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HATCHDATE DISTRIBUTIONS AND GROWTH RATES OF ANCHOVY (*Engraulis encrasicolus*) IN THE SOUTHERN BENGUELA ECOSYSTEM

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How many are your works, O LORD!
In wisdom you made them all;
The earth is full of your creatures.
There is the sea, vast and spacious,
Teeming with creatures beyond number –
Living things both large and small.
There the ships go to and fro,
And leviathan, which you formed to frolic there.

These all look to you to give them their food at the proper time.
When you give it to them, they gather it up;
When you open your hand, they are satisfied with good things.
When you hide your face, they are terrified;
When you take away their breath, they die and return to the dust.
When you send your Spirit, they are created,
And you renew the face of the earth.

(Ps 104: 24-30, NIV)

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DECLARATION

I hereby declare that the contents of this dissertation represents the result of research carried out by myself under the supervision of Dr Suzanne Painting and Dr Michael Kerstan at Marine and Coastal Management, MCM, Cape Town and Prof. John Field in the Zoology Department and Marine Biology Research Institute of the University of Cape Town. All the age readings and calculations were carried out by myself, and the age data and the ideas presented in this thesis are largely my own, although colleagues and my supervisors made valuable comments on various drafts. Although I participated in the cruises, the collection of length-frequency and acoustic data at sea was primarily made by the scientific and technical staff of MCM. Computer programmes to process statistics, and compile length-frequency distributions from acoustic surveys were designed and written by staff at MCM, and the data and methods were kindly made available for this study by Carl van der Lingen, Dagmar Merkle, Janet Coetzee and Mark Prowse. Students and MCM technicians assisted in otolith removal, mounting and grinding as well as in taking digital light micrographs. Miranda Waldron, UCT Electron Microscope Unit, assisted in taking digital scanning electron micrographs. Sea surface temperature data from satellites were made available to me by Kobus Agenbag, Herve Demarcq and Claude Roy. Egg abundance data were collected on the November Spawner Biomass cruises of MCM and kindly provided by Carl van der Lingen. Egg and larval distributions and abundance during Sardine and Anchovy Recruitment Programme, SARP, data were kindly provided by Jenny Huggett.

No portion of this thesis has been previously submitted in support of an application for any other degree or qualification at this or any other university.

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Margit Renate Wilhelm Date

ABSTRACT

Larval and juvenile Cape anchovy (*Engraulis encrasicolus*) of the particularly strong 1999/2000 year-class were collected during two consecutive surveys in March and May 2000 in the southern Benguela region off South Africa. Otoliths from sub-samples were examined to calculate hatchdate distributions and growth rates to estimate the main apparent spawning peaks of the 2000 year-class from both surveys, and to look for possible correlations between spawning, survival and growth of anchovy on the one hand, and the prevailing environmental conditions on the other. Sub-samples were chosen proportional to the length-frequency distributions at each stratum or station at each survey. Otoliths of 193 specimens (14-70 mm standard length, SL) from the March survey and 80 specimens (52-114 mm SL) from the May survey were successfully prepared for light microscopy and electron microscopy respectively. Daily increments were counted and otolith radii were measured. The age-structure of the anchovy population at the time of each survey was calculated from length-frequency distributions using age-length-keys. Mortality rates, hatchdate distributions and growth rates were estimated. Instantaneous mortality rates calculated from the catch curves were $0.0353 \cdot day^{-1}$ for larvae caught in March 2000 and $0.0202 \cdot day^{-1}$ for juveniles caught in May 2000. These compared with previous laboratory studies and mathematical models in the literature and were, thus, used to back-calculate hatchdate distributions. Resulting hatchdate distributions of larvae and pre-recruits caught in March 2000 showed two apparent hatching peaks, late September - late October 1999 and late December - early January 2000. Thus, either 1) spawning peaked in those two periods or 2) continuous spawning took place between August 1999 and March 2000, but survival of eggs and young larvae peaked in September/October and January/February. The hatchdate distribution of juveniles caught in May 2000, showed peaks in early September - October and late November - December. Therefore, apparent hatching peaks were dissimilar between the two samples of the same year-class, taken three months apart. Thus, higher age-selective mortality of larvae younger than 75 days old in March 2000 (hatched after 17 December 1999) is likely to have taken place in 2000. Large areas of > 19 °C sea surface temperatures (SST) throughout the period from August to March indicated that spawning is likely to have been continuous. Conditions, especially in December-January, when upwelling was reduced because of a cessation in south-easterly winds, may have been conducive to survival of eggs and yolk-sac larvae, due to reduced offshore losses. The period of weak upwelling was subsequently followed by a period of strong upwelling from March to May 2000. This is likely to have increased availability of planktonic food for post-larvae and juveniles. On the other hand, upwelling may have caused offshore dispersal of food patches needed by younger larvae, which could lead to age-selective mortality caused by starvation. The *critical period* (Hjort 1914) thus seemed to be at a later stage than the first-feeding stage. Mean larval growth rates were estimated between 0.33 and 0.36 mm $SL.day^{-1}$ using three different growth functions (linear $r^2 = 0.90$, Laird-Gompertz $r^2 = 0.90$, and von Bertalanffy $r^2 = 0.89$ growth functions). Juvenile growth rates were estimated at 0.22-0.24 mm $SL.day^{-1}$ ($r^2 = 0.45$, 0.48, 0.47 for the three functions respectively). These rates were slower than previously reported rates, possibly due to the high density of larvae present and hence less *per capita* food availability. However, reduced food availability did not affect survival in 2000 and, therefore, does not support the *Growth-mortality* hypothesis (Ware 1975).

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I really would not have managed without you all!

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CHAPTER ONE

INTRODUCTION

1.1. Importance of clupeoid fish and recruitment studies

The order Clupeiformes or *clupeoids* are a group of small, generally short-lived, fast growing pelagic fishes ocurring in large populations. They are characteristic of upwelling regions of the world and typically live close to shore. In the Benguela current system, three species of clupeoids are abundant: Cape anchovy *Engraulis encrasicolus*, sardine or pilchard *Sardinops sagax* and round-herring *Etrumeus whiteheadi* (Whitehead *et al.* 1988). Larval forms of all three species were described by Olivar and Fortuño (1991). The Cape anchovy species, formerly known as *Engraulis capensis*, was thought to be endemic to southern Africa, but it is now considered to be the same species as the European anchovy *E. encrasicolus* (Whitehead 1990). Throughout this dissertation, references to what was formerly called *Engraulis capensis* will be made as *Engraulis encrasicolus* or Cape anchovy.

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Clupeoids are of great commercial and socio-economic value worldwide as they constitute about a third of the 93 million metric tons (mt) of global marine fish catch (FAO 2001). The purse-seine fishery on the resources of these three species in the southern Benguela system has been a very important socio-economic factor since the early 1950s. From 1994 to1996, the total annual wholesale value of the landings from the South African pelagic fishery exceeded US$ 80 million (Cochrane *et al.* 1998), and the fishery provided employment for over 6000 people; particularly along the west coast fishing is an important employment opportunity (Cochrane and Payne 1998). Clupeoids also play an important ecological role, as they provide a food source for many larger fish, seabirds and marine mammals (Crawford 1987), and are thought to control population sizes of both their zooplanktonic prey and their predators in a "*wasp-waist*"-type ecosystem (Cury *et al.* 2000).

Like all major upwelling systems, the Benguela system typically shows large interannual fluctuations in the population sizes of clupeoids (Lluch-Belda *et al.* 1989, Schwarzlose *et al.* 1999). Following the marked decline of the pilchard catches in the mid-1960s, Cape anchovy has formed the dominant component of South African purse-seine catches (Crawford *et al.* 1987) with average annual landings of 254 000 mt fluctuating between 41 000 and 596 000 mt, 1970-1997 (Barange *et al.* 1999) (Fig. 1.1).

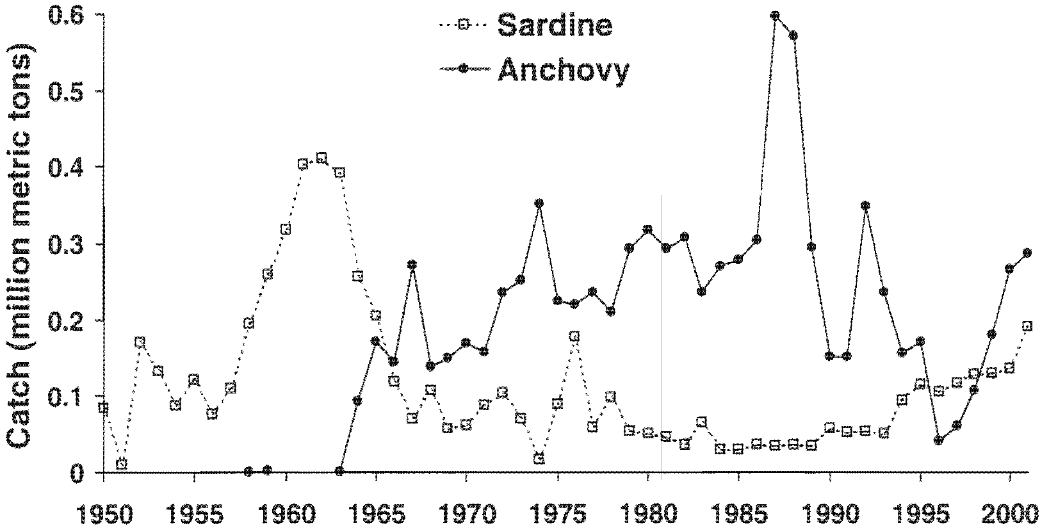

Figure 1.1. Trends in catches of pilchard and anchovy off South Africa, 1950 – 2001 (after Schwarzlose *et al.* 1999 and courtesy C. van der Lingen, *MCM pers. comm.*)

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In 2000, Cape anchovy have reached record high recruitment levels, after an apparent collapse towards the end of the 1990s (Coetzee *et al.* 2000), and have kept at that level in the following two years.

In view of the far-reaching ecological, social and economic implications of fluctuations in the abundance and availability of Cape anchovy, it is important that the exploitation of the stocks is managed in a sustainable way (Cochrane *et al.* 1998).

Population collapses of clupeoids have been observed in other upwelling systems in the past, for example sardine off California (Schwarzlose *et al.* 1999) and, more recently, pilchard in the northern Benguela off Namibia (Boyer *et al.* 1997, 2001). Fishing pressures may have been partially responsible (Lasker 1985), but it is becoming increasingly evident that natural variability also causes significant fluctuations of clupeoid population sizes (Beverton 1990, Kawasaki 1992). Shifts in the relative abundances of anchovy and sardine have been observed in all upwelling systems, and have been termed *regime shifts*. Long-term evidence for this has also been provided by retrospective studies, which have been aimed at reconstructing population sizes and species compositions from fossilised fish scales in the Santa Barbara Basin (Soutar and Isaacs 1969, 1974, review Shackleton 1987).

Generally, clupeoids show a high natural mortality, reflected by thousands of eggs spawned by one female, which are, on average, reduced to only two adult fish (Bakun

1985). Cape anchovy have a short lifespan (3 years) resulting from an early age at first maturity (1 year) combined with a high natural mortality (Shelton and Hutchings 1981). Because of the short lifespan of many clupeoids, purse-seine catches are largely dependent upon the success of new *recruits* into the fishery (Lasker 1985). Throughout this dissertation, the term *recruitment* refers to the "*quantity of younger fish surviving the egg-, larval- and juvenile stages to reach a size at which they become susceptible to fishing gear and thus begin to be sampled by the fishery*" (see Bakun 1985). In the southern Benguela, approximately 70 % of the purse-seine catches are made up of these 0-year-old recruits (Armstrong and Butterworth 1986). Inter-annual fluctuations in population size are thus largely due to variations in recruitment size in any year (Butterworth and Le Clus 1979).

Recruitment may vary inter-annually by factors of up to 20-fold (Naidoo and Verheye, Eds. 2000) and factors responsible for this extreme inter-annual recruitment variability are the focus of research programmes worldwide. The ultimate objective of many of these studies is to develop the ability to predict (forecast) recruitment of the commercially important species from one year to the next (Bakun 1985).

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1.2. Recruitment hypotheses

Recruitment of pelagic fish is generally poorly correlated with the stock size of the spawning adults (Hjort 1926, Cushing and Harris 1973, Lasker 1985, Cochrane and Starfield 1992, Cochrane and Hutchings 1995). Johan Hjort (1914) was the first to propose a link between feeding, larval survival and recruitment. His work has resulted in a paradigm shift in recruitment studies, which now generally focus less on the accessibility of adult fish to the fishery, but rather place increased emphasis on studying the early life history stages of populations to identify factors affecting recruitment success (Solemdal and Sinclair 1989). Hjort's (1914) hypothesis stated that the early post yolk-sac stage of the larval fish establishes the strength of a year-class. He proposed that when food availability was limited during this period, proportionally more larvae would die of starvation. He extended his hypothesis in 1926, also suggesting advection as a mechanism that could carry eggs and larvae out of productive areas, which would increase early larval mortality. Many hypotheses attempting to link different parameters influencing early life history stages to recruitment success have emerged since Hjort's "*Critical Period*" *hypothesis* (May 1974) in 1914 (see Table 1.1 for a summary).

Table 1.1. Recruitment hypotheses describing factors, which may control early life stages of clupeoid fishes, including the Cape anchovy *Engraulis encrasicolus* (adapted from Bakun 1985, Anderson 1988, Cury *et al.* 1995, Fowler 1998 and Hutchings *et al.* 1998).

HYPOTHESES	AUTHORS
Starvation hypotheses	Hjort 1914
Critical period: From yolk-sac stage to 1^{st} feeding	Hjort 1914, 1926
Match-mismatch: Matching of spawning onset with annual production onset	Cushing 1975, 1982, 1990
Productivity of a system: Variations in seasonal / annual food production changes carrying capacity	Parrish and MacCall 1978, Bakun and Parrish 1980, Roel *et al.* 1994
Vertical stability: Turbulent mixing of fine-scale food particle strata increases larval mortality	Lasker 1975, 1978, 1981 Shelton and Hutchings 1990
Type of potential food organisms: influences survival and growth	Lasker *et al.* 1970, Lasker 1975
Small Scale Turbulence: Increases encounter rate between larvae and food particles	Rothschild and Osborn 1988, MacKenzie and Leggett 1991
Resource use competition: High competition with other planktivores means low survival of larvae	Fraser 1970, Frank 1986
Advection hypotheses	Hjort 1926
Transport-retention: Removal of eggs and larvae from favourable habitat, exposure of larvae to damage in surf-zone, Disruption of 'normal' current patterns, that reproductive habits are tuned to	Parrish *et al.* 1981, Hewitt and Methot 1982, Husby and Nelson 1982 Shelton 1981, Shelton and Hutchings 1981, 1982, Norcross and Shaw 1984 (review)
Offshore advection of eggs and larvae: NW winds off Columbine and SE wind at Cape Point – starvation mortality of early-stage larvae	Shelton *et al.* 1985, Shannon *et al.* 1996
Moderate advection of warm water is advantageous, strong warming not	Boyd *et al.* 1992, 1998
Optimal environmental window hypothesis	Cury and Roy 1989
Starvation and advection (trade-off): Upwelling which is too weak or too intense increases mortality with food and turbulence being the limiting factors, respectively	Wroblewski *et al.* 1989, Roy *et al.* 1992, Waldron *et al.* 1997
More than one key factor, all dependent on upwelling intensity	Cury *et al.* 1995
Triad hypothesis *Enrichment, retention, concentration (and temperature)*	Bakun 1993, 1996
Predation hypotheses	Bailey and Houde 1989 (review)
Gelatinous zooplankton predator: Decreased survival of larvae	Fraser 1970, Hunter and Kimbrell 1980
Fish predator / cannibalism: Decreased survival of larvae – often density dependent	Øiestad 1985, Alheit 1987, Valdés Szeinfeld and Cochrane 1992
Prolonged *juvenile predation:* Long post-larval to recruitment stage - predation mortality accumulates	Sissenwine 1984
Growth - mortality hypothesis: Slow growth means higher mortality as predation decreases with increasing size	Ware 1975, Shepherd and Cushing 1980
– Affected by temperature	King *et al.* 1978, Brownell 1983, Pepin 1991
Disease	Sissenwine 1984 (review)
Infectious outbreaks, *transmission:* critical in high population densities	Sindermann 1970
Temperature: too low – causes physiological stress, possibly disease outbreak	

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Cushing (1975, 1982, 1990), extending in concept on Hjort's (1914) hypothesis, suggested that if the annual phytoplankton bloom and a subsequent production of copepod nauplii occurred at a different time to the start of the annual fish production cycle, they would be *"mismatched"* (Hjort 1914) and poor survival and therefore poor recruitment would occur. This hypothesis assumed that the phytoplankton blooms as well as the production cycle of fish larvae take place over a relatively short period, typically a spring bloom in temperate latitudes. More realistically for pelagic species, Parrish and MacCall (1978) and Bakun and Parrish (1980) suggested that recruitment is limited by the seasonal as well as annual food production, which regulates the annual carrying capacity of a system, extending the concept to include upwelling ecosystems in which the production can extend over many months.

Lasker's (1975) *Stability hypothesis* states that a stable water column is needed for "*chlorophyll maximum layers*" to form and be maintained. He concluded that first-feeding northern anchovy (*Engraulis mordax*) larvae need to take advantage of these strong chlorophyll maximum layers in stable ocean environments to be able to survive (Lasker 1978, 1981). In determining whether starvation is a mechanism that limits recruitment, other factors need to be considered in conjunction with estimates of prey density, such as: relationships between food abundance and larval ingestion rates (MacKenzie *et al.* 1990) and the type of zooplankton food particle present which may enhance enhance survival of older anchovy larvae (Lasker *et al.* 1970). The concentrations of food patches available to fish larvae on a micro scale (Leggett and Deblois 1994), the small-scale turbulence effect that would increase encounter rates between larvae and their prey (Rothschild and Osborn 1988, MacKenzie and Leggett 1991) and competition with other planktivores also play a role in limiting feeding and hence survival.

Peterman and Bradford (1987) and Peterman *et al.* (1988) found that there was no relationship between the abundance of first-feeding northern anchovy larvae and age-1-recruits, and concluded that there is evidence to doubt the general hypotheses of Hjort (1926) and Lasker (1975), and that the "critical stage", if any, is more likely at a stage closer to recruitment. First-feeding larvae, having had a favourable survival rate because of calm periods, may later have decreased feeding success because of increased turbulence (Leggett and Deblois 1994).

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The *Advection hypotheses* state that variations in prevailing currents are responsible for either retaining eggs and larvae in an environment suitable for their growth, or removing eggs and larvae from favourable environments. Variations in the prevailing currents may thus lead to variability in egg and larval survival (Hjort 1926, Parrish *et al.* 1981). Several authors have demonstrated that spawning of clupeoids is adapted to current features and occurs during periods when offshore losses are reduced (Shelton 1981, Shelton and Hutchings 1981, 1982; see Shelton *et al.* 1985 and Norcross and Shaw 1984 for a review). However, evidence for the various physical dispersal hypotheses is not conclusive for specific predictions of recruitment strength (Wooster and Bailey 1989).

The *Optimal Environmental Window* hypothesis relates recruitment to upwelling intensity. Cury and Roy (1989) showed that a dome-shaped relationship between recruitment and upwelling intensity exists for small pelagic fish in upwelling ecosystems. This suggests that moderate upwelling may provide the best environment for the survival of fish until recruitment, and ties in both the *advection* and *starvation* hypotheses: too little upwelling means that fish are food limited, while very intense upwelling results in turbulences, strong advective currents and offshore losses, which decrease survival of larvae and post-larvae. Wroblewski *et al.* (1989) provided additional evidence for this in their models of northern anchovy *E. mordax* and Waldron *et al.* (1997) provided evidence for this in the southern Benguela ecosystem (*E. encrasicolus*). Cury *et al.* (1995) concluded, even more comprehensively, that recruitment is non-linearly related to many different key factors, which are all dependent on upwelling intensity. They showed that moderate upwelling intensity is best for larval survival.

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Bakun (1993, 1996) reviewed evidence from the California current, the Benguela current as well as the southwestern Atlantic / Patagonian shelf system, and summarised both starvation and advection hypotheses into a *Triad* of environmental processes that, when acting in concert are considered to provide optimal conditions for larval survival:

1) nutrient *enrichment* of a certain area, for example by upwelling, as shown for Pacific sardine *Sardinops sagax* (Parrish and MacCall 1978), and Pacific mackerel *Scomber japonicus* (Bakun and Parrish 1980), where recruitment was positively correlated with the upwelling index,

2) *larval retention* in near-shore productive areas, for example by eddy circulation, which

allows larvae to avoid offshore dispersal by advective currents (Parrish *et al.* 1981, Shelton and Hutchings 1982) and

3) food particle *concentration* by *stability* in the spawning and nursery areas increases the availability of food particles and thus contributes towards spawning or recruitment success (Lasker 1975, 1978, Husby and Nelson 1982, Peterman and Bradford 1987, Shelton and Hutchings 1990). Bakun (1993) also provided examples of both positive and negative correlations between recruitment and sea temperature.

Various authors have related larval survival to *predation* on eggs and larvae by invertebrates (Fraser 1970, Hunter and Kimbrell 1980), other fish (Øiestad 1985) and fish of the same species (Alheit 1987, Valdés Szeinfeld and Cochrane 1992), but could not accurately measure predation rates in the field and the extent to which predation alone limits recruitment is still unclear (Anderson 1988, Bailey and Houde 1989, Leggett and Deblois 1994).

Ware (1975) and Shepherd and Cushing (1980) argued that a significantly slower *growth rate* results in larvae being at smaller sizes and vulnerable life history stages for longer, thereby being exposed to *predation* for longer, resulting in increased *mortality*. Growth rates are in turn affected by temperature (King *et al.* 1978, Brownell 1983, Pepin 1991).

Negative relationships between chemical composition of the water column and disease outbreaks during larval and juvenile periods and subsequent recruitment have also been reported (Sindermann 1970).

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1.3. Life history of Cape anchovy Engraulis encrasicolus and recruitment

The life history of Cape anchovy *Engraulis encrasicolus* in the southern Benguela system is well understood (see Fig. 1.2 for an outline). In the 1980s and early 1990s, the greater part of the adult stock spawned on the western Agulhas bank, approximately between Cape Point and Cape Agulhas (Crawford *et al.* 1987, Hampton 1987, Armstrong *et al.* 1988, Shelton *et al.* 1993, Roel *et al.* 1994). Since 1996, the preferred spawning area of anchovy seems to have shifted eastwards, and more than 70 % of anchovy eggs are now found on the central and eastern Agulhas banks, possibly due to the increasing abundance of sardine in the southern Benguela system (van der Lingen *et al.* 2002).

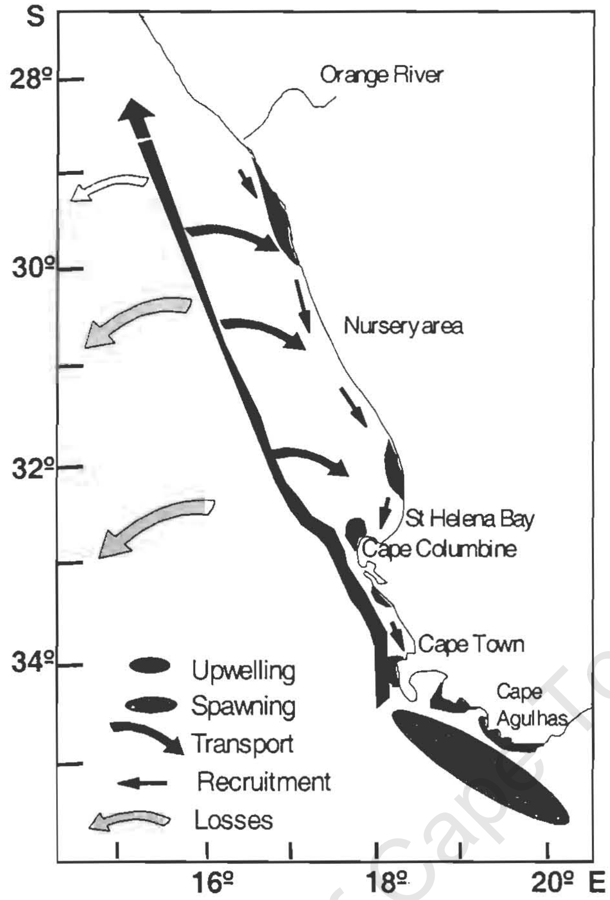

Figure 1.2. Map showing the general hypothesis on the life history of the Cape anchovy *Engraulis encrasicolus* (after Hutchings 1992, Hutchings *et al.* 1998). Since 1994, the spawning areas appear to have shifted further east (van der Lingen *et al.* 2001, 2002).

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Cape anchovy spawn during spring and summer, September to March, with an apparent peak in spawning in late spring / early summer (Shelton and Hutchings 1981). They are serial or "batch" spawners (Alheit 1989), histological studies indicate that females spawn between 14 and 20 times within this long spawning period (Melo 1994b).

In the 60s and 70s most Cape anchovy spawning took place over a temperature range of 16–19°C (Anders 1965, King 1977, King *et al.* 1978). More recent studies suggest that the preferred spawning range of Cape anchovy in November is between 17.4 and 21.1°C (van der Lingen *et al.* 2001). Sea surface temperatures may directly affect the spawning duration of anchovy because cold temperatures may increase oocyte atresia, the net effect of which is that spawners resorb their eggs (Hunter and Macewicz 1985, Melo 1994a). This may have important implications for the total number of eggs spawned in a season, and therefore for subsequent recruitment strength (Richardson *et al.* 1998, Korrûbel *et al.* 1998, Painting and Korrûbel 1998, Miller 2001, Miller and Field *submitted*).

Serial egg production requires a lot of energy (Armstrong *et al.* 1991, Melo 1994a), and the availability of food to spawners on the Agulhas bank may also influence the frequency and duration of spawning. Prolonged lack of food may result in irreversible oocyte atresia, and cessation of spawning activity (Hunter and Macewicz 1985, Melo 1994a, b). If this occurs in the early or middle periods of the spawning season, it may have a negative impact on recruitment (Richardson *et al.* 1998, Korrûbel *et al.* 1998, Painting and Korrûbel 1998).

Peaks in Cape anchovy egg abundance have been recorded in December (1965–1967, Crawford 1981), October and January (1977/1978, Shelton and Hutchings 1990), October-November (1993-1995, Fowler and Boyd 1998) and November-December (1995/1996, Huggett *et al.* 1998). Northward-flowing jet currents transport eggs and larvae from the Agulhas bank along the shelf edge onto the west coast shelf nursery area downstream from the active upwelling cells (Shelton and Hutchings 1982, Boyd and Hewitson 1983, Shannon 1985, Armstrong *et al.*1987, Boyd *et al.* 1992, Fowler and Boyd 1998).

Juvenile anchovy are removed by the fishery on the west coast from April onwards, each year. The peak of the fishing season is between May and July when recruit sizes are 80–100 mm standard length (SL) (Crawford *et al.* 1987). Later in the year, surviving recruits undergo a return migration onto the Agulhas bank, where they recruit to the spawning population at age 1. Spawner sizes in November are usually > 100 mm SL (Barange *et al.* 1999).

Since 1984, two biomass assessment surveys have been conducted annually by Marine and Coastal Management (MCM), Department of Environmental Affairs and Tourism, South Africa, to estimate the *recruitment* biomass in May/June and spawning adult biomass in November, using hydro-acoustic techniques, supplemented by midwater trawling (Hampton 1987, 1992, 1996, Barange *et al.* 1999). The mid-year surveys provide an estimate of recruitment strength, while the November surveys provide an estimate of the stock size of spawners.

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Recruitment strength in May is dependent upon successful spawning on the Agulhas bank and subsequent survival of eggs, larvae and pre-recruits on the west coast. Recent studies have shown that recruitment success is influenced by a number of factors affecting the different life history stages, and support a number of the hypotheses summarised in Table 1.1, particularly the *Starvation*, *Advection*, *Triad* and *Optimal Environmental Window* hypotheses.

These factors include:

1) Food availability to and condition of spawners as well as temperature on the spawning grounds (Bloomer *et al.* 1994, Cochrane and Hutchings 1995, Schülein *et al.* 1995, Boyd *et al.* 1998, Painting and Korrûbel 1998, Korrûbel *et al.* 1998, Richardson *et al.* 1998),

2) Successful transport of eggs and larvae to the nursery ground (Shelton and Hutchings 1982, Shelton *et al.* 1985); slackening or too strong movement of the jet current responsible for transport of eggs and larvae to the west coast nursery area could result in displacement of larvae west into mid-oceanic waters of low productivity. This could cause a high mortality of larvae due to starvation (Shelton and Hutchings 1981, Huggett *et al.* 1998, Mullon *et al.* 2002).

3) Wind and upwelling could alter the food availability to larvae and pre-recruits in the west coast nursery areas for (Waldron *et al.* 1997, Painting and Korrûbel 1998, Boyd *et al.* 1998).

Intensive research over the past few decades in the southern Benguela system and elsewhere has shown that starvation, advection and predation are most likely to limit larval and pre-recruit survival, and are therefore probably the primary causes of recruitment variations. However, it appears that there is no simple unifying hypothesis that can be used to explain recruitment in all species and all systems at all times. This may be a result of the above factors being interdependent, to some extent. For example, starvation, which may have resulted from transport into unfavourable areas, may facilitate predation when larvae are too weak to escape their predators, or low levels of oxygen may be a result of an increased coastal upwelling (Hunter 1981, Castro and Hernández 2000). In the southern Benguela system, a number of models have been constructed to incorporate many factors

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simultaneously to relate to or predict recruitment success (Table 1.2). Within season, many factors may play a cumulative role, with the relative importance of each factor differing between seasons and year-classes (Hutchings 1992, Hutchings *et al.* 1998).

