal range) were correlated with puerulus settlement and juvenile abundance to establish their relationship and the time lags associated with these relationships. A simultaneous ADL model was used to estimate the most accurate combination of time lags of all environmental factors affecting puerulus settlement and juvenile abundance. The periodic transformation of the x-axis was included to account for any seasonal effects in the independent and dependent variables.

CHAPTER 3: Results

3.1 Temporal variation in puerulus and juvenile abundance

Puerulus and juvenile abundance data from oyster bags, oyster crates and Booth crevice collectors was analysed for temporal variation by means of periodic regression analysis (circular statistics) and multiple range analysis. The abundance of the transparent and pigmented puerulus stages was analysed separately for oyster bags and crates. However, for the crevice collectors, data for the two puerulus stages was pooled due to the low number of observations. Seasonal patterns in puerulus and juvenile abundance were compared between oyster bags, crates and collectors, and presented below.

Periodic regression analysis showed that there was a seasonal trend in puerulus and juvenile lobster abundance. The seasonal cycle of the puerulus and juvenile abundance was expressed by the following polynomial and linear regression models 1 and 2 respectively:

$$1 \quad Y = M + B_1 \sin(R'X) + B_2 \cos(R'X)$$

Where: Y = Puerulus abundance

B₁ = Multiple regression coefficient of Sin(R'DOY)

B₂ = Multiple regression coefficient of Cos(R'DOY)

R'X = Time (Day of the Year (DOY) for bags and crates & Month of the Year (MOY) for collectors) in Radians

M = Mesor (multiple regression coefficient of the intercept)

$$2 \quad Y = M + A \cos(R'X - \hat{\phi})$$

Where: Y = Juvenile abundance

M = The mesor

A = The amplitude

R'X = Time (DOY or MOY) in radians

$$\partial = \text{Arctan}(B_1 / B_2) + \text{QC}$$

where QC = Quadrant correction factor (See Bell, 2000)

Periodic regression analysis revealed that puerulus abundance recorded on oyster bags and crates during the study period showed a significant seasonal pattern ($p < 0.10$) with peak settlement during August-September (Table 3.1). The recruitment of transparent pueruli started to increase from June with peak settlement observed in late August on oyster bags and early in September on crates (Fig. 3.1). Transparent puerulus abundance at peak recruitment was estimated at 1.66 transparent puerulus/bag/day and 2.23 transparent puerulus/crate/day on oyster bags and crates, respectively. The linear relationship between transparent puerulus abundance on oyster bags and crates and angular transformed time was respectively described as follow:

$$Y_{pt} = 0.873 + 0.916\cos(R'DOY - 3.898) \text{ on bags, and}$$

$$Y_{pt} = 1.860 + 0.764\cos(R'DOY - 4.201) \text{ on crates,}$$

where a decline in transparent puerulus recruitment on bags and crates was observed from October onwards with the lowest recruitment occurring between December and May.

Table 3.1 Periodic Regressions showing time of peak abundance in puerulus (P) transparent puerulus (Pt) and pigmented puerulus (Pp) abundance on oyster bags, crates and collectors for the period November 1999 to July 2003. {DOY = day of year (0th DOY= 1 January- 364th DOY=31 December); R' = time transformation to radians}.

SAMPLE UNIT	Stage	Regression form	Peak Time	*F	*P	*R ²
BAGS	Transparent puerulus	Y(Pt) = 0.873 0.628sinR'DOY 0.667cosR'DOY	226 th DOY ~26 August	23.532	2.450E-06	0.104
	Pigmented puerulus	Y(Pp) = 3.149 2.203sinR'DOY 2.508cosR'DOY	221 st DOY ~10 August	38.891	2.576E-09	0.161
CRATES	Transparent puerulus	Y(Pt) = 1.860 0.666sinR'DOY 0.374cosR'DOY	244 th DOY ~2 September	2.3253	0.129	0.017
	Pigmented puerulus	Y(Pp) = 6.917 2.674sinR'DOY 1.288cosR'DOY	247 th DOY ~5 September	3.7791	0.054	0.027
COLLECTORS	Puerulus	Y(P) = 5.230 7.294sinR'MOY 4.509cosR'MOY	7 th MOY ~ August	5.904	0.17	0.496

*F= F statistic; P= significance of F; R²= correlation coefficient

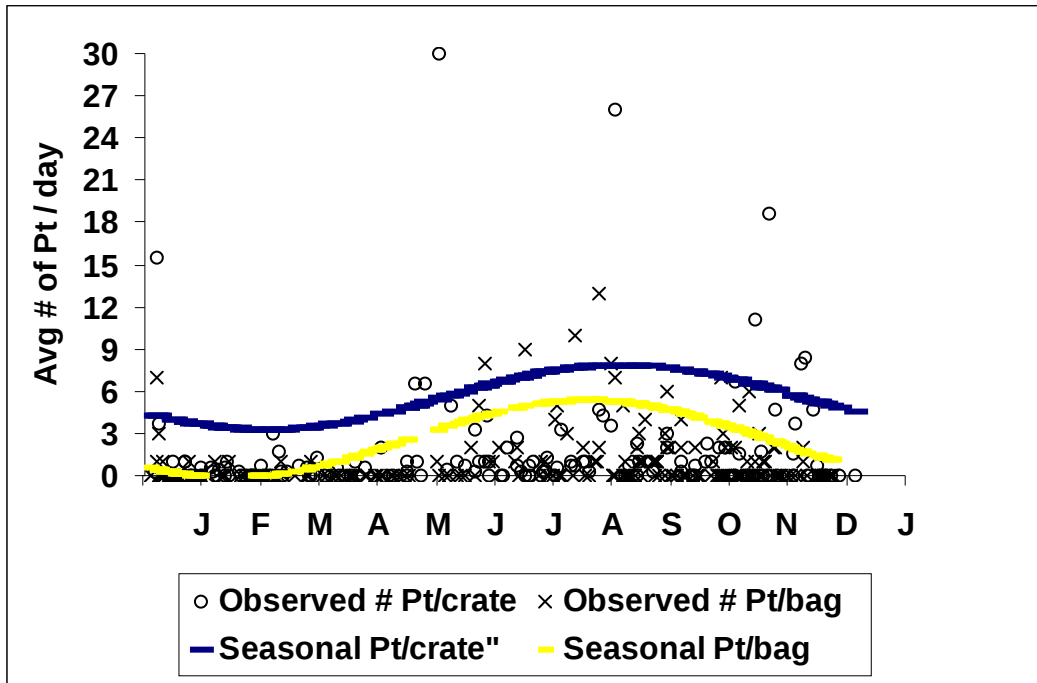


Figure 3.1 The predicted seasonal cycle in transparent puerulus (Pt) recruitment plotted against observed transparent puerulus abundance on oyster bags and crates at Lüderitz oyster farm. Peak abundance occurred in the August-September period.

The approximated seasonal cycle of pigmented puerulus abundance on oyster bags and crates is presented in Fig. 3.2 with the statistical significance of peaks highlighted in Table 3.1. Pigmented puerulus abundance on oyster bags and crates mirrored that of transparent puerulus settlement with an observed increase from June and peak abundance from August to September. The estimated peak in pigmented puerulus abundance was 2.03-pigmented puerulus/bag/day and 6.72-pigmented puerulus/crate/day on oyster bags and crates, respectively. The respective linear relationships of pigmented puerulus abundance with angular transformed time was described as

$$YP_p = 3.150 + 3.224\cos(R'DOY - 3.821) (R^2 = 0.161) \text{ on bags, and}$$

$$YP_p = 6.917 + 2.968\cos(R'DOY - 4.263) (R^2 = 0.027) \text{ on crates,}$$

where pigmented puerulus abundance on oyster bags and crates started declining from November with the lowest abundance observed from end of December through May.

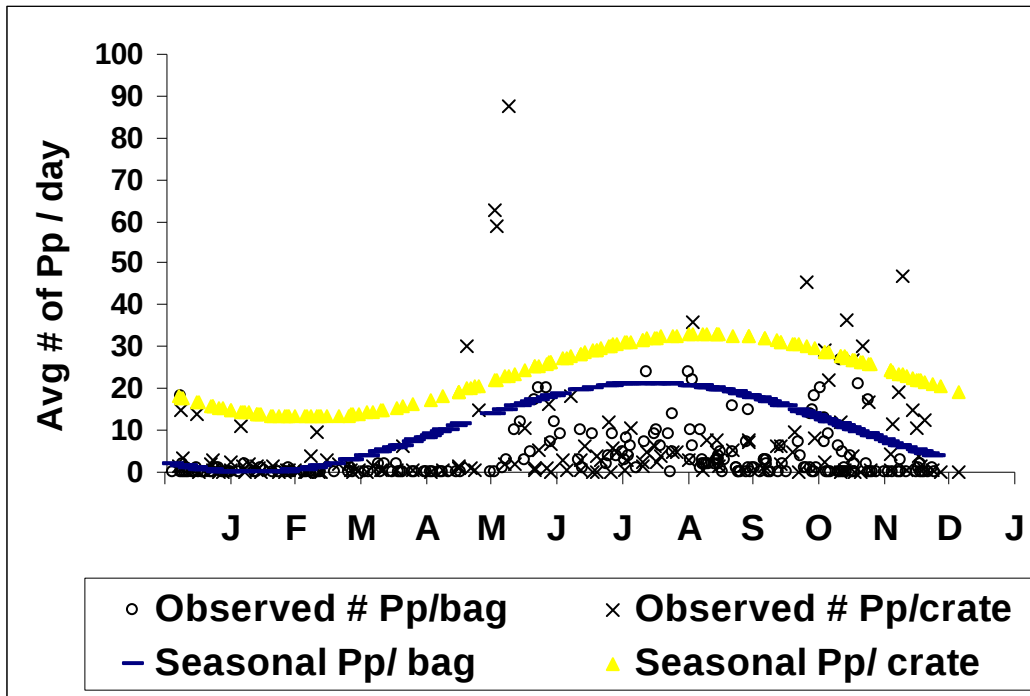


Figure 3.2 The seasonal cycle in pigmented puerulus recruitment plotted as observed abundance on oyster bags and crates at Lüderitz oyster farm from August 2001 to February 2003. Peak abundance occurred in early August.

The approximated seasonal pattern in juvenile abundance on oyster bags and crates is presented in Fig. 3.3. Juvenile abundance on oyster bags and crates started increasing around August/September with peak abundance observed from November to January. The estimated peak in juvenile abundance was 28.87 juveniles/bag/day around 17-November on bags and 16.44 juveniles/crate/day around 10-December on oyster crates. The linear relationship of juvenile abundance with angular transformed time are respectively described for bags and crates as follow:

$$Y(J) = 16.63 + 12.376 \cdot \cos(R'DOY - 5.505) \quad (R^2 = 0.220) \text{ on bags, and}$$

$$Y(J) = 20.013 + 7.794 \cdot \cos(R'DOY - 5.907) \quad (R^2 = 0.060) \text{ on crates,}$$

where juvenile abundance on oyster bags and crates declined from end of January with the lowest abundance (0-5 juveniles/ bag or crate per day) observed from March through May-June.

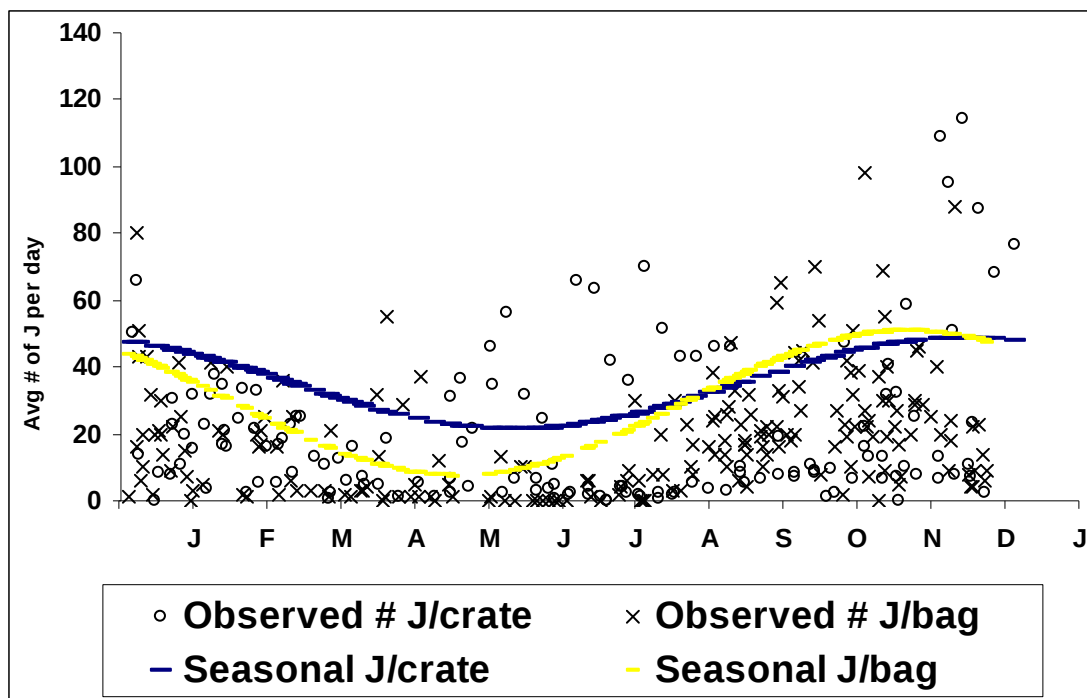


Figure 3.3 The periodic cycle in juvenile lobster abundance on oyster bags Lüderitz oyster farm from August 2001 to February 2003 and on oyster crates from November 1999 to July 2003 at Lüderitz oyster farm. Peak abundance on bags occurred around the 343rd DOY (day of the year) which corresponds to the date 10 December and that on crates around the 320th DOY (day of the year) which corresponds to the date 16 November.

Fewer data were available for puerulus and juvenile settlement on the collectors, which reduced the statistical power of the regression analyses. Puerulus settlement on collectors showed a weak seasonal pattern ($p=0.17$) and was therefore regarded as non- seasonal for the purpose of data analysis. As with the oyster bag and crate data, periodic regression analysis approximated the peak in puerulus settlement on collectors to occur in August with an observed average of 12 pueruli/collector (Table 3.1). There was no clear trend as to when puerulus settlement on collectors started increasing (Fig. 3.4). However, high numbers of pueruli recruited on collectors during August 2002 (average=18.83/collector)

and October-November 2002(15.05 pueruli/collector) with the highest numbers caught during the second week of August (24.00 pueruli/collector) and the last week of October (20.60 pueruli/collector)(Fig. 3.4).

Juvenile abundance on collectors revealed a weak seasonal pattern with periodic regressions significant at 92 % level of significance (Table 3.1). Juvenile lobsters began to recruit onto collectors in July 2002 with the rate gradually increasing during mid August with increasingly high numbers recruiting in October and December when peak juvenile abundance was recorded. Observed data for juvenile abundance on collectors showed a second smaller peak during April 2003 (5 juveniles/collector). Juveniles recruited in lower numbers than pueruli at the collector sites on average with a juvenile recruitment lagging that of pueruli by two to three months. Periodic regression analysis approximated peak juvenile abundance to occur during December, which reflected the pattern observed in bags and crates. The average juvenile abundance during the peak period was 7.32 juveniles per collector.

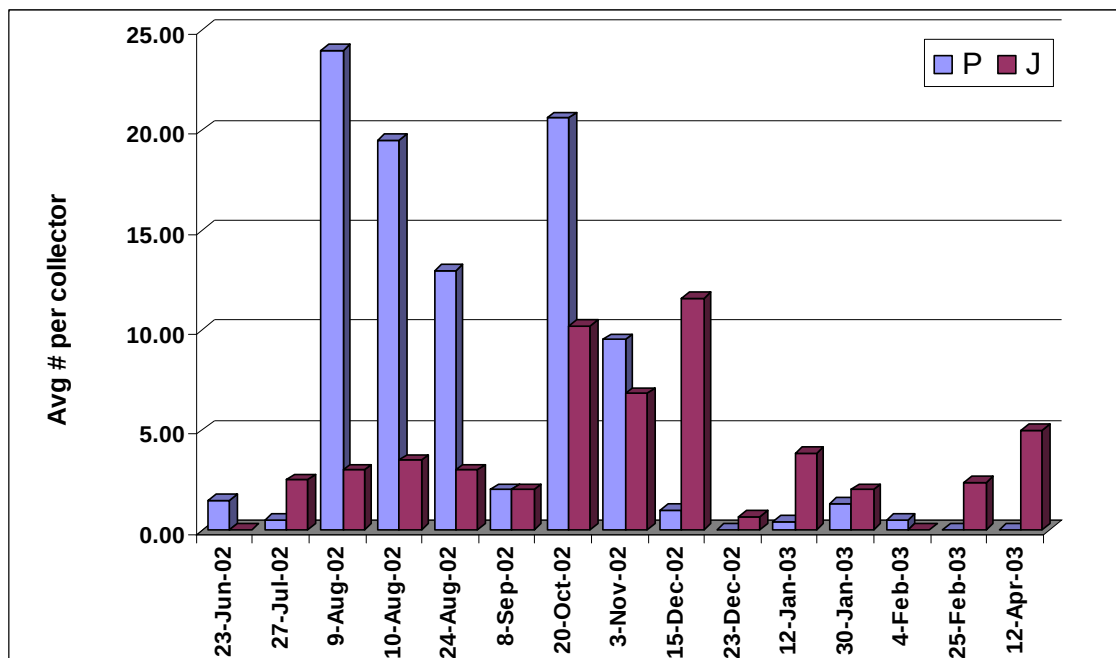


Figure 3.4 Average puerulus and juvenile recruitment on collectors at Lüderitz lagoon from June 2002 to April 2003.

Interannual variation in puerulus and juvenile abundance peaks

Peak puerulus abundance on crates during 2000 (May) was significantly higher than that observed in 2001 and 2002, with similar puerulus settlement peaks observed in 2001 and 2002. Puerulus abundance on bags during the peak puerulus settlement months (August–November) was significantly higher during 2002 compared to 2001. Juvenile abundance peaks on crates were significantly higher during 1999 compared to 2000, 2001 and 2002 (Table 3.2). Juvenile abundance during peak months on bags was not significantly different between years.

Table 3.2 Interannual variation in peak abundance of puerulus (P) and juvenile (J) lobsters on bags and crates. Peak abundance periods were compared pairwise using Tukey's HSD test and only peaks, which differed significantly, are listed. *P* denotes the level of significance of the difference in abundance between yearly peaks. The average (avg) number of each stage lobster (P and J) per bag or crate for each respective peak month (or period) is indicated in brackets.

SAMPLE UNIT	Stage	Group 1	>	Group 2	<i>P</i>
CRATES	P	May'00 (avg=55.5)		Jul – Aug'01 (avg= 3.3)	<0.0001
		May'00 (avg=55.5)		Aug – Sep'01 (avg= 5.1)	<0.001
		May'00 (avg=55.5)		Jul – Aug'02 (avg= 5.5)	<0.008
		May'00 (avg=55.5)		Sep – Oct'02 (avg=13.8)	<0.04
	J	Nov'99 (avg=60.0)		Nov'00 (avg=18.5)	0.01
		Nov'99 (avg=60.0)		Dec'00 (avg=15.4)	0.03
		Nov'99 (avg=60.0)		Nov'01 (avg = 5.1)	<0.001
		Nov'99 (avg=60.0)		Dec'01 (avg = 2.7)	0.03
		Nov'99 (avg=60.0)		Nov'02 (avg=15.1)	0.001
		Dec'99 (avg=88.3)		Nov'00 (avg=18.5)	<0.001
		Dec'99 (avg=88.3)		Dec'00 (avg=15.4)	<0.001
		Dec'99 (avg=88.3)		Nov'01 (avg = 5.1)	<0.001
		Dec'99 (avg=88.3)		Dec'01 (avg = 2.7)	<0.001
		Dec'99 (avg=88.3)		Nov'02 (avg=15.1)	<0.001
		Dec'99 (avg=88.3)		Dec'02 (avg=22.8)	<0.001
BAGS	P	Aug - Nov'02 (avg=3.1)		Aug - Nov'01 (avg=2.0)	<0.01

Time lags between puerulus and juvenile abundance peaks

Peaks in puerulus settlement were related to subsequent peaks in juvenile abundance on bags, crates and collectors at time lags ranging from 11 days up to 2 months (Table 3.3). Auto distributed lag analysis revealed that transparent and pigmented puerulus abundance on bags and crates was significantly correlated over the study period, indicating that there were no time lags between the recruitment of the two puerulus stages (ADL; $p < 0.001$). Peaks in juvenile abundance correlated most significantly with peaks in transparent puerulus abundance lagged by 11 days on bags and up to 9 weeks (2 months) on crates (ADL; $p < 0.05$). Monthly puerulus settlement on collectors was most significantly correlated with juvenile abundance time lagged by 2 months (83%; $p = 0.17$). The variation in the duration of the puerulus stage may be influenced by water temperature with increased water temperatures shortening duration significantly. Biologically it is possible that puerulus lobster can metamorphose into juveniles within 2 weeks, depending on the water temperature where higher water temperatures increases the metamorphose processes. A very low predicted R-value for the 11-day time lag indicated that this may not be realistic time lag between puerulus settlement and juvenile peaks and that it is more likely that the time lag is 2 months as indicated by the highly significant p-statistics and high R-values.

Table 3.3 Distributed time lag analysis indicating significant time lag intervals between peak puerulus (P), transparent puerulus (Pt), pigmented puerulus (Pp) and juvenile (J) abundance on oyster bags, crates and collectors. R refers to the multiple regression or Pearson's correlation coefficient, R^2 and P denotes the significance of the time lag relationship between Pt, Pp and J.

