# BIOLOGY AND ECOLOGY OF THE DEEP-WATER ROCK LOBSTERS *PALINURUS GILCHRISTI* AND *PALINURUS DELAGOAE* IN RELATION TO THEIR FISHERIES

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# DECLARATION

This thesis documents original research which has not previously been submitted in whole or in part for any degree at any other university. Much of the information presented here is original, and all other sources are fully acknowledged and referenced. All uncited interpretations are my own, and I bear their full responsibility.

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J.C. Groeneveld
15-11-2000

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# ABSTRACT

Recent declines in the biomass of the closely-related deep-water rock lobsters *Palinurus gilchristi* and *P. delagoae* off South Africa suggest that both these resources are currently overfished, and that the existing management procedures are inadequate. A lack of detailed fisheries, biological and ecological knowledge is partly to blame, as this deficiency limits the scope and utility of resource assessments, and impairs the capacity of managers to formulate species-specific management strategies.

This thesis aimed to expand the biological and ecological bases on which effective resource assessment rests, and to recommend methods to improve the management of these deep-water rock lobster populations. The steps taken were: (1) determination and interspecies comparison of biological parameters, including spatial and temporal size composition trends, somatic growth rates, size at sexual maturity, female fecundity, mortality rates, moulting, recruitment and migration; (2) assessment of the effect of fishing with different gear types or arrays on abundance and its indices; and (3) incorporation of new information into resource assessments, with recommendations aiming to improve the management of the fisheries.

Research on deep-water rock lobster populations is complex, as *in situ* visual observations without the use of expensive submersibles / ROVs is not feasible. Methods used here were developed or adapted from known procedures, ultimately including dedicated observer-based surveys and field experiments, and a long-term tag-recapture project coupled to aquarium and laboratory studies. General linear models (GLMs) were successfully used to elucidate population characteristics relative to combinations of physical gradients, and to establish standardized abundance indices for management purposes.

Both species grow at similarly slow rates consistent with their deep cold-water habitats. However, two growth regimes existed for *P. gilchristi* - relatively fast growth in the region between the Agulhas Bank and Port Elizabeth and relatively slower growth at Port Alfred, where average carapace length (CL), size of attainment of sexual maturity and female fecundity were also smaller. No spatial disparity in growth rates or size at sexual maturity occurred in *P. delagoae*, although average CL varied with depth and latitude.

Pleopod and tag-recapture indices, developed to determine the moult state and moulting season of *P. gilchristi*, both indicated a peak moulting season in early summer (November and December), but that the moulting season is size-dependent, with individuals with a CL < 70 mm commencing in October and those with a CL > 70 mm moulting from November onwards.

An experimental fishery to determine the potential of exploiting *P. delagoae* using traps was conducted annually over a 4-year period. The experiment consisted of systematic grid surveys followed by commercial fishing phases, and showed a depth-related recruitment pattern. Juveniles settle in deep water (> 400 m) and then gradually migrate inshore, effectively separating the juvenile and adult populations. Results showed that trap-fishing in combination with the traditional multi-species trawl-fishery would not be sustainable on a commercial scale. This is because high fishing mortality rates of juvenile and small adult lobsters caused by both gear types in deeper (>350 m) water resulted in the adult population becoming vulnerable to trap-fishing, indicated by a rapid decline in measured abundance.

An effort-reduction experiment was designed to explore the theory that increased fishing effort in recent years has biased the abundance index (a GLM-standardized CPUE series) for *P. gilchristi* downwards because of effort-saturation. Hypotheses based on the effort – CPUE relationship in several area-season combinations of reduced and increased effort produced no support for effort saturation. Hence it was concluded that the decline in the abundance index of this species accurately reflects a decrease in biomass.

Tag-recapture information showed that juveniles of both species migrate long distances along-shore, counter to the direction of the prevailing south-west flowing Agulhas Current. An eastward migration pathway for *P. gilchristi* originates at Cape Agulhas (where a population of post-settlement juveniles occurs), follows the shelf-edge, and culminates in one of two regions, either the eastern Agulhas Bank (after 2 years) or Mossel Bay - Port Elizabeth (after covering a straight-line distance of 800 km over 3 years). The migration pathway stops short of Port Alfred (the eastern-most site), and based on this information and dichotomous growth, size at maturity, average CL and female fecundity, two separate sub-populations are proposed for *P. gilchristi* - one at Port Alfred and the other between Cape Agulhas and Port Elizabeth. Juvenile *P. delagoae* migrate north-eastwards along-shore, also against the prevailing current. For both species, migrations appear to be an adaptation to counter displacement of the adult populations by downstream dispersal of pelagic phyllosoma larvae.

In conclusion, recommendations made in this thesis for the management of the fishery for *P. delagoae* have resulted in trap-fishing being curtailed, and effort-limited trawl-fishing being allowed to continue. Recommendations for the *P. gilchristi* fishery include a closed fishing season over the peak moulting period and a reduction in fishing effort – both these strategies are currently being implemented. The possible occurrence of two sub-populations of *P. gilchristi* needs to be further investigated in a genetic study, as two populations with contrasting production rates may require separate management strategies.

# Chapter 1

# Introduction

Two spiny-lobster species of the genus *Palinurus* are the subject of this thesis; *Palinurus gilchristi*, first described by Stebbing (1900) from False Bay (Western Cape, South Africa) and *P. delagoae*, described by Barnard (1926) from the region around Delagoa Bay (Mozambique). Both occur in the southern hemisphere only, and are restricted to the South-West Indian Ocean. *P. gilchristi* is a continental species, and is endemic to the deeper shelf regions along the southern coast of South Africa. *P. delagoae* is more widespread, including a continental population along the deep outer edge of the shelf of eastern South Africa and southern Mozambique, and insular populations off the southern coast of Madagascar and at isolated submerged points along the Madagascar Ridge to the south of this island. Both species support substantial commercial fisheries and are well-known on international markets. However, comparatively little is known about the biology and ecology of either species, or in fact, of the genus *Palinurus* in general. It is the purpose of this introductory chapter to summarise the available knowledge of *P. gilchristi* and *P. delagoae*, within the context of the genus and the family. Furthermore, the objectives of this thesis are stated, and a preview of the issues addressed in each chapter is provided.

## 1.1. Palinurid systematics

The decapod crustacean family Palinuridae comprises 49 species (Phillips *et al.*, 1980), which are grouped into eight genera, based on differences in four major morphological characteristics: relative size and disposition of the supraorbital processes; the elevation of the eyestalks; the structure of the pleopod on the second abdominal segment of the female; and the general shape of the carapace (George and Main, 1967; Holthuis, 1991; Lipcius and Cobb, 1994). George and Main (1967) have placed six genera, *Palinurus,* *Panulirus, Linuparus, Justitia, Puerulus* and *Palinustus,* in a group of spiny lobsters known as the Stridentes (sound producers that possess a stridulatory apparatus), whereas two, *Jasus* and *Projasus,* are placed in a separate group, the Silentes (lacking a sound-producing stridulatory apparatus). Despite the fact that the two lineages, Stridentes and Silentes, apparently evolved independently from each other during the course of hundreds of millions of years, extant species within these two groups share a large number of characteristics, in terms of morphology, behaviour and certain life history patterns (Pollock, 1995).

The genus *Palinurus* has a fossil record dating to the Cretaceous (Glaessner, 1969) including some fossil remains from the Miocene and others probably dating from the Oligocene and Eocene. George and Main (1967) considered that later, towards the close of the Pliocene epoch, a deeper-water *Palinurus*-type ancestor gave rise to a shallower-water genus, *Panulirus*. The ancestral *Palinurus* remained in deeper water and its modern descendants are considered to exhibit more primitive characteristics than the genus *Panulirus.*

## 1.2 Fisheries background

Palinurid lobsters sustain major commercial fisheries world-wide, as well as supporting small-scale fisheries in remote coastal locations and islands (Lipcius and Cobb, 1994). The world catch of palinurids is ~ 75 000 t per year (Lipcius and Egglestone, 2000); by mass, most of this consists of *Panulirus* lobsters (~ 73 %), with *Jasus* and *Palinurus* species respectively accounting for roughly 19 % and 8 % of the total.

Fisheries for *Panulirus* lobsters are distributed throughout the tropical and subtropical regions of the world, including the Caribbean (Cuba, Brazil and Florida), north-west and east Africa, the Indian subcontinent, western Australia, north-eastern Australia and Indonesia, Japan and the Hawaiian archipelago, and the west coast of north and central America (Lipcius and Cobb, 1994). *Jasus* is restricted to temperate waters in the southern hemisphere, where it supports commercial fisheries along the coasts of south-western Africa, southern Australia and New Zealand, and at remote islands and submerged seamounts in the south Atlantic, Indo-Pacific and south-west Pacific regions (Lipcius and Cobb, 1994).

The genus *Palinurus* consists of five extant species which all support commercial fisheries in moderately deep water (10 – 600 m) in temperate regions. The southern hemisphere species *P. gilchristi* and *P. delagoae,* occur along the southern and south-eastern African coast, from False Bay in South Africa (~ 18°20' E) to central Mozambique (17° S), and are fished by South African, Mozambican and Japanese fishing vessels (Holthuis, 1991; Palha de Sousa, 1992). The northern hemisphere species, *P. elephas*, *P. charlestoni* and *P. mauritanicus,* are restricted to the north-eastern Atlantic, from southern Norway (62° N) and the United Kingdom to the Cape Verde Islands and southern Senegal (14° N), and to the Mediterranean (Ansell and Robb, 1977; Holthuis, 1991; Ceccaldi and Latrouite, 1994; Hunter *et al.*, 1996). Fishers from France, Portugal, Spain, Ireland, England, Wales and Corsica all exploit these species (Ceccaldi and Latrouite, 1994).

The commercial fisheries for the *Palinurus* lobsters have much in common: high product value; diminishing catches (Ceccaldi and Latrouite, 1994; Groeneveld and Cockcroft, 1997); multi-national fishing fleets; multiple gear types; unreliable fisheries information and ineffective management strategies. The ineffective management of these fisheries is related to the distribution of the stocks in deep offshore waters and across international boundaries, and to the participation in the fisheries of a multitude of vessels from different countries. The diversity of data from various gear types further impedes the collection of biological information necessary for resource assessments. The gear includes traps and trawl nets off south-east Africa, and traps (pots), trammel and tangle nets in the northern Atlantic and Mediterranean (Holthuis, 1991). The selective impacts of the various fishing methods and types of gear have been noted by Hepper (1977) and Hunter *et al.* (1996). Also, as a result of their diverse origins, fisheries data are fragmented and not always reliable (Ceccaldi and Latrouite, 1994).

*P. delagoae* is typical of the lobsters of this group. It is distributed across an international boundary, occurs in deep water (100 – 600 m), has supported trap-fisheries and trawl-fisheries in Mozambique and off South Africa, and is characterised by a scarcity of biological and fisheries data. The trap and trawl fisheries target different depth zones, and impact on different (though related) components of the *P. delagoae* population (Cockcroft *et al.*, 1995). Catches of this species have plummeted on most fishing grounds since 1994 (Groeneveld and Cockcroft, 1997).

*P. gilchristi* is confined to areas within the South African exclusive fishing zone, where foreign lobster fishing vessels are prohibited (Pollock and Augustyn, 1982; Stander, 1991). It occurs only on rocky substrata between 50 and 200 m deep, but its distribution along the outer edge of the continental shelf, up to 250 km offshore on the Agulhas Bank off the southern Cape coast, gives the trap-fishery for this species a deep-water character. Existing fisheries management procedures include annual stock assessments and a total allowable catch. However, despite restricted local participation, issues surrounding fishing behaviour have thus far complicated attempts at management, which is reflected in steadily declining catch rates. Furthermore, a lack of knowledge of the basic biology and ecology of *P. gilchristi* has contributed to uncertainty about stock assessments.

### 1.3 Research up to 1995

Biological research on *P. gilchristi* and *P. delagoae* off South Africa and Mozambique is complicated by the deep-water nature of their fisheries. Research on lobsters in deep water cannot rely on diving surveys, or on *in situ* visual observations. Fisheries research vessels operating off southern Africa are, furthermore, not rigged to operate long-line trap-fishing gear. Researchers are therefore largely dependent on the commercial fisheries for information, and most sampling is conducted by on-board observers on ships of convenience. A drawback of this method of sampling is that time-series data at distinct locations are difficult to obtain because vessels move around continuously. Hire of commercial fishing vessels for dedicated field experiments is prohibitively expensive, and regular large samples of animals are difficult to obtain because of the high unit prices of spiny lobsters.

Despite these difficulties, researchers from South Africa did manage to document several aspects of the fisheries and biology of *P. delagoae* in the 25 years between 1969 and 1994. The earliest literature on *P. delagoae* off southern Africa (Berry, 1969; Berry and Heydorn, 1970) described the occurrence of an external spermatophoric mass, and suggested an external fertilization mechanism. Berry (1971a) described the geographical distribution of *P. delagoae* (then thought to be two varieties of *P. gilchristi*, namely var. *natalensis* and var. *delagoae*). He also provided insights into the biology and trawl fisheries for this species (Berry, 1972; 1973). It was not until 1973, however, that Berry and Plante (1973) revised the genus *Palinurus* in the south-west Indian Ocean, raising *P. delagoae* to specific rank. More recently, Groeneveld and Melville-Smith (1995) and Fennessy and Groeneveld (1997) described trends in catches and catch rates from South African and Mozambican trawl fishing grounds for the 1987 – 1993 period.

Past research on *P. delagoae* in Mozambique has focussed on its distribution, densities and aggregation behaviour (Koyama, 1971; Berth *et al.*, 1984), reproduction (Kondritskiy, 1976), basic biology (Brinca and Palha de Sousa, 1983; 1984), and stock assessment (Palha de Sousa, 1992). Except for a single report on an experimental fishery in Madagascar (Roullot, 1988), little is known of *P. delagoae* in that region.

Prior to 1973, *P. gilchristi* was considered to be rare (Berry, 1971a). The discovery of commercially viable densities in 1973 and the development of the fishery between 1974 and 1980 were first described by Pollock and Augustyn (1982). These authors showed that size composition depended on area, and that average lobster size declined during the first years of fishing. They also provided basic measures of growth, maturity, and fecundity. Stander (1991) and Pollock (1994) reviewed the management of the fishery, for the periods 1974 to 1991 and 1984 to 1991 respectively. Groeneveld and Melville-Smith (1994) related size at sexual maturity to area, and Groeneveld and Rossouw (1995) found that breeding periods were size dependent, and restricted to the austral autumn, winter and spring.

## 1.4 Stock assessment and management

Although the initial phases of the fishery for *P. gilchristi* were regulated only by limiting the number of traps permitted per vessel, an annual total allowable catch (TAC) was eventually introduced in 1984 and trap limitations were abolished in 1988. The TAC was initially based primarily on the performance of the fishery in preceding years, and remained stable at approximately 1025 t whole mass per year until 1993. A more rigorous stock assessment procedure was developed in 1994, using a Bayesian approach to fit a surplus production model to commercial catch and effort data (Butterworth *et al.*, 1994a; 1994b) with later model improvements also incorporating growth parameters from a long-term tagging programme and catch-at-size information. Both CPUE trends and the surplus production model have indicated a continuous decline in resource biomass since 1989. In response, a programme of phased TAC reductions was initiated in 1994/95.

In contrast to the catch-control strategy utilised in the fishery for *P. gilchristi*, an effort-control strategy is used to manage the multispecies crustacean trawl fishery off eastern South Africa; this fishery produced all the catches of *P. delagoae* in South African waters up to 1993. Eight fishing vessels have been permitted onto the trawling grounds, and their annual catches of *P. delagoae,* prawns, langoustines, crabs and fish have fluctuated greatly, but are currently much lower than prior to 1990 (Berry, 1972; Groeneveld and Melville-Smith, 1995). No formal annual stock assessments are performed for this fishery.

The apparent declines in the biomass of both species under consideration suggest that the resources are currently being overfished, and that the existing management procedures are inadequate. Various explanations can be given for the failure of management in these cases, i.e., insufficient biological information, sparse data (particularly at the start of exploitation), limited manpower and ineffective enforcement of regulations. Crucial among these is a lack of detailed biological and ecological knowledge about *P. gilchristi* and *P. delagoae*, resulting not only in inadequacies of data to be used in resource assessments, but also in interpretation of these results and findings. This thesis is dedicated to overcoming this problem, by broadening the biological and ecological bases on which effective assessment and management rest.

### 1.5 Contents of this study

This chapter sets the background against which the study was undertaken. Chapter 2 reviews the commercial trap and trawl fisheries for *P. gilchristi* and *P. delagoae* in more detail, focussing on its origin and early history, the development of fishing gear and markets, and trends in effort and catches, up to the latter half of the 1990s. Chapter 3 compares length-mass relationships between the two species.

*P. delagoae* is the focal point of Chapters 4 to 6. Chapter 4 describes the methodology, and results after four years, of a large-scale trapping experiment developed to determine the relative abundance and potential of *P. delagoae* for a trap-fishery in South African waters. Chapter 5 addresses the recruitment of juveniles to the adult population, and migration patterns relative to physical gradients of depth, latitude and the width of the continental slope. In Chapter 6, growth rates, size at sexual maturity and natural mortality rates are estimated, and used as input parameters in a deterministic length-based cohort analysis to assess the impacts of the trap and trawl fisheries on the resource. The results of the model, together with economic and ecological criteria, are used to suggest the most appropriate fishing method for this species in South African waters.

Chapters 7 to 10 are dedicated to the biology and fisheries ecology of *P. gilchristi.* In Chapter 7, spatial variation in somatic growth and fecundity are investigated, followed by a discussion of the likely causes of gradients and the implications thereof to managers. Chapter 8 concentrates on the development of seasonal moulting-indices based on pleopod cuticular development, tag-recapture information and shell-condition. Moulting seasons are defined relative to lobster size and relevant management options are discussed. In Chapter 9, long-term tagging data and spatial variations in size composition and sex ratios are used to investigate migration along the south coast of South Africa. The implications of a long-distance migration pattern relative to recruitment and stock separation is highlighted. Chapter 10 describes a field experiment specifically designed to investigate whether effort-saturation can be implicated in the decline seen in the relative abundance index of this species. The scale and complexity of this experiment required the cooperation of scientists of various disciplines and organisations, as well as the financial and operational goodwill of the South Coast Rock Lobster Association.

This thesis is concluded by integrating the newly obtained biological and fisheries ecological information into a management plan for the future sustainable use of the *P. delagoae* and *P. gilchristi* resources.

# Chapter 2

# A review of the commercial fisheries for *P. delagoae* and *P. gilchristi* in the South -West Indian Ocean

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## 2.1. Introduction

The commercial fisheries for *P. delagoae* and *P. gilchristi* are restricted to the continental shelf of southern and south-eastern Africa, between Cape Point (18° 20' E) in the west and central Mozambique (17° S) in the north-east (Berry, 1971a; Pollock and Augustyn, 1982; Brinca and Palha de Sousa, 1983; Palha de Sousa, 1992, 1998; Pollock *et al.*, 2000). The fisheries for these two species do not overlap geographically, and separate fleets are used for their exploitation. *P. gilchristi* is fished along the outside edge of the Agulhas Bank (up to 200 km offshore of Cape Agulhas), and along the South African south coast between Danger Point (19° E) and East London (28° E), at depths of 50 – 200 m (Fig. 2.1). *P delagoae* is fished patchily on suitable bottom types between depths of 100 and 600 m, northwards from 31° S (south of Durban) up to central Mozambique (17°S) (Fig. 2.1). *P. gilchristi* occurs on rocky substrata only, and is fished exclusively with traps, whereas *P. delagoae* occurs on rocky as well as trawlable softer substrata, and is fished with traps and with trawls.

The trawl fisheries for *P. delagoae* are complex, as they additionally exploit various crustacean, fish and cephalopod species. They are further complicated by the participation of a multi-national fishing fleet off Mozambique. Whereas *P. gilchristi* occurs entirely within South African waters, and is managed nationally, *P. delagoae* straddles the border between South Africa and Mozambique, and is managed according to two completely separate management strategies.

This chapter is broadly descriptive, and reviews the history of the commercial fisheries for *P. delagoae* and *P. gilchristi* as a background to the main body of the thesis.

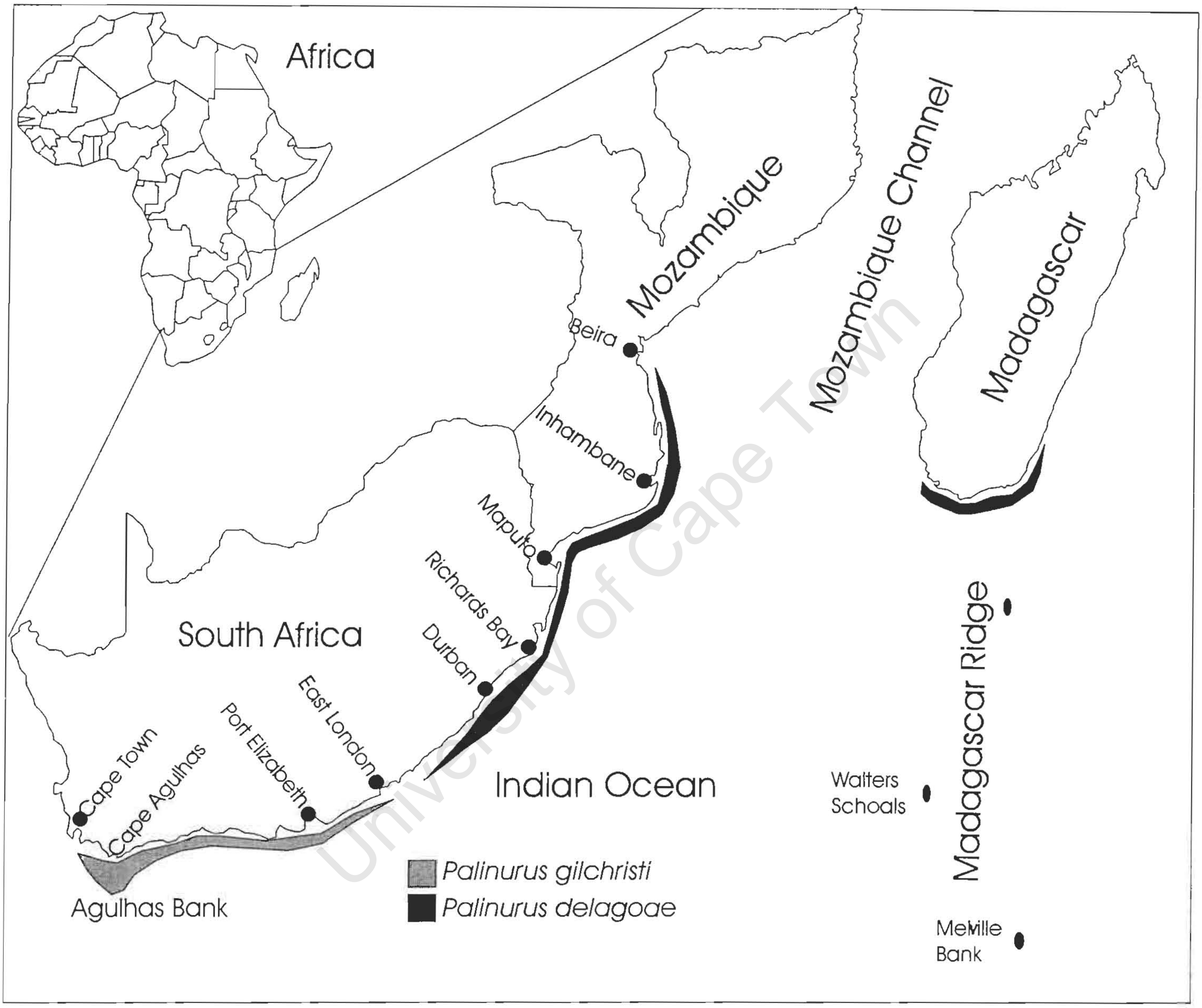

Figure 2.1: The distribution of *P.gilchristi* along the southern coast of South Africa and of *P.delagoae* along the South African east coast, Mozambique, southern Madagascar and the Madagascar Ridge.

## 2.2. The trap and trawl fisheries for *P. delagoae* off South Africa and Mozambique

### *2.2.1. Trawl fisheries – South Africa*

Exploratory trawling by the S.S. "Pickle" in 1920 first revealed the existence of large quantities of *P. delagoae* (then considered to be a variety of *P. gilchristi*; Berry and Plante, 1973) off the Kwazulu-Natal coast (Gilchrist, 1920). The "Pickle" found *P. delagoae* to be distributed over ~ 600 miles$^2$ of trawlable ground, sometimes in great abundance. Gilchrist (1920) cites a catch of over 10 000 lobsters taken in a 1.5 hour drag by the trawler "John C. Meickle" in what must have been one of the first commercial catches of this species ever made, and later records of jackpot catches noted in the literature up to 1970 include a catch of five tons made in a single drag by the "David Davies" in 1969 (Berry, 1972) and two drags of four and five tons each, made on consecutive days by a Japanese vessel fishing south of Durban in 1970 (Koyama, 1971).

Jackpot catches gradually became rare, and after the 1960s the lobster-directed trawl fishery progressively diversified to catch other species. This multi-species fishery targets deep-water knife prawns *Haliporoides triarthrus,* red prawns *Aristaeomorpha foliaceae*, langoustines *Metanephrops mozambicus* and *Nephropsis stewartii*, red crabs *Chaceon macphersoni* and several species of fish and cephalopods, as well as *P. delagoae* (Fennessy and Groeneveld, 1997). The species mixture is achieved by trawling on a variety of substrata at different depth intervals between 100 and 600 m, with species availability and product value determining the fishing strategy (Groeneveld & Melville-Smith, 1995).

Information on the catches of *P. delagoae* and other crustaceans by the trawl fishery is sketchy for the period between 1961 and 1970, and completely absent for the period between 1971 and 1984. A report of a commission of enquiry into the fishing industry (cited by Berry, 1972) show that annual catches during the 1960s were 300 t (in 1961), 200 t (in 1962, 1964 and 1965 respectively), and 100 t (in 1963, 1966, 1969 and 1970 respectively). The report does not distinguish between catches made in South Africa or in Mozambique, and furthermore admits that all the catches made during the period were not declared. Information on fishing effort was not provided.

Catch and effort data from the South African trawling grounds are reliable for the period 1985 – 1994 (Table 2.1), during which all the trawlers fishing off Kwazulu-Natal belonged to a single compliant fishing company. Annual yields from that period fluctuated between 59.9 t and 13.7 t, taken in 1986 and 1990 respectively. The smaller lobster catches made in 1990 were as a result of lower fishing effort on the offshore (100 – 600 m) fishing grounds during that year, when some vessels diverted to inshore (< 100 m) fishing grounds to take advantage of a temporary high abundance of penaeid prawns (pers. comm., J. Walsh, Spray Fishing). Catch records are incomplete for the 1995 – 1999 period (Table 2.1) as a result of some fishing vessels failing to return catch statistics.

Interpretation of the trawl catch rates of *P. delagoae* is complicated by the multi-species nature of the fishery. The complication arises from the inclusion in the lobster CPUE data series, of lobster catch rates resulting from trawls directed at prawns or langoustines. These data frequently originate from depths (or substrates) with low lobster densities, and yield catch rates much lower than those in the optimal depth range of 200 - 400 m for *P. delagoae.* Mean catch rates per depth interval (± SD) are 8.4 ± 5.8 kg whole mass per hour trawled in the 200 - 300 m depth interval, 2.0 ±1.8 kg (300 - 400 m), 1.0 ± 0.6 kg (400 - 500 m) and 1.3 ± 1.8 kg (500 - 600 m) (Groeneveld and Melville-Smith, 1995). Effort targeted at *P. delagoae* in the 200 - 400 m depth range increased nearly threefold between 1991 and 1993 (1408 hrs in 1991; 3169 hrs in 1992; 2943 hrs in 1993) leading to substantial increases in catches (Table 2.1) and catch rates (4 kg/hr in 1991, 9 kg/hr in 1992 and 8 kg/hr in 1993). The concentration of effort in the 200 – 400 m depth interval in 1992 – 1993 was a likely precipitated by reduced availability of knife prawns in depth intervals > 400 m in 1992, and reduced catches of shallow water prawns (*Penaeus* spp.) on the Tugela Bank in 1993 (Groeneveld and Melville-Smith, 1995).

Table 2.1: Information on catches of *P. delagoae* in the trap and trawl fisheries of South Africa and Mozambique.

| Year | South Africa | | | | Mozambique |
|---|---|---|---|---|---|
| | Trawl fishery | | Trap fishery | | Trap and trawl fisheries |
| | Catches (t) | Boats (n) | Catches (t) | Boats (n) | Catches (t) ** |
| 1985 | 27.2 | 3 | | | No data |
| 1986 | 59.9 | 4 | | | No data |
| 1987 | 36.8 | 5 | | | 224 |
| 1988 | 30.5 | 6 | | | 231 |
| 1989 | 16.3 | 7 | | | 167 |
| 1990 | 13.7 | 4 | | | 207 |
| 1991 | 22.2 | 5 | | | 341 |
| 1992 | 37.3 | 5 | | | 156 |
| 1993 | 37.8 | 5 | | | 443 |
| 1994 | 24.4 | 4 | 89.5 | 3 | 261 |
| 1995 | 13* | 2 | 50.0 | 2 | 179 |
| 1996 | 10* | 4 | 39.5 | 2 | 132 |
| 1997 | 10* | 4 | 7.4 | 1 | 156 |
| 1998 | 11* | 4 | | | No data |
| 1999 | 12* | 4 | | | No data |

* Does not include catches of all vessels

** Mozambique registered catches; not all catches were declared (Anon., 1998).

The highest seasonal trawl catch rates for *P. delagoae* off South Africa occur in April to September; this coincides with the formation of breeding or moulting aggregations on trawlable substrata (Koyama, 1971; Berry, 1973).

The trawl fishery operates on a year-round basis (except for an inshore component which targets penaeid prawns in depths < 100 m), and is managed by controlling the number of vessel permits; only eight permits, all to South African registered vessels, are issued per year. There are no minimum size limits applied to *P. delagoae* caught by the trawl fishery, neither are there regulations to prohibit the capture of egg-bearing females.

### *2.2.2. Trawl fisheries – Mozambique*

A deep-water trawl fishery with a multi-species character similar to the South African trawl fishery has been active in Mozambique since at least 1960 (Palha de Sousa, 1998). In addition to its multi-species nature, the Mozambican trawl-fishery has been exploited by, among others, vessels of South African, Spanish, Russian and German origin (Berth *et al.* 1984; Torstensen and Pacule, 1992). Much of the catches made by these vessels has gone undeclared, and no accurate estimates of catches and CPUEs of *P. delagoae* by this fishery are available. Saetre and Silva (1979), cited in Palha de Sousa (1998), provide an isolated record of 77 tons for 1977, and Palha de Sousa (1998) estimates catches in more recent years to have been ~ 60 tons / year.

### *2.2.3. Trap-fisheries – Mozambique and Madagascar*

A long-line trap-fishery directed at *P. delagoae* in Mozambican waters commenced in 1980, and rapidly developed to cover extensive fishing grounds in the Bazaruto area (21°S – 24°30' S), on the Boa Paz Bank (24°30' – 25°40' S) and at Inhaca island (25°40' – 26°50' S) (Palha de Sousa, 1992, 1998). Initial catches in 1981 and 1982 were approximately 300 tons of lobster per year, but this declined to 100 – 200 tons per year in the following two years; no trap-fishing took place in 1985 (Palha de Sousa, 1998). Between 1980 and 1984 catch rates declined by more than 50%, from 1.67 to 0.75 kg. trap-haul $^{-1}$ (Palha de Sousa, 1998). Trap catches between 1986 and 1992 remained relatively stable, at roughly 150 t per year; this yield appears to have increased substantially in 1993 and 1994 (Table 2.1; Anon, 1998) with the introduction of two more Japanese trap-fishing vessels into the fishery. The large catches made in 1993 and 1994 was followed by a gradual decline in the fishery, culminating in the withdrawal (possibly temporarily) of the Japanese trap-fishing vessels from Mozambican waters in 2000 (B. Palha de Sousa, Instituto de Investigacão Pesqueira, Maputo, pers. comm.). The decline in the catch rates of this fishery is difficult to interpret, mainly because of the lack of information on the spatial distribution of catches. A more detailed account of the history of the trap-fishery in Mozambique and the catch rates on the main fishing grounds is provided by Palha de Sousa (1998).

Exploratory trapping for *P. delagoae* has been undertaken off southern Madagascar (Roullot, 1988; Holthuis, 1991), and on submerged sea-mounts to the south of Madagascar by South African fishing vessels (see Fig. 2.1). However, no commercially viable quantities of *P. delagoae* have yet been uncovered in this region.

### *2.2.4. Trap-fisheries – South Africa*

An experimental long-line trap-fishery, similar to the Mozambican trap-fishery, was initiated off South Africa in 1993. The fishery was structured as an experiment to determine the potential of trap-fishing for *P. delagoae* on rocky substrata off South Africa (Groeneveld and Cockcroft, 1997). Theoretically, rocky substrata are not accessible to trawl nets, and a trap-fishery would therefore have access to previously unfished lobster stocks. A catch of 89.5 tons of *P. delagoae* was recorded in 1994, with an additional bycatch of ~ 30 tons of slipper lobster *Scyllarides elisabethae* (Groeneveld *et al.*, 1995). Catches of *P. delagoae* declined sharply in subsequent years, to 50 t in 1995, 30.5 t in 1996, and 7.8 t in 1997 (Table 2.1). Catch rates in 1997 had similarly declined by ~ 75%, compared to those recorded in 1994. Based on these results, the experiment was terminated in 1997, thereby suspending *P. delagoae* trapping in South African waters. A detailed description of the experimental trap-fishery and its results is provided in Chapter 4 of this thesis.

## 2.3 The South African trap-fishery for *P. gilchristi*

### *2.3.1. History of the fishery*

Prior to 1973, specimens of *P. gilchristi* were occasionally caught on the Agulhas Bank by trawlers fishing for soles at a depth of about 70 m (Berry, 1971a). The subsequent discovery of a commercially viable resource and the early history of its exploitation (1974 – 1980) is described in detail by Pollock and Augustyn (1982) and Stander (1991); only a brief summary of the events up to 1980 is therefore provided here.

Commercial exploitation of *P. gilchristi* originated in 1974, after the discovery of concentrations of rock lobsters on rocky ground at a depth of ~ 110 m off Port Elizabeth. Numerous local and foreign fishing vessels were attracted by the discovery (42 vessels are cited for 1974; Stander, 1991), giving rise to the expansion of the fishery, eastward to Port Alfred by 1976 and westward to the Agulhas Bank by 1977 (Pollock and Augustyn, 1982). The combined catches of local and foreign vessels peaked at 973 t tail mass (equivalent to 2092 tons whole mass) in 1975, whereafter it declined to 122 t tail mass (or 262 t whole mass) by 1979/80 (Table 2.2). The rapid decline in catches was partly as a result of the withdrawal of the foreign vessels from South African waters in 1976, when South Africa declared its EFZ and recognized its jurisdiction over the *P. gilchristi* resource, since it is a sedentary species and confined to the continental shelf of this country. However, there is little doubt that the primary reason for the decline in catches had been a serious depletion of the resource as a result of fishing. Low catch rates had forced several of the remaining local fishing vessels out of the fishery by the end of the 1970s.

Gradual recoveries of catches between 1980 and 1984, and of catch rates between 1980 and 1982 were accompanied by a resurgence in interest in the fishery by fishers who had previously withdrawn. To avert the threat of over-fishing, a total allowable catch (TAC) was introduced into the fishery in 1985, and quotas were given to companies then active in the fishery (Stander, 1991). This measure effectively limited the number of participants

Table 2.2: Records of effort, catch and CPUE in the fishery for *P. gilchristi*

| Season (4) | TAC | Number of active boats | Recorded catches (3) | | Effort (2) | CPUE (1) |
|---|---|---|---|---|---|---|
| | Tail mass (tonnes) | | Tail mass (tonnes) | Whole mass (tonnes) | Thousands of trap-hauls | kg tails / trap |
| 1974 | | 12 | 372 | 800 | | 0.78 |
| 1975 | | 19 | 973 | 2092 | | 0.41 |
| Jan-Jun76 | | 36 | 551 | 1185 | | 0.35 |
| 76/77 | | 33 | 712 | 1531 | | 0.25 |
| 77/78 | | 26 | 667 | 1434 | 3461 | 0.21 |
| 78/79 | | 20 | 461 | 991 | 2212 | 0.2 |
| 79/80 | | 18 | 122 | 262 | 644 | 0.17 |
| 80/81 | | 15 | 176 | 378 | 696 | 0.24 |
| 81/82 | | 18 | 348 | 748 | 1529 | 0.21 |
| 82/83 | | 16 | 407 | 875 | 2078 | 0.19 |
| 83/84 | | 17 | 524 | 1127 | 2687 | 0.19 |
| 84/85 | 450 | 17 | 450 | 968 | 1090* | 0.15 |
| 85/86 | 450 | 14 | 450 | 968 | 1043* | 0.15 |
| 86/87 | 450 | 15 | 450 | 968 | 690* | 0.19 |
| 87/88 | 450 | 14 | 450 | 968 | 634* | 0.21 |
| 88/89 | 452 | 13 | 452 | 972 | 933* | 0.19 |
| 89/90 | 452 | 14 | 452 | 972 | 817* | 0.21 |
| 90/91 | 477 | 13 | 477 | 1026 | 1084* | 0.17 |
| 91/92 | 477 | 15 | 477 | 1026 | 2889 | 0.16 |
| 92/93 | 477 | 12 | 477 | 1026 | 2844 | 0.17 |
| 93/94 | 477 | 15 | 477 | 1026 | 3167 | 0.16 |
| 94/95 | 452 | 13 | 452 | 972 | 3442 | 0.13 |
| 95/96 | 427 | 14 | 427 | 918 | 3217 | 0.13 |
| 96/97 | 415 | 12 | 415 | 892 | 3624 | 0.11 |
| 97/98 | 402 | 13 | 402 | 864 | 4036 | 0.09 |
| 98/99 | 402 | 13 | 402 | 864 | 4206 | 0.08 |

* Effort between 1984/85 and 1990/91 does not represent the full effort of the fishery.

(1) CPUE has been standardised by a GLM.

(2) Effort is given as the total trap-hauls, irrespective of soaktimes.

(3) Catches made after 1984/85 are assumed to be equal to the TAC.

(4) A split-season which opens on 1 October (November in some years) and continues until 30 September (30 June or 31 August in some years) was introduced for administrative purposes in 1976.

in the fishery. The TAC restricted the total catch of *P. gilchristi* to 450 t tail mass (970 t whole mass) per year; fluctuations in the TAC up to 1994 included the addition of two tons (tail mass) for research purposes in the 1988/89 fishing season, and the addition of 25 tons in 1990/91. The latter increase was justified by the inclusion of a previously unfished area off the Ciskei coast (between 27° 10' E and 27° 40' E) after 1990 (Anon., 1994). The TAC remained stable at 477 tons up to the 1993/94 fishing season (Table 2.2).

A rigorous procedure for the assessment of the resource, consisting of a surplus production model fitted to a CPUE index, somatic growth parameters and catch-at-size information was developed in 1994 (Butterworth *et al.*, 1994a, 1994b; Butterworth and Van der Riet, 1994). The assessment indicated that an annual catch of 477 t could not be sustained, and consequently, a program of phased TAC reductions was initiated in 1994/95, reducing the TAC in steps of 25 tons per year. To date (1999/2000 fishing season) the TAC has been reduced to 377 tons tail mass (810 tons whole mass), however, the most recent assessment has indicated that the reductions have failed to impact significantly on the trend of declining abundance (Geromont and Butterworth, 1999). It appears that the relative abundance of *P. gilchristi* now stands at < 50 % of its 1989/90 level (Glazer, 1999a; 1999b; 2000), and that further reductions in the TAC will be necessary.

### *2.3.2. Fishing gear and vessels*

Fishing gear in 1974 comprised individually buoyed traps deployed by fairly small vessels (Pollock and Augustyn, 1982). However, the relatively low densities of *P. gilchristi* generally encountered are better exploited by employing a long-line system consisting of large numbers of light plastic traps attached to bottom long-lines. The change towards using long-lines with multiple traps occurred as early as 1974 (Pollock and Augustyn, 1982). Large (25 to 60-m long) steel ocean-going vessels (adapted from side or stern trawlers) are used in the fishery; these vessels are suitable for the relatively distant, offshore conditions encountered in the fishery, and are able (generally after a small modification) to carry large numbers of traps.

The numbers of active fishing vessels (Table 2.2) declined after the introduction of the TAC (from 17 in 1984/85 to 14 in 1985/86), but remained relatively stable (between 11 and 15 vessels) up to 1999, despite the decline in the TAC experienced in recent years. However, the recent introduction of a new fisheries policy (embodied in the Marine Living Resources Act of 1998), which aims to broaden access to South African commercial fisheries, has resulted in fishing rights for *P. gilchristi* being granted to a number of new fishing companies, by reducing the tonnage granted to established companies by equivalent quantities. This move has led to an upheaval in the fishery in 2000, with the possible introduction of additional fishing vessels by new companies, and threats pertaining to the withdrawal of operational vessels by established companies. To date, the issue remains unresolved, with three new fishing vessels poised to enter the fishery.

### *2.3.3. Effort, catch and CPUE*

The past decade has seen a substantial increase in fishing effort for *P. gilchristi* (Table 2.2); this was achieved without an increase in the number of active fishing vessels, and reflects an increase in the quantity of gear used per vessel. The trend towards increasing the gear compliment per vessel stems from the removal of a regulation (Act 12 of 1973; Stander, 1991), which, up to 1988, limited the number of traps allowed per fishing vessel. The removal of this regulation allowed fishing vessels to deploy more traps on the fishing grounds than previously. The impact of this increase in fishing effort on the CPUE and management of the fishery is addressed in Chapter 9.

The catch trend for the 1974 – 2000 period (Table 2.2) can be subdivided into three distinct periods: 1974 – 1979/80, during which a sharp decline in catches and a near collapse of the stock can be attributed to excessive effort by a multitude of fishing vessels; 1980/81 – 1983/84, during which a recovery of the stock may be attributed to a period of reduced effort; and 1984/85 to the present, a period of relatively stable, though declining, catches. Catches in the latter period varied within a few tons of the TAC set for the fishery.

The CPUE trend for the period between 1974 and the present (Table 2.2) can likewise be divided into three periods: 1974 – 1979/80, during which a decline from 0.78 to 0.17 kg. trap $^{-1}$ was recorded; 1980/81 – 1989/90, during which the CPUE fluctuated between 0.15 and 0.24 kg. trap $^{-1}$; and 1990/91 to the present, during which the CPUE steadily declined, by nearly 50 %, from 0.17 to 0.08 kg. trap$^{-1}$ in 1998/99. The CPUE trend shown in Table 2.2 is a GLM-standardized trend, which accounts for the influences of vessel differences, and spatial and temporal variation in lobster catchability. The integrity of this trend, relative to changes in fishing strategy, is addressed in Chapter 9.

### *2.3.4. Production and markets*

Vessels discharge their catches in Cape Town and Port Elizabeth harbours, where factories for the processing and distribution of products are located. Products are generally exported to the United States, Europe and the Far East, either as live lobsters or packed as frozen lobster tails or whole frozen lobsters. Frozen lobster tails remain the most popular product of the fishery, but the live lobster category has increased in popularity throughout the 1990s (Figure 2.2). Total annual exports to the value of U$ 50 - 70 million are commonly realized. The South Coast rock lobster sector of the South African Fishing Industry employs ~ 700 workers, mostly from lower socio-economic groups.

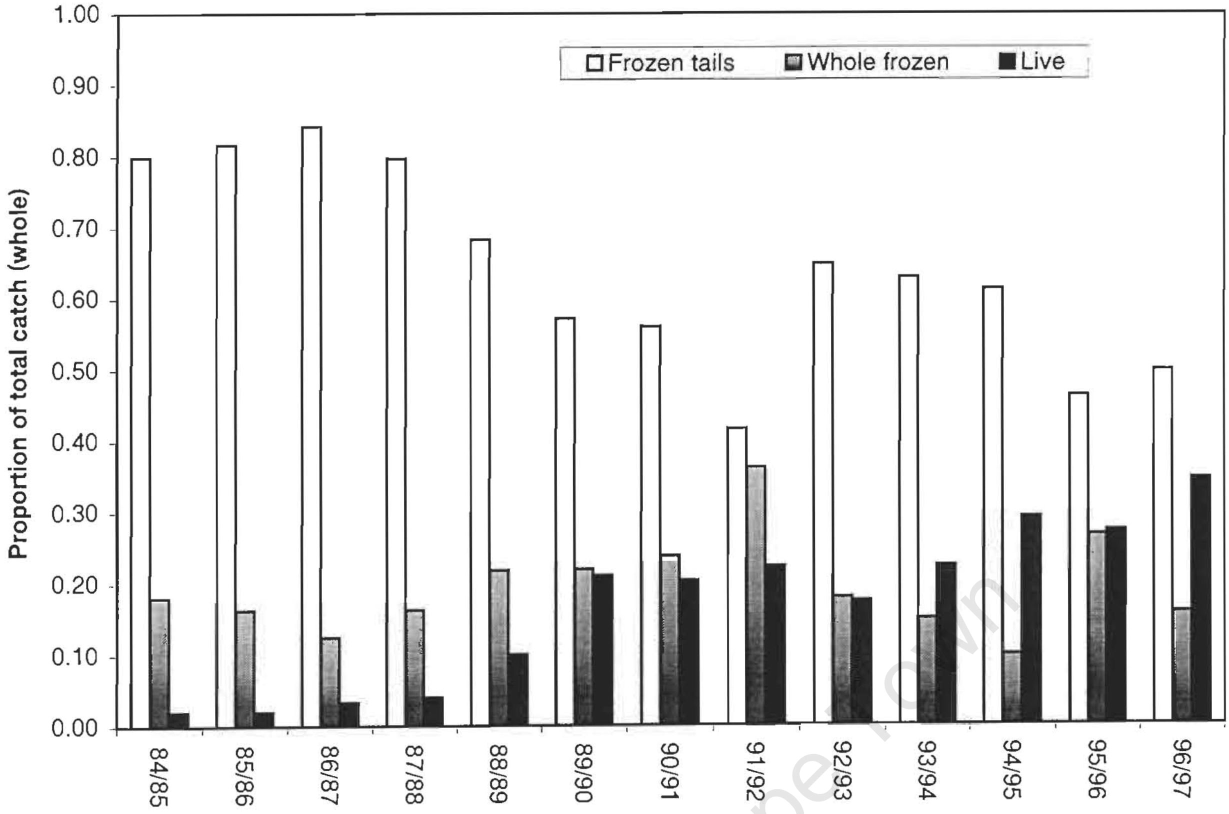

Figure 2.2. Production of South Coast rock lobster commodities

# Chapter 3

# A revision of the length-mass relationships of *P. delagoae* and *P. gilchristi* with implications for management

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## 3.1. Introduction

Within the genus *Palinurus,* the degree of morphological difference, even between the North Atlantic and Indian Ocean species, is very small (Berry and Plante, 1973). As a result, expert advice is usually needed to distinguish between specimens of *P. delagoae* and *P. gilchristi*. Their physical likeness is further reflected in their past taxonomic classification as three varieties of the same species; up to 1973 *P. delagoae* was regarded as two varieties of *P. gilchristi*, namely *P. gilchristi* var. *delagoae* from Mozambique and *P. gilchristi* var. *natalensis* from South Africa (Barnard, 1926). Berry and Plante (1973), in their seminal study on the taxonomy of the genus, merged these two varieties and raised *P. delagoae* to specific rank.

Berry and Plante (1973) summarized the main differences between *P. delagoae* and *P. gilchristi*. Briefly, the 2nd to 5th abdominal segments of *P. gilchristi* each have well-developed anterior and posterior grooves filled with short dense setae; these grooves are linked on either side of the median keel to give a distinct H-shape. In *P. delagoae* the anterior transverse groove is virtually non-existent, and is not medially linked to the posterior groove . Setae in the grooves of *P. delagoae* are sparse and inconspicuous.

The merus of the walking legs of *P. gilchristi* is triangular in cross-section and the flattened outer surface of these legs is covered in a conspicuous strip of short, dense setae. In *P. delagoae*, the merus is cylindrical and lacks setae. The entire dorsum of the cephalothorax of *P. gilchristi* is strongly tuberculate, and is covered in a dense mat of short setae between spines. In *P. delagoae* the precervical region is devoid of setae and is shiny; only towards the posterior region of the carapace are there a few setae clustered around the bases of some of the tubercles.

Several early studies on the length-mass relationships of *P. gilchristi* and *P. delagoae* suggested that there may also be morphometric differences between these two species (Berry, 1973; Pollock and Augustyn, 1982; Brinca and Palha de Sousa, 1983). However, these studies were all conducted in isolation, and standard sampling methods were not always followed. As a result, length-mass relationships obtained for the two species by different researchers are not directly comparable.

Despite the morphological and morphometric differences mentioned above, identification of the two species remain difficult. Considering that both species support lucrative commercial fisheries, and that these fisheries are located adjacent to each other and are often exploited by vessels of the same company, misidentification could result in a lack of control over the quantity of each species landed. It is therefore important that alternative characteristics that more readily distinguish between *P. delagoae* and *P. gilchristi* be sought.

Accurate length-mass relationships are also important in stock assessments where they are used to convert commercial catches (mass in tons) to numbers of lobsters captured per length category. In the fishery for *P. gilchristi,* where the total allowable catch (TAC) is measured in tail mass (TM), a whole mass (WM) to TM conversion factor is used in cases where live lobster or whole frozen lobster products are sold. Also, fishing companies can utilise information on the relationship between TM and WM, relative to species and sex, to maximize financial yield per lobster.

The aims of this chapter are to establish standardised length-mass relationships for *P. delagoae* and *P. gilchristi* and to compare these to obtain a further means of distinguishing between the two species. The management implications of the length-mass relationships, relative to species and sex, are also discussed.

Table 3.1:Regression statistics for the morphometric relationships for male and female *P.delagoae* and *P.gilchristi*

| Relationship ($y = a x^{b}$) | Regression statistics | | | | | | | | Size range (mm) |
|---|---|---|---|---|---|---|---|---|---|
| | ln a | SE of ln a | b | SE of b | $r^2$ | n | F-value | p | |
| ***P.delagoae*** | | | | | | | | | |
| $TM_M = 0{,}0061\ CL^{2{,}2664}$ | -51,066 | 0,1391 | 22,664 | 0,0300 | 0,9899 | 60 | 5690 | 0,0001 | 55 - 185 |
| $TM_F = 0{,}0019\ CL^{2.5502}$ | -62,520 | 0,1835 | 25,502 | 0,0411 | 0,9867 | 54 | 3857 | 0,0001 | 55 - 135 |
| $TM_{M+F} = 0{,}0052\ CL^{2{,}312}$ | -52,605 | 0,1476 | 23,129 | 0,0324 | 0,9785 | 114 | 5086 | 0,0001 | 55 - 185 |
| $WM_M = 0{,}0017\ CL^{2.7757}$ | -63,766 | 0,0949 | 27,757 | 0,0205 | 0,9968 | 60 | 18318 | 0,0001 | 55 - 185 |
| $WM_F = 0{,}0016\ CL^{2{,}7951}$ | -64,315 | 0,1548 | 27,951 | 0,0346 | 0,9921 | 54 | 6511 | 0,0001 | 55 - 135 |
| $WM_{M+F} = 0{,}0018\ CL^{2{,}770}$ | -63,375 | 0,0834 | 27,704 | 0,0183 | 0,9951 | 114 | 22901 | 0,0001 | 55 - 185 |
| $TM_M = 1{,}1026\ WM^{0{,}8169}$ | +0,0976 | 0,0543 | 0,8169 | 0,0083 | 0,9940 | 60 | 9586 | 0,0001 | 55 - 185 |
| $TM_F = 0{,}6808\ WM^{0.9124}$ | -0,3845 | 0,0561 | 0,9124 | 0,0092 | 0,9947 | 54 | 9790 | 0,0001 | 55 - 135 |
| $TM_{M+F} = 1{,}0207\ WM^{0{,}836}$ | +0,0204 | 0,0573 | 0,8364 | 0,0091 | 0,9870 | 114 | 8484 | 0,0001 | 55 - 185 |
| ***P.gilchristi*** | | | | | | | | | |
| $TM_M = 0{,}0007\ CL^{2{,}8316}$ | -72,793 | 0,1944 | 28,316 | 0,0443 | 0,9803 | 84 | 4086 | 0,0001 | 46 - 132 |
| $TM_F = 0{,}0004\ CL^{2.9935}$ | -78,895 | 0,3052 | 29,935 | 0,0705 | 0,9725 | 53 | 1801 | 0,0001 | 53 - 125 |
| $TM_{M+F} = 0{,}0007\ CL^{2\ 8460}$ | -73,074 | 0,1864 | 28,460 | 0,0427 | 0,9705 | 137 | 4439 | 0,0001 | 46 - 132 |
| $WM_M = 0{,}0014\ CL^{2{,}8564}$ | -65,661 | 0,1622 | 28,564 | 0,0369 | 0,9864 | 84 | 5967 | 0,0001 | 46 - 132 |
| $WM_F = 0{,}0010\ CL^{2.9445}$ | -69,129 | 0,2566 | 29,445 | 0,0528 | 0,9797 | 53 | 2467 | 0,0001 | 53 - 125 |
| $WM_{M+F} = 0{,}0013\ CL^{2{,}870}$ | -66,123 | 0,1404 | 28,701 | 0,0322 | 0,9833 | 137 | 7956 | 0,0001 | 46 - 132 |
| $TM_M = 0{,}4604\ WM^{0{,}9922}$ | -0,7757 | 0,0436 | 0,9922 | 0,0073 | 0,9956 | 84 | 18519 | 0,0001 | 46 - 132 |
| $TM_F = 0{,}4201\ WM^{1{,}0176}$ | -0,8673 | 0,0623 | 10,176 | 0,0106 | 0,9944 | 53 | 9102 | 0,0001 | 53 - 125 |
| $TM_{M+F} = 0{,}4644\ WM^{0{,}994}$ | -0,7671 | 0,0440 | 0,9944 | 0,0074 | 0,9925 | 137 | 17926 | 0,0001 | 46 - 132 |

All regressions of CL (mm) vs TM (g), CL vs WM (g) and WM vs TM were of the type $y = ax^{b}$. Data were thus In transformed so that the linear relationships (*ln y = ln a + b ln x*) could be used to test regressions for significance within the size range (CL, mm) that was measured for each species.

