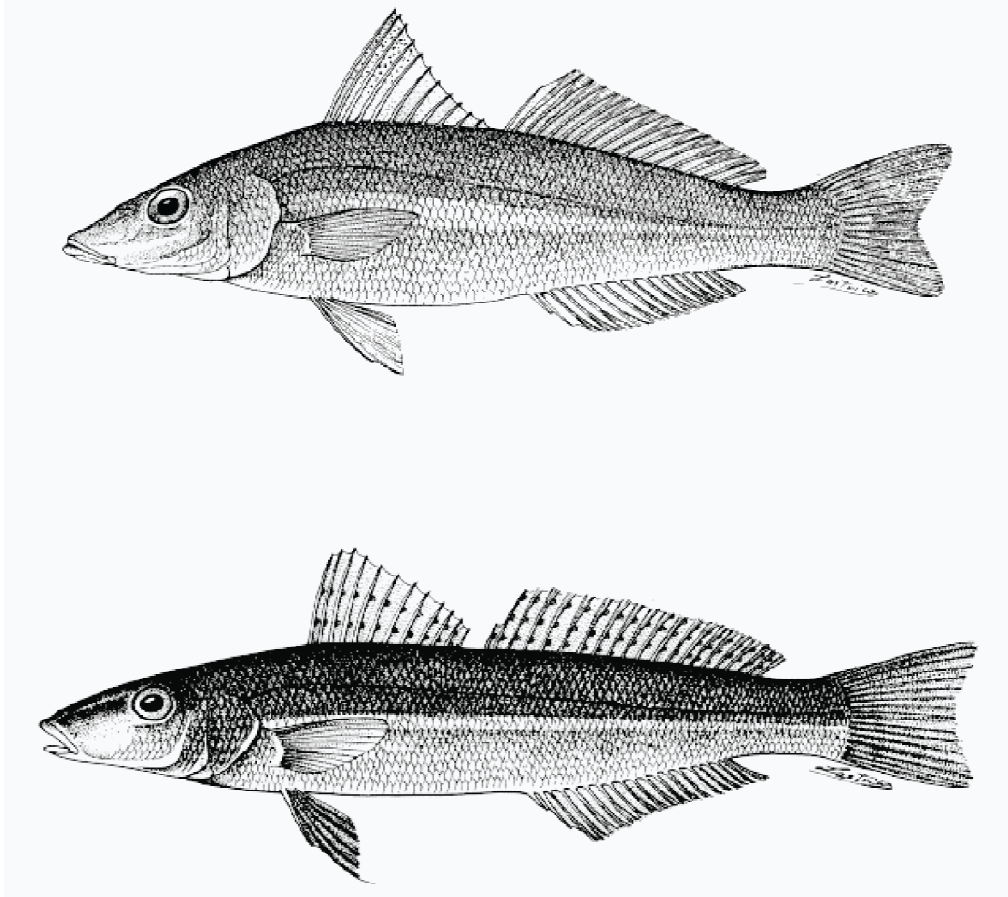


Comparisons between the biology of two species of whiting (Sillaginidae) in Shark Bay, Western Australia



By Peter Coulson

Submitted for the Honours Degree of Murdoch University

August 2003

Abstract

Golden-lined whiting *Sillago analis* and yellow-fin whiting *Sillago schomburgkii* were collected from waters within Shark Bay, which is located at ca 26°S on the west coast of Australia. The number of circuli on the scales of *S. analis* was often less than the number of opaque zones in sectioned otoliths of the same fish. Furthermore, the number of annuli visible in whole otoliths of *S. analis* was often less than were detectable in those otoliths after sectioning. The magnitude of the discrepancies increased as the number of opaque zones increased. Consequently, the otoliths of *S. analis* were sectioned in order to obtain reliable estimates of age. The mean monthly marginal increments on sectioned otoliths of *S. analis* and *S. schomburgkii* underwent a pronounced decline in late spring/early summer and then rose progressively during summer and autumn. Since these trends demonstrated that opaque zones are laid down annually in the otoliths of *S. analis* and *S. schomburgkii* from Shark Bay, their numbers could be used to help age this species in this marine embayment.

The von Bertalanffy growth parameters, L_{∞} , k and t_0 derived from the total lengths at age for individuals of *S. analis*, were 277 mm, 0.73 year⁻¹ and 0.02 years, respectively, for females and 253 mm, 0.76 year⁻¹ and 0.10 years, respectively. Females were estimated to attain lengths of 141, 211, 245 and 269 mm after 1, 2, 3 and 5 years, compared with 124, 192, 224 and 247 mm for males at the corresponding ages. The maximum ages recorded for females and males were 6 and 8 years, respectively, and the maximum lengths for females and males were 320 and 283 mm, respectively. The von Bertalanffy growth parameters derived from the total lengths at age of individuals of *S. schomburgkii* were 346 mm, 0.47 year⁻¹ and -0.09 years,

respectively, for females and 294 mm, 0.59 year⁻¹ and -0.06 years, respectively, for males. Females initially grew at a similar rate as males, attaining total lengths of 139, 216, 265 and 296 mm after 1, 2, 3 and 4 years, compared with 136, 206, 245 and 266 mm for males at the corresponding ages. The maximum ages recorded for females and males were 10 and 9 years, respectively, and the maximum lengths for females and males were 383 and 299 mm respectively. The likelihood ratio test demonstrated that the growth curves of the females and males of both *S. analis* and *S. schomburgkii* in Shark Bay were significantly different ($P < 0.001$). Since, throughout the full range of ages, the differences between the estimated lengths at age for *S. schomburgkii* in the subtropical environment of Shark Bay and those recorded previously for this species over 800 km further south in temperate waters never exceeded 5%, any differences in the estimated lengths at age are too small to be of any biological significance.

Monthly trends exhibited by the gonadosomatic indices and prevalence of the different gonad maturity stages demonstrate that *S. analis* and *S. schomburgkii* both have protracted spawning periods from October to April and from August to March, respectively. Hyndes and Potter (1997) found females and males of *S. schomburgkii* with mature and spent ovaries at stages V-VII in six months, *i.e.* October to March, in temperate waters over 800 km further south on the lower west coast of Australia. Higher average water temperatures are thus accompanied by a longer spawning period.

Since the distributions of the oocyte diameters in the ovaries of mature females of both *S. analis* and *S. schomburgkii* in Shark Bay are essentially continuous, and as mature ovaries contain oocytes at different stages in development, including “intermediate” stages such as the cortical alveolar stage, these species have

indeterminate fecundity. Thus, implicitly, *S. analis* and *S. schomburgkii* are also multiple spawners.

The females and males of *S. analis* typically attain maturity (L_{50}) at 216 and 184 mm, respectively, and maturity is typically reached by the end of their fourth years of life. The L_{50} s for female and male *S. schomburgkii* were 237 and 192 mm, respectively, and maturity is typically attained by the end of their fourth and third years of life, respectively. The above L_{50} s for the females and males of *S. schomburgkii* in Shark Bay are very similar to those estimated by Hyndes and Potter (1997) for this species in temperate waters on the lower west coast of Australia. There are indications that the length at maturity for *S. analis* and *S. schomburgkii* in Shark Bay may have decreased during the last 30 years, which may represent a response of these two *Sillago* species to fishing pressure. Preliminary mortality estimates suggest that, in Shark Bay, *S. analis* is more heavily fished than *S. schomburgkii*.

Table of contents

Abstract	1
Table of contents	5
Acknowledgments	7
Introduction	8
1.1 Ageing.....	8
1.1.1 Ageing structures	8
1.1.2 Ageing validation.....	10
1.2 Reproduction	12
1.2.1 Gonadal assessment.....	12
1.2.2 Maturity.....	13
1.2.3 Determinate and indeterminate fecundity.....	13
1.3 Nearshore habitats	14
1.4 Golden-lined, <i>Sillago analis</i> , and yellow-finned, <i>Sillago schomburgkii</i> , whiting	16
1.5 Shark Bay	19
1.6 Shark Bay Beach Seine and Mesh Net Managed Fishery.....	20
1.7 Aims of study	21
Materials and Methods	23
2.1 Sampling regime.....	23
2.1.1 Location and timing	23
2.1.2 Sampling methods	23
2.2 Environmental data.....	25
2.3 Laboratory procedures	25
2.4 Age and growth	25
2.4.1 Age determination and ageing techniques	25
2.4.2 Age validation.....	26
2.4.3 Growth.....	27
2.5 Mortality.....	29
2.5.1 Natural mortality	29
2.5.2 Total mortality	30
2.6 Reproduction	32
2.6.1 Macroscopic identification.....	32
2.6.2 Gonadosomatic indices	32
2.6.3 Ovary histology.....	32
2.6.4 Sexual maturity	33
2.6.5 Spawning mode.....	33
Results	35
3.1 Environmental measurements	35
3.1.1 Environmental measurements for Herald Bight and Dubaut Inlet.....	35
3.2 Age composition and growth of <i>Sillago analis</i>	35
3.2.1 Scales vs sectioned otoliths	35
3.2.2 Whole otoliths vs sectioned otoliths.....	35
3.2.3 Marginal increment analysis.....	36
3.2.4 Length-frequencies and age composition of <i>Sillago analis</i>	37
3.2.5 von Bertalanffy growth curves for <i>Sillago analis</i>	37
3.2.6 Growth rates	38
3.2.7 Mortality estimates of <i>Sillago analis</i>	38

3.2.8	<i>Length weight relationship</i>	39
3.3	Age and growth of <i>Sillago schomburgkii</i>	40
3.3.1	<i>Scales vs sectioned otoliths</i>	40
3.3.2	<i>Marginal increment analysis</i>	40
3.3.3	<i>Length-frequencies and age composition of Sillago schomburgkii</i>	40
3.3.4	<i>von Bertalanffy growth curves for Sillago schomburgkii</i>	41
3.3.5	<i>Growth rates</i>	42
3.3.6	<i>Mortality estimates of Sillago schomburgkii</i>	43
3.3.7	<i>Length weight relationship</i>	44
3.4	Reproduction of <i>Sillago analis</i>	44
3.4.1	<i>Gonadosomatic indices</i>	44
3.4.2	<i>Gonadal development of Sillago analis in Shark Bay</i>	45
3.4.3	<i>Description of macroscopic and histological stages of ovarian development</i>	46
3.4.4	<i>Length and age of Sillago analis at first maturity</i>	46
3.4.5	<i>Oocyte diameter frequency distributions of mature Sillago analis</i>	48
3.5	Reproduction of <i>Sillago schomburgkii</i>	49
3.5.1	<i>Gonadosomatic indices (GSI)</i>	49
3.5.2	<i>Gonadal development of Sillago schomburgkii in Shark Bay</i>	49
3.5.3	<i>Length and age of Sillago schomburgkii at first maturity</i>	50
3.5.4	<i>Oocyte diameter frequency distributions of mature Sillago schomburgkii</i> ...	51
	51
Discussion	52
4.1	Ageing structure and age validation	52
4.1.1	<i>Scales</i>	52
4.1.2	<i>Otoliths</i>	53
4.1.3	<i>Marginal increment analysis</i>	54
4.2	Length and age compositions and growth rates	55
4.3	Spawning time and period.....	56
4.4	Maturity.....	58
4.5	Spawning mode	59
4.6	Mortality.....	60
References	63

Acknowledgments

Many thanks must go to Prof. Ian Potter for giving me this opportunity to further my knowledge in fish biology. Also for his interest in the project and support throughout its duration, continued feedback allowing for greater understanding of various aspects of fish biology, and for editing my thesis. Many thanks must go to Assoc. Prof. Norm Hall for his amazing statistical input into the project and for help in editing various parts of this thesis. I would also like to thank the Fisheries Research and Development Corporation and Murdoch University for the funding of this project which made it possible. Thanks to Dr Glen Hyndes for providing data from a previous study. Thanks must also go to the Denham Fish Factory and Seafresh, Innaloo, for their help in obtaining market samples.

Many thanks must also go to Dave Fairclough for his help and advice on several field trips to Shark Bay and for showing me some great fishing spots and also for his continued help in the lab. A big thanks must also go to Alex Hesp who gave me a great deal of his time and advice in the lab with many queries, for his help in the field, and for his tireless efforts in editing, editing and further editing my thesis. I would also like to thank other members of the Murdoch University Fish Research Group and friends for their help in sampling trips: Dan French, Justin King, Bryn Farmer, Chris Marsh, Nathan Beal, Brian Coulson, Aaron Schonberg, Edmund Fenney, Claire Watterson, and Bradley Watterson. Thanks to Will “choleric” White for his help with many last minute queries. I must also thank Gordon Thompson for his expertise in sectioning continuous numbers of ovaries. Thanks.

I would also like to thank my Mum and Dad who kindly left the country and left me the house so that I could do my studies in peace and quiet and for their continued support and encouragement from such distance. I must also thank my brother “Buzz” for his help financially during my honours and for helping me keep everything in perspective. Finally, I must thank my beautiful girlfriend Claire for being loving, understanding and patient.

Chapter 1

Introduction

1.1 Ageing

Reliable determinations of age are essential for fisheries management, and the procedures used to obtain such determinations must be sound and provide valid results (Casselman, 1987). Accurate determination of age and growth can be used to provide reliable stock assessments of a species and thereby assist in conserving the stocks of this species and their sustainable utilisation (Booth *et al.*, 1995). Accurate information on age is essential for reliable calculations of growth rate, mortality and productivity, ranking it among the most important of biological variables from a fisheries point of view (Campana, 2001).

1.1.1 Ageing structures

Several calcified structures in fish undergo periodic changes in growth during the year, and thus produce “annually” formed growth zones that can be used for age determination, *e.g.* otoliths, scales, fin rays/ spines, cleithra, and opercula (Demory, 1972; Casselman, 1973; Rooper *et al.*, 2000; Kocovsky & Carline, 2000; Sipe & Chittenden, 2001). Whilst all of the above structures have been used to age fish, otoliths are the most widely used (Beamish, 1979; Maceina & Betsill, 1987; Hyndes *et al.*, 1992; Fowler & Short, 1998). The occurrence of annual rings in hard structures is associated with differences in the proportions of protein and calcium deposited during alternating slow, *i.e.* autumn/winter, and fast, *i.e.* spring/summer, phases of growth (Campana & Neilson, 1984). In general the opaque zones represent

periods of slow growth, whereas translucent zones represent periods of fast growth (Campana & Neilson, 1984).