Table 1.2. Key models investigating the influence of more than one factor on recruitment success of Cape anchovy *Engraulis encrasicolus* in the southern Benguela (after Hutchings *et al.* 1998). See also Figure 1.2

MODELS	FACTORS	AUTHORS
Rule-based model	Wind frequency and velocity, SST, spawner biomass	Bloomer *et al.* 1994
Correlation analyses	Wind, copepod biomass and production, spawner biomass, spawning area, % females with oocyte atresia, SST, fish condition, predation	Cochrane and Hutchings 1995
Expert system	Same as Cochrane and Hutchings 1995	Korrûbel *et al.* 1998
Deterministic Expert system: 1994-1995	S wind anomaly, distance offshore of 16°C isotherm, % starvation stations on Agulhas bank, daily egg prod, % females with oocyte atresia, monthly oil:meal ratio	Painting and Korrûbel 1998
Deterministic Expert system: (& classification trees) (update)	% females with oocyte atresia, weekly SST Dec & Jan (CT & Hondeklip B), Cape Agulhas pressure anomaly, 16-19°C area on WAB	Miller 2001, Miller and Field (*submitted*)

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Lasker (1985) answers the question "*what limits clupeoids*?" with "*almost everything*". He argues that rather, we will be more successful in answering the question: "*what limits clupeoids mostly*?" He suggests that the most useful studies on recruitment are those like the age study described by Methot (1983), who was the first to investigate changes within a spawning season, rather than averaging variables over an entire spawning season, by comparing monthly larval production to hatchdate distributions from juveniles. He concluded that the seasonal larval survival differences were enough to account for the differences in recruitment strength observed.

1.4. Age, hatchdate distribution and growth studies

Studies of daily growth increments from otoliths have provided ecologists with a powerful method for examining changes in age and growth of larval and juvenile fish specimens from the field (see Morales-Nin 1992 for a review), and have been geared particularly towards recruitment questions (Methot 1983, Yoklavich and Bailey 1990, Hernández and Castro 2000, Quiñonez-Velázquez *et al.* 2000).

A hatchdate distribution is the frequency distribution of hatching dates in a population, and is also the mirror image of an age-frequency distribution, drawn up from age-structure from fish otoliths. In the absence of selective mortality, the hatchdate distribution drawn up directly from the number of larvae hatched should be identical to one drawn up from a back-calculated age-frequency distribution. Differences between the two distributions would suggest that the survival of larvae hatched on certain dates was enhanced relative to those hatched on other dates (Campana and Jones 1992). This is useful for recruitment studies for testing the *matching* of hatching dates with the monthly production of the system (Methot 1983). Similarly, analyses of hatchdate distributions of larval and juvenile Cape anchovy and correlations of these distributions with egg abundances each month during a number of spawning seasons may reveal factors affecting larval growth rates, survival and recruitment variability in the southern Benguela (Huggett *et al.* 1998, Painting *et al.* 1998).

Hatchdate distributions of Cape anchovy recruits in previous studies usually spanned from July until March the following year, but shapes have differed widely showing peaks in: October-November (1984/85, 1988/89, 1993/94, all different shapes, Waldron *et al.* 1992, Bloomer 1995), and December-January (1992/93, Bloomer 1995). Length-frequency distributions estimated during recruitment surveys are available for the other years since 1984. These are subject to differences in growth rates and the dates of the cruises every year. Still, a very young year-class was shown in May 1993 (peak at 45-50 mm SL), which possibly was picked up again as 1-year-olds in the recruitment survey in 1994 (105-110 mm SL). All other length-distribution peaks and ranges differed widely (Barange *et al.* 1999), and it is still unclear whether differences in peak spawning, early larval survival versus late larval survival, growth rates, a combination of any two or three, or all four mostly make up these variable shapes of the apparent age and hatchdate distributions at recruitment.

The monthly distribution of hatchdates drawn up for Cape anchovy has previously always been correlated with the factors that may have affected spawning in that month, and survival of eggs and larvae was assumed equal for each monthly batch (Waldron *et al.* 1992, Bloomer 1994, 1995, Huggett *et al.* 1998). However, many factors may cause differential larval survival at different ages. For example, Thomas (1985a, 1985b and 1986) conducted daily age studies on larval and juvenile pelagic fish in the Benguela region, mostly

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focusing on South West African (Namibian) pilchard. Results of his studies showed that anchovy of the 1983/84 year-class caught off Namibia were spawned mostly in December 1983 and larval survival appeared to be higher for fish spawned earlier in the season. This age-specific survival may have significant impacts on recruitment.

Little is known about age-specific mortality at the early life history stage of Cape anchovy and their contribution towards recruitment variability. Links between prevailing environmental conditions, and changes in the apparent hatchdate distribution from the larval to the juvenile stage should provide a greater understanding of the dynamics that influences survival in the early life history stages of anchovy.

The change in length of a fish during a phase of its life history (e.g. larval), represent the duration of the phase. Growth rates can be calculated from the change in length over time. Variations in growth of pre-feeding larvae are positively correlated with recruitment variability (Pepin and Myers 1991). It is proposed that, as the duration of the stage increases, cumulative mortality increases (Ware 1975, Smith 1985, Pepin 1991), resulting in greater recruitment variability (see also Table 1.1).

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In the southern Benguela region, Waldron *et al.* (1989) studied daily growth of juvenile Cape anchovy and suggested that the large interseasonal variability of daily growth possibly resulted from localised variation in the zooplankton food supply. Waldron (1995) calculated the growth of juvenile Cape anchovy in 1991 from otolith rings, which showed large variations in lengths at all ages. In 1991, average sea surface temperatures (SST) were higher than usual with great fluctuations, which may have produced these large variations. It appeared that short-term changes of SST might be the main cause for fluctuating growth rates in juvenile anchovy. Preliminary results reported by Bloomer (1994) indicated average growth rates of juvenile Cape anchovy of the 1992/1993 year-class of 0.42 mm.day^{-1}. This value is faster than would be expected considering the late and relatively poor recruitment in 1993.

The 1999-2000 spawning season investigated in this study gave rise to the highest recruitment of Cape anchovy recorded since acoustic biomass surveys started in 1984 (Coetzee *et al.* 2000), despite showing a below-average pre-recruit density in March 2000 (van der Lingen and Merkle 2000). It seems then that conditions were particularly favourable for the survival of anchovy larvae and juveniles in 1999/2000 (Roy *et al.* 2001a), making this year-class an important one for studying differential egg, larval and pre-recruit survival; and calculating growth rates for samples from March and May surveys in 2000 will throw more light on the development of larvae and pre-recruits and on the relationship between growth rates and recruitment strength in Cape anchovy.

1.5. Aims and structure of this dissertation

1) The primary objective of this study was to calculate the hatchdate distributions of Cape anchovy larvae (caught in March 2000) and juveniles (caught in May 2000) in the southern Benguela region in order to investigate:

i) which part of the spawning-period most survivors stemmed from in each case,
ii) the difference between the two apparent hatchdate distributions, in order to test for possible age-selective mortalities and
iii) the effects that temperature may have had on both i) and ii).

2) A further objective of this study was to estimate growth rates of Cape anchovy larvae and juveniles in the year 2000 from age-length relationships. These were used to:

i) compare larval and juvenile growth in 2000 and
ii) compare growth rates in 2000 to growth rates in previous years in order to assess the relationship between growth rates and mortality rates in 2000 and to
iii) assess the relationship between growth rates and temperatures.

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3) These data could then be used to examine two recruitment hypotheses:

i) The *Match/mismatch* hypothesis (Cushing 1990), that the onset of spawning is matched with the onset of primary production. The hypothesis would be supported through those larvae that were hatched during favourable environmental periods constituting most of the year-class.

ii) The *Critical period* hypothesis (Hjort 1914) that the survival at first-feeding is critical in determining recruitment strength. In order for Hjort's hypothesis to be supported, larvae and juveniles should show similar hatchdate distributions indicating that year-class strength was determined at first-feeding.

iii) The Growth/mortality hypothesis (Ware 1975, Shepherd and Cushing 1980, Anderson 1988) that mortality is related to growth because larvae that grow faster within a year-class will spend less time in the early vulnerable life-history stage, and in that way will be less vulnerable to predation and survive better. This hypothesis would be supported if larvae and juveniles of the strong 2000 year-class showed a relatively high growth rate compared to a relatively low mortality.

The dissertation is divided into four further chapters. In Chapter 2, the methods for sample collection, age sub-sampling, otolith mounting, preparation and reading as well as calculations for ageing precision, mortality rates, hatchdate distributions and growth rates of anchovy in March and May 2000 are described. The results of ageing precision, mortality rates and hatchdate distributions for both March and May are presented in Chapter 3. The growth rate results for March and May are presented in Chapter 4. Chapter 5 includes the description of the temperature environment over the relevant period, a summary of the results of Chapters 3 and 4, as well as a comparison of the March and May data with each, other with other year-classes, a discussion of these in the light of the prevailing environmental conditions. Chapter five then concludes with the discussion of hypotheses i), ii) and iii) in the light of all the results presented.

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CHAPTER TWO

METHODS: DATA COLLECTION AND ANALYSIS

2.1. Sample collection: Pelagic biomass surveys

Cape anchovy samples were collected during routine surveys of pelagic fish in the southern Benguela region conducted by Marine and Coastal Management (MCM), Department of Environmental Affairs and Tourism, South Africa. Both surveys were done on the *RS Algoa*; survey names, months and collection methods are outlined in Table 2.1 below.

Table 2.1. Summary of the pelagic surveys conducted in 2000 from which samples of Cape anchovy were collected for this study.

Month in 2000	Survey name	Standard length range of population surveyed	Method of catching	Start of time-series	Reference
March (9 – 23)	Pre-recruit (Voyage 071)	10 – 95 mm	Methot frame trawl	1991	van der Lingen and Merkle 1999
May/June (13 – 9)	Recruit biomass (Voyage 074)	35 – 120 mm	Engels 308 midwater trawl	1984	Barange *et al.* 1999

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2.1.1. Larvae and pre-recruits: Pre-recruit survey

The pelagic pre-recruit survey in March 2000 covered the west coast nursery area between the Orange River mouth and Table Bay, Cape Town (see Fig. 2.1). Twenty-two randomly distributed lines were sampled. Each line was perpendicular to the shoreline and extended across the continental shelf to approximately 60–80 nautical miles (nm) offshore. Sampling stations were positioned every 10 nm. Eleven of the lines were sampled during the night from inshore to offshore with Station 01 as close inshore as possible. These nighttime stations were termed 'Methot stations' (dots, Fig. 2.1). Standardised oblique 'Methot frame trawls' (Methot 1986, O'Toole and Crous 1989) were done at each Methot station. The 5-m^2-frame net was deployed to 35-m depth, where it was towed at 1 m.s^{-1} for two minutes. Net retrieval (0.5 m.s^{-1}) was stepwise, fishing for two minutes (1 m.s^{-1}) at every 5-m-depth interval, before it was brought aboard. The net was immediately rinsed and all clupeiform fish were identified, sorted, counted and measured to the nearest 1.0 mm total length (TL) from the snout to the tip of the tailfin. During the day, oceanographic data were collected on the other 11 lines, sailing from offshore to inshore and no Methot hauls were done during the day.

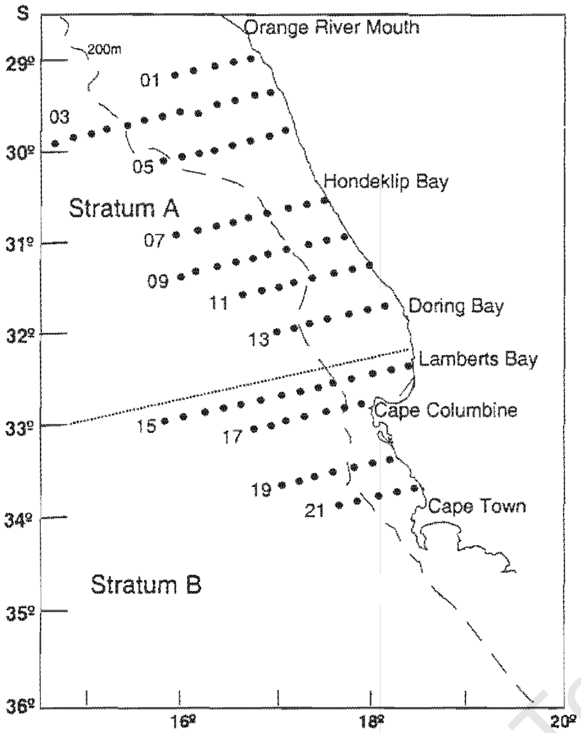

Figure 2.1. Map showing the area sampled during the March 2000 pelagic pre-recruit survey. Dots indicate the Methot frame trawl positions and each Methot transect is numbered. The dashed line indicates the approximate position of the boundary between Stratum A and B (adapted from van der Lingen and Merkle 2000).

The volume of water filtered during the tow was measured by a calibrated manual flowmeter fitted in the mouth of the Methot net. Larval catches were standardised to densities (D), no.1000 m^{-3}, at each station by the equation:

$$D = 1000 \times N/V \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2.1),$$

where N is the number of larvae in the sample and V is the volume of water filtered during each trawl, m^3 (C. van der Lingen and D. Merkle, *MCM*, *pers. comm.*).

A mean survey density, no.1000 m^{-3}, was calculated after Jolly and Hampton (1990). All samples were frozen on-board and stored for laboratory analysis.

2.1.2. Juvenile recruits: Recruit biomass survey

The recruit biomass survey in May 2000 covered the area between the Orange River mouth on the west coast and Port Alfred on the south coast of South Africa (see Fig. 2.2). The

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survey grid was based on the random stratified design of Jolly and Hampton (1990). From results of previous biomass surveys conducted for anchovy and sardine, the coastline was divided into eight pre-determined density strata with 7–10 transect lines perpendicular to the shoreline in each stratum covering the continental shelf, typically extending 40-50 nautical miles offshore. Strata with expected higher densities had a smaller surface area, and hence sampling was intensified in these. Anchovy abundance in each stratum was estimated from acoustic density estimates according to standard echo-integration methodology (MacLennan and Simmonds 1992), averaged over the line and weighted by transect length (Hampton 1987). Seventy-two target identification tows were made using the standard Engels 308 midwater trawl (dots, Fig. 2.2). The frequency of trawls made on biomass surveys is dependent upon acoustic targets available, and is decided whilst underway.

Random samples of at least 100 individuals at each trawl were measured to the nearest 5 mm standard length (SL) from the tip of the snout to the posterior end of the vertebral column, at the start of the tail fin. For the purpose of this study, bags of random samples of anchovy were frozen from each trawl for age sub-sampling at a later stage.

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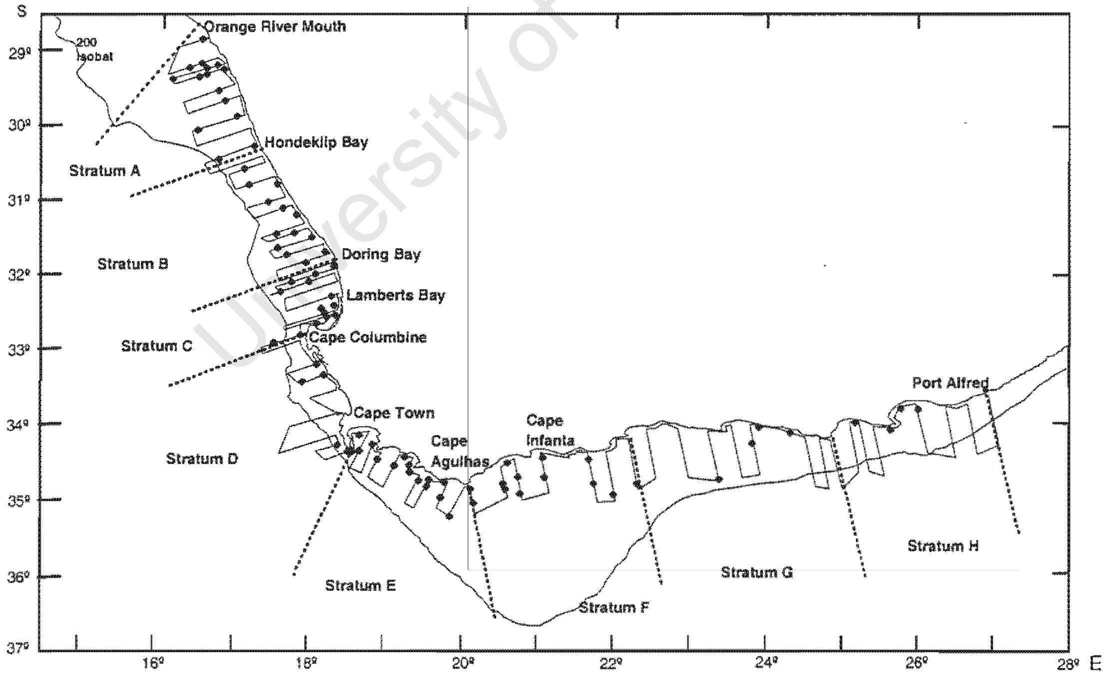

Figure 2.2. Map showing the area sampled during the May/June 2000 pelagic recruit biomass survey. Solid lines perpendicular to the shoreline indicate the cruise track and dots indicate positions of the midwater trawls. Dotted lines mark the end of each stratum, labelled A-H (adapted from Coetzee *et al.* 2000 and MCM Sailing Orders, *RS Algoa* Voyage 074).

2.2. Age sub-sampling

The number of sub-samples from every length-class was selected carefully in order to get an accurate estimate of birthdate distributions and growth rates of the whole population. The age-length key (*ALK*) method for estimating age composition of a fish population was used to do this (Fridriksson 1934). This is a double sampling technique consisting of i) simple random sampling to get a large length-frequency sample (which was done during the surveys) and ii) age sub-sampling (Cochran 1977, Lai 1993).

2.2.1. Length-frequency corrections

2.2.1.1. Larvae and pre-recruits: Pre-recruit survey

Length-frequency distributions from the pre-recruit survey were constructed from on-board measurements using 1-mm-TL-classes. From on-station densities per 1000 m^3, D (equation 2.1), on-station densities per km^2, K, were calculated by:

$$K = D/1000 \times M \times KM \text{ ....(2.2),}$$

where M = maximum depth sampled = 35 m

(assuming that all fish are homogenously distributed throughout the top 35 m depth range)

and $KM = m^2.km^{-2} = 1\ 000\ 000$.

The length measurements at each station were then raised to *in situ* densities, $no.km^{-2}$ by: fraction at TL-class * $no.km^{-2}$ at that station. Raised length frequencies at each station were then pooled to obtain the overall pre-recruit TL-frequency distribution (C. van der Lingen and D. Merkle, *MCM*, *pers. comm.*).

2.2.1.2. Juvenile recruits: Recruit biomass survey

On the recruit biomass survey, each trawl represents an acoustic biomass in a certain area. To weight individual trawls, firstly a trawl-weighting factor is calculated that converts the total acoustic weighting (mass) to an acoustic weighting factor in terms of numbers:

$$Q_{ij} = \frac{Z_{ij}}{X_{ij}} \text{ ....(2.3),}$$

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where Q_{ij} is the trawl weighting factor (numbers) of sample j in Stratum i, Z_{ij} is the total acoustic weighting of that sample (mass) and X_{ij} is the average mass of one anchovy in the trawl sample.

The length frequencies from each trawl sample are then multiplied by that particular trawl's weighting factor and summed across trawls to get a number at length at the stratum level. The weighted length frequency in Stratum i is the vector $(T)_i$:

$$(T)i = \sum_j (T)ij \times Qij \text{ ....}(2.4),$$

where vector $(T)ij$ is the vector of numbers in sample j of Stratum i (with the different elements of the vector corresponding to the counts at each 5-mm-SL-class from trawl samples).

To get the total numbers at each length, $(N)i$, in Stratum i, each stratum is weighted to the total acoustic biomass of the survey:

$$(N)i = (T)i \times \left(B \middle/ \sum_j Z_{ij} \right) \text{ ....}(2.5),$$

where B is the total acoustic biomass of the survey, and the term $(\mathrm{B}/\sum_j Z_{ij})$ is the weighting factor for Stratum i.

The numbers at length are then summed across strata to obtain the overall numbers at length in the recruit survey (J. Coetzee, C. van der Lingen and M. Prowse, *MCM, pers. comm.*). This provides composite estimates for population age structure (Hampton 1992). The frequency is expressed as the number of fish in each 5-mm-SL-class.

2.2.2. *Optimal sample size*

Baird (1983) suggests a formula that calculates a minimum sample size required for a "coefficient of variation" (*CV*), of 20 % or less for each age. This is not a true *CV* in the sense that there is no mean involved in the calculations, so for the purposes of this study, we will call it *Baird's index of variation* (*BIV*). The *BIV* for catch-at-age is calculated for

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a given "shape" of a catch-frequency curve accompanied by an age-length key (ALK) from historical data. Historical ALKs for Cape anchovy were obtained from Thomas (1986), Prosch (1986), Waldron (1995), Waldron *et al.* (1992) and Bloomer (1995). The following parameters were used to calculate *BIV* for each age (Baird 1983):

N_i = number at each length (from the survey estimates)
n_i = the number aged at length i (chosen sample size)
p_i = proportion at age for a given length i (from ALK)
N = catch-at-age

To calculate the *BIV* at each age, firstly variance of the catch at each age group, $Var(N_ip_i)$. is required:

Catch-at-age, $N = \sum N_i p_i$ ....(2.6)

and $Var\ (N_ip_i)\ = (N_i)^2\ Var\ (p_i) + (p_i)^2\ Var\ (N_i)$ ....(2.7)

= (Sampling error of ageing plus sampling error of length measurement).

The assumption is that the *ALK* has a binomial distribution, thus the second term in equation 2.7 can be ignored because of the magnitude of the first term. An adequate approximation for variance at each length is then:

$$Var\ (N_ip_i) = N_i^2\ Var\ (p_i) \quad \text{..........(2.8),}$$

where
$$Var(p_i) = \frac{p_i(1-p_i)}{n_i} \quad \text{..........(2.9).}$$

The variance of catch-at-age is calculated by summing the variances at each length group, $Var\ (N_ip_i)$ (equation 2.8):

$$VarN = \sum N_i^2 \cdot Var(p_i) \quad \text{..........(2.10)}$$

Baird's index of variation (*BIV*) is then calculated from equations 2.10 and 2.6:

$$BIV = \frac{\sqrt{VarN}}{N} \times 100 \quad \text{..........(2.11)}$$

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Baird (1983) indicates this index of variation as *VarN/N*, which seems to be a typographical error, since this does not render the results given in his tables of calculations. Equation 2.11 is used here. This method was followed for each age.

The area surveyed during the recruit biomass survey was sub-divided into strata (Jolly and Hampton 1990) (see Fig. 2.2). Survey strata were used in *Baird's index of variation* (*BIV*) equations, calculating variance at age in the same way as variance of density:

$$Var(N) = \frac{\sum A_i^2 Var(N_i)}{(\sum A_i)^2} \quad \text{...(2.12)}$$

where A_i is the area for each stratum and $Var\ (N_i)$ in this case is the variance of catch-at-age in each stratum (equation 2.10).

The area for each stratum (A_i) was calculated using an Underway Mapping System, UMS, C. Zauner and M. Berryman, *MCM*, *pers. comm.* For the purpose of comparison, *Baird's index of variation* at each larval and pre-recruit age-class was calculated in the same way as for recruits. The pre-recruit survey area was divided into two strata; the area for Stratum A was taken from line 01 to half-way between line 13, and Stratum B spanned from the end of Stratum A until line 21 (see Fig. 2.1).

A computer programme (*TrueBasic*) was written to compute *Baird's index of variation* (*BIV*) for each age at different sub-sample sizes, as well as the minimum sample size required for a *BIV* of 20 % or less (see Appendix 1). This programme incorporated:

i. The proportional age sub-sampling technique, in which sub-samples were selected proportional to their abundance in each 5-mm-SL-class, according to the length-frequency distributions calculated from the surveys. This was preferred to the stratified sub-sampling technique, because that usually introduces a larger variance (Kimura 1977, Lai 1993).

ii. The larger size-classes (38–95 mm SL) caught in the pre-recruit survey contained negligible numbers compared to the other size-classes (10–37 mm SL). Larger size-classes are likely to be undersampled by the Methot net, yet abundance in these size-

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classes was unusually high in 2000 compared to other years, and may have contributed significantly to the recruitment later that year (van der Lingen and Merkle 2000). For these reasons, one sub-sample from each 1-mm-SL-class was selected in the larger size-classes. This way, length-based age sub-sampling was combined with proportional age sub-sampling to improve precision for samples of rare and older fish (Ketchen 1949, Fournier 1983, Lai 1993).

iii. Further increasing sample sizes, in those lengths that gave the largest variance (equation 2.8; Baird 1983).

2.3. Otolith mounting and preparation

Microstructural examination of otoliths followed a procedure consisting of three steps: 1) otolith mounting, 2) preparation and 3) observation and ring enumeration. All the techniques used in this study were described in detail by Campana and Neilson (1985), Morales-Nin (1992) and Secor *et al.* (1992).

2.3.1. Larval and pre-recruit otoliths (pre-recruit survey)

Thawed specimens were measured to the nearest 1.0 mm TL as well as SL. Both *sagittae* (largest otolith of three pairs) could be easily seen under a dissecting microscope lens with polarised light. Larvae were fixed on a microscope slide with a drop of water and otoliths were removed by teasing apart the cranial region with dissecting needles. The debris was removed, otoliths were cleaned with distilled water and left to dry. Otoliths were then fixed to the slide (lateral side up, where distinguishable) by adding a drop of clear Crystalbond^{TM} resin, heated on a laboratory heating plate and flattened by carefully adding a coverslip.

Larval otoliths are thin enough that only optical sectioning (focussing the plane of maximum clarity) is necessary to make total increment counts (Brothers *et al.* 1976). Otoliths of Cape anchovy larger than about 35 mm SL, however, were too thick to transmit sufficient light for viewing the increments. Material was removed by grinding them in the sagittal plane (see Fig. 2.3) (after removing the coverslip again), with a series of 1500 to 2000 grit water paper. This was done until the primordium and all rings were clearly visible. Cleaning otoliths with a drop of immersion oil enhanced the images.

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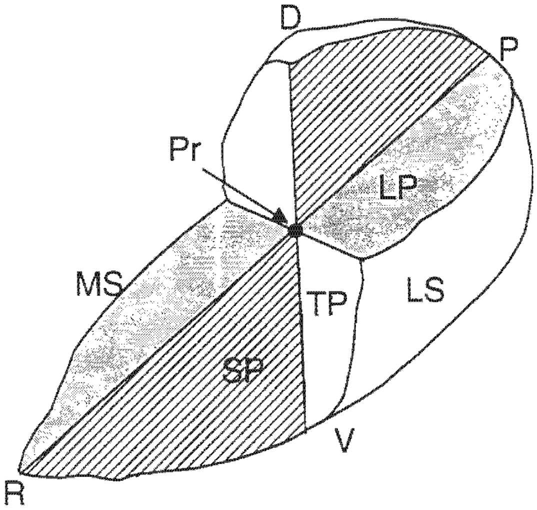

Figure 2.3. Schematic representation of a sagittal otolith showing the planes for sectioning:
P: Postrostrum
R: Rostrum
D: Dorsal side
V: Ventral side
Pr: Primordium
LS: Lateral side
MS: Medial side
SP: Sagittal plane
LP: Longitudinal plane
TP: Transversal plane.
(after Kerstan and Waldron 1995)

The otoliths with the clearest rings were chosen for analysis, and were examined at 1000 x magnification with a *Zeiss* Diaplan transmission light microscope and immersion oil. A series of digital photographs of 193 otoliths of larval and pre-recruit anchovy were taken using a *Leica* Axiocam digital camera mounted on the light microscope in conjunction with *AxioVision*2.0 imaging software.

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2.3.2. Juvenile recruit otoliths (recruit biomass survey)

Thawed juvenile anchovy were measured to the nearest 1.0 mm SL and right-side sagittae of *circa* 400 anchovy were extracted by removing the gill arches and breaking the skull on a line through the otic capsules at the base of the skull (Melo 1984). Otoliths were immediately placed in a 0.5 % potassium hydroxide solution for 2–7 days. They were then washed with distilled water and dried by placing them on the back of a hand with a pair of tweezers. Lastly, they were dipped in 90 % ethanol to ensure quick and complete drying, and each otolith was left to dry thoroughly for 3–4 days.

Dried otoliths were then prepared for scanning electron microscopy (SEM). They were embedded separately in blocks of LR White (London Resin Co.) resin cast in silicon moulds and left to dry for 2–8 hours. Otoliths in their mounts were then ground on the lateral side to the mid-sagittal plane (see Fig. 2.3), with a series of 1500 to 2000 grit water paper. The primordium was presumed exposed when both the rostral and the postrostral tips were just exposed. Otoliths were then polished on a rotating table with a felt disc covered with 0.3 µm Alumina powder and water to remove rough scratches, and finally with 0.01 µm grain

Alumina paste until no scratches were visible under a dissecting microscope. The polished blocks were rinsed with distilled water and mounted onto large SEM stubs with silver (Ag) paint (for better conduction of the electrons in the electron mircroscope).