Table 3.2: Results of Student's t-test between regression slopes and elevations of morphometric relationships for male and female *P. delagoae* and *P. gilchristi*

| Comparison | Hypothesis | Significance | | df |
|---|---|---|---|---|
| | | Slopes | Elevations | |
| CL vs TM | $P.delagoae_M = P.delagoae_F$ | $p < 0,001$* | $p > 0,1$ | 111 |
| CL vs WM | $P.delagoae_M = P.delagoae_F$ | $p > 0,5$ | $p > 0,05$ | 111 |
| CL vs TM | $P.gilchristi_M = P.gilchristi_F$ | $p > 0,2$ | $p > 0,1$ | 85 |
| CL vs WM | $P.gilchristi_M = P.gilchristi_F$ | $p > 0,5$ | $p > 0,2$ | 85 |
| CL vs TM | $P.delagoae_M = P.gilchristi_M$ | $p < 0,001$* | $p > 0,1$ | 108 |
| CL vs WM | $P.delagoae_M = P.gilchristi_M$ | $p < 0,05$* | $p > 0,05$ | 108 |
| CL vs TM | $P.delagoae_F = P.gilchristi_F$ | $p < 0,001$* | $p > 0,1$ | 88 |
| CL vs WM | $P.delagoae_F = P.gilchristi_F$ | $p > 0,1$ | $p > 0,1$ | 88 |
| TM vs WM | $P.delagoae_{M\&F} = P.gilchristi_{M\&F}$ | $p < 0,001$* | $p > 0,1$ | 199 |

* Significant difference

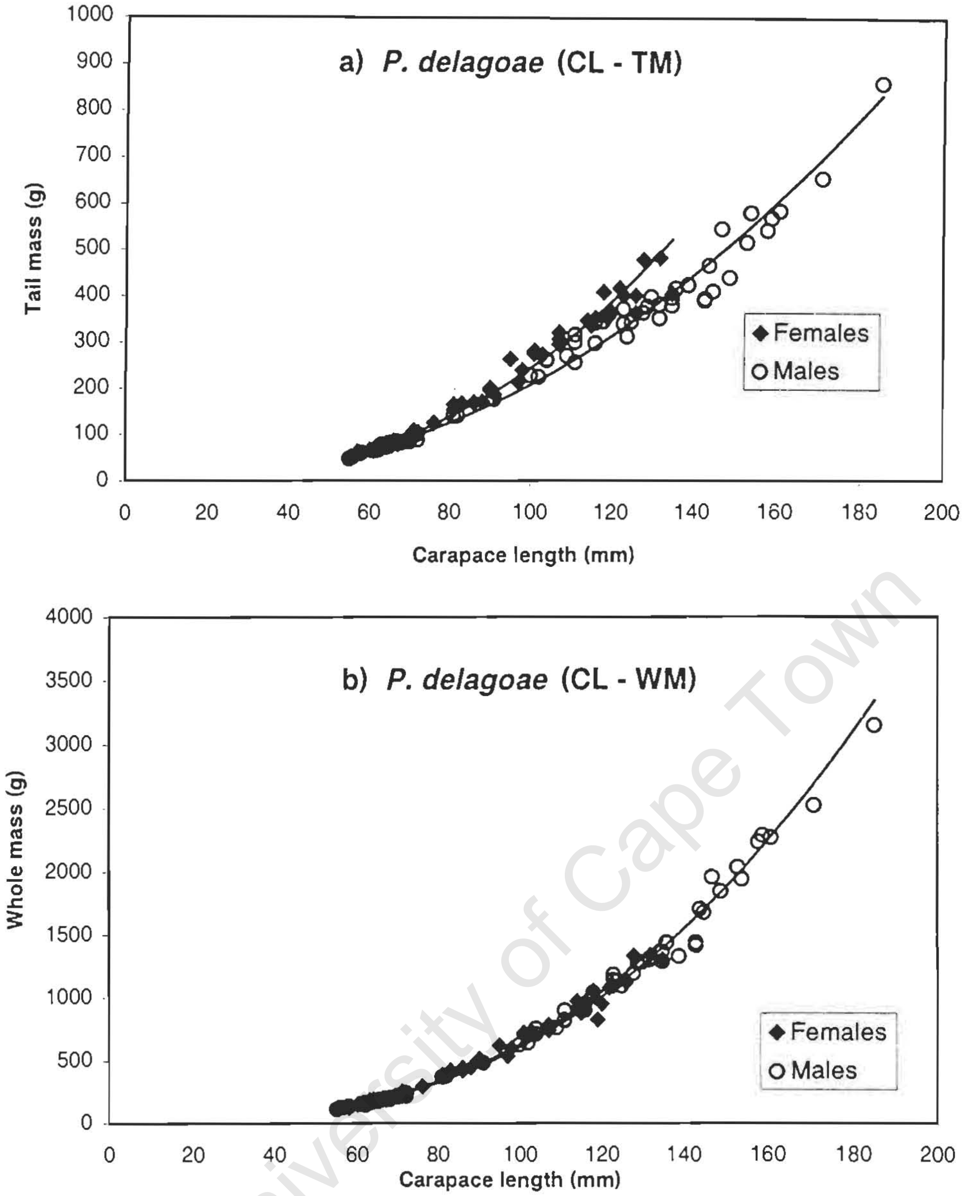

Figure 3.1: Relationships between CL and TM (a) and CL and WM (b) of male and female *P. delagoae*

## 3.2. Material and methods

A standard method was used to collect carapace length (CL) and mass measurements. To ensure a uniform distribution of data points, the first five lobsters of each sex per 5-mm CL-interval were selected from the live-lobster holding tanks used by a commercial fishing company. The widest possible CL range was covered, and only lobsters that were undamaged, with no missing or regenerated appendages, were selected. The CL was measured (± 0.1 mm) mid-dorsally from the posterior edge of the carapace to the anterior tip of the rostral spine. Whole wet mass (WM) was determined after shaking excess water from the gill chambers and tail wet mass (TM) was determined from tails that had been removed in a commercial manner (i.e. by removing the tail along with the abdominal musculature that extends into the carapace). WM and TM were measured to the nearest gram. Egg-bearing females were excluded from the samples.

Regressions of the data were non-linear, and consequently data were log-transformed. Length-mass relationships were compared by sex and between species, using Student's *t*-tests (Zar, 1984) for significant differences ($p < 0.05$) between regression slopes and elevations.

## 3.3. Results

Table 3.1 lists the relationships as $y = a x^b$ (fitted to the raw data) and as $\ln y = \ln a + b \ln x$ (fitted to the log-transformed data) for *P. delagoae* and *P. gilchristi*. All relationships were significant ($p < 0.0001$) and the high $r^2$ values indicated that the data fitted the models well.

The slopes of the relationships between CL and TM differed significantly between male and female *P.delagoae* (Table 3.2), reflecting that the TM of females became progressively heavier relative to males as CL increased (Fig. 3.1a). The WM of female *P.delagoae* was marginally greater for a given CL than for males, but neither regression slopes nor elevations differed significantly (Table 3.2, Fig. 3.1b). In the case of *P. gilchristi,* both TM and WM at a given CL were proportionally greater in females than in males, but the differences were not

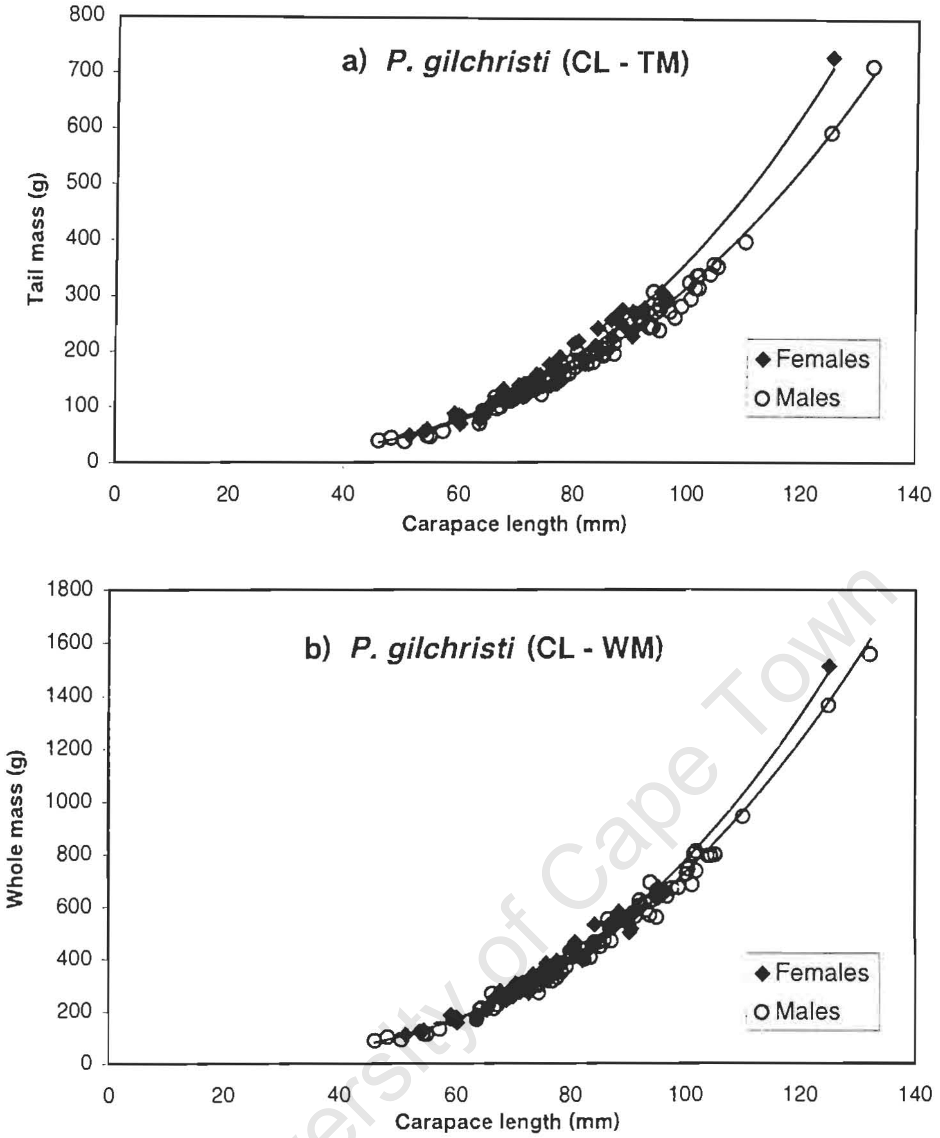

Figure 3.2: Relationships between CL and TM (a) and CL and WM (b) of male and female *P. gilchristi*

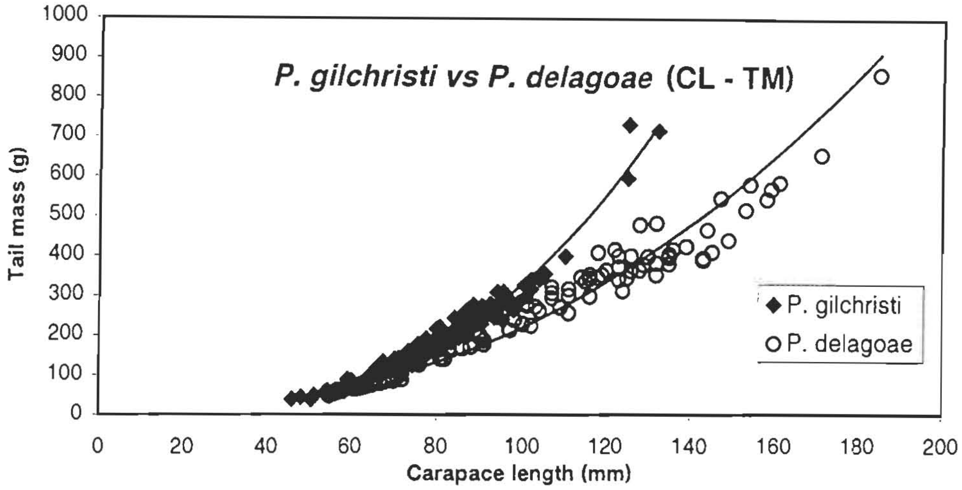

Figure 3.3: Comparison of the relationships between CL and TM of *P. delagoae* and *P. gilchristi*

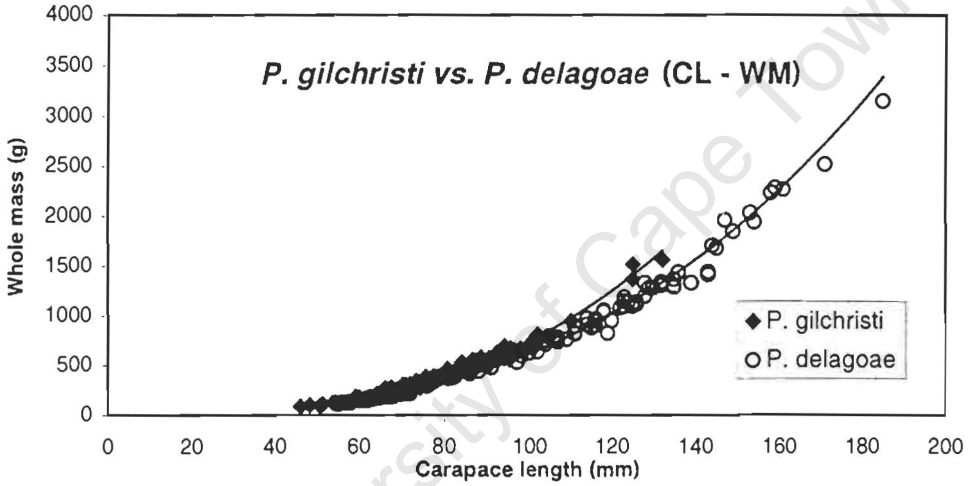

Figure 3.4: Comparison of the relationships between CL and WM of *P. delagoae* and *P. gilchristi*

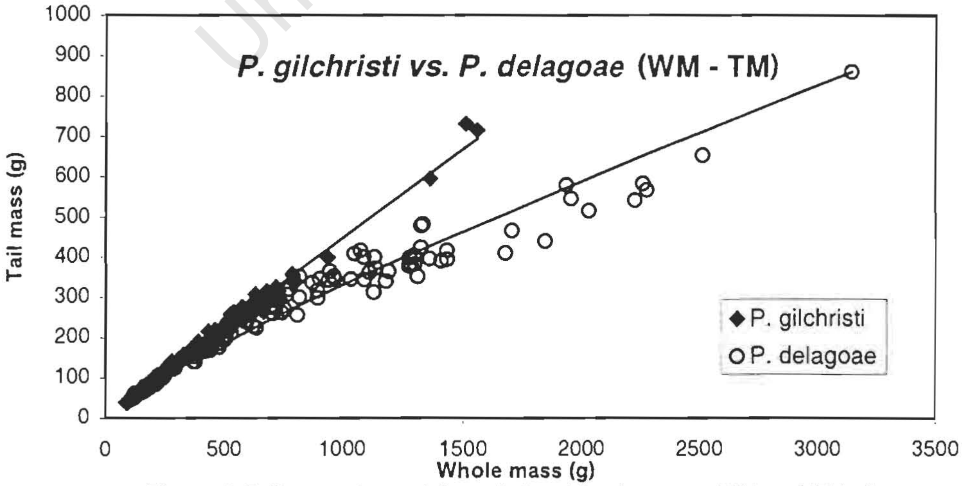

Figure 3.5: Comparison of the relationships between WM and TM of *P. delagoae* and *P. gilchristi*

significant (Table 3.2, Figs. 3.2a and b).

Differences between the species are shown in Figures 3.3 to 3.5, using data for both sexes combined. Both the TM and WM of *P. gilchristi* of a given CL were significantly heavier than those of *P. delagoae* of the same CL, with the discrepancy increasing as CL increased (Figs. 3.3 and 3.4). A comparison of the regressions of WM to TM showed that, compared to *P. delagoae*, a significantly larger proportion of the mass of whole *P. gilchristi* consisted of tail (Table 3.2, Fig. 3.5). Also, the TM proportion of *P. delagoae* decreases as WM increases (the TM of a small *P.delagoae* of 150 g WM is 44,9 % of its WM, whereas that of a large specimen of 1590 g is 30,6 %). In contrast the TM proportion in *P. gilchristi* is constant over the full size range (45,1 % of the WM of a 165 g lobster and 44,5 % of that of a 1500 g lobster).

### 3.4. Discussion

The length-mass relationships obtained in the present study differed substantially from those shown in earlier studies. The difference is attributed to the previous absence of a standard measurement for CL or TM. CL in the present study was measured mid-dorsally from the posterior edge of the carapace to the anterior tip of the rostral spine. However, in a previous study on *P.delagoae*, Berry (1973) measured CL from the base instead of from the tip of the rostrum.

The measurement of TM in the present study, and in the studies by Pollock and Augustyn (1982) and Brinca and Palha de Sousa (1983), conform to the commercial method of tailing, in which the abdominal musculature that extends into the carapace is removed along with the tail. However, in his study on *P. delagoae* in 1973, Berry defined TM as the mass of the abdomen cut off flush with the anterior edge of the first abdominal segment. As expected, the parameters obtained for the CL - TM relationships by him indicate a smaller TM at similar CL, with relationships of $TM_M = 0.0040\ CL^{2,3098}$ (Table 3.3) compared to the current regression of $TM_M = 0,0061\ CL^{2.2664}$ (Table 3.1), and $TM_F = 0,0013\ CL^{2,6017}$ (Table 3.3) compared to $TM_F= 0,0019\ CL^{2.5502}$ (Table 3.1).

Table 3.3: Relationships of *P. delagoae* and *P. gilchristi* documented in previous studies off South Africa and Mozambique

| Relationship ($y = ax^b$) | $r^2$ | n | Size range (mm CL) | Source |
|---|---|---|---|---|
| ***P.delagoae*** | | | | |
| $TM_M = 0{,}0040\ CL^{2,3098}$ | | 135 | 55-150 | Berry 1973 |
| $TM_F = 0{,}0013\ CL^{2.6017}$ | | 10 | 54-122 | Berry 1973 |
| $WM_M = 0{,}0015\ CL^{2,6389}$ | 0,9983 | 63 | 52-145 | Brinca & Palha de Sousa 1983 |
| $WM_M = 0{,}0017\ CL^{2.5950}$ | 0,9958 | 61 | 52-140 | Brinca & Palha de Sousa 1983 |
| $WM_F = 0{,}0017\ CL^{2,6116}$ | 0,9978 | 49 | 52-140 | Brinca & Palha de Sousa 1983 |
| $WM_F = 0{,}0019\ CL^{2,5287}$ | 0,9975 | 64 | 52-135 | Brinca & Palha de Sousa 1983 |
| $WM_{M+F} = 0{,}0017\ CL^{2,5930}$ | 0,9968 | 294 | | Brinca & Palha de Sousa 1983 |
| $WM_M = 0{,}0016\ CL^{2,7985}$ | | 271 | 55-155 | Berry 1973 |
| $WM_F = 0{,}0019\ CL^{2,7620}$ | | 122 | 54-122 | Berry 1973 |
| ***P.gilchristi*** | | | | |
| $TM_M = 0{,}0045\ CL^{2.3940}$ | | 80 | 59-102 | Pollock & Augustyn 1982 |
| $TM_F = 0{,}0016\ CL^{2,6577}$ | | 63 | 59- 97 | Pollock & Augustyn 1982 |
| $TM_{M+F} = 0{,}0028\ CL^{2,5144}$ | | 143 | 59-102 | Pollock & Augustyn 1982 |
| $WM_M = 0{,}0057\ CL^{2.5129}$ | | 78 | 59-102 | Pollock & Augustyn 1982 |
| $WM_F = 0{,}0034\ CL^{2,6400}$ | | 63 | 59- 97 | Pollock & Augustyn 1982 |
| $WM_{M+F} = 0{,}0044\ CL^{2,5748}$ | | 141 | 59-102 | Pollock & Augustyn 1982 |

Despite using similar methods to mine to determine the length-mass relationships of *P.gilchristi*, the CL - TM regressions determined by Pollock and Augustyn (1982) differed substantially from mine. For males, Pollock and Augustyn (1982) found that $TM_M = 0{,}0045\ CL^{2{,}3940}$ (Table 3.3) which does not compare well with the present relationship of $TM_M = 0{,}0007\ CL^{2{,}8316}$ (Table 3.1), and for females their relationship of $TM_F = 0{,}0016\ CL^{2{,}6577}$ (Table 3.3) also differed from the present $TM_F = 0{,}0004\ CL^{2{,}9935}$ (Table 3.1). Both studies predict similar TM values between 55 - 85 mm CL, but the regressions diverge at the larger (>85 mm CL) and smaller (<55 mm CL) length classes. As a larger size range was sampled in the present study (46 - 132 mm CL) compared to the previous study (53 mm - 102 mm CL) the present relationships are likely to be more reliable, especially for small and large lobsters.

Forest and Postel (1964), based on a photograph of *P. delagoae*, stated that this species could clearly be distinguished from *P. mauritanicus* and *P. charlestoni* by the relative lengths of carapace and abdomen. Likewise, the present study shows that *P. gilchristi* has a considerably heavier TM than *P.delagoae* of the same CL (Fig. 3.3). TM makes up 45% of the WM of *P.gilchristi* compared to 30,6% - 44,9% of *P.delagoae*, depending on lobster size. Also, it appears that unlike *P.gilchristi*, in which TM remains a relatively constant proportion of WM, in the case of *P. delagoae* the TM proportion decreases as lobster size increases. In practice, the heavier TM of *P.gilchristi* implies that a larger yield per lobster is realised by catching and tailing *P.gilchristi* compared to *P.delagoae* of the same CL. Packing frozen tails of *P.delagoae* leads to a larger carapace-discard per unit TM packed than for *P.gilchristi*.

Commercial catches of *P. gilchristi* are controlled in TM units, and the mass of live lobsters caught (and packed) is converted to tail mass using a fixed conversion factor. Until recently (May, 2000) a conversion factor of 0.465 was used, higher than the value of 0.450 determined in this study. The revision of the WM to TM conversion factor from 0.465 to 0.450 will result in a slight increase in total landed catches, because companies that pack whole lobster products will now be able to convert the whole lobster mass packed to TM (for control purposes) according to a slightly more favourable ratio, so gaining 15 kg of lobster per ton of whole lobster packed.

To summarize, the distinct length-mass relationships of *P. gilchristi* and *P. delagoae* can be used, together with the physical differences noted by Berry and Plante (1973), to differentiate between these two species. Further, the revision of the length – mass relationships carries important implications for estimations of the impacts of TACs (set as a mass) on actual numbers of animals that will be caught. The revised relationships have now (from 2000 onwards) been incorporated into the assessment, management and exploitation control aspects of the fishery for *P. gilchristi*.

# Chapter 4

## A systematic grid-survey to determine the relative abundance of *P. delagoae* off South Africa

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### 4.1. Introduction

Commercially exploitable densities of *P. delagoae* occur on rocky and organically rich muddy or sandy substrata (Berry, 1971a; Berry and Plante, 1973), and can therefore be fished with traps (on rocky substrata) and with trawl-nets (on mud or sand substrata) (see Chapter 2). Both gear types have successfully been used in Mozambican waters (Palha de Sousa, 1997, 1998; Groeneveld and Melville-Smith, 1995) since 1980. Up to 1993, however, only trawl-nets were used off South Africa. An experimental trap-fishery for *P. delagoae* on rocky substrata off South Africa was first permitted in 1994. A precautionary approach (limited entry, strictly controlled catches, and a systematic experimental procedure) was adopted for this fishery, as was later prescribed for the development of new fisheries off South Africa in the Marine Living Resources Act (Cockcroft and Payne, 1997). The cautious development of new fisheries is aimed at reducing the initial risk of overfishing and stock collapse. Examples of such collapses of similar resources are the depletion of *Jasus tristani* within two years of discovery on the summit of the Vema seamount in the South Atlantic ocean (Heydorn, 1969a), and the intensive fishing and large scale catches of *P. gilchristi* in 1974 to 1977, followed by a near-collapse of the stock in 1980 (Pollock and Augustyn, 1982).

The approach used for *P. delagoae* included a structured sampling procedure to determine the relative abundance trends of the population over the first few years of fishing. The preferred sampling method was a systematic grid-survey design (instead of a random sampling design). Such grid-surveys are generally efficient in terms of ships time and the locations of sample points, permitting a more precise mapping of spatial patterns of density and boundaries of distributions, reducing the risk of missing high density concentrations, and facilitating comparisons of distribution and density patterns over time (Hilborn and Walters, 1992). The grid-survey included a 1-year pilot study to determine the distribution of *P. delagoae* south of the Mozambique border, and consisted of two distinct phases; an experimental grid-sampling phase, and a commercial fishing phase to allow fishers to recover costs.

The information collected by on-board observers during the 4-year experimental trap-fishery for *P. delagoae* formed the basis of an investigation into the potential of the resource for trap-fishing. This chapter (the first of three on *P. delagoae*) describes the systematic grid-survey developed for this species and area and its results over 4 years (see Cockcroft *et al.*, 1995; Groeneveld *et al.*, 1995; Groeneveld and Cockcroft, 1997). These results were used to investigate 1) the impact of four years of trap-fishing on the catch rates, relative abundance and size composition of *P. delagoae* in South African waters, and 2) the advisability of continuing a trap fishery in parallel with the trawl fishery (see Chapter 6).

## 4.2. Material and methods

A pilot study, conducted in 1994, sampled an area along the South African coast extending from the Mozambique border (27°S) to south of Port St Johns (32°S). This study consisted of 14 transects (set roughly perpendicular to the coast), at distances of ~ 35 km apart. Longlines with traps were set roughly parallel to the coast at depths of 75, 150, 250, 300, 350 and 400 m along each transect.

The area south of 31°S and depths < 112.5 m were excluded from sampling after 1994, as the species was not recorded there (Cockcroft *et al.* 1995). The remaining area was stratified into sampling blocks based on depth and latitude. Depth intervals were 112.5 - 200 m, 200 - 275 m, 275 - 325 m, 325 - 375 m and 375 - 425 m. Latitudinal boundaries were set at 6' intervals starting at 27°S and ending at 31°S (Fig. 4.1). To concentrate the experimental effort on the regions that showed potential for commercial fishing, sampling from 1996 onwards was focussed on three promising regions between 200 and 425 m depth: North region, extending along the seawards edge of the Maputaland marine reserve between 27°S and 27°36'S and

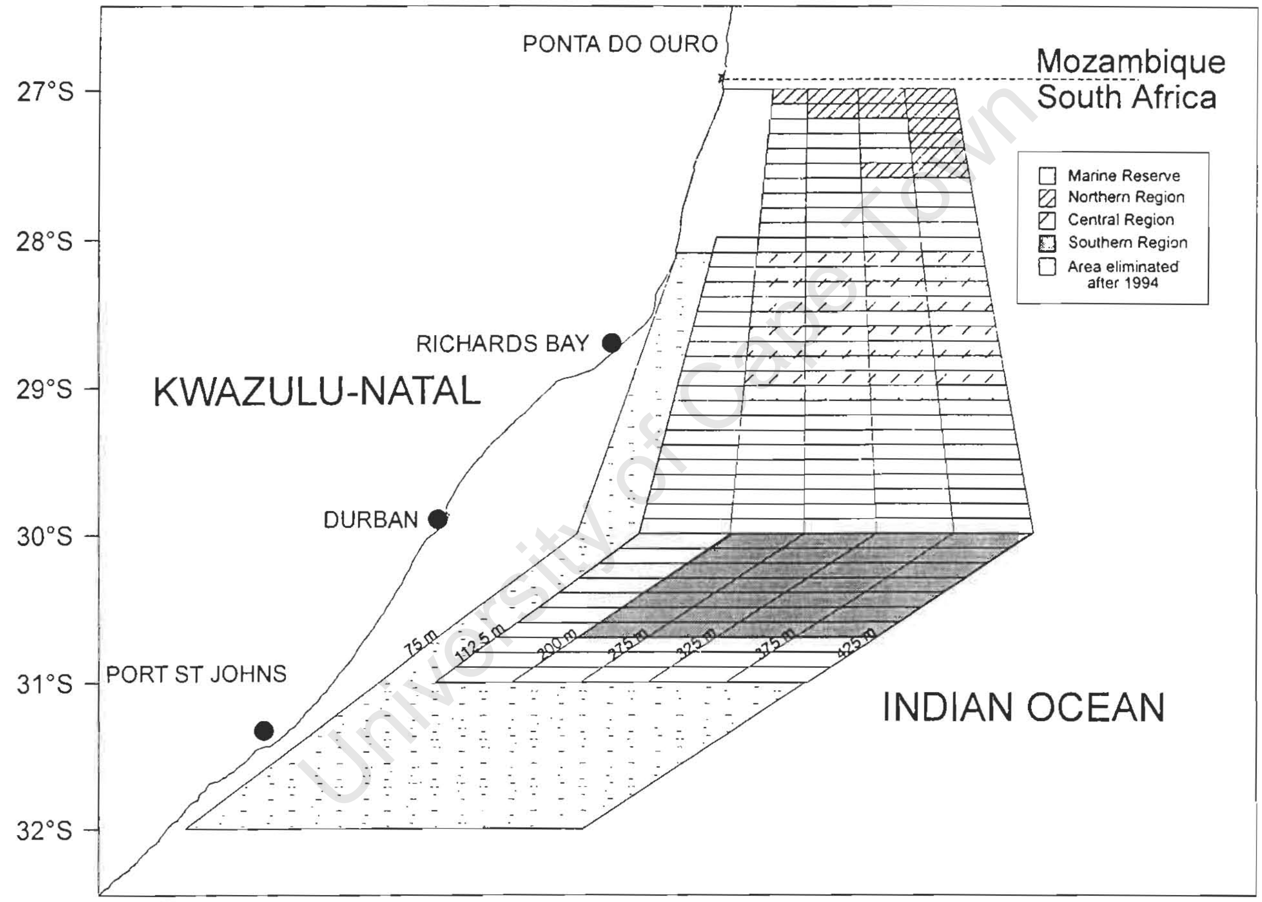

Figure 4.1: Diagram of the sampling area along the Kwazulu-Natal coast of South Africa, showing the North, Central and South regions. Sampling blocks, obtained by stratifying according to depth and latitude, are not to scale.

consisting of 12 sampling blocks (92.3 km$^2$); Central region extending from 28°S to 29°S and consisting of 40 blocks (340.7 km$^2$); and South region extending from 30°S to 30°42'S and consisting of 28 blocks (413.9 km$^2$) (Fig. 4.1).

Together, the three regions consisted of 80 sampling blocks and covered 846.9 km$^2$. The area of each sampling block was calculated from its average width (the distance in km between depth contours, measured from SAN series hydrographic charts, Scale 1 : 150 000) and its length, 10.57 km, the equivalent of 6' intervals. Areas of blocks ranged from 4.01 to 24.10 km$^2$ (mean 10.59 km$^2$ ± 5.64 s.d.) depending on the steepness of the sea bottom. The data collected in these three regions in 1994, 1995, 1996 and 1997 form the basis of this study.

Two discrete sampling regimes were conducted in each region in each year. First, in an experimental phase, each block was sampled (at its average depth) with two long-lines consisting of 70 - 150 plastic top-entry barrel traps set for 24 - 96 hours. This phase allowed the calculation of a representative abundance index based on a stratified sampling design method (Jolly and Hampton, 1990). A commercial phase followed immediately, with no restriction on location of trap deployment. In the analysis, the two types of samples were treated separately.

Surveys were conducted during winter (May to September) in all four years. Three vessels took part in 1994, two in 1995 and 1996, and only one in 1997.

An experimental quota of 104 tons, including both *P. delagoae* and Cape slipper lobster *Scyllarides elisabethae*, was set for 1995, 1996 and 1997. The quota was based on trap catches of the two species made in the pilot study in 1994, on trawl catches of *P. delagoae* off Kwazulu-Natal in 1992 and 1993, and on the size of the Kwazulu-Natal fishing grounds, relative to the fishing grounds for *P. gilchristi* along the South Coast (Groeneveld, 1995).

The data for each long-line hauled were recorded, resulting in multiple samples (both experimental and commercial) per block. Effort was standardized as the number of traps hauled per long-line. The numbers and sex of rock lobsters caught were recorded per long-line, and the carapace lengths (CL ± 1 mm) of the first 100 caught with each long-line were measured mid-dorsally from the posterior edge of the carapace to the tip of the rostral spine. Immature females, identified by the absence of ovigerous setae (Groeneveld and Melville-Smith, 1994), and the frequency of egg-bearing females in samples were also recorded.

Carapace length (mm) of each lobster was converted to whole mass (WM in g), according to the equations of Groeneveld and Goosen (1996):

$$WM_M = 0.0017\ CL^{2.7757}$$
$$WM_F = 0.0016\ CL^{2.7951}$$

Catch (kg whole mass) for each long-line was then calculated by multiplying the average weight per lobster with the number of lobsters caught, and CPUE (kg whole mass per trap) was obtained by dividing catch by the number of traps on the line.

Generalized linear models (GLMs) using SAS (Anon., 1989) were used to investigate the influence of year (1994 - 1997), region (North, Centre and South), sampling phase (experimental or commercial), month (May - September) and soak-time (< 36 hrs, 36 - 72 hrs, and > 72 hrs) on CPUE.

To calculate the abundance of *P. delagoae* effort and catches from all the long-lines hauled were summed per sampling block, so that the CPUE per block could be obtained. Block-CPUE was weighted according to the area of the block, and summed over the blocks in the region. To obtain an estimate of overall abundance per year, regional CPUEs were weighted according to area and summed.

## 4.3. Results

### *4.3.1. Sampling effort and catches*

Not all the blocks within each region were sampled during the experimental phase of the study in each year, usually as a result of adverse weather and sea-current conditions. However, in general a high percentage (43 - 100 %) of coverage was achieved (Table 4.1).

The relatively low percentage coverage of blocks in the Central and South regions in 1994 is a result of the somewhat different trap-deployment pattern used during the pilot study phase (Cockcroft *et al.* 1995; Groeneveld *et al.* 1995). Coverage during the commercial phases was, as expected, more patchy, as skippers were free to fish where they wished.

The sampling efforts during the experimental and commercial phases of the experiment are given in Table 4.2. Although every long-line hauled during the experimental phase was sampled, the large number of long-lines set during the commercial phase required subsampling. The proportion of the commercial-phase catch sampled (based on catches of *P. delagoae*) ranged from 4 - 51 % (Table 4.3).

*P. delagoae* constituted the bulk of the catches (~ 85 % by mass), with the remainder consisting of *S. elisabethae.* Total trap catches (including both species) during the experimental and commercial phases of the study were 120 tons in 1994, 59.8 tons in 1995, 38.1 tons in 1996, and 9.4 tons in 1997. This was despite the 104 ton quota (both species included) allocated to the study in 1995 to 1997. *P. delagoae* catches were 89.5 tons in 1994, 50.0 tons in 1995, 30.9 tons in 1996, and 7.4 tons in 1997; of this, 28.1 t (16 %) originated from the experimental phases of the study (Table 4.3). In addition to the lobster catches, 19.8 tons of east coast red crab *Chaceon macphersoni* were caught in 1996, and 20.2 tons in 1997.

### *4.3.2. Biological information*

Catches of *P. delagoae* consisted of equal proportions of males and females (Table 4.4). Most females were sexually mature; exceptions were the North region in 1995 and 1996, and the South region in 1997, where > 50 % of the females were immature. Few ovigerous females were captured throughout, except in 1996 when 70.3 % of the females caught in the South were egg-bearing. The size composition (both sexes combined) of trap-catches differed considerably among the North, Central and South regions (Table 4.4; Fig. 4.2). Small lobsters (CL < 75 mm) dominated catches in the North region, with only a small proportion of lobsters being > 75 mm CL. In the Central region catches consisted mainly of large lobsters with a CL of 90 - 130 mm, with a fair proportion of very large (> 130 mm CL) and small lobsters also present. Although the bulk of the catches made in the South region consisted of

Table 4.1: Number of sampling blocks fished and area covered during the experimental and commercial sampling phases.

| | Total | | Sampled | | | |
|---|---|---|---|---|---|---|
| | | | Experimental phase | | Commercial phase | |
| | Blocks (No.) | Area (sq. km) | Blocks (No.) | Area (sq. km) | Blocks (No.) | Area (sq. km) |
| North region | | | | | | |
| 1994 | 12 | 92.2 | 10 | 77.2 | 12 | 92.2 |
| 1995 | 12 | 92.2 | 10 | 77.2 | 0 | 0 |
| 1996 | 12 | 92.2 | 11 | 83.3 | 5 | 42.7 |
| 1997 | 12 | 92.2 | 12 | 92.3 | 0* | 0 |
| Central region | | | | | | |
| 1994 | 40 | 340.7 | 18 | 158.1 | 9 | 60.8 |
| 1995 | 40 | 340.7 | 34 | 285.3 | 12 | 122.8 |
| 1996 | 40 | 340.7 | 39 | 334.6 | 22 | 189.7 |
| 1997 | 40 | 340.7 | 38 | 326.3 | 0* | 0 |
| South region | | | | | | |
| 1994 | 28 | 413.9 | 12 | 229 | 0 | 0 |
| 1995 | 28 | 413.9 | 28 | 413.9 | 11 | 191.4 |
| 1996 | 28 | 413.9 | 25 | 401.8 | 11 | 152.3 |
| 1997 | 28 | 413.9 | 27 | 401.9 | 0* | 0 |

* There was no coverage of the commercial phase by observers in 1997.

Table 4.2: Sampling effort expressed as the number of long-lines and traps hauled in the experimental and commercial phases of the study in each year.

| | Experimental phase | | | Commercial phase | | |
|---|---|---|---|---|---|---|
| | Lines | Traps | Traps/line | Lines | Traps | Traps/line |
| 1994 | 105 | 11 450 | 109 | 45 | 5 400 | 120 |
| 1995 | 146 | 17 623 | 120.7 | 114 | 13 370 | 117.3 |
| 1996 | 150 | 19 108 | 127.4 | 250 | 29 687 | 118.7 |
| 1997 | 154 | 19 245 | 124.9 | 0 | 0 | 0 |

Table 4.3: Catches made in the experimental and commercial phases of the fishery

| | Experimental phase (t) | Commercial phase (t) | Total (t) |
|---|---|---|---|
| 1994 | 7.1 | 82.4 (4.2)* | 89.5 |
| 1995 | 10.8 | 39.2 (34.7) | 50.0 |
| 1996 | 6.8 | 24.1 (51.0) | 30.9 |
| 1997 | 3.4 | 4.0 (-) | 7.4 |

* The percentage of the commercial catch that was sampled by observers is shown in parenthesis

Table 4.4: Mean carapace length, sex ratio, and the percentages of females that were immature or egg-bearing in samples taken in each year and region.

| | Sample size (n) | Mean CL (mm) | Sex ratio (M:F) | Immature females (%) | Egg-bearing fem. (%) |
|---|---|---|---|---|---|
| North region | | | | | |
| 1994 | 12 335 | 76.1 | 51 : 49 | 21.2 | 0.4 |
| 1995 | 1 927 | 72.9 | 47 : 53 | 57.6 | 14.3 |
| 1996 | 2 826 | 71.2 | 52 : 48 | 57.3 | 1.6 |
| 1997 | 1 263 | 71.9 | 53 : 47 | 47.2 | 1.3 |
| Central region | | | | | |
| 1994 | 5 363 | 101.7 | 51 : 49 | 5.8 | 3.5 |
| 1995 | 8 684 | 110.1 | 49 : 51 | 5.6 | 5.2 |
| 1996 | 11 891 | 105.2 | 50 : 50 | 5.5 | 20.5 |
| 1997 | 3 018 | 95.1 | 48 : 52 | 3.1 | 33.4 |
| South Region | | | | | |
| 1994 | 2 963 | 88.1 | 48 : 52 | 24.5 | 3.3 |
| 1995 | 8 579 | 85.8 | 51 : 49 | 35.4 | 4.3 |
| 1996 | 7 213 | 81.3 | 44 : 56 | 30.5 | 70.3 |
| 1997 | 1 610 | 72.1 | 50 : 50 | 57.1 | 12 |

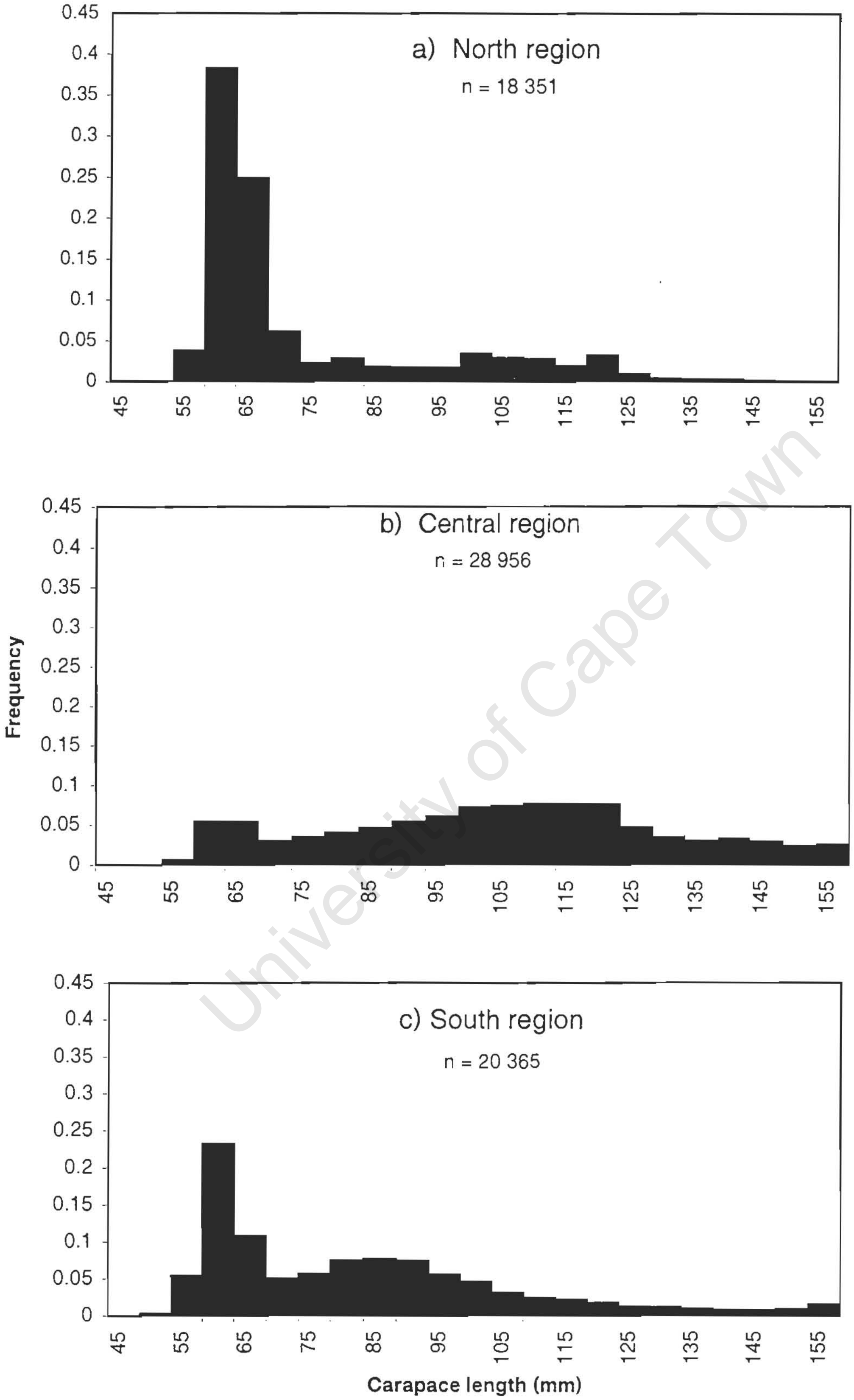

Figure 4.2: Size distribution of *P. delagoae* (sexes combined) caught in traps in the North, Central and South regions during the four years of the experiment

lobsters of 70 - 105 mm CL, a conspicuous peak occurred in the 60 - 69 mm CL interval. These patterns were consistent between years (Groeneveld and Cockcroft, 1997).

There was a consistent decline in the average size of lobsters in two of the three regions over the four years of the study (Table 4.4); average size decreased by 4.2 mm and 16.0 mm CL in the North and South regions respectively. A decrease of 15.0 mm CL (measured over the last three years of the study) was noted in the Central region.

### *4.3.3. Generalized linear model analysis*

Catch per unit effort (CPUE) as the dependent variable was fitted to the independent variables year, region, sampling phase, month and soak time. The model used was of the form

$$ln\,(\text{CPUE} + \delta) = \alpha + \beta_{\text{year}} + \gamma_{\text{region}} + \varrho_{\text{sampling phase}} + \tau_{\text{month}} + \lambda_{\text{soak-time}} + \varepsilon;$$

The independent variables were treated as boolean, taking on a value of either 1 or 0, with the constants $\alpha$, $\beta$, $\gamma$, $\varrho$, $\tau$ and $\lambda$ to be estimated. A constant ($\delta = 0.05$ of the mean CPUE) was added to allow for the occurrence of zero CPUE values. The error term, $\varepsilon$, was assumed to follow a normal distribution.

The GLM residuals (Fig. 4.3) were normally distributed and there was no obvious indication of bimodality or skewness. The model statistics and parameter estimates are listed in Table 4.5. The $r^2$ value indicates that 26.5 % of the variance is explained by the model. Parameter estimates that were significantly different from zero ($p < 0.05$) were $\beta_3$, $\beta_4$, $\gamma_3$, $\varrho_2$ and $\tau_5$. Soak time was not significantly different from zero and therefore does not contribute substantially to the model. Treating soak time as a continuous rather than as a boolean variable made no difference to the model. Month was significant with traps set in September catching less than in other months. Sampling phase was significant, with traps set during the commercial phase catching more than in the experimental phase.

Standardised CPUE was then calculated by applying the formula

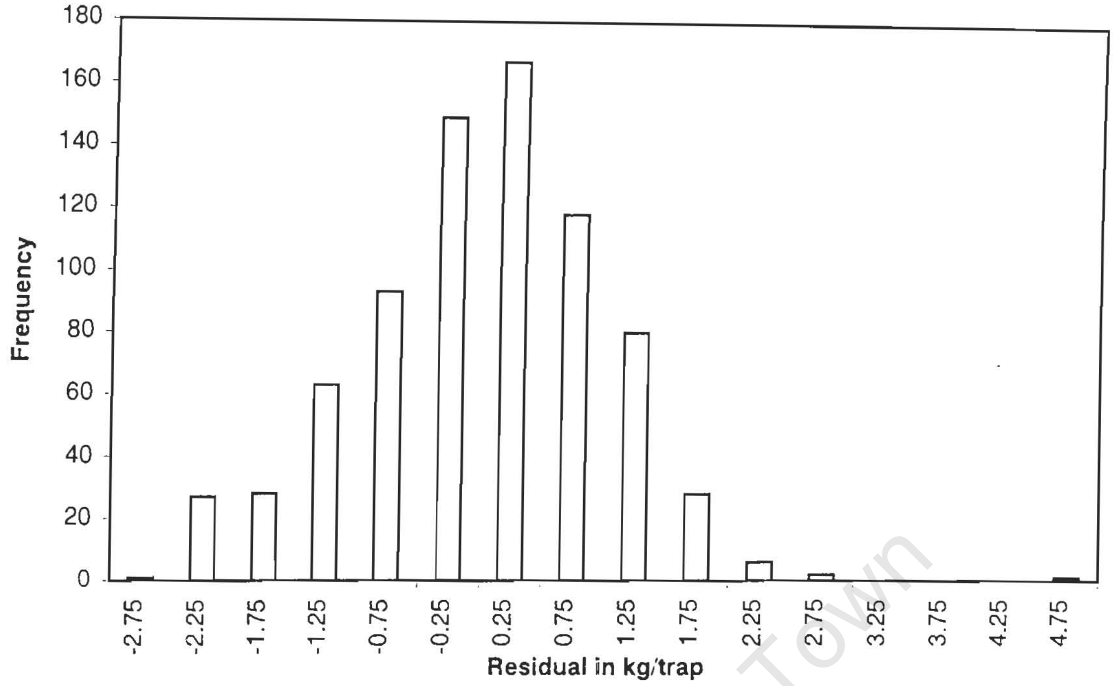

Figure 4.3: Frequency distribution of the residuals resulting from the fit of the GLM model of CPUE versus year, region,sampling phase, month and soak time

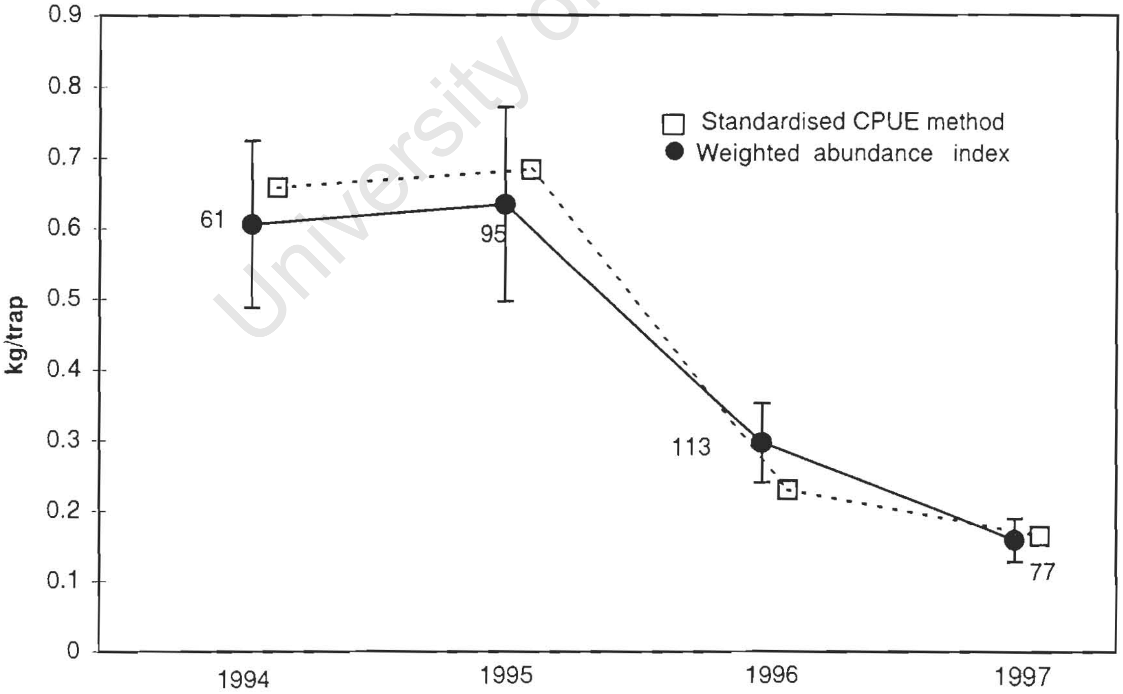

Figure 4.4: Comparison of the overall trends in abundance according to a standardised CPUE (scaled according to a standard month (July), soak-time (36 hrs< soak time < 72 hrs) and sampling phase (commercial phase)) versus an area weighted abundance index

Table 4.5: Estimates of the parameter values of the generalized linear model used to examine the relationships between CPUE for *P. delagoae* and year, region, sampling phase, month and soak-time.

Model statistics are: $r^2 = 0.265$; CV = 77.32; df = 12; F = 26.97, p = 0.0001.

p** , probability associated with the t-test for the H0 hypothesis that the parameter is zero;

* indicates significantly different from zero.

| Variable | Parameter | Estimate | t | p** | s.e. |
|---|---|---|---|---|---|
| ***Intercept*** | $\alpha$ | -1.0117 | -5.56 | 0.0001* | 0.182 |
| ***Year*** | | | | | |
| 1995 | $\beta_2$ | 0.0435 | 0.37 | 0.7092 | 0.1168 |
| 1996 | $\beta_3$ | -0.8153 | -5.51 | 0.0001* | 0.148 |
| 1997 | $\beta_4$ | -1.1317 | -7.65 | 0.0001* | 0.1479 |
| ***Region*** | | | | | |
| Central | $\gamma_2$ | 0.1925 | 1.87 | 0.0621 | 0.1031 |
| South | $\gamma_3$ | -0.3605 | -3.3 | 0.001* | 0.1093 |
| ***Sampling phase*** | | | | | |
| Commercial | $\varrho_2$ | 0.6317 | 7.16 | 0.0001* | 0.0882 |
| ***Month*** | | | | | |
| June | $\tau_2$ | 0.2421 | 1.88 | 0.0602 | 0.1287 |
| July | $\tau_3$ | -0.091 | -0.66 | 0.5126 | 0.1389 |
| August | $\tau_4$ | -0.0688 | 0.44 | 0.6623 | 0.1577 |
| September | $\tau_5$ | -0.9206 | -3.78 | 0.0002* | 0.2438 |
| ***Soak-time*** | | | | | |
| 36-72 hr soaks | $\lambda_2$ | 0.1317 | 1.68 | 0.0924 | 0.0782 |
| > 72 hr soaks | $\lambda_3$ | 0.1539 | 1.66 | 0.0963 | 0.0924 |

$$\text{CPUE}_{\text{STD}} = (e^{\alpha + \beta\ \text{year} + \gamma\ \text{region} + \varrho\ \text{sampling phase} + \tau\ \text{month} + \lambda\ \text{soak-time}} - \delta) * \text{Area}.$$

The standard set of conditions selected were sampling phase ($\varrho_2$, commercial phase), month ($\tau_3$, July) and soak-time ($\lambda_2$, 36 hrs < soak time < 72 hrs). Regional values were weighted according to area and were summed across areas to yield an annual trend. A slight increase in standardised CPUE in the second year of the study (from 0.658 to 0.683 kg/trap) was followed by sharp declines in 1996 (to 0.23 kg/trap) and in 1997 (0.165 kg/trap) (Fig. 4.4).

### *4.3.4 Estimates of abundance*

A combined annual abundance index (including data from the experimental and commercial phases) increased from 0.606 kg/trap in 1994 to 0.634 kg/trap in 1995, but then declined to 0.297 kg/trap in 1996 and 0.159 kg/trap in 1997 (Fig. 4.4); this trend is similar to that shown by the standardised CPUE series.

Estimates of abundance calculated for each of the three regions indicated that the commercial-phase indices were in most cases higher than experimental-phase indices (Fig. 4.5a-c), a result expected given the earlier GLM analysis.

Trends in indices based on the experimental and commercial phases were similar in the North and Central regions (Fig. 4.5a-b). Indices based on the experimental phase increased in both areas in 1995 and then decreased substantially (by 67 % in the North region and by 74 % in the Central region) over the next two years. Indices based on the commercial phase decreased by 38 % between 1994 and 1996 in the North region and by 59 % in the Central region; no commercial fishing was done in any of the three regions in 1997.

In the South region, marked declines were evident in both sampling phases and, for all except the first year, indices were lower than for the other two regions (Fig. 4.5c). Indices based on the experimental phase declined by 84 % over the three year period (from 0.691 to 0.112 kg/trap), and indices based on the commercial phase declined by 51 % between 1995 and 1996 (from 0.54 to 0.26 kg/trap).

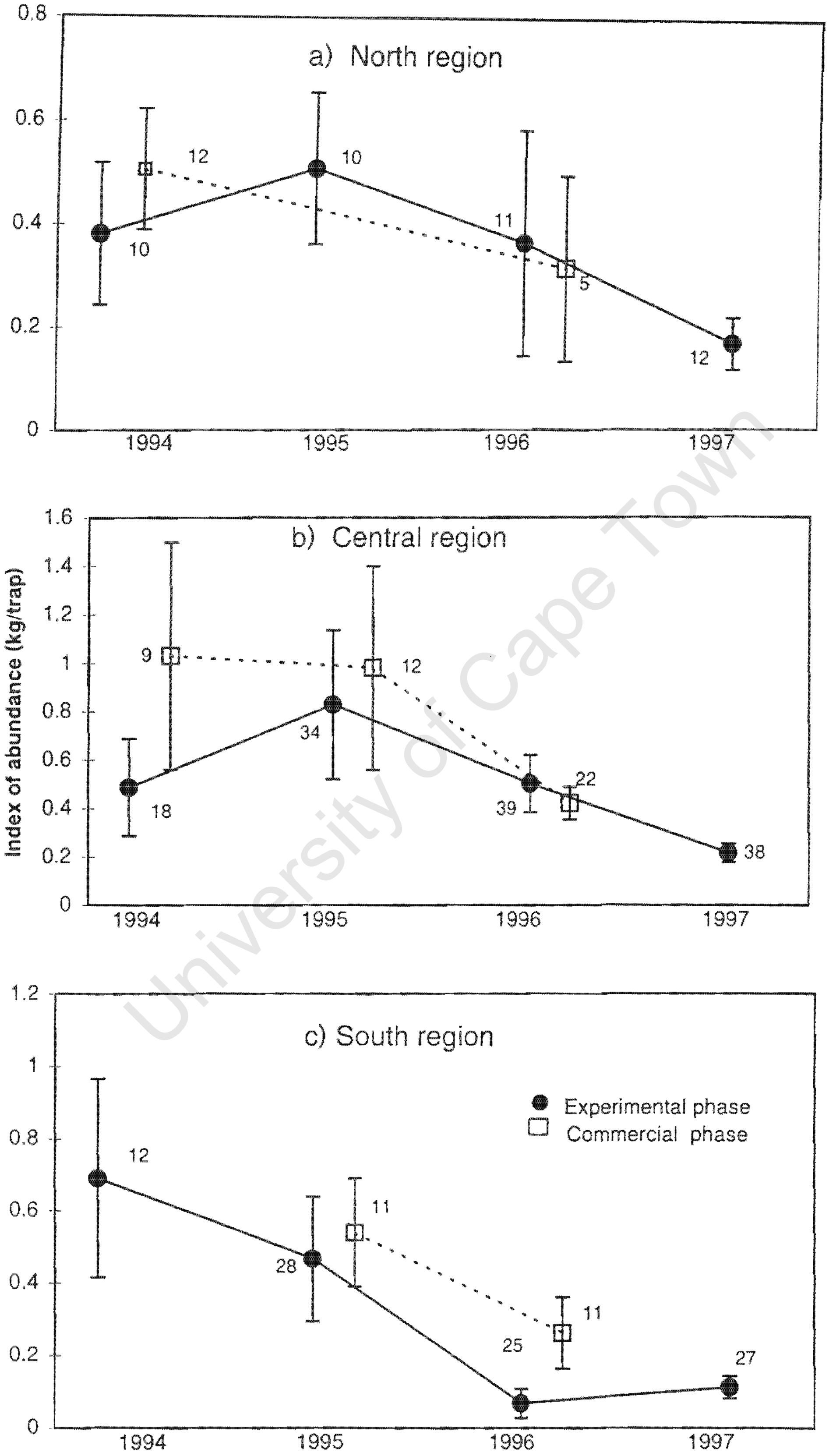

Figure 4.5: Abundance indices calculated from experimental-phase data and commercial-phase data for (a) the North, (b) the Central; and (c) the South regions of the experiment

### 4.4. Discussion

A well-designed abundance survey should accomplish at least two objectives; it should provide an estimate of average lobster density over the entire spatial range where the stock might be found, and it should permit mapping of the spatial distribution of density within this range (Hilborn and Walters, 1992). To meet the second objective, the survey has to deliberately extend beyond the known boundaries of the population distribution. This objective was only partly achieved in the present study. Traps could not reach deeper than 450 m (although trawlers catch *P.delagoae* up to 600 m depth), nor was the population occurring north of the Mozambique border sampled. The pilot study did, however, indicate that *P. delagoae* does not extend beyond 31°S nor to depths < 112 m (Cockcroft *et al.*, 1995).