Scales used to be the most widely employed structure for determining the age of a fish, because they can be obtained without killing the fish and are the least time consuming to collect and the least expensive to prepare (Pannella, 1974; Kocovsky & Carline, 2000). The use of scales in ageing studies, however, poses problems. One of these problems is that, because scale growth is proportional to body growth, the annuli become closely apposed on the edges of scales of older fish, which makes the identification of all of these annuli in older fish difficult (Borkholder & Edwards, 2001). Another source of error is that scales tend to be resorbed during periods of food deprivation or severe stress. Further misinterpretation of growth rings on scales may arise from damage to this external structure (Campana & Neilson, 1984; Hammers & Miranda, 1991; Rooper *et al.*, 2000). For these reasons, the use of scales has often been shown to underestimate the age of fish (Boxrucker, 1986; Beamish & McFarlane, 1987).

Of the three pairs of otoliths that occur in teleost fish, the sagittae, which are usually the largest, are the most commonly used in ageing studies (Campana & Neilson, 1984). Otoliths are considered the best structure for age estimation for most species, in part, because otolith growth is not directly linked to somatic growth (Kocovsky & Carline, 2000). Thus, it has been shown that, for several species otolith growth becomes “uncoupled” from somatic growth as the latter slows, with otolith growth continuing in an incremental manner independent of somatic growth. Otoliths are also an internal structure and are not thus subject to damage in the same way as scales (Campana, 1990; Casselman, 1990).

However, the use of otoliths also has problems. The annuli become very closely apposed at the edge of the otolith in older fish and thus, difficult to distinguish from one other. Furthermore, as a fish becomes older, the centre of the otolith becomes thicker and observing annuli in this area also becomes more difficult (Beamish & McFarlane, 1987). Because of this problem, many researchers section otoliths in order to be able to detect more readily all of the growth zones that are present (Beamish, 1979; Hyndes *et al.*, 1992). Sectioning of otoliths enhances the ability to differentiate between the outer opaque and translucent zones and often reveals one or more additional inner opaque zones in older fish (Hyndes *et al.*, 1992)

1.1.2 Ageing validation

One of the requirements for ageing a species is that the ageing method is validated. Validation of an absolute age is equivalent to determining the accuracy of an age estimate (Campana, 2001). A variety of methods can be used to validate that it is appropriate to use the number of annuli on the hard structures of fish for ageing purposes. These include analysis of cohorts in length-frequency and age composition data, analysis of the changes in the edge of the ageing structure, *i.e.* marginal increment analysis, the use of known-age fish through marking and tag and release programs (Bagenal & Tesch, 1978), captive rearing, radiochemical dating, and elemental and isotopic cycles (Campana, 2001).

The trends exhibited by modes in sequential length-frequency distributions may be used to determine the number of age classes present when, at any one time, the population consists of a series of discrete age groups. Each group is thus represented by a mode in the length-frequency distribution (Cadwallader, 1978). However, as growth slows as the individuals become older, the length distributions of

the different age classes increasingly overlap and thus their modes are no longer discrete (Cadwallader, 1978).

Marginal increment analysis is the most commonly used method for validating that the growth zones in calcified tissue are formed annually. The marginal increment on each otolith is the distance between the outer edge of the outermost opaque zone and the edge of the otolith (Maceina & Betsill, 1987; Campana, 2001). The popularity of marginal increment analysis can be attributed to its modest sampling requirements and low cost. However, this is one of the most difficult validation methods to carry out properly, due to the technical difficulties associated with viewing a partial increment affected by variable light refraction, through an edge which becomes increasingly thin as the margin is approached, as well as light reflection off the curved surface of the edge (Campana, 2001). Validating that the opaque zones in otoliths are formed annually is carried out by analysing the trends exhibited throughout the year by the marginal increments. The marginal increment is usually presented as a proportional state of completion (Campana, 2001).

The release of known age and marked fish and their subsequent recapture is probably the most rigorous method for the age validation for many species, since the absolute age of the recaptured fish is known without error (Campana, 2001). Natural markers, *i.e.* caused by a natural phenomena in the wild (radiocarbon dating, bomb radiocarbon, ^{14}C), may be used to validate ageing or marks may be produced by a variety of manipulations in the field or laboratory, including modification of food available, water temperature and light, and the exposure to a variety of chemicals such as tetracycline (Quinn *et al.*, 1981; Fowler, 1990; Francis *et al.*, 1992; Newman *et al.*, 1996; Fowler & Short, 1998; Cappel, *et al.*, 2000), acetazolamide, or strontium (Brothers, 1987).

The prevalence and impact of inaccurate age determinations on the accuracy of estimates for various population parameters studies cannot be overstated and there are many instances in which ageing error has contributed to the serious overexploitation of a population or species. The problem is usually one of age underestimation, rather than overestimation (Campana, 2001).

1.2 Reproduction

Reproductive studies of a species are typically aimed at determining the size and age at first maturity, the timing and duration of the spawning period, and fecundity, all of which require knowledge of the stage of gonadal development in individual fish (West, 1990). Reproduction is obviously an essential link in the life history of fish, with the perpetuation of any species depending on successful reproduction (deVlaming, 1983).

1.2.1 Gonadal assessment

There are several methods for determining the spawning period of a species including gonadal size, macroscopic staging and histology. Gonadal size alone is not a very useful measure because, irrespective of any maturation process, gonad size will increase in size as the size of the fish increases (West, 1990). Thus, gonadal indices (gonad weight relative to body weight) were introduced as a simple and objective measure of gonadal development (*e.g.* Le Cren, 1951). Gonad weights provide an easily measured record of changes in gonad condition (Crossland, 1977). Macroscopic staging of gonads is one of the most widely-used techniques for assigning a gonad to a particular stage in development. Macroscopic staging is the assignment of a numerical stage based on the external appearance of the ovary and the characteristics

of its oocytes, as viewed with the naked eye (West, 1990). Gonad staging on a descriptive scale allows a rapid quantitative assessment of the breeding state of fish (Crossland, 1977). The main macroscopic criterion as to whether oocytes are mature is whether they are visible through the ovarian wall and are opaque. However, accurate macroscopic staging of gonads requires considerable experience on the part of the researcher (West, 1990). Histological examination of ovaries allows for greater accuracy when assigning a particular developmental stage to an ovary through the examination of whole oocytes. In most studies, ovaries are classified according to the most advanced type of oocyte present, regardless of how numerous they are (West, 1990).

1.2.2 *Maturity*

Because growth rates of individuals and the reproductive potential of a fish population may be linked by the size and age at which individuals reach sexual maturity, it is essential to include these parameters in any investigation of population dynamics and stock assessment models (Cole, 1954; Beacham, 1982; Hannah, *et al.*, 2002). Length at first maturity is a very important parameter, particularly for commercially and recreationally important fish species, as it is frequently used as a basis for setting the minimum legal lengths at capture of a fish species.

1.2.3 *Determinate and indeterminate fecundity*

Fecundity estimates are a fundamental component of fishery science. Fecundity estimates are important because, when combined with estimates of the abundance of eggs released by mature females, they can be used to estimate the biomass of a stock (Hunter *et al.*, 1992). Annual fecundity is defined as the total

number of eggs spawned by a female in a single year and is related to the size of the female (Hunter *et al.*, 1985; Hunter, *et al.*, 1992). Just prior to spawning, females with a determinate fecundity will have a fixed number of advanced-yolked oocytes that are separated from the other less developed oocytes by a distinct gap in size. These eggs can either be spawned in batches or all at once (Nichol and Acuna, 2000). Batch fecundity, defined as the number of eggs released at one time by a female fish, can be estimated from counts of hydrated oocytes as long as the female has been caught during the hydration period and there is no evidence of recent ovulation or spawning (Hunter *et al.*, 1985; Hunter, *et al.*, 1992). Fish species with indeterminate fecundity possess ovaries that are characterised by the presence of oocytes that form continuous size distributions, reflecting the continuous maturation of oocytes throughout the spawning season. These species will typically develop multiple groups of oocytes with size distributions that overlap (Nichol & Acuna, 2000).

1.3 Nearshore Habitats

Shallow water environments are important habitats for many fish species. They are found in estuaries (Dando, 1984; Potter *et al.*, 1990; Potter & Hyndes, 1999), seagrass beds (Bell & Pollard, 1989; Ferrell & Bell, 1991; Jenkins *et al.*, 1997), protected embayments (Blaber & Blaber, 1980; Lenanton, 1982; Wright, 1988), sandy surf-zones (Ayvazian & Hyndes, 1995; Clark *et al.*, 1996) and mangroves (Bell, *et al.*, 1984; Robertson & Duke, 1987). Shallow water habitats are particularly important nursery areas for many fish as they are typically productive and contain warm water temperatures, and thus facilitate a faster rate of metabolism and thus growth. They also reduce the likelihood of predation from large piscivorous fish (Bell, *et al.*, 1984).

The value of estuaries as fish nursery areas has been attributed to the fact that, because they are very productive ecosystems, they enable fish to grow rapidly and thereby become less susceptible to predation. Furthermore, since the prevalence of large carnivorous fish is lower in estuaries than open marine waters, the degree of piscivorous predation on the juveniles of marine fish species will presumably be less in estuaries than in their natal environment (Blaber, 1980; Blaber & Blaber, 1980; Russell & Garrett, 1983).

Fish assemblages associated with seagrass beds consist mainly of small, inconspicuous species and juveniles of larger species (Bell & Pollard, 1989). The structural complexity associated with seagrass beds provides protection from predators and supplies food through the production of an abundant epifauna on the blades or indirectly through the generation of detritus (Ferrell & Bell, 1991).

Nearshore sandy beach environments provide an important alternative habitat to estuaries (Lenanton, 1982). The use of surf zones by large numbers of juvenile fishes is almost certainly related to the fact that these areas contain rich food resources in the form of zooplankton and provide protection from predation through the shallowness, turbidity and turbulence of these waters (Lasiak, 1986). Large accumulations of detached macrophytes often occur in these nearshore regions, which also provide a source of food and shelter for the juveniles of some fish species (Lenanton, 1982; Robertson & Lenanton, 1984; Lenanton & Caputi, 1989).

Mangrove habitats have long been considered major feeding sites for juvenile fish and crustaceans because they produce large quantities of detrital material. Mangrove creeks afford shelter to small fishes because they are too shallow for most piscivorous fish (Robertson & Duke, 1987). The pneumatophores and exposed roots of mangroves lining the creek banks provide both further shelter from predators, such

as birds, and increase the surface area available for epiphytic algae. Since plankton and other invertebrates are channeled through drainage creeks during ebb tides, the availability of such food types in these creeks provide is greater than in unvegetated habitats (Bell *et al.*, 1984).

Although many fish species use nearshore habitats as juveniles, some species, such as *Sillago bassensis*, *Sillago vittata*, *Sillago burrus* and *Sillaginodes punctata*, move offshore into deeper waters when they become adults. Others remain in nearshore areas for the whole of their lives, such as *Sillago analis*, *Sillago schomburgkii*, and *Sillago ciliata*. Alternatively, other species, such as *Sillago robusta* never use inshore areas, and thus spend their entire lives in offshore waters (Lenanton, 1970; Morton, 1985; Weng, 1986; Hyndes *et al.*, 1996b; Hyndes & Potter, 1996, 1997). When various teleost species are found in the same environment, the potential for interspecific competition is often reduced by the partitioning of resources amongst those species. Thus, such co-occurring species may feed on different types of food, occupy different habitats or utilize resources at different times (Schoener, 1974; Helfman, 1978; Ross, 1986).

1.4 Golden-lined, *Sillago analis*, and yellow-finned, *Sillago schomburgkii*, whiting

The perciform family Sillaginidae (whiting and sand smelts) contains three genera, three subgenera and thirty-one species of small to moderate size. The members of this family are found mainly in shallow coastal waters of the Indo-Pacific, where they contribute to both the commercial and recreational fisheries. Sillaginids are highly-valued as food in many tropical and temperate waters. Two of the three genera in the family Sillaginidae, namely *Sillaginodes* and *Sillaginopsis*, are

monotypic, whereas the third genera, *Sillago*, includes twenty-nine species (McKay, 1992).

One *Sillago* species, the golden-lined whiting (*Sillago analis*), also known as the rough-scale whiting, inhabits tropical environments from 7-30°S (McKay, 1992; Allen, 1997). It is found in the south-western Pacific and south-eastern Indian Oceans and occurs northwards from Shark Bay, Western Australia, throughout the Northern Territory and Queensland, and southwards to Moreton Bay. This species is also found on the southern coast of New Guinea, where it is commonly referred to as *Sillago nierstraszi* (McKay, 1992; Allen, 1997). The main diagnostic feature of this species is its possession of 16-18 dorsal soft-rays. The lower part of the body is light silver, whilst the dorsal surface is slightly darker in colour. A dull golden silver to golden yellow stripe is present below the lateral line of this species. The pelvic and anal fins are pale yellow to bright yellow and the pectoral fin has a darker 'dusting' of fine black and/or brown spots. *Sillago analis* attains a maximum total length of 450 mm (McKay, 1992, Allen, 1997).

The golden-lined whiting spends its entire life cycle in the protected nearshore waters of marine embayments (Hyndes and Potter, 1997). The juveniles of this species, together with the yellow-fin whiting (*Sillago schomburgkii*), occur in shallow waters around mangroves. In contrast, mature *S. analis* prefer muddy, tidal streams (McKay, 1992). *Sillago analis* is a nocturnally-feeding carnivore (Brewer and Warburton, 1992) and its 'preferred' prey is bivalve molluscs, such as *Mesodesma eltanae* (Gunn & Milward, 1985), and the siphon tips of the bivalve *Glaucanome virens* (Brewer & Warburton, 1992). Other prey include polychaetes, brachyurans, penaeids, thalassinids, mysids, amphipods, copepods, alpheids and many other crustaceans (Brewer & Warburton, 1992; Gunn & Milward, 1985; McKay, 1992).

During a study by Lenanton (1970) of the whiting fishery in Shark Bay (26°S), a large marine embayment, it was found that *S. analis* spawned over a relatively long period from November to March. The mean total length at maturity for females and males was estimated to be 210 and 180 mm, respectively.

The yellow-fin whiting (*Sillago schomburgkii*) is endemic to Australia, and inhabits subtropical and temperate waters between 20 and 36°S. This species is found in the eastern Indian Ocean, southwards from Dampier to Albany in Western Australia, and also occurs in the St Vincent and Spencer Gulfs in South Australia. It is not known whether it occurs in the intervening waters. The main diagnostic feature of *S. schomburgkii* is its possession of 19-22 dorsal soft-rays. This species attains a maximum total length of 420 mm and a maximum age of 12 years (Hutchins & Swainston, 1986; McKay, 1992).