The backscatter detector (BSD) method for viewing otoliths was preferred over the secondary electron detector (SED) because it did not require etching of the otoliths. Preparation time was thus reduced, the variability of etching was removed, and a larger percentage of increments could be seen (Waldron and Gerneke 1997). For the BSD method, stubs were cleaned ultrasonically, carbon-coated in a vacuum-evaporator and (vacuum-stored or) immediately examined under a Leica S440 SEM (mostly 15 KV voltage, and 800 pA current) at 1500–3000 times magnification, depending on otolith size and increment width. A series of digital photographs was taken of otoliths that showed the primordium and clear increments between the primordium and the postrostral tip using Leica Electron Optics (LEO) software (see Fig. 2.3). This was only possible for 25 % of the prepared samples.

The light microscope technique used for reading otoliths of pre-recruit samples proved more successful - for fish up to 70 mm SL. Because it was less time-consuming and costly, this method was thus also applied on juvenile otoliths later to fill in smaller size-classes (35–55 mm SL) as well as juvenile size-classes, for which only a few otoliths were extracted. The medium used to mount these otoliths on glass slides was Saarchem DPX mountant. Compared to Crystalbond^{TM}, this resin took longer to set (24–36 hours), and could not be melted again after mounting; thus otoliths could not be moved or turned over after mounting. However, it supplied a firmer hold for larger otoliths on glass slides. Otoliths were ground in the same way as larger pre-recruit otoliths, described in section *2.3.1.*

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2.4. Daily increment observations

Fish otoliths, in particular the sagittae form concentric layers of a calcareous secretion known to have seasonal growth rings (Rounsefell and Everhard 1953, Blacker 1974). A daily growth increment consists of two distinct parts, one light continuous / incremental unit, 0.5-1.0 μm wide, and one dark check unit, 0.5-2.5 μm wide (Pannella 1971).

Sagittae in this study were analysed from the digital images using *OPTIMAS 6.2* software (Optimas Corporation 1997) and an automating macro for counting and measuring daily increment widths on otoliths, developed for *OPTIMAS* by Donohoe (2000). Increments (rings) were clearly seen spreading from the primordium to the edge (see Fig. 2.4a and b). They were similar in appearance to those that others have demonstrated in the laboratory to be daily increments (Brothers *et al.* 1976) or indicated with micrographs of otoliths collected from the field (Palomera *et al.* 1988, Thorrold 1988, Thorrold and Williams 1989).

Brothers *et al.* (1976) have validated daily rings of northern anchovy *Engraulis mordax* as the smallest cyclical units (1-2 µm thick) for up to 100 days. Thomas (1986) counted daily rings on laboratory-reared Cape anchovy *E. encrasicolus* larvae. He found that the largest difference between true and counted ages was seven days on presumed 35-day-old specimens. This was taken as the time from hatching to first increment formation. Waldron (1994) used daily rings on Cape anchovy otoliths for annual ring validation. She showed that one annual growth ring comprised close to 365 daily rings. The light increments between two dark rings seen under the light and electron microscopes were thus taken to represent one day of age of the fish.

Sub-units were often seen after about the first five narrow increments. The appearance of these sub-daily units is common and has been related to daily variations in environmental temperature (Pannella 1980) or to feeding frequency (Tanaka *et al.* 1981). They were regarded as sub-daily rings following the same pattern of counting as demonstrated on light micrographs by Campana (1992), Palomera *et al.* (1988) and Morales-Nin (1987). The increments of juvenile otoliths were similar to those demonstrated on SEM micrographs by Thomas (1985a, b), Kerstan and Waldron (1995) and Waldron and Gerneke's (1997) introduction to using the BSD method on fish otoliths (Fig. 2.4.b).

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Figure 2.4.a. Light micrographs showing the primordium (Pr) and daily increments (d) of a larval Cape anchovy *Engraulis encrasicolus* otolith. This fish (P105) was caught at station 17-07 (see Fig. 2.1) offshore off Cape Columbine in March 2000, and was aged as 22 days and 12 mm SL at capture. Original magnification: 1000x.

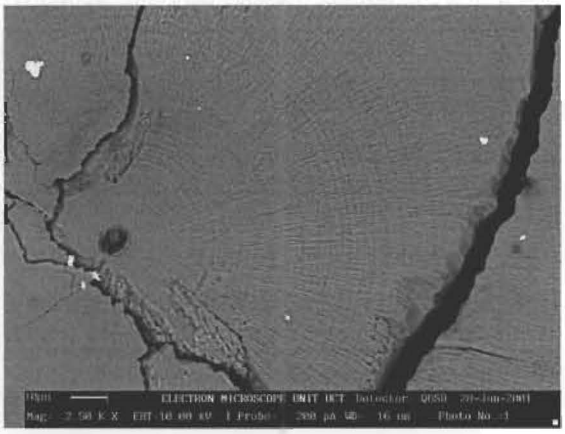

Figure 2.4.b. Scanning electron micrograph (backscatter technique) of the primordium and the first daily increments of a juvenile Cape anchovy otolith. This fish (RD137) was caught in Stratum D, Station 32-01, inshore, south of Saldanha Bay In May 2000 (see Fig. 2.2). It was aged as 155 days, 87 mm SL at capture. Original magnification: 2500x

The length (from the rostral to the postrostral tip), radius (from the primordium to the postrostral tip) (see Fig. 2.3), and distance from the core to the first increment (Secor *et al.* 1992) were measured where possible. All increment widths were measured and the total number of increments was counted. Increment widths and radii were measured in the direction of maximum growth (i.e. posterior otolith radius) or on the line at which they were best visible (Campana 1992). For areas where increments were not clearly visible, counts were interpolated from adjacent counts (Methot 1983).

Otoliths of 193 larval and pre-recruit Cape anchovy (14–74 mm SL) from the March pre-recruit survey were analysed in this way (see Table 2.2). This is a 91 % success rate. From the May recruit survey, 322 otoliths were prepared and viewed under the SEM. They were often disregarded, however, when either 1) the primordium was not seen (under- or over-ground) or 2) more than 20 % of the distance along the axis of maximum growth had no clearly visible increments. Only 80 otoliths of juvenile anchovy (52–114 mm SL) from 15 stations of Strata A–D and F of the recruit biomass survey (see Table 2.2 and Appendix 3.B) provided reliable increment counts. This is a success rate of 25 %.

The total survey area, number of length samples measured, and number of age sub-samples taken from each SL-class from each survey are outlined in Table 2.2. Note that the "age sub-sample size" column represents the number of otoliths that were successfully prepared and read. In the case of the recruitment survey, this number is not the same as the optimal sample size (see section *2.2.2*) because of time constraints and a very low success rate of the otoliths prepared for SEM purposes. *Baird's index of variation* and hence the

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new optimal sample sizes were re-calculated later with the new age-length key from this study, and are presented in Chapter 3. Optimal sample sizes calculated using historical *ALK* are presented in Appendix 3.A. Appendices 2 and 3.B show a detailed outline of the number of samples successfully analysed from each SL-class from each station or stratum of each survey.

Table 2.2. Survey areas and total number of length-frequency samples measured and age sub-samples taken from each standard length (SL)-class from each survey.

Survey area	March - Pre-recruit survey 58 953 km²		May - Recruit biomass survey 74 673 km²	
SL (mm)	Total number measured	Total number aged	Total number measured	Total number aged
10	336	12		
15	1599	47		
20	1184	36		
25	861	30		
30	420	18	1	
35	95	11	7	5
40	15	6	5	3
45	15	7	9	4
50	20	4	45	5
55	31	6	84	3
60	67	7	208	4
65	44	4	385	7
70	17	5	712	11
75	6		755	9
80	4		838	9
85	1		629	7
90			610	4
95			588	4
100			584	4
105			299	1
110			218	
115			101	1
120			140	
125			84	
130			29	
135			13	
140			5	
SUM	**4715**	**193**	**6349**	**81**

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2.4.1. Ageing precision

59 % of the larval and pre-recruit otoliths and 59 % of the recruit otoliths were read at least two times, on different occasions by the same reader. The mean of the readings was taken as the age. Ageing precision was calculated by two methods:

1) *Average percent error (APE)*, defined as:

$$\mathrm{APE}_j = 100\% \times \frac{1}{R}\sum_{i=1}^{R}\frac{\left|x_{ij} - x_j\right|}{x_j} \qquad \text{(2.13)},$$

where x_{ij} = the ith age determination of the jth fish

x_j = the mean age estimate of the jth fish

R = the number of times each fish is aged.

This becomes an index of average percent error when averaged over many fish (Beamish and Fournier 1981).

2) Coefficient of variation (*CV*) of age estimates, expressed as the ratio of the standard deviation to the mean:

$$CV_j = 100\% \times \sqrt{\sum_{i=1}^{R}\frac{\left(x_{ij} - x_j\right)^2}{R-1}} \Big/ x_j \qquad \text{(2.14)},$$

where CV_j = the age precision estimate of the jth fish.

This can also be averaged across fish to produce a mean *CV* (Chang 1982).

2.5. Data Analysis

2.5.1. Length-frequency distributions

2.5.1.1. Larvae and pre-recruits: Pre-recruit survey

Each line on the March-2000-pre-recruit survey was sampled within a 24-h period. Sampling spanned a period of 14 days (9–23 March 2000) from line 01 to line 21. This time difference between the lines needed to be taken into account for length-frequency calculations. The adjusted TL-frequency for each line (see section *2.2.2*) was raised to the mid-date of the survey (16 March) by adding or subtracting 0.448 mm TL for each day that the line was sampled before or after the survey mid-date (Suthers and Sundby 1993). This growth rate was calculated from a linear regression fitted to TL in mm against age in days, see Appendix 4.

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The new TL-frequencies for each line sampled before 16 March were thus calculated by:

$$N_{ij} = ((G_j - nGj)\ N_{(i\text{-}nGj)j}) + ((nGj+1\text{-}G_j)\ N_{(i\text{-}nGj+1)\,j}) \quad \text{.................(2.15)}$$

where N_{ij} = frequency at TL-class i at line j

G_j = absolute growth of pre-recruits sampled along line j

= 0.448 mm TL $.\text{day}^{-1}$ * days to 16 March

nGj = integer G_j (rounded down)

$N_{(i\text{-}nGj)j}$ = frequency at TL-class $(i - nGj)$ in line j

Equation 2.15 needed to be changed for lines that were sampled after the 16 March:

$$N_{ij} = (G_j - n_{Gj})\ N_{(i\text{-}nGj+1)\,j}) + ((nGj+1\text{-}G_j)\ N_{(i\text{-}nGj)j}) \quad \text{.................(2.16)}$$

Resultant frequencies were summed across lines to get a survey TL-frequency distribution.

The TL and standard length, SL measured from thawed specimens before otolith extraction, were used to construct a "*TL-SL key*", the proportion of each 1-mm-SL-class present at each 1-mm-TL-class, see Appendix 5. Multiplying the TL-frequency (vector) by the *TL-SL key* (matrix) then gave a 1-mm-SL-frequency distribution. The 1-mm-SL-frequency distribution was then converted to a 5-mm-SL frequency distribution by pooling the frequencies of five 1-mm-SL-classes at a time.

2.5.1.2. Juvenile recruits: Recruit biomass survey

Most strata were sampled over a period of 3 days. Within a stratum, 5-mm length-frequencies were assumed to have remained the same over the period of 3 days, because no fish would have grown more than 0.552 mm, at an average growth rate of 0.184 mm SL $.\text{day}^{-1}$over three days. Standard length-frequencies were raised to the fourth-last day of the survey (30 May 2000), because this was 75 days after the 16 March, survey mid-date of the pre-recruit survey; and in this way, their hatchdate-classes, dated back in 15-day intervals, would coincide. The lengths of each stratum were raised to 30 May by adding the average rate of 0.184 mm SL $.\text{day}^{-1}$ (see Appendix 6). Assuming that lengths are equally distributed within one 5-mm-SL-class, 1/5 (20 %) of the frequency of the previous

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SL-class was added to each new SL-class for each 1-mm growth in each stratum. The new length-frequency would then be calculated by:

$$N_{ij} = (((5 - G_j)/5)\ N_{ij}) + ((G_j/5)\ N_{(i-1)j}) \quad\text{.....................................}(2.17)$$

where N_{ij} = frequency at SL-class i in Stratum j

G_j = absolute growth of Stratum j

= 0.1842 mm SL $.\mathrm{day}^{-1}$ * (number of days to 30 May)

$N_{(i-1)j}$ = frequency at SL-class (i-1) in Stratum j

Historically, all strata east of Stratum F (see Fig. 2.2) have been excluded from the model used to calculate cumulative weighted length-frequencies, and have been considered to have negligible influence on recruitment age-structure. The main reasons for this were that few anchovy were caught in these strata, and most of the anchovy that were caught here were larger than 100 mm SL. Stratum F was thus the only stratum sampled after the "mid-survey" date (30 May) during this study, which was taken into account for length-frequency calculations. The equation for the length-frequency of Stratum F was thus:

$$N_{ij} = (((5 - G_j)/5)\ N_{(i-1)j}) + (G_j/5\ N_{ij}) \quad\text{.......................................}(2.18)$$

Numbers at length were then summed across strata to obtain the overall numbers at each 5-mm-SL-class.

2.5.2. *Age-frequency distributions* (*by the age-length key*)

An age-length key (*ALK*), the proportion of the number aged in each 5-mm-SL-class allocated to each 15-day-age-class, was calculated for each survey (Kimura 1977) (see Appendices 7 and 8).

Multiplying the SL-frequency (vector) of each survey by the *ALK* (matrix) gave an age-frequency distribution of the Cape anchovy population at the time of each survey. *Baird's index of variation* was then calculated for each age-class at each survey.

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2.5.3. Mortality

Mortality is estimated by measuring the decline in abundance over time of a cohort; a cohort being defined as "*a batch of fish, all of approximately the same age*" (Sparre and Venema 1998), "*a closed group of fish that, once born, can only decrease in abundance*" (Campana and Jones 1992). Mortality is calculated from the age-distribution using the negative exponential model of decay, which, together with the growth equation, forms the basis of the theory of exploited stocks (Beverton and Holt 1957):

$$N_t = N_0 e^{-Zt} \quad \text{(2.19)}$$

where Z = the instantaneous daily mortality rate
N_t = the number of individuals at age-class t
N_o = the number of individuals at age-class 0
t = age in days,

and taking natural log of both sides:

$$\ln N_t = \ln N_0 - Zt \quad \text{(2.20)}$$

Thus, drawing a linear regression of *ln* catch-at-age ($\ln N_t$), starting at the highest point, against age t gives a negative slope of Z and an intercept of the natural log of the population size at age 0 ($\ln N_0$).

2.5.4. Hatchdate analysis

The hatchdate distribution of a population is normally presented as the mirror image of an age-frequency distribution with the hatchdates calculated by subtracting the age in days from the day of capture. There is instability in the hatchdate distribution calculated directly from the age distribution of larval or juvenile fish. A monthly cohort's contribution to the hatchdate distribution is a function of the spawning rate during that month, the mortality rates experienced by that cohort over time and the age of that cohort when sampled. Larvae that were hatched earlier in the season would have been exposed to a greater cumulative mortality than those that were hatched later in the season, and the early season larvae will be under-represented in the back-calculated hatchdate distribution

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relative to the late season larvae. Therefore, cumulative mortality corrections need to be applied to stabilise hatchdate distributions before one can interpret the resultant hatchdate distributions as differences in age-specific larval survival (*sensu* Methot 1983, Yoklavich and Bailey 1990, Campana and Jones 1992 and Quiñonez-Velázquez *et al.* 2000). The mortality correction is not related to the interpretation of the results, but is a uniform mortality that applies across all cohorts (Campana and Jones 1992).

The number of individuals present at time 0 (N_0) was thus back calculated from the number of individuals at a certain age (N_t) considering mortality rate Z by rearranging equation 2.19 for N_0:

$$N_0 = N_t / e^{-Z.t} \quad \text{.......(2.21)}$$

Because the values for mortality calculated by Shannon's model (1995) (Z = 0.0315 and 0.0460 for pre-recruits 101-179 days) coincided closely with estimates from field samples in this study, a combination of *Z* estimates from this study was used for equation 2.21. I assumed that larvae showed a higher than natural mortality in the laboratory (Brownell 1983) due to frequent handling and stress levels.

2.5.5. Growth rates

I did not apply corrections for growth between hatching and the deposition of the first growth check, because the growth of yolk-sac larvae differs from that of feeding larvae (Zweifel and Lasker 1976, Methot and Kramer 1979). For simplicity, I considered the day of first increment formation as the first day of growth in these results (Thomas 1986).

To enable comparisons with other studies, I corrected larval lengths for shrinkage due to handling and net abrasion during capture (Theilacker 1980). Lengths measured on-board were adjusted to live lengths using the relationship given by equation 2.22 proposed by Theilacker (1980) for larval northern anchovy *Engraulis mordax*:

$$ln\, L_l = ln\, L_c + P_1\, exp(-P_2\, L_c\, t^{P_3}) \quad \text{.......(2.22),}$$

where L_l = live length (mm)

$P_1 = 0.289$

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$P_2 = 0.434$

$P_3 = -0.68$

L_c = handled / preserved length (mm)

t = combined net treatment and handling time (minutes)

Assuming an average t of 40 minutes (20 minutes average tow duration, 20 minutes average handling time) resulted in shrinkage factors that were very similar to those used by Brownell (1983). He estimated shrinkage of 20 % for 6–8 mm larvae, 15 % for 8–12 mm, 10 % for 12–20 mm, 8 % for 20–35 mm, and 5 % for larvae longer than 35 mm SL. For consistency, juvenile lengths were corrected for shrinkage using the same equations.

I plotted live SL corrected for shrinkage against the number of increments, and used three models to describe the growth rates of Cape anchovy: the linear, Laird-Gompertz, and von Bertalanffy growth functions.

The linear growth model has the form:

$$l_t = l_o + gt \quad \text{.........(2.23)}$$

where l_t = length at age t

t = age in days

l_o = length at $t = 0$

g = mean daily growth rate.

Von Bertalanffy (1938) described the rate of change of weight w of an organism, dw/dt, as $\eta w^m - kw^n$, all arbitrary constants. Substituting for w in terms of linear dimension, length l, the equation becomes:

$$l_t = l_\infty - (l_\infty - l_o)e^{-Kt} \quad \text{.........(2.24)}$$

where l_∞ = asymptotic length (theoretical maximum)

K = a growth coefficient

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and putting $l = 0$ at $t = 0$ gives the von Bertalanffy growth function, VBGF (Beverton and Holt 1957):

$$l_t = l_\infty \left[1 - e^{-K(t - t_0)} \right] \text{.......................................}(2.25)$$

I fitted the VBGF to the data to be able to compare growth rates of Cape anchovy in 2000 with anchovy off Namibia and South Africa collected over the period 1973–1994 (Thomas 1985a, b, 1986, Prosch 1986, Waldron *et al.* 1989, Bloomer 1994, 1995, Waldron 1995).

The Gompertz model (Gompertz 1852) is used to describe an asymmetric sigmoid curve. It describes the early growth of a group of organisms, which is fundamentally exponential growth, and undergoes intrinsic (as opposed to environmental) retardation by some unknown physiological mechanism. Laird *et al.* (1965) and Laird (1969) proposed the Laird-Gompertz model to describe larval fish growth that took the following into account: 1) a moderate increase in length during the interval following hatching that is followed by 2) a period of minimal growth accompanied by nearly uniform variability and 3) at the onset of feeding, the mean size increases rapidly with variability proportional to the square of the mean size. This Laird-Gompertz model has an asymmetric sigmoid curve of the form:

$$l_t = l_0 \exp\left[C\left\{1 - \exp(-at)\right\}\right] \text{..................................}(2.26)$$

where C = a constant

a = rate of decay of exponential growth.

All three growth curves, linear, VBGF and Laird-Gompertz were fitted to the data using the statistical software package STATISTICA 6.0 (StatSoft, Inc. 2001). Models were fitted using the quasi-Newton least squares estimating procedure to describe growth on a coarse time scale (Zar 1999).

Average lengths-at-age t (l_t) were then calculated for each model at daily intervals by substituting ages $t = 1$ to 268 into the respective equations. Instantaneous growth rates (G) at age t were then calculated by:

$$G = l_{(t+1)} - l_t \text{..}(2.27)$$

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CHAPTER THREE

AGEING, MORTALITIES AND HATCHDATE DISTRIBUTIONS OF LARVAL AND JUVENILE CAPE ANCHOVY OF THE 1999/2000 YEAR-CLASS

This chapter provides estimates of *CV* of ageing precision, length-frequency distributions, age-length keys, age-frequency distributions, mortality rates and hatchdate distributions of Cape anchovy larvae and pre-recruits caught during the pre-recruit survey in March 2000 and juvenile recruits caught during the recruit biomass survey in May 2000. A brief discussion on the potential biases and assumptions underpinning mortality rate estimates is included.

3.1. Ageing precision

Average percentage error, *APE* (see equation 2.13, section *2.4.1*) of counts on otoliths of larval and pre-recruit Cape anchovy caught in March was 6.1 %, corresponding to a mean *CV* (see equation 2.14) of 8.6 %, ranging between 6.0 % and 13.7 % at different age-classes. The variation of ageing precision seems independent of age (Fig. 3.1).

APE of first and second ring enumeration on otoliths of juvenile anchovy was 17.1 %, corresponding to a mean *CV* of 24.5 %, ranging from 4.3 to 43.6 % between different ages (black columns, Fig. 3.2). Taking the mean of the second and third counts, the *APE* and ageing *CV* were calculated again. This time the *APE* was reduced to 7.6 % and mean *CV* to 11.8 %, and a range of 4.8 to 22.8 % (grey columns, Fig. 3.2). The second and third counts were considered to be better estimates, because they were done after I had gained more knowledge and experience and had started using *OPTIMAS* image analysis software (Optimas corporation 1997); thus the first count was disregarded. Age from the first count was underestimated by a mean of 24 days. Note that the mean age changed from the first two to the third count. Moreover, only two counts were done on some otoliths; therefore, no *CV* is indicated for some ages in Fig. 3.2, grey columns.

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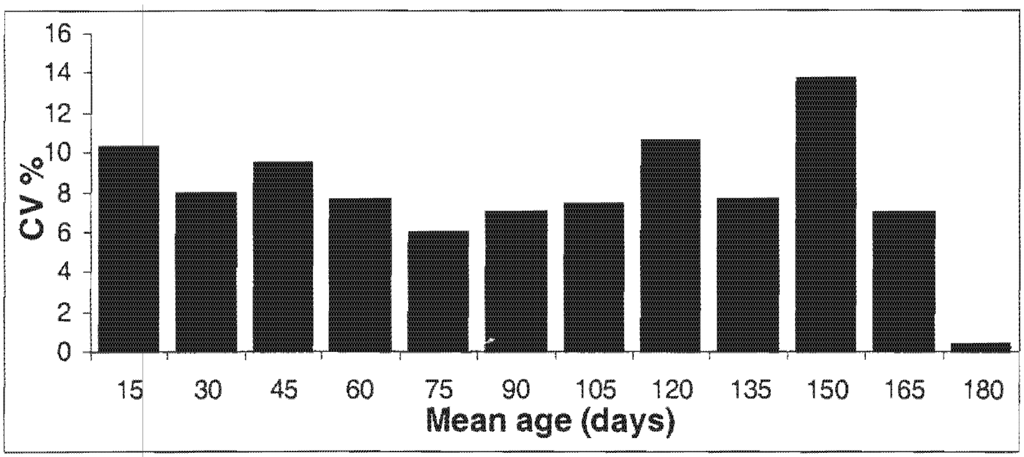

Figure 3.1. Coefficient of variation (*CV*) values by mean age class for age estimates of larval and pre-recruit Cape anchovy sampled in March 2000.

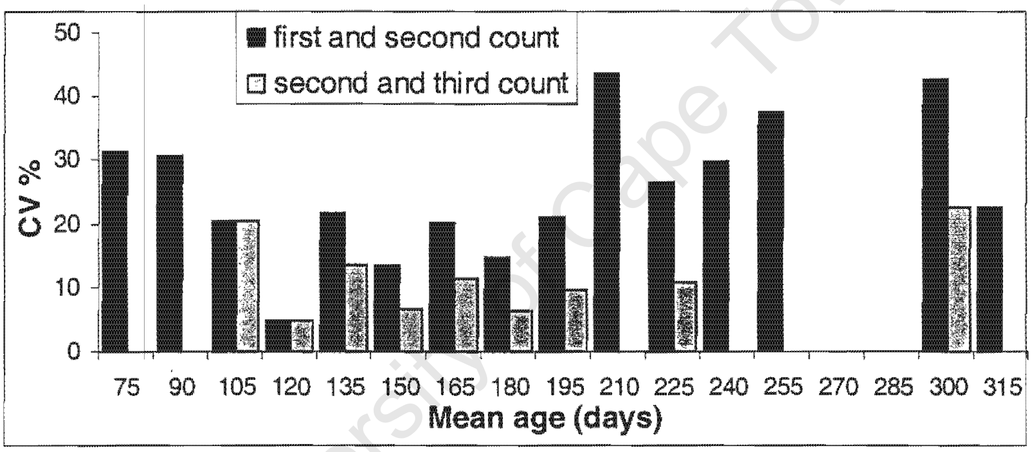

Figure 3.2. Coefficient of variation (*CV*) by mean age class of the first two (black bars) and second and third counts (grey bars) on otoliths of juvenile Cape anchovy sampled in May 2000.

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3.2. Larvae and pre-recruits caught in March 2000

The *length-frequency distribution* of Cape anchovy larvae and pre-recruits caught in March 2000 showed 16 standard length (SL)-classes from 10 to 85 mm SL, with a large mode (35 % of the population) at 15 mm SL (Fig. 3.3). Figure 3.4 shows the natural log (*ln*) of the catch-frequency against SL. The relatively high number of > 45 mm SL anchovy caught during the pre-recruit survey in 2000 (more than 5 % of all captured fish being > 45 mm SL) was an unusual feature compared to other years (van der Lingen and Merkle 2000).

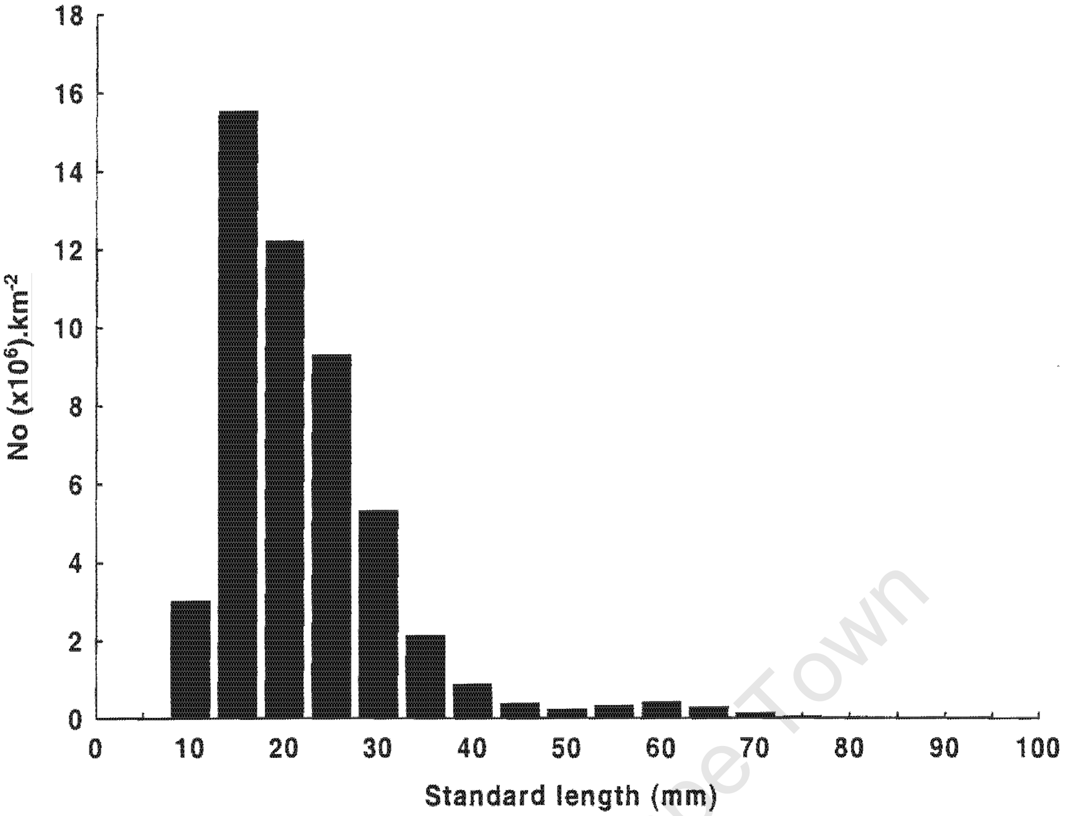

Figure 3.3. Length-frequency distribution (number in millions. km^{-2}) of Cape anchovy caught in Methot frame trawls during the pre-recruit survey in March 2000 off the west coast of South Africa. Frequencies were corrected to 16 March.