While stratum boundaries should be treated as fixed in the analysis of any data set where the sampling locations were defined in relation to these boundaries, it is not wise to treat these boundaries as immutable from year to year (Hilborn and Walters, 1992). Most often, as was the case in the present study, the first few surveys reveal that the boundaries could initially have been better placed; the survey design can be improved over time by adjusting stratum boundaries according to this information. However, care must be taken, particularly in the selection of sample sites within each stratum, to ensure that the overall abundance index remains comparable over time (Hilborn and Walters, 1992). The first two surveys of *P. delagoae* (1994 and 1995) clearly showed that this species rarely occurs in the area between Richards Bay and Durban (most likely because of an unsuitable bottom type in this area; *pers. obs.*), and this area was subsequently eliminated from the surveys performed in 1996 and 1997 (Groeneveld, 1996). However, the abundance trends in the three regions (North, Central and South) could be compared over time, as the sampling sites within each remained similar over the 4-year period.

The incorporation of both an experimental and a commercial phase in the sampling strategy makes this study unique compared to other pre-exploitation studies on lobsters (Uchida and Tagami 1984; Polovina 1994). The combination of the two sampling phases provided an economic incentive for fishers to participate in the survey, and provided valuable insights into the resource which would have been missed by using only one approach (an example is the mapping of hotspots and their rates of decline).

Abundance estimates obtained during the commercial phase of the study were higher than those obtained during the experimental phase. During the commercial phase only areas of high abundance were fished, whereas the experimental phase demanded a much wider trap deployment which included areas of both high and low densities of lobster.

The increases in the experimental-phase abundance indices in 1995 in the North and Central regions (Fig. 4.5 a, b) are considered to have resulted from local immigration into areas depleted by fishing in 1994. The slight decrease in the commercial-phase abundance index in the Central region in 1995 (Fig. 4.5 b) and the coinciding increase in mean lobster size in this region (Table 4.4) supports this hypothesis.

Fishing mortality is considered to have been the most likely cause of the decline in both the experimental- and commercial-phase abundance indices in all regions after the second year. Although a decline in catch rates is an expected consequence of the exploitation of a new stock (Hilborn and Walters 1992), the relative scarcity of patches of hard substrata which harbour high densities of *P. delagoae*, and the rapid decline of catches in these 'hotspot' areas suggest a relatively low trap-fisheries potential for this species in South Africa. Rocky patches within the preferred depth range of this species (200 - 450 m) are distributed intermittently along the coast and occur in a narrow band owing to the steepness of the continental shelf in the region. No areas of high lobster density could be found in an extensive area of soft / muddy substrata between Richards Bay (~ 29° S) and Durban (~ 30°S).

There is no evidence to substantiate the notion that the decline in the abundance index over the four years of the survey was as a result of a decline in lobster catchability by traps, or as a result of variable catch rates. Miller (1990) reviewed the many factors that may affect catch rates by traps, e.g. soak time, trap saturation, the physical habitat, trap design, bait, and the life cycle of the target species. This study was designed to circumvent many of these factors:

the same fishing vessels were used each year, standard plastic traps were used throughout, and a standard bait was used. Furthermore, to minimize variations in catchability as a result of fishing during different stages of the life cycle of *P. delagoae*, the experiment was conducted during the same months in each year (May to September). Monthly variations in catch rates observed during this period were accounted for in the GLM standardization.

The influence of soak-times on catch rates was investigated in the GLM, and was found to be insignificant; this could be explained by trap saturation within the shortest soak time period considered, by rapid depletion of lobster in the area of bait attraction or by the loss of bait or bait attraction after a relatively short period of immersion. Trap saturation within 36 hours (the shortest soak time considered) is unlikely, because many traps came up empty or with small catches adjacent to traps with larger catches (traps spaced 10 fathoms apart). The lack of difference in trap-catches after soak-times of < 36 h, 36 - 72 h or > 72 h suggests either that the lobster numbers within the area of bait attraction were depleted rapidly or that the bait lost its attraction or was consumed after 36 hours. Mackie *et al.* (1980) showed that the release rate of amino acids from fish flesh decreased by an order of magnitude over 24 h, and Zimmer-Faust (1993) found that the attractiveness of mussel flesh to spiny lobster decreased by about two-thirds after being aged in seawater for 24 h. Also, Loewenthal *et al.* (2000) showed that bait inundated for longer than 12 hrs resulted in a decline in catch rates of *J. lalandii.*

The size compositions of lobsters caught in the three regions were distinctive, with mostly small lobsters being caught in the North region. Larger lobsters, and a wider range of sizes, were caught in the Central and South regions, with the Central region having the largest lobsters on average (Fig. 4.2). Chapter 5 addresses depth distribution, recruitment and migration, and their effect on the size composition in the different regions.

The average size of lobsters caught in the North and South regions declined markedly over the four-year period. Large lobster are more valuable than the smaller size classes and were therefore targeted during the commercial phase of the study, by fishing in the 200 - 300 m depth zone (see Chapter 5). The increase in the mean size of lobsters caught in the Central region in 1995 suggests the discovery of unexploited patches of lobster in that year, or that large lobsters had immigrated into the fishing grounds. A sharp decrease in mean lobster size in the Central and South regions in 1996 and 1997 clearly reflects a rapid depletion of the larger size classes in these regions. No obvious trends in sex ratios were evident in the trap catches during the study period, with males and females equally represented in each of the three areas.

The survey was initially designed to fall outside the peak summer breeding season for this species (Berry 1973; Kondritskiy 1976; Brinca and Palha de Sousa 1983) and, as expected, the frequency of egg-bearing females in all three regions was generally low throughout the study. The notable exception in the South and Central regions in 1996 is considered to be largely as a result of a delayed breeding season rather than the one-week earlier start to sampling in that year. Fluctuations in the timing of breeding seasons have also been shown for *Panulirus argus*, *P. guttatus*, *P. interruptus*, *P. japonicus* and *Jasus lalandii* (Chubb, 1994), and the control thereof depends on a suite of environmental conditions (Chittleborough 1976; Lipcius 1985; Lipcius and Herrnkind 1987; Deguchi *et al.* 1991).

The combination of experimental and commercial sampling phases over the four-year survey has highlighted the relative scarcity of patches of hard substrata that harbour high densities of *P. delagoae*, and the 75 % decrease in the combined abundance index together with a marked decrease in mean lobster size demonstrates the vulnerability of these hotspots to trap-fishing. The next two chapters further investigate the biology of *P. delagoae* relative to the trap-fishery, focussing on the recruitment of juveniles to the fishing grounds (Chapter 5) and on developing the most appropriate way in which biological and economic aims can be achieved in the fisheries for this species (Chapter 6).

# Chapter 5

# Recruitment and migration of *P. delagoae*

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## 5.1. Introduction

Anecdotal information dating from the 1970s suggests that *P. delagoae* is a migratory species. Based on the composition of trawl catches, Berry (1972, 1973) noted that constant local movement occurs and that males and females, and juvenile and adult lobsters, appear to segregate during certain times of the year. The tendency of egg-bearing females to gather in dense concentrations in shallow water (150 – 160 m) in summer, as well as an off-shore movement to deeper water (>300 m) in autumn and winter was also noted by various researchers (Koyama, 1971; Berry, 1972, 1973; Kondritskiy, 1976). Furthermore, Berry (1972, 1973) noted that small, sexually immature *P. delagoae* tend to occur in the deepest extreme of the depth range inhabited by this species, whereas sexually mature animals inhabit shallower areas. Juvenile specimens with a CL < 50 mm are altogether absent from trawl catches at all depths; this was apparent even when using a prawn trawl net with a 40-mm mesh in the cod-end (Berry, 1973). All these observations point towards migratory behaviour. However, to date, no study has been dedicated towards clarifying the patterns of migration exhibited by this species, or towards establishing the advantages or ecological gains of these migrations.

Generally, migrations of spiny lobsters have been shown to achieve a variety of specific biological needs, such as food, shelter, genetic mixing, reproduction or recruitment (Herrnkind, 1980). Clearly, such migrations must have evolved as a response to the physical and oceanographical characteristics of the region inhabited by the population. In the case of *P. delagoae*, it is likely that migration behaviour developed as an adaptation to their existence in a narrow shelf-region dominated by a strong well-defined western-boundary current system; the Agulhas Current flows swiftly (with speeds of > 2 m.s $^{-1}$ at its core; Schumann, 1987) and deeply along the east coast of South Africa. The current and narrow shelf structure serve to characterise this east coast coastal ocean as an identifiable entity, in which the effect of the current extends well onto the shelf, although at a decreased speed on the inshore boundary (Schumann, 1987).

Herrnkind (1980) reviews the research approaches used to assess palinurid movements. He lists (1) monitoring the biological attributes of the commercial catch; (2) wide-area tag and recapture programs; (3) direct collection and observation by divers; (4) ultrasonic telemetry; (5) monitoring of physical variables concurrent with field sampling; and (6) correlated behavioural and physiological study of captive specimens. Of these methods, monitoring of the commercial catch has the advantages that it covers wide geographical areas and consistently produces large quantities of data over a long term, at a low cost. It generally reveals major redistributions of migrants and their biological features (e.g., size and stage of sexual development). More precise information on movements, i.e. distance and direction moved and rate of movement, may be provided by tag-recapture studies; reviews of the techniques used for spiny and clawed lobsters are presented by Herrnkind (1980) and Haakonsen and Anoruo (1994).

Based on the observations made by earlier researchers (Koyama, 1971; Berry, 1972, 1973; Kondritskiy, 1976), and the possible effect of the Agulhas Current on the ecology of *P. delagoae*, I proposed three distinct migration pathways for *P. delagoae*: recruitment of juveniles from the deeper extreme of the depth range to the more inshore adult population; seasonal inshore-offshore migrations of adult lobsters for reproductive and moulting purposes; and longshore migration. It was the aim of this chapter (the second of three chapters based on the 4-year trap-survey undertaken off the eastern coast of South Africa) to investigate these proposed migration patterns of *P. delagoae* using tagging data and information on size composition collected across gradients of depth, latitude and the width of the continental slope. The likely influence of the Agulhas Current on the ecology of the population, and the advantages of migration as an adaptation for survival under these conditions, are discussed.

## 5.2. Materials and methods

Information on the size composition and sex ratios of *P. delagoae* in relation to depth, latitude and the width of the continental slope was collected in 1994, during the pilot study of the 4-year experimental trap-fishery for this species (see Cockcroft *et al.*, 1995; Groeneveld *et al.*, 1995; Chapter 4). Three commercial fishing boats were used to deploy standard commercial bottom long-lines in accordance with the sampling schedule listed in Table 5.1. Each long-line was equipped with 110 - 135 top-entry plastic traps or, in some cases, with 70 - 135 top-entry steel traps. The fishing vessels carried 8, 10 and 20 long-lines respectively.

The study area (Fig. 5.1), extending from the Mozambique border at 27°00'S to just south of Port St Johns (31°55'S), was sampled along 14 transects spaced at 15' intervals north of 28°S and at 25' intervals south of 28°S (Table 5.1). Transects extended from east to west (Fig. 5.1) and, where conditions allowed, long-lines with traps were set roughly parallel to the coast at depth intervals of 75 m, 150 m, 250 m, 300 m, 350 m and 400 m along each transect (Table 5.1). Limited time, the steep gradient of the sea-floor in the northern sector and in the southern extreme of the southern sector, and weather and current conditions influenced the numbers of traps that could be set at each transect. Traps remained underwater for a standard soak time of 36 - 72 hours. Data derived from longer soak-times were excluded from the analyses, because it was suspected that lobsters are able to escape from traps after an extended period of entrapment.

The numbers and sex of rock lobsters caught were recorded by depth and latitude, and the carapace lengths (CL ± 1 mm) of the first 100 caught with each long-line measured. Carapace lengths were measured dorsally from the posterior edge of the carapace to the tip of the rostral spine.

Generalized linear models (*GLMs*) were used to examine relationships between CL, depth and latitude. The influence of continental slope-width on CL was examined by using the same models, but by replacing the latitude variables with a single slope-width covariate, which was

Table 5.1: Latitudes of sampling transects, width of the continental slope between the 200- and 500-m depth contours at each transect, and fishing effort expressed as the numbers of traps soaked for 36-72 h.

| Transect number | Latitude | Slope width (km) | Numbers of traps by depth (m)* | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | 75 | 150 | 250 | 300 | 350 | 400 |
| 1 | 27° 00'S | 4.9 | MR | 270 | 0 | 405 | 1015 | 750 |
| 2 | 27° 15'S | 5.2 | MR | MR | MR | 70 | 205 | 955 |
| 3 | 27° 30'S | 4.4 | MR | MR | 135 | 405 | 340 | 345 |
| 4 | 27° 45'S | 3.7 | MR | MR | MR | 220 | 220 | C |
| 5 | 28° 00'S | 4.8 | MR | MR | 330 | 770 | 440 | C |
| 6 | 28° 25'S | 4.0 | 490 | 490 | 330 | 1575 | 330 | 245 |
| 7 | 28° 50'S | 7.6 | 490 | 865 | 440 | 1860 | 110 | 710 |
| 8 | 29° 15'S | 8.3 | 220 | 330 | 110 | 1100 | 0 | 0 |
| 9 | 29° 40'S | 5.0 | 220 | 220 | 110 | 110 | 220 | 0 |
| 10 | 30° 05'S | 8.0 | 110 | 110 | 330 | 660 | 220 | 110 |
| 11 | 30° 30'S | 5.2 | 0 | 220 | 465 | 805 | 0 | 0 |
| 12 | 30° 55'S | 0.8 | 0 | 220 | 110 | 220 | 110 | 0 |
| 13 | 31° 20'S | 2.8 | 0 | 220 | 220 | 0 | 0 | C |
| 14 | 31° 55'S | 2.8 | 0 | 110 | 330 | 110 | 110 | C |

* MR denotes a marine reserve that extends three nautical miles offshore, and C denotes strong currents that prohibited sampling in deep water. No traps were set in some positions because of bad weather, limited time or proximity to shipping.

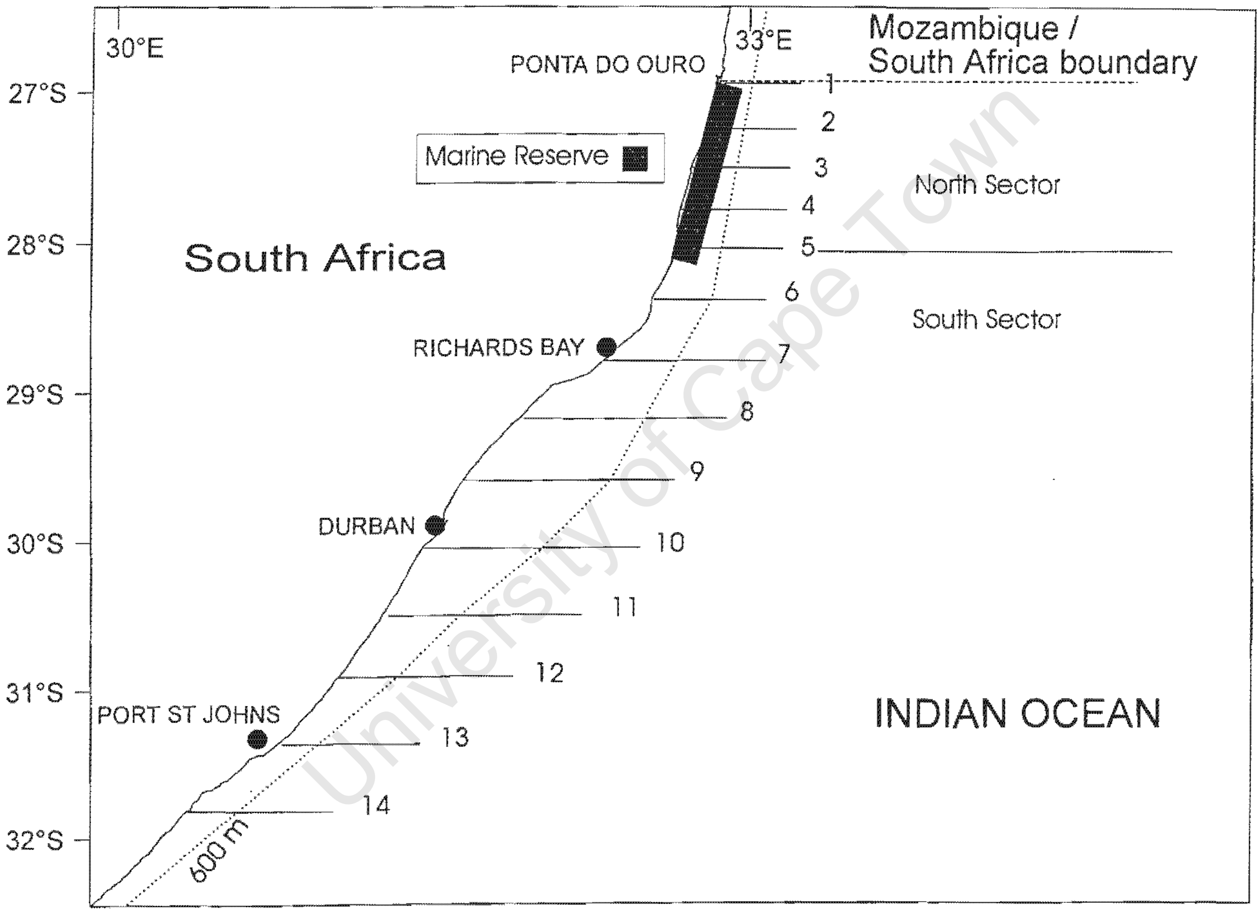

Figure 5.1: Diagram of the sampling area along the Kwazulu-Natal coast of South Africa showing the 14 transects at which long-lines with traps were set (not to scale).

obtained by measuring the distances between the 200 m and 500 m depth contours on each transect, using charts (SAN Series, Scale - 1: 150 000) (Table 5.1). The distances were converted to km, and ranged from 0.8 to 8.3 km. The SAS software system (Anon., 1989) was used to perform the analyses.

Healthy lobsters of all sizes and both sexes were tagged, and were released within an hour after tagging, after recording sex, CL, location, depth and date of release. Standard plastic T-bar tags (Hallprint, TBA-1) were used; these are 5 cm long, of which 4 cm consists of a bright yellow plastic strip bearing a unique identifying number. Tags were inserted into the abdominal musculature of each lobster, dorso-laterally between the posterior edge of the carapace and first abdominal segment, or between the first and second abdominal segments. On-board observers, commercial trawl fishers in South Africa, and commercial trap and trawl fishers off Mozambique returned recaptured tagged lobsters, along with information on the date and location of recapture.

Lobsters that had moved < 20 km were assumed not to have migrated alongshore; this cut-off distance was based on the characteristics of the fishery, which employs a long-line system of trap-deployment. Long-lines with traps are generally 1 – 2 nm (1.9 – 3.6 km) long, and the reported capture location of a tagged lobster can therefore not be considered to be more accurate than the actual recapture location ± 3.6 km. Strong ocean currents pre-dominate in the sampling area, and the recorded tag-release location (at the sea surface) is therefore expected to be inaccurate, taking into account current-driven displacements over the 150 – 400 m descent to the sea-bottom. No formal estimate of the error was made, however, it is unlikely that the horizontal displacement will exceed 2.5 nm (4.6 km). The combined maximum error associated with distance moved by lobsters is therefore 8.2 km.

## 5.3. Results

No *P. delagoae* were captured in traps set at 75 m depth, and this depth interval was therefore excluded from further analyses. A total of 19 435 lobsters was captured in the 22 500 traps set at other depths during 1994, and 48.2% of these were males. Sex ratios, shown as the ratio of males to females, remained equal at 250 m (1:1.03), 300 m (1:1.05), 350 m (1: 0.97) and 400 m (1: 1.06), but at 150 m, where the sample size of 633 lobsters was relatively small, males were in a distinct minority (1: 3.12). Carapace length of captured lobsters ranged between 50 and 170 mm, lobsters < 50 mm being conspicuously absent from trap catches.

Catch rates of steel and plastic traps were not significantly different (t-test, $p>0.05$) in 13 long-line sets (six lines with 135 steel traps and seven with 135 plastic traps) of 48-h duration at a depth range of 300-400m along Transect 1.

As a first investigative model, CL as dependent variable was fitted to the independent variables sex, depth and latitude. The model used was of the form

$$CL_{M+F} = \alpha + \beta \text{ sex} + \sum_{i=1}^{4} \tau_i \text{depth}_i + \sum_{i=1}^{13} \delta_i \text{lat}_i \quad (1).$$

Here sex, $\text{depth}_i$, and $\text{lat}_i$ are boolean variables, taking the value of either 0 or 1, with the constants $\alpha$, $\beta$, $\tau_i$ and $\delta_i$ to be determined.

The model was fitted to the data shown in Figs. 5.2 (males) and 5.4 (females), with resulting statistics $r^2 = 0.71$ and C.V. = 154. The model results showed that males at a given depth and latitude were on average 6.02 (± 2.89 SE) mm larger than females, a t-test indicating that the probability of the null hypothesis, $\beta = 0$, being true was 0.011. The probability that $\alpha = \tau_i = \delta_i = 0$ was also insignificant ($p < 0.0001$). Further analyses were therefore carried out separately for males and females.

### *5.3.1. Male carapace length by depth, latitude and width of slope*

The model was subsequently modified to exclude the sex variable. Fitting it to the data in Fig. 5.2 gave a value of $r^2$ of 0.758. The results showed that male CL decreases as depth increases from 150 m to 400 m (Fig. 5.2). An example of this can be seen at 28°50'S (Transect 7), where small numbers of large individuals with an average CL of 140 (± 16.96 SD) mm occurred in shallow water (Fig. 5.2a), compared to larger numbers of small individuals with

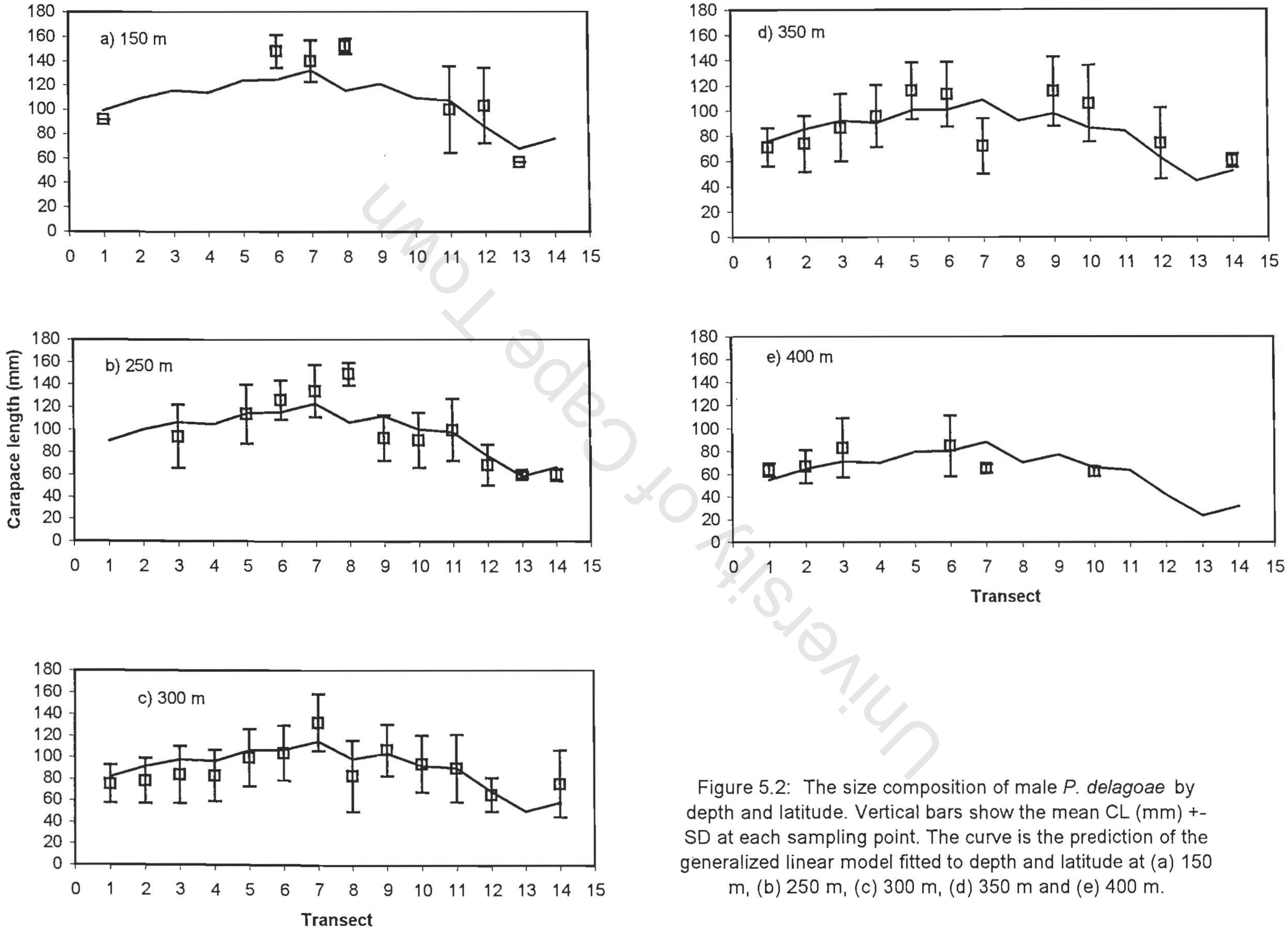

Figure 5.2: The size composition of male *P. delagoae* by depth and latitude. Vertical bars show the mean CL (mm) +- SD at each sampling point. The curve is the prediction of the generalized linear model fitted to depth and latitude at (a) 150 m, (b) 250 m, (c) 300 m, (d) 350 m and (e) 400 m.

an average CL of 64.75 (± 3.74 SD) mm in deeper water (Fig. 5.2e).

The largest male lobsters at all depths were caught between 28° (Transect 5) and 29°40'S (Transect 9, Fig. 5.2), mean CL declining sharply towards the north and south of these latitudes. The parameter estimates of the CL, depth and latitude model (Table 5.2) were large negative values for the area south of 30°30'S ($\delta_{12}$, $\delta_{13}$ and $\delta_{14}$), indicating small sizes, as opposed to large positive values for the area between 28° and 29°40'S ($\delta_5$ to $\delta_9$), indicating larger sizes there. Parameter estimates indicated intermediate sizes at 27°15'S ($\delta_2$), 27°30 ($\delta_3$), 27°45'S ($\delta_4$), 30°05'S ($\delta_{10}$) and 30°30'S ($\delta_{11}$).

The influence of width of the continental slope on CL was examined next, using the same model as before, but by replacing the latitude variables with a single slope-width covariate. The model (Fig. 5.3), with an $r^2$ of 0.41, showed that slope-width had little influence on male CL, because the parameter estimate for slope width (3.19 ± 1.86 SE) mm was not significant ($p = 0.0702$).

### *5.3.2. Female carapace length by depth, latitude and width of slope*

As with males, a model with female CL as dependent variable was fitted to the independent variables depth and latitude ($r^2 = 0.745$). This indicated that depth affected the size distribution of females in a manner similar to that of males (Fig. 5.4). Larger females were found at 150 m, and size decreased out towards 400 m.

The largest females at all depths occurred between 27°45'S (Transect 4) and 28°50'S (Transect 7) and at 29°40'S (Transect 9), size declining sharply south of this last latitude (Fig. 5.4). The parameter estimates for the area south of 30°30'S ($\delta_{12}$, $\delta_{13}$ and $\delta_{14}$) were large negative values (Table 5.3), indicating small females. Females at 29°15'S (Transect 8) were much smaller than at surrounding latitudes (Fig. 5.4), but this estimate is likely to have been biased by the fact that females were captured at only a single depth (300 m).

In the model where female CL was fitted to width of the continental slope and depth, slope-width was, as before, taken as a covariate and the depth variables as boolean. The model (Fig.

Table 5.2: Generalized linear models examining the relationships between male CL, depth, latitude and the width of the continental slope between the 200- and 500-m isobaths

<table>
<tr><th>Variable</th><th>Parameter</th><th>Estimate</th><th>t#</th><th>p</th><th>SE</th></tr>
<tr><td colspan="6">Depth and latitude<br>$$CL_M = \alpha \sum_{i=1}^{4} \tau_i depth_i + \sum_{i=1}^{13} \delta_i lat_i$$<br>$r^2 = 0.758$, mean CL = 89.66 mm, CV = 170.74, df = 17, F = 5.35</td></tr>
<tr><td>Intercept</td><td>$\alpha$</td><td>99.28</td><td>6.47</td><td>0.0001**</td><td>15.34</td></tr>
<tr><td>250 m</td><td>$\tau 2$</td><td>-9.09</td><td>-0.61</td><td>0.545</td><td>14.86</td></tr>
<tr><td>300 m</td><td>$\tau 3$</td><td>-17.45</td><td>-1.22</td><td>0.232</td><td>14.29</td></tr>
<tr><td>350 m</td><td>$\tau 4$</td><td>-23.71</td><td>-1.54</td><td>0.135</td><td>15.43</td></tr>
<tr><td>400 m</td><td>$\tau 5$</td><td>-44.33</td><td>-2.9</td><td>0.007*</td><td>15.28</td></tr>
<tr><td>Transect 2</td><td>$\delta 2$</td><td>9.43</td><td>1.12</td><td>0.27</td><td>8.38</td></tr>
<tr><td>Transect 3</td><td>$\delta 3$</td><td>16.1</td><td>2.02</td><td>0.053</td><td>7.94</td></tr>
<tr><td>Transect 4</td><td>$\delta 4$</td><td>14.46</td><td>0.66</td><td>0.516</td><td>21.99</td></tr>
<tr><td>Transect 5</td><td>$\delta 5$</td><td>24.3</td><td>2.52</td><td>0.018*</td><td>9.65</td></tr>
<tr><td>Transect 6</td><td>$\delta 6$</td><td>24.98</td><td>3.24</td><td>0.003*</td><td>7.71</td></tr>
<tr><td>Transect 7</td><td>$\delta 7$</td><td>32.78</td><td>4.52</td><td>0.001*</td><td>7.24</td></tr>
<tr><td>Transect 8</td><td>$\delta 8$</td><td>16.12</td><td>0.83</td><td>0.412</td><td>19.36</td></tr>
<tr><td>Transect 9</td><td>$\delta 9$</td><td>21.77</td><td>1.53</td><td>0.136</td><td>14.19</td></tr>
<tr><td>Transect 10</td><td>$\delta 10$</td><td>10.25</td><td>1.17</td><td>0.252</td><td>8.77</td></tr>
<tr><td>Transect 11</td><td>$\delta 11$</td><td>7.95</td><td>0.97</td><td>0.339</td><td>8.19</td></tr>
<tr><td>Transect 12</td><td>$\delta 12$</td><td>-13.48</td><td>-0.73</td><td>0.474</td><td>18.57</td></tr>
<tr><td>Transect 13</td><td>$\delta 13$</td><td>-31.72</td><td>-1.35</td><td>0.186</td><td>23.55</td></tr>
<tr><td>Transect 14</td><td>$\delta 14$</td><td>-23.75</td><td>-1.29</td><td>0.208</td><td>18.43</td></tr>
<tr><td colspan="6">Depth and width of the continental slope<br>$$CL_M = \alpha + \beta slope\ width + \sum_{i=1}^{5} \tau_i\ depth_i$$<br>$r^2 = 0.41$, mean CL = 88.33 mm, CV = 230.21, df = 5, F = 5.78</td></tr>
<tr><td>Intercept</td><td>$\alpha$</td><td>93.16</td><td>4.56</td><td>0.0001**</td><td>20.43</td></tr>
<tr><td>Slope width</td><td>$\beta$</td><td>3.19</td><td>1.86</td><td>0.0702</td><td>1.71</td></tr>
<tr><td>250 m</td><td>$\tau 2$</td><td>-19.43</td><td>-1</td><td>0.3238</td><td>19.45</td></tr>
<tr><td>300 m</td><td>$\tau 3$</td><td>-11.78</td><td>-0.64</td><td>0.528</td><td>18.5</td></tr>
<tr><td>350 m</td><td>$\tau 4$</td><td>-24.82</td><td>-1.29</td><td>0.2034</td><td>19.21</td></tr>
<tr><td>400 m</td><td>$\tau 5$</td><td>-42.58</td><td>-2.26</td><td>0.0292*</td><td>18.84</td></tr>
</table>

* Significantly different from the intercept of the model

** Significantly different from zero

# t-test for the H0 hypothesis that the parameter = 0

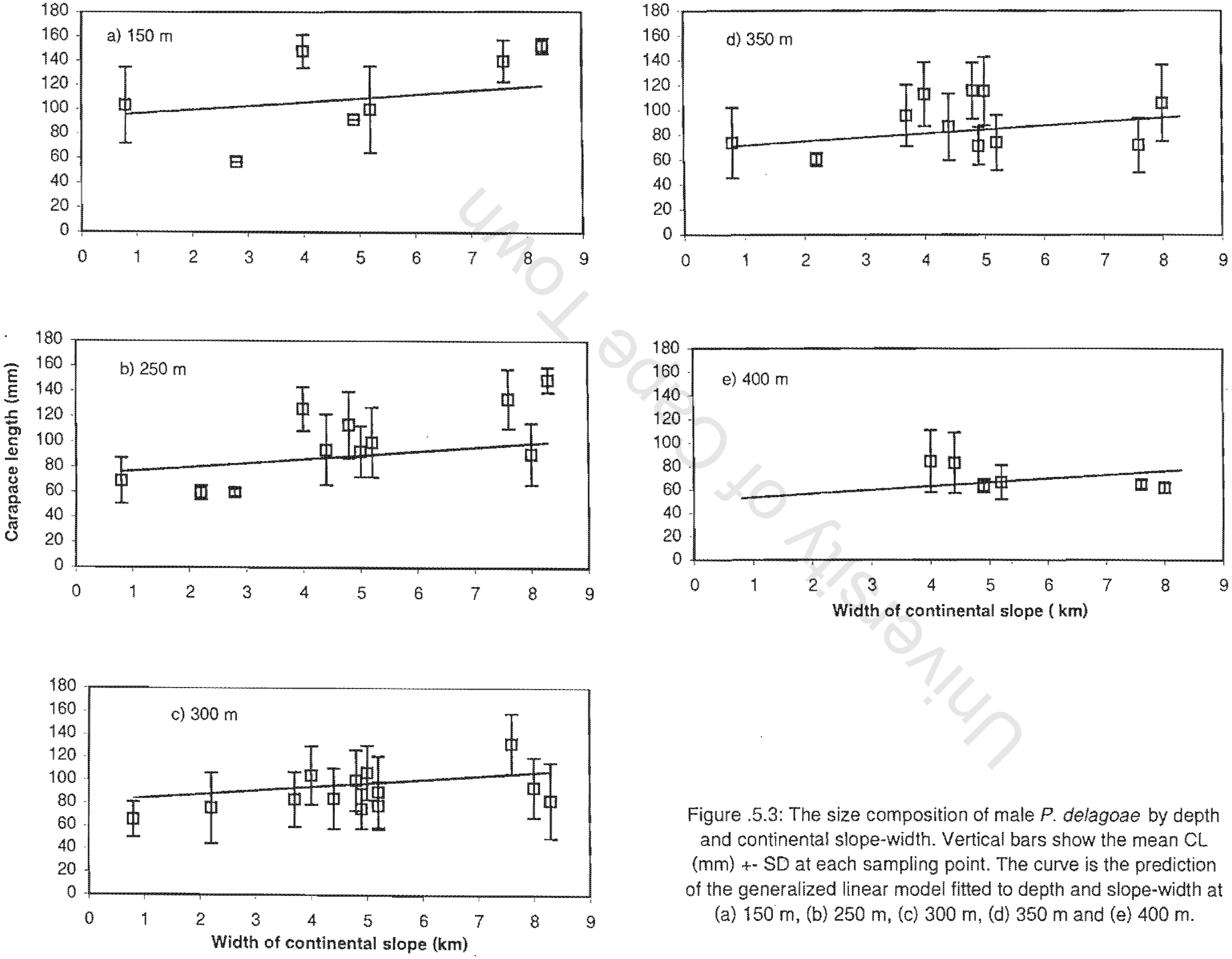

Figure .5.3: The size composition of male *P. delagoae* by depth and continental slope-width. Vertical bars show the mean CL (mm) +- SD at each sampling point. The curve is the prediction of the generalized linear model fitted to depth and slope-width at (a) 150 m, (b) 250 m, (c) 300 m, (d) 350 m and (e) 400 m.

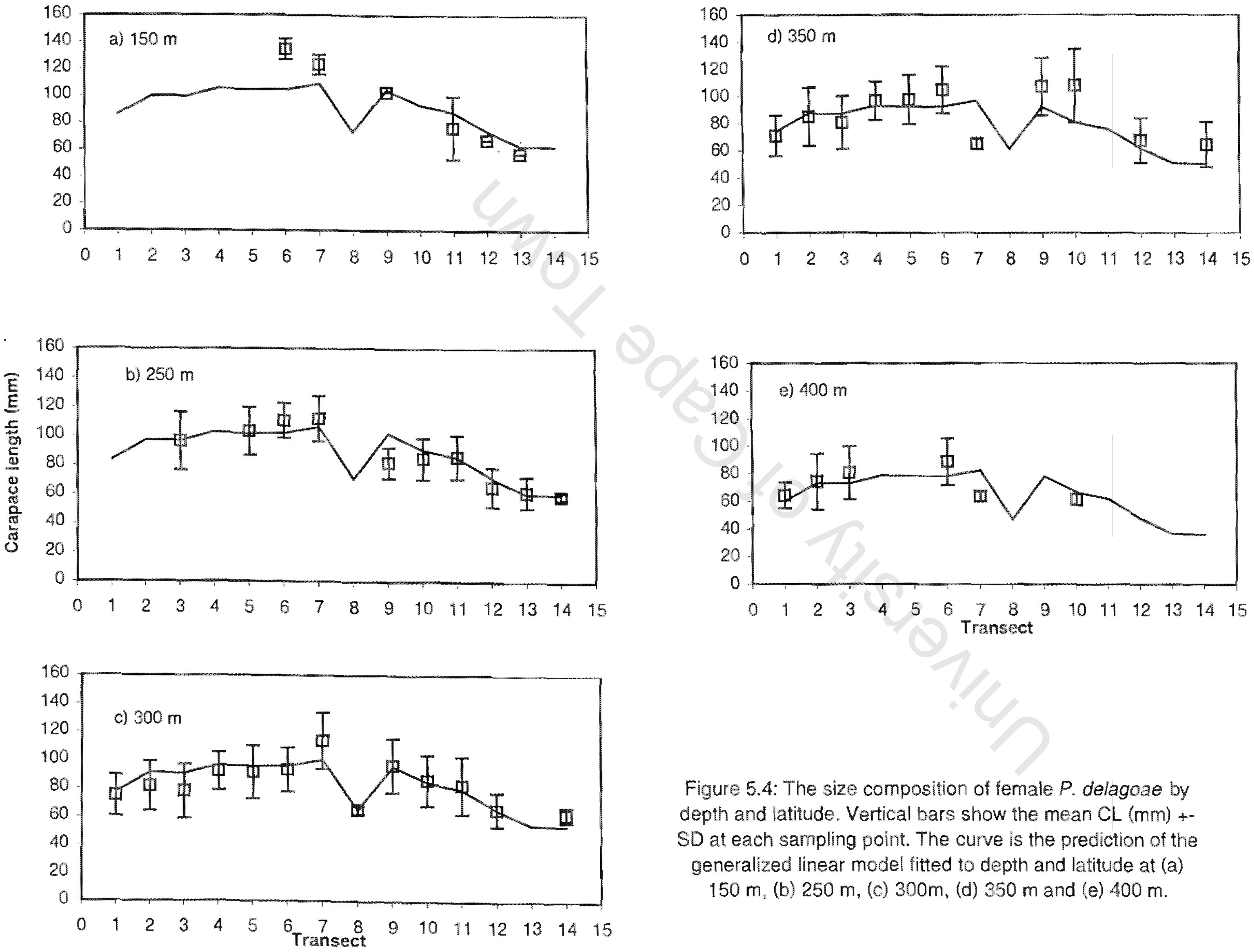

Figure 5.4: The size composition of female *P. delagoae* by depth and latitude. Vertical bars show the mean CL (mm) +- SD at each sampling point. The curve is the prediction of the generalized linear model fitted to depth and latitude at (a) 150 m, (b) 250 m, (c) 300m, (d) 350 m and (e) 400 m.

Table 5.3: Generalized linear models examining the relationships between female CL, depth, latitude and the width of the continental slope between the 200- and 500-m isobaths

| Variable | Parameter | Estimate | t# | p | SE |
|---|---|---|---|---|---|
| Depth and latitude | | | | | |
| $CL_F = \alpha \sum_{i=1}^{4} \tau_i \, depth_i + \sum_{i=1}^{13} \delta_i \, lat_i$ | | | | | |
| $r^2 = 0.727$, mean CL = 83.68 mm, CV = 147.56, df = 17, F = 4.08 | | | | | |
| Intercept | $\alpha$ | 86.23 | 10.22 | 0.0001** | 8.44 |
| 250 m | $\tau 2$ | -2.53 | -0.31 | 0.758 | 8.15 |
| 300 m | $\tau 3$ | -8.65 | -1.2 | 0.242 | 7.24 |
| 350 m | $\tau 4$ | -12.13 | -1.41 | 0.169 | 8.59 |
| 400 m | $\tau 5$ | -26.24 | -3.21 | 0.004* | 8.19 |
| Transect 2 | $\delta 2$ | 13.29 | 2.17 | 0.039* | 6.13 |
| Transect 3 | $\delta 3$ | 12.91 | 2.09 | 0.046* | 6.17 |
| Transect 4 | $\delta 4$ | 18.92 | 1.56 | 0.13 | 12.11 |
| Transect 5 | $\delta 5$ | 17.76 | 2.41 | 0.024* | 7.38 |
| Transect 6 | $\delta 6$ | 18.22 | 2.95 | 0.007* | 6.17 |
| Transect 7 | $\delta 7$ | 22.48 | 3.62 | 0.001* | 6.21 |
| Transect 8 | $\delta 8$ | -12.98 | -0.55 | 0.586 | 23.51 |
| Transect 9 | $\delta 9$ | 18.07 | 1.47 | 0.154 | 12.31 |
| Transect 10 | $\delta 10$ | 6.73 | 0.91 | 0.37 | 7.36 |
| Transect 11 | $\delta 11$ | 1.71 | 0.27 | 0.789 | 6.3 |
| Transect 12 | $\delta 12$ | -12.5 | -0.88 | 0.388 | 14.24 |
| Transect 13 | $\delta 13$ | -23.5 | -1.26 | 0.217 | 18.58 |
| Transect 14 | $\delta 14$ | -23.81 | -1.19 | 0.247 | 20.08 |
| Depth and width of the continental slope | | | | | |
| $CL_F = \alpha + \beta \, slope\ width + \sum_{i=1}^{5} \tau_i \, depth_i$ | | | | | |
| $r^2 = 0.33$, mean CL = 83.68 mm, CV = 188.76, df = 5, F = 3.85 | | | | | |
| Intercept | $\alpha$ | 86.86 | 7.38 | 0.0001** | 11.76 |
| Slope width | $\beta$ | 1.54 | 1.11 | 0.2722 | 1.38 |
| 250 m | $\tau 2$ | -3.93 | -0.4 | 0.694 | 9.91 |
| 300 m | $\tau 3$ | -6.7 | -0.76 | 0.4499 | 8.79 |
| 350 m | $\tau 4$ | -12.31 | -1.26 | 0.2141 | 9.74 |
| 400 m | $\tau 5$ | -23.94 | -2.64 | 0.0119* | 9.07 |

* Significantly different from the intercept of the model

** Significantly different from zero

\# t-test for the H0 hypothesis that the parameter = 0

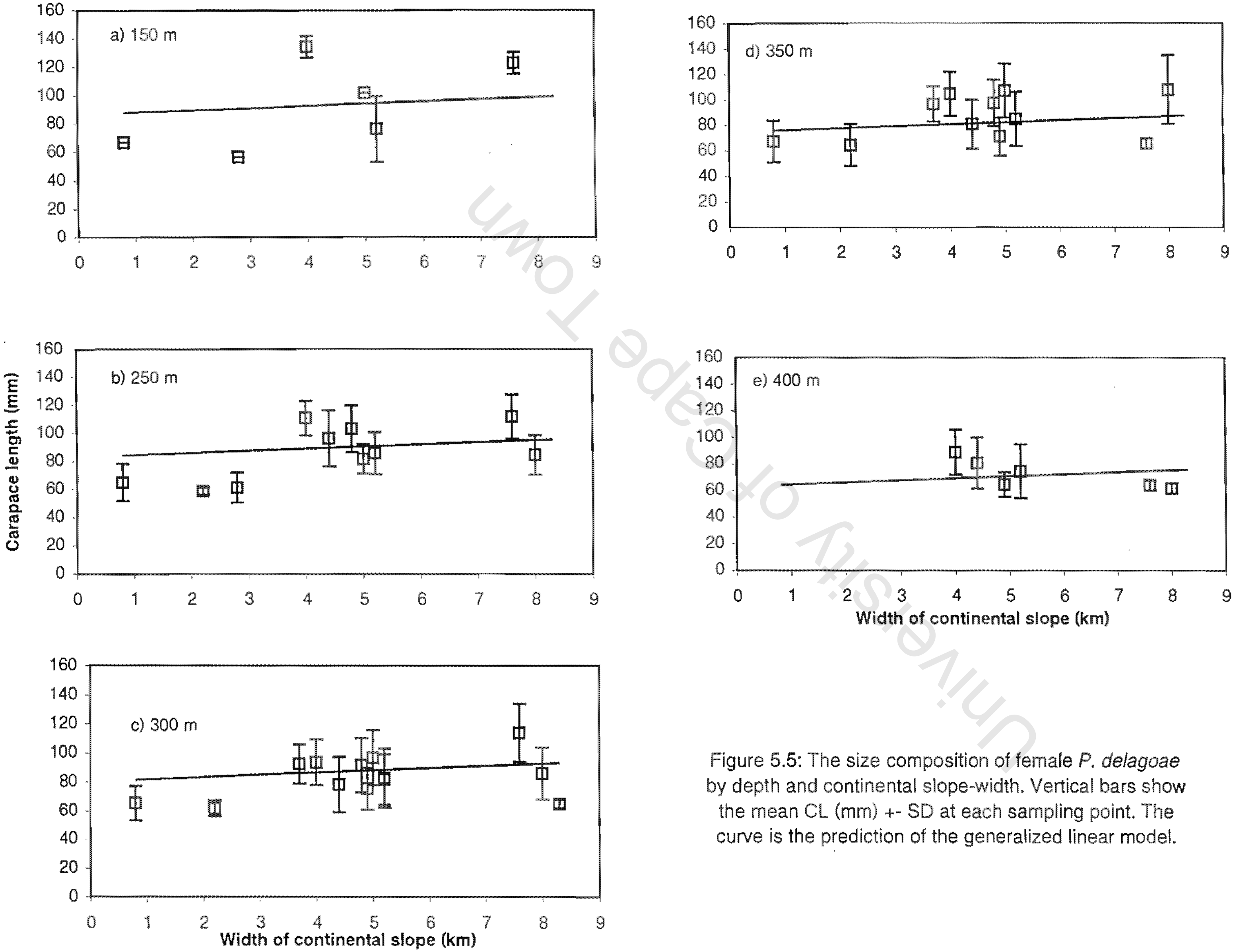

Figure 5.5: The size composition of female *P. delagoae* by depth and continental slope-width. Vertical bars show the mean CL (mm) +- SD at each sampling point. The curve is the prediction of the generalized linear model.

5.5) did not fit the data well ($r^2 = 0.33$) and the parameter estimate for slope-width was not significantly different from zero ($p = 0.2722$; Table 5.3) indicating that slope-width has no significant influence on female CL. The magnitude of the female slope-width parameter (1.54 ± 1.11 SE) was comparable to the equivalent parameter obtained for males ($\beta_M = 3.19$ mm).

### *5.3.3. Analysis of tag-recaptures*

A total of 7654 lobsters was tagged between 1995 and 1997; 4130 in 1995, 1524 in 1996 and 2000 in 1997. Of these, 383 (5.0 %) had been recaptured by March 2000. Most of the recaptures (342 or 89.3 %) were made between 1995 and 1997, by the trapping vessels participating in the experimental fishery. Thirty-five recaptures (9.1 %) were made by South African trawlers on the fishing grounds between Durban and the Mozambique border, between 1998 and 2000. Seven lobsters (1.8 %) were recaptured north of Maputo in Mozambique, between July and November of 1999 (Fig. 5.6).

The time period between tagging and recapture ranged between 28 and 940 days (~ 3 years) (Table 5.4), with the median times at large indicating that most tagged lobsters were at liberty for at least a year before being recaptured. This year-interval is as a result of the short annual fishing seasons (May to September), with tagging normally taking place towards the latter half of each fishing season. Lobsters were therefore more likely to be caught in subsequent fishing seasons, than in the short period between tagging and the closure of fishing in that season.

The proportions of recaptured lobsters that had moved alongshore, the straight-line distances covered and the direction of movement (north-eastward or south-westward) are shown in Table 5.4. Of the 363 recaptures which had information on recapture location, 320 (88.2 %) had moved < 20 km. Forty-seven lobsters (12.7 % of the recaptures) had moved > 20 km alongshore; most of those (33 lobsters) had moved > 100 km (Table 5.4). The direction of the alongshore movement was overwhelmingly north-eastward (88.4 % of migrants moving > 20 km), with the remaining 11.6 % (5 lobsters) having moved south-westward (Fig. 5.6). Only a NE – SW axis of movement was considered because the narrow continental slope between 100 – 400 m depth along the stretch between Durban and the Mozambique border restricts

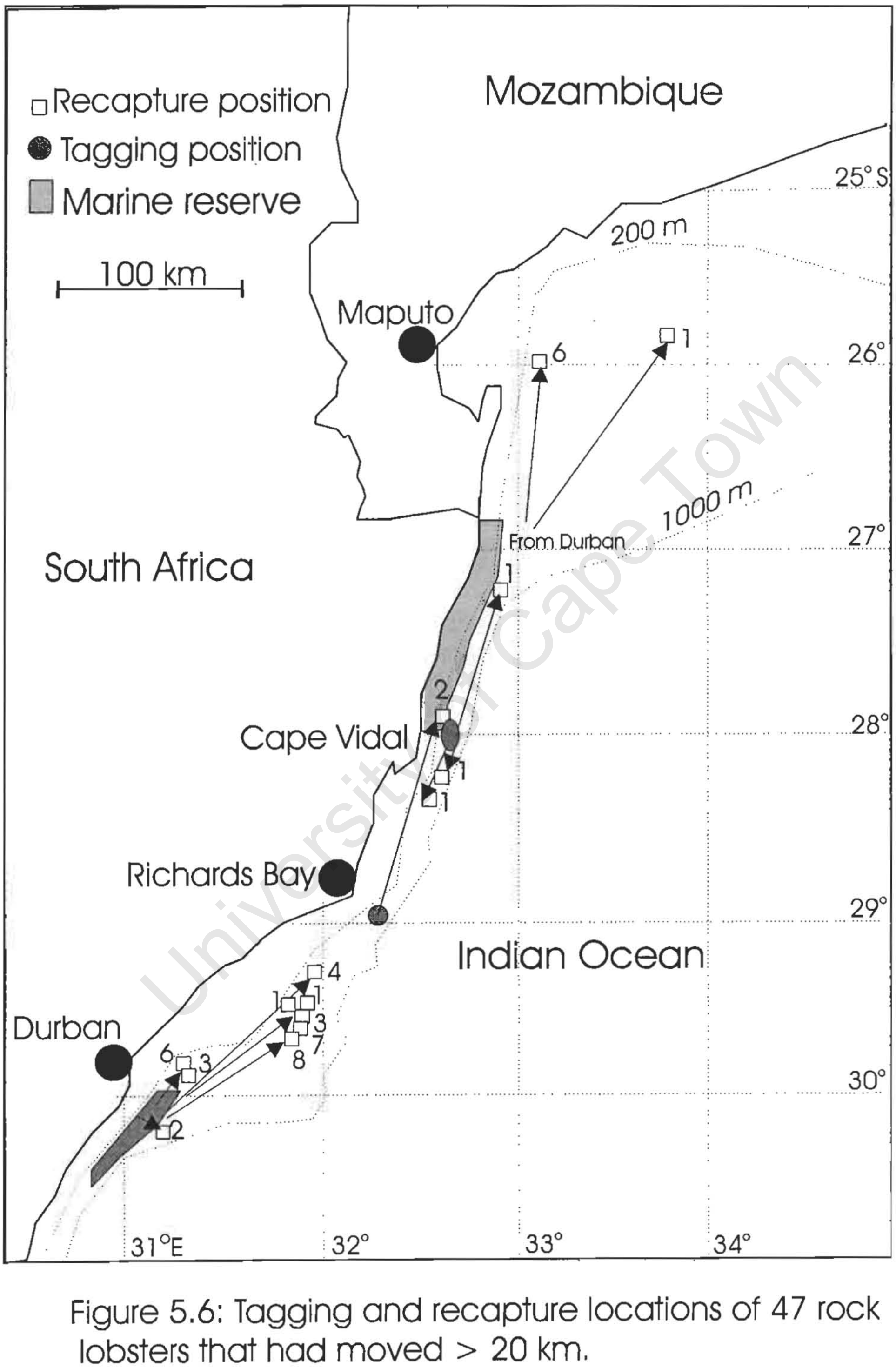

Figure 5.6: Tagging and recapture locations of 47 rock lobsters that had moved > 20 km.

Table 5.4: Summary of distances and directions migrated, and time at liberty of tagged *P. delagoae*.

| Distance categories (km) | Recaptures per category | | | | | | Time at liberty | |
|---|---|---|---|---|---|---|---|---|
| | Totals | | Males | | Moved northwards | | Range (days) | Median (days) |
| | (n) | (prop.) | (n) | (prop.) | (n) | (prop.) | | |
| 0 - 10 | 296 | 0.82 | 100 | 0.34 | | | 28 - 716 | 315 |
| 11 - 20 | 24 | 0.07 | 10 | 0.42 | | | 36 - 359 | 280 |
| 21 - 50 | 3 | 0.01 | 1 | 0.33 | 2 | 0.67 | 357 - 940 | 387 |
| 51 - 100 | 7 | 0.02 | 3 | 0.43 | 6 | 0.86 | 183 - 940 | 512 |
| 101 - 200 | 27 | 0.07 | 6 | 0.22 | 24 | 0.89 | 292 - 689 | 547 |
| > 200 | 6 | 0.02 | 3 | 0.50 | 6 | 1.00 | > 700 | |

movement along the NW – SE axis to distances < 20 km.

Recaptures of male and female tagged lobsters in the sample that had moved > 20 km suggest that both sexes participate in the alongshore migration (Table 5.4). The preponderance of females in recaptures is as a result of their abundance in the original tagging samples; in 1996 the sex ratio of the tagging sample was 533 males vs. 991 females (35 % males).

The size composition of tagging samples show that only small lobsters (CL < 65 mm) migrated substantial distances alongshore (Fig. 5.7). The ratio of migrants (lobsters that had moved > 20 km) to residents in the 55 mm CL-class indicate that most tagged individuals (63 %) in that size class had migrated > 20 km alongshore before recapture. The ratios of migrants to residents were much lower in the 60 mm CL-class (37 %) and especially in the 65 mm CL-class (4 %), showing that lobsters with a CL > 65 mm do not move alongshore in substantial numbers. Considering that the CL at which *P. delagoae* females reach 50 % maturity lies between 67 mm CL (where 50 % of females have ovigerous setae, i.e. they are theoretically mature) and 72 mm CL (the minimum length at which 50 % of females bear eggs, i.e they are functionally mature; Groeneveld, 2000), the alongshore migration appears to be limited to juvenile or sexually immature lobsters. This theory is strongly supported by field data; none of the migrant females (n = 30) exhibited well-developed ovigerous setae at the time of tagging.