Sample Unit	Group 1	Group 2	Time lag	R^2	P
BAGS	Pt	Pp	0 days	0.90	<0.0001
	Pt	J	11 days	0.05	<0.04
CRATES	Pt	Pp	0 days	0.65	<0.0001
	Pt	J	9 weeks	0.42	<0.0001
COLLECTORS	P	J	8 weeks	0.95	<0.17

3.2 Environmental correlations

In this section I attempted to determine whether there was a relationship between local environmental factors for which data was available and puerulus and juvenile abundance on oyster bags, crates and crevice collectors. The environmental factors of interest were Sea Surface Temperature (SST), the north-south (N-S) component of wind direction, wind speed, the moon phases, tidal range and sea swell height. Crate puerulus abundance data was correlated with the above-mentioned environmental parameters for the period from November 1999 to July 2003, and bag puerulus abundance data for the period from August 2001 to February 2003. Collector abundance data was correlated with the above-mentioned environmental factors for the period from June 2002 to April 2003.

Before correlation analysis was performed, continuous variables such as abundance data, SST, wind speed, swell height and tidal range were analysed for seasonality so that the seasonal component of those variables with significant seasonal cycles could be removed. Environmental factors such as sea surface temperature (SST), wind speed, swell height and tidal range data were analysed for seasonality using the periodic regression analysis methods employed in analysing lobster abundance for seasonality in Section 3.1. Variables with the underlying seasonal cycle removed were referred to as anomalies, which are the significant deviations from the expected value that is the anomaly for which we seek a correlation with puerulus abundance. In cases where no direct correlation was evident between environmental factors (or environmental anomalies) and puerulus and juvenile abundance (or their anomalies) at the time of the study (t_{x-0}), Auto distributed time lag analysis (ADL) was used to correlate environmental factors lagged in time (t_{x-i}) with puerulus and juvenile abundance. The seasonality of each environmental factor and its relationship with puerulus and juvenile abundance is presented in the separate subsections below.

Sea surface temperature and lobster abundance

Sea surface temperature data recorded during the sample period for bags, crates and collectors had a significant seasonal cycle ($p < 0.01$). In section 3.1 it was shown that transparent and pigmented puerulus and juvenile abundance on oyster bags was seasonal. Therefore de-trended (with the seasonal component removed) values of sea surface temperature, sea surface temperature anomalies (SSTAnom) and transparent and pigmented puerulus anomalies (PtAnom and PpAnom) were used to establish the correlation between sea surface temperature and lobster abundance. Observed values for puerulus abundance (P) on collectors were correlated with SSTAnom.

Puerulus settlement on oyster bags, crates and collectors peaked less than 1 week after low sea surface temperatures averaging around 12.0°C were experienced during the years 2000 through 2002 at Lüderitz Bay (Table 3.4). Transparent and pigmented puerulus settlement on oyster bags and crates was not correlated with sea surface temperature at the time (time x) of collection of the pueruli ($p > 0.05$). Therefore transparent and pigmented puerulus abundance was correlated with SSTAnom temperature anomalies. Time lag analysis (ADL) revealed that peak transparent puerulus settlement was significantly correlated with low sea surface temperatures averaging around 12.6°C recorded 2 days prior to the time of sampling of bags and crates (Table 3.4). Below average sea surface temperature of 11.4°C was observed 2 days prior to peak transparent puerulus settlement on crates during the year 2000, compared to average sea temperatures of 12.3°C and 13.5°C recorded 2 days prior to peak transparent puerulus settlement on bags and crates during 2001 and 2002, respectively (Table 3.5). Tukey's multiple range test revealed that peak transparent puerulus settlement was significantly higher during 2000 compared to that observed during 2001 and 2002. Pigmented puerulus abundance on bags and crates, respectively peaked 1 and 4 days after low sea surface temperatures averaging around 12.4°C were recorded ($p < 0.05$; Table 3.4). Average sea surface temperatures recorded 1-4 days prior to peak in pigmented puerulus settlement during the year 2000, was very low averaging around 11.6°C , compared to higher average temperatures of 12.7°C and 12.5°C experienced during the years 2001 and 2002 (Table 3.5). Tukey's multiple range test revealed that peak pigmented puerulus abundance was

significantly higher during 2000, compared to peak pigmented puerulus abundance observed during 2001 and 2002. Below average sea surface temperatures ($<12.0^{\circ}\text{C}$) one to four days appeared to be related to highest puerulus settlement peaks during 2000.

Spearman's Rank correlation analysis revealed that observed puerulus abundance on collectors was not correlated with SSTAnom. However, observed puerulus settlement on collectors at the time of the study was inversely correlated with observed sea surface temperature ($R = -0.762$; Table 3.4). Peak puerulus settlement on collectors was related to low sea surface temperature with an average of 12.1°C during the August 2002 and October 2002 puerulus abundance peaks on collectors when sea surface temperatures of 12.3°C and 11.9°C were recorded, respectively.

Table 3.4 Relationship between sea surface temperature anomalies and transparent puerulus and pigmented puerulus abundance on oyster bags, crates and collectors. Sea surface temperature anomalies were lagged in time as indicated by x-i where x is the date at which lobster abundance was sampled minus i, the number of days by which SST anomalies are lagging lobster abundance. Y= abundance where Pt and Pp denotes observed transparent puerulus abundance and pigmented puerulus abundance, respectively. De-seasonalised Pt abundance and sea surface temperature are indicated with PtAnom and SSTAnom, respectively.

Sample Unit	Stage	Regression form	Time Lag	*F	*P	*R ²
BAGS	Transparent puerulus	$Y(Pt) = -0.0687 - 0.233 * SSTAnom_{(x-2)}$	x-2 days	4.865	0.029	0.044
	Pigmented puerulus	$Y(Pp) = -0.8256 - 0.588 * SSTAnom_{(x-1)}$	x-1 days	6.635	0.011	0.059
CRATES	Transparent puerulus	$Y(Pt) = -2.5183 - 0.144 * SSTAnom_{(x-2)}$	x-2 days	2.488	0.06	0.082
	Pigmented puerulus	$Y(Pp) = -10.7873 - 0.528 * SSTAnom_{(x-4)}$	x-4 days	4.870	0.004	0.150
COLLECTORS	Stage	Regression form	Time Lag	*F	*P	*R
	Puerulus	$Y(Pt) = -2.161 - 0.476 * SST_{(x-0)}$	x-0 days	3.805	0.07	-0.762

* F= F-statistic; P= probability or significance of F; R and R²= correlation coefficients

Table 3.5 Predicted relationship of sea surface temperature (SST) in degrees Celsius (°C) with transparent puerulus and pigmented puerulus abundance on oyster bags, crates and crevice collectors. $X_{(y*)}$ is the time (date) when lobster abundance (y) was sampled and t lags is the number of days by which sea surface temperature is lagging lobster abundance.

SAMPLE UNIT	Stage	Time Lag	SST at $X_{(y*)} - t$ lags		
			2000	2001	2002
BAGS	Transparent puerulus	x-2 days	-	11.9°C	13.7°C
	Pigmented puerulus	x-1 days	-	12.8°C	13.8°C
CRATES	Transparent puerulus	x-2 days	11.6°C	12.6°C	13.3°C
	Pigmented puerulus	x-4 days	11.6°C	12.6°C	11.2°C
COLLECTORS	Puerulus	x-0 days	-	-	11.9°C
Average SST (°C) at average time lag per year	Puerulus	0-4 days	11.6°C	12.5°C	12.8°C
Average SST during peak P settlement months	Puerulus	30 days	12.3	12.1	12.3

Effect of Wind stress on lobster abundance on oyster farm

Wind speeds in the Lüderitz area vary seasonally with very strong periodic south-westerly winds prevailing during summer months, and generally light south winds during winter (May-June). Moderate to strong uninterrupted south winds are predominant during spring from September-December. Wind speeds generally exceed $5 \text{ m} \cdot \text{sec}^{-1}$ during spring months (Grobler & Noli-Pear, 1997). Wind direction was reported as north and south components during the study period since southerly winds dominate the wind field by more than 80% and is responsible for upwelling, which occurs throughout the year at Lüderitz (Bailey 1979, Tomalin 1993). Puerulus abundance on oyster bags and crates were compared during periods of north and south winds. Puerulus abundance on oyster bags,

crates and collectors did not differ significantly during north and south prevailing wind conditions over the study period (Kruskal-Wallis ANOVA, $p > 0.05$).

Wind speed recorded during the time bags were sampled had a seasonal cycle at the 90% level of significance. De-trended values of wind speed, which revealed wind anomalies (windAnom), were therefore used in all correlation analyses. Wind speeds observed during the study period for the crates, from November 1999 to July 2003, was not seasonal ($p > 0.10$). Observed values of all parameters were therefore used in the correlation analysis. During the period in which the collectors were monitored wind speed was not seasonal, and was not related to puerulus recruitment on collectors ($p > 0.10$). Multiple Regression analysis showed that the relationship between wind speed and transparent and pigmented puerulus abundance on bags and crates was not significant during the study period ($p > 0.05$). Using Auto Distributed Lag (ADL) analysis wind speed anomalies were lagged by various time intervals to obtain the most significant relationship with puerulus abundance observed during the study period. These relationships are described in Table 3.6.

High transparent puerulus settlement on oyster crates and bags was related to moderate south winds with an average speed of $7.6 \text{ m}\cdot\text{sec}^{-1}$ observed 4-10 days earlier (Table 3.6 and 3.7). The highest transparent puerulus abundance peak was recorded in 2000 when moderate to strong south winds with an average speed of $9.8 \text{ m}\cdot\text{sec}^{-1}$ prevailed 4-10 days earlier. A smaller peak in transparent puerulus settlement was observed during 2001 compared to peaks observed during 2000, and was predominantly related to north winds with low average speeds of $4.5 \text{ m}\cdot\text{sec}^{-1}$ that prevailed 4-10 days prior to peak transparent puerulus settlement. Wind speeds in 2000 ($9.8 \text{ m}\cdot\text{sec}^{-1}$, S) and 2002 ($9.6 \text{ m}\cdot\text{sec}^{-1}$, S) were similar during peak transparent puerulus settlement on bags and crates, however transparent puerulus recruitment during 2002 was less than half the strength of that observed during 2000 and marginally higher than that during 2001. It appears that moderate to strong south winds enhanced peak transparent puerulus recruitment during the study.

The relationship of wind speed with pigmented puerulus did not indicate a clear trend. Pigmented puerulus abundance on crates and bags peaked 4-7 days after low to moderate south winds averaging around $8.5\text{m}\cdot\text{sec}^{-1}$ were prevalent (Table 3.6 and 3.7). Below average wind speeds of $4.7\text{m}\cdot\text{sec}^{-1}$ was observed 4 days prior to the peak in pigmented puerulus abundance observed in 2000. Pigmented puerulus abundance was highest during May 2000, which was related to low southerly winds averaging around $2.9\text{m}\cdot\text{sec}^{-1}$ that prevailed 4 days earlier. Peak pigmented puerulus abundance during 2001 was less than that during 2000 and was related to moderate southerly winds with an average of $8.8\text{m}\cdot\text{sec}^{-1}$, experienced 4-7 days earlier. Moderate to strong southerly winds with an average speed of $10.1\text{m}\cdot\text{sec}^{-1}$ was prevalent 4-7 days prior a moderate peak in pigmented puerulus abundance during 2002. It appears that stronger peaks in pigmented puerulus abundance are experienced after south winds of low to moderate speeds 4-7 days earlier.

Table 3.6 Relationship of wind speed with transparent and pigmented puerulus abundance on oyster bags and crates. Wind speed anomalies were lagged in time as indicated by x-i where x is the date at which lobster abundance was sampled minus i, the number of days by which wind speed anomalies are lagging lobster abundance. Y= abundance where Pt and Pp denotes observed transparent puerulus abundance and pigmented puerulus abundance, respectively. De-seasonalised Pt abundance and wind speed are indicated with PtAnom and WindAnom, respectively.

SAMPLE UNIT	Stage	Regression form	Time Lag	*F	*P	*R ²
BAGS	Transparent puerulus	$Y(\text{PtAnom}) = 0.3315 - 0.068 * \text{WindAnom}_{(x-10)}$	x-10 days	3.637	0.06	0.034
	Pigmented puerulus	$Y(\text{PpAnom}) = -0.9057 + 0.221 * \text{WindAnom}_{(x-7)}$	x-7 days	5.678	0.001	0.142
CRATES	Transparent puerulus	$Y(\text{Pt}) = 1.8928 - 0.177 * \text{Wind}_{(x-4)}$	x-4 days	2.383	0.08	0.111
	Pigmented puerulus	$Y(\text{Pp}) = 4.1279 - 0.324 * \text{Wind}_{(x-4)}$	x-4 days	3.947	0.012	0.170

* F= F-statistic; P= probability or significance of F; R²= correlation coefficients

Table 3.7 Wind speed ($\text{m}\cdot\text{sec}^{-1}$) and direction recorded at the time lags predicted for transparent puerulus and pigmented puerulus abundance on oyster bags and crates by Auto distributed lag analysis. $X_{(y*)}$ is the time (date) when lobster abundance (y) was sampled t lags is the number of days by which wind speed is lagging lobster abundance. N and S indicate north and south wind direction, respectively.

SAMPLE UNIT	Stage	Time Lag	Wind speed ($\text{m}\cdot\text{sec}^{-1}$) at $X_{(y*)} - t$ lags		
			2000	2001	2002
BAGS	Transparent puerulus	10 days	-	6.12 (S)	12.83(S)
	Pigmented puerulus	7 days	-	11.45 (S)	12.98 (S)
CRATES	Transparent puerulus	4 days	9.79 (S)	2.81 (N)	6.29 (N)
	Pigmented puerulus	4 days	4.73 (S)	6.06 (S)	7.16 (S)
Average wind speed ($\text{m}\cdot\text{sec}^{-1}$) at average time lag per year	Puerulus	0-4 days	7.26	6.61	8.03
Average wind speed during peak P abundance month	Puerulus	30 days	6.32	4.80	5.44

Effect of Moon Phase and tidal range on lobster abundance

No clear relationship between peak puerulus abundance and moon phase was evident in the data. Puerulus recruitment on collectors did not differ significantly between the different moon phases (Kruskal-Wallis ANOVA $p > 0.05$). However, Kruskal-Wallis ANOVA and Tukey's HSD tests revealed that pigmented puerulus abundance on oyster bags was higher during last quarter moon phases compared to first quarter moon phases at a 93% level of significance (Table 3.8). Transparent puerulus settlement on oyster crates was higher during new moon than that during full moon at a significance level of $p = 0.07$ (Tukey's HSD; Table 3.8). Therefore during the study period it appeared that puerulus of *J. lalandii* at Lüderitz recruited in large numbers during any moon phase.

Table 3.8 Tukey's HSD multiple range test highlighting the moon phases (FM= full moon; LQ= last quarter; NM= new moon; FQ= first quarter) during which transparent puerulus settlement (Pt) on crates and pigmented puerulus settlement (Pp) on oyster bags differed significantly. Group 1 indicates moon phases during which average (avg) lobster abundance per unit was significantly higher per sample day and group 2 moon phases during which average (avg) lobster abundance per unit was significantly less per sample day.

SAMPLE UNIT	Group 1	Group 2	Pt		Pp	
			P	DF	P	DF
BAGS	FQ (avg=3.9 Pp/day) >	LQ (avg=2.1 Pp/day)	-	-	0.07	200
CRATES	NM (avg=1.9 Pt/day) >	FM (avg=1.6 Pt/day)	0.04	137	-	-

Puerulus settlement on bags, crates and collectors peaked with average increased tidal ranges of 1.32m that were associated with new moon, full moon and the last quarter moon phases (following the full moon phase) (Table 3.9 and 3.10). Puerulus settlement on collectors was highest but similar during new moon and full moon phases when average large tidal ranges of 1.43m was observed during the study period ($p < 0.05$; Table 3.9, Table 3.10). Puerulus settlement on bags and crates was not significantly correlated with tidal range during the study period. Increased transparent puerulus settlement on bags and crates was related to increased tidal ranges with an average of 1.02m observed 1-2 days earlier ($p < 0.05$; Table 3.9). The extensive peak in transparent puerulus abundance during 2000 was related to large tidal ranges averaging around 1.62m observed 1-2days earlier during the new moon phase (Table 3.10). Low tidal ranges of 0.91m and 0.84m were related to small peaks in transparent puerulus settlement observed 1-2days later in 2001 and 2002. The lunar calendar indicated that the lunar cycle was in the first quarter moon phase 1 day before the peak time of transparent puerulus settlement in August 2001 and in the full moon phase 1 day prior to peak transparent puerulus settlement during August 2002.

Auto distributed lag analysis revealed that there was no significant relationship between pigmented puerulus settlement on bags and tidal range either over the sample period or at

any realistic time lag ($p > 0.05$; Table 3.9). Auto distributed lag analysis predicted an inverse relationship between high pigmented puerulus abundance on crates and low tidal range observed 2 days earlier. A large tidal range averaging around 1.08m was observed 2 days prior to peak pigmented puerulus abundance recorded on crates during 2000, 2001 and 2002 (Table 3.10). An extensive peak in pigmented puerulus abundance observed during 2000 was related to an increased tidal range of 1.22m observed during the new moon phase 2 days earlier. A large tidal range of 1.26m during the full moon phase was related to the small peak in pigmented puerulus abundance observed 2 days later during 2001. A low tidal range of 0.77m was observed during the last quarter moon phase 2 days prior to the peak in pigmented puerulus during 2002, which was higher than the 2001 peak. The relationship between peak pigmented puerulus abundance and tidal range is not clear. Nonetheless, it appears that pigmented puerulus recruit in large numbers with increased tidal ranges during new moon and full moon phases and during the initial days of the last quarter moon immediately after the full moon phase.

Table 3.9 Relationship between tidal range with transparent and pigmented puerulus abundance on oyster bags and crates. Tidal range is lagged in time as indicated by $x-i$ where x is the date at which lobster abundance was sampled minus i , the number of days by which tidal range is lagging lobster abundance. Y = abundance where P_t and P_p denotes observed transparent and pigmented puerulus abundance respectively. De-seasonalised P_t abundance is indicated with P_tAnom .

SAMPLE UNIT	Stage	Regression form	Time Lag	*F	*P	*R ²
BAGS	Transparent puerulus	$Y(P_tAnom) = -0.9635 + 0.956 * Tide_{(x-1)}$	1 days	3.950	0.049	0.034
	Pigmented puerulus	-	-	-	-	-
CRATES	Transparent puerulus	$Y(P_t) = -1.3921 - 1.561 * Tide_{(x-2)}$	2 days	2.516	0.06	0.082
	Pigmented puerulus	$Y(P_p) = -4.2646 - 5.240 * Tide_{(x-2)}$	2 days	3.970	0.011	0.124
COLLECTORS	Puerulus	$Y(P) = 14.1011 + 0.554 * Tide_{(x-0)}$	0 days	5.747	0.03	0.253

* F= F-statistic; P= probability or significance of F; R²= correlation coefficients

Table 3.10 Tidal range (in meters: m) and moon phases recorded at the time lags predicted for tidal range with transparent and pigmented puerulus abundance on oyster bags, crates and crevice collectors indicated by Auto distributed lag analysis. $X_{(y*)}$ is the time (date) when lobster abundance (y) was sampled and t lags is the number of days by which the moon phase is lagging lobster abundance. NM, FQ, FM and LQ indicate new moon, first quarter moon, full moon and last quarter moon phases, respectively.

SAMPLE UNIT	Stage	Time Lag	Tidal range (m) at $X_{(y*)} - t$ lags				
			1999	2000	2001	2002	Average
BAGS	Transparent puerulus	x-1 days	-	-	0.78 (FQ)	1.21 (FM)	0.99
	Pigmented puerulus	-	-	-	-	-	-
CRATES	Transparent puerulus	x-2 days	-	1.62 (NM)	1.03 (FQ)	0.46 (LQ)	1.15
	Pigmented puerulus	x-2 days	-	1.22 (NM)	1.26 (FM)	0.77 (LQ)	1.08
COLLECTORS	Puerulus	x-0 days	-	-	-	1.43 (NM & FM)	1.43

Effect of Sea Swell on lobster abundance

Sea swell height during the sampling period for the bags and crates showed significant seasonality, whereas swell height during the shorter sampling period for the collectors was not seasonal.

Peak puerulus settlement on bags and crates was related to moderate swells with an average height of 2m observed 0-6 days earlier. Puerulus abundance on oyster bags was not significantly related to the swell conditions observed at the time of collection (Multiple Regression $p > 0.05$), however auto distributed time lag analysis (ADL) revealed that transparent puerulus settlement on bags was positively related to swell conditions observed 6 days earlier ($p < 0.05$; Table 3.11). Puerulus abundance on oyster crates was significantly related to swell height anomalies during the study period. Puerulus abundance on bags and crates peaked when moderate swell conditions with average swell heights of 1.24m were prevalent 0-6 days earlier (Table 3.11 & 3.12). Peak transparent

puerulus abundance on crates coincided with moderate sea swells (1.7 – 3.0m) observed 0-6 days earlier. High pigmented puerulus abundance on bags and crates was positively related to moderate sea swell height lagged by 0 and 6 days at a 90% level of significance (Table 3.11). Moderate swells of 2m and 2.3m (observed 0-6 days earlier) were related to an exceptionally high peak and an intermediate peak in pigmented puerulus abundance observed during 2000 and 2002, respectively (Table 3.12). The lowest level of pigmented puerulus recruitment observed in 2001 was related to large swell conditions of 3m observed 6 days before the estimated peak in pigmented puerulus settlement (Table 3.12). Anomalies in puerulus abundance on collectors were not significantly correlated to swell height during the study period or at any realistic time lag. Moderate swells averaging around 1.24m were observed during the time of peak puerulus settlement on collectors (Table 3.12).

Table 3.11. The relationship of swell height with transparent and pigmented puerulus abundance on oyster bags and crates. Swell height is lagged in time as indicated by x-i where x is the date at which lobster abundance was sampled minus i, the number of days by which swell height is lagging lobster abundance. Y= abundance where Pt and Pp denotes observed transparent puerulus and pigmented puerulus abundance, respectively. De-seasonalised Pt abundance and swell height are indicated with PtAnom and SwellAnom, respectively.