Sillago schomburgkii generally frequents inshore waters over sand banks, bars and spits, and congregates in sandy hollows (McKay, 1992) and, like *S. analis*, remains in sheltered nearshore waters throughout its entire life cycle (Hyndes & Potter, 1997; Hyndes *et al.*, 1997a). At high tide, *S. schomburgkii* move in schools across sand flats and retreat to the slopes of banks when the tide falls. Juveniles inhabit either mangrove-lined creeks or protected inshore areas, over muddy bottoms or seagrass (McKay, 1992). Like several other whiting species, crustaceans and polychaetes are the prey that are most frequently ingested by *S. schomburgkii* (Hyndes *et al.*, 1997a).

During his study on whiting in Shark Bay, Lenanton (1970) found that *S. schomburgkii* spawned between September and March and that, on average, the females and males of this species mature at total lengths of *ca* 230 mm and 200 mm, respectively. In contrast to these findings for Shark Bay, Hyndes and Potter (1997)

found that, in nearshore waters on the lower west coast of Australia (*ca* 32°S), *S. schomburgkii* spawn between October and February and reach maturity at a similar size to that found by Lenanton (1970) for individuals of this species in Shark Bay, *i.e.* 230 mm and 200 mm females and males, respectively.

1.5 Shark Bay

Shark Bay is situated *ca* 800km north of Perth at *ca* 26°S, 114°E in Western Australia, and was inscribed on the World Heritage List in 1991. The Shark Bay World Heritage Property that encompasses the westernmost point of Australia occupies a total area of 2.2 million hectares, 71% of which consists of marine habitat containing more than 1500 km of mostly pristine coastline (Walker *et al.*, 1988; Marsh, 1990).

Shark Bay stretches from the north end of Bernier Island (24°45'S, 113°10'E) to the south end of Freycinet Harbour (26°36'S, 113°41'E). Shark Bay is a large (13 000 km²), shallow (mainly <15 m) basin with an average depth of 9 m and a maximum depth of *ca* 29 m (Walker *et al.*, 1988; Marsh, 1990). The bay is enclosed by Bernier, Dorre and Dirk Hartog Islands and is subdivided internally by dune ridges and submerged banks or sills into numerous inlets, gulfs and basins (Marsh, 1990). Shark Bay is characterised by two important features: extensive intertidal and shallow subtidal sandflats with seagrass beds containing a remarkable number of species of plants and a gradient of increasingly saline water which reaches 65 ppt in the distal parts of the bay farthest from the open sea (Black *et al.*, 1990).

The total area of mangroves in the Shark Bay region, from Miaboolia Beach north of the Gascoyne River to South Passage, Shark Bay, is 1700 hectares, excluding the mangrove area of Dubaut Inlet. This area includes saltmarsh, front-flats and back-

flats. The two main species of mangroves in the Gascoyne region are *Avicennia marina* and *Aegialitis annulata* (Johnstone, 1990; Pedretti & Paling, 2001).

1.6 Shark Bay Beach Seine and Mesh Net Managed Fishery

Seine netting for scale fish in Denham, Shark Bay, started in the late 1920s. Pearl luggers in Denham supplemented their income by shipping fish to Singapore and the eastern states. With the availability of road transport (1942), freezer storage (1948) and later, an air service, the market flourished. The number of men and boats and the annual catch continued to rise until about 1963. In the late 1960s, research indicated that the whiting stocks were declining as a result of overfishing (Shaw, 2000). Recommendations were made for the fishery to be managed, which resulted in a reduction in the number of fishing units from of 17 in 1964 to nine at the current time (Shaw, 2000).

In the Shark Bay Beach Seine and Mesh Net Managed Fishery, each unit has one primary vessel, a maximum of three netting dinghies and a team of no more than three fishers. Most of the whiting are caught between April and September, when the high tides allow netting on the majority of the shallow banks. Since the winds are usually lighter in these months of the year, it is usually easier to fish during this period (Shaw, 2000).

The Shark Bay Beach Seine and Mesh Net Managed Fishery takes a mixed catch of whiting (Sillaginidae), sea mullet (*Mugil cephalus*), tailor (*Pomatomus saltrix*) and yellowfin bream (*Acanthopagrus latus*). Whiting is the main target species in Shark Bay, with the overall catch consisting primarily of two species of whiting, *i.e.* *S. schomburgkii* and *S. analis* (Anon., 2002).

This fishery, although relatively small-scale, makes a significant contribution to the Denham economy and community. The commercial production during the 2001 season was 259 tonnes (all finfish), of which 115.3 tonnes were whiting. The estimated annual value for the 2001 season was \$750 000 (all finfish), of which whiting accounted for \$414 000 (Anon., 2002).

1.7 Aims of study

The overall aims of this study were to determine the size and age compositions, growth rates and aspects of the reproductive biology of *Sillago analis* and *Sillago schomburgkii* in Shark Bay and to compare these results with those recorded by Lenanton (1970) for Shark Bay and by Hyndes and Potter (1997) for the lower west coast of Australia. Although some very useful information was provided by Lenanton's (1970) study on the life cycles of these two whiting species in Shark Bay, the present study provides data produced using methods and techniques that were unavailable when these fish were previously studied. The specific aims of the present study were to determine the following for *Sillago analis* and *Sillago schomburgkii*:

1. The most appropriate structure for ageing these fish and whether growth zones are formed annually.
2. Length and age compositions and growth rates.
3. Time and duration of spawning.
4. Total lengths (*i.e.* L_{50}) and ages at which females and males first attain maturity.
5. Whether these species are multiple spawners and whether they have determinate or indeterminate fecundity.

6. Whether there is evidence that either species is suffering high fishing mortality.
7. Compare the results obtained for these two species in the present study with those obtained by Lenanton (1970) during the late 1960s and 1970s to determine whether any aspect of the biology of the two species of whiting have changed as a response to a marked reduction in fishing pressure.
8. Finally, aspects of the biology of *Sillago schomburgkii* in Shark Bay will be compared with those in other regions in Australia to determine whether differing environmental effects influence the biological characteristics of this species.

Chapter 2

Materials and Methods

2.1 Sampling regime

2.1.1 Location and timing

Sampling for juvenile and adult *Sillago analis* and *Sillago schomburgkii* was concentrated in nearshore, shallow waters at Herald Bight and Dubaut Inlet on the western side of Peron Peninsula, Shark Bay, situated on the mid-west coast of Australia (Map 1). These two sites contain intertidal mangroves and creeks and are bordered by open sand flats (Plate 1). Herald Bight has a total mangrove area of *ca* 100 ha (Johnstone, 1990). The total area of mangroves at Dubaut Inlet is unknown. Additional opportunistic samples of juveniles and adults were obtained from Bush Bay, Uendoo Creek, Oyster Creek, and Cape Peron and South Passage respectively (Map 1). Sampling for both juvenile and adult fish was always conducted during the day.

2.1.2 Sampling methods

Samples of juvenile *S. analis* and *S. schomburgkii* were obtained using a 21.5 m seine net, which comprised two 10 m long wings, each consisting of 6 m of 9 mm mesh and 4 m of 3 mm mesh, and a 1.5 m long pocket of 3 mm mesh. The net fished to a maximum depth of 1.5 m and covered an area of *ca* 116 m² (Plate 2). Four replicate seines were dragged on each sampling occasion at each site. The seine net was deployed in a circle in both mangrove inlets and along mangrove edges on the bordering sand flats at Herald Bight and Dubaut Inlet (Plate 3). Six opportunistic

seine net samples were also obtained at each of Uendoo Creek, Bush Bay and Oyster Creek in September and November 2002 and January, February, June and July of 2003. Sampling was carried out in the same way as described above for replicate sampling.

Adult fish were sampled using gill nets at Herald Bight and by rod and line fishing at Dubaut Inlet on each sampling occasion and opportunistically at other sites around Cape Peron (Map 1). The four gill nets used were 21 m in length and each consisted of three equal sized panels with different mesh sizes (*i.e.* 50, 75, and 100 mm mesh). The gillnets fished to a maximum depth of 1 m. Gill nets were set perpendicular to the mangroves bordering the sand flats. One end of the gill net was attached to the mangroves while the other end was either attached to a stake that was hammered into the sediment or tied to a weight and float (Plate 4). A total of four replicate samples were collected on each sampling occasion, two on the sand flats and two in the inlet in every second month from December 2001 through to August 2002 at Herald Bight. Gill nets, the same as above as well as a further four nets, each consisting of a single panel of 50 mm mesh, were also set opportunistically during September and November of 2002, and January, February, March of 2003 at Herald Bight. When sampling using rod and line, size 8 and 10 long shank hooks were used. Coral prawns were found to be the most suitable bait. Fish were also obtained from the wholesale fish market in Shark Bay and from retail fish markets in Perth, when available, to supplement samples.

2.2 Environmental data

Water temperature was recorded on each sampling occasion at Herald Bight and Dubaut Inlet using a Yellow Springs Instruments Salinity, Conductivity and Temperature meter (Model YSI 30).

2.3 Laboratory procedures

The total weight (TW) and total length (TL) of each *S. analis* and *S. schomburgkii* were recorded to the nearest 1 g and 1 mm, respectively.

2.4 Age and growth

2.4.1 Age determination and ageing techniques

The sagittal otoliths of each individual of both *Sillago* species were removed, cleaned, dried and stored in labeled envelopes. A preliminary examination of both whole and sectioned otoliths from fish of various sizes was conducted to determine whether the clarity of the opaque zones was improved by sectioning. Whole otoliths were placed in a small black dish and covered with methyl salicylate and examined under reflected light using a dissecting microscope. The number of opaque zones that were visible on each otolith was recorded. The same otoliths were then mounted in clear epoxy resin and cut transversely through their primordia into *ca* 0.6 mm sections using an Isomet Buehler low-speed diamond saw. The sections were ground with fine wet and dry carborundum paper (Grade 1200) and mounted on glass microscope slides with DePX mounting adhesive and a cover slip. Subsequently, each slide was placed on a black surface and viewed in the same manner as whole otoliths, and the number of visible opaque zones was recorded. Since the opaque zones typically were more clearly visible on sectioned otoliths, the otoliths of all fish were sectioned for

ageing purposes. The number of opaque zones on each otolith was recorded. To determine if there was any reader bias in the ageing of these fish, comparisons were made between the number of opaque zones that could be observed on sectioned otoliths of 100 fish from a wide size range by the author and an experienced reader of otoliths (Alex Hesp – Murdoch University Fish and Fisheries Research Centre).

Scales were removed from a subsample of 100 *S. analis* and 80 *S. schomburgkii*, representing individuals in each 10 mm size class from 70 to 290 mm and 70 to 350 mm, respectively, to determine whether scales could be used for ageing these two *Sillago* species. A minimum of five scales were removed from just behind the pectoral fin on the left-hand side of each fish, dried and then stored in labelled envelopes. These scales were later placed between two glass microscope slides that were taped together with cellulose tape and viewed using the computer package Leica Image Manager 1000 (Leica Microsystems Ltd., 2001), which obtained the image via a video camera (Leica DC 300) attached to a Leica M27₅ dissecting microscope using reflected light. The scale with the clearest circuli was used for providing counts of the growth zones of each fish. Counts of the number of circuli on each scale and the number of opaque zones on the corresponding sectioned otolith of each fish were recorded.

2.4.2 Age validation

Whenever possible, a minimum of 20 otoliths per month for both *Sillago* species were used for age validation. The distance between the primordium and both the outer edge of the otolith and the outer edge of the single zone when only one zone was present and between the outer edges of the two outermost opaque zones when two or more opaque zones were present were all measured along the same axis, *i.e.*

perpendicular to the opaque zone (*e.g.* Hyndes *et al.*, 1992, 1996a). The marginal increment, *i.e.* the distance between the outer edge of the single or outermost opaque zone and the periphery of the otolith has been calculated for each otolith. Measurements were recorded to the nearest 0.1 mm using a dissecting microscope with a graticule in the eyepiece under reflected light. Since the number of otoliths containing \geq four opaque zones was far less than those with one, two and three zones, the marginal increment values for all otoliths with \geq four opaque zones in each month have been pooled (see results section).

The trends shown by the mean monthly marginal increments on otoliths with differing numbers of opaque zones were examined to determine whether the marginal increment underwent a single decline and rise each year, and thereby demonstrated that one opaque zone was formed annually and that the number of opaque zones could thus be used to ascertain determining the ages of *S. analis* and *S. schomburgkii*.

2.4.3 Growth

A birth date was assigned to *S. analis* and *S. schomburgkii*, based on the estimated peak time of spawning, which was determined from the monthly trends exhibited by gonadosomatic indices, gonadal maturity stages and oocytes stages. von Bertalanffy growth curves were fitted to the lengths of individuals of both sexes at the estimated age at the time of capture by using SPSS (SPSS Inc., 2001). The lengths at age of juvenile fish of both *Sillago* species < 80 mm TL, which could not be sexed macroscopically, were alternately allocated to the female and male data sets used for calculating the von Bertalanffy growth curves. The von Bertalanffy growth equation is

$$L_t = L_\infty [1 - \exp^{-k(t-t_0)}],$$

where L_t is the length (mm TL) at age t (years), L_∞ is the mean asymptotic length predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length if growth had followed that predicted by the equation. The growth equations for female and male *S. analis* and *S. schomburgkii* in Shark Bay were compared using a likelihood-ratio test (see Kimura, 1980). The hypothesis of a common growth curve for the two sexes, was rejected at the $\alpha = 0.05$ level of significance if the test statistic, calculated as twice the difference between the log-likelihood obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two approaches (e.g. Cerrato 1990). The log-likelihood, λ , for each curve, ignoring constants, was calculated as $\lambda = -\frac{n}{2} \ln\left(\frac{ss}{n}\right)$, where n refers to the sample size, \ln is the natural logarithm, and ss refers to the sum of the squared residuals between the observed and expected lengths at age.

A likelihood-ratio test was also used to compare the growth curves derived by Hyndes and Potter (1997) for each sex of *S. schomburgkii* at ca 32°S on the lower west coast of Australia and those derived in the present study at ca 26°S in Shark Bay. The question of whether the lengths at age of the growth curves of *S. schomburgkii* for the two latitudes differed at each of the ages 1, 2, and 3 years was explored by reparameterising the von Bertalanffy growth equation in terms of the lengths at two reference ages (Schnute, 1981) and the growth coefficient k . Growth curves were fitted simultaneously to both data sets, using a penalty function to ensure that the difference between the calculated values of t_0 for the two curves was negligible. For each of the specified reference ages, 1, 2, 3, and 4 years, separate curves were first

fitted to the data sets for the two different latitudes. Subsequently, these growth curves were constrained such that the length at this reference age was common to both curves. The difference between the log-likelihoods for these two analyses was tested using the likelihood ratio test to determine whether the length of the specified age differed between the two data sets.

