The biology of four commercial fish species

in a seasonally closed estuary

by

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Declaration

I declare that the information contained in this thesis is the result of my own research unless otherwise cited.

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Abstract

The aim of this study was to determine the size and age compositions, growth rates, reproductive biology, dietary compositions and mesh selectivity of the King George whiting *Sillaginodes punctata*, the Australian herring *Arripsis georgiana*, the yelloweye mullet *Aldrichetta forsteri* and the sea mullet *Mugil cephalus* in Wilson Inlet. These biological variables were chosen for analysis since the resultant data would be of use for managing these commercially important marine species in this seasonally closed estuary, which is located on the southern coast of Western Australia.

Samples of each of the above species were typically collected, in at least every other month between April 1988 and April 1990, by using seine netting and gill netting at several sites, distributed at regular intervals throughout the 48 km² basin of Wilson Inlet, and by gill netting at one site in each of two tributary rivers. The ages of *Sillaginodes punctata*, *Aldrichetta forsteri* and *Mugil cephalus* were determined using the annuli on scales, whereas those of *Arripsis georgiana* were determined using the annuli on otoliths. The annuli on the above hard structures of the four species were shown to be formed annually before they were used for aging purposes.

Although at least four year classes of each species were found in Wilson Inlet, the 0+ year class of none of the species was well represented in this estuary. The paucity of this age class was probably attributable, in most cases, to the spawning grounds of these species being located some distance away on the lower west coast of Australia. However, the absence of any 0+ *S. punctata* in one year was attributed to the mouth of Wilson Inlet being closed at a crucial time, which thereby prevented the recruitment of this species into this estuary.
Virtually all of the *S. punctata* caught in Wilson Inlet were less than the $L_{59}$ at first maturity, which implies that none of this species return to this estuary after they have emigrated to sea, matured and spawned. However, appreciable numbers of each of the other three species were found at lengths greater than their respective $L_{50}$s. There was clear evidence that large *A. forsteri* tended to leave the estuary soon after the bar at the estuary mouth was breached. In contrast, length-frequency distributions indicated that large *A. georgiana* often tended to remain in the estuary, even when they exceeded the $L_{59}$ at first maturity and the estuary mouth was open. The maximum lengths attained by *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* were 491, 373, 430 and 525 mm, respectively, while the maximum ages attained by these four species were 5+, 7+, 5+ and 4+, respectively. While there was no significant difference between the growth rates of the two sexes of either *S. punctata* or *M. cephalus*, the overall growth rates of the females of *A. georgiana* and *A. forsteri* were both greater than those of their males.

Each fish was assigned a maturity stage using the criteria of Laevastu (1965). The maximum maturity stage recorded for the gonads of *S. punctata* was IV (maturing). The fact that no *S. punctata* with spawning (stage VI), spent (stage VII), recovering spent (stage VIII) or resorbing gonads were found provides overwhelming evidence that this whiting species neither spawns in Wilson Inlet nor returns to this estuary after it has spawned at sea. Furthermore, spawning and recently-spent gonads were never found in individuals of either *A. georgiana, A. forsteri* or *M. cephalus*, which implies that these species also do not spawn in the estuary. However, some *A. georgiana* and *A. forsteri* with recovering spent gonads were found in Wilson Inlet, which indicates that some individuals of these two species enter the estuary after spawning at sea. There was no indication that this also applied with *M. cephalus*. Yet, the gonads of some individuals
of this latter species and also of *A. georgiana* contained resorbing gonads, *i.e.* gonads that had reached a reasonably advanced stage, but not maturity, and which were now undergoing regression. The fish with these gonads had presumably been trapped in the estuary at the time their gonads were developing and could not therefore emigrate out to their marine spawning areas.

The dietary compositions of the four species were shown to be significantly different. *Sillaginodes punctata* and *A. georgiana* fed mainly on benthic macroinvertebrates, while all but the smallest *M. cephalus* were detritivores and *A. forsteri* was an omnivore. Furthermore, *S. punctata* fed mainly on errant polychaetes and nemerteans, whereas *A. georgiana* ingested decapods, mysids and other teleosts. The diets of each species underwent size-related changes. The differences in dietary compositions among and within species would reduce the likelihood of inter- and intraspecific competition for food resources.

Comparisons have been made between traditional methods for estimating the selectivity of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* in gill nets and a new method of analysis developed (with Dr. N. Hall), which incorporates the best features of the traditional methods.
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Chapter 1

General Introduction

1.1 Bar-built estuaries

On the basis of their geomorphology, Ketchum (1983) has classified estuaries into four main types, *i.e.* drowned river valleys, fjords, deltaic formations and bar-built estuaries. The estuaries of south-western Australia are all bar-built and connected to the ocean by narrow entrance mouths that restrict the exchange of water between their large central basins and the ocean (Hodgkin 1998, Hodgkin and Hesp 1998). Tidal transport through the entrance is thus limited and circulation patterns within the estuary are often determined more by wind and changes in barometric pressure than tidal flow (Hodgkin and Lenanton 1981).

In the geological past, the estuaries of south-western Australia were part of a system of large open seaways (Hodgkin and Hesp 1998). Flood tide deltas formed within these estuaries during the Holocene, blocking flow channels, narrowing entrance channels and aiding in the formation of ocean sand bars at the mouths, thus forming the bar-built estuaries that exist today (Hodgkin 1998, Hodgkin and Clark 1988, Hodgkin and Hesp 1998). These bar-built estuaries can be separated into groups according to the extent of their connection with the ocean, *i.e.* permanently open, seasonally open, permanently closed and normally closed (Hodgkin and Hesp 1998). To a large degree, the extent of the connection determines the hydrology of the estuary, which, in turn,
affects the distribution and abundance of the fish species within each system (Lenanton & Hodgkin 1985, Potter and Hyndes 1999).

1.2 Wilson Inlet and its catchment area

Wilson Inlet is located on the south coast of Western Australia between latitudes 34°38’ and 35°02’ S and longitudes 117°18’ and 117°29’ E (see Fig. 2.1 for map). The system is open to the sea seasonally, and a sand bar blocks the narrow and shallow entrance channel, preventing an exchange of water with the Southern Ocean for periods which can last up to several months. Although the large shallow basin of the estuary can become 4 to 5 m deep in winter, the average depth is typically less than 2 metres. The lagoonal-like basin is 14 km long, 4 km wide and has a total surface area of 48 km² (Hodgkin and Clark 1988).

The estuary basin is fed by two large rivers, the Denmark and Hay Rivers, and four smaller tributaries, the Sleeman River, Cuppup Creek, Lake Saide Drain and Little River (Fig. 2.1). The catchment of the estuary has a total area of 2823 km², with those of the Denmark River and the Hay Rivers comprising 89% of the total catchment area (Lenanton 1974, Humphries et al. 1982).

1.3 The fish fauna of Wilson Inlet

The fish assemblage of Wilson Inlet is dominated by estuarine species, i.e. species capable of completing their life cycles within the estuary (Potter et al. 1993). The two most abundant species in the deeper waters of Wilson Inlet are the estuarine catfish *Cnidoglanis macrocephalus* and the blue spotted flathead *Platycephalus speculator*. Both species are represented by discrete populations in coastal marine waters, but, in Wilson Inlet, they have become adapted to completing
their life cycles in this seasonally-closed estuary (Hyndes et al. 1992b, Laurenson et al. 1993b, Potter et al. 1993). Cnidoglanis macrocephalus and P. specular are ranked first and second, respectively, in terms of their economic importance to the commercial fishery in Wilson Inlet (Hyndes et al. 1992a, Laurenson et al. 1993a).

The presence of relatively high salinities and sheltered habitats in the basin of Wilson Inlet also make it possible for many species of marine teleosts to remain for lengthy periods in the system, where they benefit from an increased availability of food and protection from predation (Potter et al. 1983). Other economically important species in Wilson Inlet include the King George whiting Sillaginodes punctata, the Australian herring Arripsis georgiana, the yelloweye mullet Aldrichetta forsteri and the sea mullet Mugil cephalus, which are all marine species. These four species spawn in the coastal marine waters of Western Australia and the resultant juveniles move inshore to sheltered marine embayments and estuaries (Thomson 1955, Dybdahl 1979, Lenanton 1977, 1978, 1982, Chubb et al. 1981, Lenanton et al. 1982, Potter et al. 1983, Lenanton and Hodgkin 1985, Lenanton and Potter 1987, Potter and Hyndes 1994, 1999, Ayvazian and Hyndes 1995, Hyndes et al. 1998, Fairclough et al. 2000b). Although Wilson Inlet provides ideal nursery habitats for large numbers of the juveniles of these species, the timing and duration of contact between the estuary and the sea directly affects the patterns of recruitment of these species into this seasonally-closed estuary and the extent to which they are subsequently retained (Lenanton and Hodgkin 1985, Potter et al. 1993).
1.4 The Wilson Inlet Fishery

Fish caught in south-western Australian estuaries contribute more than 12% by weight to the total finfish catch of all commercial fisheries in Western Australia (Lenanton and Potter 1987). Wilson Inlet supports the largest professional and amateur estuarine fishery on the south coast of Western Australia (Lenanton and Hodgkin 1985). The two main target species of the commercial fishery in Wilson Inlet are *C. macrocephalus* and *P. speculator*, which contributed ca 49 and 10%, respectively, to the total landed weight of the commercial catch in Wilson Inlet between 1987 and 1990 (Australian Bureau of Statistics 1991). However, substantial numbers of *A. forsteri*, *A. georgiana*, *M. cephalus* and *S. punctata* are caught on occasions (Australian Bureau of Statistics 1991) and, between 1987 and 1990, the average percentage contribution by weight to the total catch in Wilson Inlet made by *A. forsteri*, *A. georgiana*, *M. cephalus* and *S. punctata* was ca 10, 9, 7 and 6%, respectively (Australian Bureau of Statistics 1991).

At the time of this study, eight of the twenty-two commercially licensed fishers operating in Wilson Inlet, fished regularly in the estuary. These fishers employ sunken gill nets with stretched mesh sizes of 76, 89 or 102 mm when targeting the valuable *C. macrocephalus* and *P. speculator*. When the catches of *C. macrocephalus* underwent periodic declines (see Laurenson 1992), fishers switched to using gill nets with a mesh size of 57 mm to catch other species, and in particular *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus*. In addition, gill nets, with a mesh size of 44 mm, were used to target the sea garfish *Hyporhamphus melanochir* on those occasions when appreciable numbers of this marine species entered Wilson Inlet. There was no restriction on the maximum lengths for either set nets or purse seines and each of the
regular commercial fishers set up to 1.5 km of gill nets in the estuary during each night of fishing. Occasionally, one commercial fisher used a purse seine to target *H. melanochir, A. georgiana, A. forsteri, M. cephalus* and the anchovy *Engraulis australis*. All commercial fishing was prohibited in the waters between the mouth of the estuary and Poison Point (see Fig. 2.1 for map).

### 1.5 Rationale for studying fish populations in Wilson Inlet

Wilson Inlet is one of the most intensively studied estuarine systems on the south-coast of Western Australia (Hodgkin and Clark 1988). Land clearing in the catchment, nutrient input and increasing conflicts between interest groups are just a few of the issues that have made the collection of data specific to this estuary a matter of priority for management authorities. Thus, previous studies have concentrated on determining the processes that led to the increasing eutrophication of Wilson Inlet (Lenanton 1974, Humphries *et al.* 1982, Lukatelich *et al.* 1984, 1986, 1987, Ranasinghe and Pattiaratchi 1994, 1998, Western Australian Waterways Commission 1995, Thompson 1997, Western Australian Water and Rivers Commission 1998).

The commercial fish catch in Wilson Inlet is contributing an increasingly significant proportion to the total catch of the South Coast Estuarine Fishery (Pearn and Capelluti 1999). Furthermore, this estuary is an extremely popular destination for recreational fishers and tourists. Thus, in recent years, attention has focused on elucidating the most appropriate ways in which the catches should be allocated between recreational and commercial fishers, regulating commercial fishing effort and the extent to which gill net mesh sizes should be increased (Pearn and Cappelluti 1999).

The successful management of a fishery is dependent on a thorough understanding of the biology of the species on which it is based (King 1995). In the
case of Wilson Inlet, there are brief descriptions of the stomach contents and spawning periods of some of the fish species (Thomson 1957a, b), and data on the age and size compositions and growth of *P. speculator* (Hyndes et al. 1992a, b) and *C. macrocephalus* (Laurenson et al. 1993a, b) and the relative abundance of the suite of teleosts that occupy this estuary (Potter et al. 1993). There are also catch and effort data for commercial fish species, including *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* from the monthly returns of commercial fishers. Previous studies of assemblages of *S. punctata, A. forsteri* and *M. cephalus* in south-western Australian estuaries have described aspects of the biology of assemblages of these species in permanently-open systems on the lower west coast, *i.e.* the Swan River Estuary, Peel-Harvey Estuary and Leschenault Estuary (Chubb et al. 1981, Potter et al. 1983, Lenanton et al. 1984, Potter et al. 2000) and on the south-west coast, *i.e.* the Blackwood River Estuary (Lenanton 1977). Studies of the biology of *A. georgiana* have been conducted on fish caught almost exclusively in the marine environment (Lenanton 1978, Fairclough et al. 2000a, b). However, little information exists on the biology of these species in Wilson Inlet.

### 1.6 Aims of this study

In view of the importance of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* to the recreational and commercial fishery in Wilson Inlet, the current study was undertaken to examine those biological aspects that are relevant to the management of these species.

The specific aims of this study of the above four species in the seasonally-closed Wilson Inlet are as follows:
1. To determine the age compositions and growth characteristics of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus*.

2. To elucidate the influence of the timing of the bar opening and length of bar opening on the recruitment of juveniles.

3. To determine the reproductive biology of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus*.

4. To determine the dietary compositions of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus*.

5. To model the selectivity of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in gill nets.

The background and rationale for the studies on each of the different aspects of the biology of the above four species is given in greater detail in subsequent chapters.
Chapter 2

General materials and methods

2.1 Sampling sites and sampling regime

*Sillaginodes punctata*, *Arripsis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus* were caught in Wilson Inlet between April 1988 and April 1990. Sampling was conducted at eight sites within the basin of the estuary and at one site in each of the Denmark and Hay Rivers (Fig. 2.1). Seine nets were used to sample nearshore, shallow waters, while gill nets were employed to sample offshore, deeper waters. The sampling regime is detailed in Table 2.1.

2.1.1 Seine netting

Seine netting with a small mesh net was carried out at site 1 in each month between April 1988 and April 1990 (Table 2.2). Random triplicate seines were made during the day in the shallows over bare sand at this site. The small mesh seine net measured 21.5 m in length and comprised two 10 m wings (6 m of 9 mm mesh and 4 m of 6 mm mesh) and a 1.5 m pocket (3 mm mesh). The net fished to a depth of 1.5 m and swept an area of 116 m².