Estimates of migration rates of lobsters that had moved > 20 km ranged between 0.03 and 0.58 $km.d^{-1}$. These estimates are based on straight-line measurements of distances migrated between tagging and recapture locations, and therefore underestimate the actual rate of movement, as it is unlikely that lobsters move along straight lines. Furthermore, it cannot be assumed that recaptures were made while individuals were *en route*, or shortly after arrival at a destination; the possible incorporation of excess time into the calculation of migration rate may further deflate estimates of rate. The highest estimates are therefore likely to more accurately reflect actual migration rates. Six lobsters (16 % of lobsters that had migrated between 20 and 200 km) recorded migration rates between 0.53 and 0.58 $km.d^{-1}$, and based on these recaptures, it is suggested that the rate of alongshore migration of juvenile *P.*

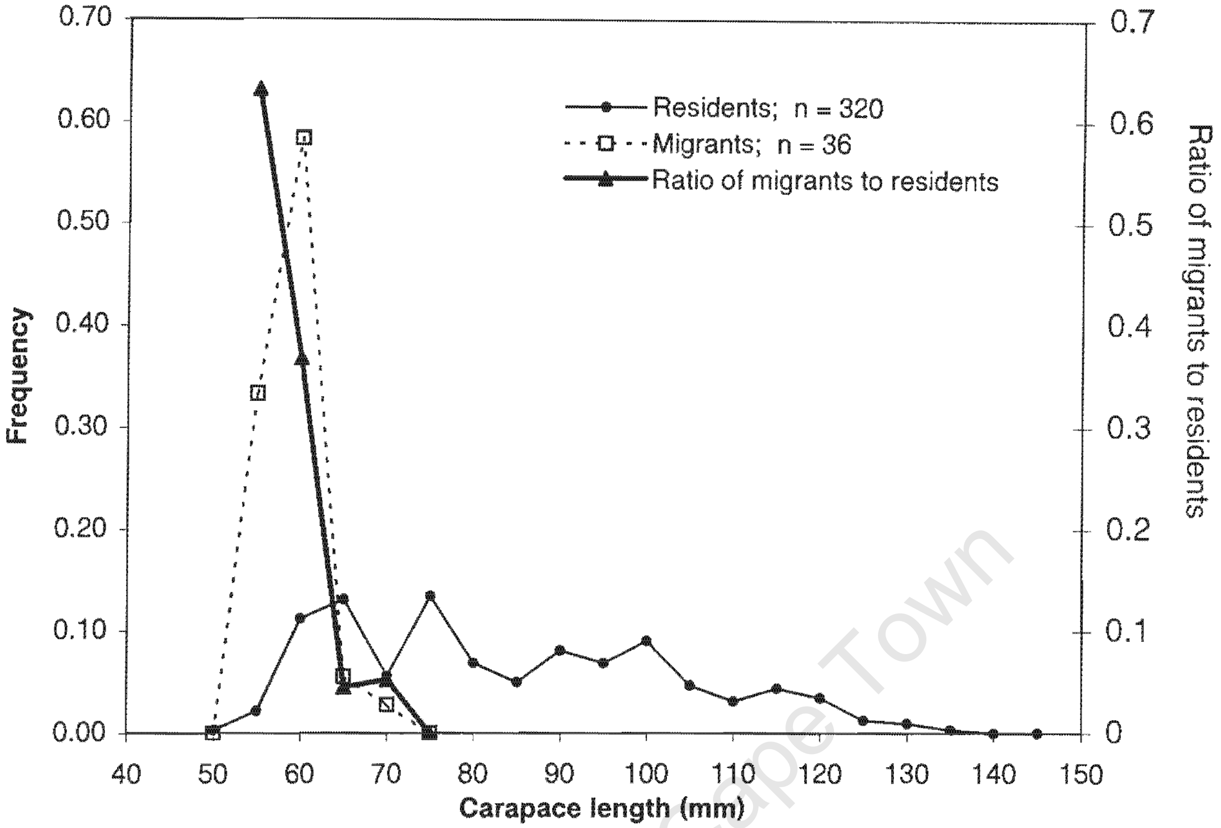

Figure 5.7: Size composition at tagging of migrant lobster versus residents, and the ratio per 5-mm size class of tagged lobsters that had migrated versus those that had not.

*delagoae* is ~ 0.55 km.d $^{-1}$.

### 5.4. Discussion

The predictive value of the GLMs used to examine CL is based on the assumption that there is no selection of size, sex or life stage by the gear. Although this assumption is not entirely valid (see Miller, 1990 for a review of the effectiveness of crab and lobster traps), the observed systematic trends in size composition across depths and latitudes suggest that any selective characteristics of the traps were overshadowed by trends in population size composition.

The GLMs indicated that depth is the most important parameter influencing the size distribution of male and female *P. delagoae.* Small lobsters occurred at the deepest interval (400 m), with CL increasing towards the shallower depth intervals; the largest individuals occurred at the shallowest 150 m depth interval. The size gradient was less evident in the 250 – 350 m depth interval, and lobsters of intermediate size were caught there. The absence of lobsters at 75 m depth indicate that the inshore boundary of the distribution of *P. delagoae* occurs somewhere between 75 and 150 m depth.

The absence of juvenile *P. delagoae* with a CL < ~ 55 mm from catches over hard-bottom substrata surveyed by traps and from traditional soft-bottom trawling grounds (Berry, 1972, 1973; Brinca and Palha de Sousa, 1983) suggests that larvae settle outside the 75 - 600 m depth range accessed by the two fishing methods. Berry (1973) postulated that larvae settle deeper than 600 m and that juveniles then migrate inshore, reaching the deeper fishing grounds (400 m) at a CL > 55 mm. Such a gradual shoreward migration of juvenile *P. delagoae,* and of adults from 400 m to 250 m, may also be inferred from the present study. Although the bulk of the adult population was observed in the 250 – 350 m depth interval during this study, it was clear that the inshore migration continues to shallower depths, culminating at ~ 150 m.

The interpretation of lobster size distribution across a depth gradient could be complicated by seasonal inshore-offshore migrations. Adults are known to migrate seasonally inshore-offshore between 150 and 350 m depth (Koyama, 1971; Kondritskiy, 1976), and such migrations have been ascribed to breeding (Berry, 1972, 1973; Koyama, 1971; Kondritskiy, 1976) and moulting (Koyama, 1971; Kondritskiy, 1976). Dense aggregations of egg-bearing females have been recorded in shallow water (155 - 300 m) during summer (Koyama, 1971; Berry, 1972). In autumn and winter the adult population migrates to depths greater than 300 m to moult and mate (Koyama, 1971; Berry, 1973; Kondritskiy, 1976). The present study was conducted during the winter of 1994 (June – August). The occurrence of the bulk of the adult population between 250 and 350 m depths confirms the findings of Koyama (1971), Berry (1973), and Kondritskiy (1976), that the adult population occurs in deeper water during the winter period.

The factors responsible for the inshore-offshore migration have not yet been established. However, considering that the Agulhas Current flows much slower on the shelf (depths < 200 m) than offshore of the shelfbreak (Schumann, 1987), it is conceivable that larvae that hatch on the shelf would be less likely to be caught up in the fast-moving core of the current than larvae that hatch in deeper water. An inshore migration of egg-bearing females to depths as shallow as 150 – 160 m may therefore have developed as a mechanism to reduce the displacement effect of the current on recently hatched larvae.

After depth, latitude was the most important parameter influencing *P. delagoae* size distribution. Size increased from 27°S (Transect 1) to 28°S (Transect 5), reached a maximum between 28° and 29° 40'S (Transects 6 to 9), and then decreased towards 30°55'S to 31°55'S (Transects 12 to 14). The small average CLs in the latter three transects occur at the southern-most extreme of the distribution of *P. delagoae;* it is likely that the small average size of lobsters in this area is related to sub-optimal habitat for this species at the extreme edge of its distribution. The smaller average CLs between 27 and 28°S (compared with those between 28° and 29°40'S) may be related to the sampling method; only deep stations (where smaller lobsters were caught) could be sampled in much of this area because of the existence of the Maputaland marine reserve which stretches 3 nm seawards from the shore, and includes most shallow stations between 27° and 28°S (see Table 5.1). No significant relationship existed between the width of the continental slope and CL of either male or female lobsters.

The results of the tagging study clearly show that north-eastward alongshore migration of both male and female juveniles of *P. delagoae* occurs along the eastern coast of South Africa, and along the southern coast of Mozambique. This alongshore migration is superimposed on the inshore migration of juveniles, from depths > 600 m to the 400 m depth interval, and to depths as shallow as 150 m by adult *P. delagoae*.

The scale of the north-eastward migration suggested in this study, both in terms of the proportion of the population involved (12.7 %) and the distance covered (mostly < 200 km), is likely to be an underestimate. Industry representatives have frequently reported the recapture of tagged lobsters in Mozambican waters, however, because of the absence of formal cooperative links between the Mozambican and South African fisheries, few of these tagged lobsters are returned to Marine and Coastal Management. The straight-line distance between the South African fishing grounds off Durban (where the lobsters recaptured in Mozambican waters had originally been tagged) and the southern-most Mozambican fishing grounds off Maputo is ~ 500 km. This indicates that the longshore migration of *P. delagoae* juveniles is more extensive than is suggested by this study.

The north-eastward migration of juvenile *P. delagoae* is directly counter to the south-westward flowing Agulhas Current in the region between southern Mozambique and Durban; the current flows swiftly (up to 2 $m.s^{-1}$; Schumann, 1987) and deeply along this stretch of the coast. Similar migrations of juvenile or small mature spiny lobsters against the prevailing current or net coastal flow (also called contranatant movement; Meek, 1915) has been shown for *J. verreauxi* off New Zealand and southern Australia, *J. edwardsii* off New Zealand (McKoy, 1983; Booth, 1984, 1997), *P. cygnus* off Western Australia (Phillips, 1983) and *P. ornatus* in the gulf of Papua New Guinea (Moore and McFarlane, 1984). The estimated migration rate of *P. delagoae* (0.55 $km.d^{-1}$) is similar to those of three other spiny lobster species, *Jasus verreauxi* (0.61 $km.d^{-1}$; Booth, 1984), *Panulirus ornatus* (0.61 $km.d^{-1}$; Moore and McFarlane, 1984) and *Panulirus cygnus* (0.62 $km.d^{-1}$; Phillips, 1983).

Long-distance contranatant movements are not restricted to spiny lobsters, but have also been shown for other decapods, such as scylarid lobsters (*Ibacus* sp.; Stewart and Kennelly, 1998) and crabs (*Cancer pagurus*; Edwards, 1967). Contranatant movement is likely to have evolved to counter the displacement effect of currents on the distribution of pelagic larvae; species distribution may otherwise be displaced in the direction of the currents that transport larvae. *P. delagoae* appears to fit this pattern, as larvae that hatch along the coast may be caught up in the Agulhas Current, and would then be displaced south-westward. It is suggested that the alongshore migration pattern for this species has developed to counteract the displacement effect of the Agulhas Current on pelagic larvae. However, this theory hinges on various unknown factors; intrinsically the potential for displacement by currents depends on the length of the larval phase and on the vertical migratory behaviour of phyllosoma larvae (see Phillips and McWilliam, 1986) – as such, the location and pattern of settlement of post-larvae are likely to be affected by advective processes in the region, such as coastal currents, eddies, wind-driven surface currents and fronts. A detailed study of the spatial and temporal distribution of phyllosoma, relative to the oceanographic features of the region, would be needed to confirm the theory that *P. delagoae* phyllosoma are, in fact, being displaced south-westward.

The long-distance migrations shown for *P. delagoae* in this study do not imply that this species does not also utilise other methods to retain phyllosoma larvae in the vicinity of the parent populations, or to return widely distributed larvae to their origin. The oceanic processes that may influence larval delivery were reviewed by Cobb (1997) and may include oceanic gyres, coastal currents, eddies, upwelling, wind-driven surface currents and fronts. In fact, the isolated populations of *P. delagoae* occurring on the seamounts south of Madagascar cannot be sustained by migration, and larval replenishment to these localities must occur through oceanic processes. Several authors have shown that advective processes alone may not be able to ensure larval delivery, and that mid and late-stage phyllosoma larvae would have to be able to position themselves in the water column (Phillips, 1981; Chiswell and Booth, 1999). Lobster pueruli are also known to be good swimmers that can sustain swimming speeds of 6 to 46 $cm.s^{-1}$ (Phillips and Olsen, 1975; Lyons, 1980; Macmillan *et al.*, 1992). None of these behavioural mechanisms have yet been investigated for *P. delagoae*, and it is quite possible that a combination of migrations by juveniles and larval behaviour is used to ensure recruitment.

Neither the size composition nor the tagging information could be used to assess the inshore-offshore migrations by adult lobsters for breeding or moulting purposes (see Koyama, 1971; Berry 1972, 1973; Kondritskiy 1976). Size composition data could not be used across seasons, because sampling was restricted to winter months only. Tagging data were considered to have too large a margin of error, associated with the location of tagging and recapture, to meaningfully support an analysis of onshore-offshore migration; the 8.2 km combined maximum error associated with the distance moved by lobsters is greater than the width of the continental slope (between 150 and 500 m) at all but one of the transects sampled. Likewise, the reported depths of tag-release and recapture were not considered to be accurate enough to support analyses of onshore-offshore migration.

It is concluded that *P. delagoae* is highly migratory, with three possible migration processes occurring during its benthic life history. Two processes, namely an inshore recruitment to the adult habitat and a north-eastward alongshore migration of juveniles were clearly identified in this chapter. The third, a seasonal inshore-offshore migration in the 150 – 350 m depth interval could not be assessed. However, the depth-based size composition analysis showed the adult population to be concentrated in the 250 – 350 m depth interval during winter; this observation agrees with those of earlier researchers.

# Chapter 6

## Stock assessment of *P. delagoae*: ecology and economics as criteria for choosing between trap and trawl fisheries

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### 6.1. Introduction

The trapping experiment for *P. delagoae* off South Africa discussed in Chapters 4 and 5 provided a time series of reliable fisheries data and ecological information for the 1994 to 1997 period. To date, this information has been used to establish the response of the population to trap-fishing, in terms of trends in relative abundance (see Chapter 4; Groeneveld *et al.*, 1995; Groeneveld and Cockcroft, 1997), and to determine the size distribution of the population relative to depth and latitude (see Chapter 5; Cockcroft *et al.*, 1995). The latter study provided insights into the recruitment of juvenile lobsters, which move from deeper water to the shallower adult population, and into directional northward longshore migrations of lobsters, against the flow of the southward-moving Mozambique Current.

In the present chapter, the trapping information, together with limited data on the size composition and catches from the multispecies crustacean trawl fishery off South Africa, is used for a stock assessment of *P. delagoae* in South African waters. More specifically, the aims of this chapter are to estimate growth rates, size at sexual maturity and natural mortality of *P. delagoae*, and to use these parameters in a deterministic length-based cohort analysis to assess the impact of the fisheries on the resource. A length-based Thompson and Bell analysis was used to predict the impact of various prospective fishing strategies on the population biomass and yield. A trade-off between the trap and trawl fisheries is discussed, and the most appropriate fishing method is suggested, based on economic and ecological criteria.

## 6.2. Materials and methods

### *6.2.1 Sampling strategy*

#### *6.2.1.1 Trapping*

A detailed description of the trap-sampling procedure followed during the 4-year experimental fishery is provided in Chapter 4. Briefly summarized, commercial rock lobster trap-fishing vessels accompanied by scientific observers sampled the South African east coast between the Mozambican border (27°S) and a point south of Port St Johns (32°S) (Fig. 6.1). The vessels followed a systematic sampling procedure (see Chapter 4; Groeneveld and Cockcroft, 1997) between 75 and 425 m depth. Light plastic traps (in sets of 100 – 200 traps per long-line) were deployed for time intervals of 24 – 96 hours. Captured lobsters were counted and sexed, and the carapace lengths (CL ± 1 mm) of random samples of lobsters were measured mid-dorsally, from the posterior edge of the carapace to the tip of the rostral spine. The presence or absence of ovigerous setae or eggs on females was also recorded.

#### *6.2.1.2. Trawling*

Catches of crustaceans made by the trawl fishery have been monitored since 1988. Catch records include the date, depth, position (Fig. 6.1) and the breakdown of trawl catches by species. Lobster catches were available in three broad commercial whole wet-mass categories: < 400 g / lobster; 401 – 1000 g / lobster; and > 1000 g / lobster, which correspond to the length categories CL < 85 mm; CL 86 - 118 mm; and CL > 118 mm (Whole wet mass $= 0.0018 \text{ CL}^{2.7704}$: see Chapter 3; Groeneveld and Goosen, 1996).

A rough length distribution was constructed by converting numbers per 5-mm length class (obtained from a historic trawling sample collected by Berry (1973)) to corresponding mass classes. These were distributed among the three broad commercial mass categories and were raised proportionally, within each category, to reflect the average catch in that category over the period 1994 to 1997. The resulting masses were then converted back to numbers per 5-mm length class, assuming that the mass distribution within each of the three commercial categories had remained constant, despite fluctuations of categories between 1969 and 1994

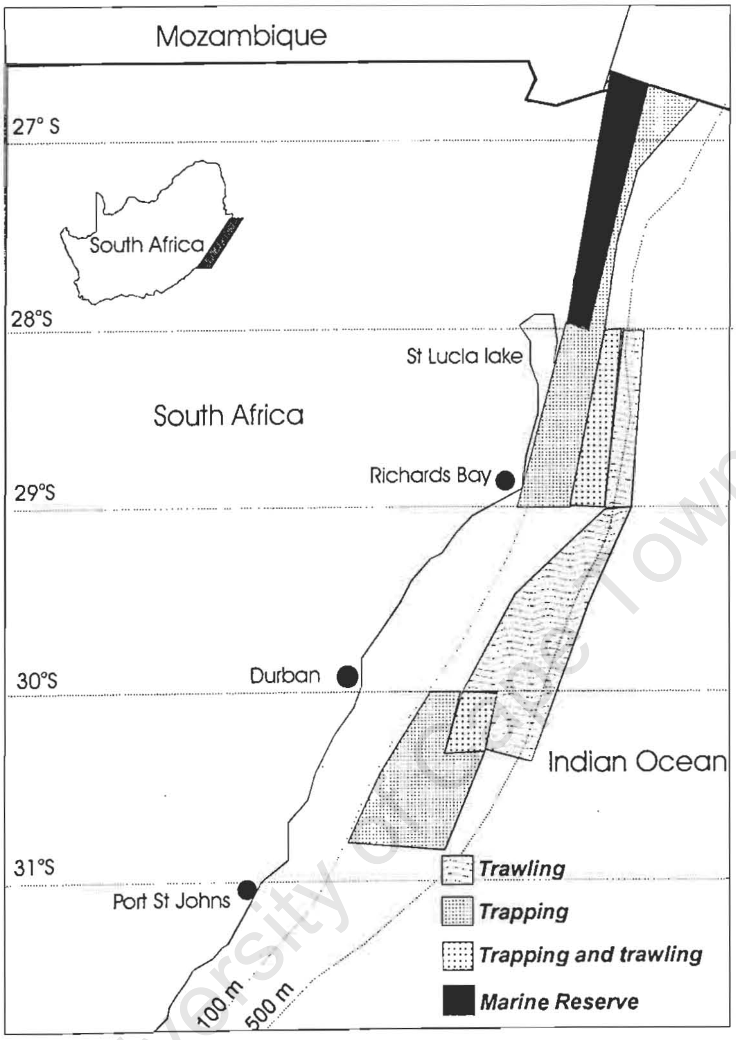

Figure 6.1: The east coast of South Africa, showing the areas exploited by trap and trawl fisheries.

(Fig. 6.2a).

### *6.2.1.3 Tagging*

Only healthy animals with all appendages present were tagged. T-bar anchor tags were inserted dorso-laterally into the abdominal muscle, between the first and second segments. Tagged lobsters were released after recording the position, depth, CL (± 0.1 mm) and sex. Fishers returned recaptured lobsters, and reported the date and position of recapture.

## *6.2.2. Data analysis*

Data collected from the trap-fishery were used to estimate population parameters for growth rate, size at sexual maturity and natural mortality. Data from the trap and trawl fisheries were combined to estimate fishing mortality at length and recruitment.

### *6.2.2.1. Size at sexual maturity*

Two methods were used to determine the size at sexual maturity of females. The first used the ratios of females with ovigerous setae to the total number of females per 1-mm CL interval (setal method). The second method used the ratio of egg-bearing females to the total number of females per 1-mm CL interval (ovigerous method). A logistic curve,

$$f_m = 1 / (1 + e^{(a - b*CL)})$$

was fitted in each case, where $f_m$ is the frequency of mature females, and a and b are constants, obtained by a non-linear search algorithm (using a least squares fitting procedure) provided by an Excel software package (Microsoft, 1997). The size at sexual maturity was defined as the CL at which 50% of females had well-developed setae, or as the CL corresponding to 50 % of the maximum egg-bearing percentage.

### *6.2.2.2. Growth*

Growth parameters ($L_\infty$ and K ) were estimated from tagging and from length-frequency information. Growth records of tagged lobsters that had been at large for 1 and 2 years, (272 - 359 days and 677 – 716 days respectively), with $\Delta L \geq 0$ mm CL were used to construct regressions of annual growth as a function of pre-moult CL (see Groeneveld, 1997), Gulland and Holt plots (Gulland and Holt, 1959), and Hiatt plots of pre-moult vs. post-moult CL (Mauchline, 1976). Annual growth and Hiatt plots relied on first-year recaptures, whereas Gulland and Holt plots relied on first- and second-year recaptures, the latter after halving the observed increments. Length-frequency data were used to estimate $L_\infty$ based on the Powell-Wetherall method (Wetherall *et al.*, 1987).

*6.2.2.3. Total Mortality (Z)*

Three equilibrium length-based approaches (using the same underlying model but differing in the way parameters are estimated) were used to estimate total mortality, Z. Linearized length-converted catch curves (Pauly, 1983; 1984a; 1984b) were used to convert length into age, using the inverse Von Bertalanffy growth equation:

$$t_L = t_0 - 1 / (K * \ln (1 - L / L_\infty))$$

where $t_L$ is the predicted age at length L (Sparre and Venema, 1998), and $t_0$ is assumed to be zero. Assumptions were that the frequency distribution of a sample reflects the behaviour of a cohort, that recruitment and mortality rates are constant and that the population is stable.

The second method (Beverton and Holt, 1956) relies on the functional relationship of Z and $L^-$

$$Z = K*[(L_\infty - L^-) / (L^- - L')]$$

where $L^-$ is the mean CL of lobster with a CL of L' and larger, and L' is the CL above which all lobsters are under full exploitation.

In the third method (Wetherall *et al.,* 1987), the following linear regression

$$L^- - L' = a + b * L'$$

was used, where $Z / K = (-(1 + b) / b)$ and $L_\infty = (-a / b)$, assuming a population at equilibrium.

A fourth method, which is independent of the assumption of a population in equilibrium, was used to calculate Z more directly, by regressing the natural logarithm of survivors (N) of one cohort against progressively increasing time intervals ($\Delta t = 1, 2, 3\ldots$ years),

$$\mathit{ln}\ [\Sigma_i N(t+1)_i] = -Z\ \Delta t + \mathit{ln}\ [\Sigma_i N(t)_i]$$

providing a straight line with a slope equal to Z (Schoeman, 1997). The only assumptions were that Z is constant within the population (which was tested by comparing mortality curves based on different starting lengths) and that growth is described by the Von Bertalanffy growth function.

*6.2.2.4. Natural mortality (M)*

Natural mortality was first estimated assuming that effort (f) and fishing mortality (F) are related in the simple manner $F = q * f$ (Paloheimo, 1958; 1961; 1980) where q is the catchability coefficient, and M the intercept of the linear regression

$$Z = M + q * f.$$

Four empirical models were also used to estimate M. Beverton and Holt (1959) suggested the simple relationship

$$M = K * [3 L_\infty / (L_m - 3)]$$

where $L_m$ is the mean CL at maturity.

A general function, originally derived for fish, was presented by Pauly (1980):

$$\ln M = -0.0152 - 0.279 * \ln L_\infty + 0.6543 * \ln K + 0.663 * \ln T$$

where $L_\infty$ is measured in cm and T is the mean annual water temperature.

Rikhter and Evanov (1976) showed a close association between M and the age at which 50 % of the population is mature ($T_{m50\%}$), namely:

$$M = [1.521 / (T_{m50\%}^{0.720})] - 0.155.$$

Alagaraja (1984) related natural mortality to longevity of fishes using the relationship

$$M_{1\%} = - \ln (0.01) / Tm,$$

where Tm represents longevity and $M_{1\%}$ is the natural mortality corresponding to a 1 % survival in the oldest cohort.

### 6.2.2.5. *Fishing mortality (F)*

Jones' length-based cohort analysis (Jones and van Zalinge, 1981) was used to estimate F-at-length separately for the trap and trawl fisheries. A combined F-array was also calculated after raising respective trap and trawl length composition samples to catch. Input into the analyses were average catch-at-length obtained over the 1994 – 1997 period. Survivors ($N_{Li}$), a F-array and a F / Z -array were calculated retrogressively from the terminal length group, CL > 155 mm, assuming the terminal F / Z to be 0.5 $y^{-1}$.

### 6.2.2.6. *Yield and biomass*

Yield and average biomass was calculated using Jones' length-based cohort analysis (Jones and van Zalinge, 1981; Pauly, 1984a, 1984b; Sparre and Venema, 1998). Input into the model were the average annual catch and F-at-length, calculated from the trap and trawl data using the method explained in section 6.2.2.5. A length-based Thompson and Bell model, with input F-at-length (from the length-based cohort analysis), the number of recruits in the smallest length group (45 - 50 mm), the natural mortality factor per length group ($H = [L_\infty - L1 / L_\infty - L2]^{M/2K}$ , where L1 and L2 are successive length groups) and the parameters of the length-mass relationship for this species (Groeneveld and Goosen, 1996) was used to predict numbers-at-length, equilibrium biomass and yield at various levels of F.

## 6.3. Results

### *6.3.1 Catches and abundance indices*

Detailed descriptions of catches and abundance indices during the 4-year trapping are provided in Chapters 2 and 4 of this thesis. Briefly, South African lobster catches declined sharply between 1994 and 1997 (Table 6.1). Annual trap catches declined by an order of magnitude, from 89.5 t to 7.4 t, and trawl catches declined from ~ 33 t in 1993 to ~10 t per year between 1994 and 1997. During the same period, trap catches in Mozambique declined from 261 to 156 t.y$^{-1}$ (- 40%).

CPUE of lobsters in trawls off South Africa declined from 2.71 to 1.06 kg.hr$^{-1}$ (61 % down) between 1993 and 1997. During the same period, the trap-based relative abundance index declined from 0.61 to 0.16 kg.trap$^{-1}$ (- 74 %; see Chapter 4).

### *6.3.2. Size composition, sex ratios and size at maturity*

Commercial packing categories show that the proportion of small lobsters in trawl catches had increased from < 60 % in 1969 (for which period a research sample was available), to > 90 % in 1988. However, the proportion of small lobsters in annual trawl catches did then remain stable between 1988 and 1997 (Fig. 6.2a.). The rough length distribution, obtained by splitting catches per packing category for the 1994 – 1997 period according to the length distribution of the 1969 research sample, suggests that recent trawl catches consist largely of lobsters of 60 – 75 mm CL (Fig. 6.2b).

Lobsters with a CL < 50 mm were rare in trap catches (n = 75 270 lobsters) (Fig. 6.2c and 6.2d). Lobsters of 60 - 64 mm CL dominated catches (~ 20 % of the total trap catch), followed by lobsters of 65 - 69 mm (~12 %). Frequencies of lobsters with a CL > 70 mm

Table 6.1: Record of catch (tonnes) and CPUE of *P. delagoae* caught in traps and trawl nets off South Africa and Mozambique.

| Year | South Africa | | | | Mozambique |
|---|---|---|---|---|---|
| | Trawl fishery | | Trap fishery | | Trap and trawls |
| | Catches (t) | CPUE (kg / hour) | Catches (t) | CPUE (kg / trap) | Catches ** (t) |
| 1985 | 27.2 | | | | |
| 1986 | 59.9 | | | | |
| 1987 | 36.8 | | | | 224 |
| 1988 | 30.5 | | | | 231 |
| 1989 | 16.3 | | | | 167 |
| 1990 | 13.7 | | | | 207 |
| 1991 | 22.2 | | | | 341 |
| 1992 | 37.3 | | | | 156 |
| 1993 | 37.8 | 2.71 | | | 443 |
| 1994 | 24.4 | 1.6 | 89.5 | 0.606 | 261 |
| 1995 | 13* | 1.3 | 50.0 | 0.634 | 179 |
| 1996 | 10* | 1.02 | 39.5 | 0.297 | 132 |
| 1997 | 10* | 1.06 | 7.4 | 0.159 | 156 |
| 1998 | 11* | | | | No data |
| 1999 | 12* | | | | No data |

* Groeneveld and Melville-Smith, 1995; does not include catches of all the active vessels

** Mozambique-registered catches; all catches were not declared (Anon., 1998)

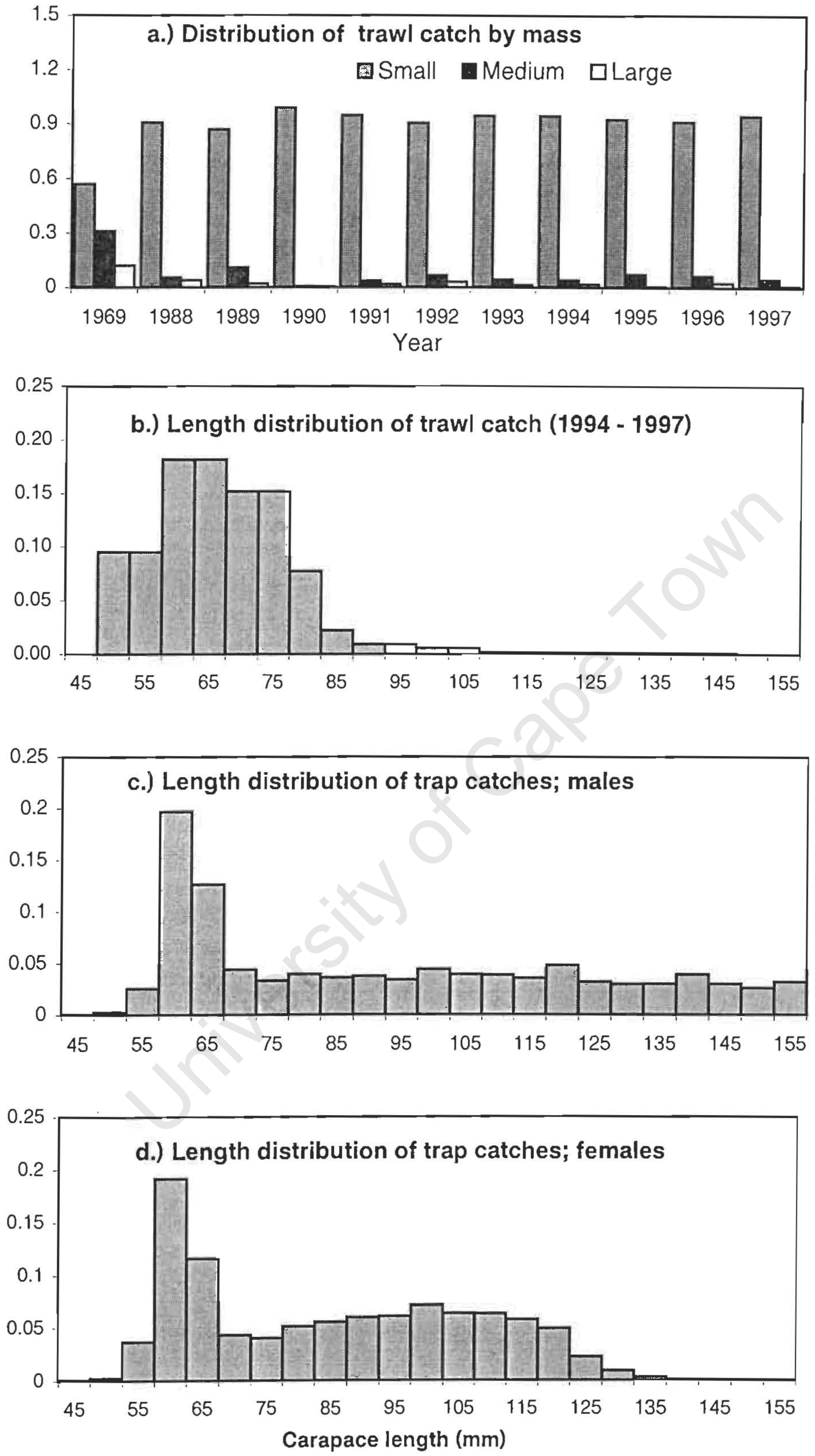

Figure 6.2: Length distribution of *P. delagoae* caught by trap and trawl fisheries during the period between 1994 and 1997 (commercial packing categories of trawl catches [2a] correspond to length classes : small, CL < 85 mm; medium, 85 mm < CL < 118 mm; and large, CL > 118 mm).

remained below 6% (of total trap catch) per 5-mm length class. A gradual inter-annual increase in catches of lobsters of 60 - 69 mm, and a decline in catches of lobsters > 70 mm CL, was observed between in 1994 and 1997 (Fig. 6.3).

Sex ratios of trap catches varied according to lobster size. Males dominated in length classes with a CL > 125 mm CL, and generally grew to larger sizes than females (Fig. 2c and 2d). Sex ratios of catches were fairly evenly spread across depth, with the percentages of males per depth interval measuring 54 % (112 – 200 m ), 46 % (201 – 275 m), 51 % (276 – 325 m), 51 % (326 – 375 m) and 50 % (376 – 425 m). Thirty-five percent of all the mature females captured between 200 and 275 m bore eggs, compared to < 10 % of females in any other depth interval.

The size at 50 % maturity of female *P. delagoae* was estimated at 67.3 mm CL using the setal method as an indicator, and at 71.2 mm CL using the ovigerous method (Fig. 6.4). These values are similar to an estimate of 65 mm CL for *P. delagoae* caught in Mozambique (Brinca and Palha de Sousa, 1983). A moult between attaining the primary characteristics of maturity (ovigerous setae) and functional maturity (bearing eggs) probably accounts for the difference between estimates using the two methods (Groeneveld and Melville-Smith, 1994).

### *6.3.3. Growth*

Of the 5654 lobsters tagged in 1995 and 1996, 256 (4.5 %) were recaptured by the trap fishers. Of these, 211 recaptures were made within the first year, and 24 within the second. Annual growth measurements varied between zero and 17.3 mm, with 29.4 % of measurements ≤ 0.5 mm (Fig. 6.5). Linear regressions of annual growth vs. CL and Gulland and Holt plots were all significant ($p < 0.05$) with negative slopes (Table 6.2); annual increments thus shorten as lobster size increases. Males grow slightly more per year than females.

Because of the absence of large lobsters in the sample (no lobsters > 125 mm CL were recaptured) and the numerous zero increments (ascribed to increments too small to detect and to lobsters that did not moult), estimates of $L_\infty$ from the tag-recaptures were consistently

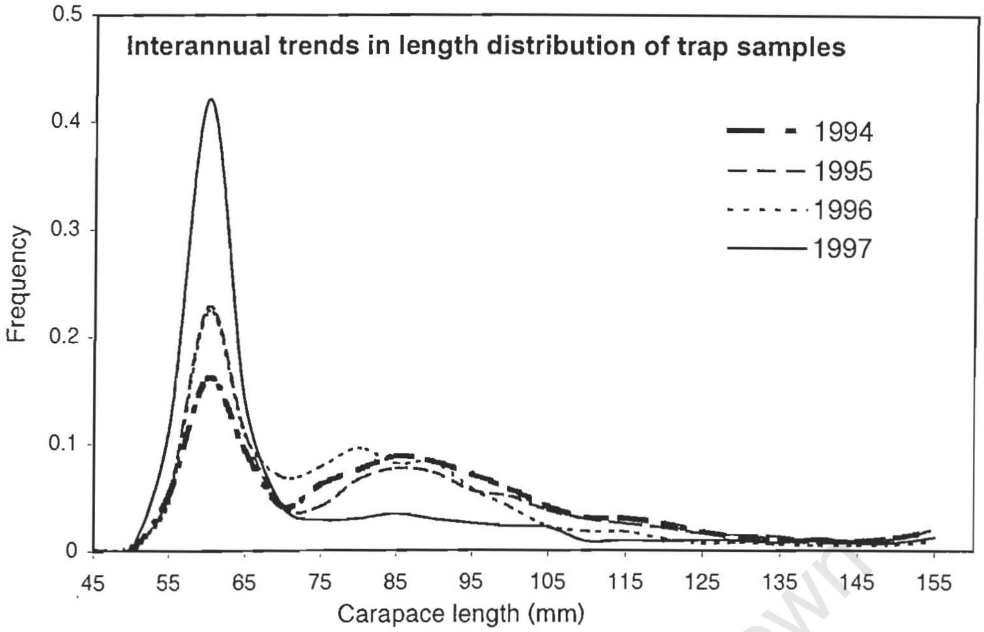

Figure 6.3: Annual trends in the length distribution of lobsters caught by traps.

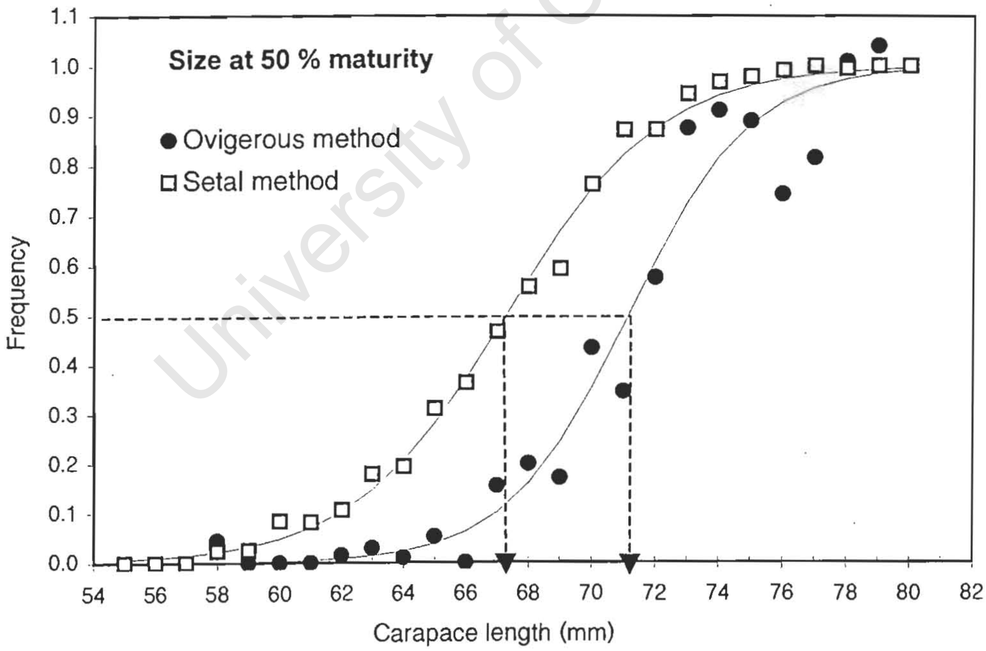

Figure 6.4: Size at 50 % maturity of female *P. delagoae*, estimated from the presence of ovigerous setae and external eggs.

lower than the observed maximum CL of ~180 mm (Table 6.2). The length-based Powell-Wetherall estimates of $L_\infty$ (both sexes combined) were more realistic, namely 162.8 mm (1994), 160.8 mm (1995), 160.8 mm (1996) and 162.8 mm (1997).

K-estimates ranged between 0.061 $y^{-1}$ and 0.071 $y^{-1}$ (Table 6.2). Slightly larger K-values for males than females reflect the fact that males approach $L_\infty$ faster than females. These estimates were similar to that of *P. elephas* (< 0.1 $y^{-1}$; Hepper, 1977) and to that of *P. gilchristi* (0.092 – 0.129 $y^{-1}$; Groeneveld, 1997), which were both obtained by using similar tag-recapture methods. The low values of K reflect slow growth towards $L_\infty$, which is consistent with the slow-growing and long-lived life strategies of temperate-water palinurid lobsters.

### *6.3.4 Total mortality (Z)*

The length-converted catch curve (Fig. 6.6) show that young lobsters have a high total mortality (0.74 $y^{-1}$) compared to intermediate (0.07 $y^{-1}$) and older lobsters (0.1 $y^{-1}$). The average over the fully exploited length-range was obtained by fitting a linear regression to the catch curve, after excluding all of the points along its ascending leg (not yet fully recruited to the fishery) and the terminal point at 155 - 159 mm CL (age – length relationship uncertain close to $L_\infty$). The consistency of the remaining data points were explored by fitting a series of regressions, starting with the first three points (65 – 69 mm, 70 –74 mm and 75 - 79 mm), and sequentially adding the next point until the 145 - 149 mm point had been reached. For each regression, 95% confidence limits were calculated, and the regressions with the most points and narrowest 95% confidence limits were chosen as the best estimates of Z (Table 6.3). The underlying assumption of the catch curve, that $Z * \Delta t < 1$, proved valid over the entire length range. On average, including the catch curve and other estimates obtained from the Powell-Wetherall and Beverton and Holt methods, Z was estimated to be ~ 0.12 $y^{-1}$.

A much higher estimate ($Z = 0.3$ $y^{-1}$) was obtained from the regression of the natural logarithm of survivors (N) of one cohort against progressively increasing time intervals. The result is important, because unlike the other methods used to obtain Z, this method is

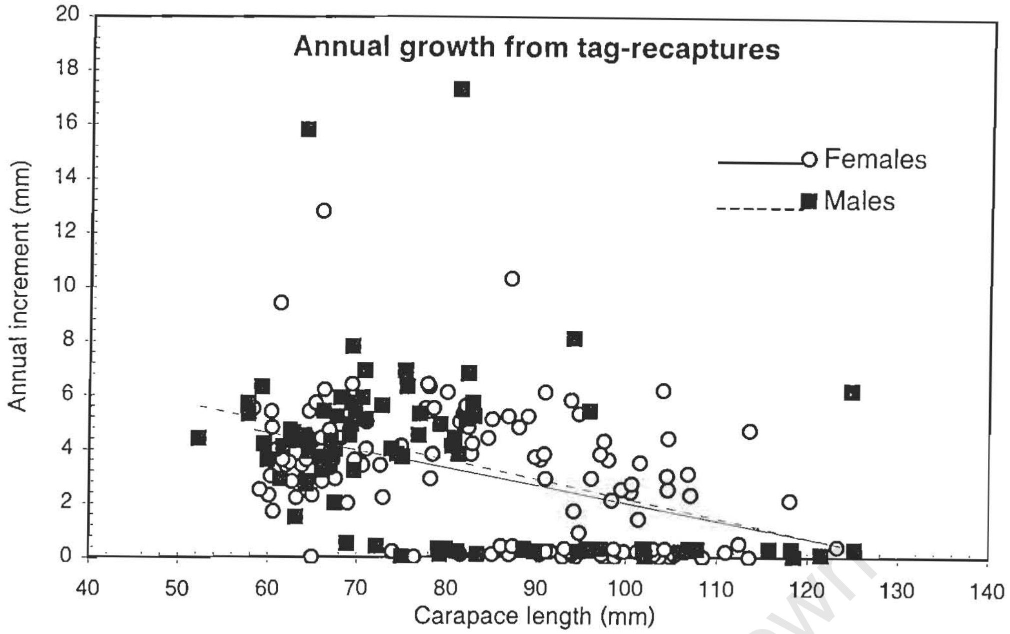

Figure 6.5: Annual growth increments (mm CL) of male and female *P. delagoae* from tag-recaptures, and regressions of annual growth versus premoult CL.

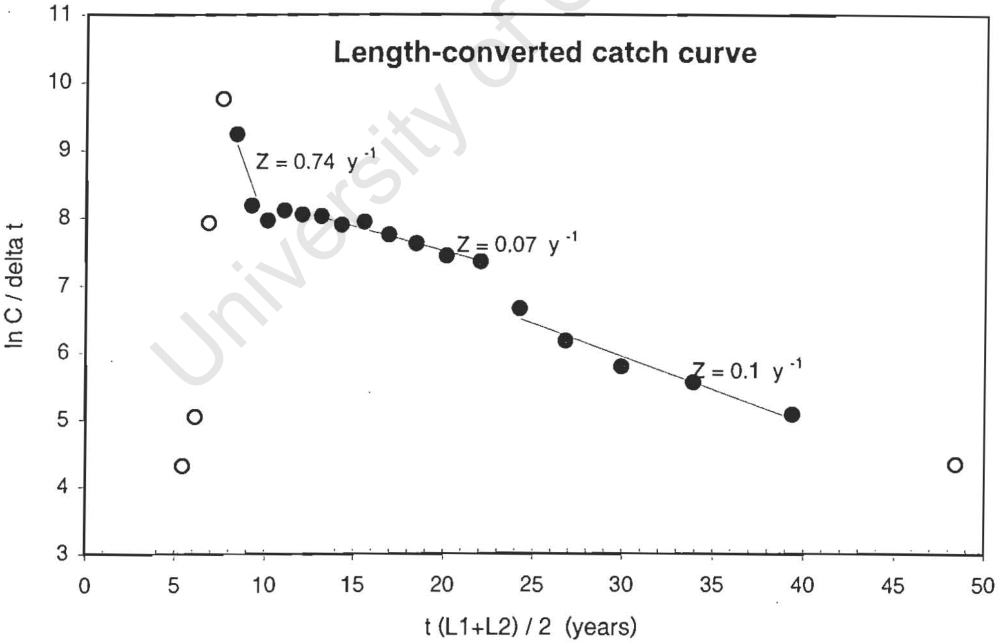

Figure 6.6: Estimates of total mortality (Z) from a length-converted catch curve based on trap catches. Open dots (omitted from the regressions) represent length classes not fully recruited to the fishery, and length-classes close to Linf

Table 6.2: Summary of growth regressions and Von Bertalanffy parameters K and $L_{inf}$ obtained with various methods

| Method | Regression equations * | n | $r^2$ | K (per year) | $L_{inf}$ (mm) |
|---|---|---|---|---|---|
| Annual growth | $A = -0.0691 * CL + 8.94$ | 211 | 0.19 | 0.0691 | 129.3 |
| Gulland and Holt | $G = -0.0611 * CL + 8.43$ | 235 | 0.14 | 0.0611 | 138.0 |
| Hiatt | $H = -0.9311 * CL + 8.85$ | 211 | 0.98 | 0.0714 | 128.5 |
| Powell-Wetherall | $P = -0.4502 * CL + 72.58$ | 4 | 0.99 | | 161.2 |

* $P(b=0) < 0.05$ for all slopes; $A = L_2 - L_1$ (mm); $G = \Delta L / \Delta t$ (mm per year); $H = L_{(t+\Delta t)}$ (mm) ; $P = L - L_1$ (mm).

Table 6.3: Summary of total mortality estimates (Z +-95% confidence interval; per year)

| Method | 1994 | 1995 | 1996 | 1997 | Combined |
|---|---|---|---|---|---|
| Catch curve | 0.14 +- 0.05 | 0.10 +- 0.02 | 0.12 +- 0.02 | 0.12 +- 0.05 | 0.12 +- 0.02 |
| Beverton and Holt | 0.199 | 0.117 | 0.133 | 0.164 | |
| Powell-Wetherall | 0.097 | 0.078 | 0.079 | 0.092 | |
| Non-equilibrium projection | | | | | 0.29 - 0.30 |

independent of the assumption of a population in equilibrium. The only assumption made, that Z is constant within the population, proved valid, with mortality remaining constant (~ 0286 - 0.3 $y^{-1}$) for mortality curves based on different starting lengths between 60 and 85 mm CL.

### *6.3.5. Natural Mortality estimates* (M)

Beverton and Holt (1959) found that values of the M/K ratio generally lie between 1.5 and 2.5; assuming a K of 0.06 - 0.08 $y^{-1}$ then results in an M of 0.1 - 0.17 $y^{-1}$ for *P. delagoae*. The linear regression of Z on effort resulted in an M (± 95 % confidence limits) of 0.0986 ± 0.14 $y^{-1}$. This regression ($r^2 = 0.2$) was based on four annual points which covered a wide effort interval (43 254 – 131 151 traps.$y^{-1}$).

Estimates of M from empirical methods were 0.255 – 0.281 $y^{-1}$ (Beverton and Holt method with a CL interval of 67 – 71 mm at 50 % maturity), 0.129 $y^{-1}$ (Pauly's empirical formula with an average water temperature of 12° C), 0.13 - 0.15 $y^{-1}$ (Rikhter Evanov formula with an age-interval of 9 – 10 years at 50 % maturity), and 0.092 $y^{-1}$ (longevity method with a survival rate of 1.31 % after 50 years).

Assuming the Beverton and Holt estimate to be an outlier, a reasonable range of M for *P.delagoae* is 0.09 – 0.15 $y^{-1}$. This compares well with estimates of M in other temperate water palinurids, i.e. 0.11 $y^{-1}$ for *P. elephas* (Hepper, 1977*)*, 0.1 $y^{-1}$ for *Jasus edwardsii* (Annala, 1979; 1980), 0.1 – 0.2 $y^{-1}$ for *J. tristani* (Pollock, 1981) and 0.1 – 0.2 $y^{-1}$ for *J. lalandii* (Pollock, 1978).

### *6.3.6. Fishing mortality (F)*

The Jones length-based cohort analysis indicates that fishing mortality (F) is highest between 60 and 69 mm CL (assuming input ranges of M = 0.09 - 0.15 $y^{-1}$ ; $L_\infty$ = 155 -165 mm and K = 0.06 - 0.08 $y^{-1}$) (Fig. 6.7), and that most of the fishing mortality in this range can be attributed to trapping. Fishing mortality attributed to trawling is relatively low compared to

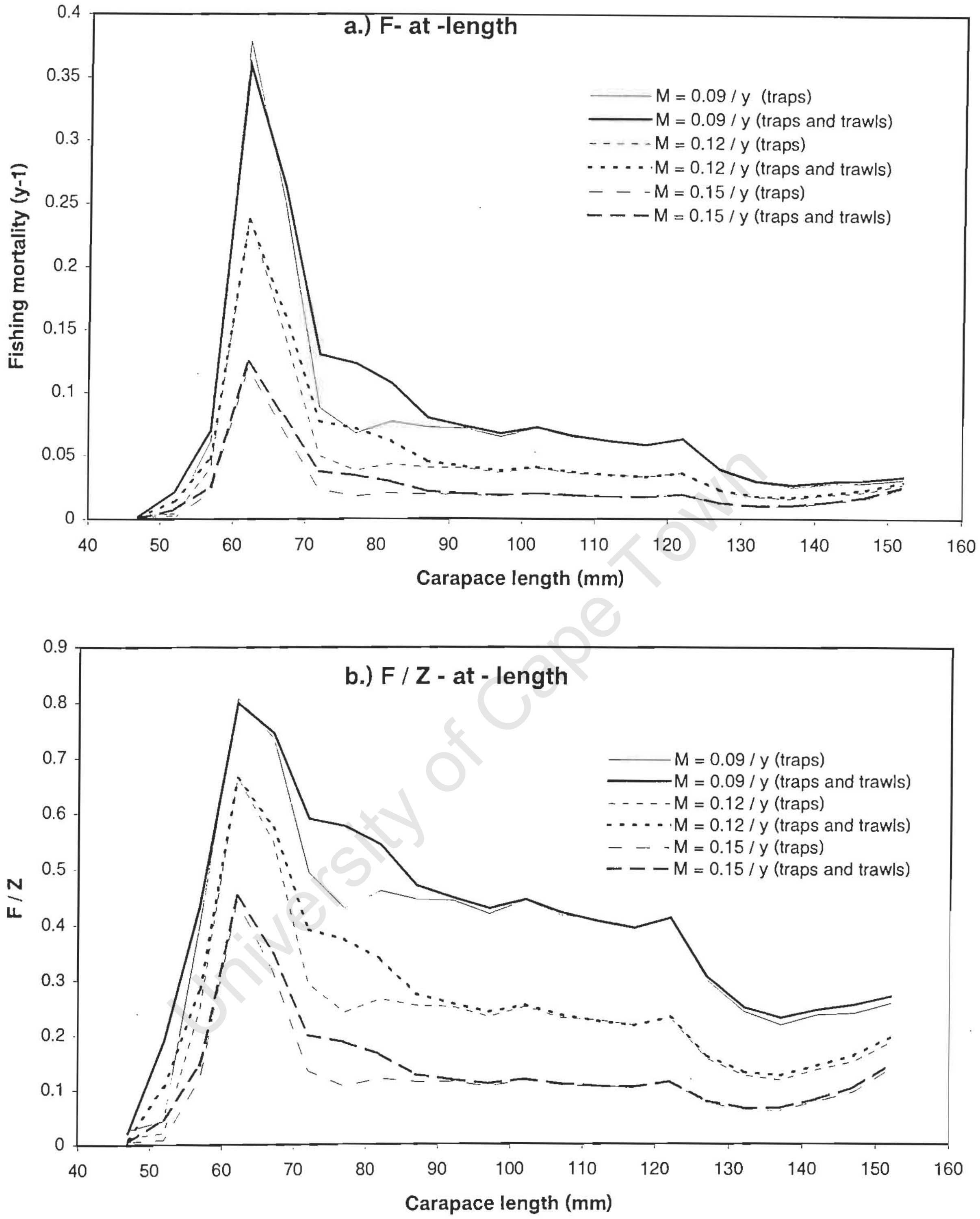

Figure 6.7: F-array (fishing mortality-at-length) and F/Z, estimated from combined trap and trawl catches and from trap catches alone (M = 0.09 to 0.15 per year).

that of trapping, except for length classes < 55 mm CL and for the 70 – 79 mm CL range.

### *6.3.7. Length-based Thompson and Bell model*

Equilibrium predictions of numbers per length-class and yield for a range of fishing strategies (expressed as the fishing mortality factor with F-factor = 1 indicating the present strategy) are presented in Fig. 6.8. A basic assumption is that recruitment into the 45 - 49 mm length-class (calculated from the length distribution and catches of trap and trawl fisheries combined) remains constant.

Figure 6.8a shows that numbers of lobsters of 45 - 59 mm CL are virtually independent of the F-factor, suggesting that fishing does not greatly impact on these length-classes. The threshold where fishing at any F-factor > 0 affects survival is at 60 mm CL. F-factors > 1 drastically reduce survivorship above 65 mm CL, so that yield (Fig. 6.8b) increasingly depends on the 60 - 69 mm length range.

Biomass projections (Fig. 6.8c) suggest that the total biomass in an unexploited population (F-factor = 0) is ~ 2466 t. The greatest proportion of this biomass is contributed by lobsters of 100 - 150 mm CL. At present (F-factor = 1) the equilibrium biomass projection is ~800 t (or 32 % of pristine), with the proportions of lobsters, by mass, spread evenly across the 50 – 150 mm size range. The spawning biomass at F-factor = 1 is expected to be ~ 29 % of that at pristine. Increasing the F-factor (F-factor > 2) results in lobsters of 55 - 59 mm CL dominating the population.

The Thompson and Bell model suggests a sustainable yield of ~ 60 t of lobster per year for both fisheries combined (Fig. 6.9). The yield curve is, however, relatively insensitive to changes in the F-factor in the 60 t region (1 < F-factor < 2.5), suggesting that an increase in effort above the 1997 level would not result in a significant increase in yield. It is important to note that the model is based on trap and trawl data, and that the 60 t would have to support both these fisheries.

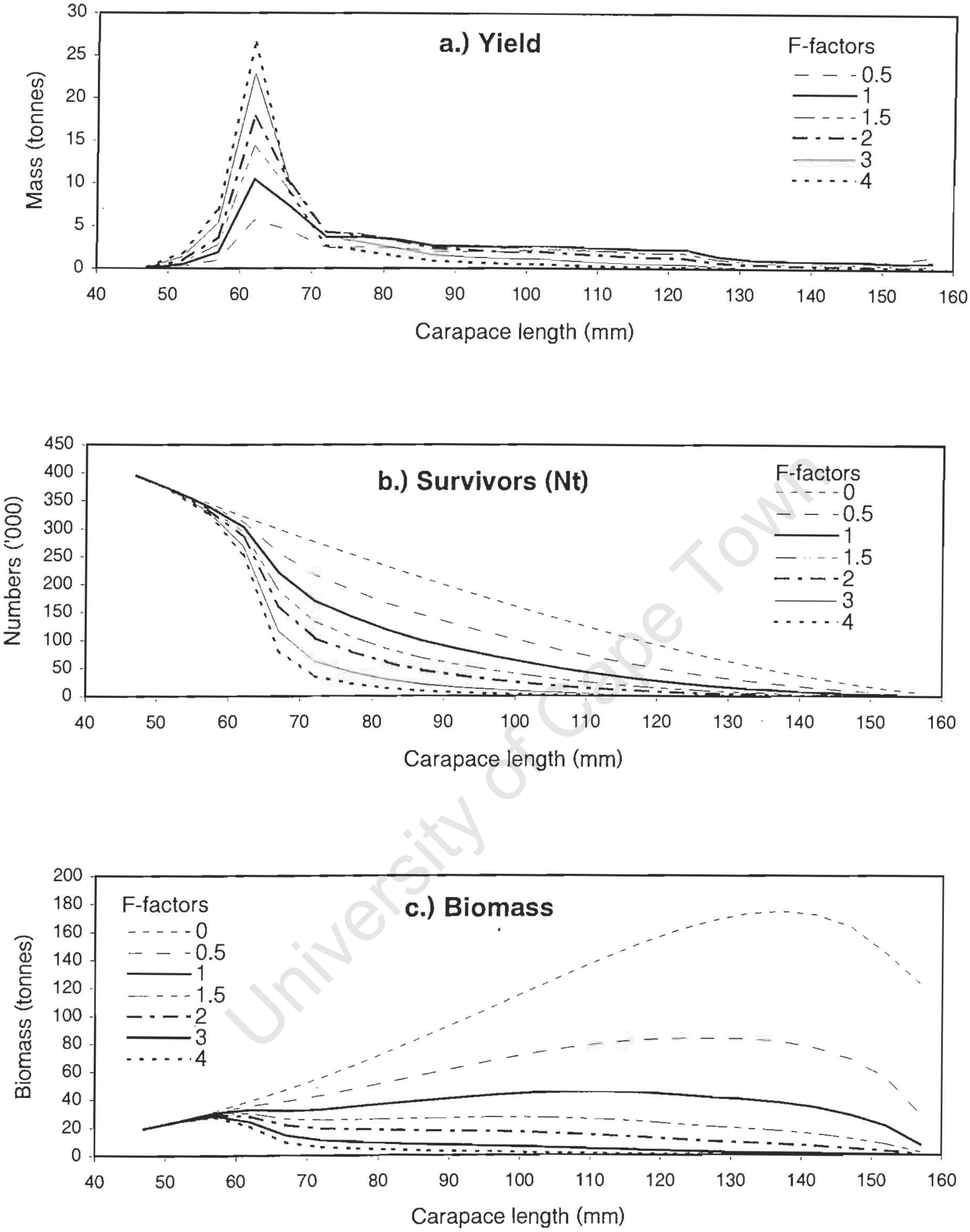

Figure 6.8: Projections of yield (a), survival (Nt) (b), and biomass (c) per length-class for a range of fishing strategies (0 < F-factor < 4; where 0 denotes no fishing and 4 denotes four times the current F).