2.5 Mortality

2.5.1 Natural mortality

Natural mortality (M) was calculated using three empirical methods, namely those of Pauly (1980), Ralston (1987) and Rikhter and Efanov (1976). Pauly (1980) developed a relationship between natural mortality rate, M , and the growth parameters k and L_∞ in the von Bertalanffy growth equation and temperature, T , using data from 175 fish stocks. In order that the 95% confidence limits were calculated a linear regression was refitted to Pauly's (1980) data. The resulting regression model using natural logarithms, is

$$\ln_e M = -0.0152 - 0.279 \ln_e L_\infty + 0.6543 \ln_e k + 0.4634 \ln_e T,$$

where T = mean annual surface temperature (°C) and L_∞ (mm) and k (years⁻¹) are the von Bertalanffy growth parameters. An estimate of M was determined for *S. analis* and *S. schomburgkii* in Shark Bay by inserting estimates of L_∞ and k , derived from their respective growth equations, into the regression model above. The mean annual surface water temperature in Denham, Shark Bay (22.5°C), was determined from data obtained by the Australian Oceanographic Data Centre (<http://www.AODC.gov.au>).

An estimate of M and its confidence limits were also calculated by refitting a linear regression to Ralston's (1987) data. The refitted version of Ralston's regression equation is

$$M = 0.0189 + 2.06 k,$$

where k (years⁻¹) is the von Bertalanffy growth coefficient.

A further estimate of M was calculated using the regression equation developed by Rikhter and Efanov (1976) who found M to relate to the age at which 50% of fish first attained maturity. Their equation is:

$$M = (1.521/Tm_{50}^{0.72}) - 0.155,$$

where Tm_{50} is the age at which 50% of *S. analis* and *S. schomburgkii* first attained maturity. The value of Tm_{50} was estimated using the following equation,

$$Tm_{50} = t_0 - 1/k \ln(1-Lm_{50}/L_{\infty}),$$

where t_0 , k and L_{∞} are the von Bertalanffy parameters and Lm_{50} is the estimated length at 50% maturity (Rikhter and Efanov, 1976).

For all these natural mortality rates, M and its 95% confidence limits were calculated for females and males. The final M was calculated by finding the mean of the female and male mortality rates, and conservative estimates of the confidence intervals were derived from the lowest and highest values of the corresponding confidence limits for females and males.

2.5.2 Total mortality

To determine the age at full recruitment for each species, a preliminary age frequency histogram was plotted for the commercial catch data. Normally, only age classes following the 'peak' on the descending limb of such a 'catch curve' are used in following analyses for calculating Z (Ricker, 1969; 1975). This approach was used for *S. schomburgkii*, however in the case of *S. analis*, this was not possible for yielding a reliable estimate of Z , as there were limited data. Therefore, in the case of *S. analis*, the age classes above, and that which included the peak, were all used to

estimate Z . Thus, the value for Z for *S. analis* is considered as a preliminary estimate, which may represent a slight underestimate for the true value for Z .

An estimate of total mortality (Z) was obtained by using the age composition data for commercial samples of *S. analis* and *S. schomburgkii* from Shark Bay collected during the study. For a fish stock that experiences a constant level of Z from the age of full recruitment (into the fishery), $a=t_c$ years, the estimated proportion, $\hat{p}_{a,t}$,

at age a is $\hat{p}_{a,t} = \frac{\exp[-(a-t_c)Z]}{\sum_{j=t_c}^A \exp[-(j-t_c)Z]}$, where A is the maximum observed age. It was

assumed that the level of annual recruitment is constant. It was also assumed that the age composition for fish of ages $t_c \leq a \leq A$ observed in year t , represents a random sample from a multinomial distribution with uniform selectivity from the age of full recruitment. Ignoring constants, the log-likelihood, λ , of the age compositions was

calculated as $\lambda = \sum_{a=t_c}^A n_{a,t} \log[\hat{p}_{a,t}]$, where $n_{a,t}$ is the observed number of fish of age a in

year t . The parameters of the model were estimated by maximizing the log-likelihood, using the SOLVER routine in Microsoft™ Excel. For each species, the data were randomly resampled and analysed to create 1000 sets of bootstrap estimates. The point estimate of Z was taken as the median of the 1000 bootstrap estimates. The 95% confidence limits were calculated as the 2.5 and 97.5 percentiles of the corresponding predicted values.

Values of Z were also estimated by using the observed maximum age (t_{\max}) for *S. analis* in all samples, as well as solely for the commercial samples, and in the case of *S. schomburgkii* in all samples, employing the following regression equation for fish by Hoenig (1983),

$$\ln(Z) = 1.46 - 1.01 \ln(t_{\max}).$$

When calculating total mortality using catch curve analysis and Hoenig's (1983) method, data for females and males were pooled.

2.6 Reproduction

2.6.1 *Macroscopic identification*

The sex of each fish > 80 mm was determined macroscopically. The gonads of each fish were removed, weighed to the nearest 0.01g, and allocated macroscopically to one of the following stages of maturity, based on the criteria of Laevastu (1965): I = virgin; II = maturing virgin; III = developing; IV = maturing; V = mature; VI = spawning; VII = spent; VIII = recovering.

2.6.2 *Gonadosomatic indices*

Gonadosomatic indices (GSI) were determined from the following equation

$$(W1 / (W2 - W1)) \times 100,$$

where W1 = gonad weight and W2 = body weight. The indices were calculated using data from fish \geq the estimated L_{50} at first maturity, i.e. 230 and 190 mm for females and males, respectively (see section 2.6.4).

2.6.3 *Ovary histology*

Ovaries of up to 10 large females collected in each month were placed in Bouin's fixative for 24 h, dehydrated in 70% ethanol and then embedded in paraffin wax. Transverse sections (6 μ m) of the mid-region of each ovary was stained with Mallory's trichrome. The terminology for the oocyte stages follows that given by Khoo (1979).

2.6.4 *Sexual maturity*

Lengths of both sexes at first maturity were estimated by fitting a logistic regression to the proportion of those fish, which, in each 10 mm class interval of *S. analis* and each 20 mm class interval of *S. schomburgkii*, possessed, during the spawning period of the species, gonads at stages III to VIII and were thus likely to have spawned during that period. The curve was fitted using SPSS (SPSS Inc., 2001). The logistic equation is

$$P_L = 1/[1 + e^{(a + bL)}]$$

where P_L is the proportion of fish with mature gonads at length interval L and a and b are constants. The L_{50} , which represents the length at which 50% of the individuals possessed gonads at stages III to VIII, was calculated from the equation $L_{50} = -a/b$.

From preliminary examinations of both *S. analis* and *S. schomburgkii* caught during their respective spawning periods, it was found that the majority of female fish ≥ 230 mm and male fish ≥ 190 mm would reach stages III-VIII and therefore be mature. Thus, trends shown by the gonadosomatic indices and gonadal development (see results section) were determined using female and male fish of both these species \geq these lengths.

2.6.5 *Spawning mode*

To determine whether *S. analis* and *S. schomburgkii* had determinate or indeterminate fecundity, sections of four randomly-selected mature ovaries from fish that were caught during the spawning period and were ≥ 230 mm total length (length at first maturity) were examined. The circumferences of 100 randomly selected oocytes were measured to the nearest 0.1 μm using a high-resolution projection screen attached to an Olympus BH-2 compound microscope. These circumferences, which

were recorded only for oocytes that had been sectioned through their nuclei, were then used to calculate the diameters of the oocytes.

Chapter 3

Results

3.1 Environmental measurements

3.1.1 *Environmental measurements for Herald Bight and Dubaut Inlet*

The mean monthly water temperatures for sampling regions in Shark Bay declined from a maximum of *ca* 29°C in mid summer to *ca* 26°C in mid autumn and then to a minimum of *ca* 17°C in late winter, before rising to *ca* 27°C in late spring (Fig. 3.1).

3.2 Age composition and growth of *Sillago analis*

3.2.1 *Scales vs sectioned otoliths*

Although the number of growth zones detected in sectioned otoliths were sometimes the same as those that were observed in scales, this frequently was not the case (Fig. 3.2). Furthermore, in these latter cases, the number of opaque zones visible in sectioned otoliths was generally greater than the number of circuli visible in the scales of the corresponding fish and, in one case, the difference in the number was as great as three (Fig. 3.2).

3.2.2 *Whole otoliths vs sectioned otoliths*

The number of opaque zones that could be detected on the otoliths of *S. analis* after sectioning were the same as those on otoliths that contained either no opaque zones or only a single opaque zone (Fig. 3.3). However, this was frequently not the case when the number of opaque zones that could be detected in sectioned otoliths

was more than one. In such cases, the number of opaque zones visible in whole otoliths was always less than that which could be detected in sectioned otoliths of the same fish. Furthermore, the magnitude of such discrepancies increased as the number of opaque zones increased, with a maximum difference of three opaque zones being recorded in the fish with the greatest number of annuli (Fig. 3.3).

3.2.3 Marginal increment analysis

The mean monthly marginal increments for sectioned otoliths of *S. analis* with two opaque zones remained at 0.48 to 0.58 between July and October, before declining precipitously to a minimum of 0.19 in November and then increasing progressively to 0.57 in March and remaining at about this level in the immediately ensuing months (Fig. 3.4). The mean monthly marginal increments for otoliths with three and or ≥ 4 opaque zones, respectively, followed essentially the same trend as that just described for otoliths with two opaque zones. Although no fish with otoliths containing one opaque zone were caught in either October or December, the mean monthly marginal increments for the otoliths of such fish in the other months of the year followed a similar trend to that just described for fish with a greater number of opaque zones (Fig. 3.4). The presence of a single pronounced decline and rise in the mean monthly marginal increment during the year demonstrates that a single opaque zone is formed annually and that the number of opaque zones in the sectioned otoliths of *S. analis* can thus be used to assist in ageing this species (Fig. 3.4).

3.2.4 *Length-frequencies and age composition of Sillago analis*

Since *S. analis* were not able to be sexed until they had reached lengths of *ca* 80 mm, the lengths at age of 0+ juveniles below this length were alternately allocated to the length-at-age data sets for females and males (Figs 3.5 and 3.6). Substantial numbers of early 0+ juveniles, ranging in length from 21-79 mm, were first caught in June (Fig. 3.5). By November, when the 0+ cohort was, on average, 10 months old, this species had attained an average length of 110 mm (range = 71-159 mm). By the end of their second, third and fourth years of life, females had attained an average length of 170, 240 and 260 mm, respectively, and males had attained an average length of 160, 220 and 250 mm, respectively (Fig. 3.5).

3.2.5 *von Bertalanffy growth curves for Sillago analis*

The von Bertalanffy growth curve fitted well the lengths at age of both female and male *S. analis* (Fig. 3.6), as is demonstrated by the relatively high values for the coefficient of determination (R^2), *i.e.* 0.80 and 0.86, respectively, and values for t_0 that were close to zero (Table 3.1). The growth coefficient (k) and asymptotic length (L_∞) of females were 0.73 years⁻¹ and 277 mm, respectively. Female *S. analis* attained lengths of 141, 211, 245 and 269 mm at 1, 2, 3 and 5 years of age, respectively (Fig. 3.6). The maximum length and age recorded for female *S. analis* was 320 mm and 6 years, respectively.

In comparison with females, the value for k for male *S. analis* was slightly higher, *i.e.* 0.76 years⁻¹, and that for the L_∞ was slightly lower, *i.e.* 253 mm (Table 3.1). Male *S. analis* attained lengths of 124, 192, 224 and 247 mm at 1, 2, 3, and 5 years of age, respectively (Fig. 3.6). The maximum length and age recorded for males was 283 mm and 8 years, respectively.

Table 3.1. von Bertalanffy growth parameters L_∞ , k , and t_0 including upper and lower 95% confidence limits, derived from length at age data for *Sillago analis* caught in Shark Bay, Western Australia. R^2 = coefficient of determination, n = sample size.

		von Bertalanffy parameters				
		L_∞ (mm)	k (year ⁻¹)	t_0 (years)	R^2	n
Female	Estimate	276.6	0.731	0.024	0.805	693
	Upper	282.7	0.797	0.095		
	Lower	270.4	0.665	-0.047		
Male	Estimate	253.2	0.757	0.105	0.862	425
	Upper	259.3	0.826	0.169		
	Lower	247.2	0.689	0.041		

3.2.6 Growth rates

The likelihood ratio test demonstrated that the growth curves of female and male *S. analis* were significantly different ($P < 0.001$). The difference between the predicted lengths of female and male *S. analis*, expressed as a percentage of the lowest value of L_∞ for the two growth curves, at ages 1, 2, 3, and 4 was 6.5, 7.2, 8.0, and 8.5%, respectively, and was always $> 5\%$ throughout the full range of ages.

3.2.7 Mortality estimates of *Sillago analis*

The point estimates for the instantaneous coefficient of natural mortality, M , for *S. analis*, derived by taking the mean of the values estimated for female and male using the regression equations refitted to the data of Pauly (1980) and Ralston (1987) were similar, *i.e.* 1.55 and 1.44 year⁻¹, respectively. However, the confidence intervals for these point estimates were very broad (Table 3.2). In contrast, the point estimate of M for *S. analis* derived for the separate sexes using the equation of Rikhter and Efanov (1976) was considerably lower, *i.e.* 0.78 year⁻¹, than those derived from the empirical equations of Pauly (1980) and Ralston (1987) (Table 3.2).

The point estimate for the instantaneous coefficient of total mortality, Z , *i.e.* 0.99 year^{-1} derived using the regression equation refitted to Hoenig's (1982, 1983) data for fish, was lower than all the point estimates calculated for M using Pauly's (1980) and Ralston's (1987) refitted regression equations, but higher than the point estimate calculated for M using Rikther and Efanov's (1976) equation (Table 3.2). However, the point estimate for Z , *i.e.* 1.95 years^{-1} for *S. analis*, calculated from catch curve analysis employing the resampling approach was higher than that derived using the refitted Hoenig (1983) equation, and also higher than all of the estimates for M . The confidence intervals for Z calculated from the catch curve analysis were far narrower than those calculated using the method of Hoenig (Table 3.2).

Table 3.2. Mortality estimates (year^{-1}) of *Sillago analis* in Shark Bay calculated using different methods. M = natural mortality, Z = total mortality, N = no value could be obtained.

Method of analysis	M or Z	Estimate	Lower 95%	Upper 95%
Refitted Pauly (1980)	M	1.55	0.44	4.53
Refitted Ralston (1987)	M	1.44	0.93	1.98
Rikther and Efanov (1976)	M	0.78	N	N
Refitted Hoenig (1983)	Z	0.99	0.32	3.10
Catch curve analysis	Z	1.95	1.70	2.27

3.2.8 Length weight relationship

The relationships between total length (TL) in mm and total weight (TW) in g for female and male *S. analis* are shown in Figure 3.7 and described by the following regression equations.