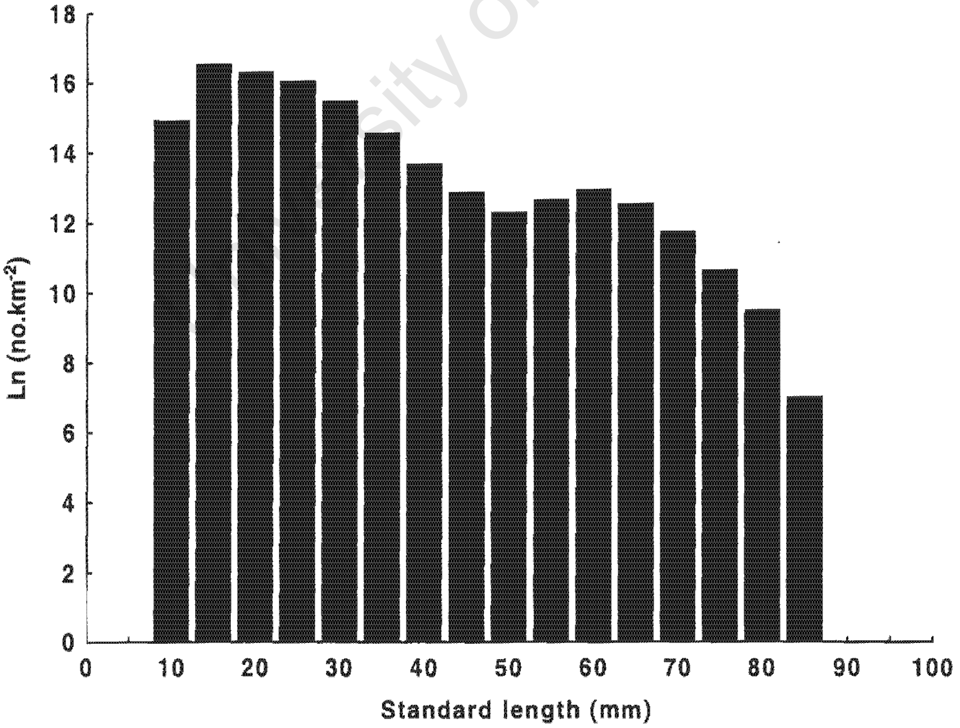

Figure 3.4. Natural log of numbers . km^{-2} at length of Cape anchovy caught in March 2000 during the pelagic pre-recruit survey off the west coast of South Africa. Frequencies were corrected to 16 March.

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The *age-length key* for larvae and pre-recruits caught during the pre-recruit survey in March 2000 (Table 3.1) roughly shows a normal distribution of lengths at most ages. The variability of catch-at-age was the highest at the 30-day age-class, with Baird's index of variation (*BIV*) at this age being 18 % and decreasing with increasing age afterwards. Since all *BIV* are below 20 %, the sample sizes taken are also the optimal sample sizes (see section 2.2.2).

Table 3.1. Age-length key and Baird's index of variation (*BIV*, %) at age of Cape anchovy caught off the west coast of South Africa in March 2000.

SL	Age (days)													
(mm)	**15**	**30**	**45**	**60**	**75**	**90**	**105**	**120**	**135**	**150**	**165**	**180**	**195**	**SUM**
10	9	3												**12**
15	14	30	3											**47**
20	2	20	13	1										**36**
25		1	7	18	4									**30**
30			2	8	5	2	1							**18**
35			1		5	4	1							**11**
40					1	1	2	1	1					**6**
45					1	2	1	2	1					**7**
50							1	1	2					**4**
55							2	2	1	1				**6**
60						1		1	3	1	1			**7**
65								1	1	1	1			**4**
70											2	2	1	**5**
SUM	25	54	26	27	16	10	8	8	9	3	4	2	1	193
BIV, %	14.4	17.9	14.8	10.6	8.85	5.72	4.38	2.47	2.48	1.20	1.07	0.34	0.28	

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The *age-frequency distribution* of larvae and pre-recruits sampled in March 2000 showed a distinct mode at 30 days decreasing exponentially towards 195 days (Fig. 3.5). The range of hatching dates was thus from the 1 March to 18 September. The mode corresponds to the 15 February (Fig. 3.5).

Fitting a regression line to the natural log of the catch-at-age between 30 and 165 days, gave an instantaneous natural *mortality rate* (*Z*) of 0.0353.day^{-1} ($r^2 = 0.98$, Fig. 3.6). The mean survival rate (e^{-Z}) for fish aged 30-165 days was thus 0.965.day^{-1}.

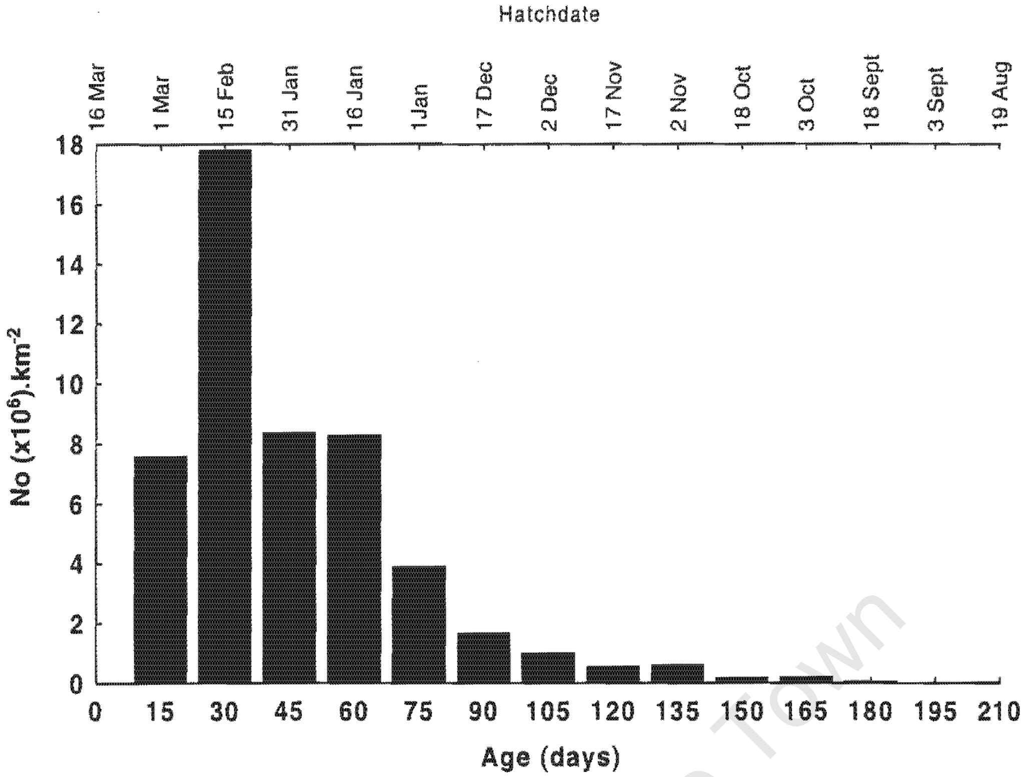

Figure 3.5. Number (in millions).km^{-2} at 15-day age-classes of Cape anchovy caught in March 2000 off the west coast of South Africa. Corresponding hatchdates (cruise mid-date less age) are presented on the second x-axis.

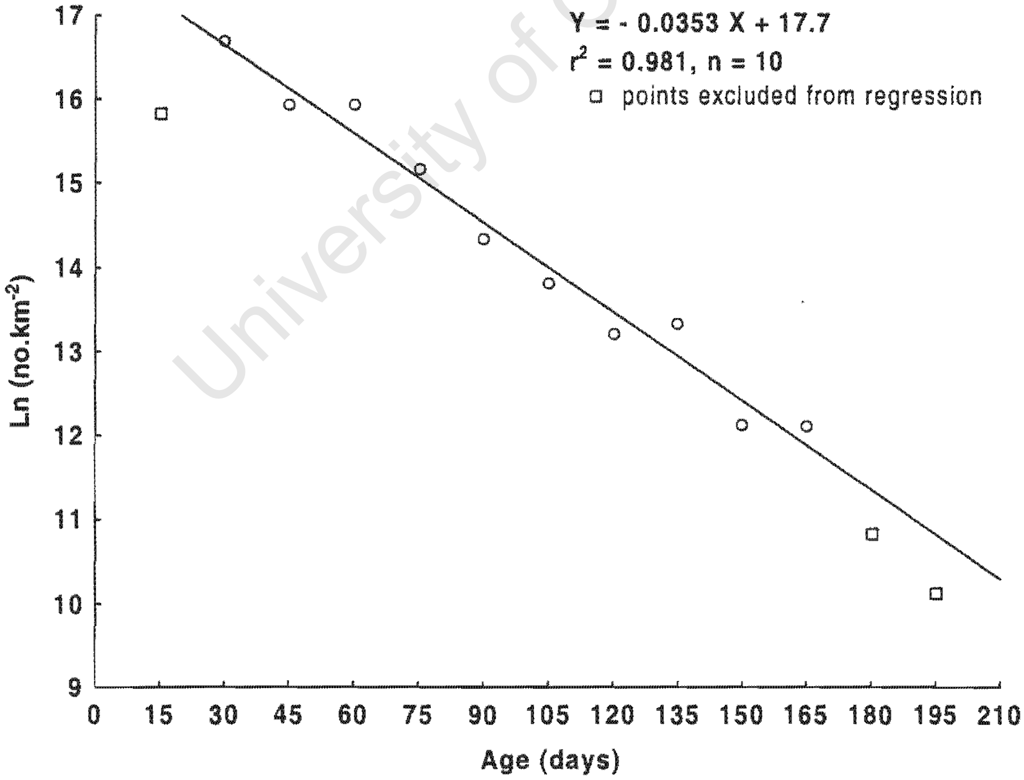

Figure 3.6. Natural log of number.km^{-2} against age in days of Cape anchovy caught in March 2000 off the west coast of South Africa. Apparent instantaneous natural mortality rate (Z) is calculated from the linear equation, $Y = Z.X + C$.

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The larval *hatchdate distribution* (after correction for mortality using a value of $0.0353.\text{day}^{-1}$ for fish <165 days and $0.0202.\text{day}^{-1}$ (see later) for fish ≥ 165 days), comprising the period from 20 August 1999 to 1 March 2000, showed a fairly flat distribution throughout, with slight bimodality shown by increased frequencies in late September-late October 1999 and late December/January-early February 2000 (Fig. 3.7).

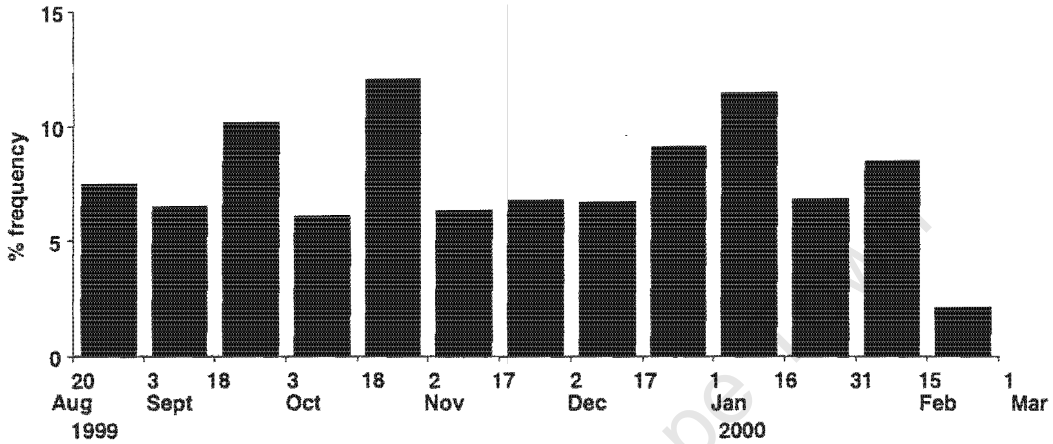

Figure 3.7. Hatchdate distributions of Cape anchovy caught in March 2000 off the west coast of South Africa. Distributions were adjusted for mortality (Z): <165 days: 0.0353 and ≥ 165 days: $0.0202.\text{day}^{-1}$.

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3.3. Juvenile recruits caught in May 2000

The *length-frequency distribution* of juveniles caught on the recruit biomass survey in May 2000 showed a normal distribution of lengths in 21 SL-classes with one mode between 75 and 80 mm SL (Fig. 3.8). Frequency is presented in total number weighted according to acoustic estimates from the recruit biomass survey and raised to the 30 May 2000 (see sections *2.2.1.2* and *2.5.1.2*). The natural log of the same number against length (Fig. 3.9) shows that the seemingly bimodal length-distribution seen in larval and pre-recruit distributions in March 2000 (see Fig. 3.4) had smoothed out in May (Fig. 3.9).

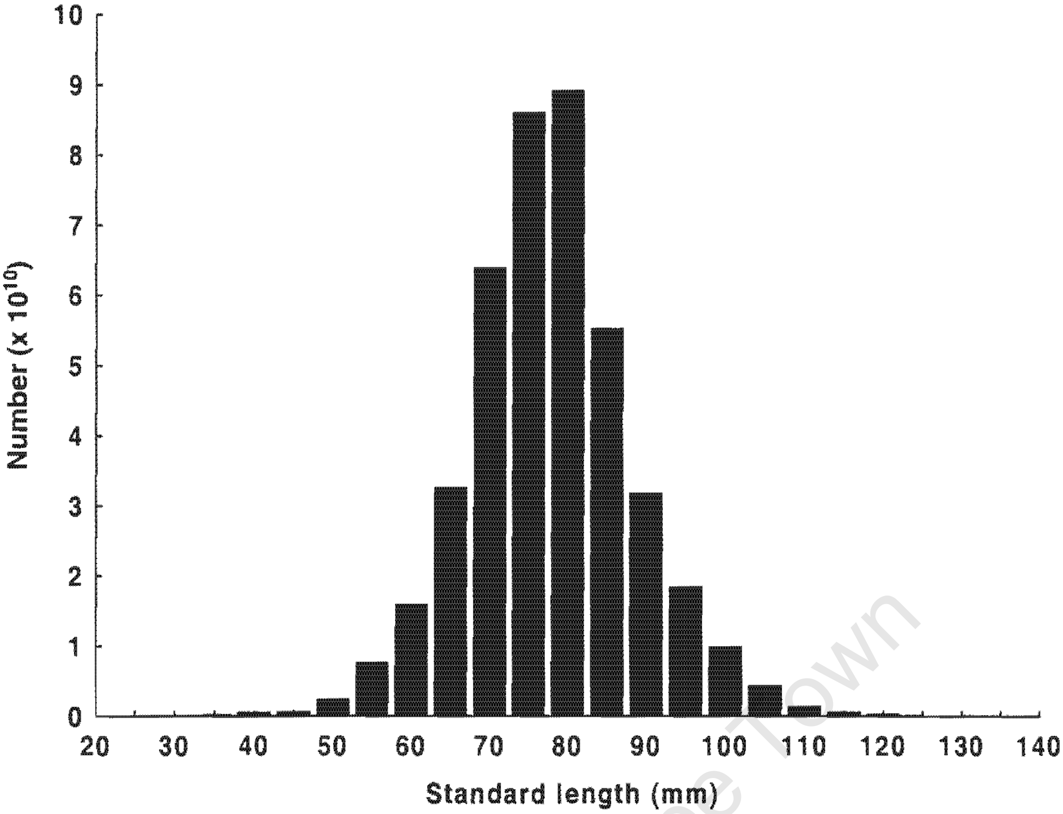

Figure 3.8. Acoustic weighted length frequency distribution, raised to 30 May 2000, of Cape anchovy caught on the recruitment survey in May 2000 off South Africa.

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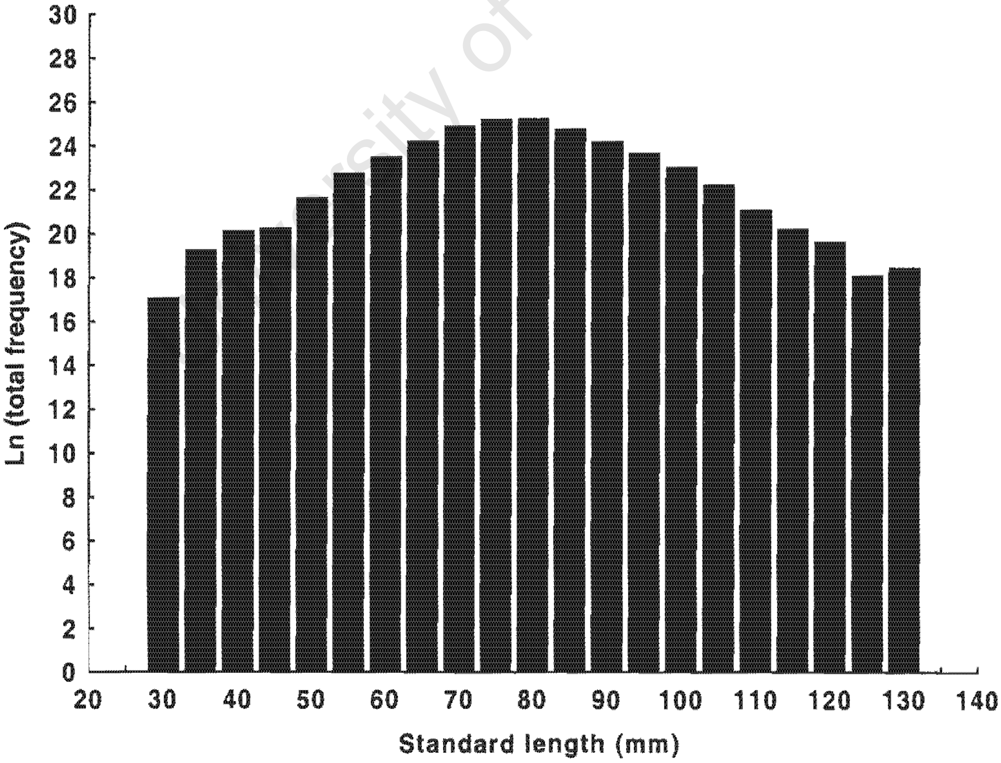

Figure 3.9. Natural log (Ln) of the frequency at length of Cape anchovy caught in May 2000 off the west coast and south coast of South Africa. Frequencies were corrected to 30 May.

The *age-length key* drawn up for juvenile recruits caught in May 2000 (Table 3.2) indicates that age-at-length for Cape anchovy was more variable in May 2000 than in March 2000. For example, the 5-mm-SL-class represents a range of 150 days in May as opposed to only 45 days in March (see Table 3.1). The number of sub-samples taken for ageing recruits caught in May was smaller than that taken from the larvae and pre-recruits caught in March 2000. Baird's index of variation (*BIV*) was up to four times higher from samples taken in May than that of samples taken in March (see Table 3.1) with the highest *BIV* in May being 82 % at age 210 days (Table 3.2). The optimal sample size (*"Opt SS"*, Table 3.2) calculated using this *ALK* represents the number of age sub-samples at each length-class that would stabilise *BIV* at circa 30 %. Any increase of sample sizes after this did not decrease the BIV significantly. Thus the aim of a 20 % *BIV* is not quite realised with the present ALK.

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Table 3.2. Age-length key and Baird's index of variation (*BIV, %*) at age of Cape anchovy caught off the west coast and south coast of South Africa in May 2000. *Opt SS* = Optimal Sample sizes: Sample size needed at each length to give a BIV of 20 %, calculated using this ALK.

SL	Age (days)																	Opt
(mm)	75	90	105	120	135	150	165	180	195	210	225	240	255	270	300	360	SUM	SS
30																	0	4
35	1	1	3														5	5
40			2	1													3	3
45				3	1												4	2
50				1	2	1	1										5	7
55						1	1	1									3	5
60				2	1			1									4	5
65			2		3	1	1										7	9
70			1	1	1	2	2	1	2				1				11	35
75			1	1			4	1	1		1						9	40
80			1	1		3		1	2			1					9	40
85				1				3		1	1		1				7	70
90						1	1					1			1		4	25
95							1	2		1							4	50
100									1			1	1	1			4	4
105																	0	4
110																1	1	4
SUM	1	1	10	11	8	9	11	10	6	2	2	3	3	1	1	1	80	308
BIV, %	0	0	0.70	0.86	1.5	0.74	0.82	65.3	59.9	82.2	64.0	68.2	56.1	0	0	0		

The *age-frequency distribution* of juveniles sampled in May 2000 shows three modes, the highest at 165 days, corresponding to the 17 December 1999 hatchdate (Fig. 3.10). Fitting a regression line to the natural log (*ln*) of the frequency against age (from the mode at 165 days), gave an *instantaneous mortality rate* (*Z*) of 0.0202.day^{-1} ($r^2 = 0.996$, Fig. 3.11). This corresponds to a survival rate of 0.980.day^{-1}or 2 % mean mortality per day.

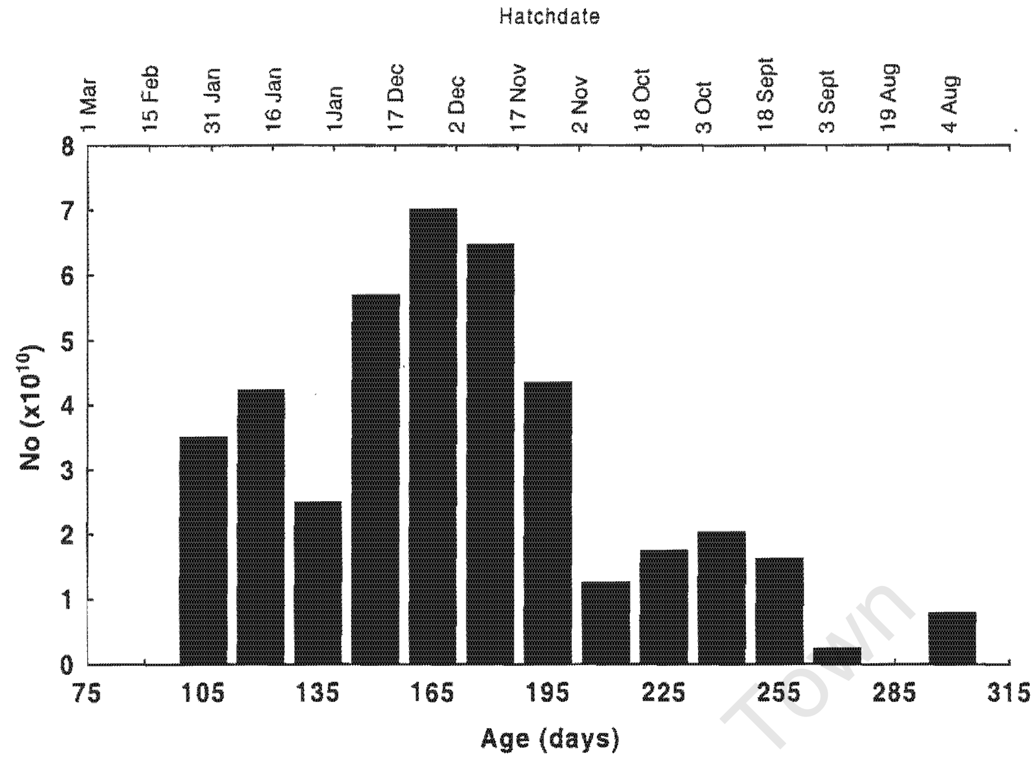

Figure 3.10. Total number of Cape anchovy at 15-day age-classes, caught in May 2000 off the west coast and south coast of South Africa. The second x-axis shows hatchdates (mid-cruise date less age in days) corresponding to each age.

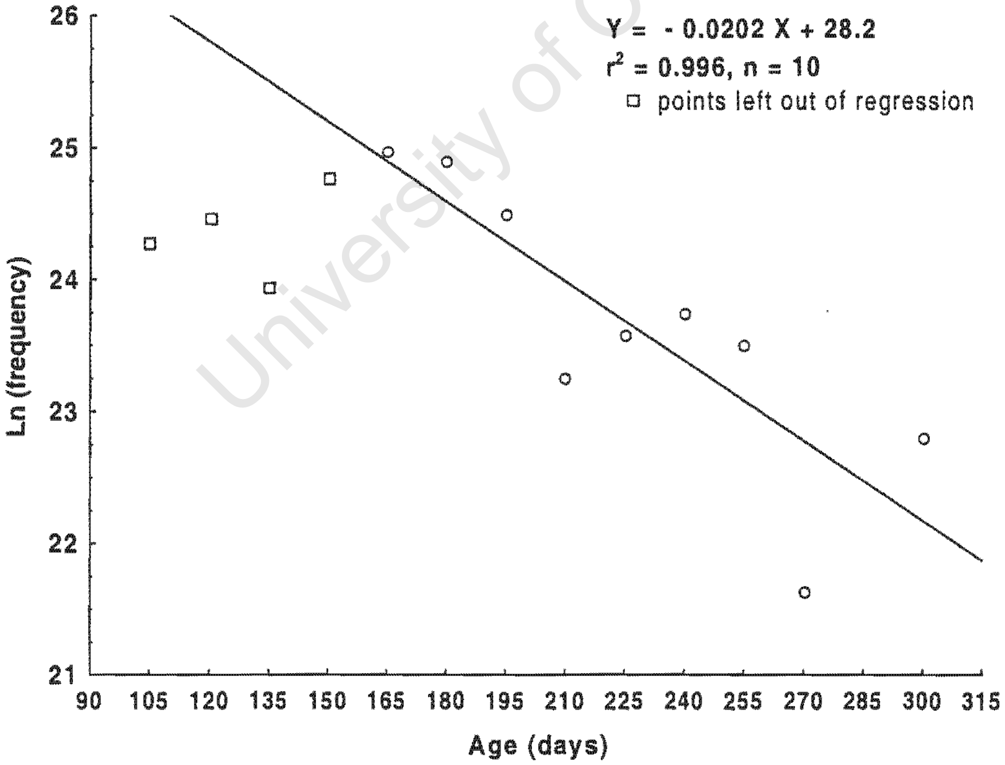

Figure 3.11. Natural log (*ln*) of frequency-at-age against age in days of Cape anchovy caught off the west coast and south coast of South Africa in May 2000. Instantaneous mortality rate (Z) is calculated from the linear regression, Y = Z X + C.

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The *hatchdate distribution* of juvenile Cape anchovy caught in May 2000 (corrected for mortality, <165 days: 0.0353 and ≥ 165 days: 0.0202.day^{-1}) shows bimodality with a mode between 2 November and 17 December 1999, and another mode between 3 September and 3 October 1999 (Fig. 3.12).

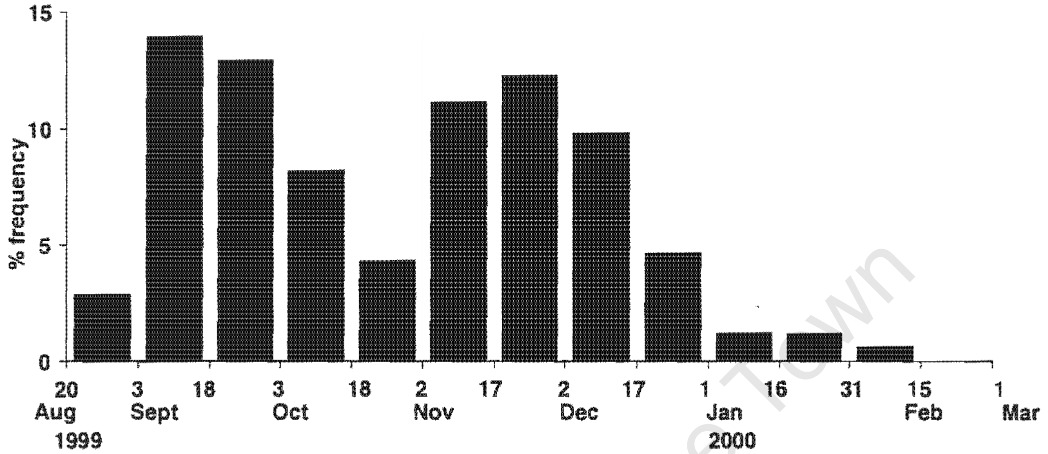

Figure 3.12. Hatchdate distribution of Cape anchovy caught in May 2000 off the west coast and south coast of South Africa. Distributions were adjusted for mortality: <165 days: 0.0353 and ≥ 165 days: 0.0202.day^{-1}.

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3.4. Evaluation of potential biases

The quality of the ageing results and the subsequent interpretation depends upon the quality of the collection and analysis of the samples. Limitations of sampling and analytical techniques may introduce biases into the data and may therefore influence their interpretation. Errors and biases can arise at three stages: during sampling, otolith preparation, and daily ring enumeration. Some of these problems are highlighted below:

3.4.1. Sampling and preparation

In general, the scanning electron microscope (SEM) method of preparing and reading otoliths was not very successful (25 % success rate). Thus, because of the poor success rate of otolith preparation, the expense and time involved in this method, based on this study, I recommend that in future studies the ageing of juvenile anchovy < 95 mm SL should be done using light microscopy. This method proved to be less time-consuming, less costly, and more successful (90 % success rate).

The variation of catch-at-age was higher for recruit samples than for pre-recruit samples (see *BIV* %, Tables 3.1 and 3.2), particularly for fish > 180 days. This is most probably due to the poorer success rate of otolith preparation for the SEM method, and therefore the smaller number of recruit age sub-samples. With increased success of otolith preparation for light microscopy, and using the thorough sampling method outlined in section *2.2.2* (see Table 3.2, Appendix 3.A), this sampling error could be minimized.

However, it seems that the calculated optimal sample size is dependent upon the age-length-key itself, seen from the difference between the optimal sample sizes from historical age-length keys (see Appendix 3.A) and from the age-length key in this study (see Table 3.2). Thus, the optimal sample size determined in this study will probably decrease as the age-length key is improved by adding samples. It is thus important to use the age-length key specific to the year-class in order to determine the age-distribution as well as the variability at age and the optimal sample size at length (Westrheim and Ricker 1978). This can be done using a pilot study on the year-class. An *ALK* could be drawn up using a smaller selective sample-size, (using proportional sub-sampling combined with length-based sub-sampling, see section *2.2.2* i. and ii.) covering the entire length-distribution of interest. *BIV* for each age should then be calculated in order to determine in which length-classes the sample sizes thereafter need to be improved, (section *2.2.2* iii.) as is presented here (Table 3.1 and 3.2).