SAMPLE UNIT	Stage	Regression form	Time Lag	*F	*P	*R ²
BAGS	Transparent puerulus	$Y(PtAnom) = -2.466 - 0.336 * SwellAnom_{(x-6)}$	x-6 days	4.679	0.032	0.043
	Pigmented puerulus	$Y(PpAnom) = 1.670 + 0.718 * SwellAnom_{(x-6)}$	x-6 days	2.689	0.09	0.071
CRATES	Transparent puerulus	$Y(Pt) = 1.926 + 0.777 * SwellAnom_{(x-0)}$	x-0 days	4.143	0.044	0.053
	Pigmented puerulus	$Y(Pp) = 7.123 + 2.355 * SwellAnom_{(x-0)}$	x-0 days	4.094	0.045	0.142

* F= F-statistic; P= probability or significance of F; R²= correlation coefficients

Table 3.12 Sea swell height (m) recorded at the time lags predicted between swell height and transparent and pigmented puerulus abundance on oyster bags, crates and crevice collectors indicated by Auto distributed lag analysis. $X_{(y*)}$ is the time (date) when lobster abundance (y) was sampled and t lags is the number of days by which swell height is lagging lobster abundance.

SAMPLE UNIT	Stage	Time Lag	Swell height (m) at $X_{(y*)} - t$ lags				
			1999	2000	2001	2002	Average
BAGS	Transparent puerulus	x-6 days	-	-	4.0	1.7	2.9
	Pigmented puerulus	x-6 days	-	-	3.0	2.3	2.7
CRATES	Transparent puerulus	x-0 days	-	2.0	1.7	1.7	1.8
	Pigmented puerulus	x-0 days	-	2.0	1.7	1.7	1.8
COLLECTORS	Puerulus	x-0 days	-	-	-	1.2	1.24
Average swell height (m) at average time lag per year	Puerulus	0-6 days	-	2.0	2.4	1.5	2.0

3.3 Cohort Identification, growth and nutritional condition

Cohort analysis

Pueruli that recruited during August 2001-June 2002 (average CL = 9.2mm) were larger but weighed less (average weight=0.25g) than those that recruited during July 2002-February 2003 (average CL = 8.9mm; average weight=0.29g) (Table 3.15; $p<0.05$). Puerulus was not included in the cohort and growth analyses since they do not change in terms of carapace length. Early juvenile recruitment occurred in distinct peaks, which made it possible to identify distinct cohorts and estimate their growth rate. Carapace length frequency data for early juveniles collected on bags at the Lüderitz Oyster farm were subjected to Modal Progression cohort analysis to identify groups of lobster of the same age and to track their growth over the study period. Modal progression analysis identified 15 cohorts (A-O) between August 2001 and February 2003 (Fig. 3.5). Two distinct major recruitment events were evident in cohort analysis, during August/September 2001 and July/August 2002, respectively (Fig. 3.5 & 3.6). Eight cohorts (A-H) of early juveniles were identified for the August/September 2001 recruitment event with cohort A presumed as the oldest recruits and H the youngest (Fig. 3.5). A group of older early juveniles (mean CL = 15.9 mm) that was only observed in the August 2001 sample (probably part of an earlier recruitment event) was labelled as cohort z. Cohort H was only observed during April 2002 at a mean carapace length of 10.8mm CL. The highest frequency of recruits (90 juveniles) from the August/September 2001 recruitment event was recorded during September 2001. These were presumably second moult stage (instar) juveniles with a mean carapace length of 10.4mm. All cohorts from the August/September 2001 recruitment event went extinct by June 2002 at mean carapace lengths in the range of 25.2-30.6mm. Seven cohorts (I-O) were identified during the July/ August 2002 recruitment event (Fig. 3.5). The first recruits (cohort J) of the July/August 2002 recruitment event were a group of presumably 1st instar juveniles (8.2-12 mm CL) with a mean carapace length of 9.9mm and a frequency at mean CL of 15 juveniles. Cohort I recruited at a mean CL of 15.4mm during September 2002 and was considered older than cohort J that recruited earlier. Each one of the cohorts K-O recruited during consecutive months starting from September 2002 (cohort K) up till

January 2003 (Cohort O). The highest frequencies (50-80 J/month) of presumably second instar juveniles in the size range of 10.0-10.8 mm CL were recorded during August 2002 (J; 55 J/month), September 2002 (K; 70 J/month), November 2002 (M; 80 J/month) and January 2003 (N; 50 J/month), respectively. The remaining two cohorts (L and O) of presumably second instar juveniles recruited during October 2002 and January 2003 at mean carapace lengths of 10.0 mm and mean frequencies of 10, and 12 juveniles per month, respectively. Cohorts I, J and K went extinct at mean CL of 18.4-18.8mm during October, November and December 2002, respectively. Animals of cohorts L, M, N and-O were still present on the oyster farm during the final month of oyster bag sampling and had mean carapace lengths of 19.5mm, 16.3mm, 14.6mm and 12.0mm. Cohort B and L had slower growing individuals resulting in the splitting of these cohorts into secondary cohorts, *B'* and *L'*. The population parameters of these secondary cohorts were not included in the growth analysis.

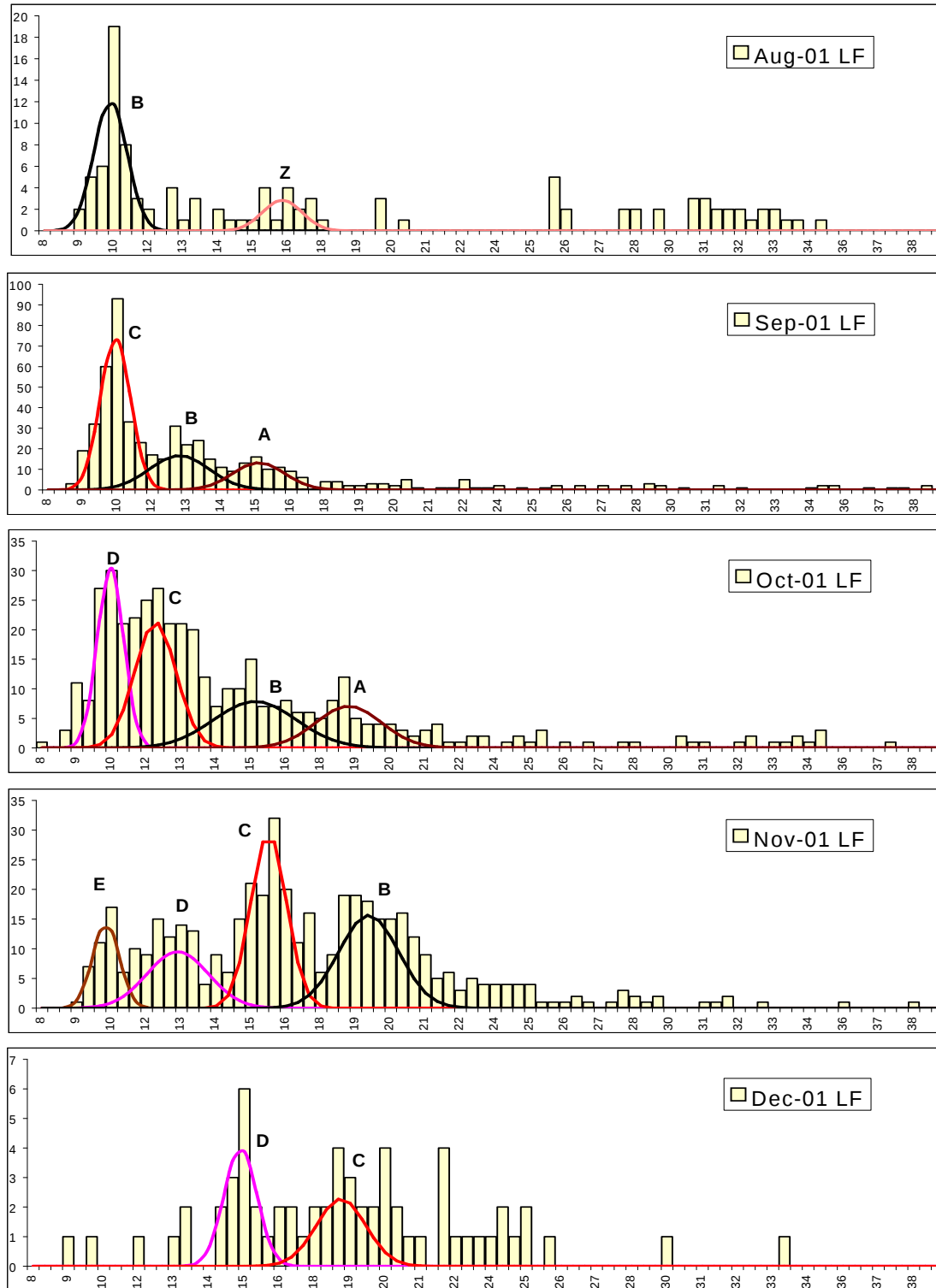


Figure 3.5 Length frequency distribution of early juveniles collected from oyster bags between August 2001 and February 2003. Groups of animals belonging to the same cohorts (selected in FISAT Bhattacharya's Method) are indicated with normal distribution curves designated by the same colour and alphabetic letter (A-O).

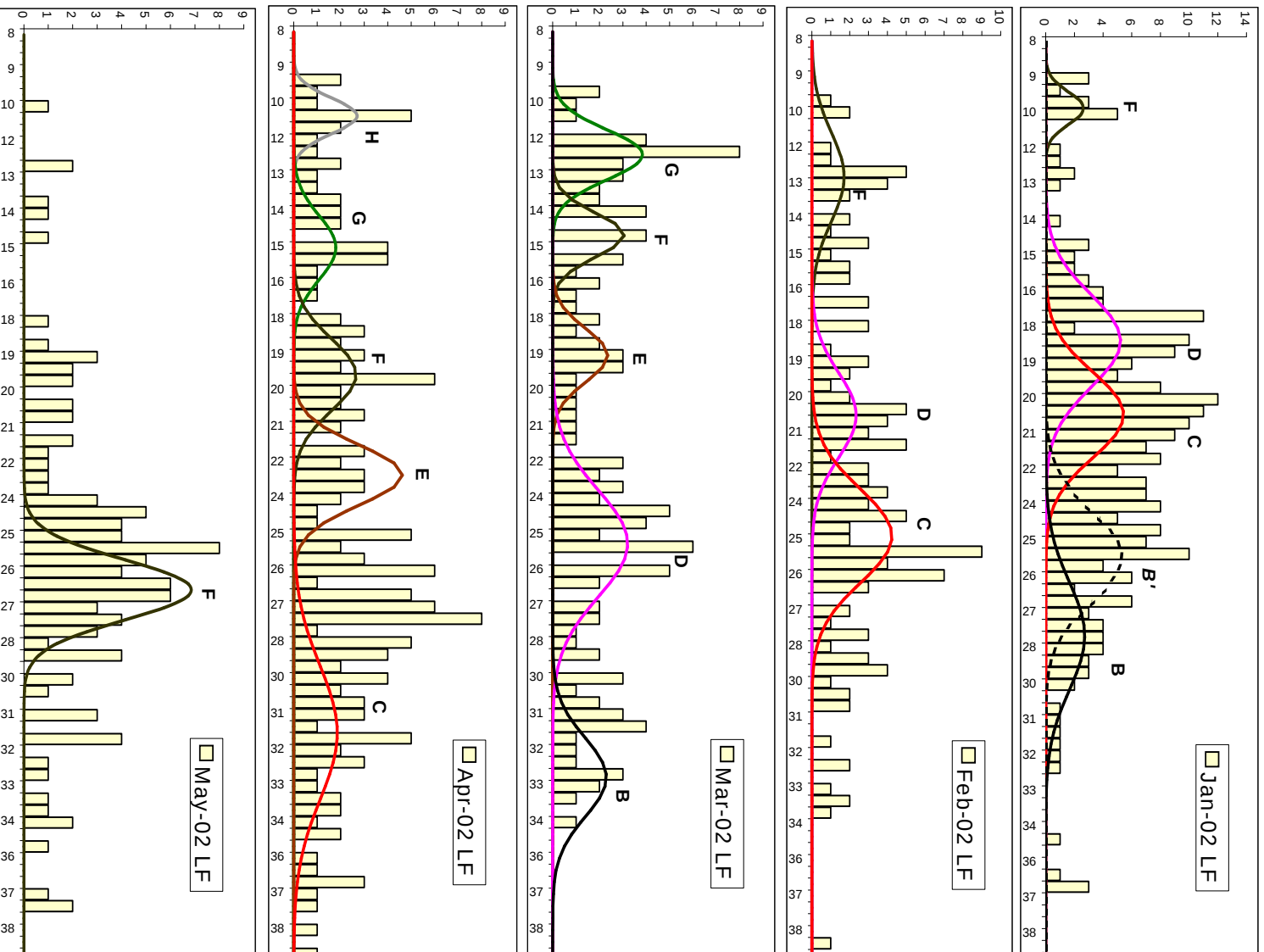


Figure 3.5 continued...

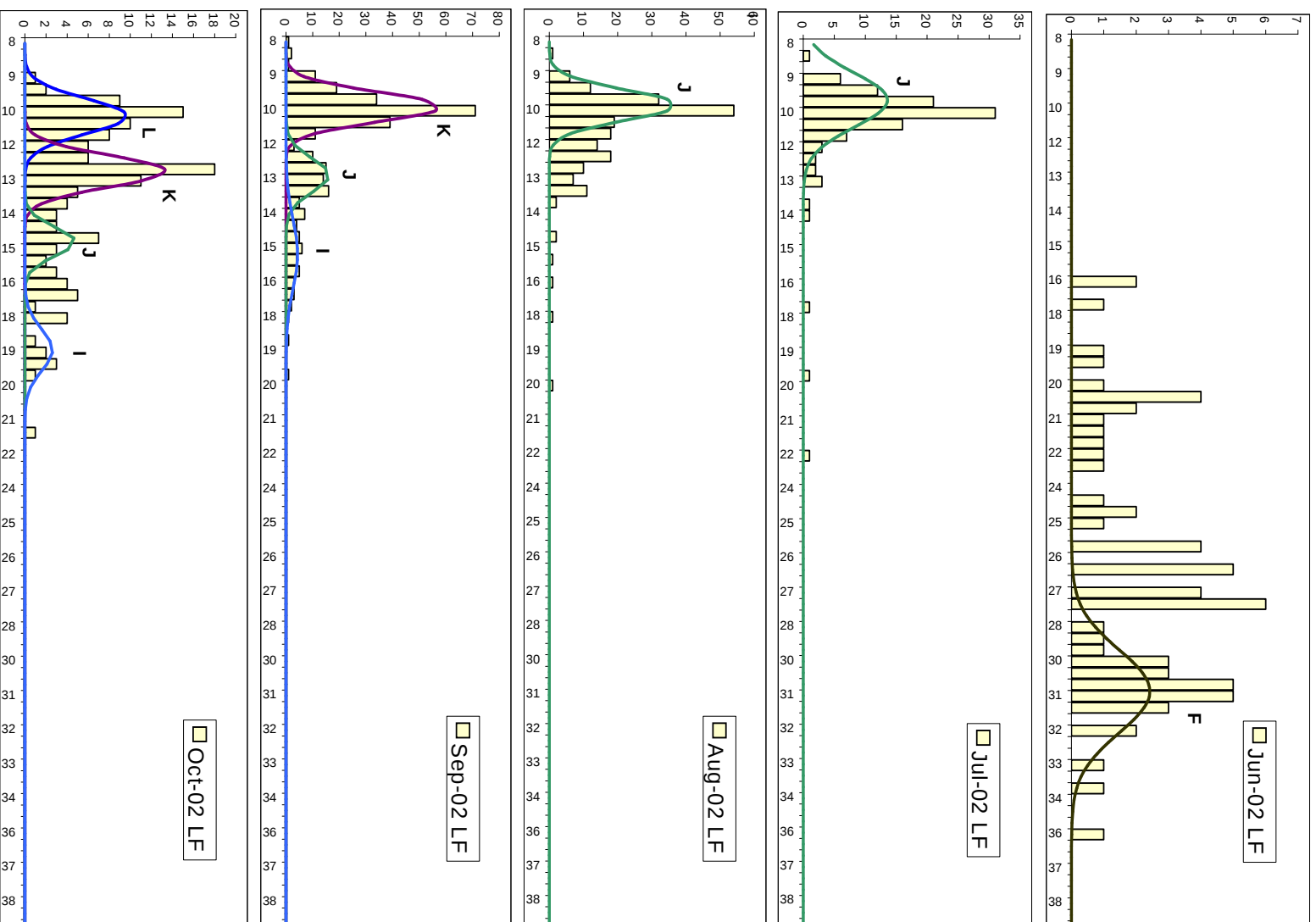


Figure 3.5 continued...

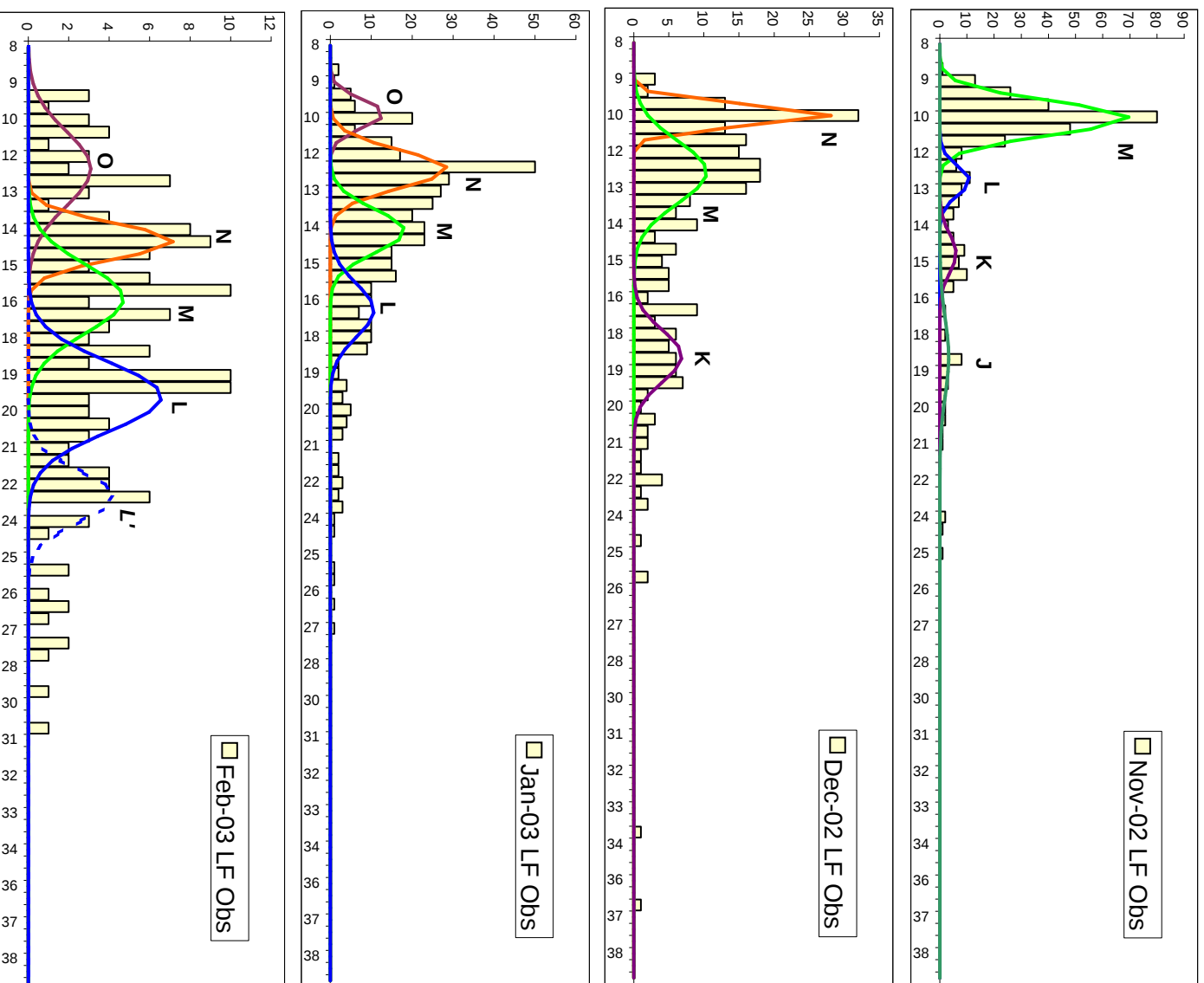


Figure 3.5 continued...

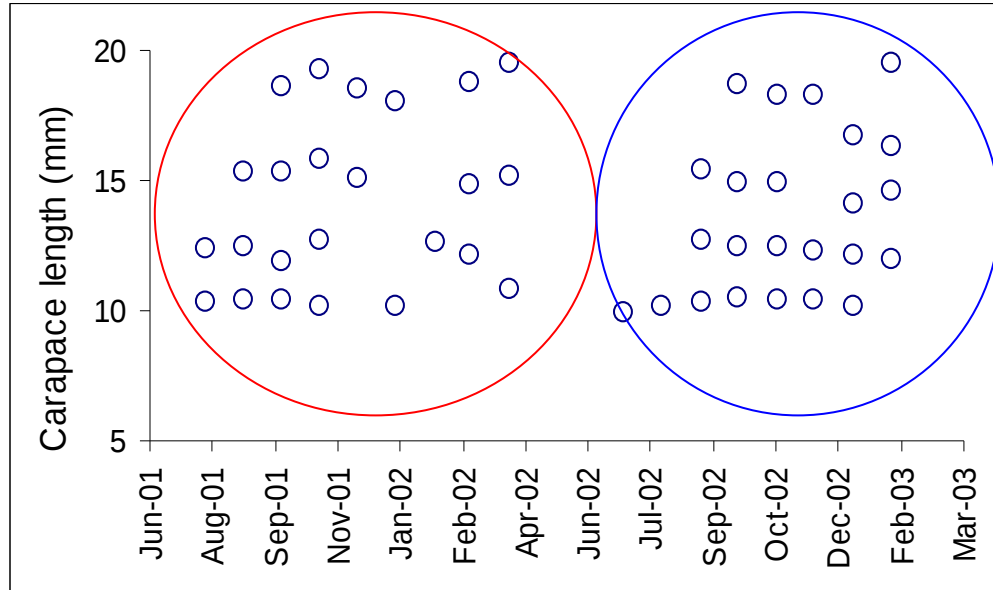


Figure 3.6 Mean carapace lengths of selected cohorts that recruited between August 2001 and February 2003. Two distinct waves of recruitment events are indicated with a red circle for 2001/2002 recruits and a blue circle for 2002/2003 recruits. A maximum size limit of 20mm CL was selected since the majority of animals from both recruitment groups fall in this size range.