Females $\ln \text{ TW} = 3.001(\ln \text{ TL}) - 11.711$ ($R^2 = 0.994$, $n = 742$)

Males $\ln \text{ TW} = 2.983(\ln \text{ TL}) - 11.611$ ($R^2 = 0.996$, $n = 429$),

where R^2 is the regression coefficient and n is the sample size.

3.3 Age and Growth of *Sillago schomburgkii*

3.3.1 Scales vs sectioned otoliths

The number of growth zones detected in sectioned otoliths that were the same as those that were observed in scales occurred only when either no opaque zones or a single opaque zone was visible in sectioned otoliths of *S. schomburgkii* (Fig. 3.8). The number of growth zones detected in scales consistently was shown to be less than that in sectioned otoliths when one or more opaque zones were visible, and in one case the difference was as great as four (Fig. 3.8).

3.3.2 Marginal increment analysis

The mean monthly marginal increments for sectioned otoliths of *S. schomburgkii* with one opaque zone remained at 0.40 to 0.49 between July and October before declining markedly to a minimum of 0.19 in November and then increasing progressively to 0.34 in March and to 0.44 in June (Fig. 3.9). The mean monthly marginal increments for otoliths with two, three or ≥ 4 opaque zones followed essentially the same trend as that described above for otoliths with one opaque zone (Fig. 3.9). As was the case for *S. analis*, the mean monthly marginal increments for otoliths of *S. schomburgkii* declined markedly only once during the year and then rose progressively, demonstrating that the opaque zones are formed annually and can thus be used to age this species.

3.3.3 Length-frequencies and age composition of *Sillago schomburgkii*

Since *S. schomburgkii* were not able to be sexed until they had reached lengths of ca 80 mm, the lengths at age of 0+ juveniles below this length were alternately allocated to the length-at-age data sets for females and males. Small numbers of early

0+ juveniles, which ranged between 11 and 79 mm, were first caught in January (Fig. 3.10). By April, when individuals of the 0+ cohort were, on average, 4 months old, they had attained an average length of 80 mm (range 61-129 mm). By the end of their first year of life, *S. schomburgkii* had reached an average length of 120 mm. By the end of their second, third and fourth years of life, female *S. schomburgkii* had attained average lengths of 210, 270 and 300 mm, respectively, and male *S. schomburgkii* had attained average lengths of 200, 250 and 270 mm, respectively (Fig. 3.10).

3.3.4 von Bertalanffy growth curves for *Sillago schomburgkii*

von Bertalanffy growth curves fitted well the lengths at age of both female and male *S. schomburgkii*, as is demonstrated by the relatively high values for the coefficient of determination (R^2), *i.e.* 0.91 and 0.86, respectively, and values for t_0 that were close to zero (Table 3.3). The growth coefficient (k) and asymptotic length (L_∞) of females were 0.47 years⁻¹ and 347 mm, respectively. Female *S. schomburgkii* attained lengths of 139, 216, 265 and 296 mm at 1, 2, 3, and 4 years of age, respectively (Fig. 3.11). The maximum length and age recorded for females was 383 mm and 10 years, respectively.

In comparison with females, the value for k was slightly higher, *i.e.* 0.59 years⁻¹, and that for the L_∞ was slightly lower for males, *i.e.* 294 mm (Table 3.3). Male *S. schomburgkii* attained a length of 136, 206, 245 and 266 mm at 1, 2, 3, and 4 years of age, respectively (Fig. 3.11). The maximum length and age recorded for males was 299 mm and 9 years, respectively.

Table 3.3. von Bertalanffy growth parameters L_{∞} , k , and t_0 including upper and lower 95% confidence limits derived from length-at-age data for *Sillago schomburgkii* caught in Shark Bay, Western Australia. R^2 = coefficient of determination, n = sample size.

		von Bertalanffy parameters				
		L_{∞} (mm)	k (years ⁻¹)	t_0 (years)	R^2	n
Female	Estimate	346.7	0.470	-0.089	0.907	900
	Upper	355.9	0.500	-0.521		
	Lower	337.5	0.439	-0.126		
Male	Estimate	293.8	0.589	-0.059	0.862	829
	Upper	305.6	0.644	-0.203		
	Lower	282.2	0.534	-0.098		

3.3.5 Growth rates

The likelihood ratio test indicated that the growth curves of female and male *S. schomburgkii* in Shark Bay were significantly different ($P < 0.001$). The difference between the predicted lengths of female and male *S. schomburgkii*, expressed as a percentage of the lowest value of L_{∞} for the two growth curves, at ages 1, 2, 3, and 4 was 0.9, 3.6, 7.0, 9.9%, respectively.

The likelihood ratio test also indicated that the growth curves of female and male *S. schomburgkii* on the lower west coast and Shark Bay were statistically different between the two regions ($P < 0.001$). The difference between the predicted lengths of male *S. schomburgkii*, expressed as a percentage of the lowest value of L_{∞} for the two growth curves, at ages 1, 2, 3, and 4 was 3.3, 3.0, 4.2, 5.7%, respectively, and remained $> 5\%$ throughout the full range of ages greater than 4. However, there was little biological difference, *i.e.* $< 5\%$, for females, between the two regions at ages 1, 2, 3, and 4 which showed values of 4.2, 3.0, 1.5, 0.1, respectively, and remained $< 5\%$ throughout the full range of ages.

3.3.6 Mortality estimates of *Sillago schomburgkii*

As was the case for *S. analis*, the point estimates for the instantaneous coefficient of natural mortality, M , for *S. schomburgkii*, derived using the regression equations refitted to Pauly (1987) and Ralston (1980) were very similar, *i.e.* 1.23 and 1.11 year⁻¹, respectively. However, the confidence intervals for these point estimates were also very broad (Table 3.4). The point estimate of M for *S. schomburgkii* derived using the equation of Rikhter and Efanov (1976) was considerably lower, *i.e.* 0.76 year⁻¹, than those derived from the equations of Pauly (1980) and Ralston (1987) (Table 3.4).

The point estimate for the instantaneous coefficient of total mortality, Z , *i.e.* 0.68 year⁻¹, derived using the regression equation refitted to Hoenig's (1982, 1983) fish data, was lower than all of the point estimates calculated for M (Table 3.4). However, the point estimate for Z , *i.e.* 0.81 year⁻¹, calculated using catch curve analysis was similar to that derived from the refitted Hoenig (1983) equation and the estimate for M derived using the Rikhter and Efanov (1976) equation, but was substantially lower than the estimates of M calculated from the refitted Pauly (1980) and Ralston (1987) equations. Whilst the confidence intervals for Z and M derived from the empirical methods were always very broad, those for the estimate of Z obtained using catch curve analysis were far narrower (Table 3.4).

Table 3.4. Mortality estimates (year^{-1}) of *Sillago schomburgkii* in Shark Bay calculated using different methods. *M* = natural mortality, *Z* = total mortality, N = no value could be obtained.

Method of analysis	<i>M</i> or <i>Z</i>	Estimate	Lower 95%	Upper 95%
Refitted Pauly (1980)	<i>M</i>	1.23	0.31	3.54
Refitted Ralston (1987)	<i>M</i>	1.11	0.64	1.63
Rikther and Efanov (1976)	<i>M</i>	0.76	N	N
Refitted Hoeing (1983)	<i>Z</i>	0.68	0.23	2.05
Catch curve analysis	<i>Z</i>	0.81	0.71	0.92

3.3.7 Length weight relationship

The relationships between total length (TL) in mm and total weight (TW) in g for female and male *S. schomburgkii* are both shown in Figure 3.12 and described by the following regression equations.

Females $\ln \text{TW} = 2.001(\ln \text{TL}) - 11.761$ ($R^2 = 0.997$, $n = 907$)

Males $\ln \text{TW} = 3.012(\ln \text{TL}) - 11.812$ ($R^2 = 0.995$, $n = 841$).

where R^2 is the regression coefficient and n is the sample size.

3.4 Reproduction of *Sillago analis*

3.4.1 Gonadosomatic indices

The mean monthly GSIs of female *S. analis* ≥ 216 mm, *i.e.* the L_{50} of females at first maturity (see section 3.4.4), rose sharply from *ca* 0.7 in July to a peak of *ca* 4.2 in January and then fell precipitously to *ca* 1.0 in April and to *ca* 0.7 in June (Fig. 3.13). The mean monthly GSIs for male *S. analis* ≥ 184 mm, *i.e.* the L_{50} of males at first maturity, followed similar trends to those of females, rising sharply from *ca* 0.3 in July to reach a peak of *ca* 2.1 in February and then falling precipitously to *ca* 0.9 in April and to *ca* 0.2 in June (Fig. 3.13).

3.4.2 Gonadal development of *Sillago analis* in Shark Bay

All females of *S. analis* that were caught during July and August and were $\geq L_{50}$ at first maturity, possessed ovaries at stage II, *i.e.* maturing virgin/resting (Fig. 3.14). The frequency of stage II ovaries in female fish declined progressively to 25% in November and then to between 3 and 5% between January and March. Stage III (developing) and IV (maturing) ovaries first appeared in September and stage V/VI ovaries (mature/spawning) in October. The prevalence of both stage III and IV ovaries declined after December, with the result that few fish with ovaries at these stages were caught from January to March. Most ovaries were at stage V/VI in January and February and stage VII (spent) ovaries were first found in March (Fig. 3.14). Although no stage V/VI ovaries were found in May and June, several fish with stage VII and VIII (recovering/spent) ovaries were found in these two months.

The trends exhibited in sequential months by the prevalence of the different stages in gonadal development of the males of *S. analis*, that were $\geq L_{50}$ at first maturity, were similar to those just described for females (Fig. 3.14).

The above trends strongly indicate that virtually all females and males with ovaries and testes, respectively, at stages III and above in October to November will progress through to maturity in the immediately ensuing months (Fig 3.14). Thus, in the following section, the regression analysis used for determining the L_{50} at first maturity employed the prevalence of fish possessing gonads at stages III to VIII in January to March, the main spawning period.

3.4.3 Description of macroscopic and histological stages of ovarian development

Descriptions of the macroscopic development of ovaries and testes and the histological stages of ovaries for *S. analis* and *S. schomburgkii* are shown in Table 3.5.

3.4.4 Length and age of *Sillago analis* at first maturity

The ovaries of all females, that were caught during the spawning period, *i.e.* January to March (see section 3.4.2) and were between 100 and 179 mm in total length, were immature (stage I/II) (Fig. 3.15). Fish with ovaries at stages III to VIII were first recorded in the 180-189 mm length class, in which they accounted for just 5% of all fish. The percentage of fish with ovaries at stages III to VIII increased in a logistic manner, with 15, 75 and 100% of fish in the 200-209, 220-229, 240-249 mm length classes, possessing ovaries at these stages, respectively. The L_{50} at which female *S. analis* first reach maturity was estimated to be *ca* 216 mm (Fig. 3.15; Table 3.6).

The percentage of males in successive length classes of male *S. analis*, which possessed testes at stages III to VIII, increased in a similar logistic manner to that just described above for females with the corresponding ovarian stages, except that “maturity” was reached at a smaller size (Fig. 3.15). Thus, although all males between 100 and 169 mm possessed testes at stages I to II, over 30% of males in the 170-179 mm length class and 66 and 100% in the 190-199 and 210-219 mm length classes, respectively, possessed testes at stages III to VIII. Furthermore, the L_{50} at which male *S. analis* first reach maturity was estimated to be *ca* 184 mm (Fig. 3.15; Table 3.6).

Table 3.5. Description of the characteristics used to distinguish macroscopic gonadal development stages of female and male *Sillago analis* and *S. schomburgkii* and the corresponding histological characteristics of these stages for females. N.B. Macroscopic stages are adapted from Laevastu (1965) and Lenanton (1970), while histological stages are modified from Wallace and Selman (1981) and Mayer *et al.* (1988.)

Stage	Macroscopic stage (female and male)	Histological stage (female)
I Virgin	Male and female gonads very small, tucked up between swim-bladder and ventral cavity wall. Female gonads colourless and transparent. No eggs visible. Male gonads black and strand-like.	Oogonia, chromatin nucleolar and perinucleolar oocytes. Oocytes organised into neat rows.
II Maturing Virgin/ resting adult	Ovaries light red in colour, but still translucent. Eggs invisible to the naked eye. Testes black and strand-like. Length of gonads half the length of the ventral cavity.	Previtellogenic oocytes present. Late perinucleolar oocytes present. Highly organised oocytes.
III Developing	Ovaries opaque, rose to light pink in colour. Small eggs visible through ovary wall. Testes dark purple and larger in size. No longer strand-like. Gonads take up $\frac{1}{2}$ of ventral cavity.	Previtellogenic oocytes present. Cortical alveoli oocytes first appear. Oocytes organised.
IV Maturing	Ovaries orange in colour with more opaque eggs visible. Red capillaries thickening. Testes light purple in colour. Larger in size. Milt present under pressure. Gonads take up $\frac{2}{3}$ of ventral cavity	Cortical alveoli oocytes dominant with previtellogenic oocytes also present. A few yolk granules oocytes first appear. Ovary starting to become tightly packed.
V Mature	Ovaries large, take up majority of ventral cavity and are yellow in colour with thick red capillaries running down the length of each lobe. Individual eggs easily discernable with naked eye. Testes large, filling ventral cavity, are light purple with white edges to lobes. Milt present under light pressure	Tightly packed yolk granule oocytes fill ovary. Cortical alveoli oocytes also present, although not as numerous as in stage V. Small numbers of previtellogenic oocytes present.
VI* Spawning	Testes occupying large percentage of ventral cavity. Lobes completely white in colour. Testes easily perforated. Milt free flowing	
VII Spent	Ovaries and testes one third the size of stage V. Ovaries light red in colour. Capillaries still present, although not a thick as in stage V. Testes pale purple in colour. Small amount of milt still present if squeezed.	Spaces in ovary. Oocytes disorganised. Ovary wall very thick.
VIII Recovering	Both ovaries and testes flaccid in appearance. Ovaries deep red in colour. A few remnant eggs may still be visible. Milt also present under pressure. Gonads occupy $\frac{1}{2}$ of the ventral cavity.	Oocytes within ovary disorganised. Scar tissue and atretic oocytes present. Previtellogenic oocytes present.

*N.B. No stage VI (spawning) ovaries were observed in the study.

No female or male *S. analis* had attained maturity by the end of their first year of life, and only a few individuals of either sex had reached maturity by the end of their second year of life. By the end of their third year of life, 20% of females and 61% of males were mature. Virtually all females and all of the males had reached maturity of the end of their fourth year of life (Fig. 3.16).

Table 3.6. Length at maturity (L_{50} and L_{95}) estimates and 95% confidence limits derived for *Sillago analis* caught in Shark Bay, Western Australia.