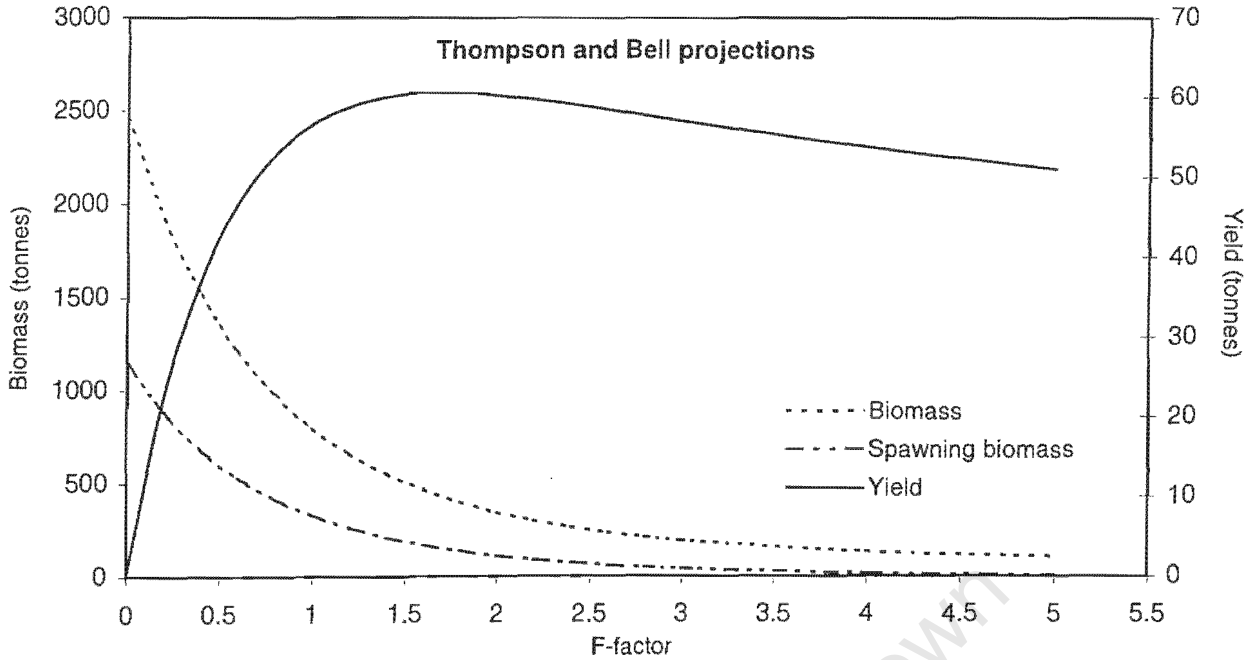

Figure 6.9: Thompson and Bell projections of total biomass, spawning biomass and yield for a range of fishing strategies (0 < F-factor < 5). Input data are from combined trap and trawl catches.

## 6.4. Discussion

### 6.4.1 Stock assessment

A general assumption behind the virtual population methods used in this study is that the stock is in a steady state, with all parameters remaining constant. This situation is, however, rarely achieved in fisheries research. The present study is no exception, and the reductions in catches, catch rates, and average lobster size suggest that the stock was in decline over the four year study period. The effect of this on the various parameter estimates is difficult to quantify, and to illustrate this uncertainty, a range of likely parameter estimates (often obtained from a variety of methods) was generally incorporated into the models.

The relatively low fishing mortality compared to natural mortality shown by the majority of equilibrium-based analyses is likely an example of bias introduced by assuming equilibrium conditions. A higher ratio would be more realistic, considering the declines in catches and catch rates. A non-equilibrium method, which relies on the progression of a single cohort over time, produced a higher total mortality (~ $0.3\ y^{-1}$ compared to $0.12\ y^{-1}$ obtained from equilibrium methods), and thus a more likely relationship between F and M. Fishing mortality obtained in this way was included in the virtual population analyses, where it corresponds to a F-factor of 3 in the plots of yield and biomass (see Fig. 6.8).

Recruitment, fishing mortality, biomass and yield were almost certainly under-estimated, when based on trapping data alone. Both trap and trawl fisheries impact on the population, especially on soft substrata in the 200 – 450 m depth interval, which can be accessed by both gear types. To improve estimates, rudimentary trawling data from the 1994 – 1997 period were included in the length-based cohort analysis, resulting in a ~ 10 % increase in recruitment in the 45 – 49 mm length-class and a slightly modified F-array (see Fig. 6.7).

Based on the Thompson and Bell projections, a sustainable yield of ~ 60 t per year for both fisheries combined may have been sustainable. Catches during 1994 and 1995 far exceeded this level, suggesting that the declines in catches and catch rates between 1994 and 1997 can be explained by overfishing.

A high impact of the trap and trawl fisheries on small lobsters may, furthermore, explain the rapid decline in trap catches. The focus of these fisheries on small lobsters is apparent in the catch size distributions (Fig. 6.2), fishing mortality array (Fig. 6.7), and in projections of yield and biomass (Fig. 6.8). It is possible for these fisheries to target small lobsters by fishing in the deeper (> 350 m) extreme of the 100 – 600 m depth range of *P. delagoae*, (Berry, 1973; Cockcroft *et. al*, 1995). These authors described a gradual inshore migration of newly recruited cohorts, which enter the fishery at ~600 m (Berry, 1973) and then migrate (while progressively increasing in size) to depths as shallow as 100 m.

Accordingly, lobsters with a CL < ~70 mm occur at depths > 350 m, whereas those with a CL > ~70 mm CL occur between 100 and 350 m. Trawlers generally focus on the 400 – 500 m depth range, so as to target the most valuable association of prawns, langoustines, red crabs and rock lobsters (Groeneveld and Melville-Smith, 1995), and consequently catch mainly juvenile or small mature lobsters (see Fig. 6.2). Survivors of the trawl fishery may continue their inshore migration, where, over time, the combination of depleted recruitment cohorts and natural mortality manifests itself in a relatively vulnerable equilibrium adult population, compared to a pristine population with larger numbers of recruits from the juvenile cohorts. A vulnerable adult population would explain the rapid decline in trap-catches of large lobsters (see Fig. 6.3), and the subsequent targeting of smaller lobsters in deeper water by trap fishers.

### *6.4.2. Management aims and selecting the most appropriate fishing method*

Given the relatively small projected yield and recent declines in catch rates, it is perceived by managers and fishers that the resource can support only one fishery. A comparison of the merits of trapping vs. trawling for *P.delagoae* encompassed three broad objectives, namely: to ensure a sustainable yield; to effect a recovery of the adult stock; and to limit unwanted bycatch. The criteria that were applied to compare the trap and trawl fisheries were: economic value (including retained bycatch species); local existing infrastructure; inherent economic risk; impact on the recovery of the adult stock; access of fishing gear to lobster habitat; and bycatch discards (see Table 6.4).

Table 6.4: Categories used to compare trap and trawl fisheries in relation to economic, biological and environmental management aims*

| Category | Trawling | Trapping |
|---|---|---|
| Wholesale value (including bycatch)** | US$ 1.511million | US$ 0.665 million |
| Local infrastructure | Established since 1960s | No investment to date |
| Economic risk | Based on several species | Based on lobster alone |
| Impact on spawning biomass | Depletes juvenile cohorts | Depletes juvenile and adult cohorts |
| Access of gear to lobster habitat | Natural refuges on rocks | Access to all habitats < 450 m |
| Mass of discarded catch | ca 1000 t per year | < 10 t per year |

* The wholesale value (landed catch(t) * product value (US$ per ton)) of lobster and its bycatch is supplied for both fisheries for 1997

** Trawl fishery: *P. delagoae*, 0.133; assorted prawns, 0.464; langoustines, 0.599; red crabs, 0.225; squid, 0.009; other fish, 0.082. Trap fishery: *P. delagoae*, 0.665 (based on a sustainable yield of 50 t per year) (Unit = Value * $10^6$)

The wholesale value of the trawl catch is ~U$ 1.5 million.$y^{-1}$, compared to ~ U$ 0.66 million.$y^{-1}$ for trap catches (Table 6.4). Trap catches consist mainly of lobster (with a small bycatch of slipper lobster *Scyllarides elisabethae*) compared to trawl catches, which include lobsters, knife prawns *Haliporoides triarthrus* and *Aristaeomorpha foliacea*, langoustines *Metanephrops mozambicus* and *Nephropsis stewarti*, red crabs *Chaceon macphersoni*, and several species of fish, squid and cephalopods (Fennessy and Groeneveld, 1997).

The trawling industry is situated in Durban, within 250 km of the furthest extent of the South African fishing grounds. The trawling infrastructure is well-established, and has been operational for ~ 35 years. The trap-fishery has, to date, operated on an experimental basis only, and hence little capital has been invested in developing infrastructure in the region. Trapping vessels rely on facilities in Cape Town (~2500 km away) and Port Elizabeth (~1500 km away).

Economic risk is spread over a number of crustacean and fish resources in the trawl fishery. The species composition of trawl catches can be manipulated by targeting different areas, so allowing fishers to shift their effort between species, depending on catch rates or market demands. The economic risk is far greater in the trap-fishery, which rely on lobster alone – declining lobster catch rates resulted in a financial loss to trap-fishers in 1997 (pers. comm., Industry representative).

Trawling has an indirect impact on the recovery of the adult stock, as it reduces the numbers of juveniles that survive to adulthood. However, trawl-nets can only access low-profile soft bottom areas, resulting in the occurrence of natural refuges against trawling in areas with high-profile rocky substrata. Conversely, traps have access to soft and rocky substrata, and are only limited by depth, to the interval < 450 m. Adult *P. delagoae* occur shallower than 450 m, and will therefore be entirely exposed to trapping.

Of the total annual trawl catch of 1500 t in 1992, 1000 t (consisting of a variety of fish, elasmobranch, crustacean and mollusc species) was discarded (Fennessy and Groeneveld, 1997). An initiative to reduce trawl bycatch by fitting excluder devices to trawl nets is currently being developed. Compared to the quantities discarded by trawlers, discards from trapping are negligible (< 10 $t.y^{-1}$) (Groeneveld, *pers. obs.*).

In conclusion, it appears that both trap and trawl fisheries exploit mainly smaller length classes, but that traps also impact heavily on the vulnerable adult population. The economic and ecological management aims defined for the *P. delagoae* stocks and fisheries can also be more easily achieved in a trawl than a trap fishery. Trawling thus appears to be the most appropriate fishing method for *P. delagoae* off South Africa, apart from its adverse bycatch effects.

# Chapter 7

## Growth and fecundity of *P. gilchristi*

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### 7.1. Introduction

The fisheries for *P. gilchristi* and *P. delagoae,* and their taxonomic relationships were addressed in the first part of this thesis (Chapters 1-3), followed by a study of the biology, ecology and management of *P. delagoae* in the second part (Chapters 4-7). The focus now shifts to the economically more important *P. gilchristi*, with the next four chapters investigating its ecology in relation to the management of its fisheries.

Estimates of growth rates are an essential component of stock assessment models, and especially in size- or length-based models such as those used in annual assessments of *P. gilchristi.* However, estimating growth in lobsters remains difficult under field conditions because all the features that can be used to determine the age of individuals are lost at moulting (Campbell, 1983). Tagging and recapturing animals provide an approach in which two easily obtainable measurements, namely the size increase between tagging and recapture and the time spent at large, can be used to determine growth rates (Aiken 1980). A tag-recapture program dedicated to measuring the growth of *P. gilchristi* was initiated in 1988, and is still continuing.

Growth rates of rock lobsters vary amongst different areas (Pollock and Beyers, 1981; Beyers and Goosen, 1987), and this variation has been ascribed to regional differences in food availability (Newman and Pollock, 1974b; Pollock and Beyers, 1981; Pollock, 1982), availability of oxygen (Pollock and Shannon, 1987) and temperature (Chittleborough, 1975). Growth rates also vary between years (Newman and Pollock, 1974b; Pollock, 1987), although the causes for this variation are not readily identified. They are, furthermore, intrinsically related to size and sex, and generally, with increasing size, the percentage moult increment decreases and the intermoult period lengthens (Hartnoll, 1985). These changes, and possible mathematical relationships involved, have been discussed in detail elsewhere (Mauchline, 1976, 1977; Hartnoll, 1978, 1982).

Pollock and Augustyn (1982) first reported on geographical differences in growth rates of *P. gilchristi*, and also showed that mean and maximum carapace lengths differed among areas. Groeneveld and Rossouw (1995) showed that at Port Alfred *P. gilchristi* tended to be smaller than in other regions, and Groeneveld and Melville-Smith (1994) found that females at Port Alfred matured at a smaller size than those occurring between the Agulhas Bank and Port Elizabeth. Female fecundity (number of eggs per female) of *P. gilchristi* has not yet been studied on a spatial basis. An association exists between male growth and female fecundity of *J. lalandii* (Melville-Smith *et al.*, 1995), so it is likely that there will be geographical differences in the fecundity of *P. gilchristi*.

The reproductive potential of a lobster resource depends heavily on growth and fecundity, and may be affected by management practices such as the timing of fishing seasons, restricted areas and a minimum size limit (Campbell and Robinson, 1983). It is therefore important that managers understand the relationships between these two parameters, and that if spatial gradients of growth and fecundity exist, they are taken into account when management decisions are made. The aims of this chapter were therefore to determine the growth rates of *P. gilchristi* in different fishing areas, using tag-recapture data, and to compare female fecundity in areas with contrasting growth rates. Physical and ecological factors that may give rise to variations in growth and fecundity are discussed.

## 7.2. Material and methods

### *7.2.1. Growth*

Tagging was conducted on board commercial fishing vessels at four traditional lobster fishing grounds: Agulhas Bank (Cape Point - Mossel Bay), St Francis (Mossel Bay - St Francis Bay), Port Elizabeth (St Francis Bay - Bird Island) and Port Alfred (Bird Island - East London) (Fig. 7.1). Plastic T-bar internal anchor tags (Hallprint TBA-1 tags) were inserted into the abdominal muscle of healthy lobsters (lively and with all appendages present) of all sizes, dorso-laterally

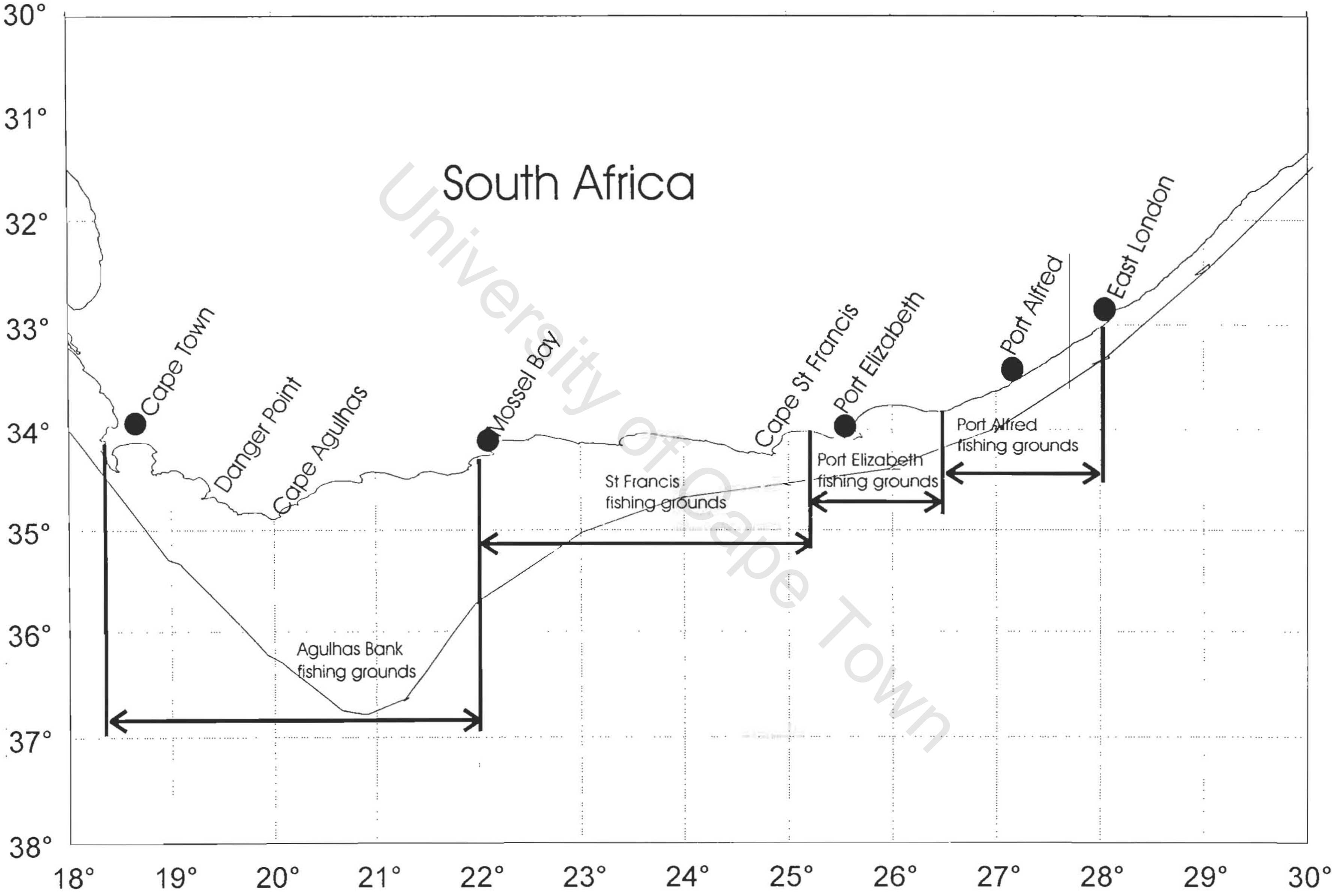

Figure 7.1: Four traditional fishing grounds for *Palinurus gilchristi* along the Cape South Coast

between the posterior edge of the carapace and the first abdominal segment, or between the first and second abdominal segments. Tag number, position and depth of release, carapace length (CL ± 0.1 mm) and sex were recorded for each lobster before it was released on the fishing grounds. Tagged lobsters caught in traps by commercial vessels were returned to Marine and Coastal Management, together with details regarding the position, depth and date of recapture.

Annual growth-at-size, i.e. the increase in *CL* (mm) per year for an individual relative to its size, was determined using the "anniversary method" of Hancock and Edwards (1967). Following this method, all growth increments of lobsters recaptured on or near the anniversary date of tagging were used, regardless of the number of moults. Linear regressions of annual growth as a function of *CL* were calculated for each area and gender, using a least-squares fit. Trends were compared using either analysis of covariance or *t*-tests (Zar 1984). When no areal difference was found, data were pooled and regressions were calculated for all areas combined.

Moult increment-at-size, i.e. the increase in *CL* (mm) per moult for an individual of a certain size, was determined after selecting animals that had moulted only once. Selection criteria were a noticeable increase in *CL* and a time at large of less than a year. It was assumed that negative growth did not occur, and that an increment of zero indicated that no moulting had taken place. Linear regressions of moult increment as a function of *CL* were calculated using a least-squares fit and were compared between areas using *t*-tests.

The number of times that lobsters of a certain size moult per year, i.e. annual moult frequency, was estimated using the two methods described by Annala and Bycroft (1988): (1) by dividing the average annual growth per 5-mm length interval by the mean moult increment in that interval, and (2) by dividing predictions of annual growth (obtained from the preceding analyses) by predictions of moult increment. Moult frequency was inverted to provide the intermoult period (the number of months between moults), which could be used in growth models based on moult increment and intermoult period.

Growth models for *P. gilchristi* were based on the assumption that juveniles recruited to the fishery at a *CL* of 50 mm, the smallest *CL* found in commercial catches. Models were constructed by combining the regressions of moult increment with intermoult period (Botsford 1985). This formed a complete description of growth after recruitment for the Agulhas Bank to Port Elizabeth region and for Port Alfred. In the models, *CL* at each moult after recruitment at 50 mm is given by the equation

$$CL_{n+1} = CL_n + m_n \quad ,$$

where $CL_n$ is the carapace length at moult $n$ and $m_n$ is the moult increment corresponding to $CL_n$, calculated from the linear regression of moult increment ($m_n = \alpha + \beta\, CL_n$). The time period $t_{n+1}$ needed to reach $CL_{n+1}$ is calculated from the equation

$$t_{n+1} = t_n + P_n \quad ,$$

where $P_n$ is the intermoult period derived from

$$P_n = m_n / a_n \quad ,$$

where $a_n$ is calculated from the linear regression of annual increment-at-size ($a_n = \gamma + \lambda\, CL_n$).

In addition to these growth models, $L_\infty$ (mm *CL*) and K (year$^{-1}$) for the generalized form of the Von Bertalanffy growth function

$$L_t = L_\infty\,(1\text{-}e^{-kt})$$

are presented for males and females from each study area. These data were derived from annual growth-at-size regressions.

### *7.2.2. Fecundity*

Females in berry (i.e. animals carrying external eggs) were collected from the Agulhas Bank in March 2000 and from Port Alfred in June 2000 (see Fig.7.1). Only females in an early berry stage (before the development of eyespots) were selected, and as wide a range of carapace lengths as possible was covered. Intact females with eggs attached were frozen at sea and transported to the laboratory where the egg-masses were removed. The CL of each female was measured to the nearest 0.1 mm, and egg-diameters were determined by measuring 10 eggs per female using a binocular microscope fitted with an eyepiece micrometer. The egg-masses were then oven-dried at 70° C for 24 hours, and the dried eggs were separated from any extraneous material such as pleopods and endopodite remains. The total egg mass produced by each individual was determined, whereafter a subsample (weighing 0.1 – 0.3 g) was taken from each female, weighed, and the eggs counted using a binocular microscope. Linear regressions of numbers of eggs per animal as a function of *CL* were calculated using a least-squares fit and were compared between Agulhas Bank and Port Alfred using *t*-tests.

## 7.3. Results

### *7.3.1. Growth*

Of 28 790 lobsters tagged during 15 tagging sessions between May 1988 and August 1998, 2256 (7.8%) were recaptured by May 1999 (Table 7.1).

All regressions of annual growth as a function of *CL* were significant ($p < 0.05$), except for females at Port Elizabeth, where the sample size was small (Table 7.2). An analysis of covariance comparing annual growth between areas indicated that growth of males and of females differed between areas. However, if the Port Alfred data are omitted from the analysis, the annual growth of males and of females did not differ significantly between Agulhas Bank, St Francis and Port Elizabeth. When pooling the data from those three areas, the regression analysis indicated that the annual growth of male and of female lobsters at Port Alfred was significantly less than in the other study areas (Fig. 7.2). In all areas, males grew slightly (but not significantly) faster per year than females.

For the determination of moult increment and moult frequency as a function of *CL*, data from Agulhas Bank, St Francis and Port Elizabeth were combined, because the growth regressions indicated that annual growth in these three areas were similar.

Table 7.1: Date of each tagging experiment for the four study areas, and the numbers of *P. gilchristi* tagged and recaptured. Recapture data up to 1 May 1999.

| Locality | Month tagged | Number tagged | Number recaptured | %recaptured |
|---|---|---|---|---|
| Agulhas Bank | May 1988 | 1997 | 196 | 9.8 |
| St Francis | May 1990 | 1499 | 238 | 15.9 |
| Port Elizabeth | Aug. 1990 | 1797 | 237 | 13.2 |
| Agulhas Bank | Feb. 1992 | 941 | 148 | 15.7 |
| Port Alfred | Jun. 1992 | 2035 | 246 | 12.1 |
| Agulhas Bank | May 1993 | 2875 | 163 | 5.7 |
| Agulhas Bank | Jun. 1995 | 1000 | 303 | 30.3 |
| St Francis | Jul. 1995 | 2136 | 56 | 2.6 |
| Agulhas Bank | Apr. 1996 | 2500 | 194 | 7.8 |
| Port Elizabeth | Jun. 1996 | 2524 | 99 | 3.9 |
| St Francis | Apr. 1997 | 4100 | 70 | 1.7 |
| Port Alfred | May 1997 | 500 | 59 | 11.8 |
| Port Elizabeth | Apr. 1998 | 1243 | 2 | 0.2 |
| Agulhas Bank | May 1998 | 2399 | 189 | 7.9 |
| St Francis | Aug. 1998 | 1244 | 56 | 4.5 |
| Total | May 1988 - Aug 1998 | 28790 | 2256 | 7.8 |

Table 7.2: Regression statistics for the annual growth and moult increment relationships for male and female *P.gilchristi* at Agulhas Bank, St Francis, Port Elizabeth and Port Alfred, and between Agulhas Bank and Port Elizabeth

| Locality | Sex | Number of days at large | Relationship ($y = a + b\,CL$) | $r^2$ | SE of y | SE of b | n | p |
|---|---|---|---|---|---|---|---|---|
| ***Annual increment-at-size*** | | | | | | | | |
| Agulhas Bank | M | 244 - 442 | $y = 10.012 - 0.0869\,CL$ | 0.20 | 0.203 | 0.0032 | 126 | $<0.001$ |
| St Francis | M | 256 - 428 | $y = 7.5972 - 0.0574\,CL$ | 0.09 | 0.329 | 0.0049 | 49 | $<0.05$ |
| Port Elizabeth | M | 250 - 445 | $y = 6.0223 - 0.0459\,CL$ | 0.11 | 0.276 | 0.0031 | 43 | $<0.05$ |
| Port Alfred | M | 232 - 307 | $y = 4.7133 - 0.0490\,CL$ | 0.07 | 0.126 | 0.0011 | 84 | $<0.025$ |
| Agulhas Bank - Port Elizabeth | M | 244 - 445 | $y = 9.6189 - 0.0837\,CL$ | 0.22 | 0.227 | 0.0051 | 218 | $<0.001$ |
| Agulhas Bank | F | 244 - 440 | $y = 10.225 - 0.0969\,CL$ | 0.32 | 0.189 | 0.0025 | 97 | $<0.001$ |
| St Francis | F | 258 - 427 | $y = 9.6004 - 0.0933\,CL$ | 0.15 | 0.335 | 0.0052 | 52 | $<0.005$ |
| Port Elizabeth | F | 250 - 426 | $y = 1.7545 - 0.0065\,CL$ | 0.001 | 0.291 | 0.0038 | 45 | $>0.25$* |
| Port Alfred | F | 231 - 307 | $y = 4.8662 - 0.0608\,CL$ | 0.12 | 0.11 | 0.0007 | 71 | $<0.005$ |
| Agulhas Bank - Port Elizabeth | F | 244 - 440 | $y = 9.2644 - 0.0906\,CL$ | 0.21 | 0.166 | 0.0026 | 194 | $<0.001$ |
| ***Moult increment-at-size*** | | | | | | | | |
| Agulhas Bank - Port Elizabeth | M | 26 - 445 | $y = 6.9185 - 0.0440\,CL$ | 0.06 | 0.135 | 0.0021 | 259 | $<0.001$ |
| Port Alfred | M | 107 - 307 | $y = 4.4228 - 0.0415\,CL$ | 0.06 | 0.119 | 0.0008 | 72 | $<0.05$ |
| Agulhas Bank - Port Elizabeth | F | 43 - 440 | $y = 6.5721 - 0.0480\,CL$ | 0.08 | 0.138 | 0.0018 | 188 | $<0.001$ |
| Port Alfred | F | 108 - 304 | $y = 3.4605 - 0.0353\,CL$ | 0.09 | 0.088 | 0.0004 | 47 | $<0.05$ |

* = Not significant

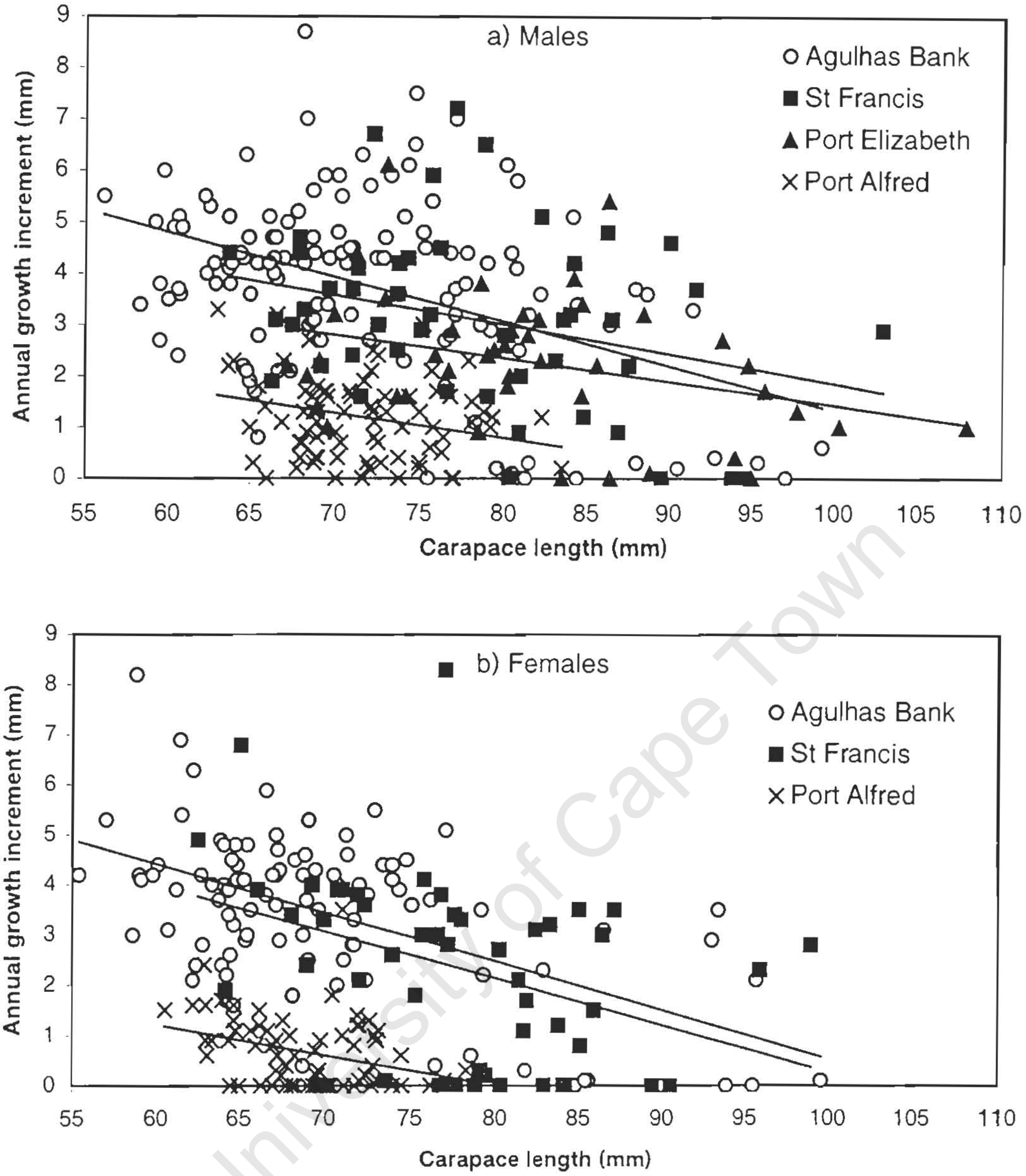

Figure 7.2: Relationships between annual growth increments and carapace length for (a) male and (b) female *P. gilchristi* at the Agulhas Bank, St Francis, Port Elizabeth and Port Alfred fishing grounds. The relationship of females at Port Elizabeth was not significant and was thus excluded from b.

All regressions of moult increment as a function of *CL* (Table 7.2) were significant ($p < 0.05$), with moult increments decreasing with increasing size. Moult increments for both males and females between Agulhas Bank and Port Elizabeth were significantly larger than at Port Alfred (Fig. 7.3). There was no significant difference in moult increment between males and females in either the Agulhas Bank to Port Elizabeth region or at Port Alfred.

Both methods used to estimate the annual number of moults for an individual of a certain size showed that *P. gilchristi* from the Agulhas Bank to Port Elizabeth region moulted more frequently than those at Port Alfred. In all regions moult frequencies decreased with increasing size (Table 7.3). Small individuals (55 - 70 mm *CL*) between the Agulhas Bank and Port Elizabeth generally moulted more than once per year, whereas small individuals (55 - 60 mm *CL*) at Port Alfred moulted annually. Larger females in both areas moulted less frequently than males of equal size.

Predictions of lobster size-at-age after recruitment (Table 7.4, Fig. 7.4) indicate slower growth at Port Alfred than between Agulhas Bank and Port Elizabeth, as a result of smaller moult increments. The model predicts that 20 years after recruitment at a length of 50 mm CL, males and females at Agulhas Bank to Port Elizabeth will, on average, attain lengths of 105 mm and 97 mm CL, respectively. These lengths are smaller than the theoretical maximum lengths ($L_\infty$) derived from the Von Bertalanffy growth function (Table 7.5), and smaller than the maximum observed lengths in the commercial fishery (c. 130 mm at Agulhas Bank to Port Elizabeth; pers. obs.). At Port Alfred, it is predicted that over a 20-year post-recruitment period male and female lobsters of 50 mm CL will, on average, grow to 80 mm and 72 mm CL, respectively. These values are also smaller than the Von Bertalanffy $L_\infty$ estimates (Table 7.5), and the maximum observed lengths (c. 110 mm; pers. obs.). This information suggests that the largest individuals in both areas are much older than 20 years. The Von Bertalanffy growth coefficients (K) were larger for lobsters from Agulhas Bank to Port Elizabeth than at Port Alfred, indicating faster growth towards maximum lengths.

### *7.3.2. Fecundity*

Mean egg diameters (± standard deviations) were identical at the Agulhas Bank (0.871 ± 0.052

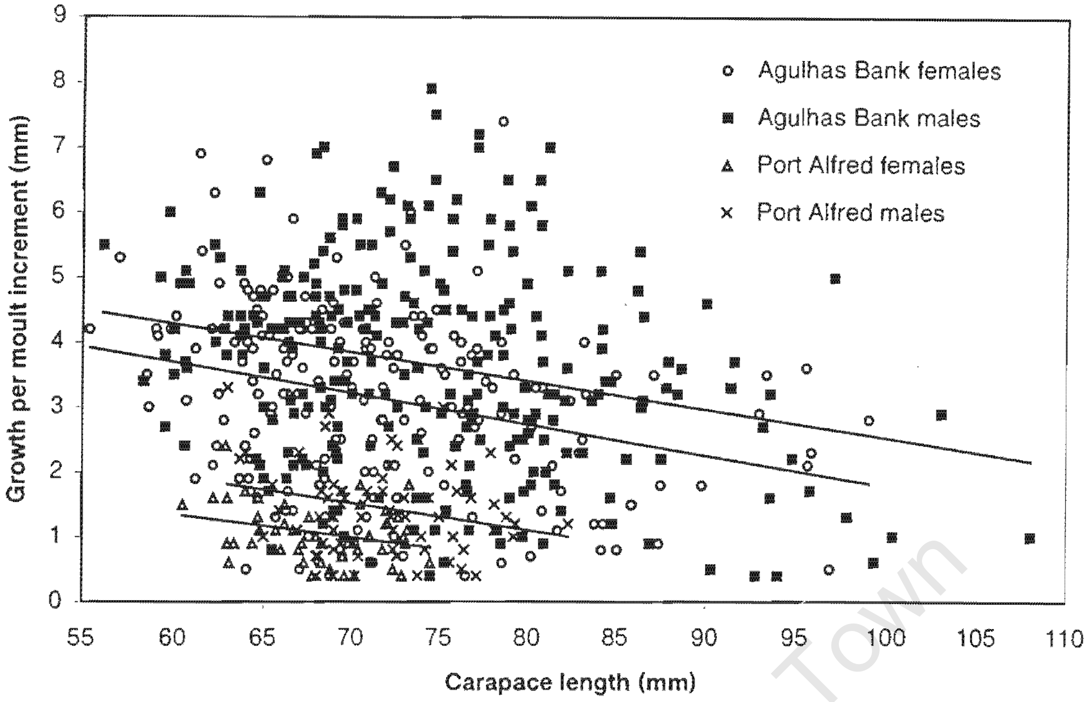

Figure 7.3: Relationships between moult increments and carapace length for male and female *P. gilchristi* between Agulhas Bank and Port Elizabeth and at Port Alfred.

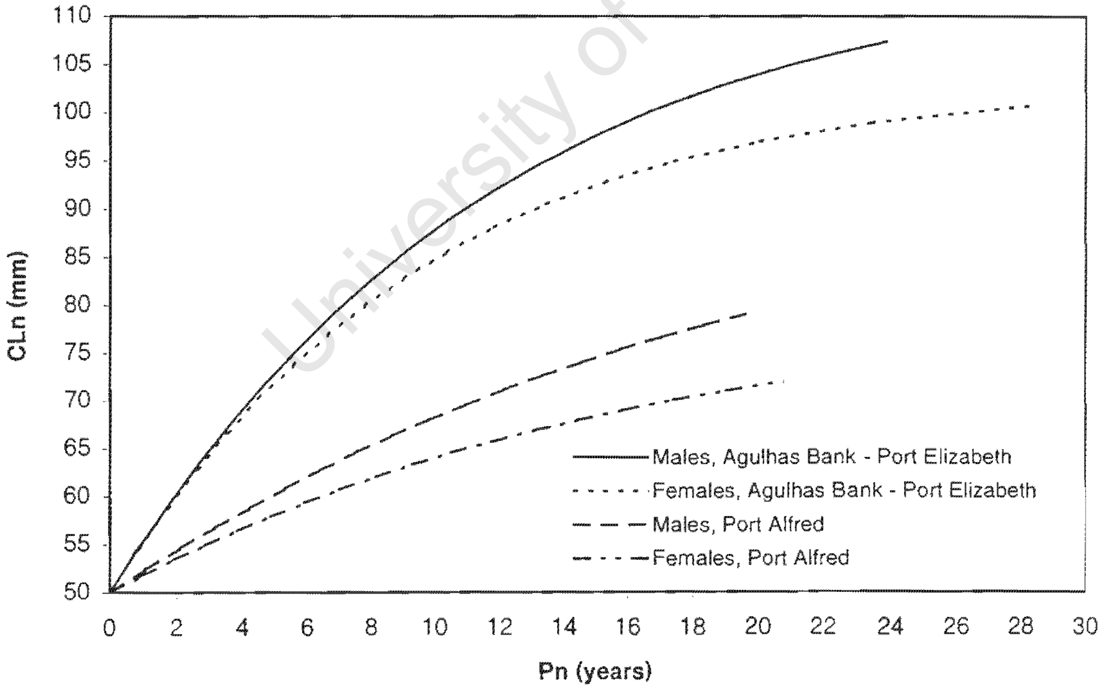

Figure 7.4: Growth models of *P.gilchristi* males and females at the Agulhas Bank to Port Elizabeth area and at Port Alfred.

Table 7.3: Annual moult frequency of male and female *P. gichristi*, estimated dividing the average annual growth increment by the moult increment per 5-mm length interval (Method 1), and by dividing the predicted annual growth by the predicted moult increment (Method 2).

| Length interval | ***Method 1*** Agulhas Bank, St Francis and Port Elizabeth | | Port Alfred | |
|---|---|---|---|---|
| (mm) | *Males* | *Females* | *Males* | *Females* |
| 55-59 | 1.00 | 1.16 | | |
| 60-64 | 1.00 | 1.01 | 1.00 | 0.92 |
| 65-69 | 1.01 | 1.08 | 0.89 | 0.57 |
| 70-74 | 1.04 | 1.03 | 0.78 | 0.64 |
| 75-79 | 0.94 | 0.71 | 0.81 | |
| 80-84 | 0.78 | 0.60 | 0.42 | |
| 85-89 | 0.70 | 0.77 | | |
| 90-94 | 0.77 | 0.40 | | |
| 95-99 | 0.19 | 0.61 | | |
| | ***Method 2*** Agulhas Bank, St Francis and Port Elizabeth | | Port Alfred | |
| | *Males* | *Females* | *Males* | *Females* |
| 55-59 | 1.10 | 1.13 | 0.93 | 0.96 |
| 60-64 | 1.05 | 1.07 | 0.90 | 0.85 |
| 65-69 | 1.01 | 1.01 | 0.87 | 0.71 |
| 70-74 | 0.95 | 0.94 | 0.82 | 0.51 |
| 75-79 | 0.89 | 0.86 | 0.76 | 0.21 |
| 80-84 | 0.83 | 0.76 | 0.67 | |
| 85-89 | 0.75 | 0.63 | 0.54 | |
| 90-94 | 0.66 | 0.47 | 0.31 | |
| 95-99 | 0.55 | 0.27 | | |
| 100-104 | 0.43 | | | |

Table 7.4: Predictions of size ($CL_n$)-at-age ($t_n$) after recruitment of male and female *P. gilchristi* for the region between Agulhas Bank and Port Elizabeth and for Port Alfred. $P_n$ and $m_n$ denote intermoult period- and moult increment-at-age respectively.

| | *Males* *Agulhas Bank, St Francis and Port Elizabeth* | | | | *Females* *Agulhas Bank, St Francis and Port Elizabeth* | | | |
|---|---|---|---|---|---|---|---|---|
| Recruitment (R) and number of moults | $t_n$ (years) | $CL_n$ (mm) | $m_n$ (mm/moult) | $P_n$ (years) | $t_n$ (years) | $CL_n$ (mm) | $m_n$ (mm/moult) | $P_n$ (years) |
| R | 0.00 | 50.00 | 4.72 | 0.87 | 0.00 | 50.00 | 4.53 | 0.84 |
| 1 | 0.87 | 54.72 | 4.51 | 0.90 | 0.84 | 54.53 | 4.28 | 0.87 |
| 2 | 1.76 | 59.23 | 4.31 | 0.93 | 1.71 | 58.81 | 4.04 | 0.90 |
| 3 | 2.69 | 63.54 | 4.12 | 0.96 | 2.60 | 62.85 | 3.82 | 0.94 |
| 4 | 3.65 | 67.66 | 3.94 | 1.00 | 3.54 | 66.67 | 3.61 | 0.98 |
| 5 | 4.64 | 71.61 | 3.77 | 1.04 | 4.52 | 70.27 | 3.41 | 1.03 |
| 6 | 5.68 | 75.37 | 3.60 | 1.09 | 5.54 | 73.68 | 3.22 | 1.08 |
| 7 | 6.77 | 78.98 | 3.44 | 1.14 | 6.63 | 76.89 | 3.04 | 1.15 |
| 8 | 7.92 | 82.42 | 3.29 | 1.21 | 7.78 | 79.93 | 2.87 | 1.24 |
| 9 | 9.13 | 85.71 | 3.15 | 1.29 | 9.02 | 82.80 | 2.71 | 1.34 |
| 10 | 10.41 | 88.86 | 3.01 | 1.38 | 10.35 | 85.51 | 2.56 | 1.46 |
| 11 | 11.79 | 91.87 | 2.88 | 1.49 | 11.81 | 88.07 | 2.42 | 1.63 |
| 12 | 13.28 | 94.74 | 2.75 | 1.63 | 13.44 | 90.49 | 2.28 | 1.85 |
| 13 | 14.91 | 97.49 | 2.63 | 1.80 | 15.29 | 92.77 | 2.16 | 2.15 |
| 14 | 16.71 | 100.12 | 2.51 | 2.03 | 17.44 | 94.93 | 2.04 | 2.61 |
| 15 | 18.74 | 102.64 | 2.40 | 2.34 | 20.05 | 96.96 | 1.92 | 3.37 |
| 16 | 21.08 | 105.04 | 2.30 | 2.78 | 23.42 | 98.89 | 1.82 | 4.88 |
| 17 | 23.86 | 107.33 | 2.20 | 3.46 | 28.30 | 100.70 | 1.72 | 9.25 |
| 18 | 27.31 | 109.53 | 2.10 | 4.65 | | 102.42 | 1.62 | |
| 19 | 31.97 | 111.63 | 2.01 | 7.28 | | 104.04 | 1.53 | |
| 20 | | 113.64 | 1.92 | | | 105.57 | 1.45 | |
| | *Males* *Port Alfred* | | | | *Females* *Port Alfred* | | | |
| R | 0.00 | 50.00 | 2.35 | 1.04 | 0.00 | 50.00 | 1.70 | 0.93 |
| 1 | 1.04 | 52.35 | 2.25 | 1.05 | 0.93 | 51.70 | 1.64 | 0.95 |
| 2 | 2.08 | 54.60 | 2.16 | 1.06 | 1.88 | 53.33 | 1.58 | 0.97 |
| 3 | 3.14 | 56.76 | 2.07 | 1.07 | 2.85 | 54.91 | 1.52 | 1.00 |
| 4 | 4.21 | 58.82 | 1.98 | 1.08 | 3.85 | 56.43 | 1.47 | 1.02 |
| 5 | 5.30 | 60.80 | 1.90 | 1.10 | 4.87 | 57.90 | 1.42 | 1.05 |
| 6 | 6.39 | 62.70 | 1.82 | 1.11 | 5.92 | 59.32 | 1.37 | 1.08 |
| 7 | 7.50 | 64.52 | 1.75 | 1.12 | 7.01 | 60.68 | 1.32 | 1.12 |
| 8 | 8.63 | 66.27 | 1.67 | 1.14 | 8.13 | 62.00 | 1.27 | 1.16 |
| 9 | 9.77 | 67.94 | 1.60 | 1.16 | 9.29 | 63.27 | 1.23 | 1.20 |
| 10 | 10.92 | 69.55 | 1.54 | 1.18 | 10.49 | 64.50 | 1.18 | 1.25 |
| 11 | 12.10 | 71.08 | 1.47 | 1.20 | 11.74 | 65.68 | 1.14 | 1.31 |
| 12 | 13.30 | 72.55 | 1.41 | 1.22 | 13.05 | 66.83 | 1.10 | 1.37 |
| 13 | 14.52 | 73.97 | 1.35 | 1.24 | 14.42 | 67.93 | 1.06 | 1.44 |
| 14 | 15.76 | 75.32 | 1.30 | 1.27 | 15.87 | 68.99 | 1.03 | 1.53 |
| 15 | 17.03 | 76.62 | 1.24 | 1.30 | 17.39 | 70.02 | 0.99 | 1.62 |
| 16 | 18.32 | 77.86 | 1.19 | 1.33 | 19.02 | 71.00 | 0.95 | 1.74 |
| 17 | 19.65 | 79.05 | 1.14 | 1.36 | 20.75 | 71.96 | 0.92 | 1.87 |
| 18 | 21.01 | 80.19 | 1.09 | 1.40 | 22.63 | 72.88 | 0.89 | 2.04 |
| 19 | 22.41 | 81.29 | 1.05 | 1.44 | 24.67 | 73.77 | 0.86 | 2.25 |
| 20 | 23.85 | 82.34 | 1.01 | 1.48 | 26.92 | 74.62 | 0.83 | 2.51 |

Table 7.5: Values of the parameters of the Von Bertalanffy growth equation estimated for male and female *P. gilchristi* between Agulhas Bank and Port Elizabeth and at Port Alfred.

| Locality | Value | | |
|---|---|---|---|
| | Sex | $L_{inf}$ (mm) | K (per year) |
| Agulhas Bank to Port Elizabeth | Male | 114.92 | 0.0837 |
| Agulhas Bank to Port Elizabeth | Female | 102.26 | 0.0906 |
| Port Alfred | Male | 96.19 | 0.049 |
| Port Alfred | Female | 80.04 | 0.0608 |

mm; n = 310) and Port Alfred fishing grounds (0.869 ± 0.045 mm; n = 210). The number of eggs per female ranged between 36 222 and 183 045 at the Agulhas Bank, and between 32 583 and 123 659 at Port Alfred, and the linear relationships between the number of eggs per female and CL (Fig. 7.5) were significant in both areas ($p < 0.05$), with the $r^2$-values of 0.90 (Agulhas Bank) and 0.72 (Port Alfred) indicating that the regressions fitted the data well. The regression equations (where E is the number of eggs per female) were

$$E = 3788.7 * CL - 215611 \quad \text{(Agulhas Bank) and}$$

$$E = 2015.7 * CL - 87325 \quad \text{(Port Alfred).}$$

The regression slopes differed significantly (t-test, $p < 0.001$), indicating a greater increase in egg-production with increasing lobster size at the Agulhas Bank than at Port Alfred. Comparisons within 5-mm size classes showed that the fecundity of females of 70.0 - 74.9 mm CL did not differ significantly between the two areas (t-test, $p < 0.05$, $n = 9$), whereas the fecundity of females of 75.0 – 79.9 mm (n = 12) and 80.0 – 84.9 mm (n = 12) were greater at the Agulhas Bank.

No comparison of fecundity between the two areas could be made in the size classes 60.0 – 69.9 mm CL, because only Port Alfred females bore eggs in these smaller size classes (Fig. 7.5).

### 7.4. Discussion

Estimates of various aspects of lobster growth, such as annual growth, moult increment and moulting frequency, are subject to the limitations of tag-recapture data, and certain assumptions need to be made. In this study, a positive increment in *CL* was assumed to be the sole indicator that moulting had taken place. In rock lobsters, moulting may occur without growth, and even with body shrinkage (Conan 1985, Cockcroft and Goosen 1995). Therefore, some animals may moult without detection. Consequently, the intermoult periods computed in the present growth models are likely overestimated, especially in the larger size-classes where moult increments

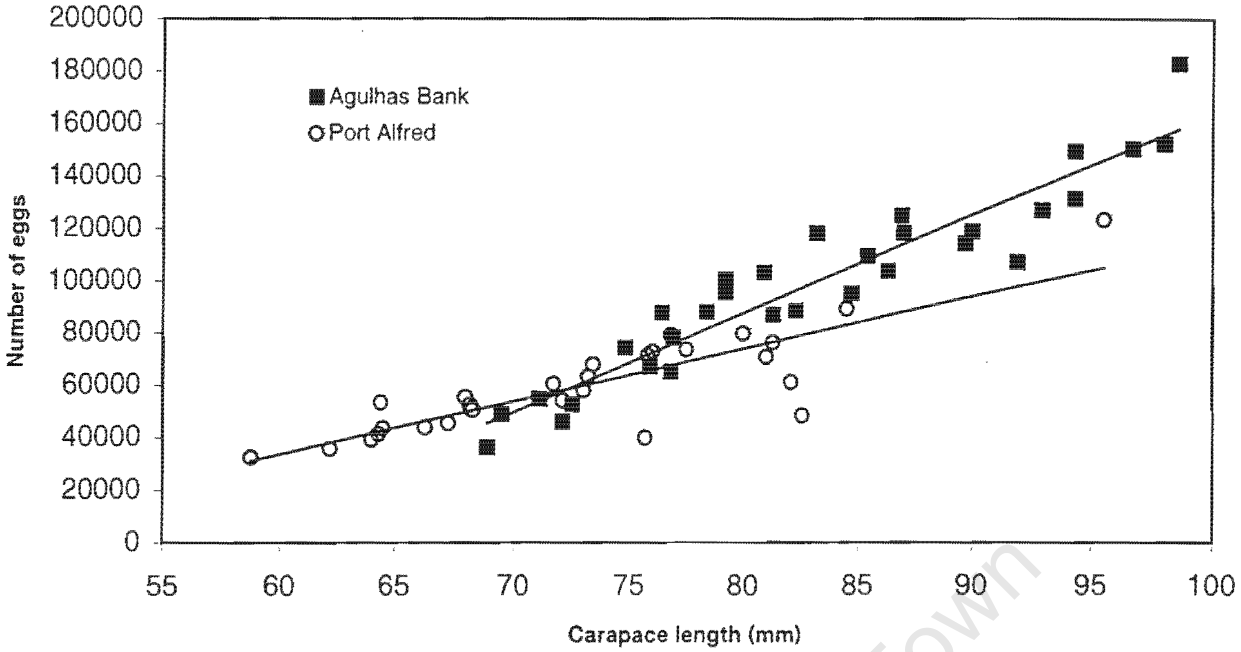

Figure 7.5: Fecundity of *P. gilchristi* at the Agulhas Bank and Port Alfred fishing grounds

are often too small to detect (see Table 7.4).

The parameters of the Von Bertalanffy growth functions were determined from annual growth increments-at-size. This eliminated the need to combine moult increments with intermoult periods and to use an increase in *CL* as an indication of moulting. The reason that the predicted maximum lengths ($L_\infty$) were considerably smaller than the lobsters sampled is probably because of the zero increments recorded for many of the larger lobsters, when increments were too small to detect.

Both the present study and that of Pollock and Augustyn (1982) indicate that the growth rate of *P. gilchristi* at Port Alfred is significantly slower than that between Agulhas Bank and Port Elizabeth. This was apparent for both sexes and all size classes tested, and appears to be because of differences in moult increments, rather than intermoult periods.

Female *P. gilchristi* grow progressively slower than males for a given length after reaching 65 - 69 mm CL at Port Alfred and 70 - 74 mm in the region between Agulhas Bank and Port Elizabeth (Table 7.4). It is around this length that females attain sexual maturity and start reproducing; in the Agulhas Bank to Port Elizabeth region they attain sexual maturity at a larger CL (63 - 71 mm) than at Port Alfred (59 - 62 mm; Groeneveld and Melville-Smith, 1994). The contrast in the size at sexual maturity shown by these authors was again highlighted in the present study, where egg-bearing females were encountered in the 60 – 70 mm size range at Port Alfred, but only in size classes > 70 mm CL at Agulhas Bank to Port Elizabeth. Reduced growth rates of females at the onset of maturity, which seems to be the case for *P.gilchristi*, is common in crustaceans (Hartnoll, 1985; Lipcius, 1985), and in the present study it appears to be because of increased intermoult periods and smaller moult increments in mature females relative to males.

Comparing the present annual growth estimates with those determined by Pollock and Augustyn (1982) from tag recaptures between 1974 and 1978 (Table 7.6), current growth appears to be somewhat lower than in the earlier study, particularly in animals in the smaller size classes. In the only direct regional comparison (for males of 65 mm CL), the declines are

Table 7.6: Annual growth increments for male and female *P. gilchristi* between Agulhas Bank and Port Elizabeth and at Port Alfred. Increments in parenthesis are from Pollock and Augustyn (1982).

| Carapace length (mm) | Agulhas Bank to Port Elizabeth | | Port Alfred | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| 65 | 4.2 (5.0*) | 3.4 | 1.5 (1.7) | 0.9 (1.3) |
| 75 | 3.3 | 2.5 | 1.0 (1.4) | 0.3 (0.7) |
| 85 | 2.5 | 1.6 | 0.5 | |
| 95 | 1.7 (1.0*) | 0.7 | | |
| 105 | 0.8 (1.0*) | 0.0 (0*) | | |

* From Rocky Bank, west of the Agulhas Bank fishing grounds

similar, i.e. 16 % between Agulhas Bank and Port Elizabeth and 12 % at Port Alfred. It should be noted that the earlier study was limited to particular size-classes and was based on small sample sizes. Also, annual fluctuations in growth rates are common in local lobster populations (Melville-Smith *et al.,* 1995).

Fecundity of females appears to be related to growth rate, being high in the fast-growth Agulhas Bank area and low in the slow-growth Port Alfred area. Similarly-linked geographical variations in growth and fecundity were found in *J. lalandii* on fishing grounds of divergent yields along the west coast of South Africa (Beyers and Goosen, 1987; Melville-Smith *et al.*, 1995). In neither species did the mean egg-numbers per size-class differ among areas when considering animals of lengths near first maturity. However, differences became progressively greater with increasing size of individuals.

The CL – fecundity relationship of females at Port Alfred in the present study is similar to that found by Pollock and Augustyn (1982). These authors based their relationship on the egg counts of 16 females ranging from 67 to 101 mm CL, but neglected to specify where they were collected. Their conclusion that the fecundity of *P. gilchristi* is very much lower than that of *J. lalandii* may therefore refer to *P. gilchristi* at Port Alfred, whereas the results of the present study indicates that the fecundity of this species in the Agulhas Bank to Port Elizabeth region is similar to that of *J. lalandii.*

In addition to growth rates and female fecundity, the average size (Pollock and Augustyn 1982, Groeneveld and Rossouw 1995) and the size at sexual maturity (Groeneveld and Melville-Smith 1994) are smaller at Port Alfred than in the Agulhas Bank to Port Elizabeth region. These factors therefore appear to be linked, either genetically or as a result of environmental induction. No genetic studies have yet been done on *P. gilchristi*, and to date the population has been presumed to be genetically coherent, with extensive larval mixing occurring during the pelagic phase of its life cycle (Pollock, 1989).

Several studies on other palinurid species have indicated that food availability is an important factor regulating growth rate (Newman and Pollock, 1974b; Chittleborough, 1975, 1976;

Pollock, 1979, 1982, 1991; McKoy and Esterman 1981, Pollock and Beyers 1981; Mayfield, 1998; Mayfield *et al*, in press). As such, lobsters from areas with contrasting growth rates have been shown to feed on different prey items, probably as a result of differences in benthic community structure (Newman and Pollock, 1974a, 1974b; Pollock *et al*., 1982; Joll and Phillips, 1984). It is quite possible that there are differences in the benthic community structures in the deeper shelf areas (> 50m) at Port Alfred as opposed to the Agulhas Bank to Port Elizabeth region, and that these differences affect growth rates and thus age-dependent parameters such as size at sexual maturity and mean CL. Assuming that the quantity and/or quality of available prey is greater between the Agulhas Bank and Port Elizabeth, and that this affects the energy available for growth and reproduction, a higher fecundity would also be expected in this combined region than at Port Alfred.