Bimonthly sampling using a large mesh beach seine was carried out during the day at four sites (2, 7 to 9) between April 1988 and April 1989 and at three sites (3 to 5) between April 1988 and August 1989 (Table 2.2). The large mesh seine was 46 m long and fished to a depth of 1.5 m and contained stretched mesh of 25 mm in the wings and 9.5 mm in the pocket.
Figure 2.1  Sampling sites in Wilson Inlet. Inset shows the location of Wilson Inlet in Western Australia.
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Table 2.1  The monthly sampling regime in Wilson Inlet. Circles represent sampling with gill nets. Closed squares represent seine netting with a large mesh net, open squares represent seine netting with a small meshed net.
<table>
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<tr>
<th>Site code</th>
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<td>6</td>
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<td>8</td>
<td>Bird Rocks</td>
<td>2</td>
</tr>
<tr>
<td>9</td>
<td>Hay River Mouth</td>
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<tr>
<td>10</td>
<td>Hay River Upstream</td>
<td>4</td>
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</table>

Table 2.2 Sites sampled in Wilson Inlet using both seine and gill nets and the maximum water depth at each site.

2.1.2 Gill netting

Fish were caught in floating, composite gill nets at nine sites (2 to 10) located throughout the basin and upper reaches of Wilson Inlet and in the Hay River (Fig. 2.1). Gill nets were set over a substrate consisting of sand, rock and the aquatic angiosperm *Ruppia megacarpa* (sites 2 to 9) and mud and rock (site 10). Water depths ranged between 2 and 4m. (Table 2.2). Gill nets were set at dusk and retrieved at first light after an average soak time of 13.5 h. Each gill net measured 180 m long with a drop of 1.5 m and comprised six 30 m long panels. The nets were manufactured from twisted multifilament nylon of mesh sizes 38, 51, 63, 76, 89 and 102 mm (manufacturer’s specifications for stretched mesh, knot to knot).

Gill netting at site 2 was carried out monthly between April 1988 and August 1989 and bimonthly between October 1989 and April 1990. Between April 1988 and April 1989, gill netting was carried out bimonthly at seven sites (3, 4, 6 to 10). Sampling at site 5 was discontinued after August 1988 because of the low catches.
that were obtained at this site. Bimonthly sampling at sites 6 and 9 was continued to April 1990.

2.1.3 Sampling the commercial catch

The catches of three commercial fishermen, operating regularly in Wilson Inlet, were sampled monthly between April 1988 and April 1990. Sampling was conducted at Rudgyard jetty as the catches were landed. Depending on the size of the catch, the total lengths of a random sample of up to thirty individuals of each species were measured to the nearest 1 mm. Wherever possible, scale samples were collected for aging. Undersized discards were occasionally retained by the fishermen and supplied for research purposes and these samples were processed in the same way as fish captured in research gill nets.
Chapter 3

Physico-chemical characteristics of Wilson Inlet and factors affecting the hydrology of the estuary

3.1 Introduction

Previous studies have shown that the hydrology of Wilson Inlet is affected by the length of time the estuary is open to the Southern Ocean, the amount of oceanic water that penetrates the estuary when the bar is open, the volume of freshwater discharged into the estuary, the extent of evaporation and the amount of mixing that is caused by wind action (Lenanton 1974, Hodgkin & Clark 1988, Potter et al. 1993).

3.1.1 The hydrology of Wilson Inlet

The estuaries of south-western Australia are subjected to similar climatic conditions and, as is the case with the other 63 estuaries of temperate Western Australia that are classified as “seasonally open”, Wilson Inlet likewise undergoes extreme seasonal fluctuations in variations in both river flow and salinity (Hodgkin and Lenanton 1981, Hodgkin and Clark 1988, Potter et al. 1993, Hodgkin and Hesp 1998). In general, salinities in Wilson Inlet remain relatively high, i.e. > 20‰ during much of the year. However, during the wet winter and early spring months, when rainfall is at its highest, freshwater discharge increases markedly and, as a consequence, salinities in the upper estuary often decline to less than 10‰. This marked increase in freshwater discharge also often causes the bar at the estuary mouth to be breached. During the
warm, dry summers, freshwater discharge virtually ceases, which, together with the presence of an open estuary mouth, results in salinities in the basin increasing to more than 25%. This results in the habitats of Wilson Inlet resembling those of the marine offshore environment (Hodgkin and Clark 1988, Potter et al. 1993).

3.1.2 The sand bar at the mouth of the estuary

Wilson Inlet becomes closed each year due to the formation of a massive sand, bar which extends from the western end of the Nullaki peninsula to the cliff behind Wilson head (Plate 3.1). The bar is breached annually on a date specified by management authorities after the water level in the Inlet exceeds 1.015 m above MSL (Hodgkin and Clark 1988). Heavy earth-moving machinery is used to excavate an initial cut through the bar. The difference in head level between the estuary and ocean then produces sufficient energy to scour a channel through the bar and thereby cause estuarine water to flow outwards through the cut. The entrance channel that forms when the sand bar is breached is short, narrow and shallow. Thus, since tidal movement through the entrance channel is limited, the amount of water exchanged between the estuary basin and the ocean is restricted (Lenanton 1974). Indeed, most of the exchange of water occurs through the effect of meteorological tides, during the passage of low pressure systems (Hodgkin and Clark 1988).

The mouth of the channel becomes closed as a result of a combination of factors, including a reduction in water level through decreased run-off and evaporation, which leads to a reduction in flow through the channel and oceanic wave action which reinforces the sand bar.
Plate 3.1  Aerial photograph taken in October 1996, showing the entrance channel of Wilson Inlet (Department of Land Administration).
3.2 Materials and methods

Measurements of surface and bottom salinities and surface and bottom temperatures were recorded at three sites (4, 7, 8) between April 1988 and April 1989 and at four sites (2, 3, 6, 10) between April 1988 to April 1990, on each occasion that gill netting and beach seining was carried out (see Fig. 2.1. for location of sampling sites and Table 2.1 for sampling times).

Rainfall and climatic data were supplied by the Bureau of Meteorology. Data on the timing, duration and position of the breaching of the sand bar at the mouth of Wilson Inlet were obtained from the Water Authority of Western Australia, the Wilson Inlet Management Authority, Lenanton (1974), Humphries et al. (1982) and Lukatelich et al. (1986).

3.3 Results

3.3.1 Salinity

The mean surface salinities at each site in the basin of the estuary exhibited similar monthly trends in both of the twelve month periods between April 1988 and April 1990 (Fig. 3.1). In April 1988, the surface and bottom salinities were the same at all sites, i.e. ca 30%. However, heavy winter rains during May and June 1988 (Fig 3.2) caused the water level in Wilson Inlet to rise from -0.5m to 1.01m in only six weeks (Hodgkin and Clark 1988). The increase in freshwater discharge led to a decline in surface and bottom salinities at all sites. Salinities continued to decline after the bar was breached in June 1988. At site 2 in the upper estuary, surface and bottom salinities decreased precipitously from 29.4% in April to a minimum of 6.0% in July 1988. Increased freshwater discharge inhibited seawater entering the system and thus
Figure 3.1  Mean salinities and temperatures recorded at the surface and bottom of the water column at sites in Wilson Inlet between April 1988 and April 1990. The open bars on the x-axis refer to autumn and spring months and the closed bars to winter and summer months. Stippled and open bars below the x-axis indicate periods when the mouth of the estuary was closed (C) and open (O).
Figure 3.2  Total monthly rainfall recorded at the Denmark P.O. gauging station between June 1987 and May 1990. (Data from the Australian Bureau of Meteorology).
an influence from the influx of seawater did not become apparent until rainfall
decreased in July. In this latter month, the bottom and surface salinities diverged
markedly at sites in the lower and middle estuary. At site 2 in August 1988, bottom
salinities reached a maximum of 35.1‰, while surface salinities increased only to
19.4‰. High levels of evaporation during the summer months led to surface salinities
at all sites increasing and, by January 1989, bottom salinities had decreased and surface
salinities had increased, with the result that there was no longer a halocline. Following
the closure of the mouth of the estuary in May 1989, continuing rainfall and increased
freshwater discharge at this time led to a decline in salinities at all sites, with, for
example, at site 2, the bottom and surface salinities decreasing from 27.6‰ in April
1989 to 14.8‰ in June 1989. Surface and bottom salinities tended to increase after July
1989, as seawater entered the estuary, following the breaching of the sand bar.

Similar seasonal trends in salinity were exhibited at each site. Marked
haloclines were formed during the winter months at sites 2, 3, 4 and 6 in the lower and
middle estuary, but these were less evident at sites 7, 8 and 9 in the upper estuary. The
lowest surface salinities, i.e. 0‰, were recorded at the sites at the mouths of the
Denmark and Hay Rivers, i.e. sites 4 and 9, respectively, during the winter months,
when rainfall was at its highest, and, as a consequence, freshwater discharge increased.

3.3.2 Water temperature

Water temperatures followed similar trends at all sites. Water temperatures were
highest during the summer months, with the maximum temperature of 23.0°C being
recorded at site 4 in February 1989, and lowest during the winter months, with the
minimum of 10.6°C being recorded at site 3 in August 1988 (Fig. 3.1).
3.3.3 Rainfall and ambient temperature

The climate in the Denmark region is mediterranean, with cool, wet winters and hot, dry summers (Fig. 3.2). Wilson Inlet lies in a high rainfall zone, with the annual rainfall in the catchment ranging from 1200 mm at the southwest township of Denmark to 700 mm at Mt. Barker in the north (Humphries et al. 1982) (Fig 3.3). Since rainfall is highest in winter, it produces maximum riverine discharge between July and October. Approximately 50 per cent of rain falls between June and August and 75 per cent of the total annual rainfall typically falls between May and October (Humphries et al. 1982) (Fig. 3.4). Although the average monthly rainfall exceeds average monthly pan evaporation for five months of the year, i.e. from May and September, high summer temperatures from December to February can cause significant rates of pan evaporation during this period (Humphries et al. 1982).

3.4 Discussion

3.4.1 Salinity and water temperature

During those periods in the summers of 1988 and 1989, when the estuary mouth was open and seawater entered the estuary, rainfall was low, freshwater flushing was minimal and evaporation was high, with the result that bottom and surface salinities throughout the system increased to between 20 and 30%. When the bar was breached during the late autumn and early winter of both 1988 and 1989, following heavy rainfall and a build up of freshwater, the increase in freshwater discharge into Wilson Inlet caused the salinity throughout the shallow estuarine basin to undergo pronounced changes. Marked haloclines were thus formed in the lower and middle estuary as bottom salinities remained high and surface salinities decreased. Sites in the upper
Figure 3.3  Total annual rainfall between recorded at the Denmark P.O. gauging station between 1976 and 1990. (Data from the Australian Bureau of Meteorology).

Figure 3.4  Mean monthly rainfall ± 1 s.e. recorded at the Denmark P.O. gauging station between 1976 and 1990. (Data from the Australian Bureau of Meteorology).
estuary did not experience vertical stratification due to the small volume of marine water that penetrated into the upper reaches of Wilson Inlet.

There were only minor variations in mean temperatures between sites in any given month. Furthermore, only minor differences were detected between surface and bottom temperatures at each site and thus there was no evidence that conspicuous thermoclines were formed. There was a direct relationship between fluctuations in temperatures and salinity at each site.

3.4.2 The effect of the sand bar on the physico-chemical characteristics of Wilson Inlet

The length of time that the estuary is connected to the sea and the season in which the bar is breached appears to have a significant effect on the physico-chemical characteristics of Wilson Inlet. The seasonal trends in salinities, that followed the opening of the channel for a short period in the late spring of 1987 (Potter et al. 1993), differ from those following the lengthy, late autumn/early winter channel openings of 1988 and 1989.

After the sand bar was opened on 13 October 1987, the influx of oceanic water caused only a slight increase in surface and bottom salinities at all sites. Indeed, salinities at all sites in the basin of the estuary remained constant, in the region of 21%, indicating that only a limited exchange of water occurred between the estuary and the ocean (Potter et al. 1993). The channel remained open for just over two months, closing on 18 December, with low rainfall, high temperatures and increased rates of evaporation resulting in a gradual increase in salinities at all sites during late summer (Potter et al. 1993).
In contrast, the breaching of the sand bar in 1988 and 1989 had a marked effect on the hydrology of Wilson Inlet. After the openings in these two years, which occurred during periods of increased winter rainfall, salinities fluctuated considerably at all sites throughout the estuary, and spring salinities, recorded when the estuary mouth was open, were considerably lower than those described by Potter et al. (1993) for the corresponding period in 1987.

3.4.3 Breaching of the sand bar

The continuing viability of Wilson Inlet is largely dependent on an appropriate frequency of opening of the sand bar connecting the estuary to the ocean (Humphries et al. 1982). However, there has been considerable conflict amongst various interest groups for many years over the timing and location of the opening of the bar.

The history of the opening of the bar is well-documented (Hodgkin and Clark 1988). After 1929, the construction of the Elleker-Nornalup railway line and the development of potato market gardens on the shores of the inlet, meant that it became necessary to consider opening the bar artificially in order to prevent periodic flooding of these low-lying areas. However, prior to 1955, the bar was usually breached naturally when the build-up of water from winter rains was sufficient to scour a channel through the bar. Between 1955 and 1970, the opening of the bar came under the control of the W.A. Public Works Department (PWD). Since 1971 the bar has been opened by the Denmark Shire Council. The positions where the channel was opened between 1955 and 1991 are given in Table 3.1. In the early years, the PWD cut the channel in the middle or the eastern side of the bar. When the Denmark Shire Council assumed control of breaching the bar, the position was moved closer to the western cliff face, but in 1990 and 1991 it reverted to the eastern side.
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</tbody>
</table>

Table 3.1 Opening and closing dates of the channel, the duration of opening, the distance of the cut from the western cliff-face and the position of the cut through the bar from 1955 to 1991. (Data from the WA Water Authority).

* Lenanton (1974) and Lukatelich et al (1986) both record that the mouth of the estuary did not open in 1959.
Prior to 1955, when the bar was allowed to breach naturally, the channel cut through the western side of the bar, close to the calcarenite cliffs. Although it has been claimed that the energy of the flow scoured a deep, wide channel, which promoted large-scale flushing of the estuary, there are insufficient data to prove that this is the case. However, there is evidence that, since the damming of the Denmark River in 1961 and the restriction of the head of water allowed to be trapped in the Inlet to less than 1.01 MSL, artificial openings have become less pronounced due to a reduction in the scouring effect at the estuary mouth.

When the channel is opened, there is a net inward transport of sand from the sea. Marine sediments have accumulated to form extensive “flood tide shoals” behind the bar and successive western breachings, over time, have resulted in the production of shallow channels which meander through the shoals, and thus lessen the amount of water exchanged with the ocean (Hodgkin and Clark 1988).