		L_{50} (mm)	L_{95} (mm)
Female	Estimate	215.7	238.2
	Upper	219.4	245.9
	Lower	211.9	230.4
Male	Estimate	183.9	209.8
	Upper	187.7	218.3
	Lower	179.8	201.4

3.4.5 Oocyte diameter frequency distributions of mature *Sillago analis*

The oocyte diameter distributions for mature ovaries (*i.e.* stage V/VI) removed from four individuals of *S. analis* captured during the spawning season in three out of the four cases, were continuous (Fig. 3.17). The two stages of previtellogenic oocytes, *i.e.* chromatin nucleolar and perinucleolar stage oocytes, when combined, always produced a prominent modal class at between 40 and 79 μm . Cortical alveoli stage oocytes, ranging between 80 and 239 μm in diameter, were present in each of the four ovaries. The yolk granule stage oocytes in those ovaries ranged in diameter from 200 and 439 μm (Fig. 3.17).

3.5 Reproduction of *Sillago schomburgkii*

3.5.1 Gonadosomatic indices (GSI)

The mean monthly GSI of female *S. schomburgkii* ≥ 237 mm, *i.e.* the L_{50} at first maturity of females (see section 3.5.3), rose from 1.2 in July to 4.2 in August and then ranged between this value and 2.4 through to December, before declining precipitously to 0.8 in January and remaining at < 1.3 through to June (Fig. 3.18).

The mean monthly GSI of male *S. schomburgkii* ≥ 192 mm, *i.e.* the L_{50} at first maturity of males (see section 3.5.3), rose from 1.1 in July to 4.0 in August and then declined to 1.3 in September. The mean monthly GSI of males then rose slightly to 2.0 in December, and then declined to 0.2 in February and remained < 1.0 until June (Fig. 3.18).

3.5.2 Gonadal development of *Sillago schomburgkii* in Shark Bay

Most of the female *S. schomburgkii*, that were caught in June and were $\geq L_{50}$, possessed stage II (maturing virgin/resting) ovaries (Fig. 3.19). Very few females contained stage IV ovaries in June and none of those caught in this month possessed ovaries at stages V/VI. However, $> 50\%$ of the females caught in August possessed stage V/VI ovaries. Fish with ovaries at this stage predominated in September and December. Fish with stage VII (spent) ovaries were first found in January and, together with some fish with stage VIII (recovering/spent) ovaries, were also present in February, March and April (Fig. 3.19).

The trends exhibited in sequential months by the prevalence of the different stages in gonadal development of the males of *S. schomburgkii* that were $\geq L_{50}$ at first maturity, were similar to those just described for females (Fig. 3.19)

The above trends demonstrate that virtually all of the females and males with ovaries and testes, respectively, at stages III and above in November will progress through to maturity in the immediately ensuing months. Thus, as was the case for *S. analis*, the regression analysis used for determining the L_{50} at first maturity employed the prevalence of fish possessing gonads at stages III to VIII in November to March, the main spawning period.

3.5.3 Length and age of *Sillago schomburgkii* at first maturity

The ovaries of all female *S. schomburgkii*, that were caught in November to March, and measured between 100 and 179 mm, were at stages I-II, *i.e.* immature (Fig. 3.20). Females with ovaries at stages III-VIII were first found in the 180-199 mm length class, where they accounted for 4% of all female fish. The percentage of females with stages III-VIII ovaries increased in a logistic manner. Thus, 7, 65, 85 and 100% of fish in the 200-219, 220-239, 260-279 and 300-319 mm length classes, respectively, possessed ovaries at stages III-VIII. The L_{50} of female *S. schomburgkii* at first maturity was estimated to be 237 mm (Fig. 3.20; Table 3.7).

The percentage of males in successive length classes with testes at stages III-VIII increased in a logistic manner similar to that just described above for females with ovaries at the corresponding stages, except that maturity was reached at a smaller size (Fig. 3.20). Thus, while all males between 100 and 159 mm possessed testes at stages I-II, 12% of those in the 160-179 mm length class and 36, 87 and 100% of those in the 180-199, 200-219, 220 to 299 mm length classes, respectively, were at stages III-VIII. The L_{50} of male *S. schomburgkii* at first maturity was estimated to be 192 mm (Fig. 3.20; Table 3.7).

Table 3.7. Length at maturity (L_{50}) estimates and 95% confidence limits derived for *Sillago schomburgkii* caught in Shark Bay, Western Australia.

		L_{50} (mm)	L_{95} (mm)
Female	Estimate	237.5	283.1
	Upper	245.7	299.9
	Lower	229.3	265.8
Male	Estimate	192.1	217.9
	Upper	196.2	229.6
	Lower	187.6	208.1

No females or males at the end of their first year of life and only 2 and 21% of females and males, respectively, at the end of their second year of life had possessed gonads at stages III to VIII. However, the vast majority of females and of males, *i.e.* 85 and 100% respectively, at 4 years of age possessed such gonads (Fig. 3.21).

3.5.4 Oocyte diameter frequency distributions of mature *Sillago schomburgkii*

The two stages of previtellogenic oocytes, *i.e.* chromatin nucleolar and perinucleolar stage oocytes, when combined, always produced a prominent modal class at between 20 to 99 μm . Cortical alveoli stage oocytes, ranging between 100 and 219 μm in diameter, were present in each of the four ovaries. The yolk granule stage oocytes ranged in diameter from 240 and 459 μm (Fig. 3.22).

Chapter 4

Discussion

4.1 Ageing structure and age validation

4.1.1 Scales

Although Lenanton (1970) used counts of the number of circuli on scales in an attempt to age *Sillago analis* and *Sillago schomburgkii*, circuli were found not to be clearly demarcated in the scales of the individuals of these species that were examined during the present study. This was particularly the case with those fish in which ≥ 3 opaque zones could be seen in their otoliths. Consequently, the use of the number of circuli on scales in the present study would have tended to yield underestimates of the ages of the individuals of these two species. Furthermore, in his study, Lenanton (1970) found that most of the scales of those *S. schomburgkii* and *S. analis* that had reached maturity showed evidence of erosion. Thus, the number of circuli may have become reduced and therefore have led to underestimates of the age of these species in his study.

The tendency for the ages of *S. analis* and *S. schomburgkii* to be underestimated through the use of scales parallels the findings of studies on several other species (e.g. Starck & Schroeder, 1970; Boxrucker, 1986; Beamish and McFarlane, 1987). This can result, under certain environmental conditions, from circuli not being formed on scales until after the completion of the second year of growth by a fish (Lentsch & Griffith, 1987). Alternatively, Casselman (1987) found that circuli were not deposited around the entire scale of the largest and oldest trout (*Salvelinus namaycush*). Such partial circuli are difficult to distinguish from “false”

rings, *i.e.* those that are not formed annually (Casselman, 1990). Furthermore, different scales from the same fish often contain different numbers of circuli and thus yield different estimates of the age of that fish (Sipe & Chittenden, 2001). The above cases show that the number of circuli on the scales of fish frequently yields an unreliable estimate of the age of fish. In contrast, the number of annuli on otoliths generally provides an accurate measure for ageing fish (Beamish & McFarlane, 1987; Campana, 2001).

4.1.2 Otoliths

A similar trend to that recorded for the scales of *S. analis* was found when otoliths were viewed whole, *i.e.* the number of annuli visible was sometimes less than those which, on the basis of an examination of sectioned otoliths, were known to be present. Previous work had also shown that it was necessary to section the otoliths of *S. schomburgkii* in order to be able to detect all of the annuli that are present in this hard structure in this species (*e.g.* Hyndes & Potter, 1997).

The present study demonstrated that, when two or more opaque zones were present, the number of annuli visible in the whole otoliths of *S. analis* was often less than that in corresponding otoliths after sectioning. The magnitude of the discrepancies increased as the number of opaque zones increased, with a maximum difference of three opaque zones being recorded in the fish with the greatest number of annuli. Sectioning of otoliths enhances the ability to differentiate between the outer opaque and translucent zones, and also often reveals one or more additional inner opaque zones, particularly in older fish (Hyndes *et al.*, 1992; Lowerre-Barbieri *et al.*, 1994). For example, Fowler and Short (1998) showed that the counts of annuli obtained using the whole otoliths of *Sillaginodes punctata* could be misleading and

that it was necessary to section otoliths to be able to obtain an accurate count of the opaque zones. Furthermore, the trends shown by the marginal increment in some long-lived fish become clear only after the otoliths have been sectioned (Campana, 1984; Collins *et al.*, 1988; Hyndes *et al.*, 1992).

4.1.3 Marginal increment analysis

The mean monthly marginal increments on the otoliths of *S. analis* underwent a single marked decline and subsequent conspicuous increase during the year, and the same was true for those of the otoliths of *S. schomburgkii* (Hyndes & Potter, 1997), demonstrating that a single opaque zone is formed annually on the otoliths of these two species. Thus, the number of annuli on sectioned otoliths can be used to age these species. In both *Sillago* species, the outermost opaque zone in the otoliths becomes delineated in either November or December, *i.e.* late spring/early summer. This demonstrates that this narrow opaque zone is formed over the cool winter and early spring months when growth is greatly reduced, and that the wide translucent zone is formed when more rapid growth occurs during the warm summer and autumn months. A narrow opaque zone is also typically formed during spring or early summer in the otoliths of other fish species in south-western Australian waters, *e.g.* the West Australian dhufish *Glaucosoma hebraicum* (Hesp *et al.*, 2002), the Australian herring *Arripis georgiana* (Fairclough *et al.*, 2000), the black bream *Acanthopagrus butcheri* (Sarre & Potter, 2000) and the western yellowfin bream *Acanthopagrus latus* (Hesp *et al.*, in press). It also parallels the situation found with numerous teleosts elsewhere in the world, *e.g.* the weakfish *Cynoscion regalis* (Lowerre-Barbieri *et al.*, 1994), and the red snapper *Lutjanus campechanus* (Wilson & Nieland, 2001). The use of marginal increment analysis has been widely accepted as an appropriate method for validating

that annuli are formed only once in each year on the hard structures of fish and, in such cases, can thus be used for ageing fish (Maccina & Betsill, 1987; Hyndes *et al.*, 1992; Campana, 2001; Escot & Grando-Lorencio, 2001).

4.2 Length and age compositions and growth rates

The fact that the growth coefficients (k) for the females and males of *S. analis* in Shark Bay, *i.e.* 0.73 and 0.76 year⁻¹, respectively, were greater than those of *S. schomburgkii* in this environment, *i.e.* 0.47 and 0.59 year⁻¹, respectively, demonstrates that the length of the former species reaches its asymptote at a faster rate. Furthermore, the asymptotic lengths (L_{∞}) of the females and males of *S. analis*, *i.e.* 276.6 and 253.2, respectively, were both far less than the corresponding values for the two sexes of *S. schomburgkii*, *i.e.* 346.7 and 293.8, respectively. Therefore, the patterns of growth of these two morphologically similar and congeneric species differ markedly, even when the two species are sympatric. However, the length at first maturity is strongly correlated with the asymptotic length in sillaginids in general (Hyndes & Potter, 1997). The fact that the *S. analis* attains maturity at a smaller size than *S. schomburgkii*, which has a greater asymptotic length, is thus consistent with the above correlation. Furthermore, the pattern of growth of *S. schomburgkii* in the subtropical embayment of Shark Bay was remarkably similar to that in the very different environment of the coastal waters of temperate Western Australia, approximately 800 km further south, in which the temperatures in the warmer months of the year are about 3°C lower (Hesp, 2003). This suggests that the pattern of growth in this species is, to a large extent, genetically fixed.

As with other sillaginid species (see Hyndes & Potter, 1996, 1997; Hyndes *et al.*, 1997b), the L_{∞} s and maximum lengths of the females of both *S. analis* and

S. schomburgkii were greater than those of their males. The attainment of a larger size by females would be of selective advantage to this sex as it would facilitate the production of the optimal amount of eggs, whereas there would not be the same selection pressures to produce extremely large numbers of sperm by the males.

4.3 Spawning time and period

Since mature (stage V) ovaries were found in some female *S. analis* in each month between October and April (Fig. 3.14), this species could potentially spawn throughout these seven months. However, the prevalences of stage V ovaries were very low in the first and last of these months and mature males were not caught until December. It is thus proposed that the majority of spawning occurs predominantly between December and March, which is very similar to the conclusion by Lenanton (1970) that the spawning period extends from November to March. The conclusion that spawning is typically completed by the end of March is supported by the high prevalences of stages VII (spent) and VIII (recovering spent) in large female fish caught between April and June and by the decline in the GSIs of both the males and females of *S. analis* to low levels after March.

The presence of mature (stage V) ovaries and testes in some of the large females and males of *Sillago schomburgkii*, respectively, in each month sampled between July and April suggests that this species spawns over this very protracted period of nine months. However, the prevalence of female fish with mature gonads was very low in the first and last of those nine months and thus spawning probably occurred mainly in the seven months between August and March. The mean monthly GSIs of females and males of *S. schomburgkii* did not show the same progressive increase and then decline as those exhibited by the two sexes of *S. analis*, which

would be consistent with the presence of a more protracted spawning period. The above estimated spawning period for *S. schomburgkii* in Shark Bay is also similar to that estimated by Lenanton (1970) for this species in this large embayment, *i.e.* September to March.

In contrast to the above findings for *S. schomburgkii* in the subtropical environment of Shark Bay, Hyndes and Potter (1997) found females and males of this species with ovaries at stages V-VII (*i.e.* mature, spawning or spent) in only six months, *i.e.* October to March, in temperate waters over 800 km further south on the lower west coast of Australia. The presence of a longer spawning period of *S. schomburgkii* in Shark Bay than in the cooler waters further south parallels the type of variation found amongst the populations of other species in which the distribution has a wide latitudinal range. For example, the bay anchovy *Anchoa mitchilli* spawns for about a month in the temperate part of its range off the east coast of northern America and over the entire year in the more southern and warmer waters of its distribution (Voughlitois *et al.*, 1987; Castro & Cowen, 1991). The more restricted spawning period of certain species of fish at higher latitudes has often been considered to reflect the fact that, at these latitudes, the amplitude in temperature is greater than at lower latitudes, and that this therefore leads to a more seasonal occurrence in the abundance and quality of food required by larval fish (Conover & Kynard, 1984). However, the difference between maximum and minimum monthly temperatures is greater in Shark Bay than in more southern temperate waters (Hesp, 2003) and yet spawning occurs over a longer period in that subtropical embayment. It is thus proposed that the presence of a longer spawning period of *S. schomburgkii* in Shark Bay than in temperate waters is related to the presence of higher water temperatures for a more protracted period. However, this trend is not exhibited by the

tarwhine *Rhabdosargus sarba* which has a very similar spawning period in Shark Bay and on the lower west coast of Western Australia (Hesp and Potter, in press).