The estimated population statistics of 13 of the 15 cohorts identified were reliable for calculating the monthly growth increments (in mm CL) of early juveniles (<20mm CL) using the Linking of Means Analysis (FISAT)(Table 3.13). Cohorts B, C, E, F, G and H recruited during the 2001/2002 recruitment event with cohorts I, J, K, L, M, N and O recruiting as part of the 2002/2003 recruitment group (Fig 3.6).

From cohort analysis it was evident that most cohorts first recruited at a mean carapace length of 10.0 to 12mm CL, cohort J was the only exception with a mean size at first recruitment of 9.9mm CL and a size range of 8.2-12mm CL. Therefore it was assumed that the first moult occurred from puerulus (9.0mm CL) to 1st instar juvenile (9.9mm CL), second moult was from first to second instar (10.0-12.0mm CL), third moult was from second to third instar (12.1-15.0mm CL), fourth moult was from third instar to fourth

instar (15.1-18.0mm CL) and fifth moult was from fourth to fifth instar (18.1-20.0mm CL). Inter-moult periods between the juvenile instars appear to be one month in duration.

Table 3.13 Population statistics as estimated by NORMSEP, of the 13 reliable cohorts identified for growth increment analysis. The mean carapace length (mean CL) of each mode that belongs to the designated cohort is indicated for the months in which the mode occurred. The spread of each mode is indicated by the standard deviation (SD), the degree of overlap indicated by the separation index (SI) with SI less than 2 designating a high degree of overlap between modes of different cohorts within the same month and R^2 is the correlation coefficient. The percentage that the number of animals belonging to a specific cohort constitutes of monthly samples is indicated for each cohort, respectively.

Cohort	Month	Mean CL(mm)	% of Sample Population	SD	SI	R^2
B	Aug-01	10.3	39	0.57	n.a.*	0.604
	Sep-01	12.5	20	1.03	3.10	0.169
	Oct-01	15.3	17	1.42	3.22	0.175
	Nov-01	19.3	22	1.03	4.20	0.589
C	Sep-01	10.4	45	0.52	n.a.*	0.816
	Oct-01	11.9	23	0.71	2.66	0.995
	Nov-01	15.8	24	0.61	3.75	0.666
	Dec-01	18.5	19	0.84	4.90	0.343
	Jan-02	20.5	19	1.44	1.66	0.817
F	Jan-02	10.2	6	0.54	n.a.*	0.998
	Feb-02	12.6	11	1.5	n.a.*	0.064
	Mar-02	14.8	16	0.73	3.44	0.713
	Apr-02	19.5	26	1.2	3.71	0.071
G	Mar-02	12.1	16	0.83	n.a.*	0.180
	Apr-02	15.2	7	1.07	4.58	0.125
H	Apr-02	10.8	6	0.59	n.a.*	0.271
I	Sep-02	15.4	11	1.21	3.04	0.502
	Oct-02	18.7	9	0.73	6.16	0.457
J	Jul-02	9.9	73	0.95	n.a.*	0.301
	Aug-02	10.2	59	0.53	n.a.*	0.650
	Sep-02	12.7	20	0.59	4.35	0.722
	Oct-02	14.9	11	0.5	4.69	0.509
	Nov-02	18.3	7	1.27	3.58	0.326
K	Sep-02	10.3	63	0.51	n.a.*	0.840
	Oct-02	12.5	33	0.55	3.31	0.568
	Nov-02	14.9	7	0.64	4.29	0.700
	Dec-02	18.3	14	0.84	6.48	0.584
L	Oct-02	10.5	27	0.61	n.a.*	0.499
	Nov-02	12.5	10	0.48	4.02	0.896
M	Nov-02	10.4	69	0.55	n.a.*	0.853
	Dec-02	12.3	26	1.03	2.75	0.984
	Jan-03	14.1	20	0.71	3.07	0.956
	Feb-03	16.3	20	1.12	2.24	0.056
N	Dec-02	10.4	23	0.34	n.a.*	0.971
	Jan-03	12.1	27	0.62	3.39	0.260
	Feb-03	14.6	16	0.58	2.62	0.962
O	Jan-03	10.2	9	0.46	n.a.*	0.583
	Feb-03	12.0	14	1.24	n.a.*	0.046

Growth

Mean carapace lengths of the identified cohorts in Modal progression analysis were used in the Linking of means analysis (also known as Peterson's growth method) to calculate the growth increments (carapace length increments) for each individual cohort per month. The monthly mean growth increments of cohorts that respectively recruited in 2001/2002 and 2002/2003 (Fig. 3.6), were plotted against their corresponding mean carapace lengths (per cohort) to give the relationship for animals smaller than 20mm CL of the 2001/2002 and 2002/2003 settlement groups (Fig. 3.7). The maximum size of 20mm CL was chosen as the cut-off size as most animals in both recruitment groups were less than 20mm CL. Growth increments of early juveniles of the 2001/2002 recruitment group generally increased as juveniles attain a larger size whereas mean growth increments of the 2002/2003 juvenile recruits only increases with mean carapace length up to a size of 15.0mm CL and remained constant for juveniles from 15.1mm CL to 20mm CL. The growth increment was significantly higher for early juveniles that recruited during 2001/2002 with a mean growth increment of 2.9mm CL per month compared to a 2.3mm CL mean growth increment of early juveniles that recruited during 2002/2003. The mean growth increment per 2-3-mm-CL size interval class followed this general increasing trend, however the monthly growth increment for the 10-12mm CL size class juveniles (3rd instar) was identical for cohorts that recruited during 2001/2002 and 2002/2003 (Table 3.14). The mean monthly growth increment of the 18.1 – 20.0mm CL size class of juveniles that recruited during 2002/2003 was greater than that of juvenile cohorts that recruited during 2001/2002.

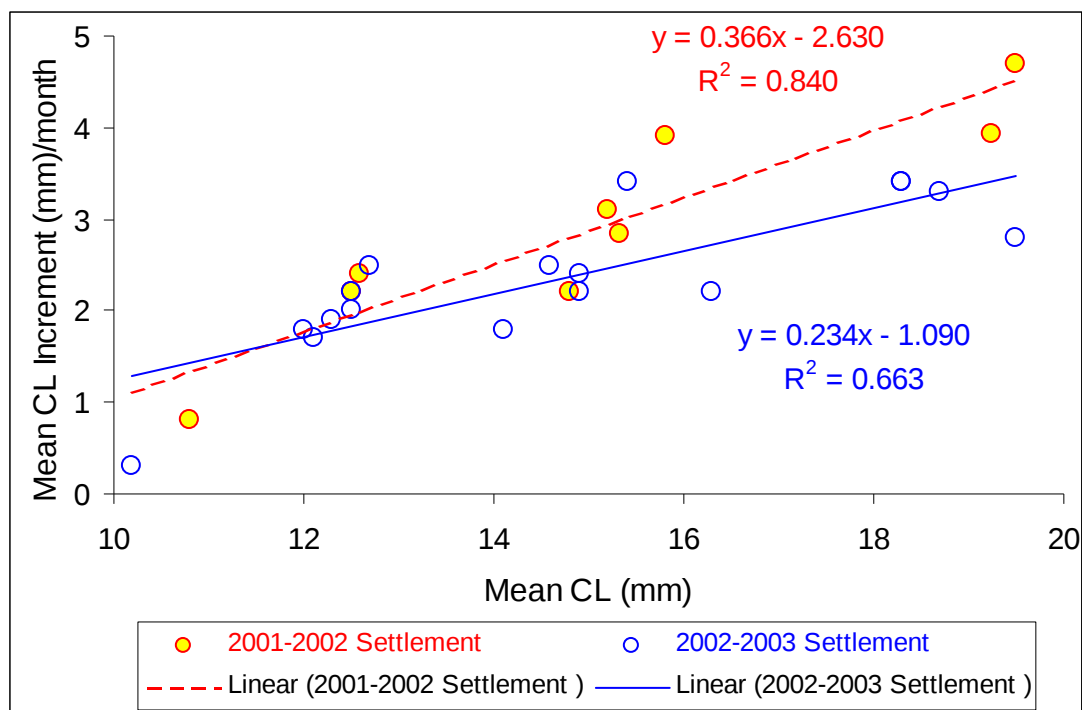


Figure 3.7 Post-settlement growth increment of early juvenile lobster calculated from the monthly mean carapace lengths of selected cohorts that recruited during the two recruitment events (2001/2002 and 2002/2003) on the Lüderitz oyster farm between August 2001 and February 2003.

Table 3.14 Mean monthly carapace length (growth) increments of selected cohorts of early juveniles (<20mm CL) that recruited during 2001/2002 and 2002/2003 at Lüderitz Oyster farm.

2001/2002 cohorts					2002/2003 cohorts			
Size class (mm CL)	Mean increment (mm CL)	% CL increase	SD	n	Mean increment (mm)	% CL increase	SD	n
< 10.0	-	-	-	213	0.3	3	-	312
10.0 - 12.0	2.8	7	0.42	432	2.0	7	0.29	818
12.1 - 15.0	3.2	16	0.69	409	2.4	16	0.53	540
15.1 - 18.0	3.6	20	0.74	337	2.8	16	0.73	261
18.1 - 20.0	2.3	19	0.40	233	2.8	16	-	94

Nutritional condition of puerulus and juvenile lobster

The nutritional condition of puerulus and juvenile lobster was evaluated by means of two nutritional condition indices, weight-length ratio (K) and percentage (%) crude fat. It was also evaluated whether the condition factor K was comparable to the % crude fat index, so that K may be used as a measure of nutritional condition in instances where only length and weight data is available and where animals cannot be sacrificed. The nutritional condition factors, K and % crude fat of pueruli collected from oyster bags, crates and booth crevice collectors (combined) during 2002 were compared between sample dates to establish the time of peak nutritional condition (Fig. 3.8). Transparent and pigmented pueruli of weekly-pooled samples were combined due to most samples containing either too few transparent pueruli or pigmented pueruli. Based on the percentage crude fat index, nutritional condition of puerulus peaked during August 2002 and October 2002 (Fig. 3.8). The weight-length index showed that nutritional condition peaked during August 2002. Linear regression analysis revealed that there was a significant correlation between percentage crude fat and weight-length ratio ($R^2=0.652$; $p<0.001$; Fig. 3.8).

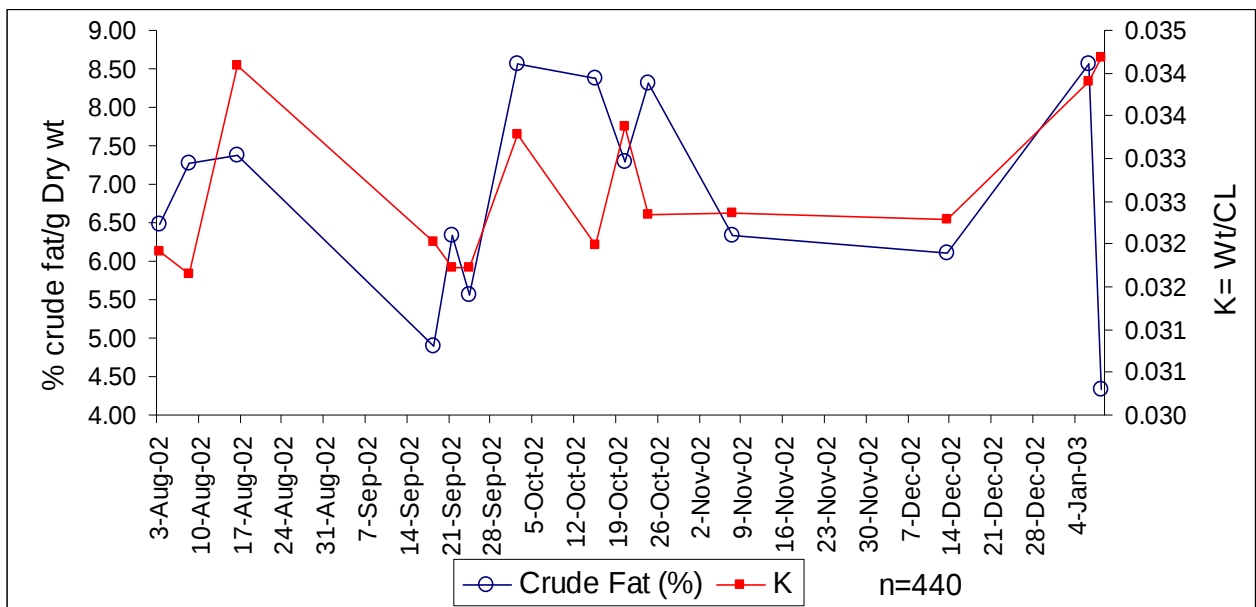


Figure 3.8 Nutritional condition indices, K (g/mm) and % crude fat (per g dry wt) of puerulus lobster recruits from selected samples collected between August 2002 and January 2003.

Similarly, nutritional condition factors, K and % crude fat of juveniles collected from oyster bags, crates and booth crevice collectors during 2002 were compared between months (Fig. 3.9). Based on the percentage crude fat index the nutritional condition of juvenile lobster peaked during August, November 2002 and January 2003 (Fig. 3.9). Weight-length ratio indicated that nutritional condition of juveniles was also highest during the same months (except for August 2002) as well as during October 2002. There was however, no significant correlation/relationship between the percentage crude fat and weight-length ratio indices for juveniles ($R=0.287$; $p>0.05$).

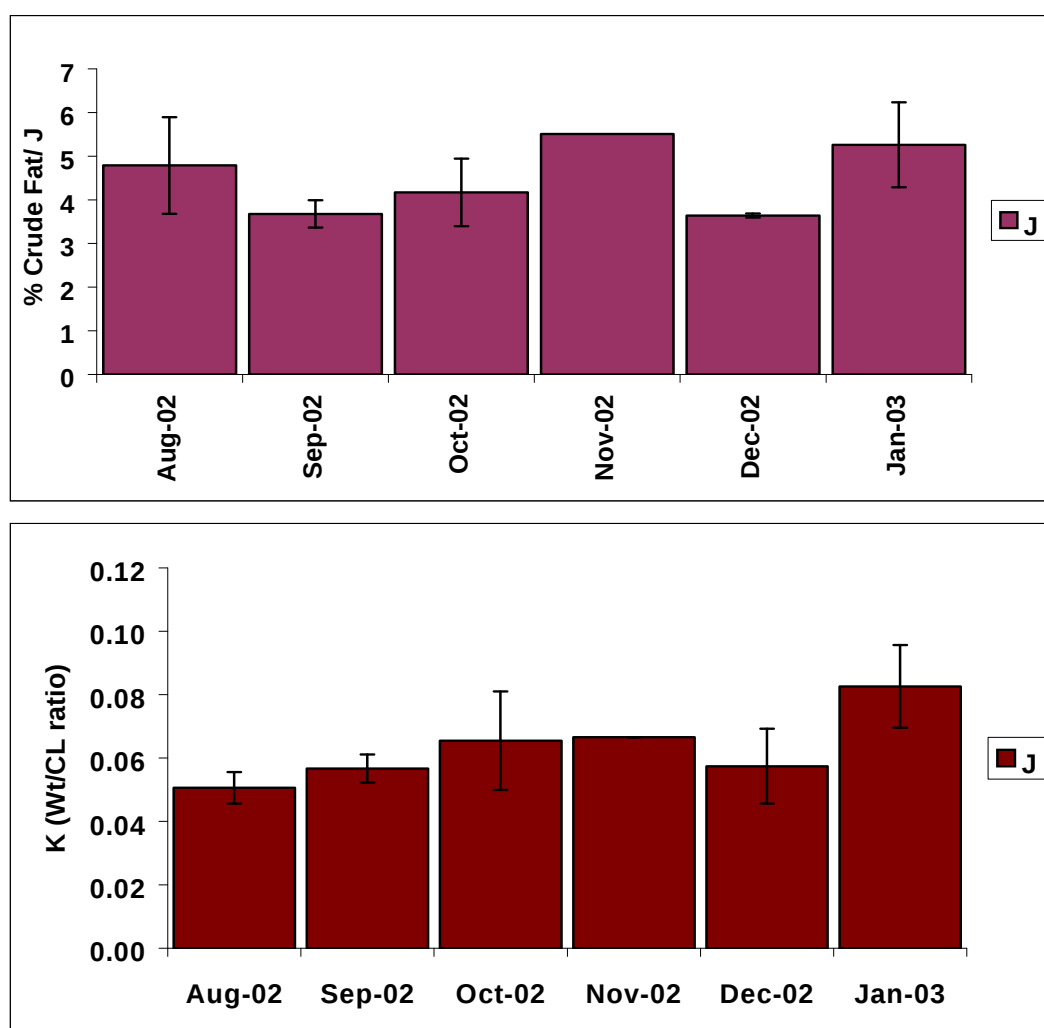


Figure 3.9 Nutritional condition of juvenile lobster based on the percentage crude fat and weight-length ratio (K) indices from selected samples collected between August 2002 and January 2003.

The significant correlation between the % fat and K condition indices for puerulus indicated that the K condition index was suitable for establishing trends in the nutritional condition of puerulus lobster. Therefore the K condition index was calculated and compared for puerulus that settled during the 2001/2002 and 2002/2003 recruitment events. Pueruli that recruited during the 2002/2003-recruitment event were in a better nutritional condition than puerulus that recruited during the 2001/2002-recruitment event ($P < 0.0001$; Table 3.15). Despite being larger in terms of carapace length puerulus of the 2001/2002-recruitment weighed less than puerulus that recruited during 2002/2003. Puerulus carapace length was neither correlated to the nutritional condition K ($R^2 = 0.001$) or to the weight ($R^2 = 0.111$) of puerulus recruits of 2001/2002 (Appendix 1). Although carapace length was not significantly correlated with nutritional condition ($R^2 = 0.260$), carapace length was correlated with weight ($R^2 = 0.619$) for puerulus that recruited during 2002/2003. Nutritional condition was strongly correlated with weight for puerulus of both the 2001/2002 ($R^2 = 0.902$) and the 2002/2003 ($R^2 = 0.864$) recruitment events.

Table 3.15. Comparison of morphometric dimensions and nutritional condition of puerulus (P) and juvenile (J) recruits between the 2001/2002 and 2002/2003 recruitment events. The average values of weight, carapace length and nutritional condition K are indicated with the standard deviation indicated with a $\pm$ sign followed by the value. P indicates the statistical significance ($p < 0.05$) of the difference in a factor between the 2001/2002 and 2002/2003 recruitment events. The total number (sample size n) of pueruli and juveniles collected are indicated for each recruitment event.

Stage	Factor	2001/2002	2002/2003	P
P	Weight (g)	0.25 ± 0.07	0.29 ± 0.05	<0.001
	Carapace length(mm)	9.2 ± 0.72	8.9 ± 0.58	<0.001
	K (g/mm)	0.027 ± 0.007	0.033 ± 0.004	<0.001
	n	422	703	<0.001
J	Weight (g)	1.35 ± 1.02	0.92 ± 0.70	<0.001
	Carapace length(mm)	13.6 ± 3.26	12.3 ± 2.64	<0.001
	K (g/mm)	0.09 ± 0.05	0.07 ± 0.03	<0.001
	n	1623	2027	<0.001

Juveniles that recruited during 2001/2002 were in a higher nutritional condition than juvenile recruits of 2002/2003 and this was also reflected in the significantly larger carapace length and higher weight of the 2001/2002 juveniles (Table 3.15). Juvenile carapace length and weight were significantly correlated with each other and with the nutritional condition K, as reflected by the R^2 - values of above 0.89 (Appendix 1).

The nutritional condition of early juveniles (across the range of size classes) showed a significant relationship with the monthly growth increments for juveniles that recruited during 2001/2002 and 2002/2003. The relationship was most evident for juvenile recruits of 2002/2003 ($R^2 = 0.62$; $P < 0.01$) compared to the marginally significant CL increment-K condition relationship of juvenile recruits of 2001/2002 ($R^2 = 0.56$; $P = 0.05$). The nutritional condition of specific size classes (2-3mm CL class intervals) of juveniles less than 20mm CL that were used in the growth increment analysis are presented in Table 3.16. Juveniles less than 12mm CL in size were in a similar nutritional state during 2001/2002 and 2002/2003. Juveniles in the 12.1mm CL to 20mm CL size classes during 2001/2002 were in a better nutritional state compared 2002/2003.

Table 3.16. Comparison of the mean nutritional condition of five 2-3 mm CL-size-interval size classes of selected cohorts of early juveniles (<20mm CL) that recruited during 2001/2002 and 2002/2003 at Lüderitz Oyster farm. The average values of weight, carapace length and nutritional condition K and their standard deviations (indicated with a $\pm$ sign followed by the value), are indicated. Significant differences (at $P < 0.05$) in a factor between the 2001/2002 and 2002/2003 recruitment events are indicated with Φ . The total number (sample size n) of pueruli and juveniles collected is indicated for each recruitment event.