A return to an opening on the eastern side was first advocated by Lenanton (1974) as a means for improving water quality and providing conditions favourable for the recruitment of fish into the estuary. On the basis that an eastern channel is the shortest physical distance providing the steepest gradient between the deep water in the inlet and the deep water of the ocean, channels on the eastern side should theoretically facilitate the maximum possible exchange between the ocean and the estuary. Lenanton (1974) recorded that the eastern breachings of 1969 and 1970 formed deep, straight channels with high flow rates and low levels of turbidity. However, a reversion to an opening on the eastern side in 1990 (WIRG 1994) was not as successful as expected. Heavy siltation caused water flow in the channel to cease and it was necessary to dredge an emergency channel.
Statistical analysis of channel openings from 1955 to 1989 shows that there is no significant relationship between the location of the cut and the length of time that the channel remains open (Laurenson 1992). However, the data for the years between 1976 and 1990 shows that there is a significant inverse correlation between the day on which the channel is opened and the length of time during which there is a connection between the estuary and the sea (Fig 3.5). In other words, breaches that occur earlier in the year result in the channels remaining open for longer than those which occur in later months. On the basis of the premise that the channel is kept open by the scouring of estuarine water through the bar, it is reasonable to conclude that rainfall, which contributes to the volume and flow energy of water in the Inlet, also determines how long the channel remains open and there is a significant positive correlation between rainfall during the period that the channel remains open and thus the length of time that the estuary is connected to the sea (Fig. 3.6).

In effect, the shoals blocking the mouth of the estuary are now so large that neither an east side nor a west side breaching can guarantee a successful flushing of Wilson Inlet. However, breaches which coincide with heavy winter rainfall form channels that remain open longer than those which are initiated during periods of low rainfall.

3.4.4 Water Quality and Eutrophication

Wilson Inlet and its environs provide a major recreational and tourist centre for south-western Australia (Caputi and Lenanton 1977) and the area has a high conservation value (Humphries et al. 1982). However, like many other south-west estuaries, Wilson Inlet is beginning to show the adverse effects of increasing human pressure, both within the lagoon itself and in the surrounding catchment area. Land
Figure 3.5  Relationship between the day of breaching and the duration of the channel opening between the years 1976 and 1990.

Figure 3.6  Relationship between the amount of rainfall recorded during the opening period and the duration of channel opening between the years 1976 and 1990.
clearing and erosion have contributed to increased salinisation of streams in the catchment and a decrease in water quality in the estuary. Since approximately 75% of the Wilson Inlet catchment area is designated farmland, the estuary experiences nutrient loading from nitrogenous and phosphate fertilisers and the input of various biocides from agricultural run-off (Humphries et al. 1982).

The nutrient budget of Wilson Inlet has been extensively studied by Lukatelich et al. (1984, 1986, 1987). The Inlet experiences an annual net retention of phosphorous and is exhibiting symptoms of eutrophication, particularly in the prolific growth of large banks of the aquatic macrophyte Ruppia megacarpa. During those periods when the bar is closed, evaporation causes a significant reduction in the non-tidal water level, exposing the shallow fringing “weed” on the banks which then decompose, causing an aesthetic nuisance to tourists and local residents.

Various plans have been proposed to solve the problem of the declining water quality of Wilson Inlet. The physical removal of Ruppia from the estuary was not a feasible solution since Lukatelich et al. (1984) cautioned that the harvesting of Ruppia would remove the main sink for excess nutrients and lead to the development of large macroalgal blooms. Although macroalgal blooms can benefit a fishery through increasing fish abundance and thus fish catches (Lenanton et al. 1984, Steckis et al. 1995), they cause a dramatic decline in water quality, hindering boating and netting activities and producing an overpowering smell when they decay, which is unattractive and affects local residents and tourists. To reduce the amount of macroalgae, Lukatelich et al. (1984) recommended the amount of nutrients retained should be decreased through decreasing the residence time of nutrient-rich river water within the Inlet. This could be achieved by opening the bar in early winter so that it coincides with maximum
river flow, and thus allows the nutrient-enriched river water to pass rapidly to the ocean and thereby prevent phosphorous and nitrogen from concentrating in the basin of the estuary.

In February 1990, a group of local residents lobbied in support of an ambitious proposal to build a retaining wall on the cliff side of the channel with the intention of creating a permanent opening to the inlet (Denmark Bulletin, no 252). This plan generated much local debate (Denmark Bulletin, no. 253) and was responsible in part, for the formation of the Wilson Inlet Restoration Group (WIRG). WIRG submitted a plan to the Environmental Protection Agency in 1994 for the dredging of a channel on the western side of the bar (WIRG 1994). To date, none of these management proposals has been implemented. The management of Wilson Inlet is now the responsibility of the Wilson Inlet Management Authority.
Chapter 4

Age and growth of *Sillaginodes punctata*, *Arripsis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus*

4.1 Introduction

It is now considered essential that those growth zones, that are present on hard structures and are to be used for aging the individuals of a fish species, are shown to be formed at regular and known intervals (Beamish and McFarlane 1983, 1987). Such validation is required to demonstrate that it is appropriate to use the number of such growth zones for aging purposes. Validation has often involved demonstrating that the trends exhibited by the size of the marginal increment, *i.e.* the zone outside the outermost annuli, are consistent with an annual formation of the growth zones.

Furthermore, any validation that the annuli on the hard structures of fish are formed annually requires that such validation is performed separately on otoliths with differing numbers of annuli (Beamish and McFarlane 1983, Hyndes *et al.* 1992a). This procedure is required to overcome any potential problems that might be posed by the annuli on older fish becoming delineated at different times to those on younger fish. It is also important because the trends exhibited by the marginal increment on otoliths with a large number of annuli may obscure those exhibited on otoliths with a small number of annuli and which, on their own, do not show a seasonal trend that is consistent with an annual formation of those annuli (Hyndes *et al.* 1992a).

The annuli on hard structures, which have been used to age *S. punctata*, *A. forsteri* or *M. cephalus*, have only occasionally been validated as being formed
annually. However, while none of the studies, which used scales for aging *S. punctata*, have validated that the annuli on that hard structure can be used for that purpose (Caton 1966, Gilmour 1969, Lenanton 1977, Jones *et al.* 1990), the annuli on the sagittal otoliths of *S. punctata* in marine waters on the lower west and south coasts of Australia have been shown to be formed annually (Fowler and Short 1998, Hyndes *et al.* 1998). Likewise, while neither of the previous studies aimed at aging *A. georgiana* using scales have validated that the annuli on this hard structure are formed annually (Stanley 1975, Lenanton 1978), a recent study has demonstrated that, in marine waters, the annuli on otoliths are formed annually (Fairclough *et al.* 2000 b). In the context of otoliths, it should be recognised that, in some species in south-western Australia, this hard structure has to be sectioned to reveal all of its growth zones in the case of larger and older fish (Hyndes *et al.* 1992a), but that this was not the case with the otoliths of *A. georgiana* (Fairclough *et al.* 2000 b).

Early attempts to use the trends exhibited by the marginal increment to validate that the annuli on scales were appropriate for aging those *A. forsteri* (Thomson 1957d) and *M. cephalus* (Thomson 1951) that are found in Western Australian estuaries were severely hampered by a lack of samples over the critical period of October to January when the annuli are likely to become delineated. However, Grant and Spain (1975) were able to use marginal increment analysis for this purpose with the scales of *M. cephalus* obtained from fish in north-eastern Australia. A few studies of *A. forsteri* and *M. cephalus* have used Petersen’s method in an attempt to confirm that the ages estimated from the number of annuli on scales or otoliths were valid (Kesteven 1942, Thomson 1951, 1957d, Harris 1968). This technique assumes that the modes in length-frequency data correspond to single cohorts or recruitment events. However, Petersen’s
method cannot be used to validate that a hard structure is appropriate for aging in the case of those species which have protracted spawning periods and live for several years, such as *A. forsteri* and *M. cephalus*. The inability to adopt this procedure in such cases is due to the fact that cohorts are recruited into a population over a period of several months and the length distributions of the different age classes thereby show an increasing tendency to overlap and are thus not represented by distinct modes in the length-frequency distributions (see Beamish and McFarlane 1983, Hilborn and Walters 1992).

The age and size compositions of *S. punctata* in marine waters have been studied by several workers (Scott 1954, Caton 1966, Gilmour 1969, Robertson 1977, Jones et al. 1990, Cockrum and Jones 1992, Jenkins et al. 1996, Fowler and Short 1998, Hyndes et al. 1998, Fowler et al. 1999, 2000). However, studies on the age and growth of this species in estuarine environments are restricted to estimates of daily growth rates of the postlarvae of this species in an estuary in South Australia (Fowler and Short 1996).

Estimates of the age and growth of *A. georgiana* are similarly restricted to fish caught in marine waters (see Stanley 1975, Lenanton 1978, Fairclough et al. 2000b). This point is important because, in comparison with the marine environment, estuaries contain a greater abundance of food, which may thus facilitate a faster growth rate of this species than that which occurs in marine waters (see Whittaker 1975, Mann 1982). In terms of managing the estuarine fisheries for *S. punctata* and *A. georgiana*, it is thus important to demonstrate that the biological parameters previously determined for marine assemblages also apply to the estuarine assemblages of those species.

A number of studies have been carried out on the age and growth of the mugilids *A. forsteri* and *M. cephalus* in permanently- open estuarine systems in Australia.
(Kesteven 1942, Thomson 1951, 1957d, Harris 1968, Grant and Spain 1975, Chubb et al. 1981, Lenanton et al. 1984) and New Zealand (Webb 1972). However, no attempt has previously been made to determine the age and growth of mugilids in the seasonally-closed estuaries of south-western Australia.

The aim of this study was to describe the size and age compositions and growth rates of the assemblages of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* found in Wilson Inlet, with emphasis first being placed on validating that an appropriate hard structure was being used for aging fish. Growth parameters have been compared with those reported for other Australian assemblages of these species. The effect of the timing and duration of the periodic opening of the sand bar on the age composition of assemblages of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* in Wilson Inlet is also considered.

### 4.2 Materials and methods

#### 4.2.1 Biotic measurements

The total length (TL) and wet weight of the individuals of *Sillaginodes punctata, Arripis georgiana, Aldrichetta forsteri* and *Mugil cephalus*, that were obtained by gill and seine netting, were recorded to the nearest 1 mm and 0.01 g, respectively. Up to thirty fish of each of the above species collected from each site on each sampling occasion were randomly subsampled to provide scales and otoliths for aging. The criteria used to assign gonads to appropriate maturation stages, which provide the data necessary for determining the spawning period and assigning birth dates, are described in Chapter 5.
4.2.2 Choice of hard structures for aging studies

Preliminary microscopic examination of the scales and otoliths of *S. punctata*, *A. forsteri* and *M. cephalus*, using transmitted light, showed that the annuli could be readily identified on the scales but not on the whole sagittal otoliths of these three species. Conversely, annuli were not clearly defined on the scales of *A. georgiana*, whereas translucent and opaque zones were easily distinguishable on the sagittal otoliths of this species, particularly in the posterior region of the otolith. Thus, the scales of *S. punctata*, *A. forsteri* and *M. cephalus* and the sagittal otoliths of *A. georgiana* were selected as candidates for aging these species.

Since the smallest *A. georgiana* collected in Wilson Inlet was 121 mm, 85 individuals of this species, that were collected from Poison Point (33°19'S, 123°55'E) between August and October 1996, and ranged in length from 31 to 76 mm, were used to provide the lengths-at-age of young fish and thus facilitate the construction of a more reliable growth curve for this species.

4.2.3 Use of scales for aging

Scales were removed from below the lateral line and beneath the distal end of the left pectoral fin of each of the *S. punctata*, *A. forsteri* and *M. cephalus* that was to be aged. The scales were cleaned, dried and stored in labelled envelopes. Damaged or regenerated scales were discarded. Scales were mounted between glass slides and viewed under transmitted light using an Olympus BH-2 microscope with a Panasonic WV-CD20 video camera that was connected to a video display unit. The focus of a scale to the outer edges of successive annuli on that scale were measured to the nearest 0.05 mm along a diagonal line from the focus to its right postero-lateral corner using
OPTIMAS software (Optimas © 1988-1994, Optimas Corporation). These measurements enabled the distance between the outer edge of the outer annulus and the outer edge of the scale (= marginal increment) to be determined. The marginal increment was expressed as the ratio of the distance between the focus of the scale and the outer edge of the annulus when a single annulus was present, and as a ratio of the distance between the outer edges of the two outermost annuli when two or more annuli were present. For convenience, these relative values are subsequently referred to just as the marginal increment. Marginal increments for scales in each corresponding month for the different years were pooled. The number of annuli on each scale was recorded.

4.2.4 Use of otoliths for aging

The sagittal otoliths of *A. georgiana* were removed, dried and stored in envelopes. Whole otoliths were immersed in methyl salicylate and examined under reflected light against a dark background using a dissecting microscope at a magnification of 25 or 50 X, depending on the size of the otolith. The whole otoliths of large fish contained a large central opaque zone (= core), surrounded by regularly alternating concentric translucent and opaque zones (= annuli). The central opaque zone was deposited immediately after fish had been spawned in the late autumn and early winter (see Results) and, for the purposes of aging, was regarded as the first opaque zone.

The distance between the outer edge of each opaque zone and the periphery of each otolith (= marginal increment ) was measured to the nearest 0.05 mm along the long axis of the otolith using an ocular micrometer. The marginal increment was expressed as a proportion of the distance between the focus and the outer edge of the opaque zone,
when only a single opaque zone, \textit{i.e.} core, was present on an otolith, and as a proportion of the distance between the two outer edges of the two outermost opaque zones, when two or more opaque zones were present. As with scales, these relative measurements are subsequently referred to just as the marginal increment. Marginal increments for otoliths in each corresponding month for the different years were pooled. The number of opaque zones on each otolith was recorded.

4.2.5 \textit{Fitting the growth model}

The age of each individual fish of each species was determined from the number of growth zones on the hard structures used for aging and the birth date assigned to that species (see Chapter 5). von Bertalanffy growth models were fitted to the length and age of each individual of each species. Note that, in the case of small fish that could not be sexed, the lengths at age of those fish were randomised and assigned alternately to the data sets for males or females.

While linear methods are traditionally used to fit the von Bertalanffy growth model to age and length data, non-linear least squares methods (Vaughan and Kanciruk 1982) are now accepted as providing the best parameter estimates of this model (Helser 1996). The non-linear form of the von Bertalanffy growth equation, which relates the predicted length of an individual fish \( l_u \) and age \( t_u \) \((u = 1, \ldots, n)\), is of the form

\[
l_u = L_\infty \left(1 - e^{-K(t_u-t_0)}\right) + \varepsilon_u
\]

where \( L_\infty \) is the asymptotic body length, \( K \) is the Brody growth coefficient, \( t_0 \) is a coefficient compensating for apparent non-zero body length at age zero and the \( \varepsilon_u \)s are
assumed to be independent, identically distributed $N(0, \sigma^2)$ random variates. The von Bertalanffy equation can be expressed as

$$l_u = f(\hat{\theta}, t_u) + \varepsilon_u$$

where $\hat{\theta}$ is a vector of the parameter estimates. The least squares estimate $\hat{\theta}$ is the parameter estimate which minimises the sum of squares of residuals

$$S(\hat{\theta}) = \sum_{u=1}^{n} (l_u - f(\hat{\theta}, t_u))^2$$

where $n$ is the sample size.