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Reading ages on otoliths under the light microscope becomes more difficult with increasing age and size of the fish as otoliths get thicker and rings get more crowded on the otoliths. Therefore, for ageing the larger size-classes (> 95 mm SL) the SEM method would be appropriate, because of its greater magnification and resolution.

3.4.2. Age enumeration

The mean *CV* of ageing precision of repeated readings of larval and pre-recruit otoliths (8.6 %, see Fig. 3.1) and of second and third counts on juvenile otoliths (11.8 %, see Fig. 3.2) showed that these age readings were repeatable. Based on reviewed literature, the median *CV* of all ageing studies was 7.6 %, the most frequently reported age enumeration *CV* for otolith studies was 5 %, and the mean *CV* for daily otolith readings was 9 % with 95 % of all reported *CV*s ranging between 6 % and 12 % (Campana 2001).

The *CV* of the first and second age readings on otoliths of juvenile anchovy (see Fig. 3.2) may be a cause for concern. However, the decrease in CV from the second and third readings showed that a reader is able to improve on the ageing precision with experience as well as using image analysis software such as *OPTIMAS* (Optimas corporation 1997). This also emphasizes the importance of building up otolith libraries, in order for readers to be consistent in long-term studies (Campana 2001). The *CV* did not increase with increasing age, showing that ageing precision was unbiased with respect to age (see Figs. 3.1 and 3.2).

The decrease in ageing precision (increase in *CV*) from light micrograph to SEM micrograph increment enumeration (see Figs 3.1 and 3.2) may be a reason why age-at-length is more variable of juvenile recruits caught in May than that of larvae and pre-recruits of the same length caught in March 2000 (see Tables 3.1 and 3.2).

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3.5. Assumptions underpinning mortality rate estimates

Three key assumptions underlie mortality estimates from field samples:

1) There is a stable age distribution, i.e. the abundance of several batches of fish at one moment is representative of one cohort as it ages through time (Lo *et al.* 1989). Because spawning happens continuously (Alheit 1989, Melo 1994b), the difference in numbers of individuals between consecutive age-classes is, in reality, the difference between mortality and numbers added by hatching within that period. We are assuming that spawning happened at equal intensity at each 15-day age-class, and that the decrease in abundance over time is only due to mortality. This may not be the case, especially in the juvenile age-distribution, in which three modes are visible (see Fig. 3.10). There may be two reasons for these modes: a) spawning may have increased over those periods, i.e. they are actually sub-cohorts or b) the three modes are simply an artifact of sampling intensity, or variability around the particular age-classes. This second reason appears likely, hence it is appropriate to calculate an overall average mortality. Apart from this, there were too few data points to calculate an average mortality for each 'sub-cohort', and hence the overall average was preferred.

2) Another assumption is that the survey area covers the whole range of the stock. There may be problems with fish appearing/disappearing from the *unit stock* due to migration out of the survey area (Vetter 1988). Also, the survey areas and methods used for the two surveys are different (see Tables 2.1 and 2.2); hence, we should view the indices as relative indices when comparing the two surveys, and not absolute indices of abundance. Because the survey areas and methods, and absolute indices of abundance, were not comparable, calculations of overall annual mortality for sub-cohorts from one survey to the next was not possible.

3) It is assumed that the fish counted and measured on the surveys are counted in proportion to their true abundance (Lo *et al.* 1989). The net retention and catchability of each length-class influences the number caught in that class. Escapement (the passage through the mesh aperture), extrusion (the forcing of fish through the mesh) and evasion (the swimming of fish out of the volume of water to be filtered) (Smith 1981) need to be considered. All of these are size-dependent, and will differ between the two methods (Methot trawls and Engels 308 midwater trawls) used to sample larval and juvenile fish in this study (Smith 1981). Efficiency of the two sampling methods is discussed below.

3.5.1. Methot net sampling efficiency

The Methot frame trawl is designed to sample selectively for 15–60 mm SL anchovy (Methot 1986). Pre-recruit surveys in South Africa are conducted in March in order to get an indication of relative abundance of late larvae and pre-recruits - as possible contributors to, and predictors of, recruitment strength in May/June the same year (O'Toole and Hampton 1989, van der Lingen and Merkle 1999). The mesh size of the inner net lining of the Methot sampler is 5.0 mm (O'Toole and Crous 1989), and targets 25–60 mm long anchovy (O'Toole and Hampton 1989). No larvae < 10.0 mm have been caught in the Methot net (Fig. 3.3; see also van der Lingen and Merkle 1999); thus it appears that anchovy of size-classes < 10 mm SL escape the net. Larvae at the 10-mm-SL-class, because of their low abundance in relation to larger size-classes, are probably partially extruded, especially during long vertical tows and in bad weather (Smith 1981).

Since this study is aimed at comparing the age-structure of Cape anchovy at the time of the pre-recruit survey to that at the time of the recruit biomass survey, the main concern is whether the two sampling methods show comparable retention and catchability at overlapping size-classes (35–100 mm SL, see Figs. 3.3 and 3.8). Results of a trial survey by O'Toole and Hampton (1989) showed that catches from Methot frame trawls and Engels 308 midwater trawls targeted at near-surface shoals of "*post-larvae and juveniles*", had very similar size-distribution ranges of young anchovy. Slight differences were evident between the relative abundance of the modal length-class (25 mm SL). The Engels 308 midwater trawl samples showed a relative abundance of 30 % and Methot trawl samples showed 50 % of all catches found at that length-class. This may suggest that the Engels midwater trawl net was under-sampling fish of 25 mm SL relative to the Methot trawl net. However, in view of the similar abundance of catches at size-classes above and below 25 mm SL, the difference in relative abundance at 25 mm SL is probably caused by the greater efficiency of the Engels midwater trawl net of sampling fish in the 40–60 mm SL-classes. Fish in these size classes constituted 6 % and 15 % in Methot net and midwater trawl catches respectively (O'Toole and Hampton 1989).

Cape anchovy larvae > 6.5 mm SL have been shown to avoid plankton nets during daylight hours. Avoidance increases with larval length (Badenhorst and Boyd 1980). Larger fish, probably ≥ 40 mm SL, tend to avoid the Methot net because of a slower towing speed and smaller mouth width than the Engels 308 midwater trawl net (van der Lingen and Merkle 2000). However, these fish are still caught, thus do not seem to completely avoid the Methot net as they are able to avoid a smaller bongo net (Clarke 1983).

To test for comparable retention and catchability one would need to examine Engels midwater trawl net:Methot net catch-ratios. To my knowledge, catchability and retention rates have not been calculated for the Methot net, and I could not use the correction factors of Somarakis *et al.* (1998), for example, because they were suggested for plankton nets and used night to daylight catch ratios. All Methot trawls in this study were done at night. The catchability of anchovy in Methot and Engels midwater trawl nets was thus assumed to be comparable. However, the abundance of pre-recruits ≥ 40 mm SL may be under-estimated, because data indicate that ancchovy at these larger size classes are not caught with 100 % efficiency by the Methot net. This undersampling of larger size classes will lead to a slight over-estimation of pre-recruit mortality rates; nevertheless examination of

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abundance at age against age of anchovy collected during the pre-recruit survey (Fig. 3.6) suggests that excluding data points ≥ 40 mm SL is unlikely to have substantial effect on the slope of the graph, although it will reduce the number of usable data points markedly. Mortality was therefore estimated between 30 and 165 days (see Fig. 3.6). Ages 180 days onwards are probably under-estimated because of a) the increased escape rate from the Methot net and b) the absence of age sub-samples from > 70 mm SL-classes (Table 3.1).

3.5.2. Engels 308 midwater trawl net sampling efficiency

The SL-distributions drawn up from Engels 308 midwater trawl samples and acoustic estimates done on recruit biomass surveys in different years differed widely. The bimodal SL-distributions in 1992 and 1996 with the first modes at 45 and 55 mm SL are particularly interesting (Barange *et al.* 1999). They indicate that when smaller size-classes were present in abundance, they were also caught in abundance by the Engels midwater trawl net. This is also shown by the mode of frequency at 50 mm SL in 1993 (Barange and Hampton 1997). In view of these data, and O'Toole and Hampton's (1989) comparative study, I assumed that there was no under-sampling of size-classes ≥ 35 mm SL by the Engels midwater trawl net, (i.e. ≥ 105 days, see Table 3.2). Mortality rates were calculated only for ages ≥ 165 days, because 165 days was the mode of the age-distribution (Beverton and Holt 1957).

At the larger size-classes of recruits, age under-sampling rather than net avoidance is a problem, as I have only aged one sample in age-classes >100 mm SL (see Table 3.2) due to difficulty of preparation and reading of samples. However, fish larger than 100 mm SL (1.63 % of catches) are considered as adults rather than 0-year-old recruits (Barange *et al.* 1999). This is also illustrated by the 110 mm SL sample aged 360 days (see Table 3.2), which usually approximately coincides with an *annulus* (Waldron 1994, 1998). Hence, fish in length-classes ≥ 100 mm SL were assumed to be 1-year-olds and thus not part of the 1999/2000 year-class.

Few samples were successfully prepared and read at size-classes ≤ 40 mm and ≥ 95 mm SL, hence age-classes 75 and 90 days, and 270 days onwards, only had one sample present in each (see Table 3.2). Age-classes between 105 and 255 days were therefore considered representative.

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CHAPTER FOUR

GROWTH RATES OF LARVAL AND JUVENILE CAPE ANCHOVY CAUGHT IN 2000

This chapter provides results from otolith analysis on larval Cape anchovy sampled in March 2000 and juvenile Cape anchovy sampled in May 2000:

1) The relationships between otolith size, standard length and age and
2) Estimates of daily growth rates of larvae (March) and juveniles (May) separately as well as overall growth in the field in 2000.

A brief discussion on potential biases is included.

4.1. Otolith radius – fish length relationships

The relationship between otolith radius and number of increments from Cape anchovy larvae and pre-recruits collected on the west coast of South Africa in March 2000 is well described by a power function ($r^2 = 0.87$, n = 168, $p < 0.0001$; Fig. 4.1).

Another power function was used to describe the relationship between otolith radius and standard length (corrected for shrinkage after Theilacker 1980) of larval and pre-recruit anchovy caught in the southern Benguela in March 2000 ($r^2 = 0.97$, n = 184, $p < 0.0001$; Fig. 4.2). According to these two relationships, a larva with one increment should have an otolith radius of 0.29 μm and a standard length of 1.3 mm.

This otolith radius – number of increment relationship seems to have inverted for juvenile recruits caught in May 2000, being a power function with an exponential less than one ($r^2 = 0.59$, n = 52, $p < 0.001$; Fig. 4.3). The relationship between live standard length and otolith radius of juveniles caught in May 2000 was described by a power function ($r^2 = 0.60$, n = 52, $p < 0.001$; Fig. 4.4).

The correlations are good enough to back-calculate growth rates from increment widths.

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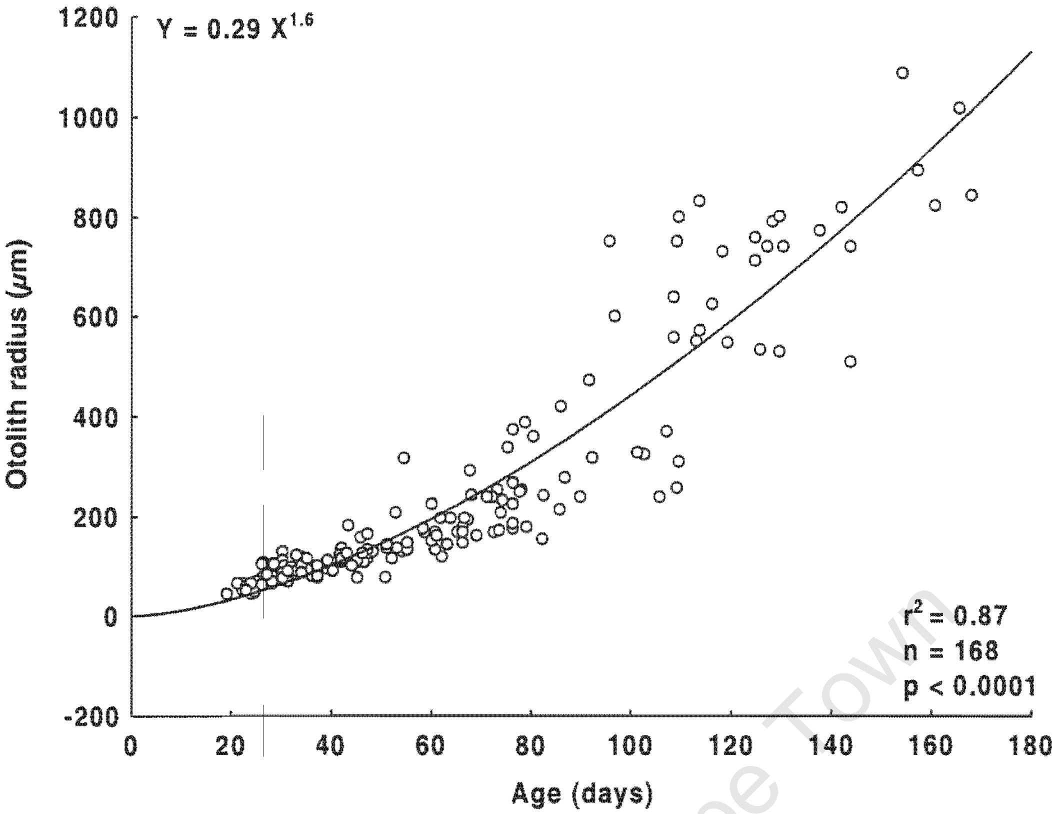

Figure 4.1. Relation between the otolith radius and the age in days of Cape anchovy larvae and pre-recruits caught off the west coast of South Africa in March 2000.

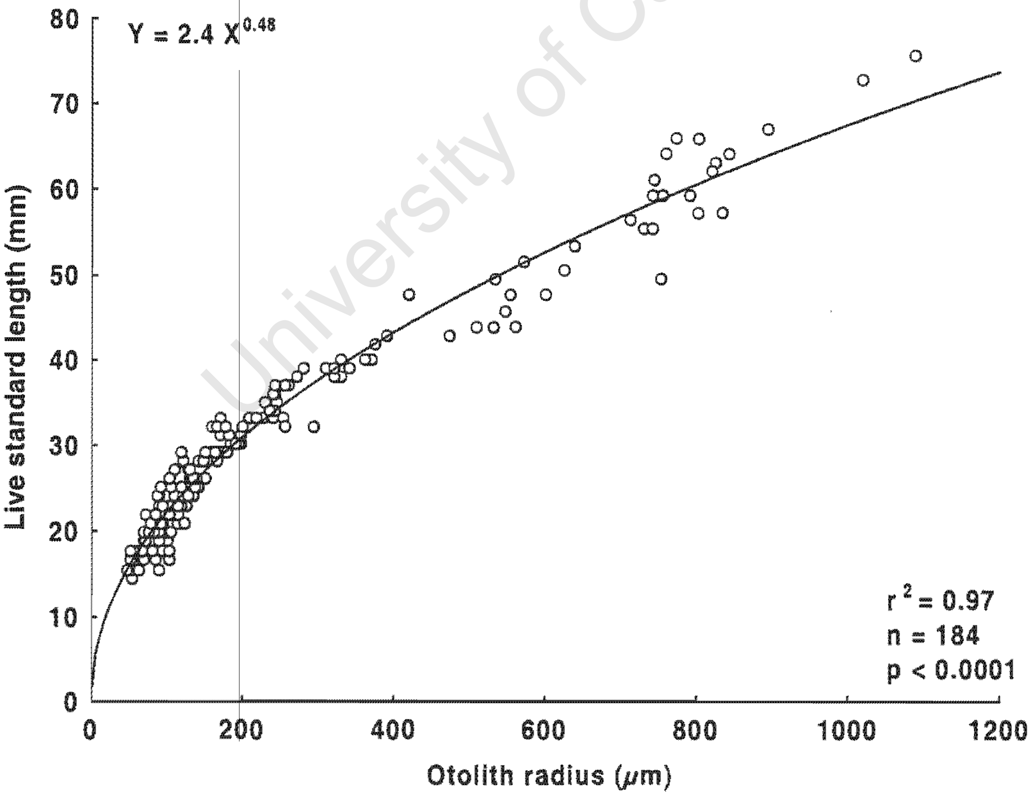

Figure 4.2. Relation between standard length and otolith radius of Cape anchovy larvae and pre-recruits caught off the west coast of South Africa in March 2000.

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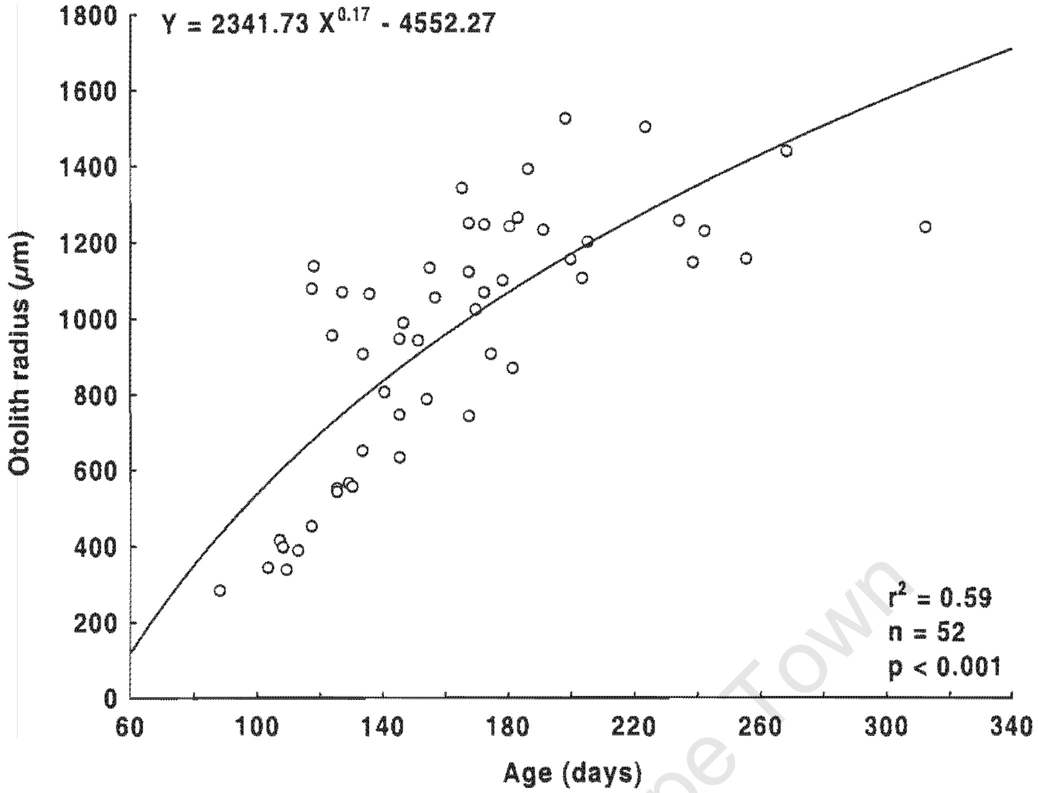

Figure 4.3. Relation between the otolith radius and age on otoliths of juvenile anchovy caught on the May 2000 recruit biomass survey off the west and south coasts of South Africa.

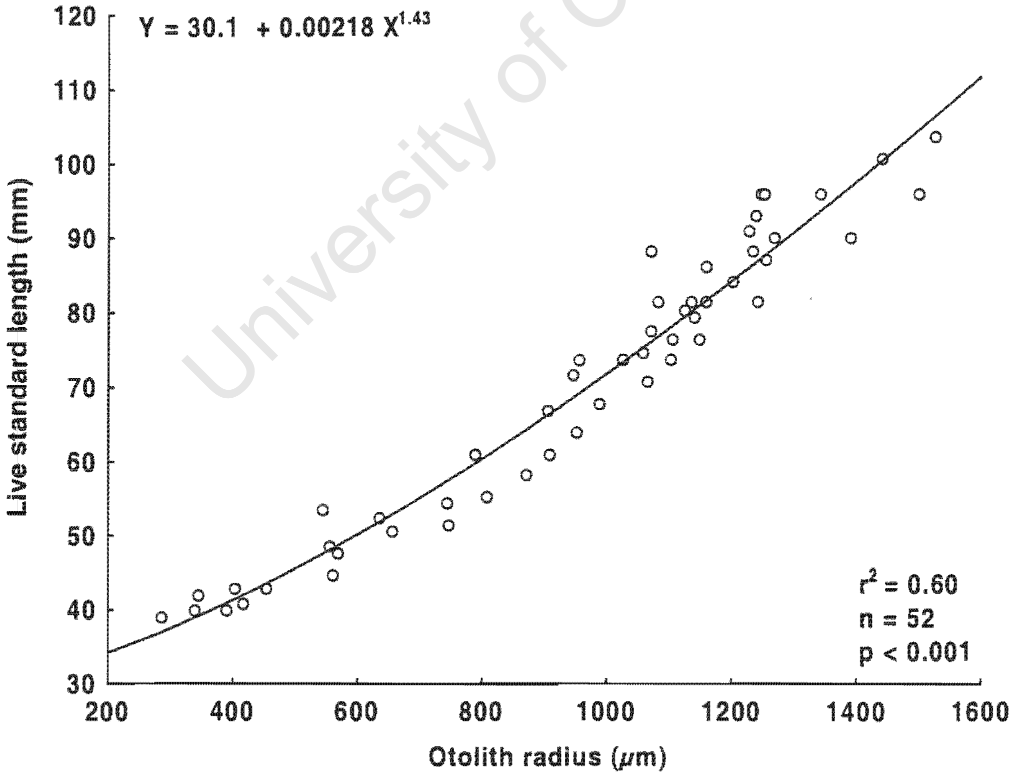

Figure 4.4. Relation between standard length and otolith radius of Cape anchovy juveniles caught off the west and south coasts of South Africa in May 2000.

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4.2. Larval and pre-recruit growth – from hatching to pre-recruit stage

The live standard length (SL) of larvae and pre-recruits caught in March 2000 ranged from 14.0 to 75.5 mm and their ages ranged between 19 and 201 days. The three growth models used to describe anchovy larval and pre-recruit growth in 2000 were all highly significant at $p < 0.00005$ (Fig. 4.5, Table 4.1).

The linear model yielded a daily growth rate of 0.36 $mm.day^{-1}$ ($n = 193$, $r^2 = 0.90$). The Laird-Gompertz model yielded a mean daily growth rate of 0.35 $mm.day^{-1}$ ($n = 193$, $r^2 = 0.90$). When the VBGF was fitted using the residual sum of squares method, the asymptotic length l_∞ was estimated at 477 mm. However, because the maximum length of anchovy caught off South Africa is only 140 mm (Barange *et al.* 1999), a VBGF was fitted, fixing l_∞ at 140 mm. This yielded a mean daily growth rate of 0.33 $mm.day^{-1}$ ($n = 193$, $r^2 = 0.89$).

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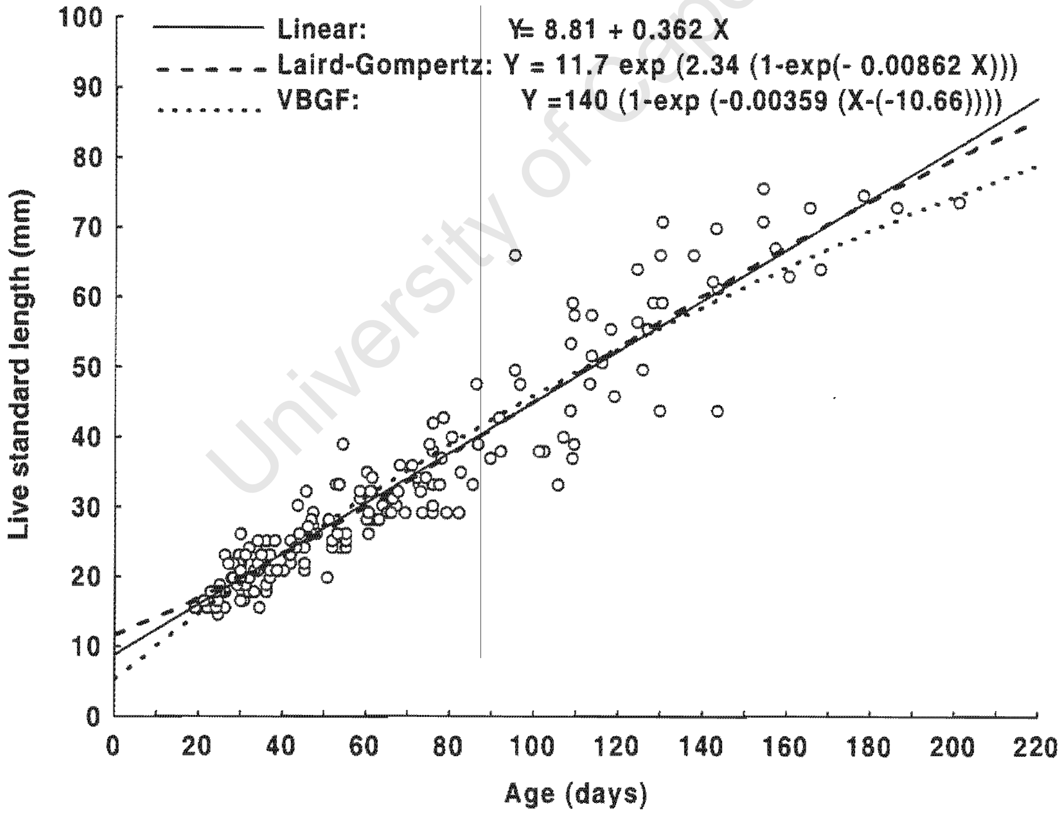

Figure 4.5. Standard length against age in days of larval and pre-recruit Cape anchovy sampled in March 2000. Models used to describe anchovy growth: Linear model (solid line), Laird-Gompertz model (dashed line), and von Bertalanffy model, VBGF (dotted line). Lengths are corrected for shrinkage. Basic statistics for each model are shown in Table 4.1.

Table 4.1. Three growth models fitted to data for Cape anchovy collected in March 2000 on the West coast of South Africa. G = growth rate (mm.day^{-1}), t = age in days, RSS = residual sum of squares, r^2 = coefficient of determination.

Larvae and Pre-recruits	Model	Parameters	RSS	r^2	P-level
Linear	$l_t = l_0 + Gt$	$l_o = 8.81$	4421	0.899	0.000000
		$G = 0.362$			0.000000
Laird-Gompertz	$l_t = l_0\ exp\ (C\ (1\text{-}exp\ (\text{-}at)$	$l_o = 11.7$	4317	0.902	0.000000
		$C = 2.34$			0.000000
		$a = 0.00862$			0.000000
Von Bertalanffy	$l_t = l_\infty(1\text{-}exp\ (\text{-}K\ (t\text{-}t_0)))$	$l_\infty = 140$, fixed	4758	0.891	
		$K = 0.00359$			0.000000
		$t_o = -10.7$			0.000056

4.3. Juvenile growth - from pre-recruit to recruitment stage

A smaller percentage of the variation in length is explained by age for the curves used to describe juvenile growth than larval growth (Table 4.2). Juvenile Cape anchovy, between 88 and 318 days old in May 2000, were growing at an average of 0.24 mm.day^{-1} according to the linear growth model ($n = 80$, $r^2 = 0.45$, $p < 0.00005$; Fig. 4.6, Table 4.2).

The Laird-Gompertz model yielded a mean growth rate of 0.22 mm.day^{-1}, with a maximum instantaneous growth rate of 0.44 mm.day^{-1} at age 88 days ($n = 80$, $r^2 = 0.48$, $p < 0.0000005$; Fig. 4.6, Table 4.2).

The VBGF had a gentler slope than the Laird-Gompertz model towards a fixed asymptotic length of 140 mm (Fig. 4.6). It yielded a mean daily growth rate of 0.24 mm.day^{-1} between 88 and 318 days, with a maximum instantaneous growth rate of 0.37 mm.day^{-1} at age 88 days ($n = 80$, $r^2 = 0.47$, $p < 0.00005$; Table 4.2).