2001/2002 cohorts						2002/2003 cohorts			
Size class (mm CL)	Mean CL(mm)	Mean Wt(g)	Mean K (g/mm)	n		Mean CL(mm)	Mean Wt(g)	Mean K (g/mm)	n
< 10.0	9.5 $\pm$ 0.36	0.37 $\pm$ 0.06	0.04 $\pm$ 0.005	213		9.5 $\pm$ 0.37	0.38 $\pm$ 0.05	0.04 $\pm$ 0.005	312
10.0 - 12.0	10.8 $\pm$ 0.65	Φ 0.55 $\pm$ 0.19	0.05 $\pm$ 0.015	432		10.7 $\pm$ 0.63	Φ 0.52 $\pm$ 0.12	0.05 $\pm$ 0.01	818
12.1 - 15.0	13.4 $\pm$ 0.94	Φ 1.07 $\pm$ 0.32	Φ 0.08 $\pm$ 0.020	409		13.3 $\pm$ 0.88	Φ 0.99 $\pm$ 0.24	Φ 0.07 $\pm$ 0.01	540
15.1 - 18.0	16.4 $\pm$ 0.86	Φ 1.99 $\pm$ 0.46	Φ 0.12 $\pm$ 0.022	337		16.3 $\pm$ 0.85	Φ 1.88 $\pm$ 0.35	Φ 0.11 $\pm$ 0.02	261
18.1 - 20.0	19.0 $\pm$ 0.58	Φ 3.26 $\pm$ 0.44	Φ 0.17 $\pm$ 0.020	233		18.9 $\pm$ 0.56	Φ 3.07 $\pm$ 0.50	Φ 0.16 $\pm$ 0.02	94

3.4 Spatial variation in puerulus and juvenile abundance

Puerulus and juvenile abundance was compared between raft areas, bags and crates on the oyster farm and between collector sites in the greater bay area. The abundance of transparent, pigmented puerulus and juvenile lobster was compared between bags that were hung from three oyster raft areas, exposed, centred and sheltered. Exposed rafts were rafts exposed to wave and swell action. Centred rafts refer to rafts that were surrounded by other raft entirely. Sheltered rafts were rafts protected from wave and swell action.

Kruskal-Wallis ANOVA and Scheffe's multiple range tests revealed that transparent puerulus settlement was not significantly different between exposed, centred and sheltered raft areas (Table 3.17). Pigmented puerulus and juvenile abundance on exposed rafts was significantly less than that on centred and sheltered rafts.

Table 3.17 Statistical differences in transparent puerulus, pigmented puerulus and juvenile abundance between exposed centred and sheltered raft areas, as determined by Kruskal-Wallis ANOVA and Scheffe's multiple range tests. Average numbers are reported with variance calculated as $\pm$ the standard deviation from the sample mean. $P < 0.05$ indicate significant differences and $p > 0.05$ indicates no significant differences in the mean abundance of Pt, Pp and J between raft areas. Sample size is denoted by n.

Stage	Average numbers per raft area per sample day			P- value
	Exposed	Centre	Sheltered	
Pt	0.093 $\pm$ 0.522 (n=18) ~	0.335 $\pm$ 0.893 (n=65) ~	0.345 $\pm$ 0.989 (n=67)	>0.05
Pp	0.309 $\pm$ 1.605 (n=60) <	1.407 $\pm$ 3.017 (n=273)~	1.195 $\pm$ 2.519 (n=232)	<0.01
J	4.358 $\pm$ 6.439 (n=841) <	7.176 $\pm$ 7.465 (n=1385)~	6.711 $\pm$ 7.170 (n=1302)	<0.01

Spatial variation in lobster abundance between rafts (bags) and longlines (crates).

Puerulus and juvenile abundance was compared between crates and bags for significant differences at $p < 0.05$ using Kruskal-Wallis ANOVA and Scheffe's multiple range tests. The results of these comparisons are presented in Table 3.18. Settlement rates of transparent pueruli on crates and bags were similar (Scheffe's test; $p > 0.05$). Pigmented puerulus abundance was significantly higher on crates compared to abundance on bags. Similarly, juvenile abundance on crates was significantly higher than that on bags.

Table 3.18 Statistical differences in transparent puerulus, pigmented puerulus and juvenile abundance on oyster crates and bags as determined by Kruskal-Wallis ANOVA and Scheffe's multiple range tests. Average numbers are reported with variance calculated as $\pm$ the standard deviation from the sample mean.

Stage	Average numbers per bag or crate per month		
	Bags	Crates	P- value
Pt	0.67 $\pm$ 0.67 (n=150) ~	1.40 $\pm$ 2.54 (n=493)	>0.05
Pp	1.12 $\pm$ 1.87 (n=565) <	6.07 $\pm$ 9.36 (n=996)	<0.05
J	6.45 $\pm$ 5.88 (n=3528) <	12.15 $\pm$ 13.57 (n=1961)	<0.05

Spatial variation in puerulus and juvenile recruitment on collectors

The hogshair collector attracted no pueruli but only larger juveniles of greater than 20mm in carapace length. Structurally the hogshair collector was not suitable for the physical conditions at Lüderitz Bay with all collectors being destroyed by moderate wave action within a period of 2 months. The hogshair collectors could not be repaired and was therefore replaced with new ones. The destruction and loss of collectors after every 2 months rendered the exercise costly and unsuccessful and therefore sampling was discontinued.

Puerulus recruitment on booth collectors was highest at the Satellite 2 and Satellite 3 sites followed by recruitment at Lagoon 2 and Satellite 1 sites (Fig. 3.10). Recruitment at the Griffith Bay and Nest Hotel sites was less with catch rates of 5.00 and 4.00 lobsters per collector per sample day, respectively. The Lagoon 1 site was sampled only once and had the lowest catch rate of 0.50 pueruli per collector. Juvenile abundance was greatest on collectors at the Satellite 2 (16.00/collector), Satellite 3(11.86/collector), Lagoon 2 (6.50/collector) and Griffith Bay sites (5.00/collector). Collectors at the Satellite 1, Nest and Lagoon 1 sites had lower catch rates of 3.83, 2.40 and 1.00 lobsters per collector per sample day, respectively.

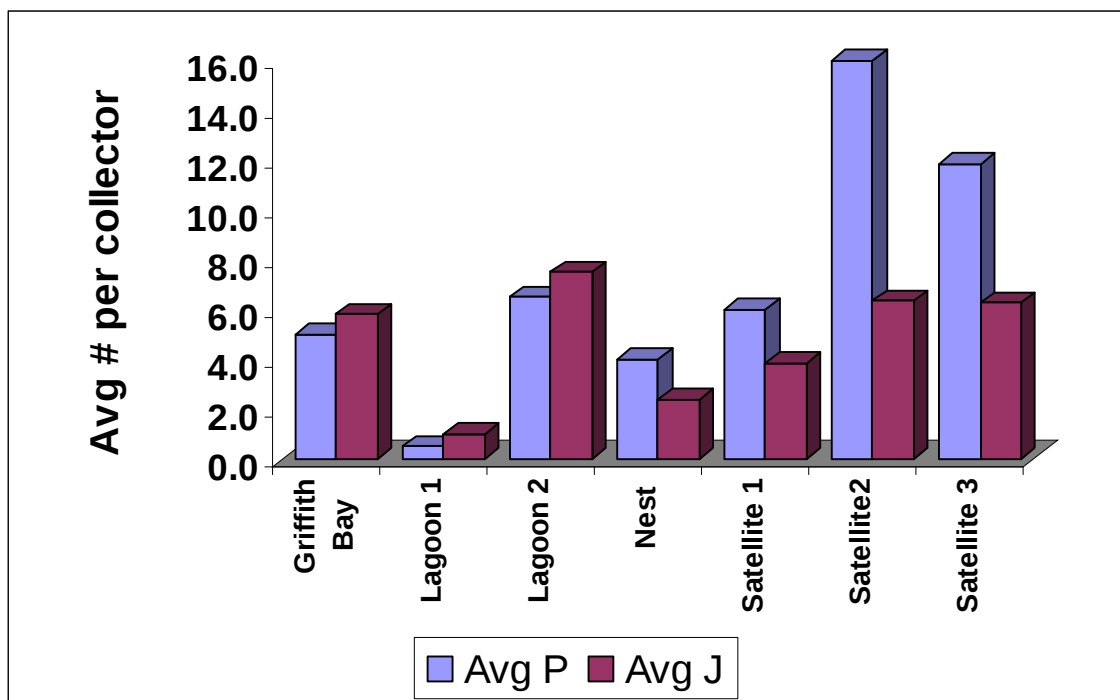


Figure 3.10 Puerulus and juvenile recruitment at the selected collector sites within Lüderitz Bay between June 2002 and April 2003.

Table 3.19 Two-tailed multiple comparisons (p- and z values) tests revealing collector sites with significantly different lobster abundance. Group 1 indicates collector sites with significantly higher puerulus settlement, and Group 2 collector sites with significant lower puerulus settlement. P-values less than 0.05 indicate a significant difference between group 1 and group 2.

Group 1	Group 2	P	Z-value
Griffith Bay	Lagoon 1	0.003	3.817
Satellite 2	Lagoon 1	0.004	3.749
Satellite 1	Lagoon 1	0.043	3.086
Satellite 3	Lagoon 1	<0.0001	5.487
Satellite 3	Nest	0.047	3.005

Puerulus settlement was significantly higher at collector sites closest to areas with a high presence of juveniles such as the satellite sites on the oyster farm and at Griffith Bay near rocky outcrops close to the entrance of the bay, that are occupied by mid-stage juveniles (*personal observation*) ($p < 0.05$; Table 3.19). Puerulus settlement at the Lagoon 1 site was significantly less compared to all other sites, except the Nest site. The recruitment of puerulus at the Satellite 3-collector site was significantly higher than that at the Nest collector site. The Griffith Bay was one of the sites with the highest puerulus recruitment.

Summary

The main findings from results section may be summarised as follows:

1. Late winter (August) to spring (September-November) was been identified as the season for peak puerulus settlement at Lüderitz Bay. The high puerulus settlement that occurred during early winter in May 2000 was an exception. The period for peak juvenile abundance was approximated to occur during late spring (November) to early summer (December). Juvenile peaks lagged by 8-9 weeks were significantly correlated with puerulus peaks.
2. Interannual variation in puerulus and juvenile abundance on crates was evident with the years 1999 and 2000 showing significantly higher juvenile and puerulus abundance peaks, respectively. The peak in puerulus abundance was significantly higher during 2000 compared to 2001 and 2002. On bags the transparent and pigmented puerulus abundance peaks of 2001 were significantly higher than that during 2002. The secondary pigmented puerulus peak during October-November 2002 was significantly higher than the October-November abundance and the August peak of 2001. There was no significant variation in juvenile abundance on bags between 2001 and 2002 peaks.
3. Peak puerulus settlement appears to be driven by the following prevailing environmental factors lagged by up to 1 week:
 - Low SST
 - Moderate to strong southerly winds
 - Moderate swells
 - Large tidal ranges associated with new moon, full moon and last quarter moon phases

Interannual variation in time lagged environmental factors associated with peak puerulus abundance was evident with the above-mentioned environmental conditions most pronounced during the year 2000. All environmental factors during the 2001

peak puerulus settlement season varied significantly from that during 2000. Lower tidal ranges during the first quarter moon and above average SST were the only factors contributing to the variation in environmental condition between 2002 and 2000.

4. Two distinct waves of early (2nd to 3rd moult) juvenile cohorts were observed recruiting during 2001/2002 and 2002/2003, respectively. Juvenile cohorts of the 2001/2002-recruitment group grew at a faster rate than the 2002/2003-recruitment group.
5. The % fat and K nutritional condition indices indicated that puerulus nutritional condition was highest during the peak settlement season in spring (August-October). Puerulus nutritional condition was higher during 2002/2003 compared to 2001/2002. Juvenile nutritional condition was highest during the peak juvenile abundance season and the 2001/2002 recruits were in a higher nutritional condition compared to 2002/2003 recruits.
6. Puerulus and juvenile abundance varied on a micro-spatial scale on the oyster rafts with pigmented puerulus and juveniles occupying more protected areas (centred and sheltered areas) on rafts. Pigmented puerulus and juveniles showed higher abundance on oyster crates compared to bags (Table 3.18). Transparent puerulus settlement was uniform over oyster rafts areas and on crates and bags.
7. Puerulus settlement was significantly higher at collector sites closest to areas with a high presence of juveniles such as the satellite sites on the oyster farm and at Griffith Bay near rocky outcrops close to the entrance of the bay, that are occupied by mid-stage juveniles (*personal observation*).

CHAPTER 4: General Discussion

4.1 Seasonal and annual puerulus recruitment patterns and the environment

The results show that puerulus settlement in *Jasus lalandii* on the oyster farm and the lagoon at Lüderitz Bay peaked annually during the late winter - early spring period (August to September). Settlement events were however not confined to this period. A major peak in puerulus settlement occurred in May 2000, prior to the predicted peak in August 2000, and in 2002, a secondary puerulus settlement peak was observed in October-November, following the puerulus settlement peak observed during August 2002.

The time of annual peak puerulus settlement events coincided at all monitoring sites throughout the bay indicating that ontogenetic, biological and oceanographic processes, as opposed to local bay scale processes, were the determining factors of puerulus recruitment in *J. lalandii* at Lüderitz Bay.

Reproductive and ontogenetic cycles

The time of peak puerulus settlement during August-September, observed during the present study was probably determined by the time of spawning one year earlier and the duration of the larval cycle. Females of the Namibian *J. lalandii* population are in berry from June to October every year. Spawning is usually observed from August to November, however 60% of females spawn between September to November (Ndjaula, MFMR, *pers. comm.*, 2002). Although the time and magnitude of spawning in *J. lalandii* off the coast at Lüderitz during the study period are not known, it is possible that variations in the timing of the spawning cycle one year earlier may have resulted in the observed variations in puerulus settlement events observed during the study. Variations in the time of spawning time of *J. lalandii* are known to occur, for example, smaller sexually mature females spawn later in the year (Lazarus, 1967; Heydorn, 1969).

Variations in the duration of the larval phase of *J. lalandii* may also be responsible for the variation in the peak time of puerulus settlement observed during the study. The duration of the larval phase of *J. lalandii* may be extended in the absence of sufficient food or unfavourable environmental conditions responsible for the transporting larvae back to their home population (Pollock, 1989, 1990).

The completion of the life cycle of *J. lalandii*, particularly the stages between egg and puerulus lobster are dependent on the physical and biological conditions of the open ocean (Lazarus, 1967; Pollock, 1986; Pollock and Goosen 1991). Pollock and Goosen (1991) proposed the path of larval circulation in the Southeast Atlantic Ocean (Fig. 4.1).

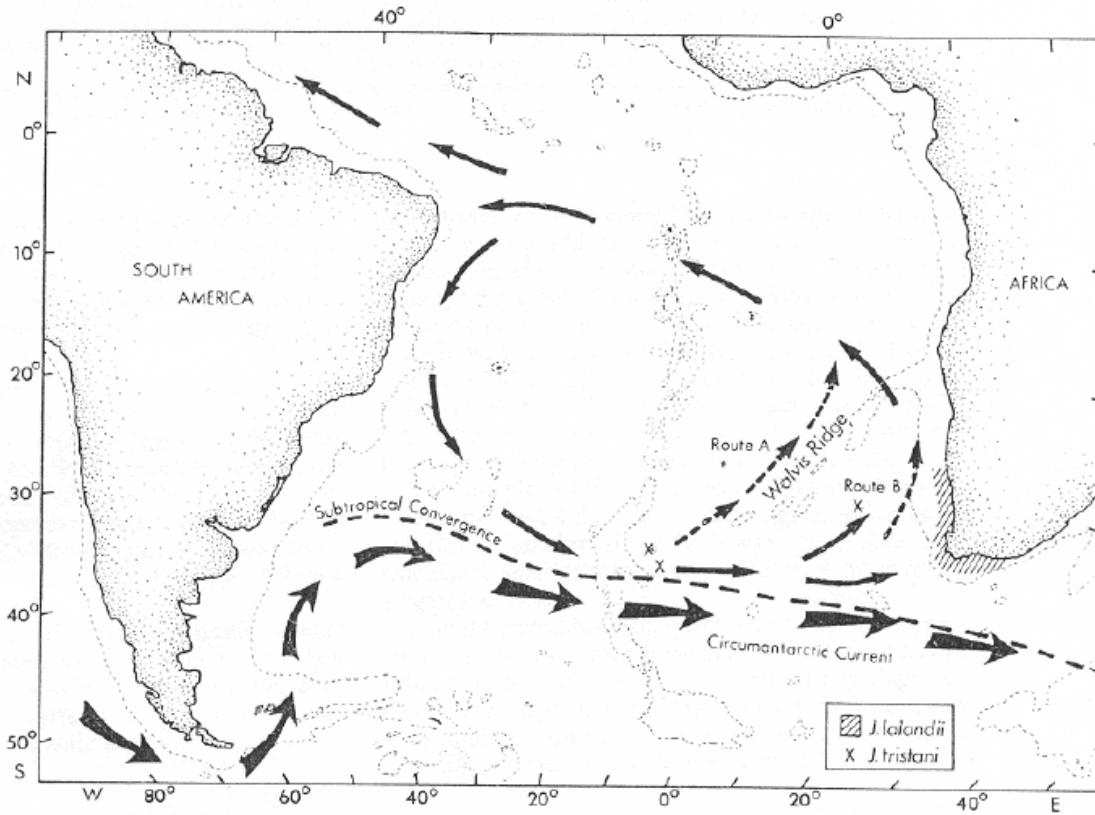


Figure 4.1 Proposed routes that larvae of *J. lalandii* pursue during their oceanic circulation in the South Atlantic Ocean (Figure from Pollock and Goosen, 1991).

Larvae hatch at the shelf break mainly in September (Pollock 1986) and upon hatching newly hatched larvae are transported offshore by the Benguela Oceanic Current (BOC) into the South Atlantic Subtropical Gyre (Fig. 4.1). The 13 stage developmental larval cycle is completed within 12 months during which larvae are circulating in the oceanic waters of the South Atlantic Subtropical Gyre. Following a complete cycle of circulating in the South Atlantic Gyre larvae are transported equatorwards by the surface BOC current and eastwards by diversions of the BOC to be concentrated at the continental shelf break along the west coast of southern Africa (Route B). At the continental shelf break final stage phyllosoma larvae metamorphose into puerulus post-larvae. Metamorphoses between larval stages and to the final puerulus stage occur once sufficient internal energy reserve levels are present (McWilliam and Phillips, 1997). Metamorphosis to puerulus may be delayed until the internal energy threshold is reached, thus resulting in a slightly extended larval cycle and a shift in the time of peak puerulus recruitment on the coast (Lemmens, 1994). The active swimming puerulus is capable of directional swimming which enables it to cross the continental shelf, with the help of wind induced surface currents, to return to its home population where it settles inshore among seaweed, rock crevices and holes in the inter-tidal region (Pollock, 1987). The puerulus stage is suspected to last 2-3 weeks (Lemmens, 1994), with post settlement duration of 2 weeks observed for *J. lalandii* (Ndjaula, MFMR, *pers. comm.*, 2002), depending on the amount of stored energy, water temperature and when suitable settlement habitat is found before it moults into a juvenile (Phillips and Booth, 1994). It is therefore a plausible hypothesis that the September peak puerulus in settlement at Lüderitz Bay occurred approximately about 12 months after eggs hatched into larvae.

Oceanographic processes and puerulus recruitment

Using the larval circulation theory proposed by Pollock and Goosen (1991) I attempt to explain how various physical and biological factors in the offshore, inshore and near-shore regions may have contributed to the temporal (seasonal and interannual) variations in puerulus settlement observed at Lüderitz Bay during the present study. The offshore region refers to the open ocean environment in waters beyond the continental shelf-break (depth >200m), the inshore region includes the area of water over the continental shelf deeper than 30m, and the nearshore region refers to waters shallower than 30 metres in depth.

Offshore

On an oceanic scale there was a paucity of information on the variability of environmental conditions affecting *J. lalandii* larval development and survival. Specifically, there is a lack of direct evidence indicating how larval hatching one year earlier may have been enhanced or reduced by environmental conditions. Neither is there any information on variations in the physical conditions and food availability in the South Atlantic gyre offshore, which may have influenced the moulting of larvae and the duration of the various larval stages. The offshore oceanic environment of the South Atlantic gyral system is more stable in comparison to the coastal upwelling region inshore of the continental shelf break (Shannon, 1985). This led Pollock and Goosen (1991) to postulate that predation levels on *J. lalandii* larvae are at a minimum in offshore waters, and highest closer inshore at the continental shelf. Therefore, despite the lack of environmental data for the offshore region, variations in larval survival and puerulus recruitment are more likely to be explained by variations of environmental factors in the inshore and nearshore regions.

Continental shelf (Inshore) region

Peak puerulus settlement during early spring (late-August to early-September) at Lüderitz Bay was correlated to low SST, moderate to strong southerly winds, and moderate swell conditions observed one week earlier. These results suggest that these coastal environmental conditions probably promoted late stage phyllosoma larval feeding, metamorphosis and the subsequent inshore movement of puerulus across the continental shelf. Late stage phyllosoma larvae are usually found at the shelf break (Lazarus, 1967; Pollock, 1986; Pollock and Goosen, 1991) where oceanic conditions are more variable and influenced by the highly variable coastal hydrographic features responsible for upwelling (Shannon, 1985). Environmental conditions experienced one week prior to peak puerulus settlement observed during the study were synonymous with environmental conditions characteristic of the spring upwelling season at Lüderitz. Tomalin (1993) distinguished three upwelling seasons that occur at Lüderitz as follow:

1. Autumn/Winter (May- August): Calm conditions are experienced in autumn-winter when wind speeds are lower. Water is warmer and large swells of long wavelength occur.
2. Spring (September-December): Upwelling can persist for up to two weeks with uninterrupted winds at a daily average of more than 5m/sec in spring. Due to these strong winds water is well mixed and very cold and swells are of moderate intensity.
3. Summer (January-April): Upwelling lasts for a few days with very strong southwesterly winds, particularly in summer. During these months, water can be highly stratified and is warmer with low swells occurring.

Environmental conditions at Lüderitz Bay are characterised by intense coastal upwelling due to the Benguela current's principle upwelling cell being situated near Lüderitz. This upwelling is driven by strong southwesterly winds that are predominant throughout the year (Grobler and Noli-Peard, 1997). A slight maximum in upwelling is reached during spring (August-September) and a slight minimum during autumn (Hardman-Mountford *et*

al., 2003). During spring strong uninterrupted southerly winds are responsible for intense upwelling of cold bottom water rich in nutrients. Thus lower than average SST were observed during spring in the present study. The general upwelling process with the associated oceanographic features are described in Chapter 2.1 to provide a context for explaining the transport and survival of lobster larvae and how these factors are related to puerulus recruitment at Lüderitz Bay.