All calculations were performed using worksheets in Microsoft® Excel for Windows™. The von Bertalanffy growth model was fitted separately to data for female and male fish and estimates of the error variances were calculated.

4.2.6 Comparison of the parameters of von Bertalanffy growth models

Of the two most commonly used techniques for simultaneously comparing von Bertalanffy parameters, the procedure based on the likelihood ratio statistic, as developed by Kimura (1980), was shown by Cerrato (1990) to be more reliable than the alternative approach, based on Hotelling’s $T^2$ statistic (see Kingsley 1979, Bernard 1981). The growth parameters of females and males of each species were compared using likelihood ratio statistics (Kimura 1980, Cerrato 1990). The null and alternative hypotheses can be stated as -
\( H_o \): that the parameters \( L_{ao}, K, \text{ and } t_o \) satisfy some set of \( q \) linear constraints

\( H_\Omega \): that the parameters \( L_{ao}, K, \text{ and } t_o \) possibly satisfy no linear constraints.

Eight models were fitted to the growth data, i.e. a six parameter model with no linear constraints, three five parameter models with linear constraints on the individual parameters of \( L_{ao}, K, \text{ and } t_o \), three four parameter models with linear constraints on the parameter pairs of \( L_{ao} \) and \( K, L_{ao} \) and \( t_o \), and \( K \) and \( t_o \), and a three parameter model with linear constraints on all three parameters. The linear constraints applied to the von Bertalanffy growth equation, the null and alternative hypotheses associated with each level of constraint and the degrees of freedom of the test statistic are given in Table 4.1. Homogeneity of variances was tested using the F-test, to determine which of the methods described below was to be used when comparing the growth models.

For two data sets with equal error variances, i.e. \( \sigma^2_1 = \sigma^2_2 \), the maximum likelihood estimate of the error variance \( \hat{\sigma}^2 \), is obtained by minimising the sum of squares of residuals resulting from the non-linear procedure used to fit \( L_{ao}, K \text{ and } t_o \), subject to \( q \) linear constraints. The equation is given by

\[
\hat{\sigma}^2 = S(\hat{\theta})/(n_1 + n_2)
\]

When error variances are not homogeneous, i.e. \( \sigma^2_1 \neq \sigma^2_2 \), the maximum likelihood estimates of the error variances, \( \hat{\sigma}^2_1 \) and \( \hat{\sigma}^2_2 \), are obtained by maximising the log likelihood resulting from the non-linear fitting procedure where

\[
LL = -0.5(n_1 + n_2)(1 + \ln 2\pi) + n_1 \ln \hat{\sigma}^2_1 + n_2 \ln \hat{\sigma}^2_2
\]

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<table>
<thead>
<tr>
<th>Model</th>
<th>Model parameters</th>
<th>Degrees of freedom ((q))</th>
<th>Number of parameters ((p))</th>
</tr>
</thead>
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<tr>
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<td>3</td>
</tr>
</tbody>
</table>

Table 4.1 The parameters of each model, the degrees of freedom associated with each hypothesis for likelihood ratio tests and the number of parameters used to calculate growth models for females \((F)\) and males \((M)\) of each species.
The likelihood ratio test statistic, for two data sets with unequal error variances and sample sizes \(n_1\) and \(n_2\), where the combined sample size is large, \(i.e. (n_1 + n_2) > 300\), is given by

\[
\Lambda^{-2/\nu} = e^{-\frac{2(L_{\omega} - L_{\Omega})}{n_1 + n_2}}
\]

where the subscripts \(\omega\) and \(\Omega\) distinguish the estimates obtained under the null and alternative hypotheses, respectively.

Under the null hypothesis, \(\Lambda^{-2/\nu}\) converges asymptotically to a random variable whose distribution under the null hypothesis is a function of the \(F\) distribution (Gallant 1975). The null hypothesis is rejected at the \(\alpha\) level of significance when

\[
\Lambda^{-2/\nu} > \left(1 + \frac{q}{f_1 + f_2} F_{a, \nu, f_1 + f_2}\right)
\]

where \(f_i = n_i - 3\).

When the error variances are homogeneous, \(i.e. \sigma_1^2 = \sigma_2^2\), \(\Lambda^{-2/\nu} = \hat{\sigma}_\omega^2 / \hat{\sigma}_\Omega^2\) (Gallant 1975) and the null hypothesis is rejected at the \(\alpha\) level of significance when

\[
\frac{S(\hat{\theta}_\omega, \hat{\theta}_{\omega 2}) - S(\hat{\theta}_\Omega, \hat{\theta}_{\Omega 2})}{S(\hat{\theta}_\Omega, \hat{\theta}_{\Omega 2})/(f_1 + f_2)} > F_{a, \nu, f_1 + f_2}
\]

where \(S\) is the sum of squares of the residuals for both data sets.

In some cases, the likelihood ratio test resulted in conflicting outcomes, \(i.e.\) a significant difference between the six parameter model and a five parameter model but no significant difference between the six parameter model and the three parameter...
model. Therefore, the selection of the more appropriate model from the set of candidate models was determined using the Bayesian Information Criterion (BIC) (Schwarz 1978). The most appropriate model was selected as that model for which the BIC produced the smallest value. When the error variances were homogenous, the BIC was calculated for each model using the formula

\[ BIC = n \log \left( \frac{S(\hat{\Theta}, \hat{\Sigma})}{n} \right) + p \log(n). \]

For two data sets with unequal error variances, the BIC was given by

\[ BIC = -2(\text{LL}) + p \log(n) \]

where \( p \) refers to the number of parameters and

\[ p = 6-q. \]

4.3 Results

4.3.1 Age and growth of Sillaginodes punctata

The mean monthly marginal increments on the scales of Sillaginodes punctata with one annulus increased slightly from 0.8 to 1.1 between April and October and then declined precipitously to <0.1 in November, before increasing progressively to 0.9 in March (Fig. 4.1). The mean monthly marginal increments on scales with two and three to five annuli collectively followed the same trends, and thus likewise underwent a precipitous decline between September and November (Fig. 4.1). The strong seasonal trends displayed by the marginal increments on the scales of S. punctata, with a
Figure 4.1  Mean monthly values ± 1 S.E. for marginal increments on the scales of *Sillaginodes punctata*, using pooled data for the corresponding months in the years 1988-90. The marginal increment is expressed as a proportion of the distance between the focus and the outer edge of the annulus, when only one annulus was present, and as a proportion of the distance between the outer edges of the two outermost annuli, when two or more annuli were present. The number of scales examined is given above each mean.

In this and Figs 4.4, 4.7 and 4.10, the open bars refer to autumn and spring months and the closed bars to winter and summer months.
pronounced decline and subsequent progressive rise occurring only once during the year, demonstrates that an annulus is formed on the scales of *S. punctata* each year and that the number of such annuli can thus be used to age this sillaginid in Wilson Inlet.

Since the spawning of *S. punctata* peaks in late July/early August in marine waters (Hyndes *et al.* 1998), this sillaginid was assigned a birth date of 1 August (for full rationale see Chapter 5). In 1988, small numbers of small 0+ recruits of *S. punctata*, with total lengths ranging from 32 to 35 mm, were first caught in Wilson Inlet in September. Since a translucent zone had not yet started to form outside the central opaque zone (= core) on the otoliths of these fish, this cohort represented the 1988 year class (Fig. 4.2). Only small numbers of this year class were caught in the next few months. The length range of the 1988 year class increased to 80-179 mm in April 1989 and then to 160-249 mm in December 1989, by which month the first annulus had become clearly discernible near the edge of their scales and the age of this cohort was about 16 months old. By April 1990, when sampling ceased, the length range of the 1988 year class was 220-319 mm. In 1989, the 0+ age class first appeared in December, by which month it had reached lengths of 40-49 mm. Large numbers of this 1989 age class were caught in January 1990, when their modal length class was 60-69 mm.

During 1988, the vast majority of fish in the monthly samples belonged to the 1986 year class. The lengths of this year class increased from 210-319 mm in April to 240-369 mm in December 1988 and subsequently to 330-429 mm in October 1989. The 1987 year class was first caught in January 1989, when it ranged in length from 150 to 249 mm and, by July 1989, just prior to entering the third year life, its modal length class had increased to 280-289 mm. The 1986 and 1987 year classes tended to decrease in number over time and neither appeared in samples collected after December 1989.
Figure 4.2  Length-frequency histograms for each year class of *Sillaginodes punctata* caught in monthly samples using seine and gill nets in Wilson Inlet. The times when the estuary mouth became opened and became closed are shown. Sample sizes are given in parentheses.
The assemblage of *S. punctata* in Wilson Inlet consisted predominantly of fish belonging to the 0+, 1+, 2+ and 3+ age classes and were generally less than 400 mm in total length (Fig 4.2 and 4.3). The asymptotic lengths ($L_\infty$) for female and male *S. punctata* were 531 mm and 480 mm, respectively, while the corresponding growth coefficients ($K$) for the two sexes were 0.40 and 0.48, respectively (Table 4.2). The oldest female and male were aged 5+ and 4+, respectively, while the maximum lengths for females and males were 491 and 417 mm, respectively, these being recorded for a 5+ and 4+ fish, respectively (Fig. 4.3).

Since the estimates of the error variances ($s^2$) of females and males were not significantly different ($P < 0.01$), it was assumed that the error variances ($\sigma^2$) of both sexes were homogenous with age and Gallant’s (1975) equation was thus used to calculate the likelihood ratio test statistic. Likelihood ratio tests showed a significant difference ($P < 0.05$) between the six parameter model and two of the five parameter models, *i.e.* those models with the linear constraints of $K_F = K_M$ and $t_0F = t_0M$, respectively (Table 4.3). The model with the least number of parameters that was not significantly different to the six parameter model was the three parameter model, and thus the conclusion from the likelihood ratio test is that the three parameter model provides the best description of the growth of female and male *S. punctata*. The model with the lowest BIC value was the three parameter model. It is therefore concluded that there was no significant difference between the von Bertalanffy parameter estimates of $L_\infty$, $K$ and $t_0$ for female and male *S. punctata*. 

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Table 4.2  von Bertalanffy growth parameters (with 95% confidence intervals) derived from length-at-age data for *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus* captured in Wilson Inlet.

$L_\infty$ is the asymptotic length, $K$ is the growth coefficient, $t_0$ is the hypothetical age at which fish have zero length, $r^2$ is the coefficient of determination, $n$ is the sample size and $s^2$ is the estimate of the error variance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>$L_\infty$ (mm)</th>
<th>$K$</th>
<th>$t_0$ (years)</th>
<th>$r^2$</th>
<th>$n$</th>
<th>$s^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sillaginodes punctata</em></td>
<td>Females</td>
<td>530.92 (497.73 - 564.12)</td>
<td>0.40 (0.36 - 0.44)</td>
<td>0.09 (0.06 - 0.12)</td>
<td>0.93</td>
<td>634</td>
<td>519.66</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>479.57 (446.26 - 512.89)</td>
<td>0.48 (0.42 - 0.54)</td>
<td>0.13 (0.09 - 0.16)</td>
<td>0.93</td>
<td>548</td>
<td>499.05</td>
</tr>
<tr>
<td><em>Arripis georgiana</em></td>
<td>Females</td>
<td>384.62 (371.72 - 397.48)</td>
<td>0.27 (0.25 - 0.30)</td>
<td>-0.35 ((-0.41) - (-0.29))</td>
<td>0.97</td>
<td>426</td>
<td>257.06</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>316.51 (303.98 - 325.18)</td>
<td>0.33 (0.31 - 0.37)</td>
<td>-0.34 ((-0.39) - (-0.29))</td>
<td>0.99</td>
<td>215</td>
<td>132.96</td>
</tr>
<tr>
<td><em>Aldrichetta forsteri</em></td>
<td>Females</td>
<td>428.38 (412.15 - 444.46)</td>
<td>0.48 (0.45 - 0.52)</td>
<td>0.14 (0.12 - 0.17)</td>
<td>0.97</td>
<td>519</td>
<td>312.21</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>356.99 (344.27 - 369.68)</td>
<td>0.62 (0.57 - 0.68)</td>
<td>0.16 (0.14 - 0.18)</td>
<td>0.97</td>
<td>422</td>
<td>238.76</td>
</tr>
<tr>
<td><em>Mugil cephalus</em></td>
<td>Females</td>
<td>584.16 (496.53 - 670.03)</td>
<td>0.39 (0.29 - 0.49)</td>
<td>0.11 (0.03 - 0.18)</td>
<td>0.86</td>
<td>281</td>
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</tr>
<tr>
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<td>Males</td>
<td>541.85 (454.85 - 609.29)</td>
<td>0.42 (0.31 - 0.53)</td>
<td>0.11 (0.03 - 0.18)</td>
<td>0.86</td>
<td>239</td>
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Figure 4.3  von Bertalanffy growth curves fitted to length-at-age data for female and male *Sillaginodes punctata*. 
Table 4.3  Likelihood ratio tests comparing von Bertalanffy growth models for females and males of *Sillaginodes punctata* and the BIC values of each model.  * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

<table>
<thead>
<tr>
<th>Species</th>
<th>Hypothesis</th>
<th>$L_m$ (females)</th>
<th>$L_m$ (males)</th>
<th>$K$ (females)</th>
<th>$K$ (males)</th>
<th>$t_o$ (females)</th>
<th>$t_o$ (males)</th>
<th>Residual Sum of Squares</th>
<th>$F$</th>
<th>BIC</th>
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<td>510.31</td>
<td>0.4282</td>
<td>0.4351</td>
<td>0.1027</td>
<td>0.1082</td>
<td>602055</td>
<td>4.24*</td>
<td>7402.95</td>
</tr>
<tr>
<td>n (males) = 548</td>
<td>H<em>ω2</em></td>
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<td>511.97</td>
<td>0.4312</td>
<td>0.4312</td>
<td>0.1067</td>
<td>0.1034</td>
<td>602376</td>
<td>4.87*</td>
<td>7403.58</td>
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<td>0.4351</td>
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<td>0.1075</td>
<td>601039</td>
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<td>7400.95</td>
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<tr>
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<td>512.52</td>
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<td>0.4309</td>
<td>0.1051</td>
<td>0.1051</td>
<td>602395</td>
<td>2.46</td>
<td>7396.54</td>
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<td>H<em>ω5</em></td>
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<td>510.22</td>
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<td>0.4343</td>
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<td>2.16</td>
<td>7395.95</td>
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<tr>
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<td>509.90</td>
<td>0.4319</td>
<td>0.4319</td>
<td>0.1106</td>
<td>0.0999</td>
<td>602546</td>
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<td>H<em>ω7</em></td>
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<td>509.53</td>
<td>0.4322</td>
<td>0.4322</td>
<td>0.1052</td>
<td>0.1052</td>
<td>603136</td>
<td>2.12</td>
<td>7390.91</td>
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</tbody>
</table>
4.3.2 Age and growth of Arripis georgiana

The mean marginal increments on sagittal otoliths of *A. georgiana* with two opaque zones rose from *ca* 0.5 in April to *ca* 0.8 in September, but then declined precipitously to *ca* 0.2 in October and *ca* 0.1 in November, before rising to *ca* 0.4 in January and *ca* 0.5 in March (Fig. 4.4). Although the number of *A. georgiana* possessing otoliths with only one opaque zone (= core) was low, the marginal increments for the otoliths of such fish still clearly followed the same trend. Similar seasonal trends were also exhibited by the mean marginal increments on otoliths with three and four to seven opaque zones, with values declining precipitously in October and then increasing over the ensuing summer months. The pronounced seasonality in the trends shown by the marginal increments, with a conspicuous decline and a subsequent progressive rise occurring only once in each 12 month period, demonstrate that the opaque zones on the sagittal otoliths of *A. georgiana* are formed annually. The number of opaque zones can thus be used to help age *A. georgiana*.