4.4 Maturity

The lengths at which female and male *S. analis* were estimated to attain maturity (L_{50}), *i.e.* 216 and 184 mm, respectively, were both slightly less than the mean lengths of 225 and 209 mm, respectively, estimated for the attainment of maturity by Lenanton (1970). Furthermore, the L_{50} s of 237 and 192 mm, estimated for the attainment of maturity by the females and males *S. schomburgkii*, respectively, in Shark Bay were also slightly less than the mean lengths of 250 and 235 mm estimated for maturity by Lenanton (1970) in this same environment.

It should be noted that, as a different method than that employed in the present study was used by Lenanton (1970) to determine the length at first maturity of the two species of whiting in Shark Bay, it is possible that the above interspecific differences in the estimates of length at first maturity between the two studies may not be “real”. However, if these differences are “real”, they indicate that the lengths at which female and male *S. analis* and *S. schomburgkii* first attain maturity in Shark Bay has declined during the last 30 years. Since several studies have shown that, during heavy fishing pressure, the size at first maturity often declines, as has been shown, for example, to be the case with the cod *Gadus morhua* and the American plaice *Hippoglossoides platessoides* (Beacham, 1983a,b), it appears relevant that both *S. analis* and *S. schomburgkii* have been fished continuously in Shark Bay by commercial fishers during this 30 year period and that such fishing pressure may have been sufficiently strong to have led to a decline in catches over this period (Shaw, 2000). Reductions in the length at maturity of fish species which have been subjected to heavy fishing

pressure have been attributed to the effects of strong selection pressures in favour of those fish that mature at a small length and young size (Beacham, 1983b, c). The smaller size of the males than females of both *S. analis* and *S. schomburgkii* at maturity, parallels the findings for various other species of sillaginid, *e.g.* *S. bassensis* and *S. robusta* (Hyndes & Potter, 1996), *S. sihama* (Jayasankar, 1991) and also species in other teleost families, *e.g.* the Australian herring *Arripis georginana* (Fairclough *et al.*, 2000).

The L_{50} s derived during the current study for the females and males of *S. schomburgkii* at first maturity in Shark Bay, *i.e.* 237 and 192 mm, respectively, are very similar to those estimated by Hyndes and Potter (1997) for this species in temperate waters on the lower west coast of Australia. This similarity in the size at first maturity of *S. schomburgkii* in the very different environments of Shark Bay and temperate coastal waters in south-western Australia indicates that, as with the similarity in the pattern of growth of these two species (see above), the size at first maturity is also, to a large extent, genetically fixed.

4.5 Spawning Mode

Since the distribution of the oocyte diameters in the ovaries of mature females of both *S. analis* and *S. schomburgkii* in Shark Bay are essentially continuous, and as mature ovaries contain oocytes of various different stages in development, including “intermediate” stages such as the cortical alveolar stage, these species have indeterminate fecundity *sensu* Hunter *et al.*, (1985). Thus, implicitly, *S. analis* and *S. schomburgkii* are also multiple spawners, *i.e.* individual females release oocytes on more than one occasion during a spawning period (de Vlaming, 1983). This conclusion was also reached by Lenanton (1970) for those species in Shark Bay and

by Hyndes and Potter (1997) for *S. schomburgkii* on the lower west coast of Australia. Multiple spawning also occurs in other species of sillaginid, *e.g.* *Sillago bassensis* (Hyndes & Potter, 1996), *Sillago ciliata* (Morton, 1985) and *Sillago sihama* (Jayasankar, 1991).

The adaptive significance of multiple spawning in fish is that it enables reproductive output to be increased (Fox & Crivelli, 1998; Burt *et al.*, 1988). Since fecundity is limited by body size, the release of eggs in batches over time enables the total number of eggs that can be produced in a spawning season to be increased (McEvoy & McEvoy, 1992). Furthermore, since, in the case of fish species that only spawn once in a spawning season, stochastic changes in, for example, food abundance could result in the loss of the annual reproductive output of that species, multiple spawning is often considered as a bet-hedging strategy (Lambert & Ware, 1984). By dispersing annual egg production in time, there is an increased chance that, at least some of the juveniles survive to reach maturity. Multiple spawning may also reduce competition for spawning sites by partitioning their use in time (Weddle & Burr, 1991).

4.6 Mortality

The estimates for natural mortality (M) varied greatly according to the type of method used, as has frequently been found to be the case for other species of fish (*e.g.* Vetter 1988, Burton, 2001, Hesp *et al.*, in press). The point estimates for M , that were derived from both the Pauly (1980) and Ralston (1987) equations, have been shown to exceed the values for total mortality (Z) derived from the Hoenig (1983) equation for western yellowfin bream in Shark Bay (Hesp *et al.*, in press) and several other species elsewhere (*e.g.* Samuel & Mathews, 1987; Burton 2001). However, natural mortality

cannot exceed total mortality. Since the estimates derived for M for both *Sillago* species using the Rickter and Efanov (1976) equation were less than those derived for Z , they are far more likely to reflect the true situation regarding natural mortality in the populations of these two species in Shark Bay.

There is yet another problem in that the value for Z obtained by catch curve analysis (1.95 year^{-1}) for *S. analis* is nearly twice that obtained using Hoenig's (1983) equation for fish. Since catch curve analysis uses all of the data on the age composition in the samples obtained from a population, it provides a better estimate of Z than the frequently used Hoenig's (1983) equation for fish, which employs only the value for the maximum age of fish in the samples and empirical data for other fish populations (Hesp *et al.*, in press).

Since the value derived for Z from catch curve analysis for *S. analis* is well over twice that of the estimate of M for derived from the Rickter and Efanov (1976) equation, this species would appear to be heavily affected by fishing pressure. However, the corresponding values for Z and M for *S. schomburgkii* are very similar which implies that this species is only lightly fished. Although this suggests that the impact of fishing pressure is far greater on *S. analis* than *S. schomburgkii*, this may reflect a greater vulnerability of this species to fishing through such factors as a more restricted distribution.

The number of fishing units in Shark Bay Beach Seine and Mesh Net Managed Fishery has declined, through regulatory action by the Department of Fisheries, from 17 at its peak in 1964 to nine at the current time (Shaw, 2000). This decrease in the number of fishing units suggests that the overall fishing pressure on targeted fish species may have declined. However, since advancements in technology are likely to have led to an increase in the efficiency of fishing, a decrease in the

number of fishing vessels would not necessarily mean that fishing pressure has decreased. Indeed, in recent years, although fishing effort (*i.e.* boat days) has decreased from a maximum of *ca* 1750 boat days in 1991 to *ca* 1250 boat days in 2002, the annual catch (tonnes) of whiting has remained essentially the same (Anon., 2002).

References

- Anon. (2002). State of the Fisheries Report, Gascoyne Coast Bioregion. Department of Fisheries, Western Australia.
- Allen, G. (1997). *Marine fishes of tropical Australia and south-east Asia*. Western Australian Museum, Perth.
- Ayvazian, S.G. & Hyndes, G.A. (1995). Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Marine Biology*. **122**: 527-536.
- Bagenal, T.B. & Tesch, F.W. (1978). Age and growth. In *Methods for assessment of Fish Production in Fresh Waters*. (Ed. T.B. Bagenal). Blackwell, Oxford. pp. 101-130.
- Beacham, T.D. (1983a). Growth and maturity of Atlantic cod (*Gadus Morhua*) in the southern Gulf of St. Lawrence. *Canadian Technical Report of Fisheries and Aquatic Sciences*. **1142**.
- Beacham, T.D. (1983b). Variability in size and age at sexual maturity of American plaice and yellowtail flounder in the Canadian Maritimes Region of the northwest Atlantic Ocean. *Canadian Technical Report of Fisheries and Aquatic Sciences*. **1196**.
- Beacham, T.D. (1983c). Variability in size and age at sexual maturity of argentine, *Argentina silus*, on the Scotian Shelf in the northwest Atlantic Ocean. *Environmental Biology of Fishes*. **8**: 67-72.
- Beacham, T.D. (1982). Median length at sexual maturity of halibut, cusk, longhorn sculpin, ocean pout, and sea raven in the Maritimes area of the northwest Atlantic. *Canadian Journal of Zoology*. **60**: 1326-1330.

- Beamish, R.J. (1979). Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. *Journal of the Fisheries Research Board Canada*. **36**: 141-151.
- Beamish, R.J. & McFarlane, G.A. (1987). Current trends in age determination methodology. In *The Age and Growth of Fish*. (Eds. R.C. Summerfelt and G. E. Hall). Iowa State University Press, USA. pp. 15-42.
- Bell, J.D., Pollard, D.A., Burchmore, J.J., Pease, B.C. & Middleton, M.J. (1984). Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Australian Journal of Marine and Freshwater Research*. **35**: 33-46.
- Bell, J.D., Pollard, D.A. (1989). Ecology of fish assemblages and fisheries associated with seagrasses. In *Biology of Seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. (Eds. A.W.D. Larkum, A.J. McComb and S. Shepherd). Elsevier, Amsterdam, pp. 565-609.
- Blaber, S.J.M. (1980). Fish of the Trinity Inlet System of north Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. *Australian Journal of Marine and Freshwater Research*. **31**: 137-146.
- Blaber, S.J.M. & Blaber, T.G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology*. **17**:143-162.
- Black, R., Robertson, A.I., Peterson, C.H. & Peterson, N.M. (1990). Fishes and benthos of near-shore seagrass and sandflat habitats at Monkey Mia Shark Bay, Western Australia. In *Research in Shark Bay: Report of the France-Australe Bicentenary Expedition Committee*. (Eds. P.F. Berry, S.D. Bradshaw and B.R. Wilson). Western Australian Museum, Perth. pp. 245-261.

- Booth, A.J., Merron, G.S. & Buxton, C.D. (1995). The growth of *Oreochromis andersonii* (Pisces: Cichlidae) from the Okavango Delta, Botswana, and a comparison of the scale and otolith method of ageing. *Environmental Biology of Fishes*. **43**: 171-178.
- Borkholder, B.D. & Edwards, A.J. (2001). Comparing the use of dorsal fin spines with scales to back-calculated length-at-age estimates in walleyes. *North American Journal of Fisheries Management*. **21**: 935-942.
- Boxrucker, J. (1986). A comparison of the otolith and scale methods for ageing white crappies in Oklahoma. *North American Journal of Fisheries Management*. **6**: 122-125.
- Brewer, D.T. & Warburton, K. (1992). Selection of prey from a seagrass/mangrove environment by golden lined whiting, *Sillago analis* (Whitley). *Journal of Fish Biology*. **40**: 257-271.
- Brothers, E.B. (1987). Methodological approaches to the examination of otoliths in ageing studies. In *The Age and Growth of Fish*. (Eds. R.C. Summerfelt and G.E. Hall). Iowa State University Press, USA. pp. 319-330.
- Burt, A., Kramer, D.L., Nakatsura, K. & Spry, C. (1988). The tempo of reproduction in *Hyphessobrycon pulchripinnis* (Characidae), with a discussion on the biology of 'multiple spawning' in fishes. *Environmental Biology of Fishes*. **22**: 15-27.
- Burton, M.L. (2001). Age, growth and maturity of gray snapper, *Lutjanus griseus*, from the east coast of Florida. *Fishery Bulletin*. **99**: 254-265.
- Cadwallader, P.L. (1978). Age, growth and condition of the common river galaxias, *Galaxias vulgaris* Stokell, in a Canterbury river, New Zealand. *Fisheries Research Bulletin, New Zealand Ministry of Agriculture and Fisheries*. **17**: 15-20.

- Campana, S.E. (1984). Comparison for age determination methods for the starry flounder. *Transactions of the American Fisheries Society*. **113**: 365-369.
- Campana, S.E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*. **47**: 2219-2227.
- Campana, S.E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*. **59**: 197-242.
- Campana, S.E. & Neilson, J.D. (1984). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*. **42**: 1014-1032.
- Cappo, M., Eden, P., Newman, S.J. & Robertson, S. (2000). A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fisheries Bulletin*. **98**: 474-488.
- Casselman, J.M. (1973). Analysis of hard tissue of pike *Esox lucius* L. with special reference to age and growth. In *The Ageing of Fish*. (Ed. T.B Bagenal). Unwin Brothers, London. pp. 13-27.
- Casselman, J.M. (1987). Determination of age and growth. In *The Biology of Fish Growth*. (Eds. A.H. Weatherley and H.S. Gill). Academic Press, London. pp. 209-242.
- Casselman, J.M. (1990). Growth and relative size of calcified structures of fish. *Transactions of the American Fisheries Society*. **119**: 673-688.
- Castro, L.R. & Cowen, R.K. (1991). Environmental factors affecting the early life history of bay anchovy *Anchoa mitchilli* in Great South Bay, New York. *Marine Ecology Progress Series*. **76**: 235-247.

- Cerrato, R.M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences*. **47**: 1416-1426.
- Clark, B.M., Bennett, B.A. & Lanmberth, S.J. (1996). Factors affecting spatial variability in seine net catches of fish in the surf zone of False Bay, South Africa. *Marine Ecology Progress Series*. **131**: 17-34.
- Cole, L.C. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology*. **29**: 103-137.
- Collins, M.R., Schmidt, D.J., Waltz, C.W. & Pickney, J.L. (1988). Age and growth of the king mackerel, *Scomberomorus cavalla*, from the Atlantic coast of the United States. *Fishery Bulletin*. **87**: 49-61.
- Conover, D.O. & Kynard, B.E. 1984. Field and laboratory observations of spawning periodicity and behavior of a northern population of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). *Environmental Biology of Fishes*. **11**: 161-171.
- Crossland, J. (1977). Seasonal reproductive cycle of snapper chrysophrys auratus (Forster) in the Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research*. **11**: 37-60.
- Dando, P.R. (1984). Reproduction in estuarine fish. In *Fish Reproduction: Strategies and Tactics*. (Eds. G.W. Potts and R.J. Wootton). Academic Press, London. pp. 155-170.
- Demory, R.L. (1972). Scales as a means of ageing Dover sole (*Microstomus pacificus*). *Journal of the Fisheries Research Board Canada*. **29**: 1647-1650.
- de Vlaming, V.L. (1983). Oocyte development patterns and hormonal involvements among teleosts. In *Control processes in Fish Physiology*. (Eds. J.C. Ranlin, T.J. Pitcher and R.T. Duggan). Croom Helm, Beckenham. pp. 176-199.