The oceanography in the Benguela region may explain the transport and survival of phyllosoma larvae and puerulus and subsequent puerulus recruitment patterns at Lüderitz Bay observed during the present study. The fast north-flowing Benguela current is thought to transport phyllosoma larvae of the *J. lalandii* population along the Namibian shelf break of the southern African West Coast after they have completed their circulation in the South Atlantic Gyral system (Pollock and Goosen, 1991). The shoreward diversion of the coastal component of the BOC south of Lüderitz appears to concentrate phyllosoma larvae at the highly productive shelf break between Lüderitz and the Orange River during late winter (Shelton *et al.*, 1985). Upwelling during winter at Lüderitz is less intense, however sufficient concentrations of nutrients required for primary productivity are present further south (Shannon and O'Toole, 1998; Campillo-Cambell and Gordo, 2004). Calmer conditions during winter reduce the advection of phytoplankton offshore. Wind mixing during winter still maintains phytoplankton at greater depths so that it is transported south of Lüderitz by the poleward undercurrent. Over the continental shelf in the south between Lüderitz and Orange River the water column is highly stratified which enables phytoplankton cells to surface to waters in the euphotic zone where sufficient light is available for photosynthesis. Over this shelf region there is a highly abundant source of plankton food throughout the year with slightly higher concentrations towards late-winter when late stage phyllosoma arrive at this shelf region. High concentrations of planktonic food at the shelf region between Lüderitz and Orange River were probably available to late stage phyllosoma larvae during late winter during the present study, which enhanced metamorphosis and survival to the puerulus stage. The eastward inshore diversion of the BOC (also present throughout the year) may have also acted as a cross shelf current transporting the newly metamorphosed puerulus

to the nearshore region at Lüderitz Bay. Although supporting evidence is lacking, there is a possibility that puerulus may have undergone vertical migration to a greater depth (100-160m) where they could have made use of the strong movement of bottom waters to shallow waters to move into the nearshore zone. Puerulus of *Palinurus cygnus* off Australia migrated vertically to depths ranging between 40m and 340m (Phillips and Pearce, 1997).

Nearshore to intertidal Region

Peak puerulus settlement was related to increased tidal height during the new moon, full moon and last quarter moon phases. In the nearshore and intertidal zone increased tidal currents associated with new moon, last quarter moon and full moon appeared to have transported puerulus into the bay area, where they settled on the crevice collectors and the oyster farm structures. The magnitude and patterns of tidal currents at the entrance and within the bay is not known. Future research on current patterns at the bay entrance and in the bay may be able to clarify the role that these circulation patterns play in puerulus recruitment into Lüderitz Bay.

Interannual variation in puerulus settlement, puerulus condition, upwelling and food availability

Our results indicated that 2000 was a “good” year for puerulus settlement at Lüderitz compared to 2001 and 2002. The 2002 puerulus settlement peak was relatively stronger than 2001.

Reproductive output data of *J. lalandii* females in the Lüderitz area was not available for the years 1999 and 2000, so that no inference could be made about its relationship with subsequent puerulus settlement at Lüderitz Bay during the present study. Ndjaula (2004) found that the fecundity of females was similar during 2001 and 2002 and higher compared 1995 and 1996. Temporal variation in food availability and environmental factors were postulated as the most likely causes of variability in reproductive output. The strong puerulus recruitment observed in 2000, in comparison to 2001 and 2002,

appears to be linked to environmental conditions. Colder SST and stronger south winds were prevalent during 2000 compared to winds and SST experienced during 2001 and 2002, suggesting that upwelling was strong during 2000. Using satellite imagery of SST and chlorophyll concentration, Campillo-Cambell and Gordo (2004) noted slight interannual variability in the strength of upwelling in the coastal zone closer inshore between 1997 and 2001 off Namibia, with low SST and high chlorophyll levels recorded during 2000. Thus abundant food in the coastal waters as a result of strong upwelling may have contributed to the “good” recruitment of puerulus into Lüderitz Bay in 2000. Information on the nutritional condition of puerulus that recruited at Lüderitz during 2000 was unfortunately not available, making it impossible to use lobster condition as an indicator of recent food availability to late stage larvae and puerulus.

The puerulus settlement peak was less pronounced during 2001 compared to 2000 and 2002 and was associated with weaker upwelling conditions. Compared to 2000 and 2002, the southerly winds were least intense and the warmest SST was experienced during the month of peak puerulus settlement in 2001 indicating that weak spring upwelling occurred during 2001. From satellite image data of SST and chlorophyll concentrations, higher SST and lower chlorophyll levels were observed off the Namibian coast during the peak upwelling season (August and September) indicated that upwelling was weaker during 2001 (Campillo-Cambell and Gordo, 2004). Low chlorophyll concentrations south of the Lüderitz upwelling cell during 2001 suggested that nutrient concentrations were low as a result of weak upwelling during this year, which possibly led to lower abundance of plankton food sources available to phyllosoma larvae. Pueruli were in a significantly poorer nutritional state during 2001 than puerulus that settled during 2002 suggesting that there may have been a lower abundance of plankton food available to late stage phyllosoma in the coastal waters in 2001. This may have resulted in fewer late stage larvae reaching the internal energy threshold required for metamorphosing to the puerulus stage during 2001, and in fewer puerulus reaching the settlement grounds at Lüderitz.

The stronger peak in puerulus settlement and higher puerulus nutritional condition during 2002 appears to be associated to stronger upwelling conditions off Lüderitz in 2002 compared to 2001. Upwelling favourable environmental conditions such as low SST and strong southerly winds were more intense during 2002 compared to 2001 thus indicating that upwelling during 2002 was more pronounced. One could hypothesise that higher puerulus condition during 2002 may have been associated with higher plankton food abundance available to late stage larvae in coastal waters. However, chlorophyll concentrations off Namibia during 2002 were not available, so no inference about coastal food productivity in relation to the higher nutritional condition of puerulus that settled at the sites monitored at Lüderitz during the present study could be made.

4.2 Factors affecting juvenile abundance and growth

Nutrition

The condition of puerulus of *J. lalandii* observed in my study did not increase with an increase in carapace length (See Appendix 1). Although pueruli of the 2001/2002 settlement were larger in terms of carapace length, they weighed less and were in a poorer nutritional state than pueruli that settled during the 2002/2003-settlement period. Therefore pueruli of *J. lalandii* with larger carapace lengths were not necessarily “better” conditioned, contrary to the positive relationship that Jeffs *et al.* (2001) found between carapace length and condition (energy reserves) of pueruli of *J. edwardsii* of New Zealand. The condition factor K of pueruli during 2001/2002 was highly correlated with weight ($R^2=0.90$). Puerulus condition increased at a rate of 0.09 per gram of weight, 0.02 units higher than that of pueruli settling during the 2002/2003 period. Transparent and pigmented pueruli had to be combined in the % fat and K analysis due to the low number of pueruli in some samples. Separating transparent and pigmented pueruli in the % fat content and K factor analysis would have provided more reliable measures of the condition of pueruli upon their arrival at the settlement grounds. Analysing the transparent and pigmented pueruli separately would also have provided an estimate of the energy (% fat) expenditure between the transparent and pigmented puerulus stages. Future research on determining the condition of puerulus lobster should study the

puerulus stages separately to understand the energy requirements of puerulus at settlement.

In contrast to the observed puerulus condition, juvenile lobsters that were present on the oyster farm during 2001/2002 were in a better nutritional condition than juvenile recruits of 2002/2003. From our results there appears to be no relationship between puerulus condition and subsequent juvenile growth rate. Despite the higher nutritional condition of puerulus of the 2002/2003 recruitment, subsequent juvenile growth during this period was lower compared to that of juveniles during 2001/2002, implying that the relatively high puerulus condition recorded in 2002/2003 did not enhance subsequent juvenile growth rates. Therefore other factors such as the food available to early juveniles governed juvenile growth at Lüderitz Bay during 2002/2003.

The monthly growth increments of early juveniles increased with size and nutritional condition at Lüderitz during our study. The nutritional condition of juveniles was significantly correlated with growth during both 2001/2002 and 2002/2003 suggesting that the growth rate and nutritional condition of juveniles may have been determined by the nutritional value of the food items juveniles consumed. The smaller growth increments and lower nutritional condition observed for juveniles of 2002/2003 were particularly evident for juveniles in the size classes between 12.1 and 20mm CL compared to the growth increments of similar sized juveniles of 2001/2002. The nutritional condition was however similar for juveniles less than 12mm CL in size for both the 2001/2002 and 2002/2003-recruitment periods, suggesting that they may have been still dependent on energy reserves built up before metamorphosis.

Juveniles of less than 11.0mm CL (1st-3rd instar) in size collected at Lüderitz oyster farm during 1999 showed slightly larger increments (1.7mm CL per month) (Grobler and Ndjaula, 2001) than similar sized juveniles that recruited during our study (1.3mm CL).

The growth rate of juvenile lobsters smaller than 20mm in carapace length in Lüderitz Bay during the present study was relatively high (2.87mm CL per month) compared to

the juvenile growth rate measured at shallow reefs off Lüderitz (1.08mm CL per month) during 1993/1994 (Grobler and Noli-Pearl, 1997). This implies that the bay at Lüderitz may possibly be a more productive habitat than juvenile nursery areas outside the bay. The growth rates measured for early juveniles (<20mm CL) in Table Bay in 1971-72 (2.65mm CL per moult) and 1996-97 (2.02mm CL per moult) during the studies by Pollock (1973) and Hazell *et al.* (2002), were closer to those recorded in the present study.¹ The average SST at Lüderitz Bay during our study was considerably colder (13.3°C) than that recorded in Table Bay (16°C) during the study of Hazell *et al.* (2001), suggesting that the high growth rates at Lüderitz Bay were due to food availability. Although no measurements of food availability were made, the shallow waters at the head of Lüderitz lagoon are clearly highly productive and with abundant zooplankton usually visible in the water column.

Validity of nutritional condition indices

A modest but significant correlation between the percentage fat and weight-length (K) indices of nutritional condition proved both methods to be efficient in determining the condition of puerulus lobster collected at Lüderitz during 2002. Although the percentage fat and K indices were not significantly correlated for juveniles that recruited at Lüderitz during 2002, both indices reflected the same time of peak juvenile condition. The K index was less variable than the % fat index for puerulus and juveniles. The time series of the % fat data is limited as samples for this analysis were only collected from mid-2002 to the beginning of 2003. The weight-length data was available from August 2001 to April 2003.

The carapace length of pueruli remains constant throughout the puerulus stage during which there are no changes in the morphometric dimension but only a change in pigmentation and weight. This was reflected in the poor relationship between carapace length and condition (K) of puerulus collected from bags during the present study. Weight-to length ratio (K) as a measure of condition has been criticised though for not

¹ Our study did not directly investigate the effect of sea surface temperature on juvenile growth and moulting, therefore we were not able to establish an inter-moult growth increment-SST relationship as was

taking the error in the shell length of crustaceans into account (Robertson *et al.*, 2000). Grobler and Ndjaula (2001) cautioned that the use of weight could be biased due to the internal retention of water, especially in pueruli of spiny lobster, *J. lalandii*. Similarly Robertson *et al.* (2000) suggested that the true measure of body weight was masked by the internal retention of water during the moulting and secondary lecithotrophic consumption of energy stored internally during the previous feeding stages of early benthic *P. argus*. The modest 65% correlation between the K and % fat condition indices for pueruli in the present study may be explained by the biased K condition index due to internal water retention.

The % fat and K condition indices were not significantly correlated for juvenile lobster (29%), but reflected the same time for peak nutritional condition, and showed similar variation. The error in carapace dimension mentioned above may be responsible for the low correlation between the K and % fat indices of nutritional condition of juveniles in the present study.

Cockcroft (1997) found the percentage lipid content of the hepatopancreas to be a reliable predictive indicator of growth in adult male *J. lalandii* lobster but this probably would not be a practical or cost effective method for predicting the growth increment of puerulus and post-pueruli of *J. lalandii* for commercial culture or for re-stocking and enhancement programs due to the small size of the animals (and the size of the hepatopancreas).

The % fat index of nutritional condition appears to be as reliable as the K condition index for detecting the reduction in internal reserves from the late stage larvae to puerulus and puerulus to juvenile stage. For rapid, quantitative and practical measurements of puerulus and juvenile nutritional condition (required for mass culture purposes), the K condition factor is recommended, whereas the % fat condition index, (though more costly) is more appropriate for qualitative measures of early lobster condition, usually required for ecological studies.

done by Hazell *et al.* (2001) for juveniles in the wild at Table Bay, South Africa.

The condition of pueruli is pre-determined during the moult from the final stage phyllosoma to puerulus depending on the food available and time spend feeding to accumulate the minimum level of internal fat reserves (Jeffs *et al.*, 1999; Robertson *et al.*, 1999; Jeffs *et al.*, 2001). These internal energy reserves are used for swimming to settlement grounds, metamorphosis to the puerulus stage, and to ensure survival to and growth of the juvenile stage (Phillips and McWilliam, 1986). The weight-length condition index, K indicated that peak puerulus condition coincided with the peak puerulus settlement events during August 2001 to February 2003. The peak in % fat of puerulus also peaked during the months of peak puerulus settlement in 2002. It is a plausible hypothesis that food consumed by the late-stage larvae around the time of peak recruitment may possibly have been of high nutritional value resulting in higher percentage of energy stored internally (% fat) and subsequent high puerulus survival until settlement. In addition, it may be possible that stronger than average surface currents moving shoreward or Ekman transport (in combination with vertical migration of puerulus) during the peak recruitment season may have assisted in transporting puerulus so that less internal energy reserves were utilised for swimming (Phillips and McWilliam, 1986).

Nutritional condition reflects the amount of energy stored internally that is required for normal physiological functioning, growth and survival of animals to the next life cycle stage (Robertson, 2000). The percentage fat condition index was useful for comparing the nutritional condition of *J. lalandii* pueruli and the subsequent juvenile stage to detect the amount of internal energy reserves used during the moulting process. Our results indicate that internal energy reserves of pueruli upon settlement were 2% higher than that of the subsequent juvenile stages. Many of the juveniles used in the nutritional condition analysis in the present study, were 2nd and 3rd moults during which they start feeding on food items at the nursery grounds. It is possible that energy from food consumed by juveniles are directly utilised in the normal physiological functioning during the juvenile stages and that little energy is stored internally. Grobler and Ndjaula (2001) suggested that the growth of 1st instar juveniles was very low due to the energy requirements of

producing a new shell and morphometric change. Subsequent 2nd and 3rd moult staged juveniles also exhibit very low growth increments of less than 17% of carapace length. Second moult stage juveniles (<10mm CL) had low internal energy reserves compared to puerulus and showed very small growth increments, suggesting that internal lipids were primarily used for morphometric changes rather than for growth. In addition, the higher lipid content of pueruli in the present study could be due to phyllosoma feeding on food with higher lipid content compared to food available to juveniles at the nursery grounds.

4.3 Spatial variation in puerulus settlement and juvenile abundance: habitat requirements

Variation between oyster farm structures

Transparent puerulus showed no preference for settling on exposed, sheltered or centre areas of oyster rafts on the Lüderitz oyster farm. Puerulus and early juvenile lobster (<30mm CL) are asocial solitary animals (e.g. *P. argus* (Butler, 2000), *J. edwardsii* (MacDiarmid, 2000) and *P. japonicus* (Yoshimura, 2000)) that do not aggregate in groups. This asocial behaviour of early benthic lobster probably also occurs in *J. lalandii* (Hazell *et al.*, 2001) and possibly played a role in the random distribution of transparent puerulus across the oyster farm at Lüderitz during our study. Transparent puerulus are still in the swimming phase at the time they reach the oyster farm, and would move through the farm until they find suitable substrate upon which to settle.

Variation between collector sites

Puerulus settlement rates were higher at the Griffith Bay and satellite collector sites, which were structurally more complex habitats than the Lagoon 2 and Nest Hotel collector sites, and thus provided relatively more shelter for young lobsters. The benthic biota at Griffith Bay is characteristic of rocky outcrops in Lüderitz Bay comprising of seaweeds, soft corals and mussels similar to that on oyster farm structures. The Nest Hotel, first and second lagoon collector sites were situated in the vicinity of the lagoon channel where the benthic structure is characterised by muddy and sandy bottoms with little or no seaweed and algal cover. Structurally the habitat at these sites provided little

shelter from predators and incoming swell, thus making them unsuitable puerulus recruitment sites.

Physical conditions at the Nest Hotel and second lagoon collector sites were more challenging for puerulus due to the high degree of exposure to swell conditions, which may have deterred puerulus from becoming resident at this site. The first lagoon site was situated just inside Radford Bay, which provided relative protection from wave action. Sampling frequency at this site was very low and therefore settlement rates could not be compared with settlement rates at other sites with sandy and muddy benthic substrate. The Griffith and Radford subsidiary bays are more sheltered from wave action and incoming swell, possibly resulting in the higher recruitment of puerulus at the Griffith Bay and satellite collector sites.

A high abundance of *J. lalandii* juveniles was observed on the rocky crevices and oyster farming structures close to the Griffith Bay and the satellite collectors, respectively during the present study. However juvenile abundance on the collectors themselves was very low compared to puerulus abundance, and to juvenile abundance in the surrounding natural habitat (*personal observation*) and oyster farm structures. Most juveniles collected from the Griffith Bay and satellite collectors were in the first and second moult stages suggesting that the juveniles migrated to the surrounding crevices soon after moulting to the second juvenile stage. The abundance of juveniles in the natural habitat at Griffith bay was not quantified and collector data at this site is limited. High puerulus settlement rates have been observed at sites with high juvenile abundance for some palinurid species (Phillips and Booth, 1994). Research on *J. lalandii* juvenile abundance in natural habitats needs to be initiated and research on puerulus settlement on collectors at Lüderitz Bay needs to be extended over a longer period to establish whether high abundance of conspecifics in the surrounding natural habitat enhances puerulus settlement at a collector site.

The circulation patterns of minor currents, and thus the transporting mechanism of *J. lalandii* puerulus into Lüderitz Bay is not known. Therefore it is not possible to speculate

on the relationship between the position Griffith Bay and satellite sites in relation to incoming currents into the bay and high puerulus settlement at these sites. It is important to establish whether collector sites positioned close to circulated currents in the bay experience higher puerulus settlement than sites further away in future since such knowledge will be valuable for selecting puerulus collection sites for the harvesting of animals for lobster aquaculture.

Collector efficiency

Booth crevice collectors proved to be efficient in collecting puerulus of *J. lalandii* at Lüderitz Bay during the present study suggesting that this type of collector provided an adequate habitat for puerulus. The booth collectors successfully detected the seasonal pattern in peak puerulus and juvenile abundance and the correlation of peak puerulus and juvenile abundance with all environmental factors, except for wind speed. Average puerulus catch rates in *J. lalandii* (18-20 puerulus per collector) during the peak settlement season in the present study were similar to catch rates for *J. edwardsii* (15-20 puerulus per collector) at Bicheno, Tasmania during peak settlement season (used as commercial puerulus harvesting site) using booth crevice collectors (Phillips *et al.*, 2003a). Unlike puerulus monitoring sites for *J. edwardsii* of Tasmania, the sites monitored during our study had low numbers of collectors, which were monitored over a short period of time (11 months) as this was an exploratory study. Our results thus suggest that the booth crevice collector is suitable for long-term monitoring of puerulus settlement sites at Lüderitz. Due to the short nature of the puerulus settlement data set for booth collectors the patterns in puerulus settlement and relationships with environmental factors need to be confirmed by deploying more collectors and monitoring them over a longer period.

The Hogshair collector attracted no pueruli but only larger juveniles of greater than 20mm carapace length. The composition of colonising organisms was not as diverse as that on oyster farm structures and booth collectors, which may have rendered the habitat provided by the Hogshair collector unsuitable for puerulus of *J. lalandii*. Structurally the Hogshair collector was not suitable for the physical conditions at Lüderitz Bay with all

collectors being destroyed by moderate wave action within a period of 2 months. The Hogshair collector frame that supported the sheets of fishing net was made of polythene piping, which collapsed during exposure to the physical conditions within Lüderitz Bay. The frame structure was probably not strong enough to support the net sheets, which became heavy with seaweed and invertebrates colonising the collector. The broken Hogshair collectors could not be repaired and were therefore replaced with new ones. The destruction and loss of collectors after every 2 months rendered the exercise costly and unsuccessful and therefore sampling was discontinued. The collector design may be improved by using a lighter material as the sheeting and a stronger type of piping such as copper piping for the supporting frame. This however may increase the cost of constructing the collector but is worth investigating. The Hogshair collector at the Lagoon 2 site remained for the longest period (6 months) but only collected juveniles. Perhaps with stronger collectors moored at the other sites, these collectors may have had enough time to condition properly with colonising organisms and provided adequate shelter for puerulus.

4.4 Implications for lobster fisheries management and aquaculture development

Implications for Namibian lobster fisheries management

In many countries puerulus settlement data is used for estimating future recruitment into the fishery and ultimately the lobster catch. Understanding the relationships between the different life history stages and the environment is important in predicting future stock biomass and catch of benthic invertebrates like spiny lobsters (Caputi *et al.*, 1995b, 1997; Cruz *et al.*, 2001; Gardner *et al.*, 2001).

We hypothesised that high puerulus recruitment was coincident with a high abundance of nutritionally fit late stage larvae one week earlier at the shelf-beak and weather conditions, which promoted the transport of pueruli inshore. Peak puerulus settlement during spring (August-September) in *J. lalandii* at Lüderitz Bay during the present study was related to strong upwelling and high productivity, which may have facilitated high food availability to the feeding late stage larvae. The environmental conditions experienced during the strong upwelling seasons in August-September at Lüderitz during the study were characterised by low SST, strong southerly winds and moderate sea swell conditions. Wind stress and SST are the most important of the three environmental factors associated with upwelling. A good year of puerulus settlement in 2000 was associated with very strong upwelling conditions with lower than average SST and stronger than average southerly winds. The intensity of these environmental factors was less pronounced during “poor years” of puerulus settlement in 2001 and 2002.