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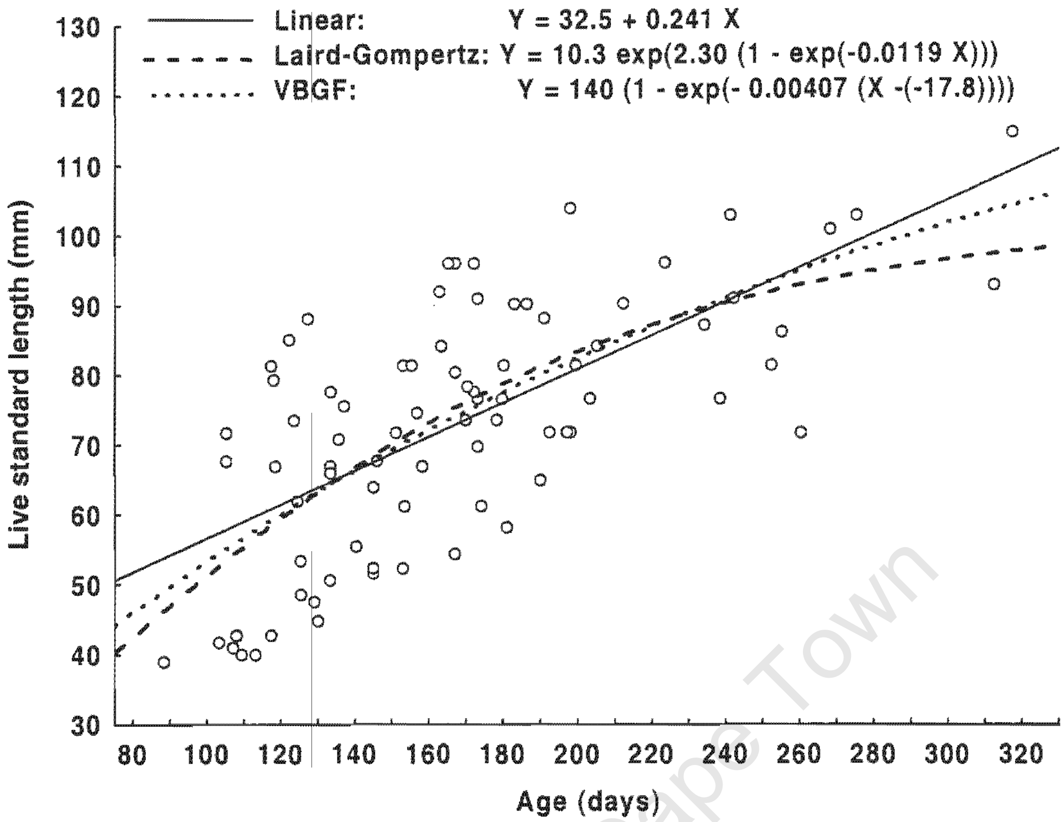

Figure 4.6. Models used to describe growth of juvenile Cape anchovy sampled in May 2000. Standard length vs. age in days: linear model (solid line), Laird-Gompertz model (dashed line), and von Bertalanffy model, VBGF (dotted line). Lengths are corrected for shrinkage. Basic statistics for each model are shown in Table 4.2.

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Table 4.2. Three growth models fitted to data for juvenile Cape anchovy collected in May 2000 on the West coast of South Africa. G = growth rate (mm.day^{-1}), t = age in days, RSS = residual sum of squares, r^2 = coefficient of determination.

Juveniles	Model	Parameters	RSS	r²	P-level
Linear	$l_t = l_0 + Gt$	$l_o = 32.5$	13436	0.452	0.00000
		$G = 0.241$			0.000013
Laird-Gompertz	$l_t = l_o\, exp\ (C(1\text{-}exp(\text{-}at)$	$L_o = 10.3$	12862	0.475	0.00000
		$C = 2.30$			0.00000
		$a = 0.0119$			0.00000
Von Bertalanffy	$L_t = L_\infty(1\text{-}exp(\text{-}K(t\text{-}t_0)))$	$L_\infty = 140$, fixed	12974	0.471	
		$K = 0.00407$			0.000047
		$t_0 = \text{-}17.8$			0.014

4.4. Mean growth in 2000 - from hatching to recruitment stage

Growth functions fitted to the combined data of March and May surveys (14–114 mm SL) yielded similar results to the larval growth curves (Fig. 4.7, Table 4.3). The linear growth model yielded an average growth rate of 0.36 mm.day^{-1} (n = 273, $r^2 = 0.81$, $p < 0.000005$; Fig. 4.7, Table 4.3), and a length at first ring deposition, l_1, of 6.4 mm (Table 4.4).

The Laird-Gompertz model yielded an average growth rate of 0.29 mm.day^{-1} between ages 1 and 318 days (n = 273, $r^2 = 0.89$, $p < 0.0000005$; Fig. 4.7, Table 4.3) with a maximum instantaneous growth rate of 0.43 mm.day^{-1}, between 74 and 94 days, and l_1 of 10.2 mm (Table 4.4).

The von Bertalanffy growth function, VBGF yielded a mean growth rate of 0.31 mm.day^{-1} (n = 273, $r^2 = 0.88$, $p < 0.1$; Fig. 4.7, Table 4.3) and a maximum instantaneous growth rate of 0.58 mm.day^{-1} at day 1; $l_1 = 2.27$ mm SL (Table 4.4).

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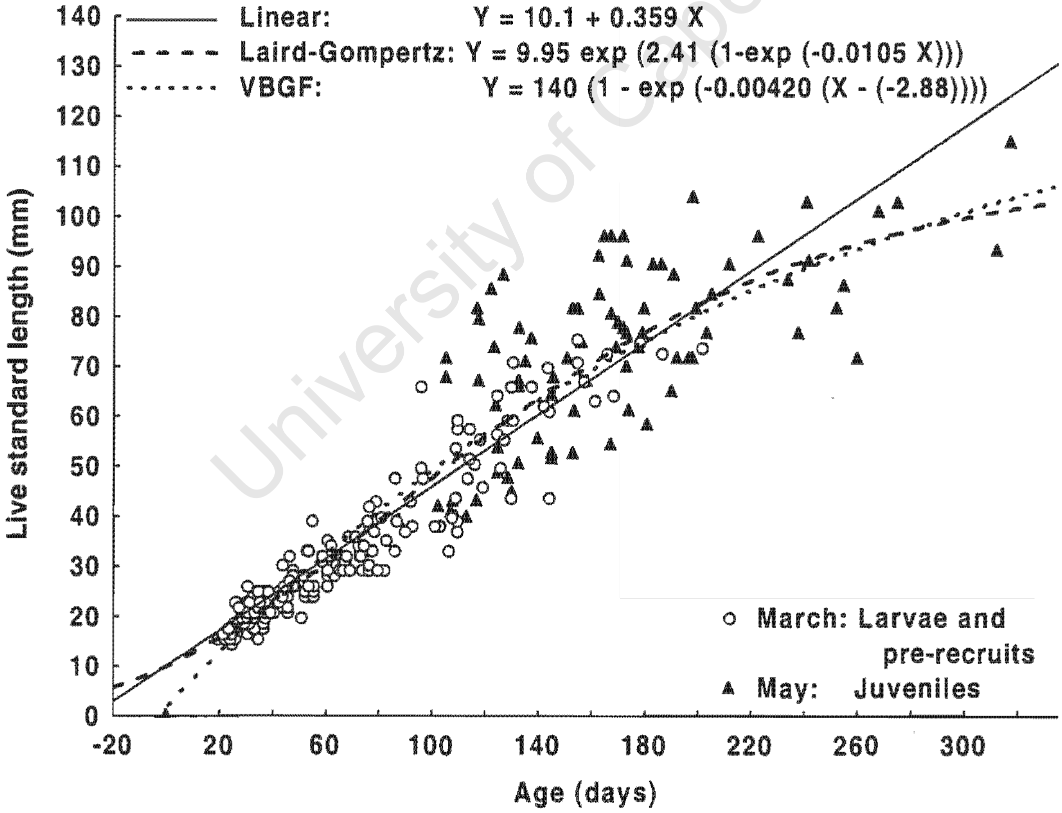

Figure 4.7. Models used to describe overall growth of the 1999/2000 Cape anchovy year-class. Circles represent anchovy caught in March 2000; triangles represent anchovy caught in May 2000. Standard Length vs. age in days: linear model (solid line), Laird-Gompertz model (dashed line), and von Bertalanffy model, VBGF (dotted line). Lengths are corrected for shrinkage. Basic statistics for each model are shown in Table 4.3.

Table 4.3. Three growth models fitted to length vs. age data for larval through juvenile Cape anchovy 1999/2000 (14–114 mm SL) collected on the West and South coast of South Africa over the entire early growth season 2000. G = growth rate (mm.day^{-1}), t = age in days, RSS = residual sum of squares, r^2 = coefficient of determination.

Model		Parameters	RSS	r²	P-level
Linear	$l_t = l_o + Gt$	$l_o = 6.00$	21264	0.811	0.000000
		$G = 0.359$			0.000006
Laird-Gompertz	$l = l_o\ exp\ (C(1\text{-}exp(\text{-}at)$	$l_o = 9.95$	18295	0.887	0.000000
		$C = 2.41$			0.000000
		$a = 0.0105$			0.000000
von Bertalanffy	$l = l_\infty(1\text{-}exp(\text{-}K(t\text{-}t_o)))$	$l_\infty = 140$, fixed	19420	0.881	
		$K = 0.00420$			0.000000
		$t_o = \text{-}2.88$			0.055

Table 4.4. Estimated mean standard length (SL) and instantaneous growth rate (G) at age of Cape anchovy, caught in the southern Benguela system in March and May 2000, from three growth equations. VBGF = von Bertalanffy growth function. See Fig. 4.7 and Table 4.3 for model equations.

	Linear model		Laird-Gompertz model		VBGF	
Age (days)	SL (mm)	G (mm.day^{-1})	SL (mm)	G (mm.day^{-1})	SL (mm)	G (mm.day^{-1})
1	6.4	0.36	10.2	0.26	2.27	0.58
15	11.4	0.36	14.1	0.30	10.1	0.55
30	16.8	0.36	19.1	0.35	18.1	0.51
45	22.2	0.36	24.7	0.39	25.5	0.48
60	27.6	0.36	30.7	0.41	32.5	0.45
75	32.9	0.36	37.0	0.43	39.1	0.42
90	38.3	0.36	43.4	0.43	45.2	0.40
105	43.7	0.36	49.8	0.42	51.0	0.37
120	49.1	0.36	55.9	0.40	56.5	0.35
135	54.5	0.36	61.8	0.38	61.6	0.33
150	59.9	0.36	67.2	0.35	66.3	0.31
165	65.3	0.36	72.3	0.32	70.8	0.29
180	70.7	0.36	76.9	0.29	75.1	0.27
195	76.0	0.36	81.1	0.26	79.0	0.26
210	81.4	0.36	84.8	0.24	82.8	0.24
225	86.8	0.36	88.1	0.21	86.3	0.23
240	92.2	0.36	91.1	0.18	89.5	0.21
255	97.6	0.36	93.6	0.16	92.6	0.20
270	103.0	0.36	95.9	0.14	95.5	0.19
285	108.4	0.36	97.9	0.12	98.2	0.18
300	113.8	0.36	99.6	0.11	100.8	0.17
315	119.1	0.36	101.1	0.093	103.2	0.16
Mean		**0.36**		**0.29**		**0.31**

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4.5. Evaluation of potential biases

Biases for sampling, otolith preparation and ring enumerations have been discussed in section *3.4.* Some biases may also occur when estimating growth rates in particular. Cape anchovy at the normal time of first-feeding, 2–3 days after hatching (King *et al.* 1978), may delay deposition of growth increments until food is provided and growth is continued (Methot and Kramer 1979). Because larvae are only about 3.7 mm SL when the first ring appears (King *et al.* 1978), estimates of the growth rates of larger larvae will not be affected (Methot and Kramer 1979). Since I only studied growth of larvae from 14 mm SL onwards, this is unlikely to have affected my estimates of growth rates.

Methot and Kramer (1979) found that increment formation slows down at very low temperatures and seriously reduced rations and can even stop at times. If length is plotted against number of increments, as opposed to true age, this will overestimate the growth rate. But since the temperatures from October 1999 to March 2000 were unusually high in the Benguela system (Roy *et al.* 2001b), I would not expect this particular problem to affect the age estimates of anchovy hatched in the 1999/2000 season.

Some biases complicate comparing growth rates between laboratory-reared larvae and field samples. Laboratory-reared larvae are hatched and grown from eggs in a relatively controlled environment and have a known age. Changes in length over time are measured on groups of live larvae or individual larvae. Growth of sea-caught larvae is estimated from one sample containing larvae of several ages, assuming that each larva had the same growth rate at different times. This method estimates growth of the population at large, i.e. the survivors, and not the individual fish.

In 2000, length-at-age data for juveniles were more variable than for larval anchovy (see r^2 values, Table 4.1; see also Tables 3.1 and 3.2). This could be because of increased natural variability in growth rates, but also because of increased ageing error due to the difficulty of preparation and reading of otoliths for SEM purposes, and the decreased precision in reading larger otoliths with more tightly packed daily rings (see *CV*s, Figs. 3.1 and 3.2).

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CHAPTER 5

DISCUSSION AND CONCLUSION

The objectives of this study were to calculate the mortality rates, hatchdate distributions, and growth rates of Cape anchovy larvae (caught in March 2000) and juveniles (caught in May 2000) in the southern Benguela region in order to compare them with each other, with other year-classes and to relate these to environmental conditions. The hypotheses tested were:

i) Cushing's (1975, 1990) *Match/Mismatch* hypothesis that the onset of spawning is matched with the onset of primary production,

ii) Hjort's (1914) *Critical period* hypothesis that the survival at first-feeding is critical in determining recruitment strength and

iii) The *Growth-mortality* hypothesis (Ware 1975, Shepherd and Cushing 1980, Anderson 1988), that mortality is related to growth because larvae that grow faster within a year-class will spend less time in the early vulnerable life-history stage, and in that way will be less vulnerable to predation and survive better.

This chapter firstly contains the description of the environment (temperature) during the period relevant for the 1999-2000 anchovy year-class (*5.1*).
The results obtained are then summarized and discussed in the light of the above objectives in the following structure:
5.2. A summary of the mortality rates in 2000 and how they compare with other studies in other years;
5.3. Anchovy spawning (temperature and egg densities), hacthing and survival (the hatchdate distributions obtained for March and May 2000 are compared with each other and age-selective larval and juvenile mortality are made) of anchovy in 2000 are discussed in the light of SST in 2000.
5.4 Growth rates obtained in this study are summarised and compared with other year-classes in relation to factors that could have affected growth in 2000.
5.5. Conclusions are drawn regarding hypotheses i), ii) and iii).

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5.1. SST changes in the Benguela environment from August 1999 to May 2000

Five-day sea surface temperature (SST) composite images were obtained from the geostationary METEOSAT satellite with a spatial resolution of 6 x 6 km and radiometric precision of approximately 0.5 °C in radiative temperature (Demarcq and Citeau 1995). Methods for temporal smoothing and conversion of METEOSAT SST to daily 1-km-resolution NOAA/AVHRR SST images were described by (Demarcq and Citeau 1995, Agenbag and Demarcq 2000, Demarcq *et al.* 2002). Daily 1-km-resolution images were then used to calculate areas of 19.1–26.0°C water in 3° by 3° blocks on (a) the Agulhas Bank, 18.0–21.0°S, 15.0–18.0°E and (b) the west coast offshore of Cape Town ("*West Coast – CT*"), 34.0–37.0°S, 18.0–21.0°E. (Fig. 5.1; K. Agenbag, *MCM*, *pers. comm.*).

Large areas of 19.1–26°C water were present on the Agulhas Bank and on the west coast of South Africa during a large part of the 1999-2000 spawning season, as shown by the weekly distribution of the area of 19.1–26°C SST water in those regions (Fig. 5.1) from the the first week of December 1999 until the end of March 2000.

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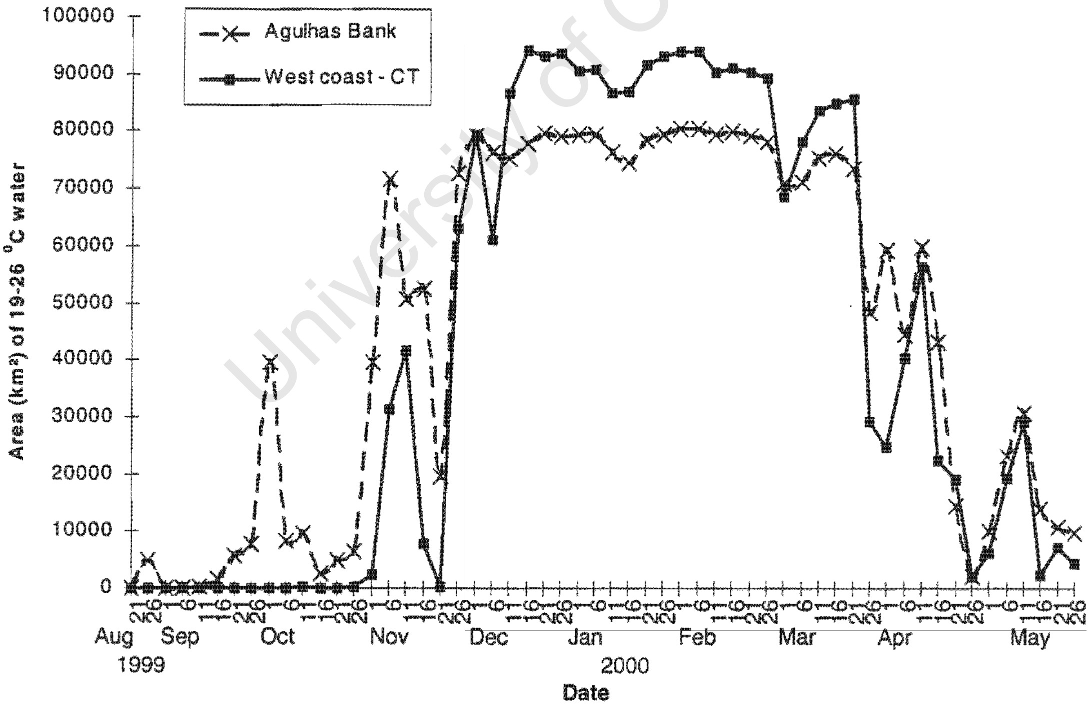

Figure 5.1. Weekly area of 19.1-26.0°C (sea surface temperature) water for the Agulhas Bank, 34-37°S, 18-21°E (smooth line and squares) and the west coast off Cape Town, 33-36°S, 15-18°E (dashed line and crosses) (K. Agenbag, *MCM, pers. comm.*).

These large areas of warm water along the west and south coasts of South Africa in December 1999 through mid-March 2000 were exceptional. The SST anomalies recorded off Cape Town during the first two weeks of December 1999 reached the second highest within a 30-year-time series at + 2.0 °C. This resulted from a collapse of upwelling over that period (Roy *et al.* 2001a). By the third week of December the entire continental shelf north of the Cape Peninsula was covered with water warmer than 19.1 °C (Fig. 5.1). During the early part of 2000 some upwelling occurred along the West coast of South Africa, but at an average level (Fig. 5.2).

Late summer and autumn, March-May 2000, was marked by cold upwelling events with little warm water present on the west and south coasts from late March 2000 (Fig. 5.2). Roy *et al.* (2001b) recorded eight major upwelling events along the west coast from the end of December 1999 to the end of April 2000, two weeks before the juvenile anchovy were caught. Roy *et al.* (2001b) used wind data to support these observations.

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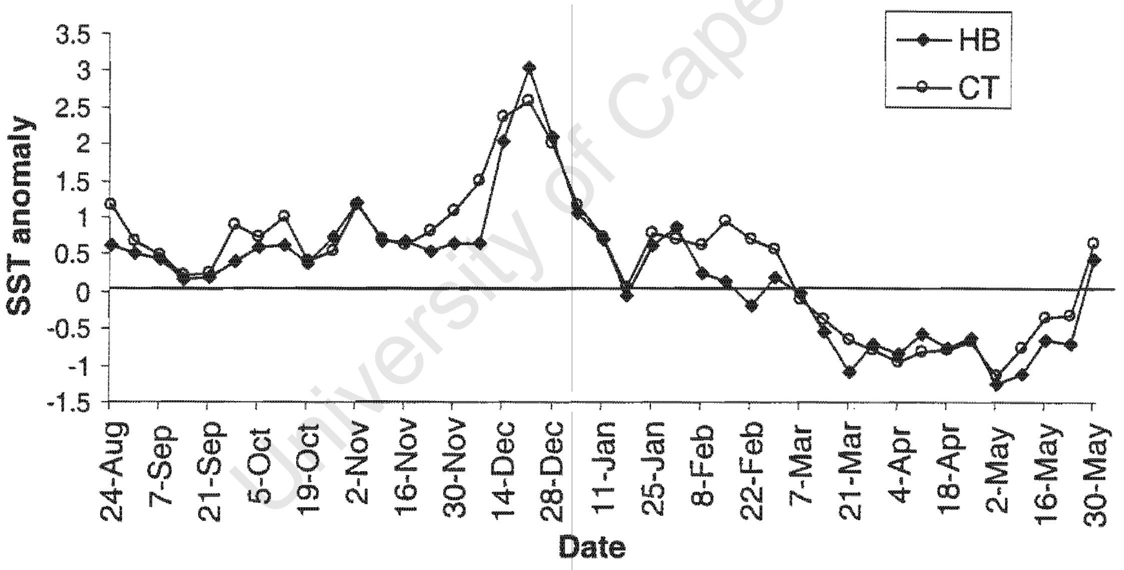

Figure 5.2. Weekly sea surface temperature (SST) anomalies from the 5-year mean, 1995-2000 off Hondeklip Bay (HB) and Cape Town (CT) (adapted from Roy *et al.* 2001b; courtesy C. Roy, *pers. comm.*)

5.2. Mortality rates

The mean instantaneous natural mortality rate (Z) calculated for Cape anchovy larvae and pre-recruits caught in March in 2000 was 0.035.day^{-1} (96 % survival). Larval survival rates in 2000 exceeded those of Brownell's (1983) laboratory-reared Cape anchovy larvae by 2.5 % (Table 5.1). To obtain mean larval and pre-recruit mortality rates separately, in order to compare them to values calculated by Shannon (1995), I split the age-frequencies from the pre-recruit survey into ages 30–90 days (larvae) and 105–165 days (pre-recruits). This gave Z values of 0.037.day^{-1} for larvae and 0.030.day^{-1} for pre-recruits (Table 5.1). This shows that survival rates increased from 96 % to 97 %.day^{-1} from larval to pre-recruit stages. Shannon (1995) and Shannon *et al.* (1996) calculated two Z values for Cape anchovy pre-recruits, at ages 101–179 days. Their first approach rendered a Z value of 0.032.day^{-1}, corresponding to a survival of 97 %.day^{-1}. Shannon's adjusted second approach, $Z = 0.046$.day^{-1} (survival rate of 96 %.day^{-1}) gave a better fit for recruitment strength (see Table 5.1).

Juvenile Cape anchovy (165–300 days) caught in May 2000, showed an instantaneous mortality Z of 0.020.day^{-1}, which corresponds to a survival rate of 98 %.day^{-1}. Valdès Szeinfeld and Cochrane (1992) estimated natural mortality, M ($M = Z -$ fishing mortality, F) for post-recruits and adults as 1.33.year^{-1}, giving M of 0.0036.day^{-1}. This is lower than Z because it does not include fishing mortality, F (see Table 5.1).

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Table 5.1. Mortality rates of larval through adult Cape anchovy *Engraulis encrasicolus* calculated from this and previous studies

Stage and Age	Z (day^{-1})	Daily survival rate (e^{-Z})	Source
1) March pre-recruit survey			
Larvae: 30-90 days	0.0365	0.964	This study
Pre-recruits: 105-165 days	0.0303	0.970	This study
Larvae and pre-recruits: 30-165 days	0.0353	0.965	This study
2) May recruit survey			
Pre-recruit to adult: 165-300 days	0.0202	0.980	This study
Larvae < 104 days	0.0629	0.939	Brownell 1983
Pre-recruits: 101-179 days	0.0315	0.969	Shannon 1995: approach 1
Pre-recruits: 101-179 days	0.0460	0.955	Shannon 1995: approach 2
Recruits and adults: 180 days +	(M) 0.00364	0.996	Valdés Szeinfeld & Cochrane 1992

Because they are comparable to model and laboratory studies, the Z values presented here are sufficient for hatchdate back-calculations. However, because of the assumptions underpinning the estimation of mortality rates from field data (see section *3.5*), they need to be viewed cautiously.

5.3. Anchovy spawning, hatching and survival in relation to SST in 2000

The hatchdates calculated in this study are actually the dates of first increment formation. This is presumed to be at first-feeding in many clupeoids (Methot and Kramer 1979), in Cape anchovy on average 2–3 days after hatching; hatching occurs 1.5–3 days after spawning, depending on temperature (King *et al.* 1978). Thomas (1985a) counted daily increments on 12 tank-reared Cape anchovy larvae, and postulated that the first increment was formed 2–7 days after hatching, 4 days on average. Thomas (1985a) also quotes Hewitt and Methot (1982) for the first ring deposition (of northern anchovy *E. mordax*) at six days after the spawning date. Brothers *et al.* (1976) estimated the date of laying down of the first ring for northern anchovy to be five days after hatching. I will thus assume first increment deposition or "hatching" as shown in the distributions, to be 6 days after the egg is spawned.

The very strong 2000-recruiting Cape anchovy year-class in the southern Benguela system seems to have been hatched mostly from mid-August 1999 to mid-February 2000 (Fig. 5.3). The hatchdate distribution of larvae caught in March (Fig. 5.3.a) shows that either: a) spawning was continuous from late August 1999 to February 2000 with enhanced survival of eggs and larvae in September-October 1999 and January-mid-February 2000 or b) there were two spawning peaks, mid-September to October and mid-December onwards, with constant survival at all ages until March.

I assumed ageing was accurate and comparable over the age ranges 30-165 days for March samples, and 105-255 days for May samples (see section *3.5*). The upper limits, ages 165 days in March and 255 days in May, both correspond to the 3 Oct hatchdate (see Figs. 3.5 and 3.10). If larvae and juveniles of all ages experienced constant mortality between the March and May surveys, the hatchdate distributions of the surveys should be similar. However, juvenile distributions differed from larval hatchdate distributions, in that the modes seemed to have been set back by 1-2 months (Fig. 5.3.b). Thus, the fish that were hatched before 17 December 1999 (> 75 days old in March) showed better survival between the March and May surveys than younger larvae, hatched after December 1999. This suggests higher selective mortality rates of larvae that were hatched after December 1999, 30-75 days old in March 2000, corresponding to lengths 10–40 mm SL (see Table 3.1).

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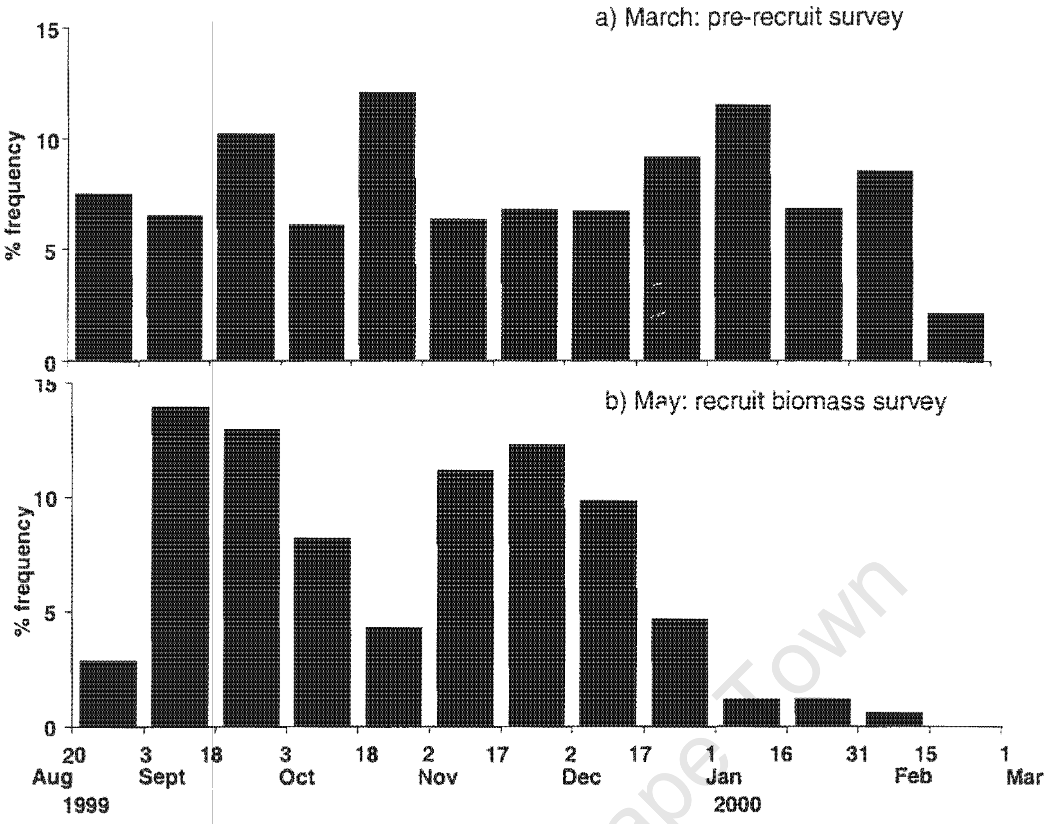

Figure 5.3. Hatchdate distributions of Cape anchovy a) larvae caught in March 2000 and b) juveniles caught in May 2000 in the southern Benguela system off South Africa. Both distributions were adjusted for mortality (Z): <165 days: 0.0353 and ≥ 165 days: 0.0202.day^{-1}.

Spawning

Egg densities are estimated during pelagic spawner-biomass surveys on the west and south coasts in November every year (van der Lingen *et al.* 1998, 2001), using Californian Vertical Egg Tow (*CalVET*) hauls (Smith *et al.* 1985). Egg densities show a steady decrease over time from 1991 onwards with a low density of 400 eggs.m^{-2} in November 1999 (Fig. 5.4).