Differences in the physical oceanography between the two areas may also affect growth rates. A possible scenario is that stronger bottom currents at Port Alfred, where the Agulhas Current flows close inshore (Schumann 1987), may limit lobster foraging efficiency (Groeneveld and Melville-Smith 1994), whereas between the Agulhas Bank and Port Elizabeth, where the core of the Agulhas Current flows farther offshore, the effect of bottom currents on foraging conditions is less severe. Support for the 'foraging efficiency' theory is provided by an experiment on *Homarus gammarus* (Howard and Nunny, 1983) in which lobster behaviour changed to include posturing and sheltering when current speeds increased.

A third mechanism that may induce retarded growth at Port Alfred is density-dependence and increased interspecific competition for available food because of limited space. In this region the continental shelf is narrow and space is restricted, compared to the Agulhas Bank, where the shelf is much wider. Some support for this theory is that the catch-per-unit-effort of lobsters, expressed as numbers caught per trap, is higher at Port Alfred than in the other areas (Table 7.7), although this could be as a result of lower fishing pressure at Port Alfred as strong currents often restrict fishing in this region (pers. obs).

The vastly different growth rates and fecundity between the two regions shown in this chapter, and the differences in average lobster size (Groeneveld and Rossouw, 1995) and size at

Table 7.7: Commercial catch-per-unit-effort, expressed as the numbers of *P. gilchristi* caught per trap for the four study areas.

| Season | Catch-per-unit-effort by locality | | | | Source |
|---|---|---|---|---|---|
| | Agulhas Bank | St Francis | Port Elizabeth | Port Alfred | |
| 1977/78 | 1.02 | 0.92 | 0.92 | 1.88 | Pollock and Augustyn, 1982 |
| 1992/93 | 1.33 | 0.87 | 0.74 | 1.78 | MCM unpublished data |
| 1993/94 | 0.88 | 0.82 | 0.84 | 1.1 | MCM unpublished data |
| 1994/95 | 1.06 | 0.69 | 0.79 | 1.2 | MCM unpublished data |

attainment of sexual maturity (Groeneveld and Melville-Smith, 1994) suggest that it may be advantageous to treat the population as two separate stocks for management purposes: the Port Alfred stock, which is less productive because of slower growth and lower fecundity, and the Agulhas Bank to Port Elizabeth stock, which is more productive because of faster growth and higher productivity. Future research to investigate the degree to which these stocks are separated should focus on genetic traits, migration routes (see Chapter 9) and larval distribution pathways.

## Chapter 8

# Moulting of *P. gilchristi:* pleopod stages, seasonality and size dependency

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### 8.1. Introduction

Predictable patterns of moulting and reproduction characterize the adult stages of many palinurid species (Aiken and Waddy, 1980). These patterns are species-specific, and their timing may depend on intrinsic factors such as size, sex and developmental status (Lipcius, 1985; Lipcius and Herrnkind, 1987), and on environmental factors such as season, temperature and photoperiod (Conan, 1985; Lipcius and Herrnkind, 1987).

An understanding of the moult and reproductive seasons of exploited lobsters are important to fisheries managers for a number of reasons. Firstly, lobsters caught during the moulting-season are often weak or soft-shelled and may die during captivity, leading to financial losses to fishers. Secondly, seasonally synchronous moulting or spawning may provide the rationale for management strategies such as closed seasons to protect lobsters during vulnerable life history stages. Thirdly, seasonal patterns in moult incidence in the population may alter the mean probability of capture by traps by affecting foraging behaviour. Such changes in catchability may occur in relation to specific size categories or sex (see Morgan 1974; Newman and Pollock, 1974a; Pollock and Beyers, 1979), and may affect estimates of abundance and mortality.

A whole suite of methods to determine moult stages and moulting seasons has been developed for crustaceans. These methods include measuring the growth of regenerating limb buds (Bliss, 1956; Skinner, 1962; Stevenson *et. al*, 1968; Stevenson and Henry, 1971; Spindler *et al.,* 1974), measuring the progressive development of gastroliths (McWhinnie, 1962; Connell, 1970; Hopkins, 1977; Rao *et al.*, 1977), determining the condition of the exoskeleton (Heydorn, 1969b), tracing the setagenic development of pleopods (Drach and Tchernigovtzeff, 1967) and calculating the monthly percentages of moulted lobsters from tag-recapture information (McKoy and Esterman, 1981). The latter three methods are used to determine the moulting stages and seasonality of *P. gilchristi* in this chapter.

The simplest method to determine the moult stage of a lobster is based on the hardness (soft or hard-shelled) and appearance (clean or encrusted with marine growth) of its exoskeleton. An early postmoult lobster may have a soft clean shell, compared to a hard, clean or encrusted shell during intermoult, or a soft encrusted shell during late premoult stages (Heydorn, 1969b). A second method, which permits a higher degree of resolution between moult stages, is based on microscopic changes to the organization of the integument. Based on the morphology of developing setae observed in the transparent edges of the pleopods of crustaceans, Drach (1939) and Drach and Tchernigovtzeff (1967) distinguished five main stages in the moult cycle: A (immediate postmoult), B (postmoult), C (intermoult), D (premoult) and E (ecdysis); each had substages. This general scheme has been widely adopted and applied to a variety of crustaceans, including crayfish (Stevenson *et al.*, 1968; Mills and Lake, 1975; Peebles, 1977; Van Herp and Bellon-Humbert, 1978), clawed and spiny lobsters (Aiken, 1973; Dall and Barclay, 1977; Lyle and MacDonald, 1983; Turnbull, 1989; Isaacs *et al. in press*), and prawns (Smith and Dall, 1985).

Recapture of tagged animals provides a method of determining moulting seasons without having to resort to moult-staging of individuals. This is achieved by calculating the incidence of moulting of recaptured animals on a monthly basis, relative to the tagging date (McKoy and Esterman, 1981). For this method to be successful, an extensive tag-recapture database is required, in which tagging dates are distributed over several months, and recapture dates are distributed at random time intervals thereafter, over a period of at least one year. It is also necessary to determine whether individuals have moulted. This is often achieved by indirect methods, such as establishing whether the size of an animal has increased.

The aims of this chapter were : 1) to develop methods to determine the moulting season of *P. gilchristi,* and; 2) to define its moulting season to provide a biological basis for the timing of seasonal fishing-ground closures. Three independent monthly indices were developed: a shell-hardness index; an index of setagenic events in the pleopods (pleopod-index) and an index based on the incidence of moulting of recaptured tagged lobsters (tag-recapture index). These indices were compared, and then used to investigate geographic variation in moulting season along the south coast, sexual dimorphism and the size-dependence of moulting.

## 8.2. Materials and methods

### *8.2.1. Setagenic moult stages (pleopod-index)*

Criteria that distinguished moult stages on the basis of the development of setae in the pleopods were determined from the pleopods of six male lobsters that had moulted in captivity (all females in captivity died within the first weeks). The male lobsters, which were kept at a constant temperature of 13°C (9 – 14°C in their natural habitat), were initially in an intermoult stage and were examined on an *ad-hoc* basis until a premoult condition could be distinguished. Thereafter the lobsters were sampled frequently on individual time scales, by excising the distal half of a pleopod and examining it at 63x or 100x magnification using a Zeiss IM35 inverted, phase contrast photo-microscope. Pleopods were photographed, and the observed changes in the morphology of setae were used to describe the moult stages according to the criteria described by Drach and Tchernigovtzeff (1967).

Monthly samples of pleopods were collected from live animals brought ashore by a commercial fishing company. The pleopods were categorized according to the moult stages as determined above, and the monthly percentage in each stage was calculated.

### *8.2.2. Shell-hardness index*

Two categories of shell-hardness were distinguished, namely soft-shelled (exoskeleton soft and pliable both laterally and dorsally) and hard-shelled (exoskeleton hard dorsally, and only slightly pliable laterally). These two categories were used to determine the monthly percentage of recently moulted lobsters (postmoult or early intermoult), as opposed to those in later inter- or premoult condition.

### *8.2.3. Tag-recapture index*

A total of 30 043 lobsters of all sizes and both sexes in four areas (Agulhas Bank [Cape Point - Mossel Bay]; St. Francis [Mossel Bay - St Francis Bay]; Port Elizabeth [St Francis Bay - Port Elizabeth]; and Port Alfred) were tagged during 16 tagging trips between 1988 and 1998 (Fig. 8.1). Carapace length (CL ± 0.1 mm), date and geographic location of release were recorded for each individual, and recaptured lobsters were returned to Marine and Coastal Management by commercial fishers, with information on the date and location of recapture.

The method of McKoy and Esterman (1981) was used to estimate moulting seasons for both male and female *P. gilchristi*, from tag-recapture information. For each tagging date, the proportions of recaptured lobsters that had increased in size (i.e. had moulted) and those that had not (i.e. had not moulted) were plotted against the number of days at large, up to one year after tagging. Over this time-scale, seasonality of moulting could be investigated by determining the months in which the frequencies of moulted individuals increased. Moulting seasonality was compared between sexes and across areas, based on tagging samples from the Agulhas Bank, St. Francis, Port Elizabeth and Port Alfred, and the moulting seasonality of small ($CL < 70$ mm CL) and large ($CL \geq 70$ mm) *P. gilchristi* was also compared by pooling tag-recapture records from all years and areas.

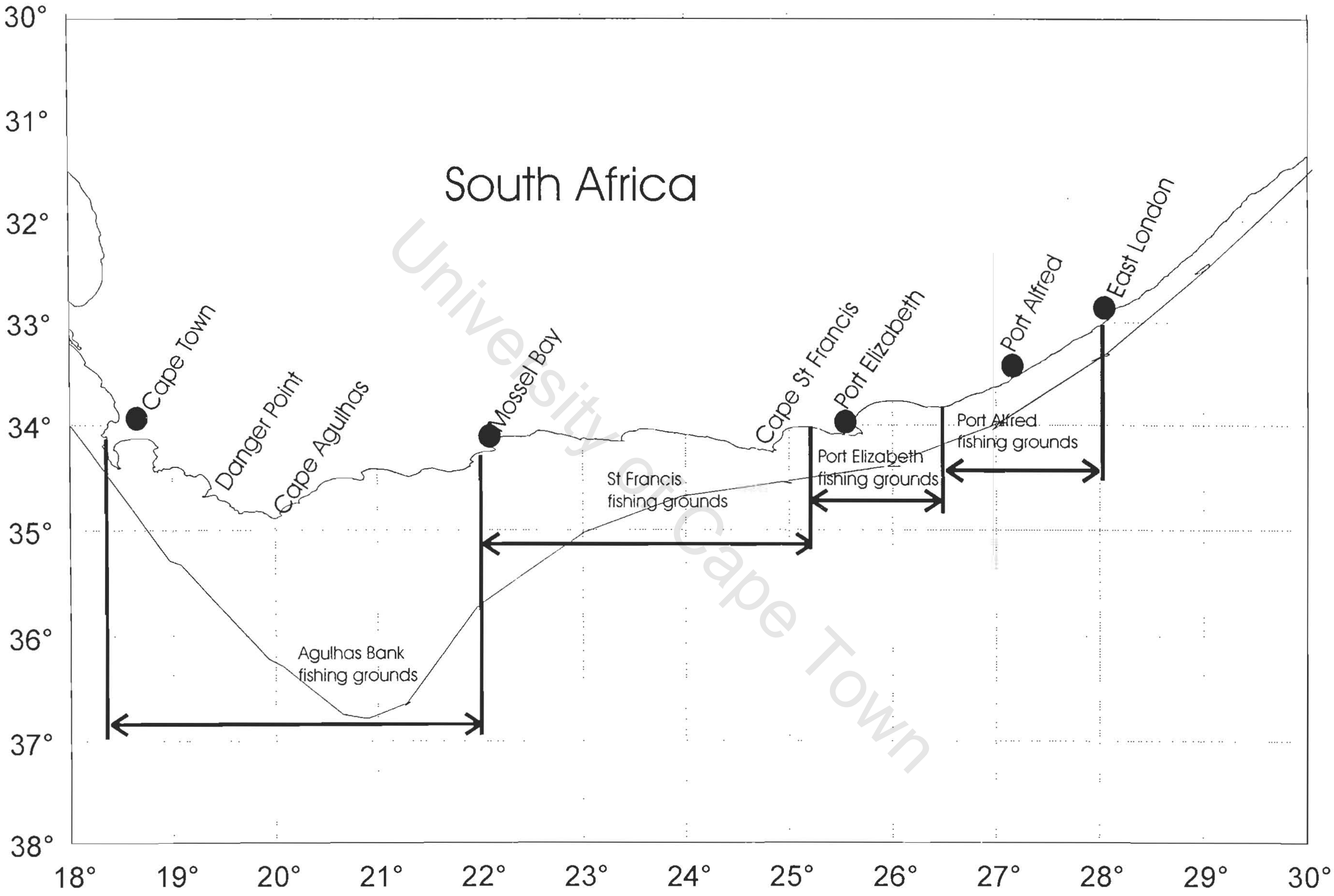

Figure 8.1: Four traditional fishing grounds for *Palinurus gilchristi* along the Cape South Coast

## 8.3. Results

### *8.3.1. Diagnostic characteristics of pleopod stages*

Moulting in *P. gilchristi* can be divided into seven relatively discrete stages and sub-stages, which can be identified by setagenic events and epidermal retraction in the cuticle and epidermis of the pleopods. The diagnostic characteristics of each stage and sub-stage are described below; the notation employed follows that of Drach (1939), which is universally used to describe the moulting stages of crustaceans.

### *8.3.1.1. Postmoult*

Stage A (Fig. 8.2): The setal lumen is wide and granular. There is little or no thickening of the setal walls and the internal walls of the setae appear rough. The cuticle is thin and consists of a single layer, and the setal bases are poorly developed.

Stage B (Fig. 8.3): The setal walls have visibly thickened, and the setal lumen is narrower and less grainy. The cuticle remains thin and undifferentiated.

### *8.3.1.2. Intermoult*

Stage C (Fig. 8.4): The characteristics of this stage vary between individuals, although consistent indicators of stage C are thick and smooth setal walls and a narrow setal lumen. The lumen is sometimes reduced or completely absent from the distal two-thirds of a shaft; often only a small triangular lumen remains near the setal base. The cuticle is mostly thick, and may have a multi-layered appearance. Setae are deeply imbedded into the cuticle and setal articulations are well developed.

### *8.3.1.3. Premoult*

Stage $D_0$ (Fig. 8.5): First signs of retraction of the epidermis from the cuticle. A narrow gap appears between the epidermis and the cuticle; the gap was sometimes first observed at the apical tip of the pleopod.

Stage $D_{1'}$ (Fig. 8.6): The epidermis retracts maximally along its entire circumference so that the cuticle is separated from the epidermis by a wide transparent zone. The new setae become visible as undifferentiated rigid conical structures in the retraction zone.

Stage $D_{1''}$, generally recognized in palinurids by the appearance of irregular flacid wisps or precursors of new setae in the retraction zone (see Lyle and MacDonald, 1983) could not be distinguished from $D_{1'}$ in *P. gilchristi* and was thus omitted.

Stage $D_{1'''}$ (Fig. 8.7): Thin walls and a lumen are faintly visible on new setae; first signs of setal invagination into the epidermis become visible.

Stage $D_2$ (Fig. 8.8): The new setae are deeply invaginated (but also extrude deeply into the retraction zone), and exhibit thin walls, a granular protoplasm and barbules. A new cuticle with setal articulations appears above the epidermis.

Once the pleopods had taken on a $D_2$ appearance, there was no further visible change until ecdysis. Stages $D_3$ and $D_4$ (identified in the pleopods of *P. marginatus* as the complete extrusion of new setae into the retraction zone (Lyle and MacDonald, 1983) or from external changes such as a softening of the exoskeleton below the ecdysial line (Turnbull, 1989)) were not distinguished in *P. gilchristi*.

The timing of the pleopod stages relative to moulting (ecdysis) is summarized in Table 8.1. The earliest indications of an impending moult were observed at 31 to 46 days prior to moulting (stage $D_{1'}$), and these were sequentially followed by stages $D_{1'''}$ (23 - 24 days prior to moulting), and $D_2$ (extending over a 2-week period directly prior to moulting). Both postmoult stages A (2 days) and B (~ 1 week) were short, with an early intermoult C stage discernible after ~ 10 days .

Figure 8.2: Stage A
SW = Setal wall, SL = Setal lumen, C = Cuticle

Figure 8.3: Stage B
SW = Setal wall, SL = Setal lumen, C = Cuticle

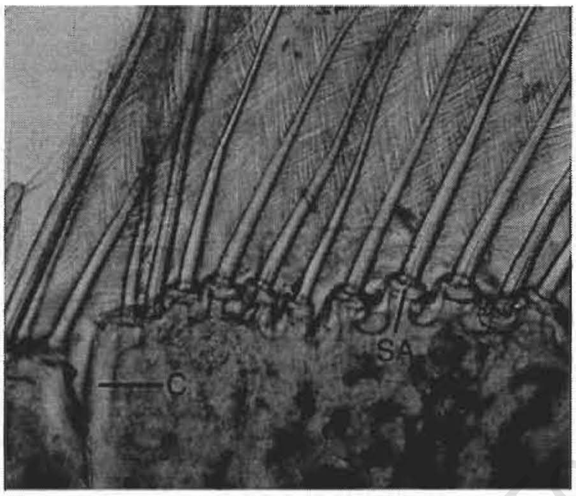

Figure 8.4a: Stage C
SW = Setal wall, SL = Setal lumen, C = Cuticle,
SA = Setal articulation

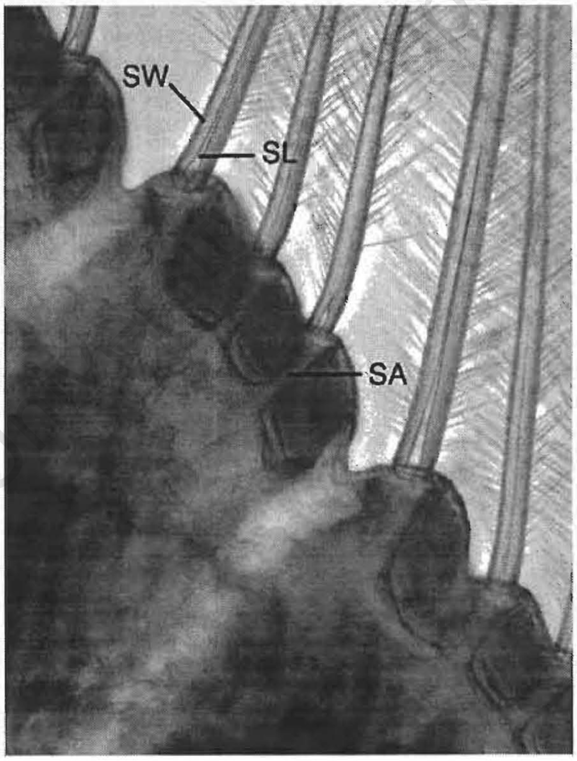

Figure 8.4b: Stage C

Figure 8.5: Stage $D_o$

RZ = Retraction zone, E = Epidermis

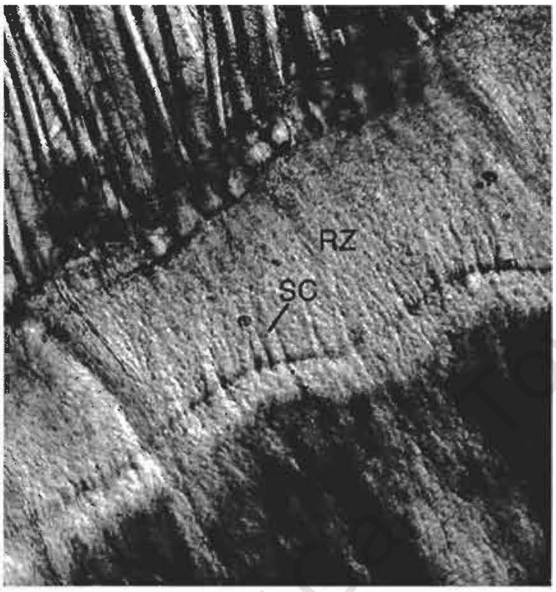

Figure 8.6a: Stage $D_1$'
RZ = Retraction zone, SC = Setal cone,
E = Epidermis

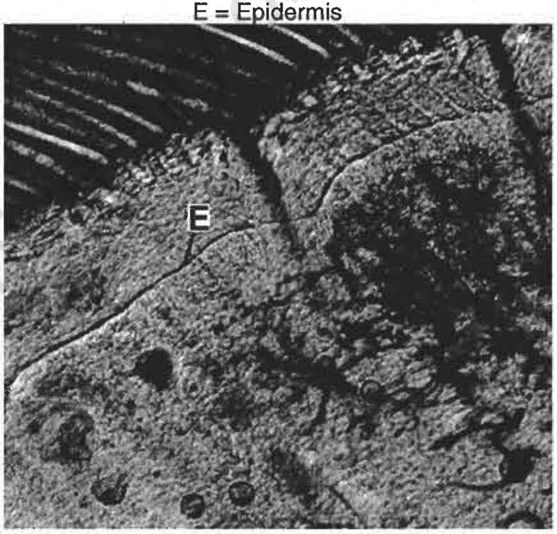

Figure 8.6b: Stage $D_1$'

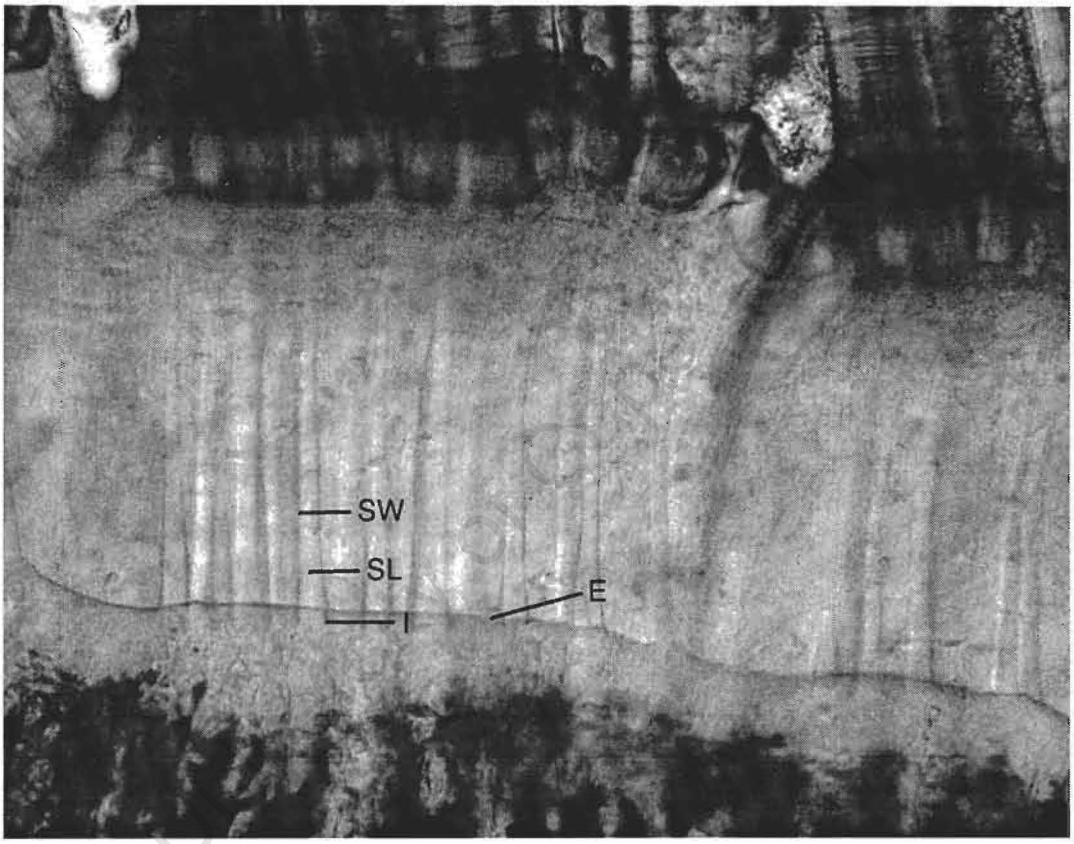

Figure 8.7: Stage $D_1$III

SW = Setal wall, SL = Setal lumen, I = Invagination, E = Epidermis

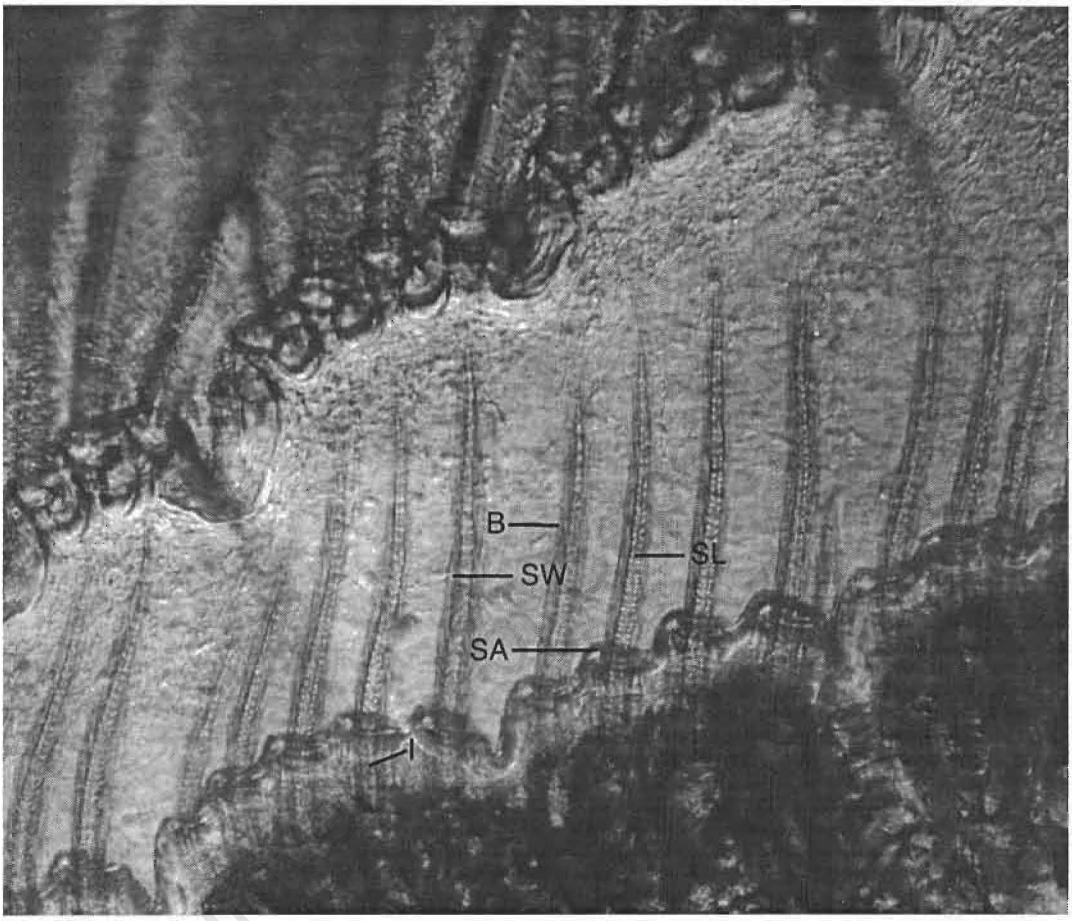

Figure 8.8: Stage $D_2$

SW = Setal wall, SL = Setal lumen, SA = Setal articulation, I = Invagination, B = Barbules

### *8.3.2. Pleopod-index from field samples*

Of the 1024 pleopods examined, 918 (90.5 %) were in an intermoult condition (stage C) compared to 96 (9.5 %) in a premoult condition (stages $D_0 - D_2$). No early postmoult pleopods (stages A or B) could be identified.

The monthly proportions of both male and female *P. gilchristi* in a premoult condition (stages $D_0$ to $D_2$) peaked between September and November (Table 8.2). During this period, the percentages of premoult males per month ranged between 26 and 39 %, compared to a somewhat lower range for females (15 – 21 %). Few premoult lobsters (0 – 7 % per month) were observed in samples taken between January and July (Table 8.2).

Of the 77 premoult lobsters captured during monthly random sampling, only 1 was in a late premoult stage (stage $D_2$), i.e., within two weeks of moulting. Fifty-one (66.2 %) were in stage $D_0$ and 25 (32.5 %) in stage $D_1$. Based on the aquarium results these stages occur between 23 and 46 days prior to moulting (see Table 8.1). Most of these lobsters were captured in September to November (see Table 8.2), and taking the time-lag into account, it is inferred, from pleopod stages, that most lobsters moult in November to December.

### *8.3.3. Shell-hardness index from field samples*

The incidence of soft-shelled lobsters (i.e. recently moulted lobsters in stages A, B or early C) in monthly samples from commercial catches remained below 13 %, discounting males in December (22 %) (Table 8.3). These low percentages suggest that the catchability of soft-shelled lobsters is low, and based on this, no inferences about moulting seasonality can be made from the shell-hardness index. A non-random sample of 4 female and 13 male soft-shelled lobsters was preferentially selected from the live lobster tanks of a fishing company in December 1999. Examination of the pleopods of these individuals showed that all were in stage C. Taking the elapsed time period from moulting to early stage C into account, it is inferred that these 17 lobsters had moulted in November or early December.

Table 8.1: Moult stages, and numbers of days prior (and subsequent) to moulting of six male lobsters kept in aquaria.

| | Individual lobsters | | | | | |
|---|---|---|---|---|---|---|
| | 68 mm CL | 64 mm CL | 79 mm CL | 72 mm CL | 80 mm CL | 74 mm CL |
| Stage | Numbers of days prior (and subsequent) to moulting | | | | | |
| D1' | 30 | | 35 | 31 - 46 | | 32 - 45 |
| D1''' | | | | 23 | | 24 |
| D2 | 14 | 4 | 2 - 5 | | | 3 - 15 |
| Moulting | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| A | 1 | 2 | | | 1 - 2 | |
| B | 8 | | | | 8 | |
| C | | | | 11 | | 15 |

Table 8.2: Numbers and frequency of lobsters in pre-moult condition in monthly samples, based on changes in pleopod morphology.

| Months | Females | | | Males | | | Both sexes | | |
|---|---|---|---|---|---|---|---|---|---|
| | Sample (n) | Premoult (n) | Proportion | Sample (n) | Premoult (n) | Proportion | Sample (n) | Premoult (n) | Proportion |
| January | 51 | 2 | 0.04 | 46 | 1 | 0.02 | 97 | 3 | 0.03 |
| February | 28 | 0 | 0.00 | 33 | 0 | 0.00 | 61 | 0 | 0.00 |
| March | 72 | 0 | 0.00 | 71 | 0 | 0.00 | 143 | 0 | 0.00 |
| April | 27 | 0 | 0.00 | 24 | 0 | 0.00 | 51 | 0 | 0.00 |
| May | 59 | 3 | 0.05 | 57 | 1 | 0.02 | 116 | 4 | 0.03 |
| June | 80 | 0 | 0.00 | 59 | 0 | 0.00 | 139 | 0 | 0.00 |
| July | 18 | 1 | 0.06 | 21 | 1 | 0.05 | 39 | 2 | 0.05 |
| August | 16 | 0 | 0.00 | 14 | 2 | 0.14 | 30 | 2 | 0.07 |
| September | 29 | 5 | 0.17 | 58 | 17 | 0.29 | 87 | 22 | 0.25 |
| October | 40 | 12 | 0.30 | 68 | 26 | 0.38 | 108 | 38 | 0.35 |
| November | 39 | 6 | 0.15 | 61 | 16 | 0.26 | 100 | 22 | 0.22 |
| December | 14 | 2 | 0.14 | 29 | 1 | 0.03 | 43 | 3 | 0.07 |

Only 1 of the pre-moult lobsters was within two weeks of moulting (I.e., in Stage D2); all the other pre-moult lobsters were in stages D0 to D1'''

Table 8.3: Numbers and frequencies of lobsters with soft shells in monthly samples.

| Month | Females | | | Males | | | Both sexes | | |
|---|---|---|---|---|---|---|---|---|---|
| | Sample (n) | Soft-shelled (n) | Proportion | Sample (n) | Soft-shelled (n) | Proportion | Sample (n) | Soft-shelled (n) | Proportion |
| January | 51 | 1 | 0.02 | 46 | 1 | 0.02 | 97 | 2 | 0.02 |
| February | 28 | 0 | 0.00 | 33 | 2 | 0.06 | 61 | 2 | 0.03 |
| March | 72 | 0 | 0.00 | 71 | 0 | 0.00 | 143 | 0 | 0.00 |
| April | 27 | 2 | 0.07 | 24 | 0 | 0.00 | 51 | 2 | 0.04 |
| May | 59 | 3 | 0.05 | 57 | 6 | 0.11 | 116 | 9 | 0.08 |
| June | 80 | 2 | 0.03 | 59 | 0 | 0.00 | 139 | 2 | 0.01 |
| July | 18 | 0 | 0.00 | 21 | 0 | 0.00 | 39 | 0 | 0.00 |
| August | 16 | 0 | 0.00 | 14 | 0 | 0.00 | 30 | 0 | 0.00 |
| September | 29 | 0 | 0.00 | 58 | 2 | 0.03 | 87 | 2 | 0.02 |
| October | 40 | 5 | 0.13 | 68 | 6 | 0.09 | 108 | 11 | 0.10 |
| November | 39 | 3 | 0.08 | 61 | 4 | 0.07 | 100 | 7 | 0.07 |
| December | 9 | 0 | 0.00 | 9 | 2 | 0.22 | 18 | 2 | 0.11 |

### *8.3.4. Tag-recapture index*

Tables 8.4 to 8.7 summarize the seasonal incidences of moulting in first-year tag-recaptures of male and female *P. gilchristi* in four fishing areas. The pooled data for the Agulhas Bank area (Table 8.4) showed a sharp increase in the incidence of moulted lobsters in recaptures made in December to February. Similar increases in December to February were shown by samples from St Francis (Table 8.5), Port Elizabeth (Table 8.6) and Port Alfred (Table 8.7). In all these areas some individuals also moult during other months of the year. In one case, the February 1992 sample on the Agulhas Bank (Table 8.4), the moulting season appears to have started in October instead of December, hence the higher percentage of moulting (18.3 %) in the pooled tagging-date-to-November category at the Agulhas Bank, compared to the other areas. The moulting incidence of females at Port Alfred (Table 8.7) is lower than in any other area, especially over the peak December to February period.

### *8.3.5. Moulting frequency relative to size*

Figure 8.9 shows the annual moulting pattern of *P. gilchristi* as a function of lobster size. Small lobsters (CL < 70 mm) of both sexes commenced with moulting in October, when the frequency of moulted males increased to 40 % (n = 20 males in October), and that of females to 47 % (n = 15). Few lobsters with a CL ≥ 70 mm moulted in October (8 %; n = 83). The same pattern was seen in November; by then 57 % of small males (n = 7 males in November) and 63 % of small females (n = 8) had moulted, compared to only 6 % of large males (n = 65) and 9 % of large females (n = 22). By December, most lobsters of both sexes and all sizes had moulted. Frequencies in the four categories were 100 % for small males (n = 22), 95 % for small females (n = 20), 76 % for large males (n = 21) and 46 % for large females (n = 19). Thus, whereas virtually all small lobsters moult within a year of tagging, up to 30 % of large lobsters do not.

## 8.4. Discussion

The morphology of the pleopod cuticle and moult stages of *P. gilchristi* are similar to those given for the Hawaiian spiny lobster *P. marginatus* (Lyle and MacDonald, 1983)

Table 8.4: Date and numbers of recaptures of male and female *P. gilchristi* in the first year after tagging, showing the monthly frequencies of moulting at the Aguihas Bank

| Month tagged | Month recaptured | Males | | | Females | | | M & F |
|---|---|---|---|---|---|---|---|---|
| | | Recaptured (n) | Moulted (n) | Moulted (%) | Recaptured (n) | Moulted (n) | Moulted (%) | Moulted (%) |
| ***Pooled sample:*** | | | | | | | | |
| | Tagging date to Nov. | 106 | 16 | 15 | 47 | 12 | 26 | 18.3 |
| | Dec. - Feb. | 79 | 72 | 91 | 64 | 54 | 84 | 81.1 |
| | After Feb. | 8 | 7 | 88 | 17 | 12 | 71 | 76.0 |
| ***Individual samples:*** | | | | | | | | |
| May 1988 | Jun. - Nov. 1988 | 0 | | | 0 | | | |
| | Dec.1988 - Feb. 1989 | 5 | 3 | 60 | 3 | 2 | 67 | 62.5 |
| | Mar. 1989 | 1 | 1 | 100 | 3 | 2 | 67 | 75.0 |
| | Apr. - May 1989 | 5 | 3 | 60 | 0 | | | 60.0 |
| Feb. 1992 | Mar. 1992 | 1 | 0 | 0 | 0 | | | 0.0 |
| | Apr. - Sep. 1992 | 0 | | | 0 | | | |
| | Oct. - Nov. 1992 | 12 | 12 | 100 | 10 | 10 | 100 | 100.0 |
| | Dec. 1992 - Feb. 1993 | 42 | 42 | 100 | 36 | 36 | 100 | 100.0 |
| May 1993 | Jun. - Aug 1993 | 0 | | | 0 | | | |
| | Sep. - Nov. 1993 | 7 | 1 | 14 | 4 | 0 | 0 | 9.1 |
| | Dec. 1993 - Mar. 1994 | 0 | | | 0 | | | |
| | Apr. 1994 - May 1994 | 2 | 2 | 100 | 2 | 2 | 100 | 100.0 |
| Jun. 1995 | Jul. - Oct. 1995 | 0 | | | 0 | | | |
| | Nov. 1995 | 9 | 1 | 11 | 3 | 1 | 33 | 16.7 |
| | Dec. 1995 - Jun. 1996 | 0 | | | 0 | | | |
| May 1998 | Jun. - Nov 1998 | 77 | 2 | 3 | 30 | 1 | 3 | 2.8 |
| | Dec. 1998 | 24 | 20 | 83 | 15 | 7 | 47 | 69.2 |
| | Jan. 1999 | 8 | 7 | 88 | 10 | 9 | 90 | 88.9 |
| | Mar. - Apr. 1999 | 5 | 4 | 80 | 12 | 8 | 67 | 70.6 |

Table 8.5: Date and numbers of recaptures of male and female *P. gilchristi* in the first year after tagging, showing the monthly frequencies of moulting at St Francis

| Month tagged | Month recaptured | Males | | | Females | | | M&F |
|---|---|---|---|---|---|---|---|---|
| | | Recaptured (n) | Moulted (n) | Moulted (%) | Recaptured (n) | Moulted (n) | Moulted (%) | Moulted (%) |
| ***Pooled sample:*** | | | | | | | | |
| | Tagging date to Nov. | 122 | 6 | 5 | 61 | 5 | 8 | 6.0 |
| | Dec. - Feb. | 14 | 11 | 79 | 16 | 11 | 69 | 73.3 |
| | After Feb. | 64 | 58 | 91 | 59 | 46 | 78 | 84.6 |
| ***Individual samples:*** | | | | | | | | |
| May 1990 | Jun. - Sep. 1990 | 6 | 1 | 17 | 5 | 0 | 0 | 9.1 |
| | Oct. - Nov. 1990 | 16 | 2 | 13 | 13 | 2 | 15 | 13.8 |
| | Dec. 1990 - Feb. 1991 | 13 | 10 | 77 | 15 | 10 | 67 | 71.4 |
| | Mar. 1991 | 7 | 7 | 100 | 6 | 4 | 67 | 84.6 |
| | Apr. - May 1991 | 11 | 10 | 91 | 11 | 8 | 73 | 81.8 |
| Apr. 1996 | May - Jul. 1996 | 62 | 1 | 2 | 28 | 2 | 7 | 3.3 |
| | Aug. - Nov. 1996 | 2 | 0 | 0 | 0 | | | |
| | Dec.1996 - Feb. 1997 | 0 | | | 0 | | | |
| | Mar. - Apr. 1997 | 23 | 20 | 87 | 15 | 13 | 87 | 86.8 |
| Apr. 1997 | Apr. - Aug. 1997 | 4 | 0 | 0 | 3 | 0 | 0 | 0.0 |
| | Sep. - Nov. 1997 | 0 | | | 0 | | | |
| | Dec. 1997 - Feb. 1998 | 1 | 1 | 100 | 1 | 1 | 100 | 100.0 |
| | Mar. - Apr. 1998 | 15 | 13 | 87 | 23 | 17 | 74 | 78.9 |
| Aug. 1998 | Sep. - Nov. 1998 | 32 | 2 | 6 | 12 | 1 | 8 | 6.8 |
| | Dec. 1998 - Feb. 1999 | 0 | | | 0 | | | |
| | Mar. 1999 | 8 | 8 | 100 | 4 | 4 | 100 | 100.0 |

Table 8.6: Date and numbers of recaptures of male and female *P. gilchristi* in the first year after tagging, showing the monthly frequencies of moulting at Port Elizabeth

| Month tagged | Month recaptured | Males | | | Females | | | M & F |
|---|---|---|---|---|---|---|---|---|
| | | Recaptured (n) | Moulted (n) | Moulted (%) | Recaptured (n) | Moulted (n) | Moulted (%) | Moulted (%) |
| ***Pooled sample:*** | | | | | | | | |
| | Tagging date to Nov. | 88 | 4 | 5 | 27 | 0 | 0 | 3.5 |
| | Dec. - Feb. | 9 | 7 | 78 | 1 | 1 | 100 | 80.0 |
| | After Feb. | 13 | 11 | 85 | 14 | 10 | 71 | 77.8 |
| ***Individual samples:*** | | | | | | | | |
| Aug. 1990 | Sep. - Nov. 1990 | 71 | 3 | 4 | 19 | 0 | 0 | 3.3 |
| | Dec. 1990 - Feb 1991 | 9 | 7 | 78 | 1 | 1 | 100 | 80.0 |
| | Mar. 1991 | 1 | 1 | 100 | 0 | | | 100.0 |
| | Apr. - Jun 1991 | 12 | 10 | 83 | 12 | 9 | 75 | 79.2 |
| Jul. 1995 | Sep. - Nov. 1995 | 17 | 1 | 6 | 8 | 0 | 0 | 4.0 |
| | Dec. 1995 - Feb. 1996 | 0 | | | 0 | | | |
| | Mar. 1996 | | | | 2 | 1 | 50 | 50.0 |

Table 8.7: Date and numbers of recaptures of male and female *P. gilchristi* in the first year after tagging, showing the monthly frequencies of moulting at Port Alfred

| Month tagged | Month recaptured | Males | | | Females | | | M & F |
|---|---|---|---|---|---|---|---|---|
| | | Recaptured (n) | Moulted (n) | Moulted (%) | Recaptured (n) | Moulted (n) | Moulted (%) | Moulted (%) |
| ***Pooled sample:*** | | | | | | | | |
| | Tagging date to Nov. | 20 | 3 | 15 | 42 | 6 | 14 | 14.5 |
| | Dec. - Feb. | 80 | 69 | 86 | 78 | 39 | 50 | 68.4 |
| | After Feb. | 24 | 20 | 83 | 23 | 17 | 74 | 78.7 |
| ***Individual samples:*** | | | | | | | | |
| Jun. 1992 | Jul. - Nov. 1992 | 0 | | | 1 | 0 | 0 | 0.0 |
| | Dec.1992 - Jan. 1993 | 0 | | | 0 | | | |
| | Feb. 1993 | 75 | 65 | 87 | 64 | 37 | 58 | 73.4 |
| | Mar. 1993 | 3 | 3 | 100 | 0 | | | 100.0 |
| | Apr. 1993 | 14 | 10 | 71 | 15 | 10 | 67 | 69.0 |
| June 1996 | Jul. - Dec. 1996 | 0 | | | 0 | | | |
| | Jan. 1997 | 3 | 2 | 67 | 6 | 3 | 50 | 55.6 |
| | Feb. 1997 | 5 | 4 | 80 | 14 | 2 | 14 | 31.6 |
| | Apr. - Jun. 1997 | 7 | 7 | 100 | 8 | 7 | 88 | 93.3 |
| May 1997 | May. - Nov. 1997 | 20 | 3 | 6 | 41 | 6 | 15 | 14.8 |

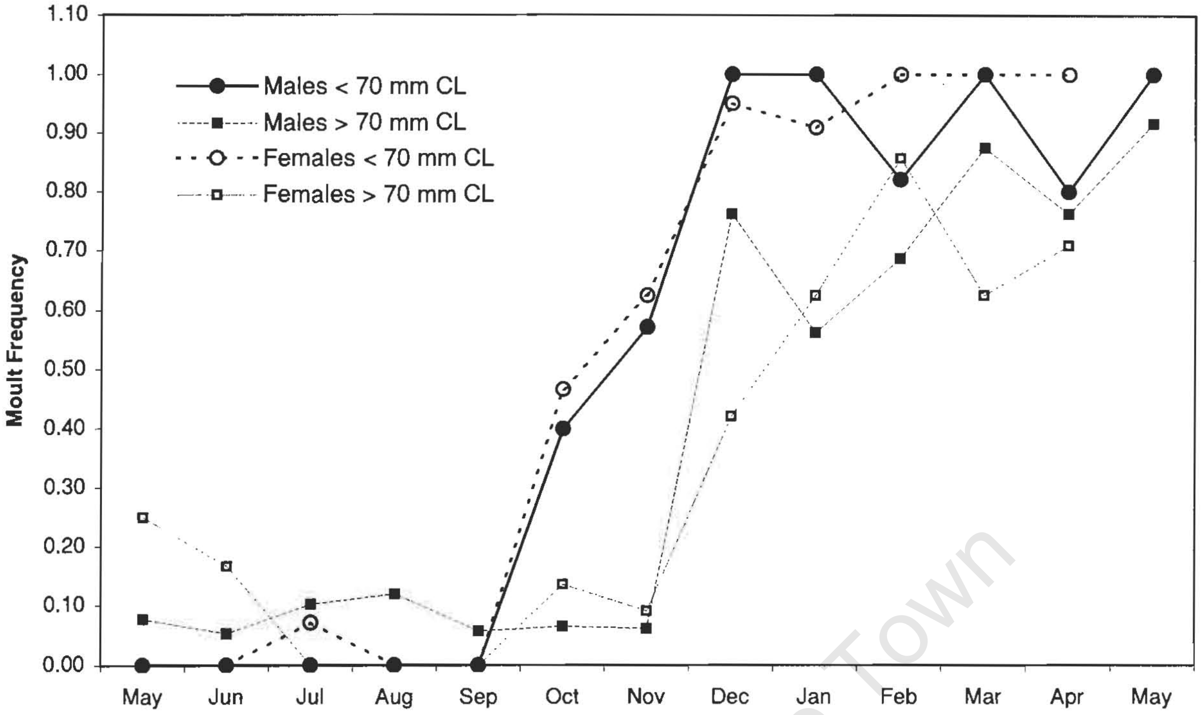

Figure 8.9: Monthly moulting frequencies of small (CL < 70 mm) and large (CL > 70 mm) *P. gilchristi* based on tag-recaptures.

and the ornate spiny lobster *P. ornatus* (Turnbull, 1989). Some differences exist, however, and contrary to *P. marginatus*, postmoult stage A of *P. gilchristi* can be distinguished from B; setae in stage B have thicker walls, a narrower lumen and a more homogenous protoplasm than those in stage A.

The intermoult stage C in *P. gilchristi* is best characterised by the very narrow, hollow appearance of the setal lumen (or its complete absence from the distal part of the setal shaft) and by a multi-layer cuticle with deeply imbedded setae in most cases. This stage was not subdivided in *P. gilchristi*; such a subdivision might have been possible based on the thickness of the cuticle and appearance of the setae, but would have been subjective and not particularly useful within the context of this study.

The premoult substages $D_{1'}$ and $D_{1''}$ in *P. gilchristi* were indistinguishable, with some pleopods simultaneously exhibiting characteristics of both. Thus the conical precursors of new setae (a characteristic of stage $D_{1''}$) develop rapidly after, or simultaneously with the retraction of the epidermis from the old cuticle. The grouping of these two substages (as $D_{1'}$) follows the pattern set for *P. ornatus*, in which a similar grouping was made when no substage $D_{1''}$ could be distinguished (Turnbull, 1989). Early formation of new setae is not uncommon, and it has also been shown to occur in stages $D_0$ and $D_{1'}$ in the crayfish *Parastacoides tasmanicus* (Mills and Lake, 1975), *Astacus leptodactylus* (Van Herp and Bellon-Humbert, 1978) and *Orconectes sanborni* (Stevenson *et al.*, 1968) and in the tiger prawn *Penaeus esculentus* (Smith and Dall, 1985).

After taking on a $D_2$ appearance (invaginated setae, setal walls, a granular protoplasm, barbules and a new cuticle with setal articulations) no further change was observed in pleopods, even in samples taken two days before moulting. Thus, similarly to *P. ornatus*, the $D_3$ and $D_4$ stages are short and cannot be identified from pleopods.

The observed time periods to moulting for different pleopod stages depended on temperature in *H. americanus* (Aiken 1973), shortening with increased temperature. To simulate its natural environment, *P. gilchristi* in the aquarium were kept at 13°C (9 –

14°C in their natural habitat), and the time periods to moulting were 30-46 days from stage $D_{1'}$, 23-24 days from stage $D_{1'''}$, and 2-15 days from stage $D_2$. These periods correspond well to that of *H. americanus* at similar temperatures (10 – 15°C): 20-40 days for stages $D_{1'}$ and $D_{1''}$ (corresponding to $D_{1'}$ in *P. gilchristi*), 15-22 days for stage $D_{1'''}$, and 3-13 days for stages $D_2$ and $D_3$ (corresponding to $D_2$ in *P. gilchristi*) (Aiken, 1973). Conversely, timing to moulting of *P. ornatus* at warm temperatures of 25 – 31°C was far quicker: 5 days from stage $D_{1'}$; 3 days from stage $D_{1'''}$, and 1-2 days from stage $D_2$ (Turnbull, 1989). The progression from early D stages to moulting is also rapid in the tropical spiny lobster *P. argus*, occurring within 10-14 days (Travis, 1955).

The pleopod index developed in this study was successfully used to determine the moulting season from field samples, however, it is constrained by the fact that most lobsters do not enter traps when moulting (Morgan, 1974). This explains the low proportion (1.0 %) of late premoult *P. gilchristi* (stage $D_2$) captured in field samples. The low proportions of early premoult lobsters in field samples are more difficult to explain, especially as lobsters in these stages ($D_0$ – $D_{1'''}$) fed actively in captivity. Premoult lobsters may, however, be less active, so reducing their catchability relative to intermoult lobsters. The total absence of postmoult lobsters (stages A and B) in field samples is almost certainly a result of these lobsters being non-feeding; this behaviour also occurs in other spiny lobster species (Travis, 1955).

The absence of a definite hard shell-state in *P. gilchristi* makes this index somewhat subjective, and the low monthly maximum incidence of soft-shelled individuals in traps reflects the non-feeding period directly after moulting. The shell-state index was therefore not considered to be a good method to determine moult seasonality in *P. gilchristi*. Nevertheless, industry personnel at commercial live-lobster facilities have regularly commented that some lobsters caught in December are soft-shelled and are therefore unsuitable for live export.

The tag-recapture index is based on a comparison of the numbers of recaptured lobsters per month that had moulted (i.e. with a positive increment in CL) with those that had not (i.e. no CL-increment). However, lobsters may moult without increasing in size, or even with body shrinkage (Conan, 1985; Cockcroft and Goosen, 1995), and thus some lobsters may have moulted without detection, so biasing the true moult incidence downwards. This bias is more likely to occur in the larger size classes where moult increments are often smaller, or in slow-growth areas, such as Port Alfred (Groeneveld, 1997). The lower moulting percentages illustrated for large lobsters in November and December in Fig. 8.9 and for females at Port Alfred in Table 8.5 are therefore likely to be artifacts of the data, although it is still possible that not all lobsters moult annually.

Taking the lag-time between the early premoult stages and moulting into account (~ 1 month) the pleopod and tag-recapture indices both indicate that most male and female lobsters moult in November and December (mid-summer) but that some individuals moult during other times of the year. The moulting season is furthermore size-dependent, with individuals with a CL < 70 mm commencing as early as October, whereas those with a CL ≥ 70 mm do not moult until December (Fig. 8.9). The smaller animals achieved a 100 % moult incidence, with larger lobsters achieving only ~ 80 %. Few lobsters with a CL < 60 mm were tagged, and no inferences were made regarding their moulting pattern.

The results of this study are supported by information on seasonal variation in hepatopancreas activity (Timme, 1995). Lobster hepatopancreas contains active proteolitic enzymes which are released in the gut to degrade proteins during active feeding stages. Timme (1995) found that firm-shelled intermoult individuals showed the highest level of hepatopancreatic and proteolitic activity, and that these peaked in January to March, and in June to August. Her study therefore confirms that *P. gilchristi* does not moult during these months, and that lobsters are in either pre- or postmoult conditions in October and November. The same author suggested an additional short moulting season in April and May, but this could not be discerned by any of the present methods.

Size-dependent moulting patterns have been shown for several lobster species, for example *P. argus* (Lipcius, 1985), *P. cygnus* (Chittleborough, 1976), and *H. americanus* (Aiken and Waddy, 1980; Ennis 1980). Lipcius (1985) presented moulting rates of *P. argus* as a function of size, and found that small immature individuals moulted at intervals throughout the year, with this pattern gradually narrowing to short seasonal moulting seasons in spring (for males) and autumn (for females) as lobsters increased in size. Individuals of intermediate size (small mature lobsters) also exhibited seasonal moulting seasons, though these commenced earlier and extended over longer time periods than in large individuals. Despite the absence of data on lobsters with a CL< 60 mm, a similar pattern is suggested for *P. gilchristi*. Accordingly, small immature *P. gilchristi* of both sexes would be expected to moult at intervals throughout the year, with the moulting season narrowing to spring and summer (from September or October onwards) in small mature lobsters (60 mm < CL < 70 mm) (see Fig. 8.9) and narrowing further to mid-summer (November and December) in larger individuals (CL > 70 mm).

The coordination of moulting and reproduction in *P. gilchristi* is unimodally synchronised, with moulting occurring in summer, and egg-bearing in winter (Groeneveld and Rossouw, 1995). Moulting in summer occurs when the water temperature at 100-m depth over the South Coast shelf area is somewhat cooler than during winter, because of an intense seasonal thermocline structure that exists during summer, but not in winter (Shannon, 1966; Schumann and Beekman, 1984; Swart and Largier, 1987; Goschen and Schumann, 1988). Winter spawning, and external egg development thereafter thus coincides with a slightly warmer temperature regime. This cycle agrees with the general pattern suggested for macruran decapods by Conan (1985), i.e.: in regions with little seasonal variation and cold water there appears to be only one moulting season shifted towards the cooler season.

The egg-bearing season of *P. gilchristi* females between June and November (Groeneveld and Rossouw, 1995) is closely followed by moulting in November and December, resulting in a 5-month (January – May) intermoult period in which large mature females (but not smaller mature females) may produce a second batch of eggs (in March or April;

see Groeneveld and Rossouw, 1995). The relatively long timespan inferred between moulting and mating (assuming that mating takes place shortly before spawning) suggests that mating takes place between hard-shelled individuals, and that it is not constrained to a few hours or days after a female had moulted, as in the genus *Jasus*; successful mating of *Jasus* lobsters only takes place between hard-shelled males and recently moulted females with soft exoskeletons (Heydorn, 1969b; Silberbauer, 1971; MacDiarmid, 1989; Lipcius and Cobb, 1994).

The separation of moulting and mating is common within the palinurid group, and frequently occurs in the closely related, but tropical genus *Panulirus* (Berry, 1971a, 1971b; Morgan, 1980; Phillips *et al.* 1980; Lyons *et al.* 1981; Lipcius, 1985). Here, the separation of moulting and mating allows females to mate and spawn repeatedly without having to moult before each mating episode, so reducing the time period between spawnings and increasing reproductive output. Similarly, the separation of moulting and mating in *P. gilchristi* may also have evolved to allow for two spawnings per year in large females.

Based on the results of the pleopod- and tag-recapture indices, a closed fishing season between October and December would coincide with moulting in *P. gilchristi*. Closure over this period would minimize financial losses to fishers resulting from weak or soft-shelled premoult or postmoult animals. However, the demand for lobsters is highest over the Christmas season (pers. comm., Industry representatives) and a closed season over December will affect marketing severely. The pros and cons of a closed season therefore needs to be debated between scientists and fishers, taking both biological and economic aspects into account.