Tomalin (1993) suggested that the Lüderitz lobster population size, and ultimately catch, was regulated by the strength of puerulus recruitment, rather than density dependent factors during the sub-legal lobster stages. This hypothesis was based on his benthic ecology study where density dependent effects, such as food availability in the nearshore region, were not related to juvenile lobster densities, and showed no temporal variability, whereas juvenile density did. He attempted to link the lobster fishery CPUE to

environmental factors but found no significant correlation between CPUE and prevailing environmental factors during spring at 0-, 1-, and 6-year lags. There was however marginal evidence that high wind stress and high sea surface temperature recorded inshore during summer 6 years earlier was inversely related to CPUE recorded for the *J. lalandii* fishery at Lüderitz.

During our study peak puerulus settlement mainly occurred during spring months which was correlated with both low SST and strong southerly wind recorded within one week earlier - in seeming contradiction to Tomalin's theory that strong wind may reduce puerulus settlement. During our study the lowest puerulus settlement rates were experienced during summer when wind stress and SST was highest. Peak puerulus settlement in the present study is in synchrony with the months during which eggs hatch into larvae one year earlier, assuming a one-year larval cycle. The negative relationship observed between puerulus settlement with strong wind during summer may simply be because pueruli do not occur in high numbers during summer since it is not the season for peak puerulus settlement. There is no data available on puerulus settlement to provide an explanation for Tomalin's (1993) correlation, and further research will be required to determine what role summer winds play in juvenile lobster survival and subsequent recruitment into the fishery.

Establishing a relationship between the puerulus settlement data obtained during the present study and CPUE will only be possible in another three to four years from now when the lobster begin to recruit into the fishery. The inter-annual variability in puerulus settlement observed during the present study where a good puerulus settlement year in 2000 was followed by poor years in 2001 and 2002 may be reflected in CPUE 6 years on during the 2006 and 2007 fishing seasons. Based on our limited data set, it can be hypothesised that the recruitment of legal size lobsters into the fishery in 2006/2007 will be relatively high and that this will be followed by two relatively poor years of recruitment. However, a longer puerulus settlement and juvenile abundance data set, including their relationship with environmental factors will be required to construct a proper catch prediction model for the *J. lalandii* fishery.

The results of the spatial variation in puerulus settlement in the present study highlighted the importance of structurally complex habitat, and the shelter it provides to post-settled *J. lalandii*. The post-settlement stages of *J. lalandii* (animals < 50mm CL in size) and the processes that regulate the abundance of post-settled lobster is poorly understood in *J. lalandii* of Namibia. Post-settlement processes may disrupt the relationship between puerulus supply and adult population. Butler and Herrnkind (2000) suggested that juvenile abundance indices are more useful for stock prediction in cases where post-settlement processes disrupt the puerulus supply-adult population size relationship. However, our results yielded a significant relationship between the abundance of puerulus and juvenile lobster stages at time lags of one to eight weeks, which suggests that the puerulus grew into juveniles, which remained in the vicinity of the oyster farm. For the purposes of predictive fisheries management it would however be prudent to monitor both puerulus settlement and juvenile abundance of *J. lalandii* in Namibia. Understanding the post-settlement processes will also shed some light on the habitat and feeding requirements, predation and thus mortality of early stage lobster which are all important for designing restocking and enhancement programs (Cruz *et al.*, 1995; Butler and Herrnkind, 1997; Herrnkind *et al.*, 1997; Nonaka *et al.*, 2000; Butler *et al.*, 2001). In addition, juvenile abundance indices may provide immediate future catch predictions in a shorter time period than puerulus settlement indices (Caputi and Brown, 1993; Caputi *et al.*, 1995a, 1995b, 2003) especially in cases where long-term puerulus data sets are not available (e.g. South African and Namibian *J. lalandii* populations).

Implications of lobster harvest for aquaculture and juvenile recruitment

The average daily standing stock of puerulus and juvenile lobsters on the oyster farm was estimated for the period between November 1999 and July 2003 (Fig. 4.2). From the oyster production records it was calculated that an average of 14700 oyster bags and 450 crates were submerged from November 1999 to July 2003. Estimates of the puerulus and juvenile standing stocks on bags and crates were based on the daily puerulus and juvenile recruitment per bag and crate, averaged for each month extrapolated for the total number of oyster bags and crates. Lobster abundance data on bags was only available from August 2001 to February. Therefore the total lobster abundance (standing stock per day)

on bags and crates are only presented for this period. The total lobster standing stock from bags and crates combined for August 2001-February 2003 averaged 123 877 lobsters per day and ranged between 22 667 and 325 312 lobsters per day. The puerulus and juvenile standing stock on crates was highest during 1999–2000, and relatively lower during 2001 and 2002, but increased again in 2003 (Fig. 4.2). For the combined bag and crate data, the highest puerulus and juvenile standing stock was observed during the months of 2002 compared to relatively lower numbers recorded in 2001 and 2003.

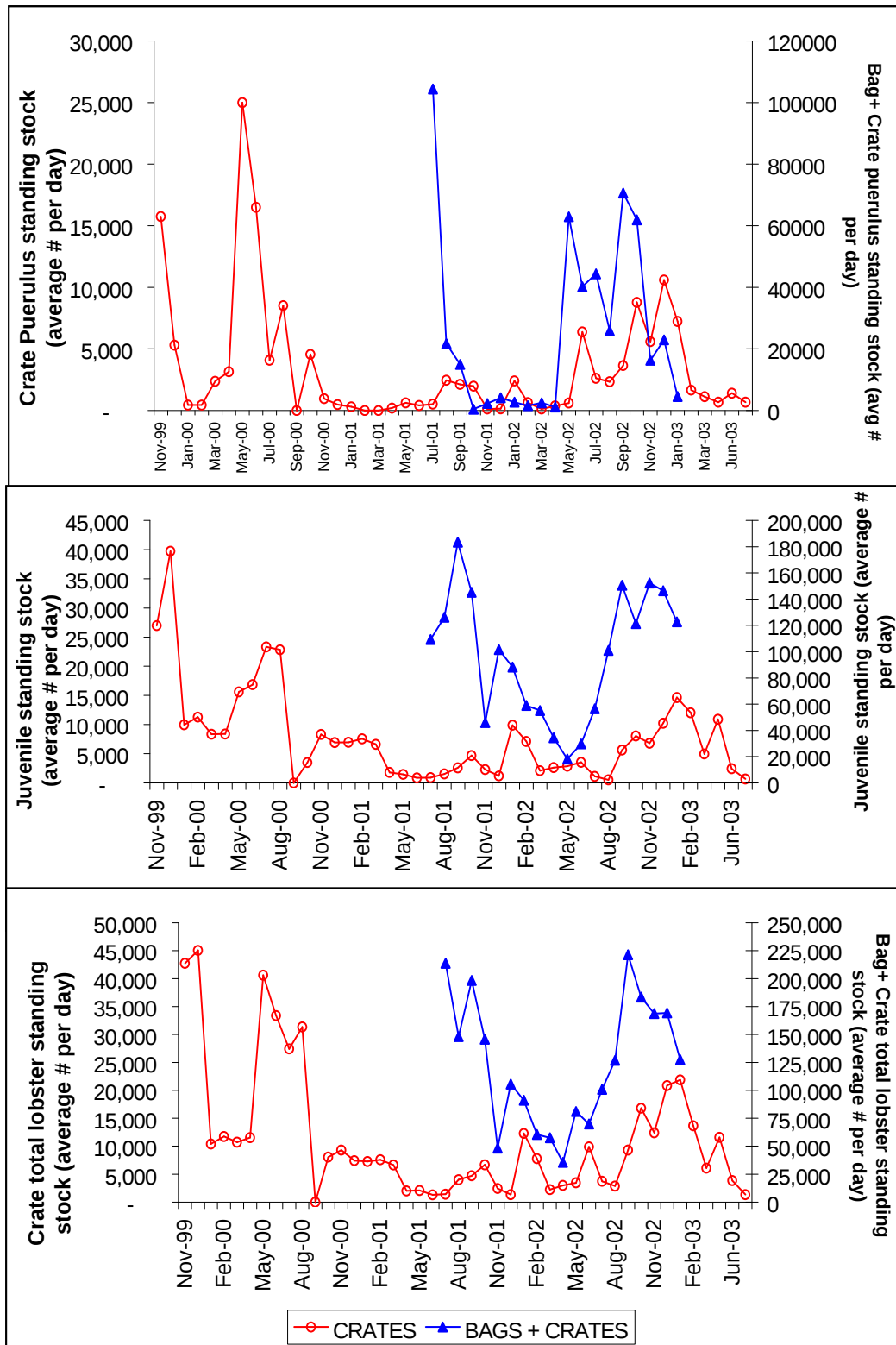


Figure 4.2. The standing stock of puerulus, juveniles and of total lobster (pueruli plus juveniles) on the oyster farm presented for oyster crates (November 1999 to July 2003) and for bags and crates combined (August 2001-February 2003).

The results of the study provide some insights into the potential effects of harvesting puerulus from the oyster farm on the recruitment of lobster into the *J. lalandii* fishery at Lüderitz Bay. Initially, fisheries managers assumed that the oyster farm at Lüderitz acted as a sink, where all puerulus and juvenile recruits on the farm structures were killed as a result of the monthly oyster sorting procedure. Lobsters in the oyster bags and crates do not survive the pressure hose cleaning process. However, it is clear from my data that there must have been a fairly rapid recolonisation of the cleaned bags that were replaced into the water, as newly settled puerulus and juvenile lobsters of up 38mm CL were usually present in the bags and crates. Based on the estimated growth rates of the juvenile lobsters, I calculate that the larger juveniles must have been present on farm structures for up to six to eight months. If the cleaning process killed all the lobsters in the bags and crates, and there was no recolonisation of juveniles, one would only expect to find recently settled puerulus and newly metamorphosed juveniles up to one month post-settlement in the bags and crates.

The data clearly show that on average there was substantial standing stock of puerulus and juveniles (123 877 lobster per day) present on the farm throughout the year ranging between 22 667 and 325 312 puerulus and juveniles per day depending on the time of year (Fig 4.2). I observed that when oyster bags and crates were removed from the water for cleaning, there were many juvenile and puerulus lobsters clinging to the outside, which escaped into the water column. Since it is clear that not all puerulus and juveniles perished during the oyster cleaning process, the oyster farm at Lüderitz may be acting as a nursery area and, contrary to the initial view that the farm was a mortality sink, it may be enhancing local lobster stocks. Juveniles became progressively less abundant as they approached 38mm CL, suggesting that they either migrated to areas which may be associated with their habitat requirements during this stage of their life cycle, or died. Further work will be required to estimate the emigration rate of lobsters off the farm and whether these lobsters enhance recruitment into the fishery.

Based on the assumption that lobsters migrate off the farm to potentially recruit into the fishery, it is important to evaluate the implications of harvesting the puerulus and juvenile standing stock more efficiently (than during oyster harvesting) for aquaculture growout. The farm supported an estimated average lobster standing stock of 123 877 lobster (puerulus and juvenile), ranging from 22 667 to 325 312 lobsters depending on season, that could be instantaneously harvested from the entire oyster farm for aquaculture growout. The potential average number of puerulus that could have been harvested per day was estimated to be 26 615 puerulus (range: 3 788- 72 968 puerulus per day). Instantaneous harvesting of the farm on a day during the peak puerulus season would potentially yield 66% more puerulus (44 210 puerulus) than the daily average puerulus standing stock (26 615) estimated from all months. The potential number of juveniles that could have been harvested on one day during the peak juvenile abundance season (129 090 juveniles per day) was estimated to be 33% more than the daily average numbers that for the entire observation period (97 262 juveniles per day).

From my data it was clear new puerulus continually settled on the farm and that juvenile lobsters rapidly re-colonised the cleaned bags, therefore year-round serial harvesting of the farm would potentially yield a bigger harvest of lobsters for aquaculture grow-out. Assuming that bags and crates are recolonised to the average levels recorded within a month, and lobster harvesting is undertaken monthly, the cumulative potential harvest can be calculated. Over my sampling period from August 2001 to February 2003, monthly harvest of lobsters from all bags and crates would have potentially yielded 2 035 388 lobsters (505 677 pueruli and 1.85 million juveniles).

Esterhuizen (2004) estimated that 500 000 pueruli are required for one commercial *J. lalandii* lobster farm to be economically viable by producing 50 tons of marketable size lobster within 5 years, assuming an 80% survival rate. Monthly harvesting of puerulus over the one-and-a-half year observation period at Lüderitz oyster farm could therefore have supplied sufficient seed for a 200t lobster production in puerulus ongrowing facilities. Taking the yearly variation in puerulus settlement into account, the potential puerulus seed supply at Lüderitz oyster farm for large-scale commercial puerulus

growout, is clearly limited. Other sites of high puerulus settlement therefore need to be identified before a commercially viable lobster aquaculture “industry” can be developed and sustained in Namibia.

Harvesting the entire potential puerulus and juvenile standing stock at Lüderitz oyster farm for aquaculture purposes means that these potential recruits are no longer available to the fishery. A policy decision will be required as to whether more efficient harvesting of lobster from the farm should be allowed. The effect of puerulus removal on the future catch of the *P. cygnus* wild fishery in Western Australia was estimated to be slight (Phillips *et al.*, 2003b). They calculated that the removal of 20 million puerulus (3.3% of the puerulus population), during a year when puerulus settlement was 600 million, would result in a 0.62% decrease in the future catch of *P. cygnus*. They surmised that the mortality of settling puerulus and juveniles is high and that this mortality has a stronger effect on the adult population size. From this example it appears that the harvesting puerulus and early juveniles would increase total lobster production since it is known that survival rates of 70-93% have been achieved in growout systems, compared to a maximum of 6 % survival in the wild (Crear *et al.*, 1998; for review see Booth and Kitakka, 2000).

Under the fisheries law of New Zealand puerulus harvesting is permitted as part of a quota trade off management strategy where a percentage of the *J. edwardsii* adult fishery quota is traded off for puerulus harvesting quota (Jeffs and Hooker, 2000). Generally 20 000 puerulus may be harvested in exchange for one ton of fishable lobster biomass. Puerulus harvesting estimates in the above examples were all based on maintaining the biological neutrality of the lobster population, which refers to the proportion of catch (TAC) forgone to compensate for the effect that puerulus harvesting for aquaculture has on the reproductive capacity of the breeding stock. The Biological neutrality strategy of sustainable puerulus harvesting considers the early life history stage indices (and their relationship with the environment), stock-recruitment relationships, and their effect on the fishery. Australia and New Zealand have collected long-term data sets of 20 to 30 years on the factors used in estimating the sustainable level of puerulus harvesting for

small-scale commercial growout. Addison (1997) highlighted possible factors that may bias the relationship between the factors used in estimating sustainable puerulus harvest and the implications for the fishery (e.g. bias abundance indices, artificial catch ceilings associated with bias quotas). A straight forward method of ensuring biological neutrality in puerulus harvesting operations for aquaculture through releasing a similar or higher number of juveniles than the number of pueruli that would have survived, one year after culture back into the wild to compensate for the puerulus removed (Gardener *et al.*, 2000). These well-researched *P. cygnus* (Australia) and *J. edwardsii* (New Zealand and Tasmania) fisheries may provide a template for the management of the *J. lalandii* fishery in the presence of puerulus removal for aquaculture in the distant future. At present knowledge on the relationship between puerulus and juvenile abundance, environmental factors, spawning stock and recruitment is insufficient to estimate the effect of puerulus removal for aquaculture on the *J. lalandii* fishery.

If puerulus removal in *J. lalandii* for aquaculture is allowed in the near future, it should be conducted on an experimental scale or small commercial scale until the potential effects on recruitment into the fishery are clearer.

REFERENCES

Addison, J.T. 1997 – Lobster stock assessment: report from a workshop; I. *Mar. Freshw. Res.* **48**: 941-944.

Anon 2001 – The South African West Coast rock lobster fishery: A review. *Anchor Environmental Consultants compilation*, Rondebosch, Cape Town, University of Cape Town: 14pp.

Bailey, G.W. 1979 – Physical and chemical aspects of the Benguela current in the Lüderitz region. M.Sc. thesis, University of Cape Town: 125pp.

Balchen, J.G. 1993 - Lobster ranching in coastal waters. In *Coastal Ocean Space Utilization III*. (Eds) Croce, N.D., Connel, S. and R. Abel. London. E & FN SPON.

Beal, B. F., Mercer, J. P. and A. O’Conghaile 2002 - Survival and growth of hatchery-reared individuals of the European lobster, *Homarus gammarus* (L.), in field-based nursery cages on the Irish West Coast. *Aquaculture* **210** (2002): 137–157.

Bell, K.N.I. 2000 – Introduction to circular and periodic variables, their statistics, and periodic regression. J.L.B. Smith Institute of Ichthyology, Grahamstown: 39 pp.

Bermudes, M. 2000 – Effects of photoperiod on survival, growth, feeding and cannibalism in early developmental stages of *Jasus edwardsii* phyllosoma larvae. In *Technical Potential for Rock Lobster Propagation in Aquaculture systems*. (Eds) Hart, P.R. and R. van Barneveld. Rock Lobster Enhancement and Aquaculture Subprogram Publication 3: 46-47.

Bhattacharya, C.G. 1967 – A simple method of resolution of a distribution into gaussian components. *Biometrics* **23**: 115-135.

Booth, J.D. 1979 – Settlement of the rock lobster, *Jasus edwardsii* (Decapoda: Palinuridae), at Castlepoint, New Zealand. *N. Z. J. Mar. Freshw. Res.* **13** (3): 395-406.

Booth, J.D. 1992 – Harvesting juvenile spiny lobster for aquaculture. *Lobster Newslett.* **5**(2): 4-5.

Booth, J.D. 2001 – Habitat preferences and behaviour of newly settled *Jasus edwardsii* (Palinuridae). *Mar. Freshw Res.* **52**: 1055-1065.

Booth, J.D. and J. Kittaka 1994 – Grow out of juvenile spiny lobster. In *Spiny Lobster Management*. (Eds) Phillips, B.F., Cobb, J.S. and J. Kittaka. Oxford, UK, Fishing News Books, Blackwell Scientific Publications: 424-445.

Booth, J.D. and J. Kittaka 2000 – Spiny lobster growout. In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillip, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 556-585.

Booth, J.D., Foreman, J.S., Strotter, D.R., Bradford, E., Renwick, J. and S.M. Chiswell 1999 – Recruitment of the red rock lobster, *Jasus edwardsii*, with management implications. *New Zealand Fisheries Assessment Research Document* **99**(10): 102pp.

Booth, J.D., Foreman, J.S., Strotter, D.R., and E. Bradford 2001a – Settlement indices for 1999 and 1999-2000 juvenile of the red rock lobster *Jasus edwardsii*. *New Zealand Fisheries Assessment Report*. **2001**(28): 34pp.

Booth, J.D., Strotter, D.R., Foreman, J.S. and E. Bradford 2001b – Juvenile abundance both mirrors and masks a settlement pulse of the rock lobster *Jasus edwardsii* (Palinuridae). *Mar. Freshw. Res.* **52**: 1067-1075.

Butler, M. 2000 – Recruitment of Caribbean spiny lobster in a dynamic nursery. P2-4 In: *Workshop on Post-settlement Processes Affecting the Southern Rock Lobster, *Jasus edwardsii*, in Southern Australia* (Eds) Frusher, S., Prescott, J., Hobday, D. and C. Gardner. University of Tasmania, Tasmanian Aquaculture and Fisheries Institute Report **10**: 28pp.

Butler, M.J. and W.F. Herrnkind 1997 – A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) population in Florida. *Can. J. Fish. Aquat. Sci.* **54**: 452-463.

Butler IV, M.J. and W.F. Herrnkind 2000 – Puerulus and juvenile ecology. In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillips, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 276-301.

Butler IV, M.J., Dolan, T., Herrnkind, and J. Hunt 2001 – Modelling the effect of spatial variation in postlarval supply and habitat structure on recruitment of Caribbean spiny lobster. *Mar. Freshw. Res.* **52**: 1243-52.

Campillo-Cambell, C. and A. Gordoia 2004 – Physical and biological variability in the Namibian upwelling system: October 1997 – October 2001. *Deep Sea Research Part II; Topical Studies in Oceanography*. **51** (1-3): 147-158.

Caputi, N. and R.S. Brown 1993 – The effect of environment on puerulus settlement of the western rock lobster (*Panulirus cygnus*) in Western Australia. *Fish. Oceangr.* **2**: 1-10.

Caputi, N., Brown, R.S. and B.F. Phillips 1995a – Prediction of catches of the western rock lobster (*Panulirus cygnus*) based on indices of puerulus and juvenile abundance. *ICES Mar. Sci. Symp.* 199: 287-293.

Caputi, N., Chubb, C.F. and R.S. Brown 1995b – Relationship between spawning stock, environment, recruitment and fishing effort for the western rock lobster, *Panulirus cygnus*, fishery in Western Australia. *Crustaceana* **68**: 213-226.

Caputi, N., Chubb, C.F., Hall, N. and A. Pearce 1997 - Relationship between different life history stages of the western rock lobster, *Panulirus cygnus*, and their implications for management. In *Developing and Sustaining World Fisheries Resources: The State of Science and Management*. (Eds) Hancock, D.A., Smith, D.C., A. and J.P. Beumer. The Second World Fisheries Conference: 579-585.

Caputi, N., Chubb, C.F. and A. Pearce 2001 – Environmental effects on recruitment of the western rock lobster, *Panulirus cygnus*. *Mar. Freshw. Res.* **52**: 1167-1174.

Caputi, N., Chubb, C.F., Melville-Smith, R., Pearce, A. and D. Griffin 2003 – Review of relationships between life history stages of the western rock lobster, *Panulirus cygnus*, in Western Australia. *Fish. Res.* **65**: 47-61.