On the basis of the time when the spawning of Australian herring peaks in marine waters (Fairclough *et al.* 2000a), the assemblage of *A. georgiana* in Wilson Inlet was assigned a birth date of 1 June (for full rationale see Chapter 5). Although *A. georgiana* was not caught by seine netting, a few small *A. georgiana* were caught by a professional fisherman using a large purse seine at site 6 in January 1989. These fish, which ranged in length from 121 to 138 mm, were smaller than the *A. georgiana* caught in gill nets, which had a minimum length of 172 mm. Since the small fish caught by purse seine possessed a central opaque zone or core but no opaque annuli on their otoliths and this species spawns between April and June (Fairclough *et al.* 2000a), they belong to the 0+ age class, *i.e.* 1988 year class.
Figure 4.4 Mean monthly values ± 1 S.E. for marginal increments on the otoliths of *Arriris georgiana*, using pooled data for the corresponding months in the years 1988-90. The marginal increment is expressed as a proportion of the distance between the primordium and the outer edge of the central opaque zone (=core), when this was the only opaque zone present, and as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. The number of otoliths examined is given above each mean.
The assemblage of *Arripis georgiana* in Wilson Inlet was represented by several year classes, some of which were sufficiently strong and consistently represented for their size distributions to be able to be traced through sequential samples (Fig. 4.5). Thus, for example, the 1986 year class increased from 190 to 239 mm in September 1988 to 200 to 249 mm in March 1989 to 210 to 259 mm in October 1989 and 230 to 269 mm in December 1989, and the 1987 year class increased from 160 to 179 mm in June 1988 to 170 to 199 mm in April 1989 to 190 to 209 mm in October 1989 (Fig. 4.5). Nine year classes were represented in the samples collected between April 1988 and April 1990, with the length ranges of these year classes frequently showing a marked overlap in the monthly samples. While large fish, *i.e.* > 300 mm, were frequently caught between April 1988 and November 1988, such fish were obtained far less frequently in subsequent months. Gill net catches between December 1988 and the end of the sampling period comprised predominantly the 1984, 1985, 1986 and 1987 year classes.

The asymptotic lengths ($L_\infty$) and growth coefficients ($K$) of female and male *A. georgiana* were 385 mm and 316 mm, respectively, and 0.27 and 0.34, respectively (Table 4.2). The oldest female and male *A. georgiana* were both aged 8+. The maximum lengths for females and males were 373 and 326 mm, respectively, these values again both being recorded for 8+ fish (Fig. 4.6).

The estimates of the error variances ($\sigma^2$) of females and males were significantly different ($P < 0.01$), indicating substantial heterogeneity in error variances ($\sigma^2$). For this reason, likelihood ratio tests were carried out using the test statistic $\Lambda^{2/n}$. Likelihood ratio tests indicated significant differences between females and males in the univariate tests of the parameter estimates of $L_\infty$ ($P < 0.001$) and $K$ ($P < 0.001$), in each
Figure 4.5 Length-frequency histograms for each year class of *Arripis georgiana* caught in monthly samples using gill nets in Wilson Inlet.

NB Although no *A. georgiana* were caught using seine nets, a few *A. georgiana* were collected by a purse seine fisher in January 1989 and the lengths of these fish are included in the length-frequency data for that month. The times when the estuary mouth became opened and became closed are shown. Sample sizes are given in parentheses.
Figure 4.6  von Bertalanffy growth curves fitted to length-at-age data for female and male *Arripis georgiana.*
of the simultaneous two parameter tests ($P < 0.001$) and in the simultaneous test of the three parameter estimates for both sexes ($P < 0.001$) (Table 4.4). Likelihood ratio tests showed that there was no significant difference between the six parameter model and the five parameter model with the linear constraint of $t_0^F = t_{0M}$. Comparison of the values of the BIC of the models resulted in the same result as the likelihood ratio tests, i.e. the most appropriate model for the description of the growth of female and male *A. georgiana* is the five parameter model (Table 4.4). It was therefore concluded that there was no significant difference between the von Bertalanffy parameter estimate of $t_0$ for female and male *A. georgiana*. However, there was a significant difference ($P < 0.001$) between the parameter estimates for $L_\infty$ and $K$ for both sexes.

4.3.3 Age and growth of Aldrichetta forsteri

The mean marginal increments on the scales of *A. forsteri* possessing one annulus increased gradually from *ca* 0.4 in April to *ca* 0.6 in June and remained at about this level until September (Fig. 4.7). They then declined precipitously to a minimum of 0.1 in October, before rising to between 0.2 and 0.3 during the ensuing spring and summer months. The mean marginal increments on the scales of *A. forsteri* with two annuli increased markedly from *ca* 0.4 in April to *ca* 0.8 in August, after which they declined precipitously to a minimum of *ca* 0.1 in October, before rising to 0.6 in November and then levelling off during the ensuing months. The monthly trends exhibited by the marginal increments on scales of *A. forsteri* possessing three to five annuli were essentially the same as those trends exhibited by scales with one and two annuli. Since the marginal increments on the scales of *A. forsteri* underwent a conspicuous decline and progressive rise only once during the year, a single annulus is formed annually in the scales of this species.
Figure 4.7  Mean monthly values ± 1 s.e. for marginal increments on the scales of *Aldrichetta forsteri*, using pooled data for the corresponding months in the years 1988-90. The marginal increment is expressed as a proportion of the distance between the focus and the outer edge of the annulus, when only one annulus was present, and as a proportion of the distance between the outer edges of the two outermost annuli, when two or more annuli were present. The number of scales examined is given above each mean.
<table>
<thead>
<tr>
<th>Species</th>
<th>Hypothesis</th>
<th>$L_m$ (females)</th>
<th>$L_m$ (males)</th>
<th>$K$ (females)</th>
<th>$K$ (males)</th>
<th>$t_0$ (females)</th>
<th>$t_0$ (males)</th>
<th>Residual Sum of Squares (females)</th>
<th>Residual Sum of Squares (males)</th>
<th>Log-Likelihood</th>
<th>$A^{2/n}$</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arripis georgiana</td>
<td>H_Ω</td>
<td>384.62</td>
<td>316.51</td>
<td>0.2741</td>
<td>0.3412</td>
<td>-0.3502</td>
<td>-0.3348</td>
<td>107698</td>
<td>26808</td>
<td>-2606.77</td>
<td>5252.32</td>
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<tr>
<td>$n$ (females) = 426</td>
<td>H_{α1}</td>
<td>363.16</td>
<td>363.16</td>
<td>0.3113</td>
<td>0.2470</td>
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<td>-0.4708</td>
<td>110794</td>
<td>32224</td>
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<td>5297.49</td>
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<td>$n$ (males) = 215</td>
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<td>0.2972</td>
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<td>-0.3972</td>
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<td>-0.3418</td>
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<tr>
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<td>0.2935</td>
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<td>-0.3665</td>
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<td>365.70</td>
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<td>367.59</td>
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<td>0.2794</td>
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<td>361.56</td>
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<td>72368</td>
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<td>5499.87</td>
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</tbody>
</table>
The birth date of *Aldrichetta forsteri* was designated as 15 June (for full rationale see Chapter 5). Small representatives of *A. forsteri*, *i.e.* with total lengths \( \leq 50 \text{ mm} \), were first caught in Wilson Inlet in September of 1988. Since these fish did not have an annulus on their scales, they were the 0+ representatives of the 1988 year class. The length distributions of the 1988 year class can be followed through each succeeding month until the completion of the study. The modal length class of the 1988 year class rose to 60-69 mm in November 1988 and then to 170-189 mm in June 1989, as these fish were entering their second year of life, and then to 190-199 mm in October 1989, when the first annulus became delineated on their scales and the members of this group were on average 16 months old. The modal length class of the 1988 cohort subsequently increased to 230-239 mm in April 1990. (Fig 4.8)

Small numbers of the 1987 year class first appeared in August 1988, at which time this cohort had a modal length class of 190-199 mm and had just entered its second year of life. Although the 1987 year class was present in August 1988 and most subsequent months, its strength was considerably weaker than that of either the 1988 or 1986 year classes. The modal length class of the 1986 year class rose from 230-239 mm in April 1988 to 260-269 mm in November 1988 and 290-299 mm in August 1989, when this cohort was just entering its fourth year of life. This year class was not present in samples collected after August 1989. Small numbers of the 1985, 1984, 1983 and 1982 year classes were caught between April 1988 and September 1989.

The assemblage of *A. forsteri* in Wilson Inlet consisted predominantly of 0+, 1+, 2+ and early 3+ fish. The oldest female and male fish were both aged 5+. The maximum lengths of females and males were 406 and 346 mm, respectively, both of which were recorded for 5+ fish (Fig. 4.9). The asymptotic lengths \( L_a \) for female and
Figure 4.8  Length-frequency histograms for each year class of Aldrichetta forsteri caught in monthly samples using seine and gill nets in Wilson Inlet. The times when the estuary mouth became opened and became closed are shown. Sample sizes are given in parentheses.
Figure 4.9  von Bertalanffy growth curves fitted to length-at-age data for female and male *Aldrichetta forsteri*.
male *A. forsteri* were 428 and 357 mm, respectively, while the corresponding growth coefficients (*K*) for the two sexes were 0.48 and 0.62, respectively (Table 4.2).

Since estimates of the error variances (*σ^2*) of females and males were significantly different (*P* < 0.01), indicating substantial heterogeneity in the error variances (*σ^2*), likelihood ratio tests were carried out using the test statistic *Λ^2n*. Likelihood ratio tests indicated significant differences (*P* < 0.001) between the six parameter model and all other models with the exception of the five parameter model with the linear constraint \( t_{0F} = t_{0M} \) (Table 4.5). The results of the BIC tests supported those of the likelihood ratio test. Thus, it was concluded that there was a significant difference (*P* < 0.001) between the von Bertalanffy parameter estimates of \( L_\infty \) and *K* for female and male *A. forsteri*.

**4.3.4 Age and growth of *Mugil cephalus***

The trends exhibited by the mean monthly marginal increments on the scales of *M. cephalus* with one annulus were essentially the same as those with two annuli (Fig. 4.10). The mean monthly marginal increments thus remained consistently high between April and August, *i.e.* > 0.4, before declining precipitously to a minimum of *ca* 0.1 in October, and then increasing during the ensuing months. Although the numbers of fish with scales with 3, 4 or 5 annuli were small, the trends exhibited by the monthly marginal increments for all such scales collectively were essentially the same as those for scales with one and two annuli, *i.e.* they declined markedly in October and then gradually rose over the following months.

The consistent trends displayed by the marginal increments on the scales of *M. cephalus*, with the mean monthly marginal increments undergoing a conspicuous
Figure 4.10  Mean monthly values ± 1 S.E. for marginal increments on the scales of *Mugil cephalus*, using pooled data for the corresponding months in the years 1988-90. The marginal increment is expressed as a proportion of the distance between the focus and the outer edge of the annulus, when only one annulus was present, and as a proportion of the distance between the outer edges of the two outermost annuli, when two or more annuli were present. The number of scales examined is given above each mean.
Table 4.5  Likelihood ratio statistics comparing von Bertalanffy growth models for males and females of *Aldrichetta forsteri* and the BIC values of each model.  * = \( P < 0.05 \),  ** = \( P < 0.01 \),  *** = \( P < 0.001 \).

<table>
<thead>
<tr>
<th>Species</th>
<th>Hypothesis</th>
<th>( L_0 ) (females)</th>
<th>( L_\infty ) (females)</th>
<th>( K ) (females)</th>
<th>( K ) (males)</th>
<th>( t_0 ) (females)</th>
<th>( t_\infty ) (males)</th>
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<th>Log-Likelihood</th>
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<th>BIC</th>
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<td>399.70</td>
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<td>1.13***</td>
<td>8098.27</td>
</tr>
<tr>
<td></td>
<td>H_{a7}</td>
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<td>400.72</td>
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<td>0.5230</td>
<td>0.1433</td>
<td>0.1433</td>
<td>177846</td>
<td>119867</td>
<td>-4041.83</td>
<td>1.15***</td>
<td>8104.20</td>
</tr>
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</table>
decline and then progressive rise only once during the year, demonstrate that an annulus is formed on the scales of this species each year. The number of annuli can thus be used for aging *M. cephalus*.

*Mugil cephalus* was assigned a birth date of 1 July (for full rationale see Chapter 5). Up to four age classes were represented in the monthly length-frequency distributions constructed using length data obtained from seine and gill net samples (Fig. 4.11). Small numbers of 0+ fish, with lengths < 45 mm, first appeared in samples in October 1988 and again in June 1989 (Fig. 4.11). The lengths of the 1989 year class increased from 20-29 mm in June 1989 to 30-79 mm in December 1989 and to 200-219 mm in April 1990. The lengths of the 1988 year class increased from 30-49 mm in October 1988 to 220-259 mm in May 1989 and to 200-289 mm in October 1989, at which time the first annulus was just becoming delineated, and then to 260-369 mm in April 1990. The 1987 year class increased in length from 220-269 mm in December 1988 to 290-329 mm in July 1989 and 340-449 mm in February 1990.

Although the 1987 year class did not first appear in gill net catches until October 1988, when it was about 15 months of age, it was represented in all subsequent months except April 1989. Very few fish belonging to the 1986 year class appeared in catches after June 1989. The 1985 year class was represented by a few 3+ fish between July 1988 and December 1988 and in May 1989. Although the monthly samples were usually dominated by the 1986-89 year classes, a substantial number of the 1985 year class was caught in December 1988. A single representative of the 1984 year class was caught in May 1989.

The oldest female and male *M. cephalus* were aged 4+ and 3+, respectively, while the maximum lengths for females and males were 525 mm and 422 mm, these
Figure 4.11  Length-frequency histograms for each year class of *Mugil cephalus* caught in monthly samples using seine and gill nets in Wilson Inlet. The times when the estuary mouth became opened and became closed are shown. Sample sizes are given in parentheses.
being recorded for 4+ and 3+ fish, respectively (Fig. 4.12). The asymptotic lengths \( L_a \) for female and male \( M. cephalus \) were 584 mm and 542 mm, respectively, and the growth coefficients \( K \) were 0.39 and 0.42, respectively (Table 4.2).