# Chapter 9

# Migration of *P. gilchristi*

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## 9.1. Introduction

Many lobster species move substantial distances to achieve biological needs such as food, shelter, genetic mixing, reproduction or recruitment (Herrnkind, 1980). These movements are often seasonal, and where predictable, dictate the spatial and temporal distribution of fisheries for spiny lobsters (Street, 1971; McKoy, 1983; Phillips, 1983; Moore and McFarlane, 1984; Booth, 1997; Noli and Grobler, 1998) as well as those for true lobsters (Cooper and Uzmann, 1971; Haakonsen and Anoruo, 1994). Migratory behaviour such as queuing (Herrnkind, 1969) and aggregating (Koyama, 1971; Kelly *et al.*, 1999) may make migrants particularly susceptible to overfishing or localized depletion, and therefore have important implications for the management of exploited lobster stocks.

Herrnkind (1980) reviewed the movement patterns of palinurid crustaceans and described three major types: (1) migrations, or the movement of a population (or a distinct part of it) within a confined time period and over relatively long distances; (2) nomadism, or the wandering of individuals without any clear start and end points; and (3) homing, involving periodic excursions from a shelter to some nearby area, with subsequent return to that shelter or others nearby.

The techniques used to assess the movements of spiny and clawed lobsters include: (1) monitoring the biological attributes of the commercial catch; (2) wide-area tagging and recapture programs; (3) direct collection and observation by divers; (4) ultrasonic telemetry; (5) monitoring of physical variables concurrent with field sampling; and (6) correlated behavioural and physiological studies of captive specimens (Herrnkind, 1980;

Haakonsen and Anoruo 1994). Monitoring the commercial catch has numerous advantages. It covers wide geographical areas and consistently produces large quantities of data over a long period and at a low cost. It generally reveals major redistributions of migrants and their biological features (i.e. juveniles, adult males and gravid females). Quantitative information on distance and direction moved and rate of movement may be provided by tag-recapture studies. These studies are particularly useful when used in conjunction with commercial catch information (Moore and McFarlane, 1984).

Migration plays a crucial role in the recruitment of postlarvae or juveniles to the adult population, because it can counter the effects of wide dispersal by currents associated with the long phyllosoma larval phases (Booth, 1997). In such species, unless there is migration against the current ("contranatant" movement; Meek, 1915) by juveniles or adults, the species distribution may gradually be displaced in the direction of the currents which transport the larvae. *P. gilchristi* must be a strong candidate for migration because of its occurrence in the vicinity of the strong westerly-flowing Agulhas Current. A mechanism must exist to counter its potential westward displacement during pelagic larval phases, either via larval retention and oceanic larval dispersal and return processes (Booth and Phillips, 1994; Cobb, 1997; Chiswell and Booth, 1999), or by migration of benthic animals. Under similar strong directional current conditions, a counter-current migration was shown for closely-related *P. delagoae* in Chapter 5, and both species may have evolved a similar mechanism to cope with larval dispersal processes.

A wider implication of migration in *P. gilchristi* involves stock identity, and the possibility of separate stocks with contrasting growth rates, fecundity and sexual maturation parameters was recognized in Chapter 7. The absence of migrations between such areas would strengthen the case for stock-separation, although no firm conclusion can be reached without a genetic study.

This chapter assesses migration of *P. gilchristi* along the south coast of South Africa using tag-recapture, size composition and sex ratio information. Based on the likely influence of the westwards flowing Agulhas Current on larvae, it is predicted that migrations will be in an eastwards direction, include both sexes, and be restricted to individuals that have not yet reproduced. Based on the migration patterns described here, and on other evidence presented in Chapter 7, it is argued that there are two separate stocks of *P. gilchristi*.

## 9.2. Materials and methods

The Cape south coast between 18° 20' and 29° 50' E and between the shore and 200 m depth was partitioned into 10 $nm^2$ (16 $km^2$) grid blocks. These grid blocks (478 in total) provided a spatial context for the analysis of tag-recapture information and size composition samples.

Lobsters were tagged at five sites, namely Cape Agulhas, West and East Agulhas Banks, Mossel Bay-Port Elizabeth (including the St Francis and Port Elizabeth fishing grounds) and Port Alfred (Fig. 9.1). These sites are geographically separate, except for West and East Agulhas Banks, which are geographically contiguous, but can be distinguished because they are inhabited by lobster populations with distinct size frequencies (see Pollock and Augustyn, 1982; Groeneveld and Rossouw, 1995). The five sites included grid blocks in which tagged lobsters were recaptured, but excluded those in which fishing occurs, but where no recaptures were made (Fig. 9.1).

Tagging was conducted annually over an 11-year period (1988 – 1998), during commercial trap-fishing operations. Lobsters were tagged with standard numbered plastic T-bar tags (Hallprint, TBA-1), which were inserted into the abdominal musculature of each lobster, dorso-laterally between the posterior edge of the carapace and first abdominal segment, or between the first and second abdominal segments. Healthy lobsters of all sizes and both sexes were tagged, and sex, carapace length (CL ± 0.1 mm, measured mid-dorsally from the tip of the rostrum to the posterior edge of the carapace), geographic location, depth and date of tagging were recorded. Lobsters were released at the sea surface, within minutes of tagging.

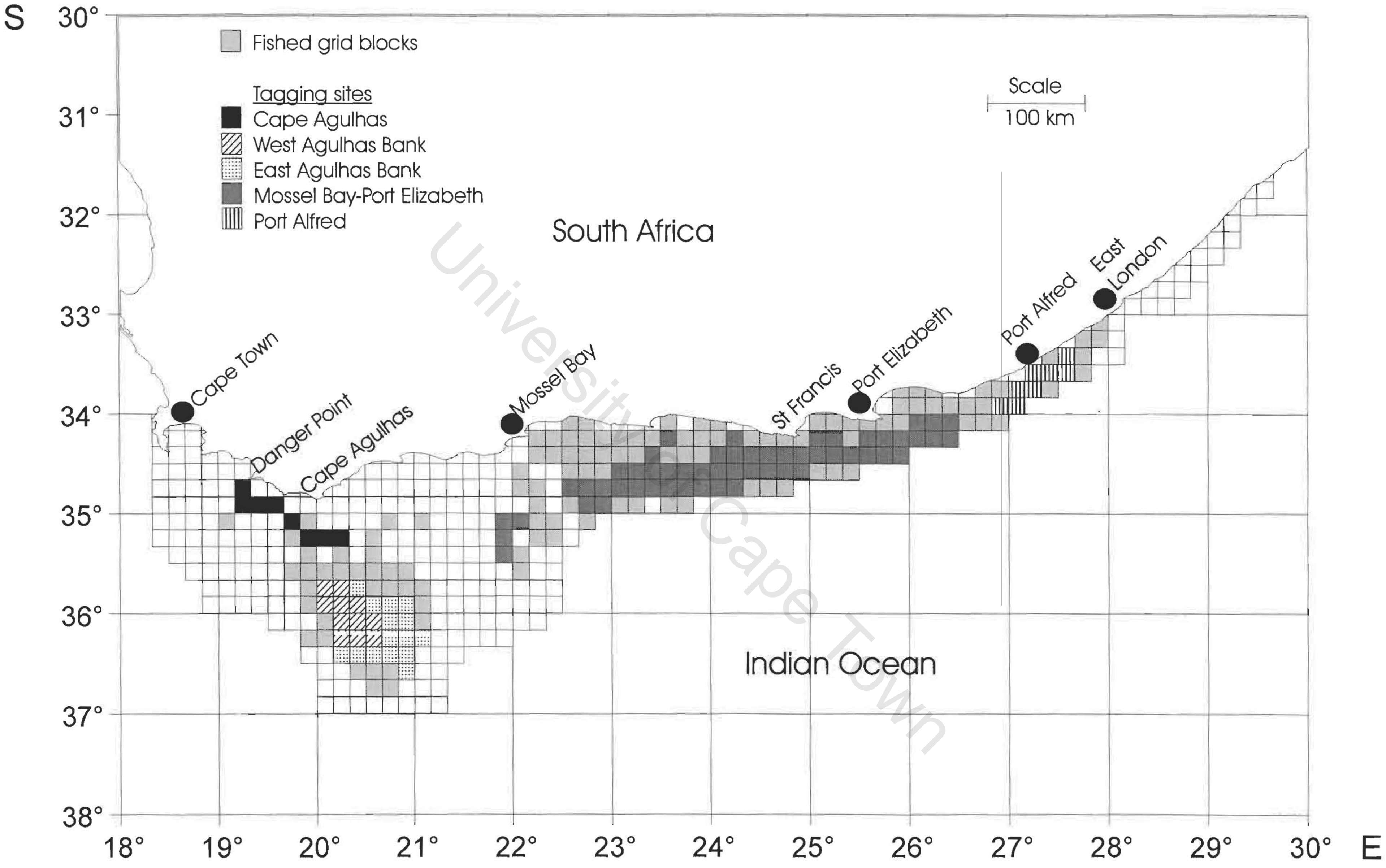

Figure 9.1: The South Coast of South Africa, showing the grid blocks that are fished and the five sites at which rock lobsters were tagged and recaptured.

A tag-reward system and tag-draw competition were used as incentives for the recovery of tagged lobsters from commercial fishers. Recaptured lobsters (with details on the date, depth and location of recapture) provided information on the time at liberty (TAL), distance and direction moved and the rate of movement of each animal.

Depths at which lobsters were captured during tagging and recapture were compared within and between sites by means of an ANOVA followed by a Tukey honestly significant difference (HSD) test (Zar, 1984).

Distances moved were calculated as the shortest distance between the release and recapture positions although this must underestimate the true distances traveled because movement will never occur in direct lines. Error estimates of distance moved were based on the characteristics of the fishery; long-lines with traps are generally 2 – 4 km long, and the reported capture location of a tagged lobster therefore has an error margin of ± 4 km. Tag-release location (at the sea surface) also has an error margin which relates to displacement of released lobsters by currents; a maximum displacement of 4 km was assumed. Based on the maximum combined error of 8 km, lobsters were classified as resident (those recaptured < 20 km from their tagging locations), short distance migrants (20 – 50 km) or long distance migrants (> 50 km).

Distance moved was compared among sites by means of an analysis of variance (ANOVA) followed by a Tukey HSD test (Zar, 1984). The data were not transformed as they met the conditions of normality and homogeneity of variance required of the ANOVA. Student's two-sample t-tests were used to compare distances moved by lobsters in two size classes (CL < 75 mm and CL > 75 mm); t-tests were performed separately for male and female lobsters at each tagging site.

The null hypothesis that lobsters moved in random directions after release was tested at each site, using $\chi^2$ tests to compare the frequency of lobsters moving short- or long-distances in each of eight directions (NE = 22.5°-67.5°; E = 67.5°-112.5°; SE = 112.5°–

57.5°; S = 157.5°-202.5°; SW = 202.5°-247.5 °; W = 247.5°-292.5°; NW = 292.5°-337.5°; and N = 337.5°-22.5°).

Migration rates (km moved per day at large) of lobsters tagged at each site were estimated from individuals that had moved > 50 km, and mean rates were compared between sites using an analysis of variance. However, means of migration rates certainly under-estimate actual rates because lobsters do not move in straight lines and time at large is likely longer than time spent migrating. Therefore the migration rates of the fastest 5 % of lobsters at each site was also calculated.

## 9.3 Results

### *9.3.1. Numbers tagged and recaptured, size composition, sex ratios and depth range*

In all, 30 043 lobsters of both sexes were tagged during 16 sampling trips undertaken between 1988 and 1998. These trips covered all the known fishing grounds between Cape Agulhas and Port Alfred, and included one sample from Cape Agulhas, four replicate samples from the Agulhas Bank, six from St Francis, three from Port Elizabeth, and two from Port Alfred (Table 9.1). Recapture rates per sample ranged from 0.16 to 15.89 % up to May 1999, with a combined rate of 7.51 % (2256 lobsters). Reliable information on tag and recapture positions were available for 2121 lobsters, and Fig. 9.2 shows the grid blocks in which these recaptures were made, relative to the five tagging sites.

The size composition at tagging of lobsters differed markedly between sites (Fig. 9.3). At Cape Agulhas, samples almost exclusively comprised small immature lobsters, average CL being 62.5 mm. The mean CL at West Agulhas Bank was 8.8 mm larger (71.3 mm), the population consisting mostly of immature and small mature lobsters. Lobsters at East Agulhas Bank had a mean CL of 75.8 mm, and the frequency distribution at that site appeared to be bimodal, suggesting the presence of a population of small lobsters (with a mode of 65 mm CL) as well as one of large lobsters (with a mode of 77 mm CL). The size frequency distributions at the last two sites were both bell-shaped, however, the

Table 9.1: Numbers of lobsters tagged per year and area, and recaptures made up to May 1999.

| Area tagged | Tag date | Tagged | | | Recaptured | |
|---|---|---|---|---|---|---|
| | | Males | Females | Total | Numbers | % |
| Agulhas Bank* | May 1988 | 1180 | 1317 | 2497 | 196 | 7.85 |
| St Francis** | May 1990 | 741 | 757 | 1498 | 238 | 15.89 |
| Port Elizabeth | Aug 1990 | 1178 | 617 | 1795 | 237 | 13.20 |
| Agulhas Bank* | Feb 1992 | 502 | 440 | 942 | 148 | 15.71 |
| Port Alfred | Jun 1992 | 800 | 1237 | 2037 | 246 | 12.08 |
| Cape Agulhas | May 1993 | 2357 | 1849 | 4206 | 163 | 3.88 |
| Agulhas Bank* | Jun 1995 | 1478 | 514 | 1992 | 303 | 15.21 |
| St Francis** | Jul 1995 | 718 | 275 | 993 | 56 | 5.64 |
| St Francis** | Apr 1996 | 1285 | 1102 | 2387 | 194 | 8.13 |
| Port Elizabeth | Jun 1996 | 814 | 1410 | 2224 | 99 | 4.45 |
| Port Alfred | May 1997 | 408 | 1089 | 1497 | 59 | 3.94 |
| St Francis** | May 1997 | 307 | 291 | 598 | 8 | 1.34 |
| St Francis** | Apr 1997 | 1151 | 1296 | 2447 | 62 | 2.53 |
| Port Elizabeth | Apr 1998 | 703 | 539 | 1242 | 2 | 0.16 |
| Agulhas Bank* | May 1998 | 1266 | 1179 | 2445 | 189 | 7.73 |
| St Francis** | Aug 1998 | 722 | 521 | 1243 | 56 | 4.51 |
| Totals | May 1988 - August 1998 | 15610 | 14433 | 30043 | 2256 | 7.51 |

* East and West Agulhas Banks combined

** Mossel Bay to Port Elizabeth

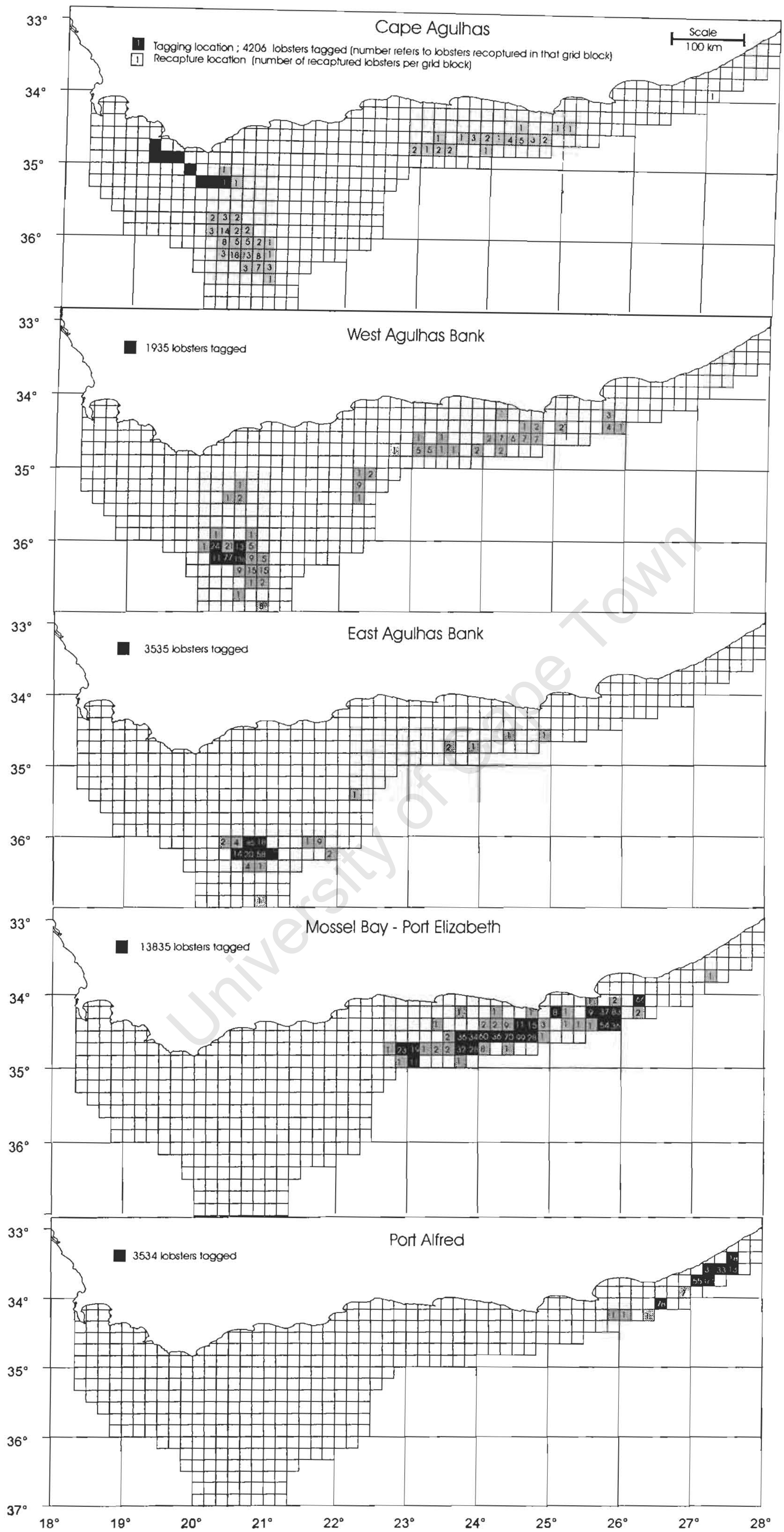

Figure 9.2: The numbers and distribution among grid blocks of recaptures for each tagging site.

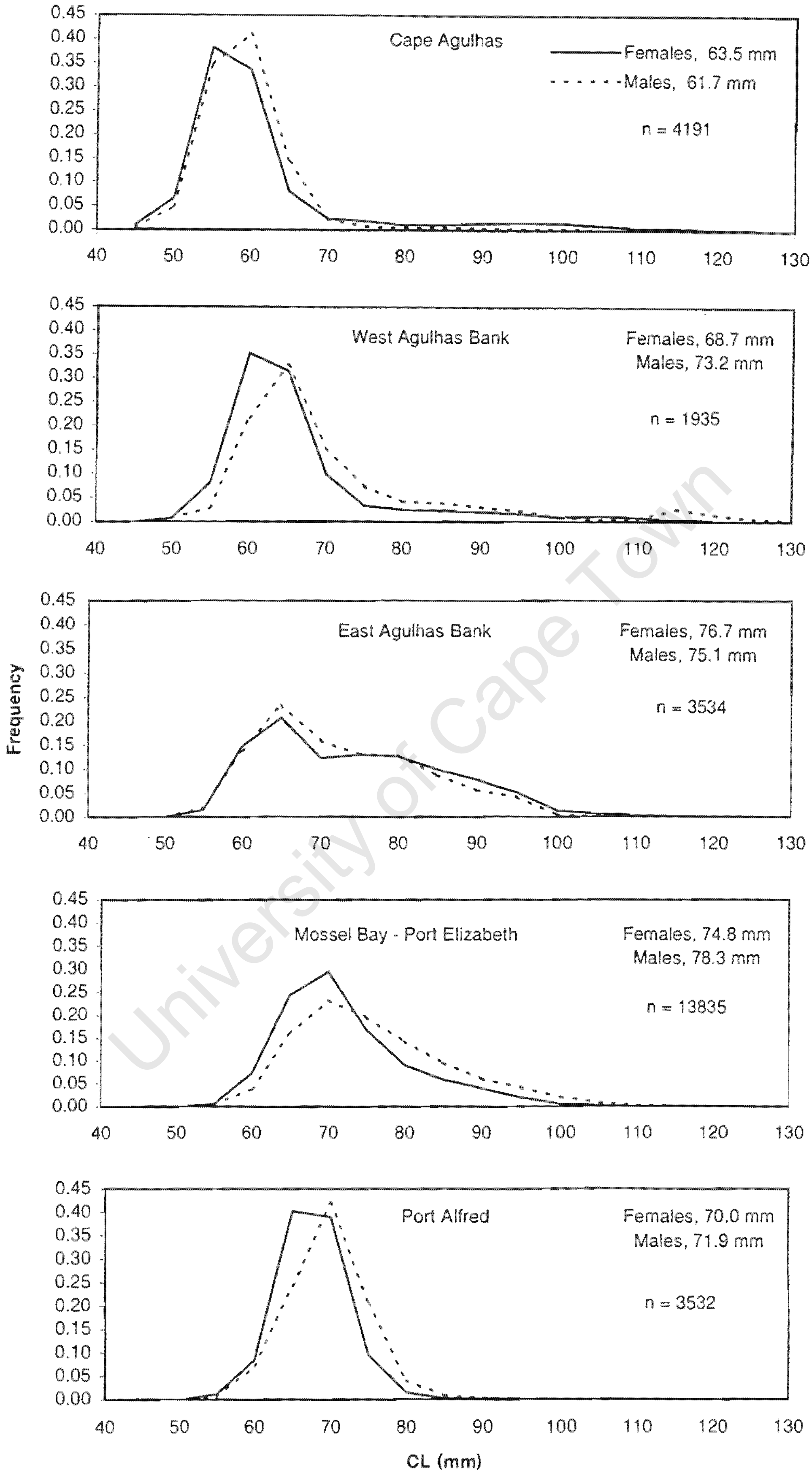

Figure 9.3: Size frequencies and mean CLs of male and female lobsters tagged at the five sites.

mean CL was 76.5 mm at Mossel Bay-Port Elizabeth compared to 70.7 mm at Port Alfred.

More males than females were tagged and recaptured at all sites except Port Alfred, where only 34 % of lobsters that were tagged were males. The proportion of males at recapture was significantly larger than that at tagging in most cases, including Port Alfred ($\chi^2$ - tests; $p<0.05$) (Table 9.2).

Depths at which lobsters were first captured differed significantly among sites (ANOVA, $F_{4,920} = 1247.7$, $p<0.001$), and this trend extended to recapture depths ($p< 0.001$). In all cases catches made at West Agulhas Bank occurred at the deepest extreme of the fished depth range for *P. gilchristi* (~ 160 m), whereas those made at Port Afred occurred at the shallowest (~ 95 m) (Table 9.3).

### *9.3.2. Distance and direction moved*

Of the 2121 recaptures with information on tagging and recapture location, 1563 (73.6 %) had moved < 20 km, and were thus considered to be resident in the areas where they were tagged. Of the migrants, 339 (52.6 %) had moved short distances (20-50 km), compared to 305 (47.4 %) long-distance migrants (50-800 km). The greatest recorded straight-line distance covered was 790 km, by a male lobster tagged at Cape Agulhas. The vast majority (97 %) of lobsters tagged at Cape Agulhas migrated long distances, with most (55 %) being recaptured 100-200 km from the tagging site (Fig. 9.4a), and a substantial proportion (27 %) being recaptured even further away (200-800 km). Sixty-two percent of recaptures from the West Agulhas Bank tagging sample remained resident (moved < 20 km) and a further 10 % migrated short distances (20 – 50 km). Similarly to Cape Agulhas, a large proportion of migrants from West Agulhas Bank (23 %) were recaptured > 100 km from tagging sites (Fig. 9.4a). Few lobsters tagged at the remaining three sites migrated > 50 km, the proportion of resident and short-distance migrants making up 93% of recaptured lobsters at East Agulhas Bank, 95 % at Mossel Bay-Port Elizabeth, and 98 % at Port Alfred (Fig. 9.4a).

Table 9.2: Proportions of males in tagging samples and in recaptures made at each site. Sites where < 20 recaptures were made are not included. Asterisks (*) indicate cases where the proportion of males at recapture was significantly different than at tagging.

| Proportion of males in tagging samples | | Proportion of males recaptured | | | | |
|---|---|---|---|---|---|---|
| | | All recaptures | West Agulhas Bank | East Agulhas Bank | Mossel Bay-Port Elizabeth | Port Alfred |
| Cape Agulhas | 0.56 | 0.59 | 0.62 | 0.57 | 0.55 | |
| West Agulhas Bank | 0.58 | 0.64* | 0.66* | 0.64 | 0.60 | |
| East Agulhas Bank | 0.59 | 0.70* | | 0.69* | | |
| Mossel Bay-Port Elizabet | 0.53 | 0.58* | | | 0.58* | |
| Port Alfred | 0.34 | 0.41* | | | | 0.41* |

Table 9.3: Mean depths at which lobsters were caught at tagging and at recapture

| Depth at tagging | | | | Depth at recapture | | | |
|---|---|---|---|---|---|---|---|
| Tagging site | Mean depth (m) | SD (m) | n | Recapture site | Mean depth (m) | SD (m) | n |
| Cape Agulhas | 119 | 11.4 | 151 | WAB | 159 | 9.2 | 75 |
| | | | | EAB | 147.5 | 9.9 | 25 |
| | | | | MB-PE | 114.9 | 9.8 | 29 |
| West Agulhas Bank | 162.3 | 9.8 | 100 | WAB | 162.5 | 4.8 | 108 |
| | | | | EAB | 155.4 | 4.9 | 42 |
| | | | | MB-PE | 118.5 | 12.3 | 45 |
| East Agulhas Bank | 141.9 | 12 | 290 | WAB | 166.2 | 3.9 | 7 |
| | | | | EAB | 138.2 | 5.6 | 218 |
| | | | | MB-PE | 126.3 | 9.1 | 11 |
| Mossel Bay-Port Elizabet | 116.2 | 8.2 | 163 | MB-PE | 114 | 14.1 | 561 |
| Port Alfred | 92.2 | 5.3 | 221 | Port Alfred | 96.4 | 12.9 | 219 |

WAB = West Agulhas Bank; EAB = East Agulhas Bank; MB-PE = Mossel Bay-Port Elizabeth

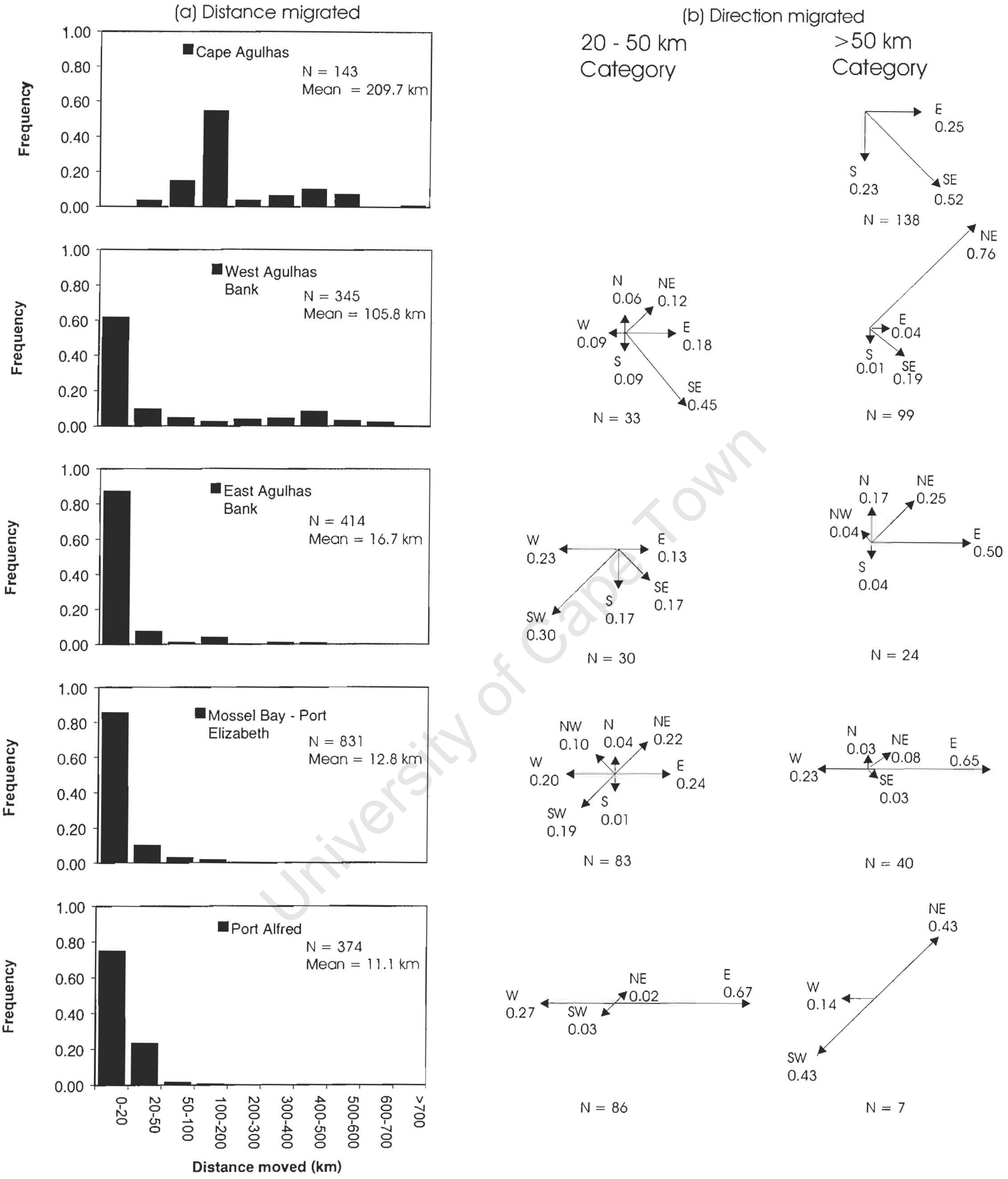

Figure 9.4: Frequency distributions of distance migrated (a) and directions taken (b). Vectors of direction are plotted for short distance (20 - 50 km) and long-distance (> 50 km) migrations

The hypothesis that lobsters moved in random directions after release was rejected in all nine cases tested ($\chi^2$ - tests; $p < 0.05$ for short and long-distance migrants at 5 sites, excluding short-distance migrants at Cape Agulhas, where the sample size was small). At Cape Agulhas, all the long-distance migrants moved offshore (S and SE) or alongshore (E) (Fig.9.4b). At West and East Agulhas Banks, long-distance migrants moved predominantly NE-wards ($p< 0.05$) and E-wards ($p < 0.05$). At Mossel Bay-Port Elizabeth, significantly more long-distance migrants moved eastwards (E and NE) than westwards ($\chi^2$ test, $p < 0.05$). At Port Alfred long-distance migrants were few in number ($n = 7$) but moved mainly on the N-NE to W-SW axis (Fig. 9.4b).

A comparison among sites of distances moved in the predominant E-NE direction showed significant differences between sites (ANOVA, $F_{3, 156} = 59.54$, $p < 0.05$; Port Alfred excluded) and a Tukey HSD test grouped migrants from Cape Agulhas (mean distance migrated in a N-NE direction = 470.9 ± 88.1 km SD) and West Agulhas Bank (408 ± 143.1 km) as separate from those at East Agulhas Bank (197.4 ± 135.4 km) and Mossel Bay-Port Elizabeth (127.6 ± 65.4 km) (Table 9.4). It is concluded that distances migrated in an eastward direction decline progressively from Cape Agulhas to Port Alfred.

### *9.3.3. Time at large (TAL) and distance moved*

Of 2121 recaptures, 1112 were at large for less than one year, 446 for 1-2 years, 251 for 2-3 years, 115 for 3-4 years and 101 for 4-5 years. A further 96 individuals were at large for 5.0 – 10.3 years. Lobsters tagged at Cape Agulhas remained at large for up to six years and were recaptured, in large numbers, at three of the five sites, throughout this period (Fig. 9.5). Recaptures occurred at West Agulhas Bank within a year of tagging (and up to 6 years thereafter), at East Agulhas Bank within two years after tagging, and at Mossel Bay-Port Elizabeth after three years. The mean distances moved by migrants from Cape Agulhas to these three sites increased from 119 km (migrants captured at West Agulhas Bank) to 461 km (at Mossel Bay-Port Elizabeth) (Table 9.5). Recaptures over a prolonged period at West- and East Agulhas Banks show that some of the lobsters that migrated here from Cape Agulhas became residents, whereas others migrated from Cape

Table 9.4: Comparison among sites of the average distance moved in each direction. Only long-distance migrants (> 50 km) were considered.

| Direction | Statistics | Tagging sites | | | | |
|---|---|---|---|---|---|---|
| | | Cape Agulhas | West Agulhas Bank | East Agulhas Bank | Mossel Bay to Port Elizabeth | Port Alfred |
| N | Mean dist.moved (km) | | | 107.5 | 52.5 | |
| | St. dev. (km) | | | 2 | | |
| | n | 0 | 0 | 4 | 1 | 0 |
| NE | Mean dist.moved (km) | | 426.3 | 365.5 | 178.9 | 69.1 |
| | St. dev. (km) | | 121.8 | 105.7 | 120.7 | 18.6 |
| | n | 0 | 75 | 6 | 3 | 3 |
| E | Mean dist.moved (km) | 470.9 | 64.3 | 113.4 | 121.6 | |
| | St. dev. (km) | 88.1 | 8.1 | 11.7 | 57.8 | |
| | n | 34 | 4 | 12 | 26 | 0 |
| SE | Mean dist.moved (km) | 149.3 | 81.5 | | | |
| | St. dev. (km) | 37.1 | 22.7 | | | |
| | n | 72 | 19 | 0 | 0 | 0 |
| S | Mean dist.moved (km) | 95.1 | 72.3 | 86.9 | | |
| | St. dev. (km) | 22.4 | | | | |
| | n | 32 | 1 | 1 | 0 | 0 |
| SW | Mean dist.moved (km) | | | | | 118.5 |
| | St. dev. (km) | | | | | 67.7 |
| | n | 0 | 0 | 0 | 0 | 3 |
| W | Mean dist.moved (km) | | | | 80.8 | 74.4 |
| | St. dev. (km) | | | | 19.4 | |
| | n | 0 | 0 | 0 | 9 | 1 |
| NW | Mean dist.moved (km) | | | 50.5 | 64.9 | |
| | St. dev. (km) | | | | | |
| | n | 0 | 0 | 1 | 1 | 0 |

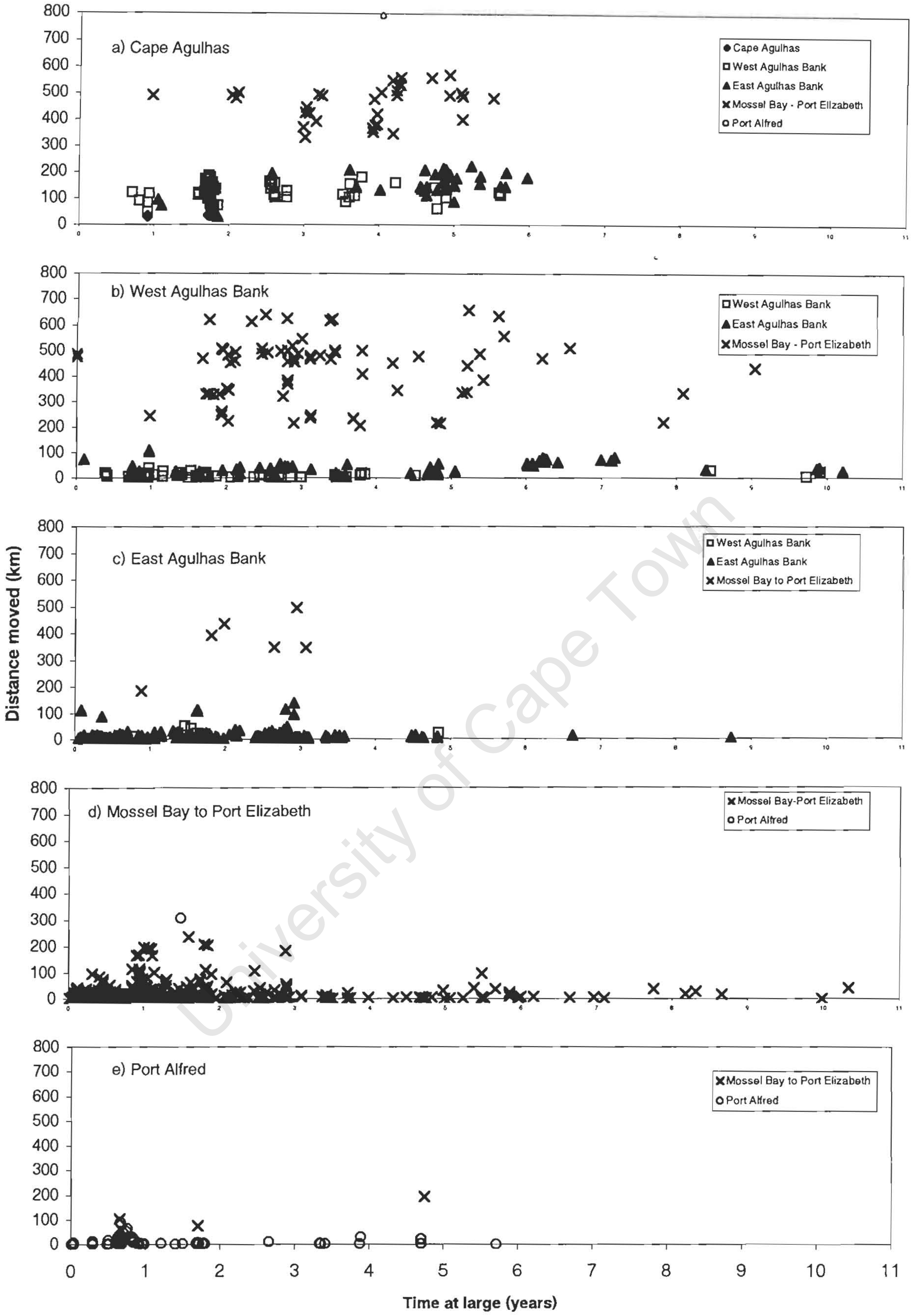

Figure 9.5: Distance moved (km) plotted against time at large (years) for lobsters tagged at each of the five sites

Table 9.5: Mean time-at-large (years) and distance moved (km) of lobsters tagged at each site.

| Tagging site | Recapture site | n | Time at large | | Distance moved | |
|---|---|---|---|---|---|---|
| | | | Mean (yrs) | SD* | Mean (km) | SD* |
| Cape Agulhas | Cape Agulhas | 3 | 1.47 | 0.48 | 33.02 | 1.78 |
| | West Agulhas Bank | 71 | 2.31 | 1.15 | 119.46 | 31.2 |
| | East Agulhas Bank | 35 | 4.34 | 1.33 | 154.02 | 46.07 |
| | Mossel Bay-Port Elizabeth | 33 | 3.77 | 1.03 | 461.19 | 68.64 |
| | Port Alfred | 1 | 4.03 | | 790.26 | |
| West Agulhas Bank | West Agulhas Bank | 146 | 1.62 | 1.55 | 8.24 | 6.46 |
| | East Agulhas Bank | 66 | 3.75 | 2.52 | 45.84 | 29.31 |
| | Mossel Bay-Port Elizabeth | 73 | 3.39 | 1.62 | 426.3 | 121.82 |
| East Agulhas Bank | West Agulhas Bank | 16 | 1.94 | 1.05 | 22.25 | 11.51 |
| | East Agulhas Bank | 392 | 1.57 | 1.34 | 11.14 | 22.27 |
| | Mossel Bay-Port Elizabeth | 6 | 2.23 | 0.83 | 365.51 | 105.67 |
| Mossel Bay-Port Elizabeth | Mossel Bay-Port Elizabeth | 844 | 1.13 | 1.34 | 12.4 | 25.87 |
| | Port Alfred | 1 | 1.49 | | 306.03 | |
| Port Alfred | Mossel Bay-Port Elizabeth | 4 | 1.95 | 1.93 | 107.47 | 59.48 |
| | Port Alfred | 269 | 0.98 | 1.22 | 10.01 | 11.66 |

* = Standard deviation (km)

Agulhas to Mossel Bay-Port Elizabeth. Three individuals were recaptured at the site of release (Cape Agulhas); but only a single lobster tagged at Cape Agulhas was recaptured at Port Alfred (Fig. 9.5; Table 9.5).

Lobsters tagged at West Agulhas Bank remained at large for up to 10.3 years, and were recaptured at three sites: West- and East Agulhas Banks, and Mossel Bay-Port Elizabeth (Fig. 9.5). At all three sites, recaptures were made over extensive periods. Lobsters that migrated to East Agulhas Bank were first recaptured within a year of tagging, and those that migrated to Mossel Bay-Port Elizabeth were first recaptured after two years at large (Fig. 9.5). On average, lobsters that remained at West Agulhas Bank moved 8 km, whereas those that moved to East Agulhas Bank and Mossel Bay-Port Elizabeth moved 45 km and 426 km, respectively (Table 9.5).

Most lobsters (95 %) tagged at East Agulhas Bank were recaptured in the same area within five years, however six had migrated to Mossel Bay-Port Elizabeth and were recaptured there after being at large for one - three years (Fig. 9.5; Table 9.5). Lobsters tagged at Mossel Bay-Port Elizabeth also remained at that site, and were recaptured over an 11-year period (Fig. 9.5; Table 9.5). A single lobster moved from this site to Port Alfred, where it was recaptured 1.5 years after tagging (Table 9.5). Lobsters tagged at Port Alfred remained resident over a 6-year period, with three exceptions; these were recaptured near Port Elizabeth (Fig. 9.5; Table 9.5).

The strong eastward movement from Cape Agulhas to Mossel Bay-Port Elizabeth clearly leads to a mixing of stock over this entire range. In notable contrast, only six individuals ever exchanged between this range and Port Alfred (Table 9.5).

### *9.3.4. Migration rate*

Mean migration rates ± SD per site (based on long-distance migrants (>50 km) but irrespective of time at large) and the migration rates of the fastest 5 % of individuals per site are shown in Fig. 9.6. Mean migration rates differed significantly between sites (ANOVA; $F_{4, 298} = 9.9$; $p < 0.001$), and a Tukey HSD test showed that the difference was

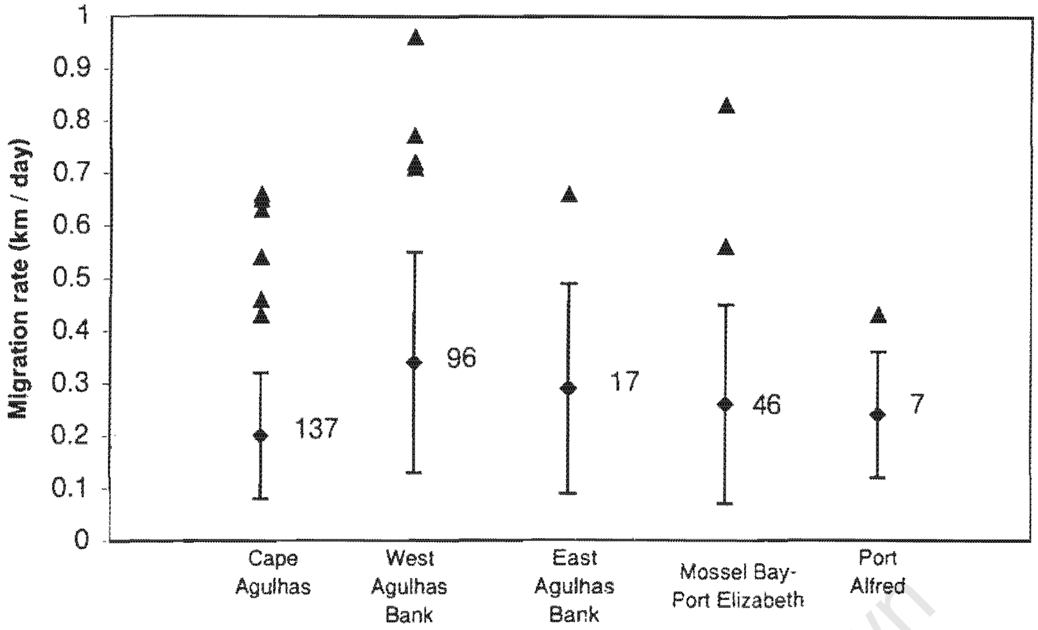

Figure 9.6: Rate of migration of lobsters at the five sites, showing means (+- standard deviation) and the fastest 5% of lobsters per site. Only lobsters that migrated > 50 km were used.

as a result of greater migration rates at West Agulhas Bank than at Cape Agulhas, Mossel Bay-Port Elizabeth and Port Alfred. Based on the fastest 5 % of lobsters, those tagged at West Agulhas Bank moved, on average, 0.78 km/day, followed by those tagged at East Agulhas Bank (0.66 km/day), Mossel Bay-Port Elizabeth (0.65 km/day) and Cape Agulhas (0.56 km/day). Lobsters tagged at Port Alfred moved the slowest (0.43 km/day).

### *9.3.5. Size of lobsters that migrate*

Plots of distance moved (km) versus CL (mm) at tagging showed that generally only lobsters < 75 mm CL migrated, and that lobsters > 75 mm CL remained resident at their respective tagging locations (Fig. 9.7). This trend was observed for both male and female lobsters, and occurred at Cape Agulhas (where the sample consisted only of lobsters < 75 mm CL, which all moved), West Agulhas Bank (where lobsters < 75 mm CL either moved or remained resident, but where all lobsters > 75 mm CL remained resident), East Agulhas Bank and Mossel Bay-Port Elizabeth (where most lobsters remained resident, but where those that moved where mostly < 75 mm CL). Student's t-tests used to compare distances moved in the two size-categories (for each site and sex separately) showed that both males and females in the < 75 mm CL-category moved significantly further than those in the > 75 mm CL-category at West Agulhas Bank ($p < 0.05$, $n = 221$ males; $p < 0.1$, $n = 124$ females) and at Mossel Bay-Port Elizabeth ($p < 0.05$, $n = 488$ males; $p < 0.05$, $n = 346$ females) and that small males at East Agulhas Bank also moved further than large males ($p < 0.05$, $n = 284$). Small females at East Agulhas Bank did not move significantly further than their larger counterparts ($p = 0.297$, $n = 125$), and neither could a difference be found between small and large males ($p = 0.315$, $n = 154$) or females ($p = 0.456$, $n = 220$) at Port Alfred. Virtually none of the Port Alfred animals could be considered as migratory.

## 9.4. Discussion

The tag and recapture method used to assess migration of *P.gilchristi* relies on five data-points that can be measured, namely the geographical positions of release and recapture, time at large and size- and sex composition. Actual distance moved, rate of migration,

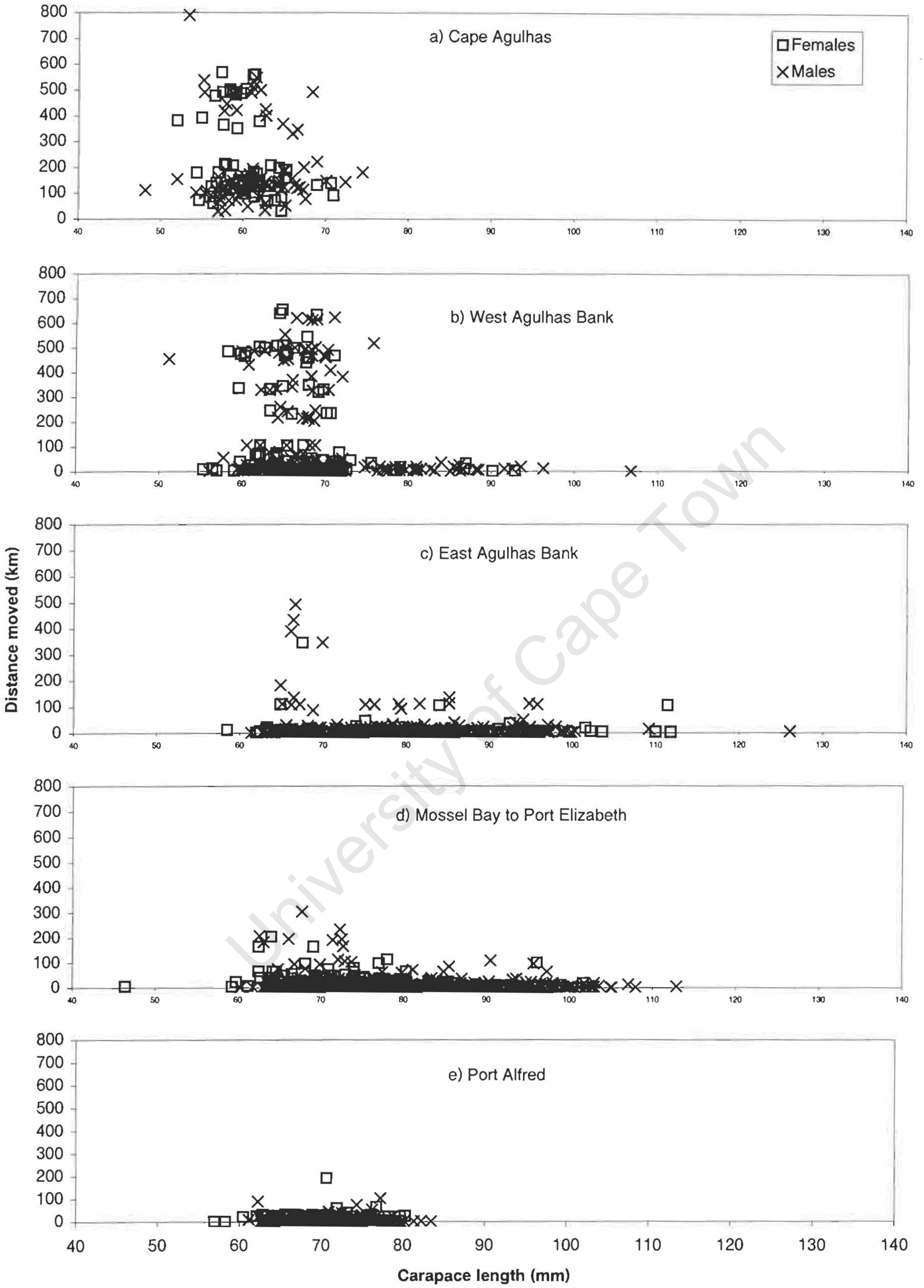

Figure 9.7: Distance moved (km) plotted against carapace length (mm) for lobsters tagged at the five sites

route taken and depth interval visited are inferred from these data, and a number of assumptions need to be made. Central to this study is the assumption that tags do not influence the behaviour of *P. gilchristi*. Many individuals retained their tags over several years, with the longest recorded period between tagging and recapture being 10.3 years. During this period an individual may moult at least 10 times (once annually; see Chapters 7 and 8), and it is therefore clear that tags that survive one moult do not easily dislodge during subsequent moults. Furthermore, growth estimates from tagging were similar to those from untagged animals in aquarium studies (see Chapters 7 and 8), and many females with tags bore eggs (pers. obs). These observations imply that tags do not influence the behaviour of *P. gilchristi* greatly.

Several sources of bias make the inferred parameters difficult to interpret; these include the assumptions that migration occurs along a straight line, and that lobsters are tagged at the outset of migration and are recaptured on arrival at its destination. None of these assumptions are likely to be true, and all three tend to bias estimates of actual distance migrated and migration rates downwards. Whereas it is difficult to correct for the under-estimate of distance migrated, migration rates can be more realistically estimated by relying on the rates of the fastest five percent of migrants at each site, instead of using mean migration rates. Results obtained in this manner (0.43 – 0.78 $km.d^{-1}$) were similar to those found in studies on *J. verreauxi* (0.61 $km.d^{-1}$; Booth, 1984), *P. ornatus* (0.61 $km.d^{-1}$; Moore and McFarlane, 1984) and *P. cygnus* (0.62 $km.d^{-1}$; Phillips, 1983).

Assuming that the numbers of males and females in the population are equal, the greater numbers of males caught in tagging and recapture samples imply that males have a higher catchability coefficient than females during most months of the year. Only at Port Alfred, where tagging was restricted to May and June, were more females than males caught (Table 9.2). Seasonal variations in sex ratio were investigated by Pollock and Augustyn (1982), and these authors concluded that males were captured more frequently than females in all months except November to March, but that this catchability trend did not extend to Port Alfred, where more females were observed, especially in size classes < 75 mm CL. The disparity in sex ratios observed in migrating lobsters in the present study is thus considered to be as a result of catchability fluctuations, and it is clear that both male and female lobsters migrate long distances.

Directional long-distance migrations have been shown for *P. delagoae* (Chapter 5) and for several *Jasus* and *Panulirus* lobster species (i.e. *P. argus, P. cygnus, P. ornatus, J. edwardsii* and *J. verreauxi;* Chubb, 1994), and the present study shows a very specific easterly migration pattern for juvenile and small adult *P. gilchristi* between Cape Agulhas and Mossel Bay-Port Elizabeth.

Data suggest that the migration originates at Cape Agulhas where the population consists almost exclusively of small juvenile lobsters with an average CL of 62.5 mm (Fig. 9.8). From Cape Agulhas, juveniles migrate offshore in a south-easterly direction, reaching West Agulhas Bank within a year, having grown to an average CL of 71.3 mm which is the size at which sexual maturity is attained (Groeneveld and Melville-Smith, 1994). From West Agulhas Bank, immature and small mature lobsters either disperse over the West and East Agulhas Banks and become resident over the next year, or migrate north-easterly and easterly to the Mossel Bay-Port Elizabeth region, which they reach within two years of tagging at West Agulhas Bank. The easterly migration of *P. gilchristi* does not extend to Port Alfred, and there is no evidence suggesting a westwards or return migration at any of the five sites.

The absence of recaptures over the inner Agulhas Bank (a rarely fished, shallower area between the coast and East Agulhas Bank), recapture of Cape Agulhas individuals at West and East Agulhas Banks and at Mossel Bay-Port Elizabeth, and recapture of West Agulhas Bank individuals at Mossel Bay-Port Elizabeth all suggest that migrants originating from Cape Agulhas and West Agulhas Bank do not cross the inner Agulhas Bank *en route* to Mossel Bay-Port Elizabeth, but that they follow the shelf-edge, first moving to deeper-water habitat at West Agulhas Bank (> 160 m), and thereafter recruiting to shallower-water adult habitat at East Agulhas Bank (~ 140 m) and Mossel Bay-Port Elizabeth (~ 120 m).

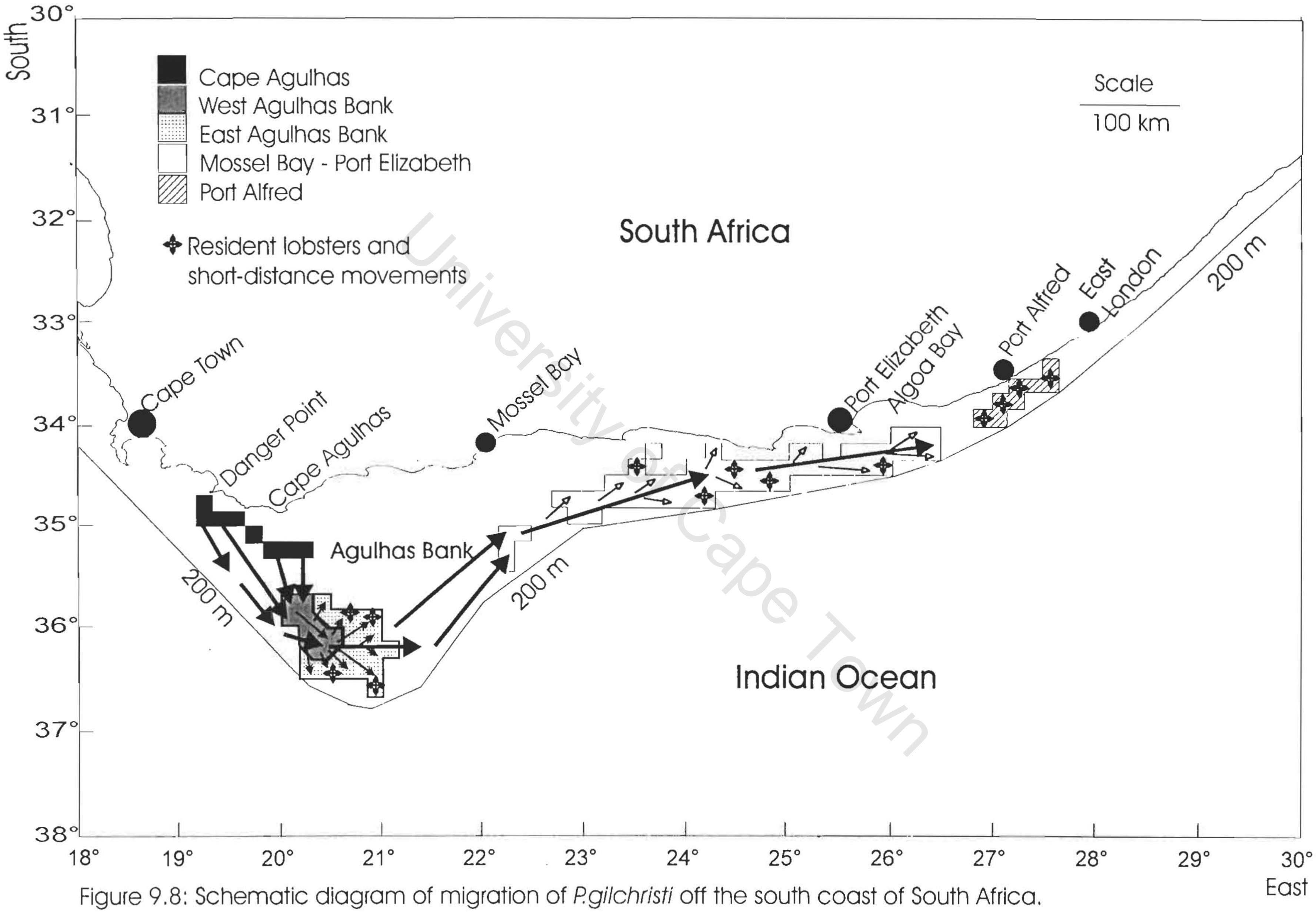

Figure 9.8: Schematic diagram of migration of *P.gilchristi* off the south coast of South Africa.