Chen, L-C. 1990 – *Aquaculture in Taiwan*. Oxford, Fishing News Books, Blackwell Scientific Publications: 273pp.

Chittleborough, R.G. 1974a – Review of prospects for rearing rock lobsters. *Aust. Fish.* **April**: 4-8.

Chittleborough, R.G. 1974b – Western rock lobster reared to maturity. *Aust. J. Mar. Freshw. Res.* **25**: 221-225.

Chittleborough, R.G. 1975 – Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). *Aust. J. Mar. Freshw. Res.* **26**: 177-196.

Chittleborough, R.G. 1976 – Breeding of *Palinurus longipes cygnus* George under natural and controlled conditions. *Aust. J. Mar. Freshw. Res.* **27**: 499-516.

Cobb, J.S., Castro, K., Wahle, R.A. and J. Catena 1998 – An artificial reef for lobsters (*Homarus americanus*) in Rhode Island, USA. In Proceedings of a Workshop on Lobster Stock Enhancement held in the Magdalen Islands (Québec) from October 2- to 31, 1997. *Can. Ind. Rep. Fish. Aqua. Sci.* **244**: 75-78.

Cockcroft, A. 1997 – Biochemical composition as a growth predictor in male west coast rock lobster (*Jasus lalandii*). *Mar. Freshw. Res.* **48**: 845-856.

Cockcroft, A.C. and A.I.L. Payne 1999 – A cautious fisheries management policy in South Africa: the fisheries for rock lobster. *Mar. Policy.* **23** (6): 587-600.

Crear, B.J. 2000 - Report on study tour to New Zealand and the United States, Hawkes Bay Aquaculture, Napier, New Zealand. In *Technical Potential for Rock Lobster Propagation in Aquaculture systems*. (Eds) Hart, P.R. and R. van Barneveld. Rock Lobster Enhancement and Aquaculture Subprogram Publication **3**: 81.

Crear, B., Mills, D., Ritar, A., Thomas, C. and P. Hart 1998 – Rock lobster (*Jasus edwardsii*) aquaculture: annual report 1997/1998. *Tasmanian Aquaculture and Fisheries Institute Internal Report*, 1998.

Crear, B.J., Thomas, C.W., Hart, P.R. and C.G. Carter 2000 – Growth of juvenile southern rock lobsters, *Jasus edwardsii*, is influenced by diet, temperature, whilst survival is influenced by diet and tank environment. *Aquaculture* **190** (2000): 169-182.

Cruywagen, G.C. 1999 – On the survivorship and historical growth of the South African Cape rock lobster. *S. Afri. J. Mar. Sci.* **21**: 279-288.

Cruz, R. and B.F. Phillips 2000 – The artificial shelters (pesqueros) used for the spiny lobster (*Panulirus argus*) fisheries in Cuba. In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillip, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 400-419.

Cruz, R., Díaz, E., Báez, M. and R. Adriano 2001 – Variability in recruitment of multiple life stages of the Caribbean spiny lobster, *Panulirus argus*, in the Gulf of Batabanó, Cuba. *Mar. Freshw. Res.* **52**: 1263-70.

Cruz, R., León, M.E. and R. Puga 1995 – Prediction of commercial catches of the spiny lobster *Panulirus argus* in the Gulf of Batabanó. *Crustaceana* **68**: 238-244.

Dennis, D.M, Pitcher, C.R. and T.D. Skewes 2001 – Distribution and transport pathways of *Panulirus ornatus* spp. Larvae in the Coral Sea, Australia. *Mar. Freshw. Res.* **52**: 1175-1185.

Eggleston, D.B., Lipcius, R.N. and J.J. Grover 1997 – Predator and shelter-size effects on coral reef fish and spiny lobster prey. *Mar. Ecol. Prog. Ser.* **149**: 43-59.

Eggleston, D.B., Lipcius, R.N., Miller, D.L. and L. Cobá-Cetina 1990 – Shelter scaling regulates survival of Caribbean spiny lobster, *Panulirus argus*. *Mar. Ecol. Prog. Ser.* **62**: 70-88.

Esterhuizen, J.A. 2004 – Towards the development of a protocol for rearing juvenile rock lobster, *Jasus lalandii*. M.Sc. thesis, Rhodes University, South Africa: v + 103pp.

FAO Fisheries Stock Assessment Tools II version 1.0.0 for windows (FISAT II version 1.0.0). Web Address (URL) <http://www.fao.org/fi/statist/fisoft/fisat/index.htm>

FAO 2003 - Statistical databases. Fishery Statistics. The global site for statistics of production, consumption, trade, fleets etc. Web Address (URL) <http://apps.fao.org>.

Gardner, C., Frusher, S.D., Kennedy, R.B. and A. Cawthorn 2001 – Relationship between settlement of southern rock lobster pueruli, *Jasus edwardsii*, and recruitment to the fishery in Tasmania, Australia. *Mar. Freshw. Res.* **52**: 1271-1275.

Gardner, C., Mills, D., Ibbott, Wilcox, S and B. Crear 2000 – Preliminary investigation towards ongrowing puerulus to enhance rock lobster stocks while providing animals for commercial culture. *Fish. Res. Rep. - FRDC Project 1999/314 June 2000*: 57pp.

Grobler, C.A.F. and H.O.N. Ndjaula 2001 – Namibian *Jasus lalandii* recruitment: size, weight and growth of pueruli and early juveniles. *Mar. Freshw. Res.* **52**: 1271-1281.

Grobler, C.A.F. and K. R. Noli-Peard 1997 - *Jasus lalandii* fishery in post-independence Namibia: monitoring population trends and stock recovery in relation to a variable environment. *Mar. Freshw. Res.* **48**: 1015-1022.

Guzmán-Del Prío, S.A., Carrilo-Laguna, J., Belmar-Pérez, J., De le Campa, S. and A.B. Villa 1996 - The puerulus settlement of red spiny lobster (*Panulirus interruptus*) in Bahía California, Mexico. *Crustaceana* **69**(8): 949-957.

Hardman-Mountford, N.J., Richardson, A.J., Agenbag, J.J., Hagen, E., Nykjaer, L., Shillington, F.A. and C. Villacastin 2003 – Ocean climate of the South East Atlantic observed from satellite data and wind models. *Prog. Oceanogr.* **59**: 181-221.

Hazell, R.W.A, Cockcroft, A.C., Mayfield, S. and M. Noffke 2001 – Factors influencing the growth rate of juvenile rock lobsters, *Jasus lalandii*. *Mar. Freshw. Res.* **52**: 1367-1373.

Hazell, R.W.A., D. S. Schoeman and M. Noffke (2002). Do fluctuations in the somatic growth rate of rock lobster encompass all size classes? A re-assessment of juvenile growth of *Jasus lalandii*. *Fish. Bull.* **100**: 510-518.

Herrnkind, W. F. and M. J. Butler IV 1986 – Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. *Mar. Ecol. Prog. Ser.* **34**: 23-30.

Herrnkind, W. F., M. J. Butler IV and J.H. Hunt 1997 – Can artificial habitats that mimic natural structures enhance recruitment of Caribbean spiny lobster? *Fisheries* **22**(4): 24-27.

Heydorn, A.E.F. 1969 – The rock lobster of the South African West Coast *Jasus lalandii* (H. Milne-Edwards). 2. Population studies, behaviour, reproduction, moulting, growth and migration. *Investl. Rep. Div. Sea. Fish. S. Afr.* **71**: 52pp.

Hilborn, R. and C. J. Walters 1992 – *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. New York; Chapman & Hall: xv + 570 pp.

Igarashi, M.A. and J. Kittaka 2000 – Water quality and microflora in the culture water of phyllosomas. In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillips, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 533-555.

Illingworth, J. and J. McDermott 1997 – Rock lobster ongrowing and enhancement using wild caught pueruli. *Aquaculture Update*, **Summer 1997**: 7-8.

Ioue, N. and H. Sekiguchi 2001 – Distribution of late-stage phyllosoma of *Panulirus japonicus* in the Kuroshio Subgyre. *Mar. Freshw. Res.* **52**: 1201-1209.

James, P.J. 1998 – Rock lobster, *Jasus edwardsii* (Hutton), growth on opened versus unopened cultured mussel, *Mytilus galloprovincialis* (Lamarck). *Aquac. Res.* **29**: 535-537.

Jeffs, A. 2003 – The potential for crayfish aquaculture in Northland. *NIWA client report*. **April**: 19pp.

Jeffs, A. and S. Hooker 2000 - Economic feasibility of aquaculture of spiny lobsters *Jasus edwardsii* in temperate waters. *J. World Aquac. Soc.* **31**(1): 30-41.

Jeffs, A. and P.J. James 2000 – Cage culture of lobster *Jasus edwardsii* in New Zealand. *Aquaculture update* **25**: 5-6.

Jeffs, A., Chiswell, S.M. and J.D. Booth 2001 – Distribution and condition of pueruli of the spiny lobster *Jasus edwardsii* offshore from north-east New Zealand. *Mar. Freshw. Res.* **52**: 1211-1216.

Jeffs, A.G., Willmott, M.E. and R.M.G. Wells 1999 – The use of energy stores in the puerulus of the spiny lobster *Jasus edwardsii* across the continental shelf of New Zealand. *Comp. Biochem. Physiol.* **123**(4): 351-357.

Johnston, J. and J. DiNardo 1997 – *Econometric methods*. 4th ed. McGraw-Hill Publishers, New York, 531pp.

Kittaka, J. 1988 – Culture of the palinurid *Jasus lalandii* from egg stage to puerulus. *Nippon Suisan Gakkaishi*. **54**(1): 87-93.

Kittaka, J. 1997 – Application of ecosystem culture method for complete development of phyllosomas of spiny lobster. *Aquaculture* **155** (1-4): 319-331.

Kittaka, J. 2000 – Culture of larval spiny lobster. In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillips, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 508-532.

Kittaka, J. and F.A. Abrunhosa 1997 – Characteristics of palinurids (Decapoda; Crustacea) in larval culture. *Hydrobiologia* **358**: 305-311.

Kittaka, J. and J.D. Booth 1994 – Prospectus for aquaculture. In *Spiny lobster management*. (Eds) Phillips, B.F., Cobb, J.S. and J. Kittaka. Oxford, U.K. Fishing News Books, Blackwell Scientific Publications: 365-373.

Kittaka, J., Iwai, M. and M. Yoshimura 1988 – Culture of a hybrid spiny lobster genus *Jasus* from egg stage to puerulus. *Bulletin of Japanese Society of Science and Fisheries*, **54**(3): 413-417.

Lazarus, B.I. 1967 – The occurrence of phyllosoma larvae off the Cape, with particular reference to *J. lalandii*. *Investl. Rep. Div. Sea. Fish. S. Afr.* **63**: 38pp.

Lee , D. O’C. and J.F. Wickens 1992. *Crustacean Farming*. 1st ed. Blackwell Scientific Publications, Oxford, 392 pp.

Lellis, W.A. 1992 – A standard reference diet for crustacean nutrition research VI response of postlarval stages of the Caribbean king crab *Mithrax spinosissimus* and the spiny lobster *Panulirus argus*. *J. World Aquacult. Soc.* **23**(1): 1-7.

Lellis, W.A. and J.A. Russel 1990 – Effect of temperature on the survival, growth and feed intake of postlarval spiny lobsters, *Panulirus argus*. *Aquaculture* **90**: 1-9.

Lemmens, J.W.T.J. 1994 – Biochemical evidence for absence of feeding in puerulus larvae of the western rock lobster (*Panulirus cygnus*; Decapoda: Palinuridae). *Mar. Biol (Berlin)* **118**: 383-391.

Lipcius, R.N. and D.B. Eggleston. 2000 – Ecology and fishery biology of spiny lobster. p1-41 In: *Spiny Lobsters: Fisheries and Culture*. (Eds) Phillips, B.F and J. Kittaka. Oxford, Fishing News Books, Blackwell Science Publications: p1-41.

Lovatelli, A. 1990 – Regional seafarming development and demonstration project. *Regional Seafarming Resources Atlas*, FAO/UNDP RAS/86/024. January 1990, FAO, Rome, Italy: 83 pp.

Lozano-Alvarez, E. 1996 - Ongrowing of juvenile spiny lobsters, *Panulirus argus* (Latreille, 1804) (Decapoda, Palinuridae) in portable sea enclosures. *Crustaceana* **69**: 958-972.

MacDiarmid, A. 2000 – Enhanced ecology of *Jasus edwardsii*. In *Workshop on Post-settlement Processes Affecting the Southern Rock Lobster, Jasus edwardsii*, in *Southern Australia*. TAFI, University of Tasmania: 4-5.

MacDiarmid, A. and J. Kittaka 2000 – Breeding. In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillips, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 485-507.

Matsuda, H. 2000 – Phyllosoma rearing of the Japanese spiny lobster, *P. japonicus*, using small rearing vessels. In: *Technical Potential for Rock Lobster Propagation in Aquaculture Systems*. (Eds) Hart, P.R. and R. van Barneveld. Rock Lobster Enhancement and Aquaculture Subprogram **Publication No. 3**: 33-34.

McWilliam, P.S. and B.F. Phillips 1997 – Metamorphosis of the final phyllosoma and secondary lecithotrophy in the puerulus of *Panulirus cygnus* George: a review. *Mar. Freshw. Res.* **48**: 783-790.

Melville-Smith, R., Thompson, A.W. and N. Caputi 2004 – Improved forecasts of recreational western rock lobster (*Panulirus cygnus*) catches in Western Australia, by predicting licence usage. *Fish. Res.* **68**: 203-208.

Mikami, S. 2000 – Investigation of the gut system; Applications for lobster aquaculture. In *Technical Potential for Rock Lobster Propagation in Aquaculture Systems*. (Eds) Hart, P.R. and R. van Barneveld. Rock Lobster Enhancement and Aquaculture Subprogram **Publication No. 3**: 50.

Mikami, S., Greenwood, J.G. and F. Takashima 1994 – Functional morphology and cytology of the phyllosomal digestive system of *Ibacus ciliatus* and *Panulirus japonicus* (Decapoda, Scyllaridae and Palinuridae). *Crustaceana* **67**(2): 212-225.

Ndjaula, H.O.N. 2004 – Fecundity, maturity and determination of reproductive potential of rock lobster *Jasus lalandii* in Namibian waters: Implications for stock recovery. M.Phil. thesis, University of Bergen, Norway: 123pp.

Nonaka, M., Fushimi, H. and T. Yamakawa 2000 – The spiny lobster fishery in Japan and restocking In *Spiny Lobsters Fisheries and Culture*. (Eds) Phillips, B.F. and J. Kittaka. Oxford, UK. Fishing News Books, Blackwell Scientific Publications: 221-242.

Pearce, A.F. and B.F. Phillips 1994 – Oceanic processes, puerulus settlement and recruitment of the western rock lobster *Panulirus cygnus*. In: *The Bio-physics of Marine Larval Dispersal*. (Eds) Sammarco, P.W. and M.L. Heron. American geophysics union, Washington. Coastal and Estuarine Studies **45**: 279-302.

Penrith, M-L and B.F. Kensley 1970 – The constitution of the intertidal fauna of rocky shores of South West Africa. Part I Lüderitzbucht. *Cimbebasia*. **1970**: 191-214.

Phillips, B.F. and J.D. Booth 1994 – Design, use and effectiveness of collectors for catching the puerulus stage of spiny lobsters. *Rev. Fish. Sci.* **2**(3): 255-289.

Phillips, B.F. and P.S. McWilliam 1986 – The pelagic phase of spiny lobster development. *Can. J. Fish. Aquat. Sci.* **43**: 2153-2163.

Phillips, B.F. and A.F. Pearce 1997 – Spiny lobster recruitment off western Australia. *Bull. Mar. Sci.* **61**(1): 21-41.

Phillips, B.F., Cruz, R., Brown, R.S. and N. Caputi 1994 – Predicting the catch of spiny lobster fisheries. In *Spiny Lobster Management*. (Eds) Phillips, B.F., Cobb, J.S. and J. Kittaka. Cambridge, MA. Blackwell Scientific Publications: 285-301.

Phillips, B.F., Cruz, R., Caputi, N. and R.S. Brown 2000a – Predicting the catch of spiny lobster fisheries. In *Spiny Lobsters Fisheries and Culture*. Phillips, B.F. and J. Kittaka (Eds.). Oxford, Blackwell Scientific Publications: 357–375.

Phillips, B.F., Pearce, A.F., Litchfield, R. and S. Guzman del Proo 2000b – Spiny lobster catches and the ocean environment. In *Spiny Lobsters Fisheries and Culture*. (Eds.) Phillips, B.F. and J. Kittaka. Oxford, Blackwell Scientific Publications: 321–333.

Phillips, B.F., Melville-Smith, R. and Y.W. Cheng 2003b – Estimating the effects of removing *Panulirus cygnus* pueruli on the fishery stock. *Fish. Res.* **65**: 89-101.

Phillips, B.F., Melville-Smith, R., Rossbach, M., Cheng, Y.W., Caputi, N., Thompson, A.W., Mills, D. and B. Crear 2003a – Towards establishing techniques for large scale harvesting of pueruli and obtaining a better understanding of mortality rates. *Fish. Res. Rep. - FRDC Project 1998/302* **144**: 140pp.

Pollock, D.E 1973 - Growth of juvenile rock lobster *J. lalandii*. *Investl. Rep. Sea. Fish. Brch. S. Afr.* **106**: 16 pp.

Pollock, D. E. 1986 – Review of the fishery for and biology of the Cape rock lobster *Jasus lalandii* with notes on larval recruitment. *Can. J. Fish. Aquat. Sci.* **43**: 2107-2117.

Pollock, D.E 1987 – Simulation models of rock-lobster populations from areas of widely divergent yields on the Cape west coast. In *The Benguela and Comparable Ecosystems*. (Eds) Payne, A.I.L., Gulland, J.A. and K. H. Brink. *S. Afr. J. Mar. Sci.* **5**: 531-545.

Pollock, D.E. 1989 – Spiny lobsters. In *Oceans of life off Southern Africa*. (Eds) Payne, A.I.L. and R.J.M. Crawford. CapeTown; Vlaeberg: 70-80.

Pollock, D.E. 1990 – Palaeoceanography and speciation in the spiny lobster genus *Jasus*. *Bull. Mar. Sci.* **46**(2): 387-405.

Pollock, D.E and P.C. Goosen 1991 – Reproductive dynamics of two *Jasus* species in the South Atlantic Region. *S. Afr. J. Mar. Sci.* **10**: 141-147.

Rahman, M.K. and B. Srikrishnadhas 1994 – The potential for spiny lobster culture in India. *INFOFISH International* **1/94**: 51.

Ritar, A.J. 2000 – Propagation of southern rock lobster (*Jasus edwardsii*) in Tasmania. In *Technical potential for Rock Lobster Propagation in Aquaculture systems*. (Eds) Hart, P.R. and R. van Barneveld. Rock Lobster Enhancement and Aquaculture Subprogram **Publication No. 3**: 42-45.

Robertson, D.N., Butler, M.J. and F.C. Dobbs 2000 – An evaluation of lipid- and morphometric-based indices of nutritional condition for early benthic stage spiny lobsters, *Panulirus argus*. *Mar. Freshw. Phys.***33**: 161-171.

Shannon, L.V. 1985 – The Benguela ecosystem part I. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Annu. Rev.* **23**: 105-182

Shannon, L.V. and M.J. O'Toole 1998 - *Integrated Overview of the Oceanography and Environmental Variability of the Benguela Current Region*: Thematic Report No: 2, Synthesis and Assessment of Information on BCLME: October 1998, UNDP, Windhoek, Namibia: 58pp.

Shelton, P.A., Boyd, A.J. and M.J. Armstrong 1985 – The influence of large-scale environmental processes on neritic fish populations in the Benguela current system. CalCOFI Rep. **XXVI**

Shioda, K., Igarashi, M.A. and J. Kittaka 1997 – Control of water quality in the culture of early stage phyllosomas of *Panulirus japonicus*. *Bull. Mar. Sci.* **61** (1): 177-189.

Tomalin, B.J. 1993 – Migrations of spiny rock-lobsters, *Jasus lalandii*, at Lüderitz: Environmental causes, and effects on the fishery and benthic ecology. M.Sc. Thesis, University of Cape Town, Cape Town: 95pp.

Tong, L.J. 1993 – Rock lobster larval culture. *Aquaculture Update*. **Spring/Summer 1993/1994**: 3-4.

Tong, L.J. and G.A. Moss 2000 – Summary of the work done in New Zealand at NIWA Mahanga Bay, on rock lobster (*Jasus edwardsii* and *Jasus verreauxi*). In *Technical potential for Rock Lobster Propagation in Aquaculture systems*. (Eds) Hart, P.R. and R. van Barneveld. Rock Lobster Enhancement and Aquaculture Subprogram **Publication No. 3**: 21-29.

Wickens, J.F and D.O'C. Lee 2002 – *Crustacean farming ranching and culture*. 2nd ed. Oxford, UK. Blackwell Scientific Publications: 446pp.

Yeung, C., Jones, D.L., Criales, M.M., Jackson, T. L. and W.J. Richards 2001 – Influence of coastal eddies and counter-currents on the influx of spiny lobster, *Panulirus argus*, postlarvae into Florida Bay. *Mar. Freshw. Res.* **52**: 1217-1232.

Yoshimura, T. 2000 – An experimental approach to post-settlement processes of *P. japonicus* using artificial structures. In *Workshop on Post-settlement Processes Affecting the Southern Rock Lobster, Jasus edwardsii, in Southern Australia*. TAFI, University of Tasmania: 4-5.

APPENDIX 1

The relationship between the morphometric dimensions, weight (wt in g) and carapace length (CL in mm) and their relationship with the nutritional condition index, K of puerulus and juvenile lobsters that recruited during the 2001/2002 and 2002/2003 recruitment events. The non-linear and linear regression equations (according to the best fit) are presented with the R^2 correlation statistic indicating the significance of these models.