The estimates of the error variances \( (s^2) \) of females and males were not significantly different \( (P < 0.01) \). Since the error variances \( (\sigma^2) \) of both sexes were assumed to be homogenous with age, Gallant’s (1975) equation was used to calculate the likelihood ratio test statistic. Likelihood ratio tests showed no significant differences \( (P < 0.001) \) between the six parameter model and either of the five, four or three parameter models (Table 4.6). Thus, since it was the least complex of the candidate models and was not significantly different to the complex six parameter model, the three parameter model provided the best description of the growth data. The lowest BIC value was recorded for the three parameter model, a result which supported that of the likelihood ratio tests. From the above, it was concluded that there was no significant difference between the von Bertalanffy parameter estimates of \( L_a, K \) and \( t_0 \) for female and male \( M. cephalus \).

4.4 Discussion

4.4.1 Validation of aging technique

The trends exhibited by the monthly mean values for the marginal increments on the scales of \( Sillaginodes punctata, Aldrichetta forsteri \) and \( Mugil cephalus \) confirmed that the annuli on the scales of these three species are formed annually and that it was thus valid to use their number to help age the individuals of each of these species. The opaque annuli on the otoliths of \( Arripsis georgiana \) were also shown to be formed annually and could thus likewise be used to age this species. Since each of the above
Figure 4.12  von Bertalanffy growth curves fitted to length-at-age data for female and male *Mugil cephalus*.
Table 4.6  Likelihood ratio statistics comparing von Bertalanffy growth models for females and males of *Mugil cephalus* and the BIC values of each model.  * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

<table>
<thead>
<tr>
<th>Species</th>
<th>Hypothesis</th>
<th>$L_\infty$ (females)</th>
<th>$L_\infty$ (males)</th>
<th>$K$ (females)</th>
<th>$K$ (males)</th>
<th>$t_0$ (females)</th>
<th>$t_0$ (males)</th>
<th>Residual Sum of Squares</th>
<th>$F$</th>
<th>BIC</th>
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<tr>
<td><em>Mugil cephalus</em></td>
<td>$H_\alpha$</td>
<td>584.16</td>
<td>541.85</td>
<td>0.3917</td>
<td>0.4198</td>
<td>0.1066</td>
<td>0.1061</td>
<td>649539</td>
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<td>$n$ (females) = 281</td>
<td>$H_{a1}$</td>
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<td>565.76</td>
<td>0.4139</td>
<td>0.3907</td>
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<td>0.0921</td>
<td>650143</td>
<td>0.48</td>
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<tr>
<td>$n$ (males) = 239</td>
<td>$H_{a2}$</td>
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<td>0.4040</td>
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<td>0.14</td>
<td>3739.11</td>
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<tr>
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<td>0.19</td>
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<td>$H_{a5}$</td>
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<td>566.34</td>
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<td>0.4026</td>
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<td>0.1082</td>
<td>654197</td>
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<td>3730.18</td>
</tr>
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</table>
species spawns in winter, the first annulus does not become delineated in their hard structures until the spring of the second year of life. However, the otoliths of *A. georgiana* contain a large central opaque core, that is laid down immediately after the fish had been spawned in winter and which could thus be considered to represent the first growth zone (see also Fairclough *et al.* 2000b).

4.4.2 *Sillaginodes punctata*

Since the growth zones on the scales of *S. punctata* become increasingly difficult to discern in older fish, scales are, in general, only reliable for aging fish less than 5 years old (see Hyndes 1996). However, the vast majority of the assemblage of *S. punctata* in Wilson Inlet were less than $3^{1/2}$ years old, none was greater than 5 years old and the annuli were still clearly visible on the scales of the older fish. Thus, the problems often associated with using scales for age determination of older age classes in *S. punctata* and other species (see Beamish and McFarlane 1987) were not encountered with *S. punctata* in this study. The annulus became delineated on the scales of *S. punctata* in Wilson Inlet during November, the same month as the annulus becomes delineated on the otoliths of this species in marine waters (Hyndes *et al.* 1998).

The fact that the von Bertalanffy growth models for male and female *S. punctata* were not significantly different contrasts with the results recorded by Hyndes *et al.* (1998) for this species in marine waters. The lack of such a difference in Wilson Inlet can almost certainly be attributed to the fact that over 95% of the fish caught in Wilson Inlet were less than $3^{1/2}$ years old and 400 mm and thus below the $L_{50}$ at first maturity of this species (Hyndes *et al.* 1998), whereas many fish were caught in marine waters at greater ages and lengths. Indeed, while the oldest female and male in Wilson Inlet were
5 and 4 years of age, respectively, those in marine waters were 14 and 13 years of age, respectively (Hyndes et al. 1998). Although the von Bertalanffy parameter estimates of the estuarine population may have been biased by the absence of older and larger fish, the 95% confidence limits for \( L_\infty \) and \( K \) for females and males in Wilson Inlet still overlapped those for the corresponding sex in coastal waters (see Hyndes et al. 1998). The implication that the growth of female and male \( S. punctata \) in Wilson Inlet during the first four years of life is similar to that of female and male \( S. punctata \) in nearshore marine waters is borne out by the similarity of the growth curves for such fish in those environments (Fig. 4.13). These results suggest that the greater contribution of high quality food items (see Edgar 1990), such as bivalve siphons, polychaetes and nemerteans, to the diet of \( S. punctata \) in Wilson Inlet (see Chapter 6, Hyndes et al. 1997) does not result in a rate of growth that is faster than that which occurs in marine populations. However, it should be recognised that Wilson Inlet is on the south coast and thus cooler than the region on the lower west coast where the study of the marine population of \( S. punctata \) was undertaken. Thus, any benefit from better quality food might have been partially offset by a lower temperature.

The fact that the assemblage of \( S. punctata \) in Wilson Inlet comprises fish that are generally less than \( 3\frac{1}{2} \) years old and 400 mm in length, and thus younger and smaller than their age and length at first maturity (see Hyndes et al. 1998), together with the paucity of sexually mature fish in the estuary, demonstrates that \( S. punctata \) leaves Wilson Inlet prior to attaining maturity for the first time. This conclusion is consistent with the fact that, as \( S. punctata \) approaches its size at first maturity in marine waters, it starts to migrate offshore from its nearshore nursery areas to its offshore spawning grounds (Hyndes et al. 1998). It is thus concluded that, when \( S. punctata \) approaches
Figure 4.13 von Bertalanffy growth curves for female and male *Silliginodes punctata* in Wilson Inlet (solid line - this study) and in coastal marine waters (open circles) derived from Hyndes *et al.* (1998).
the size at maturity in Wilson Inlet, it leaves this estuary for its spawning areas at sea
(see Chapter 5).

Although *S. punctata* of 300-400 mm were relatively abundant in Wilson Inlet,
fish > 300 mm are rarely found in other south-western Australian estuaries, such as the
Blackwood River Estuary on its south-western corner (Lenanton 1977, Valesini
*et al.* 1997) and the Swan River, Peel-Harvey and Moore River estuaries on its lower
appears relevant that, in comparison with the lower west coast, the shoreline of the south
coast is relatively more exposed and contains fewer sheltered marine habitats (Hegge
*et al.* 1996). Thus, there is a greater advantage to *S. punctata* remaining in the protected
environment of Wilson Inlet for a longer time than would be the case with the estuaries
on the lower west coast of Australia.

Since, in south-western Australia, *S. punctata* spawns between early autumn and
early spring (Hyndes *et al.* 1998), the new 0+ recruits of this species are well placed to
enter the seasonally-closed estuaries of this region during the spring, when increased
freshwater discharge usually breaches the sand bars which form at the mouths of these
estuaries and re-establishes their continuity with the sea. This would account for
juvenile *S. punctata* first appearing in the samples from Wilson Inlet in September 1988,
when their lengths were 32 to 35 mm. These lengths are greater than the 14 to 24 mm
recorded by Hyndes *et al.* (1998) for 0+ *S. punctata* when they first appeared in late
September in nearshore marine waters on the lower west coast of Australia. The greater
size of 0+ recruits in Wilson Inlet at first recruitment in September and, even more
importantly, their low numbers in the ensuing months, is consistent with the conclusion
that, since *S. punctata* spawns mainly around offshore reefs along the lower west coast
(Hyndes et al. 1998), the new 0+ recruits typically have to travel far greater distances from the spawning grounds to their nursery areas. The fact that substantial numbers of 0+ recruits have settled into nearshore marine areas by mid-November (Hyndes et al. 1998), whereas 0+ recruits did not appear in Wilson Inlet until as late as December in 1989, provides further circumstantial evidence that S. punctata juveniles are travelling long distances from the spawning grounds to reach Wilson Inlet.

The mouth of Wilson Inlet remained open during the typical recruitment period of S. punctata on the lower west coast, i.e. September to November (Hyndes et al. 1998), in each year between 1980 and 1990, except for 1982 and 1987 (Fig. 4.14). In 1987, the estuary remained closed during the first months of the typical recruitment period, i.e. from September to mid-October. The only year classes caught in Wilson Inlet between April 1988 and December 1989 were the 1985, 1986 and 1988 year classes and thus did not include representatives of the 1987 year class. However, the 1987 year class was caught in considerable numbers in January 1989, i.e. when they were about 16 months old. This suggests that the 1987 year class sheltered in alternative nursery areas before entering Wilson Inlet as relatively large 1+ fish. Since there is a paucity of suitable nearshore nursery areas along the south-west coast (Ayvazian and Hyndes 1995), that alternative nursery may have been provided by another estuary that was open at the crucial time. The preceding data provide clear evidence that the closure of the mouth of Wilson Inlet during the recruitment period of 0+ juveniles can have significant effects on the age at which S. punctata is recruited into Wilson Inlet.
Figure 4.14 Months when the mouth of Wilson Inlet was opened and closed in each year between 1980 and 1990. Cross-hatching represents the period when *Sillaginodes punctata* spawns in marine waters and months in which 0+ juveniles typically recruit into south-western Australian estuaries (spawning and recruitment periods from Hyndes *et al.* (1998)).
4.4.3 *Arrapis georgiana*

The opaque zone on the otoliths of *A. georgiana* became delineated, through formation of a translucent zone on the outer edge of otoliths, during October, the same month that the annuli became likewise delineated on the scales of this species (Lenanton 1978).

The assemblage of *A. georgiana* in Wilson Inlet comprised mainly fish of the 2+ to 7+ age classes. While gear selectivity could have accounted for the poor representation of smaller and younger fish in gill net samples, intensive seine netting throughout this study failed to capture any 0+ fish and obtained only a few 1+ individuals of this species. Indeed, small numbers of 0+ *A. georgiana* were caught in Wilson Inlet on only one occasion, namely January 1989, by a fisher using a commercial purse seine, and even then the numbers were low. Further evidence that the 0+ age class of *A. georgiana* is poorly represented in Wilson Inlet is provided by the fact that this species was never found in the gut contents of pied and black cormorants in Wilson Inlet, despite the preference by those avian piscivores for small teleosts as a source of food (Humphries *et al.* 1992).

The lack of recruitment of 0+ fish in 1988, 1989 and 1990 occurred even though Wilson Inlet was connected to the sea during those months that the 0+ individuals of this species are recruiting into nursery areas in coastal marine waters (Lenanton 1982, Fairclough *et al.* 2000b) (Fig. 4.15). This suggests that the recruitment into Wilson Inlet does not typically occur during the first year of life. A comparable delay in the recruitment of juveniles of *A. georgiana* into estuaries occurs in permanently-open systems elsewhere in south-western Australia (Lenanton and Potter 1987).
Figure 4.15  Months when the mouth of Wilson Inlet was opened and closed in each year between 1980 and 1990. Cross-hatching represents the period when *Arripis georgiana* spawns in marine waters and months in which 0+ juveniles typically recruit into southwest estuaries (spawning and recruitment periods from Fairclough *et al.* (2000a)).
The significant difference found between the von Bertalanffy growth parameters \( L_a \) and \( K \) determined for male and female *A. georgiana* in Wilson Inlet parallels the results of Fairclough *et al.* (2000b) and is consistent with the conclusions of Stanley (1975) that, in marine waters, the females reached a greater length than males of the same age. The von Bertalanffy growth parameters for female and male *A. georgiana* in Wilson Inlet did not lie within the range of those values reported by Fairclough *et al.* (2000b) for *A. georgiana* in marine waters (Fig. 4.16), but appeared similar to those calculated using data for female and male *A. georgiana* in nearshore marine waters presented in Stanley (1975). Stanley's (1975) results do not agree with those of Fairclough *et al.* (2000b), despite the fact that both studies were based on fish obtained from coastal marine waters in south-western Australia. However, it should be noted that, based on Stanley's length-at-age data, the asymptotic length estimates \( (L_a) \) of female and male *A. georgiana* are 482 mm and 705 mm, respectively. Since these values far exceed the total length of the largest specimen recorded for *A. georgiana*, *i.e.* 411 mm (Hutchins and Thompson 1983), Stanley's (1975) age estimates must be treated with caution, particularly considering that Fairclough *et al.* (2000b) have shown that age estimates derived from the number of annuli on scales can underestimate the real age of *A. georgiana* by up to four years.

While the maximum ages attained by females and males in Wilson Inlet are similar to those recorded for the corresponding sexes in south-west marine waters, likelihood ratio tests (see Appendices 1 and 2) showed that the von Bertalanffy parameter estimates for the asymptotic lengths \( (L_a) \), the growth coefficients \( (K) \) and the apparent ages at zero length \( (t_a) \) of female and male *A. georgiana* in Wilson Inlet were
Figure 4.16  von Bertalanffy growth curves for female and male *Arripis georgiana* in Wilson Inlet (solid line - this study) and in coastal marine waters (open circles) derived from Stanley (1975) and (crosses) derived from Fairclough *et al.* (in press b).
significantly different ($P < 0.001$) to those recorded by Fairclough et al. (2000b) for *A. georgiana* in coastal marine waters (Fig. 4.16).

Despite the fact that the same prey items, *i.e.* teleosts and crustaceans, dominate the diets of *A. georgiana* in both Wilson Inlet and inshore marine waters (Anon. 1987, Chapter 6), *A. georgiana* reach a larger size in Wilson Inlet than those of the same age in marine waters in south-western Australia and females $> 300$ mm and males $> 250$ mm are relatively far more numerous in Wilson Inlet than in these marine waters (Fairclough et al. 2000b). Furthermore, *A. georgiana* with total lengths $> 290$ mm have not been recorded during studies of permanently open south-western Australian estuaries, such as the Normalup-Walpole Estuary (Potter and Hyndes 1994) and the Blackwood River Estuary (Lenanton 1977, Valesini et al. 1997) or in lower west coast estuaries, such as the Peel-Harvey Estuary (Potter et al. 1983). The presence of larger fish in the data set used to fit von Bertalanffy growth models for female and male *A. georgiana* in Wilson Inlet partially accounts for the asymptotic lengths estimated for this species in this estuary being greater than those for fish in coastal marine waters.