- Escot, C. & Grando-Lorencio, C. (2001). Validation of the otoliths for age determination in *Barbus sclateri* (Günth.). *Ecology of Freshwater Fish*. **10**: 122-126.
- Fairclough, D.V., Dimmlich, W.F. & Potter, I.C. (2000). Length and age compositions and growth rates of the Australian herring *Arripis georgiana* in different regions. *Marine and Freshwater Research*. **51**: 631-640.
- Ferrell, D.J. & Bell, J.D. (1991). Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Marine Ecology Progress Series*. **72**: 15-24.
- Fowler, A.J. (1990). Validation of annual growth increments in the otoliths of small, tropical coral reef fish. *Marine Ecology Progress Series*. **64**: 25-38.
- Fowler, A.J. & Short, D.A. (1998). Validation of age determination from otoliths of the King George whiting *Sillaginodes punctata* (Perciformes). *Marine Biology*. **130**: 577-587.
- Fox, M.G. & Crivelli, A. (1998). Body size and reproduction allocation in a multiple spawning centrarchid. *Canadian Journal of Fisheries and Aquatic Science*. **55**: 737-748.
- Francis, R.I.C.C., Paul, L.J. & Mulligan, K.P. (1992). Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. *Australian Journal of Marine and Freshwater Research*. **43**: 1069-1089.
- Gunn, J.S. & Milward, N.E. (1985). The food, feeding habitats and feeding structures of the whiting species *Sillago sihama* (Forsskal) and *Sillago analis* Whitley from Townsville, North Queensland, Australia. *Journal of Fish Biology*. **26**: 411-427.

- Hammers, B.E. & Miranda, L.E. (1991). Comparison of methods for estimating age, growth and related population characteristics of white crappies. *North American Journal of Fisheries Management*. **11**: 492-498.
- Hannah, R.W., Parker, S.J. & Fruh, E.L. (2002). Length and age at maturity of female petrale sole (*Eopsetta jorani*) determined from samples collected prior to spawning aggregation. *Fishery Bulletin*. **100**: 711-719.
- Helfman, G.S. (1978). Patterns of community structure in fishes: summary and overview. *Environmental Biology of Fishes*. **3**: 129-148.
- Hesp, S.A. (2003). Biology of two species of sparid on the west coast of Australia. PhD thesis, Murdoch University, Western Australia.
- Hesp, S.A. & Potter, I.C. (in press). Reproductive biology of *Rhabdosargus sarba* (Sparidae) in Western Australian waters, in which it is a rudimentary hermaphrodite. *Journal of the Marine Biological Association of the United Kingdom*.
- Hesp, S.A. Potter, I.C. & Hall, N.G. (2002). Age and size compositions, growth rate, reproductive biology and habitats of West Australian dhufish, *Glaucosoma hebraicum*, and their relevance to the management of this species. *Fishery Bulletin*. **100**: 214-227.
- Hesp, S.A., Hall, N.G. & Potter, I.C. (in press). A Bayesian approach for overcoming inconsistencies in mortality estimates, using, as an example, data for *Acanthopagrus latus*. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Hoening, J.M. (1982). A compilation of mortality and longevity estimates for fish, molluscs, and cetaceans, with a bibliography of comparative life history studies. GSO Technical Report Reference No. 82.
- Hoening, J.M. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*. **82**: 898-903.

- Hunter, J.R., Lo, N.C.H. & Leong, R.J.H. (1985). Batch fecundity in multiple spawning fishes, In *An egg production method for estimating spawning biomass of the pelagic fish: application to the northern anchovy, Engraulis mordax*. (Ed. R. Lasker). U.S. Department Commerce, NOAA technical Report NMFS 36. pp. 67-78.
- Hunter J.R., Macewicz, B.J., Lo, N. C-H. & Kimbrell, C.A. (1992). Fecundity, spawning and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fishery Bulletin*. **90**: 101-128.
- Hutchins, B. & Swainston, R. (1986). *Sea fishes of southern Australia*. Swainston Publishing, Perth.
- Hyndes, G.A. & Potter, I.C. (1996). Comparisons between the age structures, growth and reproductive biology of two co-occurring sillaginids, *Sillago robusta* and *S. bassensis*, in temperate coastal waters of Australia. *Journal of Fish Biology*. **49**: 14-32.
- Hyndes, G.A. & Potter, I.C. (1997). Age, growth and reproduction of *Sillago schomburgkii* in south-western Australia, nearshore waters and comparisons of life history styles of a suite of *Sillago* species. *Environmental Biology of Fishes*. **49**: 435-447.
- Hyndes, G.A., Longergan, N.R. & Potter, I.C. (1992). Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fishery Bulletin*. **90**: 276-284.
- Hyndes, G.A., Potter, I.C. & Hesp, S.A. (1996a). Relationships between the movements, growth, age structures and reproductive biology of the teleosts *Sillago burrus* and *Sillago vittata* in temperate marine waters. *Marine Biology*. **126**: 549-558.

- Hyndes, G.A., Potter, I.C. & Lenanton, R.C.J. (1996b). Habitat partitioning by whiting species (Sillaginidae) in coastal waters. *Environmental Biology of Fishes*. **45**: 21-40.
- Hyndes, G.A., Platell, M.E. & Potter, I.C. (1997a). Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. *Marine Biology*. **128**: 585-598.
- Hyndes, G.A., Platell, M.E., Potter, I.C. & Lenanton, R.C.J. (1997b). Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia. *Fishery Bulletin*. **96**: 258-270.
- Jayasankar, P. (1991). Sillaginid fishes of Palk Bay and Gulf of Mannar with an account of the maturation and spawning of Indian sand whiting, *Sillago sihama* (Forsskal). *Indian Journal of Fisheries*. **38**: 13-25.
- Jenkins, G.P., May, H.M.A., Wheatley, M.J. & Holloway, M.G. (1997). Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. *Estuarine, Coastal and Shelf Science*. **44**: 569-588.
- Johnstone, R.E. (1990). *Mangroves and mangrove birds of Western Australia*. Perth, W.A., Western Australian Museum.
- Kocovsky, P.M. & Carline, R.F. (2000). A comparison of methods for estimating ages of unexploited walleyes. *North American Journal of Fisheries Management*. **20**: 1044-1048.
- Khoo, K.H. (1979). The histochemistry and endocrine control of vitellogenesis in goldfish ovaries. *Canadian Journal of Zoology*. **57**: 617-626.

- Kimura, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*. **77**: 765-776.
- Laevastu, T. (1965). *Manual of Methods in Fisheries Biology*. Rome: FAO.
- Lambert, T.C. & Ware, D.M. (1984). Reproductive strategies of pelagic and demersal spawning fish. *Canadian Journal of Fisheries and Aquatic Sciences*. **41**: 1561-1569.
- Lasiak, T.A. (1986). Juveniles, food and the surf zone habitat: implications for teleost nursery areas. *South African Journal Zoology*. **21**: 51-56.
- Le Cren E.D. (1951). The length weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology*. **20**: 201-219.
- Lenanton, R.C.J. (1970). The biology of commercially fished whiting (*Sillago* spp.) in Shark Bay, Western Australia. M.Sc. Thesis, University of Western Australia, Perth.
- Lenanton, R.C.J. (1982). Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Australian Journal of Marine and Freshwater Research*. **33**: 881-900.
- Lenanton, R.C.J. & Caputi, N. (1989). The roles of food supply and shelter in the relationship between fishes, in particular *Cnidoglanis macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. *Journal of Experimental Marine Biology and Ecology*. **128**: 165-176.
- Leica Microsystems Ltd. (2001). Leica Image Manage 1000, user manual. Heerbrugg. p. 638.

- Lentsch, L.D. & Griffith, J.S. (1987). Lack of first-year annuli on scales: frequency of occurrence and predictability in trout of the western United States. In *The Age and Growth of Fish*. (Eds. R.C. Summerfelt and G.E. Hall). Iowa State University Press, USA. pp. 177-188.
- Lowerre-Barbieri, S.K., Chittenden, M.E. Jr. & Jones, C.M. (1994). A comparison of a validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional method. *Fishery Bulletin*. **92**: 555-568.
- Maceina, M.J. & Betsill, R.K. (1987). Verification and use of whole otoliths to age white crappie. In *The Age and Growth of Fish*. (Eds. R.C. Summerfelt and G.E. Hall). Iowa State University Press, USA. pp. 267-278.
- Marsh, L.M. (1990). Mermatypic corals of Shark Bay, Western Australia. In *Research in Shark Bay: Report of the France-Australe Bicentenary Expedition Committee*. (Eds. P.F. Berry, S.D. Bradshaw and B.R. Wilson). Western Australian Museum, Perth. pp. 115-128.
- Mayer, I., Shackley, S.E. & Ryland, J.S. (1988). Aspects of the reproductive biology of the bass, *Dicentrarchus labrax* L. I. A histological and histochemical study of oocyte development. *Journal of Fish Biology*. **33**: 609-622.
- McEvoy, L.A. & McEvoy, J. (1992). Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. *Journal of Fish Biology. Supplement B*. **41**: 125-136.
- McKay, R.J. (1992). FAO Species Catalogue. Sillaginid fishes of the world (family Sillaginidae). An annotated and illustrated catalogue of the *Sillago*, smelt or Indo-Pacific whiting species known to date. FAO Fish. Synops. No. 125, Vol. 14.
- Morton, R.M. (1985). The reproductive biology of summer whiting, *Sillago ciliate* C. & V., in northern Moreton Bay, Queensland. *Australian Zoology*. **121**: 491-502.

- Newman, S.J., Williams, D, McB. & Russ, R.R. (1996). Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lujanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from central Great Barrier Reef, Australia. *Marine and Freshwater Research*. **47**: 575-584.
- Nichol, D.G. & Acuna, E.I. (2000). Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering Sea. *Fishery Bulletin*. **99**: 108-122.
- Pauly, D. (1980). On the interrelationships between M, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer*. **39**: 175-192.
- Panella, G. (1974). Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In *The Ageing of Fish*. (Ed. T.B. Bagenal). Unwin Brothers, London. pp. 28-40
- Pedretti, Y.M. & Paling, E.I. (2001). *WA Mangrove Assessment Project 1999-2000*. Murdoch University, Perth, W.A.
- Potter, I.C. & Hyndes, G.A. (1999). Characteristics of ichthyofaunas of south-western Australian estuaries, including comparisons with holarctic estuaries and estuaries elsewhere in temperate Australia. *Australian Journal of Ecology*. **24**: 295-421.
- Potter, I.C., Beckley, L.E., Whitfield, A.K. & Lenanton, R.C.J. (1990). Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environmental Biology of Fishes*. **28**: 143-178.
- Quinn, T.P., Nemeth, R.S. & McIsaac, D.O. (1991). Homing and straying patterns of fall chinook salmon in the lower Columbia River. *Transactions of the American Fisheries Society*. **120**: 150-156.

- Ralston, S. (1987). Mortality rates of snapper and groupers. In *Tropical snappers and groupers. Biology and fisheries management*. (Eds. J.J. Poloviina and S. Ralston). Westview Press, Boulder, USA. pp. 375-404.
- Ricker, W.E. (1969). Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *Journal of the Fisheries Research Board of Canada*. **26**: 479-541.
- Ricker, W.E. (1975). Growth rates and models. In *Fish Physiology. Vol. III. Bioenergetics and growth*. (Eds. W.S. Hoar, D.J. Randall, and J.R. Brett). Academic Press, New York. pp. 687-743.
- Rikhter, V.A. & Efanov, V.N. (1976). On one of the approaches to estimation of natural mortality of fish populations. *ICNAF Research Document*. 79/VI/8.
- Robertson, A.I. & Duke, N.C. (1987). Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Marine Biology*. **96**: 193-205.
- Robertson, A.I. & Lenanton, R.C.J. (1984). Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. *Journal of Experimental Marine Biology and Ecology*. **84**: 265-283.
- Rooper, C.N., Bryant, M.D. & McCurdy, S.J. (2000). Use of scales to assess summer growth of resident cutthroat in Margaret Lake, Alaska. *North American Journal of Fisheries Management*. **20**: 467-480.
- Ross, S.T. (1986). Resource partitioning in fish assemblages: a review of field studies. *Copeia*. **1986**: 352-388.
- Russell, D.J. & Garrett, R.N. (1983). Use by juvenile barramundi, *Lates calcarifer* (Bloch), and other fishes of temporary supralittoral habitats in a tropical

estuary in northern Australia. *Australian Journal of Marine Freshwater Research*. **34**: 805-811.

Samuel, M. & Mathews, C.P. (1987). Growth and maturity of four *Acanthopagrus* species. *Kuwait Bulletin of Marine Science*. **1987**: 159-171.

Sarre, G.A. & Potter, I.C. (2000). Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors. *Fishery Bulletin*. **98**: 785-799.

Schoener, T.W. (1974). Resource partitioning in natural communities. *Science*. **185**: 27-39.

Schnute, J. (1981). A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences*. **38**: 1128-1140.

Shaw, J. (2000). *Fisheries Environmental Management Review Gascoyne region*. Fisheries Environmental Management Review No. 1. Fisheries Western Australia. pp. 83-86

Sipe, A.M. & Chittenden Jr, M.E. (2001). A comparison of calcified structures for ageing summer flounder, *Paralichthys dentatus*. *Fisheries Bulletin*. **99**: 628-640.

SPSS Inc. (2001). SPSS-X 11.0. Spss Inc, Chicago.

Starck, W.A. & Schroeder, R.E. (1970). Investigations of the grey snapper, *Lutjanus grieseus*. In *Studies in Tropical Oceanography*. Vol. 10. University of Miami Press, Coral Gables.

Vetter, E.F. (1988). Estimation of *M* in fish stocks: a review. *Fishery Bulletin*. **86**: 25-43.

- Vouglitois, J.J., Able, K.W., Kurtz, R.J. & Tighe, K.A. (1987). Life history and population dynamics of the bay anchovy in New Jersey. *Transactions of the American Fisheries Society*. **116**: 141-153.
- Walker, D.I., Kendrick, G.A. & McComb, A.J. (1988). The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. *Aquatic Botany*. **30**: 305-317.
- Wallace, R.A. and Selman, K. (1981). Cellular and dynamic aspects of oocyte growth in teleosts. *American Zoology*. **21**: 325-343.
- Weddle, G.K. & Burr, B.M. (1991). Fecundity and the dynamics of multiple spawning darters: an in-stream study of *Etheostoma rafinesquei*. *Copeia*. **1991**: 419-433.
- Weng, H.T. (1986). Spatial and temporal distribution of whiting (Sillaginidae) in Moreton Bay, Queensland. *Journal of Fish Biology*. **29**: 755-764.
- West, G. (1990). Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine and Freshwater Research*. **41**: 199-222.
- Wilson, C.A. & Nieland, D.L. (2001). Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. *Fisheries Bulletin*. **99**: 653-664.
- Wright, J.M. (1988). Seasonal and spatial differences in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. *Marine Biology*. **100**: 13-20.