The easterly migration of juvenile and small adult *P. gilchristi* is against the south-westwards flowing Agulhas Current; this current flows swiftly (up to 300 cm/s) and deeply along South Africa's south and east coasts (Boyd *et. al*, 1992; Boyd and Oberholster, 1994). Similar migrations of juvenile or small mature spiny lobsters against the prevailing current or net coastal flow (also called contranatant movement; Meek, 1915) have been shown for *J. verreauxi* off New Zealand and southern Australia, *J. edwardsii* off New Zealand (McKoy, 1983; Booth, 1984, 1997), *P. cygnus* off Western Australia (Phillips, 1983) and *P. ornatus* in the gulf of Papua New Guinea (Moore and McFarlane, 1984). These contranatant movements are not restricted to spiny lobsters, but have also been shown for other decapods, such as scylarid lobsters (*Ibacus* sp.; Stewart and Kennelly, 1998) and crabs (*Cancer pagurus*; Edwards, 1967).

Contranatant movements likely evolved to counter displacement effects of currents on the distribution of pelagic phyllosoma larvae (Herrnkind. 1980). *P. gilchristi* larvae at East Agulhas Bank and Mossel Bay-Port Elizabeth hatch inshore of the core Agulhas Current (the inner boundary of the Current is located between the 200 m and 1000 m depth contours between the eastern Agulhas Bank and Algoa Bay; Boyd and Oberholster, 1994; Lutjeharms, 1991) and it is probable that a large proportion of phyllosoma larvae remain between the Current and the coast, where their dispersal is regulated by coastal currents, eddies, upwelling, wind-driven surface currents, fronts and behavioural adaptations (Phillips and McWilliam, 1986: Cobb, 1997; Chiswell and Booth, 1999) (Fig. 9.9). Despite regular reverse counter-currents and variable long-shore currents that prevail inshore of the Agulhas Current. the net flow along the Cape south coast is westerly (Boyd and Oberholster, 1994), and it is therefore likely that larvae will gradually be transported in the direction of Cape Agulhas. It is suggested that Cape Agulhas serves as an important settlement area for larvae originating from East Agulhas Bank and Mossel Bay-Port Elizabeth, and that the easterly migrations shown in this study serve to counter this displacement.

The presence of lobsters < 65 mm CL at sites other than Cape Agulhas suggests that some settlement occurs throughout the distribution range of this species, although to a

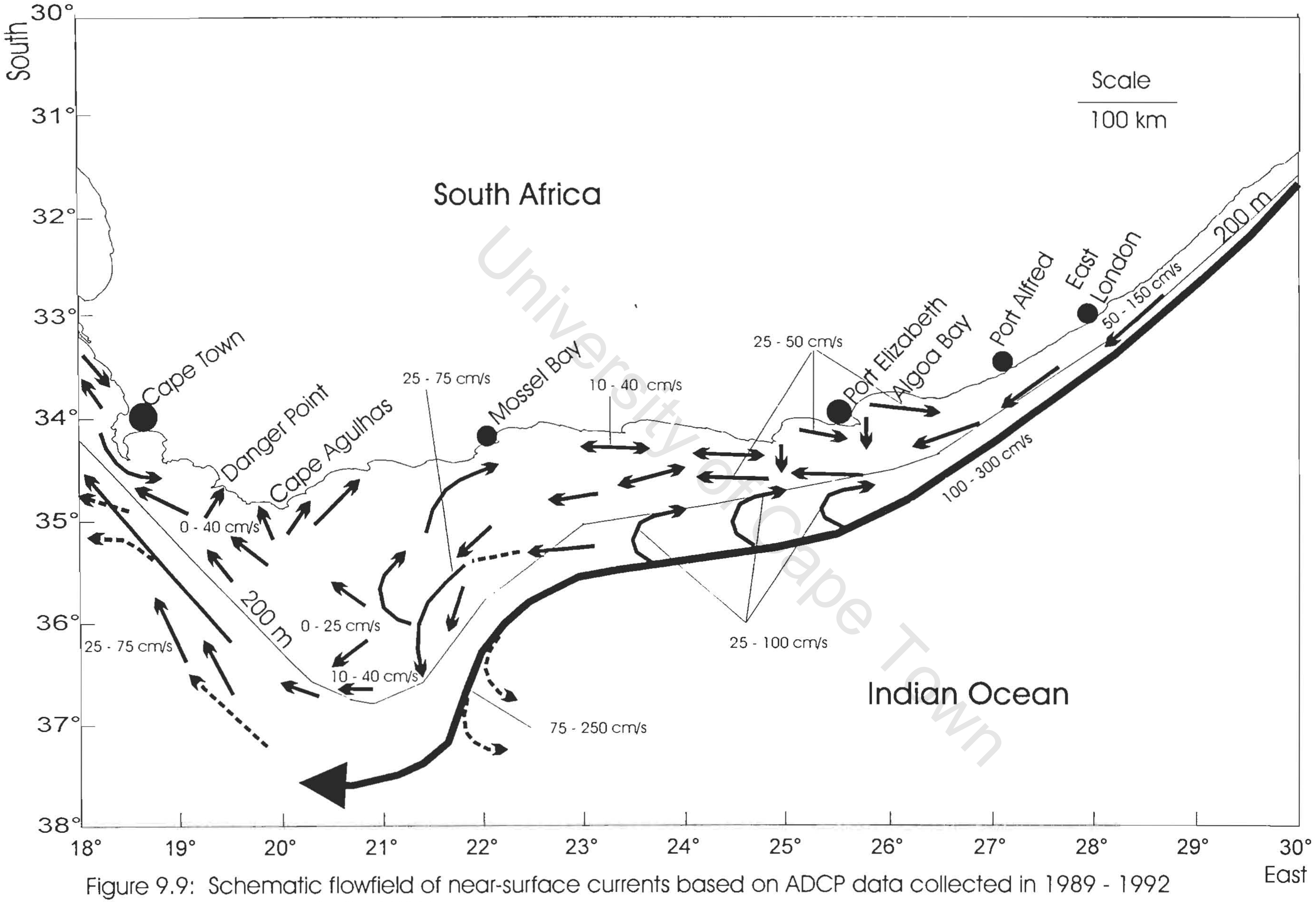

Figure 9.9: Schematic flowfield of near-surface currents based on ADCP data collected in 1989 - 1992 (redrawn from Boyd *et al.*, 1992)

lesser degree than at Cape Agulhas. However, it is difficult to assess the importance of the Cape Agulhas settlement area and the easterly migration relative to recruitment to the adult population in the absence of information on the distribution and dispersal mechanisms of *P. gilchristi* larvae and the distribution of juveniles < 50 mm CL; lobsters of these small sizes are not captured by commercial traps, and a survey with smaller-mesh traps by Pollock and Augustyn (1982) failed to locate other concentrations of juveniles. Furthermore, the cues for settlement of spiny lobster post-larvae are unclear (Cobb, 1997; Phillips and Pearce, 1997), although some crab species have been shown to metamorphose in response to water-soluble cues associated with major components of preferred adult habitat (Weber and Epifanio, 1996), or to the presence of adult crabs or sediment from adult habitats (O'Connor, 1991).

At Port Alfred *P. gilchristi* is essentially non-migratory, and juveniles and small adults in this region do not move directionally. It is inferred that larvae originating from this site are not transported to Cape Agulhas, but utilize different dispersal and return strategies to counter current-related displacements. The continental shelf at Port Alfred is very narrow and steep, and the Agulhas Current flows closer inshore there than at sites to the west of Port Elizabeth. Consequently, this site experiences greater exposure to the Current (Schumann, 1987, Schumann *et al.* 1991), which reaches a south-westerly velocity of 100 - 300 cm.s$^{-1}$ (Boyd *et al.*, 1992; Boyd and Shillington, 1994). Larvae that hatch at Port Alfred are thus more likely be swept into the core of the Current, to be transported rapidly offshore and to the south-west. A return-mechanism (although not for this site specifically) has been postulated by Pollock (1989): accordingly larvae taken up in the Agulhas Current are transported towards the Agulhas Current retroflection, from where they are returned eastwards to Port Alfred via the eastwards-flowing Agulhas return current or the South-Indian ocean gyre. An extended larval period would be required for such a long journey, and Cobb (1997) summarizes the findings of various authors that spiny lobster larvae have comparatively long larval periods, which can be further extended by mark-time moulting.

The marked differences in migration behaviour of *P. gilchristi* at Port Alfred compared to those at Cape Agulhas to Mossel Bay-Port Elizabeth, and the proposed dichotomy in larval distribution mechanisms suggest that there are two stocks of this species and that they are geographically separated. Support for this separation is provided by the population characteristics of lobsters occurring at Port Alfred compared to those at Cape Agulhas to Mossel Bay-Port Elizabeth. *P. gilchristi* at Port Alfred are smaller (Groeneveld, 1993; Groeneveld and Rossouw, 1995), reach sexual maturity at a smaller CL (Groeneveld and Melville-Smith, 1994), grow slower (Groeneveld, 1997; Chapter 7) and are less fecund (Chapter 7) than their counterparts at Cape Agulhas to Mossel Bay-Port Elizabeth. The separate-stock theory needs further investigation, as it has implications for the management of the fishery for this species. Genetic analyses are an obvious way forward.

It is concluded that lobster size and location both influence migration, with small lobsters at Cape Agulhas and West Agulhas Bank being the most active migrants, and those at Port Alfred not migrating at all. All migrants move eastwards, counter to the Agulhas Current, and this movement pattern is likely a mechanism to redress displacement of larvae by the net westwards flow in the region. Based on biological characteristics, migration and the inferred influence of the Agulhas Current on phyllosoma larvae, two geographically separated stocks appear to exist.

## Chapter 10

# Testing the potential effect of effort saturation on the abundance index of *P. gilchristi*

### 10.1. Introduction

Stock assessment of the fishery for *P. gilchristi* off South Africa is based on monitoring the catches of lobster traps, and includes the entire commercial catch of this species. Catch rates provide information on the distribution of stocks and, in a standardized format, provides an index of the relative abundance of the population along a time scale. The abundance index is obtained from a general linear model (GLM), which accounts for the influences that the following factors have on trap catch rates: vessel characteristics, trap soak-times, month of the year, geographic location and depth (see Glazer, 1999a for a description of the GLM developed for this fishery).

There has been concern, however, that the index may underestimate lobster abundance at high levels of fishing effort (Bergh and Barkai, 1996). Conceptually, such an under-estimate would occur when traps placed at high densities compete with one another for the available lobsters in the area (i.e. effective areas fished by traps on adjacent lines overlap; see Eggers *et al.*, 1982; McQuinn *et al.*, 1988) and/or when an increase in the numbers of traps in the fishery results in a greater proportion of the total trap-compliment being placed in sub-optimal fishing areas because of space limitations on optimal fishing areas (i.e. increased occupancy of the fishing grounds). Both these practices could result in lower catch rates being recorded, and incorporated into the CPUE database. These lower catch rates would not necessarily reflect an actual decline in lobster abundance, but may simply be a result of effort saturation, relative to periods of lower effort. In this context, effort saturation is defined as a decrease in CPUE caused by an increase in the numbers of traps relative to available lobsters in an area or to fishing space, and should not be confused with trap-saturation, which is generally defined as a reduction in catch rate with increasing catches per trap (Beverton and Holt, 1957; Miller, 1979, 1990).

The past decade has seen a substantial increase in fishing effort for *P. gilchristi* (Pollock *et al.*, 2000). In the late 1980s a restriction on the number of traps allowed per fishing vessel was removed (Stander, 1991). This deregulation, together with the purchase of larger fishing vessels by some companies in the early 1990s, allowed fishers to try to increase their daily catches by increasing fishing effort. This occurred via two simultaneous processes, namely an increase in the numbers of traps per daily set (i.e. the number of traps that a vessel can set and haul over a 24-hour period), and an increase in the numbers of sets deployed by a skipper. At first, skippers used a single set of traps, which was hauled and reset over 24-hour periods, however, during the 1990s this strategy evolved to the deployment of multiple sets by each skipper; these sets would then be hauled over periods of 48 h (two sets) or 72 h (three sets), instead of the customary 24 h sets (pers. obs.) The longer trap soak-times had the advantage of a somewhat higher instantaneous CPUE than the original 24-hour sets, and with more gear, skippers could now passively occupy favorite fishing areas with surplus sets. The motivation to increase catch rates, despite a fixed or declining total allowable catch (TAC) for the fishery, arose from competition between skippers within each company for the largest share of that company's quota (Bergh and Barkai, 1996, 1998), and reflects a policy of rewarding skippers on the basis of catch rates.

The increase in effort in the fishery for *P. gilchristi* coincided with a gradual downwards trend in the GLM-standardized abundance index from 1990 onwards. It was thus unclear whether this trend was as a result of a decline in lobster biomass, or whether it reflected effort saturation. This study investigates whether effort saturation can be implicated in the decline seen in the relative abundance index of *P. gilchristi*. Specifically, the aims of this chapter were to quantify the increase in fishing effort and gear, and to initiate a reduced-effort experiment to test the hypothesis that the standardized CPUE is independent of the effort exerted in the fishery. The effort reduction experiment is unique from a number of perspectives. 1) Its aim is simply to test the integrity of the abundance index, as opposed to the more common aims of effort reduction exercises, namely to allow recovery of decreased biomass and eventually increase economic returns (see Reid *et al.*, 1993; Pascoe, 1997). 2) It sought immediate CPUE responses to effort reduction rather than longer-term population responses, such as, for example, the increase in abundance resulting from effort reduction in the Florida Keys trap-fishery for *Panulirus argus* (Hunt, 1994; Muller *et al.*, 1997). 3) Its design incorporated alternate full and reduced effort treatments among sub-areas, so as to offset the potential confounding of results by normal inter-annual fluctuations in catchability (see Butterworth and Brown, 1998). This design is considered preferable to the more commonly used method of reducing the effort of a fishing fleet without considering control areas.

The null hypothesis ($H_0$) tested in this chapter states that there will be no difference in the CPUE measured in areas where full commercial effort is exerted as compared to areas of reduced fishing effort (i.e. there is no relationship between effort and CPUE). The alternative hypothesis ($H_A$), that there is a difference in CPUE between areas of commercial and reduced effort, assumes an inverse relationship, in which reduced effort results in an increased CPUE.

## 10. 2 Materials and Methods

### *10.2.1. Trends in fishing effort*

Skippers in the South Coast rock lobster fishery are, by law, expected to provide records of the daily fishing effort exerted; these comprise the number of traps hauled per fishing day, the soak-time of each set, and its geographic location. Two separate effort indices were calculated for this study, namely the total numbers of traps hauled by the fishery (irrespective of soak-times), and the total number of trap-days (trap-hauls * days set). The time factor included in the latter index gives an indication of the occupation of the fishing grounds (and possible saturation thereof) by increased amounts of fishing gear. As such, it was assumed that soak-times of ≤ 24 hrs (1 day), 24 - 48 hrs (2 days), 49 - 72 hrs (3 days) and >72 hours (4 days) implied that one, two, three or four sets of traps had been deployed. Effort (in this case defined as the occupation of the fishing grounds by gear) was calculated by proportionally raising trap-hauls by the days factor.

### *10.2.2. Effort reduction experiment, 1998 – 1999*

#### *10.2.2.1. Sampling area*

The sampling area included all the fishing grounds for *P. gilchristi* along the South Coast of South Africa, stretching from Cape Point in the west (~ 18° 20' E) to East London (~ 28° E) in the east (Fig. 10.1). Along this stretch only rocky patches within the depth interval of 50 – 200 m are actively fished for *P. gilchristi*; these patches (shaded in Fig. 10.1) are geographically separated into two regions by a corridor (21°E – 22° E) that is infrequently fished for *P. gilchristi*. The natural boundary zone provided by the corridor was used to subdivide the sampling area into two experimental areas, namely the Agulhas Bank (west of 22° E) and the Eastern fishing grounds (east of 22° E).

#### *10.2.2.2. Design and scope of the experiment*

All commercial fishing during the period December 1998 to May 1999 was structured as an effort reduction experiment. The experiment comprised two elements: full effort in which the fleet fished with its full gear compliment (including multiple sets per vessel), and reduced effort in which the fleet was restricted to a reduced gear compliment (equivalent to a single 24-hour set per vessel). The two experimental areas, Agulhas Bank and the Eastern fishing grounds were alternatively fished with full and reduced gear compliments, over three 2-month periods, following the schedule shown in Table 10.1. Observers were stationed on all vessels during the experiment; they were tasked with recording the numbers of traps used and trap soak-times.

#### *10.2.2.3. Modeling the impact of effort reduction on CPUE*

The influences of year and month of fishing, trap soak-time, depth of set, geographical area fished and vessel efficiency on CPUE were standardized by applying a GLM to the data. The GLM, developed by Brown *et al.* (1995), Brown (1996a; 1996b; 1997a; 1997b; 1998) and Glazer (1999a; 1999b), was specified as follows:

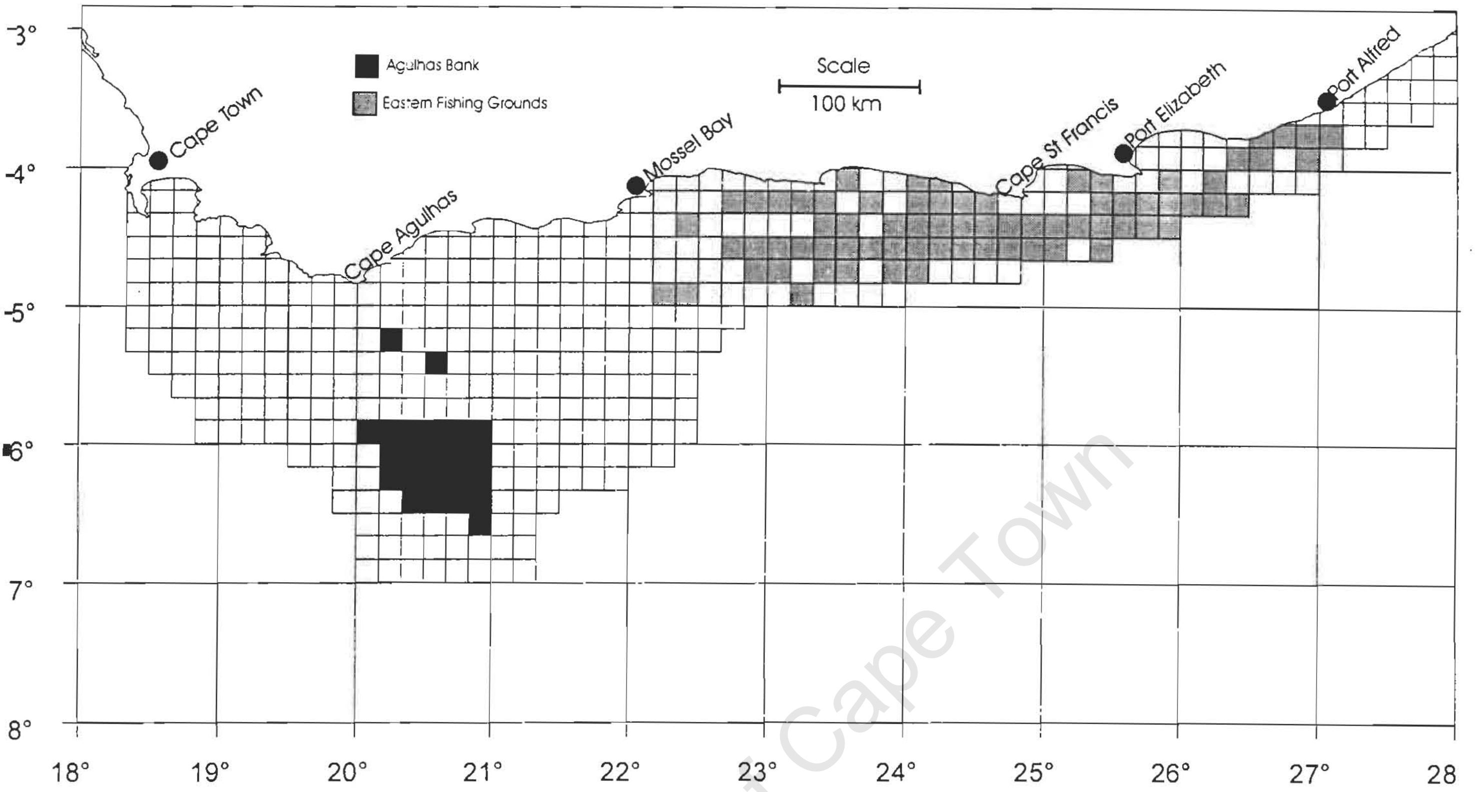

Figure 10.1: The South Coast rock lobster fishing grounds showing the grid-blocks in the two area (Agulhas Bank and Eastern fishing grounds) that were sampled during the effort- reduction experiment in 1998/99.

Table 10.1: Schedule of full commercial and reduced effort exerted in the two fishing areas during the effort- reduction experiment

| | Agulhas Bank | Eastern fishing grounds |
|---|---|---|
| December and January | Full effort | Full effort |
| February and March | Reduced effort | Reduced effort |
| April and May | Reduced effort | Full effort |

$\ln(\text{CPUE} + \delta) = \text{Int} + \alpha_{year} + \beta_{\text{month-group}} + \varphi_{\text{soak-time}} + \gamma_{depth} + \eta_{grid} + \varkappa_{boat} + \varrho\,(\text{traps}) + (\text{year*month-group*area-group})$

where $\delta$ is a constant (assumed to be 10 % of the average CPUE) added to the CPUE to allow for the occurrence of zero CPUE values;

Int is the model intercept;

*year* is a factor with eight levels (covering the split-year fishing seasons between 1991 and 1999);

*month-group* is a factor with three levels, covering the three 2-month periods represented during the experiment, i.e.:
December to January,
February to March, and
April to May;

*soak-time* is a factor with five levels, corresponding to the duration of trap sets, i.e.:
≤ 24 hours,
24 – 48 hours,
49 – 72 hours,
73 – 96 hours;

*depth* is a factor with five levels, corresponding to the depth of trap-sets:
< 100 m,
100 – 150 m,
151 – 200 m,
201 – 250 m, and
> 250m;

*boat* is a factor with 18 levels, each representing individual fishing vessels active between 1991 and 1999;

*grid* is a factor with 197 levels, where each grid-level depicts a specific area of 100 nm$^2$ on the fishing grounds, either at Agulhas Bank or at the Eastern fishing grounds;

(traps) is the effort index, representing the numbers of traps hauled; and

(year*month-group*area-group) is a three-way interaction, which describes how the CPUE differs with respect to the months-groups within each area, within each year (see Hilborn and Walters, 1992).

CPUE for each of the three 2-month periods in each area (Agulhas Bank and Eastern fishing grounds) for the 1998/99 fishing season (experimental season) and for the corresponding 2-month periods in each of the normal fishing seasons between 1991/92 and 1998/99 were calculated using the following equation (Glazer, 1999b):

$$\text{CPUE}_{y,\,m,\,a} = e^{(\text{Int} + \text{year} + \text{month-group} + \text{average soak-time} + \text{average depth} + \text{median grid estimate} + \text{median boat estimate} + \varrho^{*}(\text{average number of traps}) + \text{year} * \text{month-group} * \text{area-group})\ -\ \delta}$$

Results of this calculation are expressed relative to an average soak-time of ≤ 24 hours, an average depth of 150 - 200 m, the median of the parameter estimates of the grid effect, and the median of the parameter estimates of the boat effect.

The ratios $\text{CPUE}_{\text{Feb, Mar}} / \text{CPUE}_{\text{Dec, Jan}}$ and $\text{CPUE}_{\text{Apr, May}} / \text{CPUE}_{\text{Dec, Jan}}$ were calculated for each fishing season between 1991/1992 and 1997/98 (normal fishing seasons for which verified catch and effort data were available), and for the experimental fishing season 1998/99. In the experimental season these ratios correspond to $\text{CPUE}_{\text{Reduced effort}} / \text{CPUE}_{\text{Full effort}}$ for the February-March effort reduction periods in both experimental areas (Agulhas Bank and Eastern fishing grounds), and to the April-May effort reduction period at the Agulhas Bank. If effort does impact on CPUE, the expectation would be that

CPUE at reduced effort should increase, leading to an increased ratio of $\text{CPUE}_{\text{Reduced effort}}$ / $\text{CPUE}_{\text{Full effort}}$ compared to ratios of $\text{CPUE}_{\text{Full effort}}$ / $\text{CPUE}_{\text{Full effort}}$ in the experimental or any other fishing season.

The probability that the experimental CPUE ratio was significantly different from the mean CPUE ratio calculated for the same area in previous years was calculated from the equation $X = \mu \pm 1.96\,\alpha$, where $\mu$ is the mean CPUE ratio for the 1991/92 – 1997/98 period and $\alpha$ is the significance level. A significant result (i.e. when the experimental $\text{CPUE}_{\text{Reduced effort}}$ / $\text{CPUE}_{\text{Full effort}}$ ratio is significantly different from the mean $\text{CPUE}_{\text{Full effort}}$ / $\text{CPUE}_{\text{Full effort}}$ ratio for the 1991/92 – 1997/98 period) would occur when the experimental CPUE ratio fell outside the 95 % probability limits calculated for the 1991/92 – 1997/98 period.

## 10.3. Results

Fishing effort over the entire fished area, measured as the numbers of traps hauled per fishing season, increased by 39.7 % (from 2.89 to 4.04 million trap-hauls) in the seven year period between 1991/92 and 1997/98 (Table 10.2). This increase in trap-hauls occurred despite a decrease in the numbers of active vessels in the fishing fleet: 15 in 1991/92; 12 in 1992/93; 15 in 1993/94; 13 in 1994/95; 14 in 1995/96; 12 in 1996/97; and 13 in 1997/98. This result implies a higher work-rate across the fleet, or a progressively greater operational efficiency.

The percentage of daily sets (≤ 24 hours) decreased from 79.4 % of the fleet's total in 1991/92 to 41.6 % in 1997/98, and the percentage of traps set over two days (25 – 48 hours) increased from 11.1 % to 42.7 % over the same period (Table 10.2). Traps set for longer than 48 hours likewise increased from 9.5 % of the total in 1991/92 to 15.7 % in 1997/98. The increase in the percentage of traps set for longer than 24 hours illustrates the increase in fishing gear used by the fishery; vessels have been setting progressively more traps in each year, and the excess traps that cannot be hauled within 24 hours remain set for 25 – 48 hours or longer.

Table 10.2 GLM standardised CPUE and effort in the South Coast rock lobster fishery. Effort is shown as the numbers of trap-hauls (irrespective of soaktimes) and as the numbers of trap-hauls * days set. Sets of 0 - 24 hrs = 1day; 25 - 48 hrs = 2 days; 49 - 72 hrs = 3 days and > 72 hrs = 4 days.

| Season | GLM standardis CPUE ** (kg tails/trap) | Effort (Thousands of trap-hauls) | Percentages of traps set for | | | | Effort (Thousands of trap-hauls*days) |
|---|---|---|---|---|---|---|---|
| | | | 0-24 hrs | 25-48 hrs | 49-72 hrs | >72 hrs | |
| 77/78 | 0.25 | 3461 | 94.3 | 4.0 | 1.0 | 0.7 | 3741 |
| 78/79 | 0.23 | 2212 | 94.8 | 3.1 | 1.4 | 0.7 | 2389 |
| 79/80 | 0.17 | 644 | 88.5 | 7.0 | 2.0 | 2.6 | 766 |
| 80/81 | 0.22 | 696 | 90.0 | 6.6 | 1.7 | 1.6 | 798 |
| 81/82 | 0.22 | 1529 | 93.8 | 5.3 | 0.4 | 0.5 | 1645 |
| 82/83 | 0.19 | 2078 | 93.0 | 3.9 | 1.7 | 1.4 | 2317 |
| 83/84 | 0.22 | 2687 | 93.1 | 4.3 | 1.7 | 0.8 | 2956 |
| 84/85* | 0.18 | 1090 | 97.9 | 0.9 | 0.7 | 0.5 | 1131 |
| 85/86* | 0.17 | 1043 | 98.3 | 0.8 | 0.2 | 0.8 | 1082 |
| 86/87* | 0.22 | 690 | 98.5 | 0.6 | 0.0 | 0.9 | 713 |
| 87/88* | 0.20 | 634 | 97.7 | 0.0 | 0.6 | 1.5 | 669 |
| 88/89* | 0.24 | 933 | 98.6 | 0.2 | 0.2 | 1.0 | 967 |
| 89/90* | 0.22 | 817 | 88.7 | 3.3 | 1.3 | 6.7 | 1029 |
| 90/91* | 0.18 | 1084 | 85.9 | 4.1 | 1.6 | 8.3 | 1432 |
| 91/92 | 0.15 | 2889 | 79.4 | 11.1 | 2.0 | 7.5 | 3975 |
| 92/93 | 0.15 | 2844 | 72.3 | 18.8 | 2.4 | 6.6 | 4081 |
| 93/94 | 0.14 | 3167 | 69.8 | 23.8 | 1.5 | 4.8 | 4469 |
| 94/95 | 0.13 | 3442 | 81.8 | 11.5 | 1.7 | 5.0 | 4471 |
| 95/96 | 0.12 | 3217 | 71.7 | 17.1 | 2.9 | 8.3 | 4755 |
| 96/97 | 0.10 | 3624 | 53.8 | 34.0 | 3.8 | 8.3 | 6030 |
| 97/98 | 0.09 | 4036 | 41.6 | 42.7 | 6.1 | 9.6 | 7414 |
| 98/99 | 0.08 | Experimental year (December 1998 to May 1999) | | | | | |

* Effort listed for these years do not represent the effort of the whole fleet

** From Glazer (2000)

The occupation of the fishing grounds by traps, indexed by proportionally raising traps set by the number of days that the traps remain on the fishing grounds, increased by 86.5 % (from 3.98 to 7.41 million trap-days) between 1991/92 and 1997/98, with the biggest increase (from 4.76 to 7.41 million trap-days) occurring in the last three years (Table 10.2). The occupation of the fishing grounds between 1984/85 and 1990/91 is difficult to assess because effort during this period was not fully reported. Prior to 1984/85, the fishing grounds were comparatively lightly occupied, mainly because of a decline in the fishery (1979/80 – 1981/82) and a fishing strategy in which few traps were set for periods longer than 24 hrs (i.e. 1-day sets were used).

Table 10.3 compares catch, effort and CPUE statistics for the Agulhas Bank area and the Eastern fishing grounds for the fishing seasons between 1991/92 and 1998/99 (year-round fishing seasons extend from the 1st of October to the 30th of September). Data prior to 1991/1992 (shown in Table 10.2) were excluded from this study because effort was underreported during some fishing seasons (1984/85 – 1990/91). Most effort, in all years, was expended at the Eastern fishing grounds, and the catches recorded for this area were also larger than at the Agulhas Bank. However, the unstandardised CPUE at the Agulhas Bank was higher than at the Eastern fishing grounds in seven of the eight fishing seasons considered. The inter-annual variation of CPUE at the Agulhas Bank was high (ranging between 0.10 and 0.25 kg tail-mass per trap) compared to the Eastern fishing grounds (0.09 – 0.16kg tail-mass per trap). The minor discrepancies between the TACs (which are caught in full in each season) and the total recorded catches (i.e. the sums of catches in the two areas) are the result of eliminating incomplete catch return information from the database.

The levels of effort reduction attained in each area and 2-month period during the experiment, expressed as numbers of traps hauled, are shown in Table 10.4a. The number of traps hauled on the Agulhas Bank, relative to full effort in December-January (100 %) increased by 47 % in February-March (in spite of this being intended as an effort-reduction period) but was reduced substantially, by 42 %, in April-May. The

Table 10.3: Comparative catch, effort and CPUE statistics for the Agulhas Bank area and the Eastern fishing ground and the total allowable catch (TAC) for the fishery.

| Season | Agulhas Bank | | | Eastern fishing grounds | | | TAC |
|---|---|---|---|---|---|---|---|
| | Catch (tons tail mass) | Effort (trap-hauls*10 $^{6}$) | CPUE (kg tails/trap) | Catch (tons tail mass) | Effort (trap-hauls*10 $^{6}$) | CPUE (kg tails/trap) | (tons tail mass) |
| 91/92 | 115.8 | 0.54 | 0.22 | 293.7 | 1.94 | 0.15 | 477 |
| 92/93 | 180.5 | 0.85 | 0.21 | 213.2 | 1.45 | 0.15 | 477 |
| 93/94 | 71.0 | 0.55 | 0.13 | 321.5 | 1.98 | 0.16 | 477 |
| 94/95 | 78.2 | 0.41 | 0.19 | 343.1 | 2.66 | 0.13 | 452 |
| 95/96 | 120.0 | 0.48 | 0.25 | 275.1 | 2.41 | 0.11 | 427 |
| 96/97 | 126.6 | 0.90 | 0.14 | 274.1 | 2.62 | 0.10 | 415 |
| 97/98 | 150.8 | 1.12 | 0.14 | 224.8 | 2.39 | 0.09 | 402 |
| 98/99 | 102.2 | 1.00 | 0.10 | 244.7 | 2.74 | 0.09 | 402 |

Table 10.4: Effort reduction achieved during the experiment, expressed as a) numbers of traps hauled (irrespective of soak-times), and b) traps*days (I.e. including soak-times).

| | Agulhas Bank | | Eastern fishing grounds | |
|---|---|---|---|---|
| a) Traps hauled in: | Traps hauled (Thousands) | Relative to (1) | Traps Hauled (Thousands) | Relative to (1) |
| December and January (1) | 233.8 | 1.00 | 533.3 | 1.00 |
| February and March | 344.9* | 1.47* | 468.9* | 0.88* |
| April and May | 135.8* | 0.58* | 651.9 | 1.22 |
| b) Traps * hours in: | Traps*hours (Millions) | Relative to (2) | Traps*hours (Millions) | Relative to (2) |
| December and January (2) | 19.7 | 1.00 | 21.8 | 1.00 |
| February and March | 11.2* | 0.57* | 13.9* | 0.64* |
| April and May | 5.7* | 0.29* | 24.5 | 1.12 |

* indicates periods in which reductions were implemented

Table 10.5: Catch and standardized CPUE recorded during the effort reduction experiment

| | Agulhas Bank | | Eastern fishing grounds | |
|---|---|---|---|---|
| | Catch (Tonnes) | CPUE (kg / trap) | Catch (Tonnes) | CPUE (kg / trap) |
| December and January | 31.65 | 0.067 | 45.72 | 0.062 |
| February and March | 34.07* | 0.055* | 48.6* | 0.071* |
| April and May | 10.37* | 0.034* | 64.34 | 0.068 |

* indicates periods in which reductions were implemented

number of traps hauled on the Eastern fishing grounds, relative to full effort in December to January, was reduced by 12 % in the February-March effort-reduction period, and was increased substantially, by 22%, in the second full effort period in April-May.

When expressed as occupation of the fishing grounds (traps set * days), the level of effort reduction attained on the Agulhas Bank was substantial in both the reduced-effort periods; -21% for February-March and -64 % for April-May (both relative to the initial December-January full effort period) (Table 10.4b). On the Eastern fishing grounds, a reduction in occupancy of -29 % was attained in the February-March reduced-effort period, followed by an increase to 25 % above the December-January full-effort period in April-May (also a full-effort period).

The quantities of lobsters captured in each area during the 6 months of the experiment were 76.1 tons tail mass at the Agulhas Bank and 158.7 tons tail mass at the Eastern fishing grounds (Table 10.5). This amounts to 58.4 % of the annual TAC of 402 tons tail mass (equivalent to 865 tons of whole lobster). The standardized CPUE recorded for each area and 2-month period fluctuated between 0.034 and 0.071 kg tail mass per trap, with the highest measurement resulting from the February-March reduced-effort period at the Eastern fishing grounds (Table 10.5).

On the Agulhas Bank, neither the experimental ratio $\mathrm{CPUE}_{\mathrm{Feb,\,Mar}} / \mathrm{CPUE}_{\mathrm{Dec,\,Jan}}$ nor $\mathrm{CPUE}_{\mathrm{Apr,\,May}} / \mathrm{CPUE}_{\mathrm{Dec,\,Jan}}$ (which both reflect $\mathrm{CPUE}_{\mathrm{Reduced\ effort}} / \mathrm{CPUE}_{\mathrm{Full\ effort}}$) were significantly different from the averages of the ratios calculated for the same 2-month periods between 1991/92 and 1997/98 (Fig. 10.2). As these two averages reflect $\mathrm{CPUE}_{\mathrm{Full\ effort}} / \mathrm{CPUE}_{\mathrm{Full\ effort\ (Dec,\,Jan)}}$ for the February-March and April-May periods for the seven years prior to the experiment, it is concluded that the null hypothesis cannot be rejected, and that CPUE at the Agulhas Bank was independent of effort reduction.

On the Eastern fishing grounds, the experimental ratio $\mathrm{CPUE}_{\mathrm{Feb,\,Mar}} / \mathrm{CPUE}_{\mathrm{Dec,\,Jan}}$ (which reflects $\mathrm{CPUE}_{\mathrm{Reduced\ effort}} / \mathrm{CPUE}_{\mathrm{Full\ effort}}$) for the February-March effort-reduction period was greater than any of the corresponding annual ratios (which reflect $\mathrm{CPUE}_{\mathrm{Full}}$

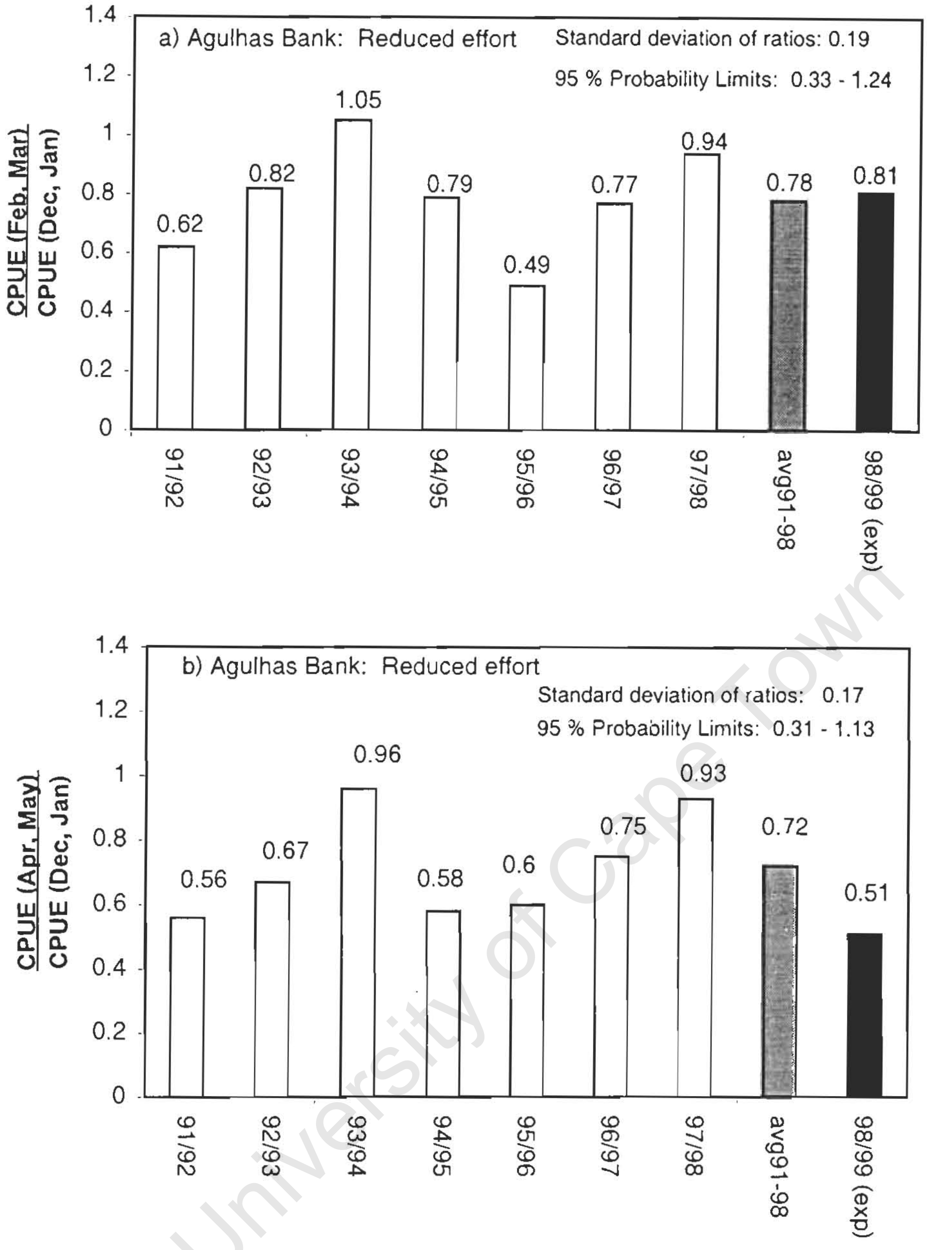

Figure 10.2: CPUE ratios for the Agulhas Bank for individual fishing seasons between 1991/92 - 1997/98 and as an average over this period, relative to the experimental ratio i 1998/99: a) February-March effort-reduction treatment, and b) April -May full-effort treatment.

${}_{\text{effort (Feb, Mar)}}$ / CPUE$_{\text{Full effort (Dec, Jan)}}$ ) calculated individually for each year in the 1991/92 – 1997/98 period, and was significantly greater ($p < 0.05$) than the average ratio for this seven year period prior to the experiment (Fig. 10.3). The null hypothesis is thus rejected, and it is concluded that CPUE on the Eastern fishing grounds did depend on the effort that was exerted, decreased effort leading to an increase in CPUE.

Remaining with the Eastern fishing grounds, the experimental ratio CPUE$_{\text{Apr, May}}$ / CPUE$_{\text{Dec, Jan}}$ (which reflects CPUE$_{\text{Full effort}}$ / CPUE$_{\text{Full effort (Dec, Jan)}}$) for the April-May high-effort period was greater than any of the annual ratios, and greater than the average ratio (these all reflect CPUE$_{\text{Full effort}}$ / CPUE$_{\text{Full effort (Dec, Jan)}}$), however, it was not significantly different from the average ratio at the 5 % level. It is concluded that the null hypothesis cannot be rejected in this control case.

### 10.4. Discussion

The main motivation for the effort-reduction experiment was that the continued decline in the standardized abundance index (Table 10.2) argues for further reductions in the TAC, unless it can be demonstrated that the decline of the index is as a result of increased effort-saturation effects, rather than lower stock biomass.

The catch rates of lobsters by traps cannot always be assumed to be proportional to the abundance of the population on the fishing grounds (Miller, 1990; Addison and Bell, 1997). This relationship may be influenced by a myriad of factors, including variations in fishing strategy, gear design and selectivity (Elner, 1980; Krouse, 1989; Addison and Lovewell, 1991), as well as physiological, behavioural and environmental impacts on lobster catchability (Bennet and Brown, 1979; Miller, 1990). In the present case, a GLM was used to account for the variation in catch rates caused by vessel characteristics, trap soak-times, depth of fishing, and seasonal and areal variations in catchability. The time factor that emerges from this GLM has, until recently, been assumed to be a reasonably good indicator of the relative abundance of the population.

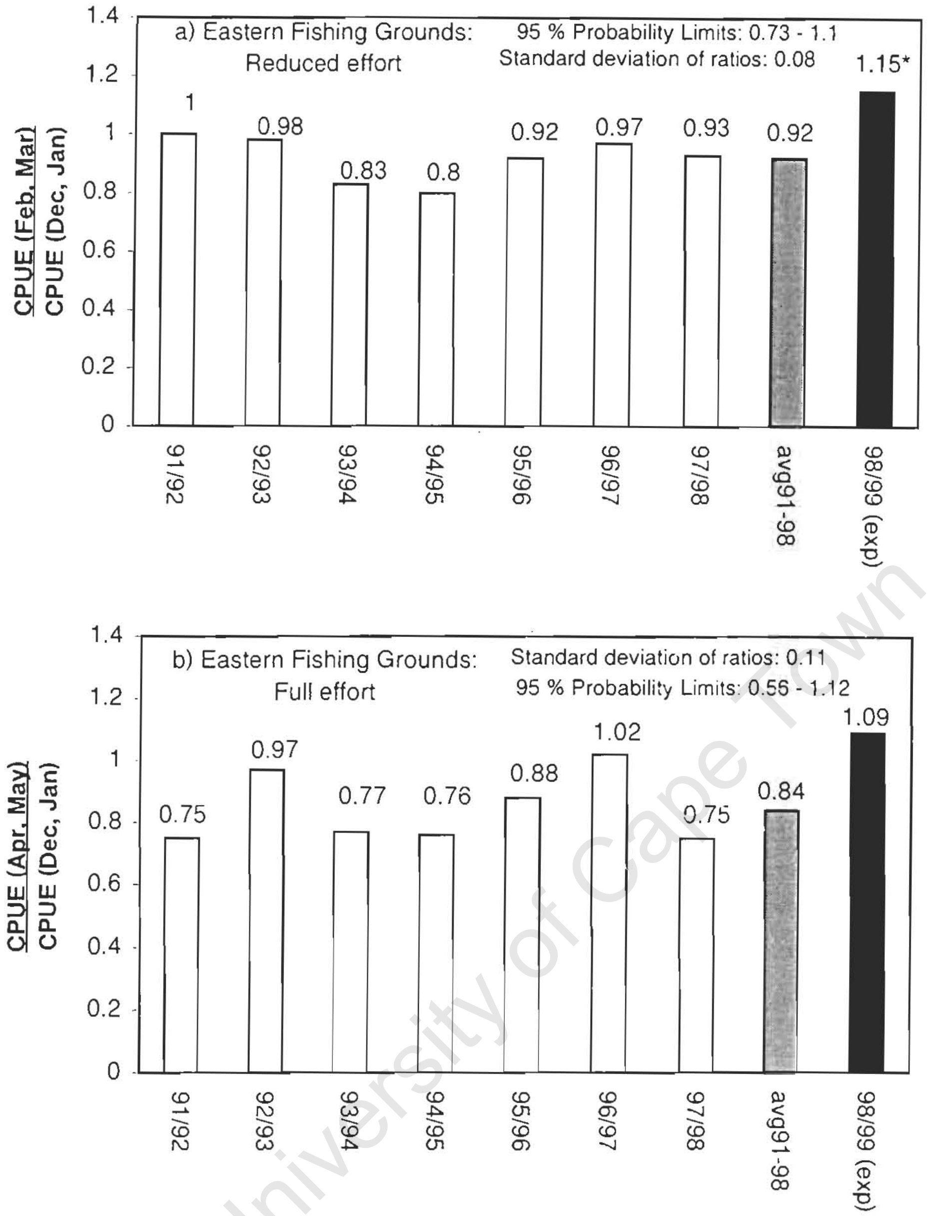

Figure 10.3: CPUE ratios for the Eastern fishing grounds for individual fishing grounds between 1991/92 - 1997/98 and as an average over this period, relative to the experimental ratio in 1998/99: a) February-March effort reduction treatment and b) April-May full-effort treatment. * Indicates a significant change in the ratio relative to that for the equivalentmonths in the previous years (1991-1998)

Effort-saturation effects at high levels of effort may, however, conceivably bias the abundance index of the South Coast rock lobster fishery downwards (Bergh and Barkai, 1996). Realistically, this bias would be difficult to separate from the abundance trend, and as such, it is likely to be difficult to detect.

The effort experiment included a number of modifications to enhance the observed responses of the CPUE ratio to effort manipulations. These included an extensive sampling procedure which covered the entire fished area, so as to reduce the impact of localized catchability fluctuations on results. Treatment periods of two months were used to account for short term (daily) catchability fluctuations; these fluctuations are common in the South Coast rock lobster fishery (pers. obs). Although no research has yet addressed catchability of *P. gilchristi*, various authors have implicated diurnal or lunar cycles (Chittleborough, 1970; Morgan, 1974; Sutcliffe, 1956; Hindly 1976), short-term temperature or salinity fluctuations (Morgan 1974; McLeese and Wilder, 1958) or water movements (Howard and Nunny, 1983) in the catchability of lobsters.

CPUE ratios (relative to the December-January full effort period), were used as response variables and were assessed in relation to corresponding ratios in the previous seven years to prevent the outcome being confounded by seasonal catchability effects. Such effects are generally caused by the impacts of weather, biological cycles and physiological condition on lobster feeding activity (Bennet, 1974; Morgan, 1974; Chittleborough, 1975; Miller, 1990). Standard traps and bait were used throughout the experiment, and a constant trap-spacing was kept along lines of traps. This diminished the potential effects of variation of gear types, bait and trap-spacing on catchability, all of which have been demonstrated by Sinoda and Kabayasi (1969) and Karnofsky and Price (1989).

Despite the above precautions, the results of the effort experiment were inconclusive, with only one out of three effort reduction treatments resulting in a statistically significant increase in the CPUE ratio. Neither period of effort reduction at Agulhas yielded an increase in CPUE. The single significant increase in CPUE occurred during

February-March at the Eastern fishing grounds, and appeared to be as a direct response to a 29 % decrease in trap-days (or a 12 % decrease in trap-hauls) relative to the initial full effort treatment in December-January. It is nevertheless an important result, because the Eastern fishing grounds are far more extensive than the Agulhas Bank (see Fig. 10.1), and are subjected to greater fishing effort (see Table 10.3). The Eastern fishing grounds also consistently produce the greatest proportion of the total annual catch; between 1991/92 and 1998/99 these fishing grounds produced 2190.2 tons tail mass compared to 945.1 tons produced by the Agulhas Bank (Table 10.3).

The above result is, however, partially negated by the result of the full effort treatment at the Eastern fishing grounds in April-May. The large (albeit insignificant) increase in CPUE ratio (see Fig. 10.3) measured after substantially increasing effort there (+ 22 % in trap-hauls, or + 12 % in trap-days, relative to the initial full effort treatment in December-January) directly contradicts the theoretical expectation of a decreased CPUE ratio during periods of increased effort. The responses to effort reduction treatments at the Agulhas Bank were also contrary to the theoretical expectation of an increased CPUE ratio at reduced effort. No significant response could be obtained for the February-March effort reduction treatment, or for the effort reduction treatment in April-May (when trap-hauls were reduced by 42 % and trap-days by 71 %). During the latter period the CPUE ratio decreased to its lowest recorded level between 1991 and 1999 (see Fig. 10.2).

Thus, in all cases except February-March at the Eastern fishing grounds, the results indicate that the effort experiment failed to separate responses to effort manipulations from seasonal and areal trends in lobster abundance. The impact of effort saturation on the abundance index appears, therefore, to be of a lesser scale than originally feared. As such its influence on the index is overshadowed by seasonal and areal variations in actual lobster abundance.

Despite its failure to conclusively address the effort saturation theory, some insight into the dynamics of the population could be obtained from the diverse seasonal trends in abundance shown for the Agulhas Bank and the Eastern fishing grounds. Inter-annual variations in catch and CPUE on the Agulhas Bank are far greater than those on the Eastern fishing grounds (Table 10.3); the trend of greater variation includes the CPUE ratios calculated for the present study (Figs. 10.2 and 10.3). These indices suggest that abundance on the Agulhas Bank is more variable than at the Eastern fishing grounds. A plausible explanation could be that lobster abundance on the Agulhas Bank depends more directly on the recruitment success of juvenile lobsters from the Cape Agulhas area (see Chapter 9). These recruiting cohorts are intensively fished during the first quarter of each year (pers. obs.); years with a large and successful recruitment cohorts will reflect a higher abundance on the Agulhas Bank than other years, extending over a longer period. It is not unlikely that a weaker recruitment cohort in the first quarter of 1999 resulted in the comparatively low abundance measured on the Agulhas Bank between February and May in 1999. The increase in abundance at the Eastern fishing grounds in 1999 is more difficult to explain, and may in fact have been an increase in catchability rather than an increase in abundance. Whereas a strong recruitment cohort in recent years could have increased abundance, factors such as mild weather conditions in 1998/99 (which would allow for more efficient fishing) or an unusually weak sea current regime during that year (which would have allowed for traps to be set in areas that are otherwise out of the reach of long-line gear) may have temporarily increased lobster catchability.

The central conclusion of this study is therefore that the effort-reduction experiment produced no support for the contention that increased effort has caused reduced catch rates; nor can the increased effort be used as a reason for not cutting TACs in response to the declines in the abundance index.

# Summary

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As a direct consequence of a lack of detailed fisheries, biological and ecological information limiting the scope and utility of resource assessments and formulation of management strategies for the deep-water rock lobsters *P. gilchristi* and *P. delagoae*, previous approaches have been inadequate, inappropriate and at times incorrect. This thesis had three aims. To recapitulate, these were: (1) the determination and interspecies comparison of biological parameters, including spatial and temporal size composition trends, somatic growth rates, size at sexual maturity, female fecundity, mortality rates, moulting, recruitment and migration; (2) assessment of the effect of fishing with different gear types or arrays on abundance and its indices; and (3) the incorporation of new information into resource assessments, with recommendations for the substantial improvement of the management of the two resources.

During the course of the thesis, the difficulties of researching deep-water rock lobster populations were confronted and resolved by developing dedicated observer-based surveys and field experiments, and combining these with aquarium observations, long-term tagging and commercial-fisheries information.

The most important findings were:

1) a distinct length-mass dichotomy between the two species, which can be used to differentiate between them, and carries important economic implications for the production of frozen lobster tails vs. whole lobster products by fishing companies, as well as estimations of the impacts of TACs (set as a mass) on actual numbers of animals that will be caught (Chapter 3);

2) that *P. delagoae* is a highly migratory species, with juveniles undertaking an inshore recruitment to a shallower-water adult habitat, so establishing a depth-related size gradient with juveniles occurring deeper than 350 m and adults occurring between 100 and 350 m. *P. delagoae* also migrates north-eastwards alongshore, sometimes for distances in excess of 200 km (Chapter 5);

3) that the *P. delagoae* population off South Africa cannot sustain simultaneous trap and trawl fisheries at commercially viable levels, because both fisheries inflict a heavy mortality on juveniles in deeper water, so limiting recruitment to the adult population, which is further heavily impacted by the trap-fishery (Chapter 4; Chapter 6);

4) that economic and ecological management aims for *P. delagoae* can more easily be achieved in a trawl than a trap fishery (Chapter 6);

5) that both *P. delagoae* and *P. gilchristi* grow at similar slow rates consistent with their deep cold-water habitat, and that both species are long-lived (Chapter 6; Chapter 7)

6) that two growth regimes exist for *P. gilchristi* (fast growth in the region between the Agulhas Bank and Port Elizabeth and slow growth at Port Alfred), and that female fecundity is higher at the former location (Chapter 7);

7) that pleopod and tag-recapture indices can be used to determine the moult state and moulting season of *P. gilchristi*, and that both these indices indicate that most male and female lobsters moult in November and December (mid-summer) but that the moulting season is size-dependent, with individuals with a CL < 70 mm commencing as early as October (Chapter 8);

8) that *P. gilchristi* juveniles migrate long distances eastwards along-shore (counter to the Agulhas current), with the migration originating from a population of small post-settlement juveniles at Cape Agulhas and following the shelf-edge (south-eastward and eastward) culminating in one of two regions; eastern Agulhas Bank (after 2

years) or Mossel Bay - Port Elizabeth (after covering a straight-line distance of 800 km over 3 years) (Chapter 9);

9) that the migrants do not move as far as Port Alfred (the eastern-most site), and based on this information and dichotomous growth, size at maturity, average CL and female fecundity, two separate populations are proposed for *P. gilchristi*; one at Port Alfred and the other between Cape Agulhas and Port Elizabeth (Chapter 9);

10) that increased fishing effort in recent years has not biased the abundance index used in the stock assessment for *P. gilchristi* downwards because of effort-saturation, and that the decline in the abundance index of this species accurately reflects a decrease in its biomass (Chapter 10).

Many of the results of this thesis could directly be applied to the management of the fisheries by their incorporation into stock assessments, and through the course of this thesis, recommendations for improved management of the two resources were made. The decision to restrict fishing for *P. delagoae* to trawling only was based solely on the results of this study, and impending initiatives regarding a closed season (during moulting) and the reduction of fishing effort in the fishery for *P. gilchristi* also stem directly from results obtained here.

Results from various chapters have indicated that two separate stocks of *P. gilchristi* may exist, and a genetic study is now necessary to determine the degree of separation. Should the separation be substantial, it will almost certainly be appropriate to develop separate management strategies to allow for the differences in productivity between the two stocks.

As with all theses, some of the results could be applied directly, whereas others generated more complex questions. Though some of these could be addressed, many others will undoubtedly perplex researchers in future.

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