In each year from 1980 to 1990, apart from two brief periods, one at the end of the 1988 spawning season and one at the beginning of the 1989 season, the mouth of Wilson Inlet was closed during those months when *A. georgiana* spawns in marine waters (Fig. 4.15). Thus, the resorption of the ovaries and the degeneration of maturing sperm in the testes of most females and males, respectively, that had reached lengths greater than their respective $L_{50}$s at first maturity (see Chapter 5), presumably reflects a response by *A. georgiana* to confinement within the estuary during the spawning season and thus prevention of their migration to the marine spawning grounds. In this context, it is relevant that laboratory-reared individuals of both *A. georgiana* (R. Lenanton pers.
comm.) and of the closely related *Arrips trutta* (Gauldie 1998) do not breed in captivity and grow to a much larger size than fish of the same age in marine waters.

Furthermore, although there is little genetic variation throughout the geographic range of *A. georgiana* (How 1997), the physical appearance of *A. georgiana* in estuaries differs from those in marine waters. *Arrips georgiana* caught in Wilson Inlet and the nearby Normalup-Walpole estuary are larger and have more visceral fat than those caught in marine waters (R. Lenanton, pers. comm.), while marine *A. georgiana* are smaller, with a more silvery-blue, "cleaner" appearance than those in estuaries (D. Fairclough pers. comm., R. Lenanton pers. comm.). From the above data and observations, it is thus concluded that the greater size attained by *A. georgiana* in Wilson Inlet reflects, in part, the diversion of energy resources towards somatic growth rather than gonadal development.

4.4.4 *Aldrichetta forsteri*

Although some researchers have had difficulty in identifying annuli on the scales of mugilids (Erman 1959, Hendricks 1961, Ibañez-Aguirre and Gallardo-Cabello 1996), such difficulties have not been encountered by other workers studying mugilids in estuaries (Thomson 1957d, Sarojini 1957, 1958, Chubb *et al.* 1981) or during the present study. However, it should be recognised that the scales of few of the few fish caught in Wilson Inlet had more than three annuli. The annuli on the scales of *A. forsteri* became delineated in October, which agrees with the results of Thomson (1957d), who recorded that that the marginal increment on the scales of 1+ and 2+ *A. forsteri* caught in Western Australian coastal waters was smallest in late September.
and early October. The first annuli became delineated on the scales of *A. forsteri* in Wilson Inlet when this species is about 14-18 months old.

The lengths and age composition of the assemblage of *A. forsteri* in Wilson Inlet is similar to that recorded for this species in other estuaries on the lower west coast of Australia, such as the Swan-Avon Estuary (Chubb *et al.* 1981), Blackwood River Estuary (Valesini *et al.* 1997), Peel-Harvey Estuary (Lenanton *et al.* 1984) and Leschenault Estuary (Potter *et al.* 2000). The new 0+ recruits of *A. forsteri* are first caught in the Swan-Avon Estuary in May (Chubb *et al.* 1981) and in the Peel-Harvey Estuary in June (Lenanton *et al.* 1984). However, 0+ *A. forsteri* did not appear in samples in Wilson Inlet until as late as September and the relative abundances of the 0+ age class in this estuary in 1988 and 1989 were appreciably less than in those other two estuaries. This difference probably reflects the fact that, since this species spawns predominantly some distance away on the lower west coast (see Chubb *et al.* 1981), their juveniles will take longer to become recruited into Wilson Inlet.

The spawning period of *A. forsteri* in Western Australian coastal waters is protracted and occurs between late autumn and early spring (Thomson 1957b, c, Chubb *et al.* 1981, Potter *et al.* 2000). Although the spawning period of *A. forsteri* is similarly protracted in eastern Australia and New Zealand, it occurs during the summer in those regions (Graham 1953, Thomson 1957b, c, d, Webb 1973a). The spawning period of this species in the Coorong in South Australia, which occurs between January and early April, is shorter than that of *A. forsteri* in both Western and eastern Australia (Harris 1968). Since the sand bars, which form at the entrance of many south-western Australian estuaries only allow access into the river systems during heavy freshwater discharge, a winter spawning is of considerable advantage to a marine-estuarine

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opportunist species that utilises estuaries extensively as a nursery area, since it allows these species to enter estuaries early in life (Potter et al. 1990, Chubb et al. 1981).

The continued presence of small fish, *i.e.* 20-40 mm, in samples collected between September and January in 1988 and between June and December in 1989 indicates that, when the estuary is connected to the sea, 0+ fish are recruited into the system over a long period. The fact that the mouth of the estuary was open for only a relatively brief period in 1987 (Fig. 4.17) could thus account for the poor representation of the 1987 cohort in the monthly samples.

The von Bertalanffy estimates for the asymptotic lengths (*Lₐ*ₙ*) and the growth coefficients (*K*) of female and male *A. forsteri* in Wilson Inlet, *i.e.* 428 and 357 mm, and 0.48 and 0.62, respectively, were greater than those obtained by fitting the von Bertalanffy growth model to length-at-age data for *A. forsteri* in the Coorong (Harris 1968), which resulted in estimates for *Lₐ* of 410 mm and 305 mm, and estimates for *K* of 0.27 and 0.49, respectively (Fig. 4.18). These parameter estimates agree with Harris’s observation that this species does not reach as large a size in the Coorong as it does in Western Australia. The estimates for *Lₐ* of female and male *A. forsteri* in Wilson Inlet were less than those calculated by Quignard and Farrugio (1981), using data in Thomson (1957d) for this species in Western Australia, *i.e.* 487 and 477 mm, respectively, and in eastern Australia *i.e.* 514 and 556 mm, respectively. However, the estimates for *K* of female and male *A. forsteri* in Wilson Inlet were greater than those calculated by Quignard and Farrugio (1981) for this species in Western Australia, *i.e.* 0.31 and 0.27, respectively, and in eastern Australia, *i.e.* 0.23 and 0.19, respectively. Since Thomson’s age estimates of *A. forsteri* in Western Australia were based on combined samples from estuaries and coastal marine waters, comparisons between these
Figure 4.17 Months when the mouth of Wilson Inlet was opened and closed in each year between 1980 and 1990. Cross-hatching represents the period when Aldrichetta forsteri spawns in marine waters and months in which 0+ juveniles typically recruit into south-western Australian estuaries (spawning and recruitment periods from Chubb et al. (1981)).
Figure 4.18  von Bertalanffy growth curves for female and male *Aldrichetta forsteri* in Wilson Inlet (solid line - this study), in Western Australia (open circles) derived from Thomson (1957), in eastern Australia (squares) derived from Thomson (1957) and in South Australia (crosses) derived from Harris (1968).
results should be made with caution. However, the asymptotic length of female
_A. forsteri_ in Wilson Inlet was greater than that of males, which agrees with previous
observations by Thomson (1957d) and Harris (1968).

4.4.5 *Mugil cephalus*

The first annulus on the scales of _M. cephalus_ became delineated in the second
October of life, _i.e._ when fish are about 16 months old. These results agree with those
of Thomson (1951) for fish in Western Australia, but contrast with the situation in north
Queensland, where the first annuli on scales becomes delineated during the monsoon
season in January and February, when fish are six months old (Grant and Spain 1975).
The fact that the _M. cephalus_ caught in Wilson Inlet were relatively young, _i.e._ generally
< 4 years old, would account for the fact that the problems experienced by other
researchers using the scales of _M. cephalus_ for age determination were not encountered
in this study. The problems encountered by those other workers included crowding of
the peripheral annuli when several annuli were present (Hendricks 1961, Grant and
Spain 1975) and the erosion of the innermost annuli in the scales of older fish (Erman

Individuals of this species spawn only once per season (Thomson 1957b,
1987, Render _et al._ 1995). Despite much conjecture in the literature, the spawning
location of _M. cephalus_ is not known. However, there is circumstantial evidence that, in
Western Australia, spawning occurs at sea over deep water (Thomson 1963).

The new 0+ recruits first appeared in Wilson Inlet in June in 1989, when their
total lengths ranged from 27 to 40 mm. The fact that recruitment started occurring one
month earlier in the Swan River Estuary would account for the smaller size of those recruits, i.e. 22-30 mm (see Chubb et al. 1981). By extrapolation from length-frequency data, Chubb et al. (1981) concluded that the spawning period of the assemblage of *M. cephalus* in the Swan River Estuary extended from March to September. Use of the same approach using length-frequency data for fish in Wilson Inlet results in a similar estimate for the spawning period, i.e. April to September. The continued presence of small fish, i.e. 30-40 mm, in Wilson Inlet from June to December 1989 is consistent with the conclusion that spawning occurs over several months and that 0+ fish are recruited at intervals into Wilson Inlet. The greater size of 0+ recruits and the later appearance of 0+ fish in Wilson Inlet reflect the time taken to travel from offshore spawning grounds to nursery areas on the south-west coast.

A protracted winter spawning season enables the juveniles of this species to become recruited into estuaries on the southern coast of Western Australia during periods when these seasonally closed systems are typically connected to the sea (Potter et al. 1990). In comparison with the situation in south-western Australia, *M. cephalus* in the tropical waters of north Queensland spawn over a relatively shorter period, i.e. between May and August (Grant and Spain 1975). In 1987, the mouth of Wilson Inlet was opened during the recruitment period of *M. cephalus* for a far shorter period than in either 1988 or 1989 (Fig. 4.19). Between April and August 1988, the only year classes present in monthly samples were those of 1985 and 1986. The 1987 year class did not appear until October 1988 when the members of this cohort were over one year old. This delay in the first appearance of the 1987 year class is almost certainly attributable to the fact that the short period when Wilson Inlet was open in 1987 would have provided 0+ fish with only a limited opportunity to enter this estuary.
Figure 4.19 Months when the mouth of Wilson Inlet was opened and closed in each year between 1980 and 1990. Cross-hatching represents the period when Mugil cephalus spawns in marine waters and months in which 0+ juveniles typically recruit into south-western Australian estuaries (spawning and recruitment periods from Chubb et al. (1981)).
The size composition of *M. cephalus* in Wilson Inlet was similar to that described by other researchers in other south-western Australian estuaries, such as the Peel-Harvey Estuary (Lenanton *et al.* 1984), the Swan-Avon Estuary (Chubb *et al.* 1981) and the Blackwood River Estuary (Valesini *et al.* 1997).

There was no significant difference between the von Bertalanffy parameter estimates for female and male *M. cephalus* in Wilson Inlet, which agrees with the findings of Kesteven (1942), Thomson (1951), Thakur (1967), Cech and Wohlschlag (1975), Grant and Spain (1975) and Ibañez-Aguirre *et al.* (1998). The von Bertalanffy parameter estimates for $L_{\infty}, K$ and $t_0$, which were recorded by Grant and Spain (1975) and those calculated by Quignard and Farrugio (1981), which were calculated from data in Thomson (1951), lie within the 95% confidence limits of the parameter estimates for females and males in Wilson Inlet (Fig. 4.20). Despite the fact that the eastern Australian and Western Australian populations of *M. cephalus* are morphometrically different (Corti and Crosetti 1996), a comparison of the plots of the growth curves of females and males from western and eastern Australia shows that the von Bertalanffy parameter estimates of each sex in each region are very similar.
Figure 4.20 von Bertalanffy growth curves for female and male *Mugil cephalus* in Wilson Inlet (solid line - this study), in Western Australia (open circles) derived from Thomson (1951) and in eastern Australia (squares) derived from Grant and Spain (1975).
Chapter 5

Reproductive biology of *Sillaginodes punctata*, *Arripsis georgiana*,
*Aldrichetta forsteri* and *Mugil cephalus*

5.1 Introduction

King George whiting *Sillaginodes punctata*, Australian herring *Arripsis georgiana*, yelloweye mullet *Aldrichetta forsteri* and sea mullet *Mugil cephalus* are each regarded as marine estuarine-opportunist species in south-western Australia, *i.e.* they spawn at sea and use estuaries as nursery areas (Potter and Hyndes 1999). There are now abundant data to show that, on the lower west coast of Australia, each of these species spawns in marine waters at some time between early autumn and early spring. However, the duration of the spawning period varies markedly among these species. For example, the two species of mullet spawn throughout all or most of that period (Chubb *et al.* 1981, Potter *et al.* 2000), while King George whiting breeds between June and September (Hyndes *et al.* 1998) and Australian herring spawns predominantly between mid-May and early June (Fairclough *et al.* 2000a).

The spawning periods of *S. punctata*, *A. forsteri* and *M. cephalus* in the coastal waters of eastern Australia differ from those in south-western Australia. Thus, *S. punctata* spawns between autumn and early winter in south-eastern Australia (Fowler and Short 1996, Fowler *et al.* 2000), *A. forsteri* breeds between mid-summer and early autumn in South Australia (Harris 1968) and during summer in Victoria and Tasmania (Thomson
1957d), while *M. cephalus* spawns between early autumn and mid-winter in south-eastern Australia (Kesteven 1942) and between late autumn and late winter in the tropical waters of north-eastern Australia (Grant and Spain 1975). Consequently, these three species spawn in other regions of Australia during the period when the seasonally-closed estuaries of south-western Australia are typically closed from the sea due to the formation of sand bars at their mouths. In contrast, these species spawn in south-western Australia in the period when these sand bars often become breached as a result of increased freshwater discharge during and following winter rains. Such breaching enables 0+ *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* to become recruited into these estuaries during periods when these systems are connected to the sea (Lenanton and Hodgkin 1985, Potter et al. 1990).

All of the available data on the reproductive biology of these species in south-western Australia are based on studies conducted in either permanently-open estuarine systems or in nearshore coastal waters (see Chubb et al. 1981, Hyndes et al. 1998, Lenanton 1977, Thomson 1951, 1957a, 1957d, Fairclough et al. 2000a). However, relatively little is known about the extent to which *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* become mature in the seasonally-closed estuaries of this region, such as Wilson Inlet. Since the mouths of these estuaries are often closed by a sand bar, during part or all of the spawning period of these species, thereby preventing emigration to sea of sexually maturing fish, the reproductive biology of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* in Wilson Inlet may be affected by the seasonal closure. Indeed, previous studies have shown that the failure of teleost species in estuaries, rivers or lakes to undertake spawning migrations inhibits the reproductive development of these fish (June 1977, Moore and Reynolds 1982, Pollock 1984, De Decker and Bennet 1985, Goodall et al. 1987, Agostinho
et al. 1993, Clearwater and Pankhurst 1997, McKinley et al. 1998) and the gonads of marine fish confined to estuaries or lakes during the spawning season typically display a high incidence of atresia (Abraham 1963, Wallace 1975, Bok 1979). Since Wilson Inlet supports a commercial and recreational fishery for the above four species, sound information on the reproductive biology of these species in this system is important for developing plans for managing the fisheries for these species (see Pearn and Cappellutti 1999).

The aim of the present study was to ascertain the reproductive status of the assemblages of S. punctata, A. georgiana, A. forsteri and M. cephalus in Wilson Inlet. Emphasis has thus been placed on determining the period during which gonadal development occurs and the stages to which gonads develop in order to ascertain whether any of these species spawn within this estuary. Attention was also focused on determining whether the prevention of fish from undertaking a seawards spawning migration, due to the closure of the estuary mouth during periods when spawning is known to occur at sea, results in these species failing to become sexually mature. An attempt was also made to determine the length and age at which maturity would typically have been attained by members of the assemblages of these species in Wilson Inlet, if they had been exposed to optimal conditions for full maturation and spawning. Establishing the timing and duration of their respective spawning periods was also important as such data are crucial for assigning a birth date to each species, which in turn is essential for accurate ageing of fish and thus also the calculation of reliable growth curves. The results of this study have been compared with those obtained for populations of S. punctata, A. georgiana, A. forsteri and
*M. cephalus* in marine waters and permanently-open estuaries in south-western and eastern Australia.