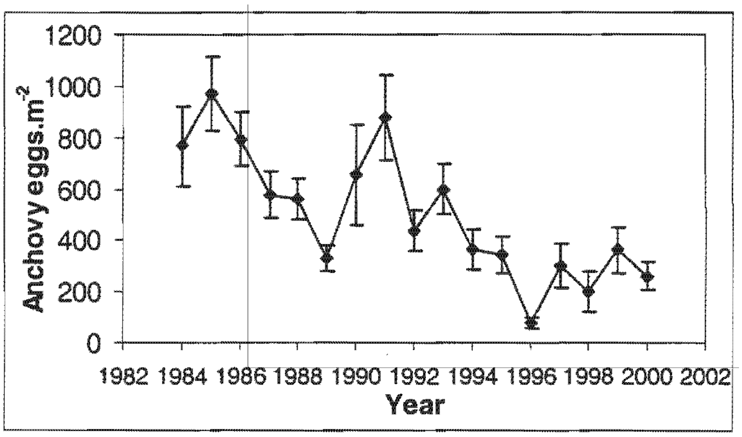

Figure 5.4.
Mean survey egg density (number m^{-2}) calculated from *CalVET* hauls on routine annual pelagic spawner-biomass surveys in November (updated from van der Lingen *et al.* 2001; courtesy C. van der Lingen, *MCM, pers. comm.*).

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Although egg density in November may have decreased over time, overall egg abundance may not have decreased. Egg density in November is not representative of the overall spawning activity during the spawning season, since only 4-6 weeks of the entire spawning period are sampled by the survey. The spawning period may have been longer in 1999/2000 due to very favourable conditions, for example, and cumulative egg abundance over the whole spawning season may have been higher.

Another indicator of Cape anchovy egg abundance in the southern Benguela region is an egg index from weekly sampling of eggs and larvae using Bongo nets along a monitoring line off the Cape Peninsula, conducted as part of the *South African Sardine and Anchovy Recruitment Programme*, SA SARP (Painting 1993, Painting *et al.* 1998, Huggett *et al.* 1998, Huggett 2002). Unfortunately, however, no samples were collected from November 1999 to January 2000 due to bad weather, so indicators of egg abundance over 1999/2000 spawning season from this monitoring line are uncertain (J. Huggett, *MCM, pers. comm.*).

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Sea surface temperatures (SST) may be good indicators of possible spawning duration and abundance; temperature ranges of 17.4–21.1°C are most conducive to Cape anchovy spawning (van der Lingen *et al.* 2001). In unfavourable temperatures, spawning may be terminated early in the season (Richardson *et al.* 1998) or abnormalities of egg development may occur in water < 14°C (King *et al.* 1978). The thermal spawning conditions seemed ideal from August 1999 to March 2000, with large areas of 16–19 °C and >19 °C water present between August and the beginning of December 1999 (see Fig. 5.1), this being much warmer than in previous years (see Fig. 5.2). Copepod production is highest in waters of 16–19°C (Richardson *et al.* 1998). It seems then, that there was no event in the spring and summer 1999/2000 that would have interrupted spawning. Thus spawning was probably continuous and reasonably abundant throughout the period.

Egg and early larval survival

Hatchdate distributions of larvae caught in March show modes in September-October and early January onwards, which seem to match high SST anomalies and warm-water events (see Figs. 5.1, 5.2 and 5.3). Warm water results from reduced southerly winds and a collapse of upwelling leading to retention of eggs and larvae in the system (Hutchings *et al.* 1998, Roy *et al.* 2001b). In the 1999/2000 season, the exceptionally warm water in December through February would have enhanced survival. Thus, larvae hatched during that time have been thought to contribute to most of the year-class strength (Roy *et al.* 2001a, b).

Post-larval and juvenile survival

However, when comparing the May - juvenile hatchdate distribution (Fig. 5.3.b) to the March - larval hatchdate distribution (Fig. 5.3.a), it is evident that age-specific mortality after March 2000 (the time of the pre-recruit survey) must have reduced the abundance of fish hatched from mid-December to mid-February (30-75 days old in March) faster relative to that of the older age-classes. Age-selective mortality is a common phenomenon in fish stocks in general, and especially in clupeiform fishes (Vetter 1988). Starvation, predation and advection are the three major hypotheses of mechanisms suggested to govern larval survival (Morse 1989; see also Table 1.1), all of which may be age-selective. These I will discuss briefly, as possible reasons for higher mortality rates of younger age-classes between March and May 2000.

5.3.1. Factors affecting age-selective mortality

i) Starvation

Early larvae (< 75 days old)

In a few studies, anchovy larvae have been reared from eggs through metamorphosis in the laboratory (Kramer and Zweifel 1970, Lasker *et al.* 1970, Hunter 1976a, Sakagawa and Kimura 1976, Brownell 1983). Laboratory-reared "first-feeding" (exogenous feeding) northern anchovy larvae survived without food for 1.5 days after yolk absorption (15–22 °C and 14-hour days). A delay in exogenous feeding beyond this resulted in mortality. After metamorphosis, larvae were able to resist starvation for up to two weeks (Lasker *et al.* 1970). In the sea, food availability is considered to be one of the major factors controlling larval survival (Cushing and Harris 1973, Lasker 1975, Castro and Hernández 2000).

Little is known about the feeding selectivity of Cape anchovy larvae (< 35 mm SL) in the wild. They presumably feed on microzooplankton (mostly copepod eggs and nauplii) and phytoplankton (Brownell 1983). For successful feeding, young anchovy larvae generally require aggregations of small food particles in the microzooplankton size range (10–50 μm) (Hunter 1981). These are often found at *chlorophyll maximum layers* or fronts (Lasker 1975, 1978, 1981). Such a front is found between the coastal upwelled water on

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the west coast of South Africa and the warmer northward-flowing Columbine jet current (Hutchings 1981, Shelton and Hutchings 1982). The proximity of the jet current to the coast, and hence offshore advection and/or starvation of young larvae is largely determined by the upwelling intensity (Shelton and Hutchings 1982, Hutchings and Field 1997, Mullon *et al.* 2002).

Larval food patches are spatially and temporally variable (Brown *et al.* 1991, Brown 1992, Dahl and Johannessen 1998, Mitchell-Innes *et al.* 1999, 2001). Factors that are important for larval survival are not only a) the food concentrations within a patch, but also b) the prey sizes available within a patch (Leggett and Deblois 1994) and c) the relationships between food abundance and larval ingestion rates (MacKenzie *et al.* 1990).

Cushing and Harris (1973) used a searching model approach to estimate daily rations of larvae from metabolic requirements for feeding success. Feeding success increased with size. Older and larger larvae would therefore be at an advantage compared to younger, smaller ones.

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In the laboratory, Hunter (1976a) showed that larvae have the ability to remain in patches of food when they find them. But even if the ephemeral food patches persist, larvae would have to move on and find other patches containing larger prey in order to survive. Whether a larva will find a concentration of food organisms of the appropriate size and whether it will be able to survive until it finds another, involves a set of interacting relationships: 1) feeding behaviour, 2) time of day and satiation, 3) starvation, 4) temperature, 5) density and distribution of food and 6) feeding success. However, it has not yet been attempted to predict the outcome of such a complex system (Hunter 1976a).

Continuous upwelling in the Benguela system from March to May (see Fig. 5.2) is likely to have dispersed plankton patches on the west coast further offshore (Hutchings 1981) preventing formation of suitable strata and hence preventing sufficient aggregation of microzooplankton patches in near-shore waters (Lasker and Smith 1977, Verheye *et al.* 1991). The absence of these would presumably lead to the starvation of young larvae.

Post-larvae and juveniles (> 75 days old)

Juvenile Cape anchovy are primarily particulate feeders, but also filter-feed on microzooplankton. Food particle size is the prime determinant of their feeding mode (King and Macleod 1976, van der Lingen 1994, Louw *et al.* 1998). They predominantly feed on crustacean eggs, nauplii, and calanoid copepods (0.5-2.0 mm) (James and Findlay 1989). In the west coast nursery area, food availability to anchovy juveniles may be directly related to upwelling strength, as upwelling results in diatom blooms, after which zooplankton, predominantly copepod grazers, become abundant (Verheye *et al.* 1992, Hutchings and Field 1997).

The strong upwelling period on the west coast in autumn 2000 (see Figs. 5.1 and 5.2) was followed by high zooplankton abundance (Hutchings *et al.* 2002). This was much higher than observed in a time-series of previous years (Verheye *et al.* 1998). Thus, abundance of larger zooplankton copepods probably lead to better feeding conditions of post-larvae and juveniles compared to younger larvae. In addition, larger copepods are able to migrate vertically thereby remaining on the shelf during strong upwelling and remaining available as prey for a longer time (Verheye and Field 1992).

Thus, the food sizes available in sufficient aggregations on the west coast (between March and May 2000) were the most likely factor to cause age-selective starvation of young larvae (hatched after December 1999, 30-75 days old when the strong upwelling started in March 2000). However, food production and particle sizes have to be monitored *in situ* to quantitatively identify modifiers of such size-selective mortality.

ii) Advection

Upwelling coincides with increased offshore advection of water masses by wind and Ekman transport (Hutchings and Boyd 1992). Larvae that are longer than 7 mm SL show development of a swimbladder and the ability to start schooling (Badenhorst and Boyd 1980). As this ability to control vertical as well as horizontal migration increases with larval length (Badenhorst and Boyd 1980), anchovy that were at post-larval and juvenile stages during strong upwelling in autumn 2000 had a greater ability to use inshore retention currents to resist offshore advection more strongly (Stenevik *et al.* 2001).

iii) Predation

Another possible influence on larval survival may be predation. Young larvae may be selectively fed on by predators, for example by adult anchovy (Alheit 1987, Brownell 1985, 1987, Valdés *et al.* 1987, Valdés Szeinfeld and Cochrane 1992). Predation (like advection) is often related to starvation since starving fish are likely to be too weak to

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escape (Hunter 1981, Morse 1989). Thus, the primary cause of mortality may still be starvation. However, to be able to define predation as the mechanism for age-selective mortality, predator abundance and ingestion rates have to be measured in conjunction with mortality.

5.4. Growth of anchovy in 2000

The growth rates decreased from larval to juvenile stages between March and May 2000 (Fig. 5.5). This is a common phenomenon, which forms the basis of the Laird-Gompertz (Laird 1969) and von Bertalanffy (Pauly 1981) models.

Prior to feeding, the only significant factors in terms of growth limitation are temperature and the size of the egg. Egg size determines volume and weight of the yolk sac at hatching and the asymptotic larval length achieved on yolk nutrition, as well as survival time in some groups (Blaxter and Hempel 1963).

When feeding starts, growth becomes a function of both temperature and abundance of food. A change in the form of the growth equation takes place at the transition from yolk-sac stage to the feeding stage (Blaxter and Hunter 1982). Since all the larvae that were studied here, were most likely post-feeding larvae (King *et al.* 1978), a single equation (linear, Gompertz or VBGF) was sufficient to describe the growth of larvae.

The linear function describes growth well until *circa* 220 days, when it starts slowing towards an asymptote. The Laird-Gompertz function (better fit than VBGF, Table 4.3) is needed to complement this for larger size-classes and ranges. According to the Laird-Gompertz function, growth increases from an initial rate of 0.26 mm $SL \cdot day^{-1}$ to 0.41 mm $SL \cdot day^{-1}$ in the first 60 days of post-hatch growth (up to 31 mm SL). A maximum rate of 0.43 $mm \cdot day^{-1}$ is reached between 75 and 90 days of growth at lengths 37–43 mm SL. Afterwards, the growth rate decreases to 0.24 $mm \cdot day^{-1}$ at 210 days (85 mm SL), thereafter decreasing continually towards 110 mm (Fig. 5.5; see also Table 4.4).

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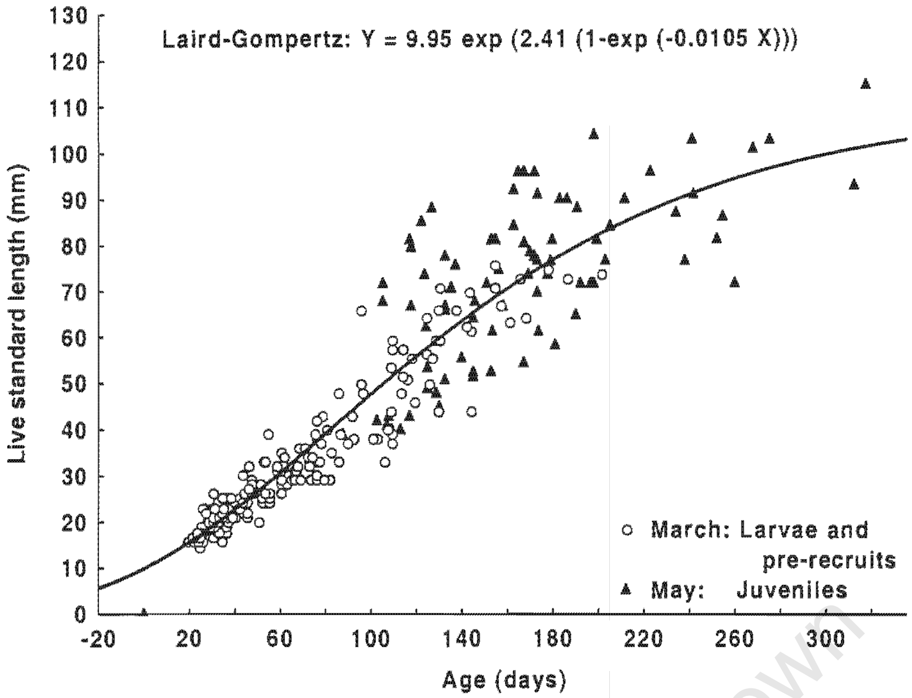

Figure 5.5. Growth rate of anchovy larvae and juveniles caught in March and May 2000 on the west coast of South Africa as described by the Laird-Gompertz growth function.

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5.4.1. Comparisons of growth in 2000 with other year-classes

The growth rates of anchovy in the wild from previous studies ranged from 0.4 to 0.6 mm·day^{-1} for larvae and from 0.3 to 0.4 mm SL·day^{-1} for juveniles. In order to compare the growth rates in 2000 with previous work as accurately as possible, I read growth rates from different size ranges from the relevant growth curves (Table 5.2). Wild Cape anchovy in previous years generally showed faster growth rates than those caught in 2000.

The comparisons only hold if there are no methodological differences between my own, and previous results. There were two important differences: 1) Sampling strategies differed as I used proportional stratified age subsampling, whereas previous authors used fixed age sub-sampling techniques (see section *2.2.2*), 2) the patchy, non-validated or non-available data of previous authors is another problem. For example, in Prosch (1986) there seems to be a typographical error, as the quoted VBGF renders a uniform line when tested, yet different mean growth rates are quoted by Waldron (1995) for Prosch's growth curves. Bloomer's (1994) results are from preliminary reports, which provide the only data available from that time. But if the growth results are comparable, we can state that Cape anchovy larvae and juveniles showed relatively slow growth rates compared to previous year-classes.

Table 5.2. Mean growth rates (mm. day^{-1}) of larval and juvenile Cape anchovy *Engraulis encrasicolus* at different size ranges using different models from this and other studies. L = Linear, LG = Laird-Gompertz, VBGF = von Bertalanffy growth function.

Location caught	**Size range**		**Growth**		**Source**	
	SL (mm)		**Model**	**(mm.day^{-1})**	**Date caught**	**Author**
South Africa	14 – 75	Larvae	L	0.36	March 2000	This study
			LG	0.35		
			VBGF	0.33		
South Africa	39 – 114	Juveniles	L	0.24	May 2000	This study
			LG	0.22		
			VBGF	0.24		
*** Growth rates read off different places off the relevant curves for comparison**						
*** South Africa**	**14 – 33**	**Larvae**	**L**	**0.26**	**March 2000**	*** This study**
Namibia	1 – 33	Larvae	L	0.60, 0.90	1978/79	Badenhorst and Boyd 1980
Namibia	3 – 30	Larvae	L	0.77	Nov 1982	Thomas 1986
	3 – 30	Larvae	L	0.55	Jan 1983	Thomas 1986
	3 – 30	Larvae	L	0.62	Feb 1983	Thomas 1986
*** South Africa**	**14 – 25**	**Larvae**	**L**	**0.21**	**March 2000**	*** This study**
South Africa	5 – 25	Larvae	L	0.44	Jan 1983	Thomas 1986
	5 – 25	Larvae	L	0.52	1982 – 1984	Thomas 1986
South Africa	2.5 – 35	Larvae	LG	0.15–0.6	Laboratory-	Brownell 1983
20 days	2.5 – 10	Larvae	LG	0.26	reared,	Brownell 1983
30 days	3 – 15	Larvae	LG	0.31	18.5–19.5°C	Brownell 1983
40 days	4 – 20	Larvae	LG	0.37		Brownell 1983
40–70 days	5 – 30	Larvae	LG	0.45		Brownell 1983
South Africa	12 – 28	Larvae	VBGF	(Equation	1983/84	Prosch 1986
	30 – 40	Pre-recruit	for all combined –		May 1983	Prosch 1986
SA and Namibia	30 – 50	Pre-recruit	does not give valid		Nov 1983	Prosch 1986
	50 – 70	Juveniles	results)		May 1983	Prosch 1986
	90 – 110	Juveniles			Nov 1984	Prosch 1986
	90	Juveniles			Jan 1979	Prosch 1986
South Africa		Larvae		0.50	1983/84	Prosch 1986 (In: Waldron
		Juveniles		0.40	1983/84	1995 & Bloomer 1994)
*** South Africa**	**60 – 114**	**Juveniles**	**VBGF**	**0.13**	**May 2000**	*** This study**
South Africa	60 – 120	Juveniles	VBGF	0.40	June 1985	Waldron 1995
*** South Africa**	**39 – 100**	**Juveniles**	**VBGF**	**0.22**	**May 2000**	*** This study**
South Africa	37 – 100	Juveniles	VBGF	0.30	June 1989	Waldron 1995
*** South Africa**	**39 – 90**	**Juveniles**	**VBGF**	**0.22**	**May 2000**	*** This study**
South Africa	37 – 90	Juveniles	VBGF	0.32	May 1991	Waldron 1995
*** South Africa**	**39 – 85**	**Juveniles**	**L**	**0.19**	**May 2000**	*** This study**
*** South Africa**	**25 – 85**	**Juveniles**	**L**	**0.34**	**March & May 2000**	*** This study**
South Africa	25 – 85	Juveniles	L	0.42	May 1993	Bloomer 1994 (prelim.)

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5.4.2. Factors affecting growth rates

Laboratory studies on young fish demonstrate that growth can be limited by temperature and ration size, stocking density and food density (Lasker *et al.* 1970, Hunter 1976b). The *type* of food particles available to larvae is also important for their growth (Lasker 1975).

Increased temperature results in increased activity, faster feeding, and increased growth rates (Hunter 1976b). Cape anchovy larvae are usually concentrated above the thermocline at about 20 m depth (O'Toole 1977). Thus, surface temperatures are probably a good indicator of the conditions that anchovy larvae were exposed to. The warm water along the west coast in September 1999 through March 2000 (see Fig. 5.1) provided excellent warm conditions for growth (Hunter 1976b). Warm water was followed by upwelling events from March 2000 to the end of April 2000, followed by enhanced primary and secondary production, after a suitable lag of one to three weeks (Hutchings *et al.* 2002). This probably provided sufficient rations for older larvae and juveniles to ensure fast growth rates during that time.

However, the growth rates measured in 2000 were slower than in previous years. Such inter-annual differences in growth rates are likely to be within the natural variability of growth that is expected of such a short-lived and highly variable species. Brownell's (1983) study gives an indication of the variability of growth rates. Even within a relatively controlled environment, where temperature and food were kept constant in laboratory tanks, the daily larval growth rates ranged from 0.15–0.6 $\text{mm}\cdot\text{day}^{-1}$ between different individuals. The growth rate estimates for Cape anchovy in this study fell within the range of Brownell's (1983) laboratory-reared anchovy larvae, corresponding to those reared at 18.5–19.5 °C and about 30–40 days of age (see Table 4.5). Apparently, obtaining enough food to survive will also mean enough food to grow rapidly, or at a standard growth within a natural variability (Methot and Kramer 1979).

The large number of recruits present in 2000 (Coetzee *et al.* 2000) suggested that growth may have been limited by a smaller *per capita* amount of food, because the increased productivity was shared out amongst a larger number of larvae and juveniles, resulting in below average growth rates, but survival of many more to recruitment. In this case, it suggests that food may have been limiting for growth, but not for survival.

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5.5. Conclusions

1) The results of this study do not fully support Cushing's (1975) *Match/Mismatch* hypothesis, that if the time of the phytoplankton bloom and the subsequent production of copepod nauplii coincided with the start of the annual fish production cycle, they would be *matched*, and good recruitment would follow. In this case, both spawning and hatching seem to have been continuous throughout spring and summer. Thus, they are unlikely to have *mismatched* one event of high productivity, but rather were consistent throughout. Survival of larvae may then have been enhanced in the period that was most favourable for transport and feeding.

This study shows that the strong year-class in 2000 corresponds to a long uninterrupted spawning period, which continuously gave eggs and larvae good opportunities for survival. Favourable conditions during this long spawning period promoted early larval survival as well as late larval and juvenile survival to recruitment age. However, larvae that were older at the time of the strong upwelling (March to May) survived better than younger larvae. This suggests that a series of strong upwelling events needs to coincide with an abundant batch of fish that will be old enough (spawned early in the season) to feed on mesozooplankton and escape offshore advection. The lag period between warm conditions promoting transport of eggs and young larvae, and strong upwelling thus is important for recruitment.

2) The *Critical period* as defined by Hjort (1914, 1926) does not seem to be at first-feeding in this study, but rather much later during the life history. As with all larval fish, survivorship of larvae of Cape anchovy *Engraulis encrasicolus* is not regulated by any one factor at any one time, but appears to be a trade-off between probability of feeding, transport and predation. The important emphasis here should be on the larger larvae that have passed the supposedly vulnerable first-feeding stage, and have been sampled by the pre-recruit survey in March. It seems that the "*critical*" stage is not at first-feeding. An array of factors may have influenced mortality of younger fish significantly between March and May, after the first-feeding stage was already passed. These data show that the majority of juvenile recruits in May consisted of older, rather than more recently spawned individuals, showing an entirely different distribution to the pre-recruits caught in March. Recruitment strength is thus dependent not only on the early larval stages, but also and maybe more importantly, on the period closer to recruitment, as suggested for other species (Smith 1985, Peterman *et al.* 1988).

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A support for this suggestion is provided by the time-series of Cape anchovy pre-recruit densities and recruitment numbers estimated during pelagic biomass cruises each. The pre-recruit densities in March do not seem to be related to May recruitment strength (Fig. 5.6). By looking at densities from the March pre-recruit surveys, it is important to consider the fish spawned earlier in the season, as they will be well advanced in their ability to escape offshore advection and predation, and feeding on larger copepods. Hence, a recruitment prediction index from the pre-recruit survey is weighted for larger sizes (van der Lingen and Merkle 1999, 2000).

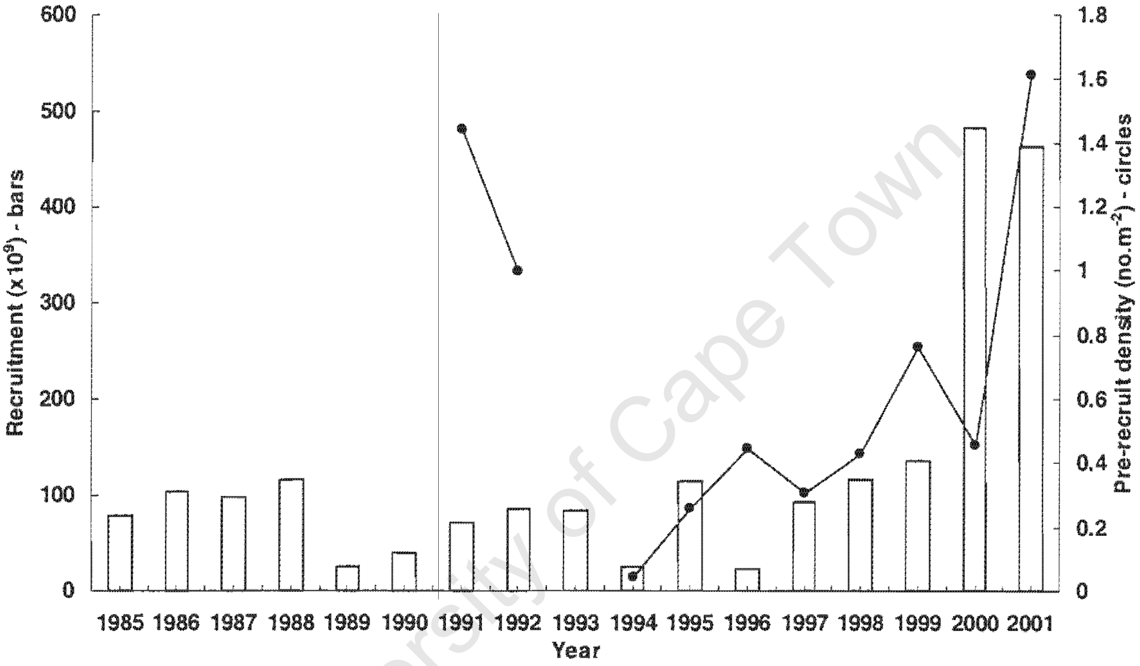

Figure 5.6. Estimates of recruitment numbers (billions) from recruit biomass surveys in May/June (bars) and pre-recruit densities (numbers.m^{-2}) from pre-recruit surveys in March (circles) in the southern Benguela system off South Africa (Recalculated from van der Lingen and Merkle 1999; courtesy C. van der Lingen, MCM, *pers. comm.*)

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The implications of this are that we need to investigate not only factors affecting spawning success and early larval survival, but also factors affecting late larval survival (e.g. size-distributions and variability of food organisms on the west coast, offshore losses, predation) in recruitment prediction programmes. To further test this, a pre-recruit density index from slightly earlier in the season than March (when September/October hatched larvae have a better catchability in the Methot net) would be useful.

3) These data do not support the *Growth-mortality* hypothesis (Ware 1975, Shepherd and Cushing 1980, Anderson 1988), that those larvae that grow faster within a year-class will have competitive advantages because they spend less time in the early vulnerable life-history stage, and in that way will be less vulnerable to predation. Hence, mortality is related to growth (Ware 1975, Shepherd and Cushing 1980, see Butler 1989). Growth rates of larvae and juveniles on the west coast were slow compared to previous data. Despite spending a prolonged time in vulnerable stages, a large abundance of juveniles was found during the recruit biomass survey. Thus, the *Growth-mortality* hypothesis does not apply. In this case, when many larvae were present at the start of the season, growth may be density limited, and therefore food limited. However, this does not seem to have seriously affected survival, as demonstrated by the record recruitment in 2000.

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APPENDICES

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Appendix 1. Programme written in *True Basic* used to calculate optimal age sub-sample sizes for Cape anchovy caught during the recruitment survey in May 2000 (for Baird's Index of variability < 20 %). Methods for all calculations and values are provided in Section 2.2.

```
DIM ALK5(107, 19)
DIM ALK15(36, 19)
DIM SL(19, 13)
DIM SLStr(19, 7)
DIM CATCHAGE(36, 7)
DIM TOTCATCHAGE(36)
DIM ni(19, 13),
DIM niStr(19, 6)
DIM niOPT(19, 6)
DIM VARpi(36, 19)
DIM VarNipi(36, 19)
DIM VarN(36, 13)
DIM AREAInfanta2(2, 6)
DIM AREAInfanta1(6)
DIM TOTVarN(36)
DIM VARIANCE(36)
DIM CV(36)
DIM OPTStr(6)


! Historical ALK for Cape anchovy
! Rows = Age (starting at 35 days, 5-day-age-classes),
! Columns = Standard Length, SL (mm)
DATA 0.0395, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0                      !35 days
DATA 0.0789, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0789, 0.0172, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.1447, 0.0172, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.1447, 0.0862, 0.0426, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0658, 0.1379, 0.0213, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0395, 0.2069, 0.0213, 0.02, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0526, 0.1552, 0.0638, 0.02, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0263, 0.1207, 0.1277, 0, 0.0638, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0526, 0.0517, 0.2128, 0.02, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0658, 0.0517, 0.1277, 0.06, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0132, 0.0517, 0.0851, 0.1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0132, 0.0172, 0.1277, 0.14, 0.0212, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0526, 0, 0.1064, 0.2, 0.1064, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0      !100 days

DATA 0.0263, 0.0172, 0, 0.12, 0.1489, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0263, 0.0345, 0.0213, 0.14, 0.1915, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0395, 0, 0, 0.1, 0.1277, 0.1064, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0132, 0, 0, 0.02, 0.1489, 0.1489, 0.075, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0.0263, 0.0172, 0, 0.02, 0.0638, 0.1277, 0.05, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0.0213, 0.02, 0.0213, 0.1702, 0.125, 0, 0.0732, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0.0213, 0.1489, 0.1, 0.05, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0.0172, 0, 0.02, 0.0213, 0.0638, 0.1, 0.125, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0.0213, 0.1064, 0.125, 0.1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0.0213, 0, 0, 0.0426, 0.125, 0.125, 0.0488, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0.0213, 0.0426, 0.125, 0.125, 0.024, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0.0213, 0.025, 0.1, 0.1707, 0.0345, 0, 0.0286, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0.05, 0.075, 0.1463, 0.1379, 0.0278, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0.0213, 0, 0.05, 0.0732, 0.1034, 0.0278, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.05, 0.122, 0.069, 0.0556, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.025, 0.0244, 0.1379, 0.0278, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0.0488, 0.1034, 0.1111, 0, 0.0286, 0.0208, 0, 0, 0, 0, 0
```

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```
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0.0244, 0.0345, 0.1389, 0.0857, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0.0732, 0.0690, 0.0833, 0.0571, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.025, 0.0244, 0, 0.0833, 0.0857, 0, 0, 0, 0, 0, 0, 0          !200 days

DATA 0, 0, 0, 0, 0, 0, 0.025, 0, 0.0488, 0.0345, 0.139, 0.1143, 0.0286, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.05, 0, 0.0345, 0, 0, 0.0571, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0.0213, 0, 0.025, 0, 0, 0.069, 0, 0.1143, 0.0571, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0.0244, 0, 0.0833, 0.0571, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0556, 0.0286, 0.0285, 0.0208, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0278, 0.0571, 0.0571, 0.0417, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0286, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.025, 0, 0, 0, 0.1429, 0.0286, 0.0208, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0286, 0.0571, 0, 0.0667, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0.025, 0, 0, 0, 0.0278, 0.0286, 0.0857, 0, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.025, 0, 0, 0.0556, 0, 0.1714, 0.0417, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0571, 0.0417, 0, 0, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0.025, 0, 0.0244, 0, 0, 0, 0.0571, 0.1042, 0.0667, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0.0244, 0.0345, 0, 0.0286, 0.0286, 0.0417, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0345, 0, 0, 0, 0.0625, 0.1, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0278, 0, 0, 0.0417, 0.0333, 0.074, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.025, 0, 0.0345, 0, 0.0571, 0.0286, 0.0417, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0.0333, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0.0333, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0667, 0.074, 0, 0, 0          !300 days

DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0345, 0, 0.0286, 0, 0, 0, 0, 0, 0.25, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0333, 0.185, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0.025, 0, 0, 0, 0, 0, 0, 0, 0.074, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0286, 0.0286, 0.0208, 0, 0.074, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.3125, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0571, 0, 0, 0.074, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0.0244, 0, 0, 0, 0, 0, 0, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0345, 0, 0, 0, 0, 0, 0, 0.1875, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0286, 0.0208, 0, 0, 0.0625, 0.25, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0417, 0, 0, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0285, 0, 0, 0, 0, 0, 0, 1
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0          !400 days

DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0.074, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0625, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0278, 0, 0.0286, 0, 0.0333, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0286, 0.0208, 0.0333, 0, 0.0625, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0
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```
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0286, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0.037, 0, 0.25, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0333, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0                          !500 days

DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.25, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.037, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0.0208, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0
DATA 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0                          !565 days
MAT READ ALK5


! Convert ALK into 15-day-age-classes from 1-day-age-classes:
FOR j = 1 TO 19
  FOR i = 1 TO 35
    LET ALK15(i, j) = ALK5((i*3-2), j) + ALK5((i*3-1), j) + ALK5((i*3), j)
  NEXT i
  LET ALK15(36, j) = ALK5(106, j) + ALK5(107, j)
NEXT j


! Total catch (May 2000) at each Stratum at each length (from SAS)
! Rows = SL(mm),  Columns = Strata (A,  inshoreA,  B,  InshoreB,  etc)
!! Only up to F1

DATA 77719052, 2922033, 0, 0, 0, 0, 0, 0, 0, 0, 0, 80641084
DATA 544033361, 20454229, 0, 0, 0, 0, 0, 0, 0, 0, 0, 564487590
DATA 414790275, 21440417, 53794222, 942982, 0, 0, 0, 0, 0, 0, 0, 0, 490967896
DATA 442262352, 39878670, 285381424, 26092764, 0, 0, 0, 0, 0, 0, 0, 0, 793615211
DATA 4420220933, 217037040, 421565797, 95665944, 282408265, 139085599, 0, 0, 0, 0, 0, 0,
5575983582
DATA 9342334338, 553829359, 1101198834, 216925997, 263316514, 139085599, 0, 0, 25139279,
1549051, 0, 0, 11643378982
DATA 15116619613, 720810494, 4495436725, 848655196, 711578825, 362761246, 81120258, 9870581,
25139279, 7800759, 0, 0, 22379792998
DATA 22184771578, 982605474, 13948230844, 1630686340, 2655142103, 1173647797, 1224148205,
242164595, 125696396, 13996962, 0, 0, 44181090339
DATA 21696766105, 947662203, 25575669898, 2685823584, 10609599172, 2486463655, 7982502194,
2416087460, 455260551, 126152714, 7647282, 4925409, 74994560306
DATA 17296826236, 726412701, 12851861857, 684472412, 26503549785, 2096871770, 16111610580,
4306905762, 979659610, 699388648, 61422468, 34477862, 82353459779
DATA 7077024079, 331128819, 9296846778, 217371920, 37651420184, 969468065, 22295552384,
2826935851, 1273249689, 1809765503, 217080405, 59104906, 84024948681
DATA 3198870224, 138171380, 5217669813, 18268526, 21884125526, 282410121, 4826073258,
365175550, 2227004095, 1974232747, 582194115, 98508176, 40812703588
DATA 2909373713, 107048891, 1115033186, 0, 9623475317, 106511170, 4104306449, 359084736,
2932264138, 2132198334, 968470952, 118209812, 24475976746
DATA 310876206, 11688131, 39706406, 0, 2355628702, 24001585, 1796423906, 132859380,
4965142554, 1252053856, 2033350042, 98508176, 13020239006
```

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```
DATA 637668766, 35673223, 109088628, 29163769, 399102806, 0, 1068531568, 79715628, 5050461816,
616518907, 1385251668, 98508176, 9509685005
DATA 0, 0, 0, 0, 598123253, 0, 0, 0, 2389724201, 216600204, 557674698, 29552453, 3791674829
DATA 0, 0, 0, 0, 0, 0, 0, 0, 1033684381, 32142332, 120545065, 0, 1186371784
DATA 0, 0, 0, 0, 0, 0, 0, 0, 477432672, 44862431, 77262989, 0, 599558096
DATA 0, 0, 0, 0, 0, 0, 0, 0, 302152757, 29908287, 0, 0, 332061045
MAT READ SL

! Add inshore SL to main Stratum SL
FOR j = 1 TO 19
  FOR s = 1 TO 6
    LET SLStr(j, s) = SL(j, (2*s-1)) + SL(j, (2*s))
  NEXT s
NEXT j


! Areas: Row 1 = A to F, Row 2 = Inshore A to Inshore F
DATA 12942.65, 10680.4, 6397.9, 8881.14, 7872.13, 4182.35
DATA 719.55, 612.42, 751.91, 904.19, 1328.34, 489.4
MAT READ AREAInfanta2


! Add inshore areas to main strata areas to get total,
! e.g. add Inshore A to Stratum A,  etc:
LET TOTAREAI = 0
FOR s = 1 TO 6                                                                      ! Strata
  LET AREAInfanta1(s) = AREAInfanta2(1, s) + AREAInfanta2(2, s)
  LET TOTAREAI = TOTAREAI + AREAInfanta1(s)
NEXT s


! Calculate catch-at-age
MAT CATCHAGE = ALK15*SLStr

FOR i = 1 TO 36
  LET TOTCATCHAGE(i) = 0
  FOR s = 1 TO 6
    LET TOTCATCHAGE(i) = TOTCATCHAGE(i) + CATCHAGE(i, s)
  NEXT s
NEXT i

! Start working out CV for each age in each stratum at diff. sample sizes
FOR n = 1 TO 36
  LET m = 0.000000000001                                      !Start with a small proportion of SL
  DO
    LET m = m + 0.000000000001
    MAT ni = m*SL                                                   !Selection of otoliths - start
    MAT niStr = m*SLStr
    MAT VarN = 0
    MAT TOTVarN = 0
    FOR s = 1 TO 6
      FOR i = 1 TO 36
        FOR j = 1 TO 19
          IF niStr(j, s) = 0 THEN
            LET VARpi(i, j) = 0
          ELSE

            IF niStr(j, s) < 1 THEN
              LET niStr(j, s) = 1
            END IF
```

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```
                LET VARpi(i, j)=ALK15(i, j)*(1-ALK15(i, j))/niStr(j, s)
          END IF
        NEXT j
      NEXT i

      FOR i = 1 TO 36
        FOR j = 1 TO 19
          LET VarNipi(i, j) = ((SLStr(j, s))^2) * VARpi(i, j)
          LET VarN(i, s) = VarN(i, s) + VarNipi(i, j)
        NEXT j

        LET TOTVarN(i)=TOTVarN(i)+(VarN(i, s)*(AREAInfanta1(s)^2))
      NEXT i
    NEXT s

    MAT VARIANCE = (1/(TOTAREAI^2)) * TOTVarN

    FOR i = 1 TO 36
      IF TOTCATCHAGE(i) > 0 THEN
        LET CV(i) = (SQR(VARIANCE(i))/TOTCATCHAGE(i))*100
      ELSE
        LET CV(i) = 0
      END IF
    NEXT i

! Test for validity (CV < 20)
    FOR i = n TO n
      LET age = 30 + (i*5)
      PRINT "age";age, "CV";CV(i), "m";m
    NEXT i

    LET niTOT = 0
    FOR s = 1 to 6
      FOR j = 1 TO 19
        LET niTOT = niTOT + niStr(j, s)
      NEXT j
    NEXT s
  LOOP UNTIL CV(n) <= 20

  FOR s = 1 to 6
    FOR j = 1 TO 19
      IF niStr(j, s) > 0 THEN
        IF ALK15(n, j) > 0 THEN
          IF niOPT(j, s) < niStr(j, s) THEN
            LET niOPT(j, s) = niStr(j, s)
          END IF
        END IF
      END IF

    NEXT j
  NEXT s
NEXT n


! Printing the calculated optimal sample size:
LET TotOPT = 0
FOR s = 1 TO 6                                                        ! Stratum A to F
  PRINT "Stratum";s
  FOR j = 1 TO 19                                                     ! SL
    IF niOPT(j, s) > 0 THEN
```

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```
      LET TotOPT = TotOPT + niOPT(j, s)
      LET OPTStr(s) = OPTStr(s) + niOPT(j, s)

      PRINT 25+(j*5);"mm"; INT(niOPT(j, s)),
    END IF

  NEXT j
  PRINT "Tot Stratum=",  INT(OPTStr(s))
NEXT s

PRINT "Optimal sample size ="; INT(TotOPT)
END
```

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Appendix 2. Table showing the number of age sub-samples selected from each mm-standard length (SL)-class at each station of the pre-recruit survey in March 2000

SL	Stations																																													
(mm)	01-02	01-05	03-01	03-02	03-03	03-04	03-08	05-04	05-08	07-02	07-03	07-05	07-06	07-08	09-01	09-02	09-05	09-06	11-03	11-07	11-08	13-01	13-02	15-05	15-07	15-08	15-09	15-10	15-11	15-13	15-14	15-15	17-04	17-05	17-06	17-07	17-08	17-09	19-03	19-04	19-05	19-07	19-08	21-04	21-05	21-06	SUM
12																																				1											1
13																												2		1						2											5
14																										1				2					1	2											6
15														1													1	1		2				1	3												9
16																												1							3	2											6
17																												1			1				5							1			1	1	10
18																												1	1		4			1	1	1	1				1				1		12
19																		1						1		1	1	1	1		1			2				1									10
20																		2			1						1		2		1				1			1				1			1		11
21																		1			1											1			1			3				1					8
22																		1			1			1				1									1	1		1							7
23																		1			1														1			1		1	1	1					7
24																								2			1																				3
25																		1		1	1			1																	1	1		1			7
26									1									1							1										1						2		3			1	10
27																								1														1						2			4
28		1																																				1						1			3
29									1															1									2								1		1				6
30																									2								2						1		2			1			8
31													2																															1			3
32					1	1																																									2
33					1								1																																		2
34			1				1																		1																						3
35			3		1																																										4
36			3	1																																											4
37			1	1																																											2
39			1																																												1
40	1			1																																											2
41				3																																											3
43				1																																											1
45			2	1																																											3
47			1					1																																							2
48								1																																							1
49																							1																								1
51								1																																							1
53										2																																					2
54										1																																					1
55																			1			1																									2
57															1							2																									3
59										1																																					1
60																						1																									1
61																						1																									1
62																1						1																									2
64												1				1						1																									3
65													1																																		1
68												1																																			1
69											1											1																									2
71																	1						1																								2
72																							1																								1
73												1																																			1
74			1																																												1
SUM	1	1	13	8	3	1	1	3	2	4	1	3	4	1	1	2	1	8	1	1	5	8	3	7	4	2	4	8	4	5	7	1	4	4	17	8	2	9	1	2	8	5	4	6	3	2	193

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Appendix 3.A. Table showing the calculated optimal sample sizes selected from each length-class at each stratum of the recruit biomass survey in May 2000. Sample sizes were calculated for a maximum of 20 % CV or *Baird's Index of Variation* (BIV) using a historical age-length key, (see programme, Appendix 1).

			Stratum				
SL (mm)	**A**	**B**	**C**	**D**	**E**	**F**	**SUM**
30	4						4
35	28						28
40	2	1					3
45	1	1					2
50	4	1	1				6
55	1	1	1		1		4
60	1	1	1	1	1		5
65	2	1	1	1	1		6
70	3	4	2	1	1	1	12
75	3	2	6	4	1	1	17
80	1	1	5	3	1	1	12
85	1	1	5	1	1	1	10
90	1	1	2	1	1	1	7
95	1	1	4	3	12	4	25
100	1	1	1	1	3	1	8
105			1		4	1	6
110					1	1	2
115					1	1	2
120					1		1
SUM	**54**	**17**	**30**	**16**	**27**	**11**	**155**

Appendix 3.B. Table showing the successful number of age sub-samples read from each length-class of each stratum of the recruit biomass survey in May 2000.

			Stratum				
SL(mm)	**A**	**B**	**C**	**D**	**E**	**F**	**SUM**
35	5						5
40	3						3
45	3	1					4
50	4	1					5
55		2	1				3
60	1	2	1				4
65	5	1	1				7
70	1	6	4				11
75	2	3	2	2			9
80	1	1	2	5			9
85			6	1			7
90	1	1	1	1			4
95	2	2					4
100		1	2	1			4
105							0
110						1	1
SUM	**28**	**21**	**20**	**10**	**0**	**1**	**80**

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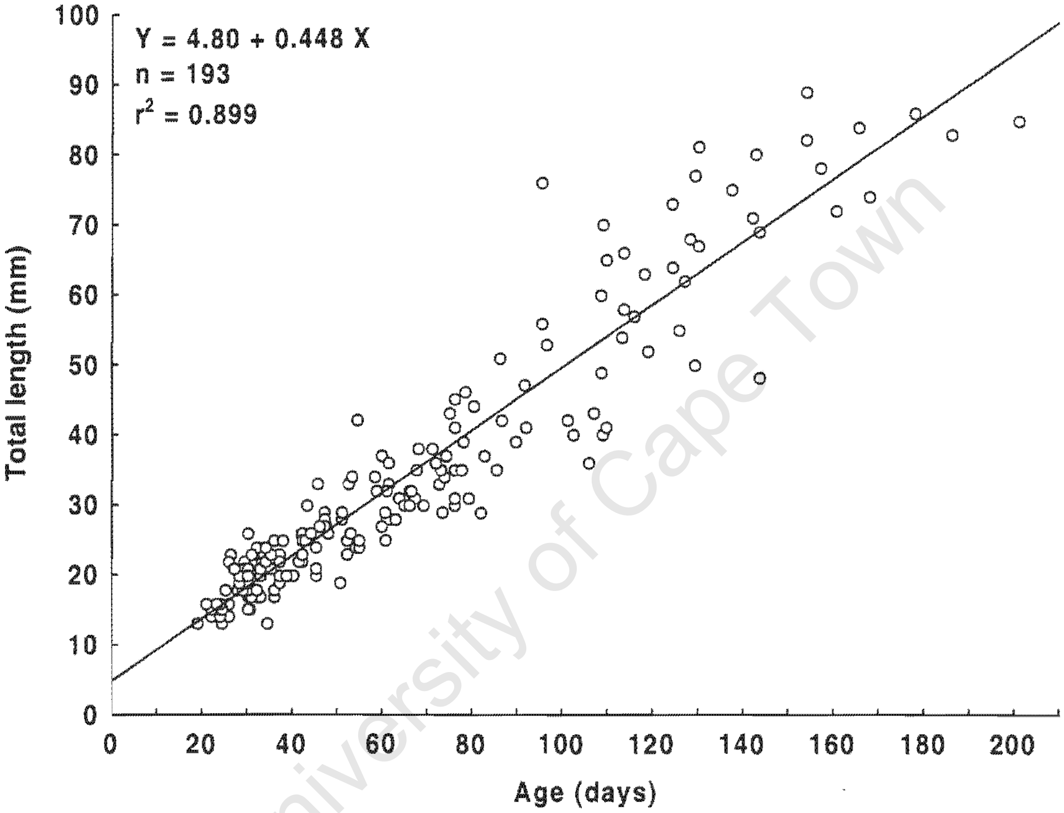
Appendix 4. Figure showing regression used for length-frequency back-calculations for the March 2000 pre-recruit survey: Total length (TL) mm against mean age (days).



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Appendix 5.A. Total Length (TL) - Standard Length (SL) key of larvae and pre-recruits caught during the pre-recruit survey in March 2000

SL	TL (mm)																																																																																						
(mm)	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	94	95	96	101	105	106	110	SUM
10	1																																																																																							1
11		1	4																																																																																				5
12			1	5																																																																																		6
13				3	7	2																																																																													12
14					1	23	3	1																																																																												28
15						3	30	18	1																																																																									52
16							2	20	28	2	1																																																																						53
17								2	14	34	8																																																																						58
18										7	42	11																																																																				60
19										2	17	33	12	2																																																																		66
20												6	36	27	4																																																																	73
21													1	11	24	5																																																																	41
22															11	28	5	1																																																																45
23																10	22	7																																																																	39
24																	4	19	17	2																																																															42
25																	1	9	16	16	1																																																														43
26																		1		14	28	6	1																																																														50
27																			1		10	26	6																																																														43
28																				1		6	20	18	1																																																											46
29																							7	20	17	6	1																																																									51
30																							1	1	16	27	10	1																																																							56
31																										10	17	10	1																																																							38
32																										1	9	14	7	2	1																																																					34
33																										1		3	16	24	6																																																							50
34																													4	10	32	7																																																						53
35																														1	16	35	8		1																																																				61
36																															1	5	26	17	1																																																			50
37																																2	2	8	13		1																																																26
38																																		1	5	10	4																																																20
39																																				4	5	2																																																11
40																																					3	8	6																																															17
41																																						2	5	7	2																																												16
42																																						1		2	10	4																																											17
43																																									1	3	2		1																																									7
44																																											3	2	1																																									6
45																																										1	3	4	5																																									13
46																																													2	3																																								5
47																																														4	4	5																																							13
48																																															1	1	1																																						3
49																																																	1	3	1																																				5
50																																																		2	4																																				6
51																																																		1	3	7	1																																		12
52																																																				1	3	2																																		6
53																																																					4	3	2	1		1																															11
54																																																							4	6				1																													11
55																																																							1	3	5	1																															10
56																																																									4	5	2																														11
57																																																										2	8	3	1																												14
58																																																										1	2	5	3	2																											13
59																																																												1	6	4	2																									13
60																																																													2	7	6	2																								17
61																																																														1	5	5	3	1																						15
62																																																														1	1	6	5	5																						18
63																																																																	1	2	4																					7
64																																																																		2	8	3																				13
65																																																																			2	7	6	1																		16
66																																																																			1	1	4	3																		9
67																																																																						3	3	1																7
68																																																																							3	1																4
69																																																																								1	3	3	1														8
70																																																																									1		2	1													4
71																																																																											2	1	2												5
72																																																																														2	1											3
73																																																																														1	2		1									4
74																																																																																1	1	1									3
75																																																																																1	2										3
76																																																																																			1								1
77																																																																																			1								1
78																																																																																	1										1
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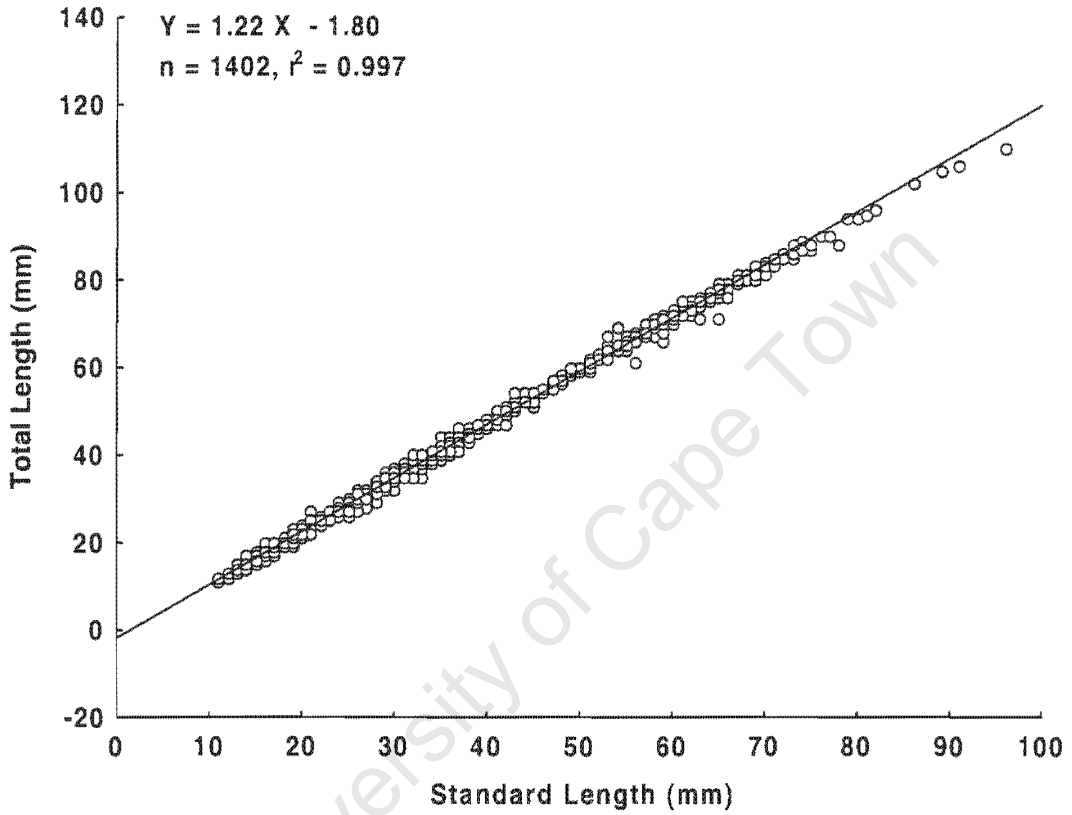
SUM	1	1	5	8	8	28	35	41	43	45	68	50	49	40	39	43	32	37	34	33	39	38	35	39	34	45	37	28	28	37	56	49	36	26	20	14	13	13	11	9	13	8	8	6	9	7	5	6	2	6	8	8	8	5	7	10	9	10	12	10	12	15	14	13	9	10	15	11	10	7	7	6	3	5	2	5	3	2	5	1	2	2	1	1	1	1	1	1	1569

Appendix 5.B. Graph showing relationship between total length (TL) and standard length (SL) of Cape anchovy larvae and pre-recruits caught in March 2000 off the west coast of South Africa.



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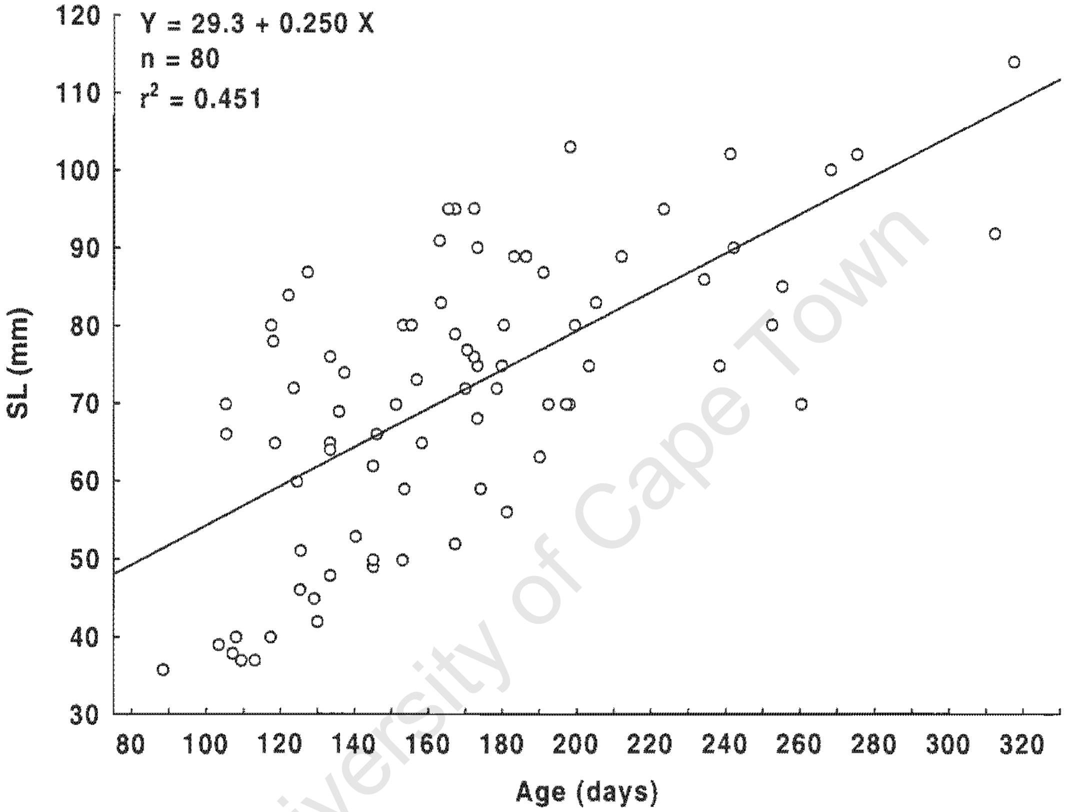
Appendix 6. Figure showing regression used for length-frequency back-calculations for the May recruit biomass survey: Standard length (SL) mm against mean age (days).



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Appendix 7. Age-length key of larvae and pre-recruits caught on the March 2000 pre-recruit survey on the west coast off South Africa. Proportion of each 15-day-age-class found at each 5-mm- standard length, SL-class.

SL	Age (days)													
(mm)	**15**	**30**	**45**	**60**	**75**	**90**	**105**	**120**	**135**	**150**	**165**	**180**	**195**	**SUM**
10	0.75	0.25	0	0	0	0	0	0	0	0	0	0	0	1
15	0.30	0.64	0.064	0	0	0	0	0	0	0	0	0	0	1
20	0.056	0.56	0.36	0.028	0	0	0	0	0	0	0	0	0	1
25	0	0.033	0.23	0.60	0.13	0	0	0	0	0	0	0	0	1
30	0	0	0.11	0.44	0.28	0.11	0.056	0	0	0	0	0	0	1
35	0	0	0.091	0	0.45	0.36	0.091	0	0	0	0	0	0	1
40	0	0	0	0	0.17	0.17	0.33	0.17	0.17	0	0	0	0	1
45	0	0	0	0	0.14	0.29	0.14	0.29	0.14	0	0	0	0	1
50	0	0	0	0	0	0	0.25	0.25	0.50	0	0	0	0	1
55	0	0	0	0	0	0	0.33	0.33	0.17	0.17	0	0	0	1
60	0	0	0	0	0	0.14	0	0.14	0.43	0.14	0.14	0	0	1
65	0	0	0	0	0	0	0	0.25	0.25	0.25	0.25	0	0	1
70	0	0	0	0	0	0	0	0	0	0	0.40	0.40	0.20	1
SUM	**1.11**	**1.48**	**0.86**	**1.07**	**1.17**	**1.07**	**1.20**	**1.43**	**1.65**	**0.56**	**0.79**	**0.40**	**0.20**	**13**

Appendix 8. Age-length key of juvenile recruits caught on the May 2000 recruit biomass survey off South Africa. Proportion of each 15-day-age-class found at each 5-mm- standard length, SL-class.

SL	Age (days)															
(mm)	**75**	**90**	**105**	**120**	**135**	**150**	**165**	**180**	**195**	**210**	**225**	**240**	**255**	**270**	**300**	**SUM**
35	0.20	0.20	0.60	0	0	0	0	0	0	0	0	0	0	0	0	1
40	0	0	0.67	0.33	0	0	0	0	0	0	0	0	0	0	0	1
45	0	0	0	0.75	0.25	0	0	0	0	0	0	0	0	0	0	1
50	0	0	0	0.20	0.40	0.20	0.20	0	0	0	0	0	0	0	0	1
55	0	0	0	0	0	0.33	0.33	0.33	0	0	0	0	0	0	0	1
60	0	0	0	0.50	0.25	0	0	0.25	0	0	0	0	0	0	0	1
65	0	0	0.29	0	0.43	0.14	0.14	0	0	0	0	0	0	0	0	1
70	0	0	0.091	0.091	0.091	0.18	0.18	0.091	0.18	0	0	0	0.091	0	0	1
75	0	0	0.11	0.11	0	0	0.44	0.11	0.11	0	0.11	0	0	0	0	1
80	0	0	0.11	0.11	0	0.33	0	0.11	0.22	0	0	0.11	0	0	0	1
85	0	0	0	0.14	0	0	0	0.43	0	0.14	0.14	0	0.14	0	0	1
90	0	0	0	0	0	0.25	0.25	0	0	0	0	0.25	0	0	0.25	1
95	0	0	0	0	0	0	0.25	0.50	0	0.25	0	0	0	0	0	1
100	0	0	0	0	0	0	0	0	0.25	0	0	0.25	0.25	0.25	0	1
SUM	**0.20**	**0.20**	**0.20**	**1.87**	**2.24**	**1.42**	**1.44**	**1.80**	**1.83**	**0.77**	**0.39**	**0.25**	**0.61**	**0.48**	**0.25**	**14**

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