### 5.2 Materials and methods

#### 5.2.1 Gonadal variables

The total length and wet weight of each *Sillaginodes punctata, Arripis georgiana, Aldrichetta forsteri* and *Mugil cephalus* that were collected by seine and gill netting were recorded to the nearest 1 mm and nearest 0.01 g, respectively (see Chapter 2). Up to 30 fish of each species from each site on each sampling occasion were randomly selected to provide gonads for reproductive studies. When the gonad could be identified as testes or ovaries, it was removed from the body cavity, weighed to the nearest 0.01 g and assigned to one of nine stages of maturation. Eight of these stages (I-VIII) were based on those of Laevastu (1965), with a ninth stage (IX) being added to represent fish with resorbing gonads (see Table 5.1 for nomenclature and descriptions of these stages). The gonadosomatic index (GSI) of each fish was calculated using the equation $\text{GSI} = \frac{W_1}{W_2} \times 100$, where $W_1$ = wet weight of gonad and $W_2$ = total wet weight of the fish.

#### 5.2.2 Length and age at first maturity

The results of this study (see later) showed that, during the respective spawning periods of the four species in marine waters, the gonads of large females and males of *A. georgiana* and *A. forsteri* in Wilson Inlet were frequently at stages IV or V, *i.e.* in the late and final phases of vitellogenesis in the case of ovaries and of the maturing and prespawning stages of development in the case of the testes, whereas those of *S. punctata*
<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
<th>Appearance of Gonad</th>
</tr>
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<tbody>
<tr>
<td>I</td>
<td>Virgin</td>
<td>Very small, colourless to grey.</td>
</tr>
<tr>
<td>II</td>
<td>Maturing virgin / Resting adult</td>
<td>Testes black, ovaries translucent, grey-red. Extend up to half the length of the ventral cavity.</td>
</tr>
<tr>
<td>III</td>
<td>Developing</td>
<td>Testes black, ovaries orange-red.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Occupy up to two-thirds of the ventral cavity</td>
</tr>
<tr>
<td>IV</td>
<td>Maturing</td>
<td>Testes grey, ovaries orange-red.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Occupy two-thirds of the ventral cavity.</td>
</tr>
<tr>
<td>V</td>
<td>Prespawning</td>
<td>Gonads fill the ventral cavity, ovaries orange, testes white and extrude small amounts of milt under pressure.</td>
</tr>
<tr>
<td>VI</td>
<td>Spawning</td>
<td>Running-ripe, roe and milt extruded under slight pressure. Visible eggs are round and translucent.</td>
</tr>
<tr>
<td>VII</td>
<td>Recently spent</td>
<td>Red with prominent blood vessels, some residual eggs are visible.</td>
</tr>
<tr>
<td>VIII</td>
<td>Recovering spent</td>
<td>Flaccid and reduced in size, organ walls striated.</td>
</tr>
<tr>
<td>IX</td>
<td>Resorbing</td>
<td>Mottled yellow, orange or grey. Hardened with a calcified appearance. Occupy up to two-thirds of the ventral cavity.</td>
</tr>
</tbody>
</table>

Table 5.1. A description of the stages of gonadal maturation based on Laevastu (1965).
and *M. cephalus* were usually at stage II, *i.e.* maturing virgin/resting adult, and had rarely advanced beyond stage III, *i.e.* developing. Thus, there was no evidence that the gonads of *S. punctata* and *M. cephalus* developed to full maturity and the lengths and ages at first maturity, *i.e.* the $L_{50}$ and $A_{50}$, were estimated only for *A. georgiana* and *A. forsteri*.

The lengths at first maturity, *i.e.* the $L_{50}$, of females and males of the first two species were estimated by fitting the logistic function to the percentage contributions of fish in each 25 mm length interval which, during the spawning period, possessed gonads at any stage between III and IX. The gonads of fish exhibiting these stages of development were either developing (stage III), maturing (stage IV), prespawning (stage V), recovering spent (stage VIII) or resorbing (stage IX) (Table 5.1).

The logistic function was fitted using the PROC NLIN procedure in SAS (SAS Institute Inc. 1988). The logistic equation is

$$P_L = \frac{1}{1 + e^{(a+bl)}},$$

where $P_L$ is the proportion of fish with developing, maturing, prespawning, spent or resorbing gonads, *i.e.* those at stages III, IV, V, VIII and IX, at length interval $L$ and where $a$ and $b$ are constants. The length at which 50% of fish possessed gonads at stages III to IX, *i.e.* the $L_{50}$, was calculated from the equation $L_{50} = -a/b$.

The ages at which 50% ($A_{50}$) of female and male representatives of *A. georgiana* and *A. forsteri* first attained maturity and their 95% confidence intervals were calculated using the parameters $L_\infty$, $K$ and $t_0$, of the von Bertalanffy growth function (Stergiou 1999). The equation is

$$A_{50} = t_0 - (1/K) \ln(1 - L_{50} / L_\infty).$$
The von Bertalanffy parameter estimates of $L_m$, $K$ and $t_0$ for *A. georgiana* and *A. forsteri* are presented in Chapter 4.

5.3 Results

5.3.1 Stages of gonadal maturity

*Sillaginodes punctata*

Most of the fish sampled for monthly gonadal studies were representatives of the 1986 year class in 1988, and the 1986 and 1987 year classes, and the 1988 year class, in 1989 and 1990, respectively (see Chapter 4). Thus, the proportion of larger and older fish used for gonadal studies was greater in 1989 than in the other two years.

The ovaries of the majority of female *S. punctata* caught in Wilson Inlet between April and September of 1988, February 1989 to May 1989 and September 1989 to December 1990 were at stages I or II (Fig 5.1). Females with stage III ovaries were present from October 1988 to January 1989 and from April 1989 to October 1989. Stage IV ovaries were found only between June and August in 1989 and in April in 1990.

The gonads of all male *S. punctata* caught between April 1988 and April 1990 were at stages I, II or III (Fig 5.1). Stage III testes were relatively abundant between April and August in 1989.

*Arripis georgiana*

Females with stage II ovaries were present in all months except April and May 1988 and stage III ovaries were found in female fish in each month from April to October of
Figure 5.1 Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of female and male *Sillaginodes punctata*. Sample sizes for each month are shown.

In this and Figs. 5.2, 5.3 and 5.4, the open bars refer to the autumn and spring months and the closed bars to the winter and summer months.
1988, and in February to June of 1989 and also in August of 1989 and February and April of 1990 (Fig. 5.2). Stage IV ovaries were recorded between April and August in 1988, from April to June in 1989 and in April of 1990. Stage V ovaries, \textit{i.e.} prespawning, were found in a small number of fish in April and May 1988, when they constituted ca 20 and 41\% of all ovaries, respectively, and in a small number of females in May 1989 and April 1990. No females with stage VI or VII ovaries, \textit{i.e.} spawning or recently spent, were caught in Wilson Inlet. Stage VIII ovaries, \textit{i.e.} recovering spent, increased in prevalence from \textit{ca} 9\% in September 1988 to \textit{ca} 34\% in October 1988, and were frequently found in August and October of 1989, when they constituted \textit{ca} 58 and 93\% of all ovaries, respectively. The characteristics of ovaries at stage VIII, showed that these gonads were in an advanced stage of recovery. Stage IX ovaries, \textit{i.e.} resorbing, were found in fish in September to November of 1988 and in December of 1989. The monthly trends in the maturity stages of the testes were similar to those exhibited by the ovaries (Fig. 5.2).

\textit{Aldrichetta forsteri}

Females with ovaries at stage II were found in all months except April, May and October of 1989, when the sample sizes were \textless{} 3 fish (Fig. 5.3). Ovaries at stages III to V were found from April to August of 1988 and from April to July of 1989. Stage VIII ovaries, \textit{i.e.} recovering spent, were recorded in a small number of females in January, August and October of 1989. These stage VIII ovaries were at an advanced stage of recovery, which suggests that spawning had occurred some weeks earlier. No ovaries at stage VI or VII, \textit{i.e.} spawning or recently spent, were found in any female \textit{A. forsteri} in any month.
Figure 5.2  Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of female and male *Arripis georgiana*. Sample sizes for each month are shown.
Figure 5.3 Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of female and male *Aldrichetta forsteri*. Sample sizes for each month are shown.
Testes at stages I or II predominated in males in all months in 1988 (Fig. 5.3). Stage III testes were found between April and August 1988 and in March and June 1989, while stage IV testes were relatively common between June and July of 1989. All fish in August 1989 had stage V testes. No testes at stages VI or VII, *i.e.* spawning or recently spent, were found in any male *A. forsteri* in any month (Fig. 5.3).

*Mugil cephalus*

The ovaries of female *M. cephalus* were usually at stages I or II (Fig. 5.4). A few females with stage III ovaries were caught in April, July and October of 1988 and in June of 1989. Stage IV ovaries were found in a few females caught in April and December of 1988, in June of 1989 and in April of 1990. A small number of females with ovaries at stage IX, *i.e.* resorbing, were caught in October and December of 1988, and in May of 1989. No females with ovaries at stages V to VIII, *i.e.* prespawning, spawning, recently spent or recovering spent, were caught in Wilson Inlet in any month. The testes of all males examined between April 1988 and April 1990 were at stages I or II (Fig 5.4).

5.3.2. *Gonadal maturity during the spawning period*

*Sillaginodes punctata*

During the period when *S. punctata* is known to spawn in the marine waters of south-western Australia, *i.e.* June to September (Hyndes *et al.* 1998), the ovaries of all female *S. punctata* < 225 mm were at stages I or II (Fig. 5.5). Stage III ovaries first appeared in the 225-249 mm length class, when they constituted *ca* 27% of all ovaries and

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Figure 5.4  Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of female and male *Mugil cephalus*. Sample sizes for each month are shown.
Figure 5.5 Percentage frequency of occurrence of sequential stages in the gonadal development in (a) each sequential 25 mm length category and (b) each age class of female and male *Sillaginodes punctata* caught between June and September, *i.e.* during the spawning period in marine waters. The sample sizes for each length and age class are shown.
Stage IV ovaries first appeared in the 275-299 mm length class when they constituted *ca* 10% of all ovaries. The ovaries of all females > 375 mm were at stages III or IV (Fig. 5.5).

During the known spawning period, the testes of all male *S. punctata* caught in Wilson Inlet were at stages I, II or III. The testes of all male *S. punctata* < 325 mm were at stages I to II (Fig. 5.5). Testes at stage III were first recorded in males in the 325-349 mm length class. The testes of all males > 350 mm were at stages II or III (Fig. 5.5).

Ovaries at stages III or IV constituted *ca* 16% of the gonads of all females at the end of their second and third years of life and *ca* 90% of those at the end of their fourth year of life (Fig. 5.5). All older females possessed ovaries at stage III. The gonads of all males at the end of their second year of life were at stages I or II. Stage III testes constituted *ca* 3% of gonads of all males at the end of their third year of life and *ca* 66% of those at the end of their fourth and fifth years of life (Fig. 5.5).

*Arripis georgiana*

During the spawning period of *A. georgiana* in marine waters, *i.e.* April to June (Fairclough *et al.* 2000a), the ovaries of all female *A. georgiana* < 200 mm total length were at stage I, while those of all females in the 200-224 mm length class were at stages II or III (Fig. 5.6). Ovaries at stages IV and V were first recorded in the 225-249 mm length class, in which they comprised *ca* 10 and 2% of all ovaries, respectively, and these subsequenty increased in prevalence with increasing length of fish, eventually comprising *ca* 89% of the ovaries of all females in the 300-324 mm length class and all of those ≥25 mm. The ovaries of the single female in the 350-374 mm length class were at stage V.
Figure 5.6 Percentage frequency of occurrence of sequential stages in the gonadal development in (a) each sequential 25 mm length category and (b) each age class of female and male *Arripis georgiana* caught between April and June, *i.e.* during the spawning period in marine waters. The logistic curve is fitted to the percentage of gonads at stages III, IV, VIII and IX in each size interval. The sample sizes for each length and age class are shown.
The length at which 50% of females first attained maturity, \textit{i.e.} the $L_{50}$, was 217.0 mm, with a 95% confidence interval of 211.4 to 219.2 mm.

The testes of all male \textit{A. georgiana} in the 200-225 mm length class during the spawning period were at stages II, III or IV (Fig. 5.6). Testes at stage V increased in prevalence with increasing length of fish, with the result that they constituted ca 11% of the gonads of males in the 225-249 mm length class and all of those \geq 300 mm. The length at which 50% ($L_{50}$) of males first attained maturity was 248.5 mm, with a 95% confidence interval of 247.8 to 248.8 mm.

The prevalence of gonads at stages III to V increased with increasing age of fish, with ovaries at these stages constituting \textit{ca} 38% of the gonads of females at the end of their second year of life and 100% of those of females at the end of their sixth year of life, and testes at these stages constituting 20% of the gonads of males at the end of their third year of life, and 100% of those of male fish at the end of their sixth year of life (Fig. 5.6). The age at which 50% of females and males first attained maturity, \textit{i.e.} the $A_{50}$, calculated from the parameters of the logistic function fitted to the percentage of gonads at stages III to IX in each year class, were 2.6 and 4.1 years, respectively, with 95% confidence intervals of 2.5 to 2.7 and 4.05 to 4.15 years, respectively.

\textit{Aldrichetta forsteri}

During the spawning period of \textit{A. forsteri} in south-western Australian marine waters, \textit{i.e.} March to September (Chubb \textit{et al.} 1981, Potter \textit{et al.} 2000), the ovaries of all female \textit{A. forsteri} \textless 200 mm in length were at stages I or II (Fig. 5.7). Ovaries at stage III were first recorded in the 200-224 mm length class, in which they constituted \textit{ca} 40% of all
Figure 5.7  Percentage frequency of occurrence of sequential stages in the gonadal development in (a) each sequential 25 mm length category and (b) each age class of female and male Aldrichetta forsteri caught between March and September, i.e. during the spawning period in permanently open estuaries and marine waters. The logistic curve is fitted to the percentage of gonads at stages III, IV, V, VIII and IX in each size interval. The sample sizes for each length and age class are shown.
ovaries. Ovaries at stages III to V increased in prevalence with increasing length of fish, with the result that they constituted ca 54% of all ovaries in the 275-299 mm length class and all of those of females ≥ 350 mm. Stage VIII ovaries, i.e. recovering spent ovaries, comprised ca 5% of the gonads of all female fish in the 325-349 mm length class. The length at which 50% of female A. forsteri first attained maturity was 268.2 mm, with a 95% confidence interval of 265.6 to 268.9 mm (Fig. 5.7).

The testes of all males that were < 175 mm total length during the spawning period were at stages I and II (Fig. 5.7). Stage III testes were first found in the 175-199 mm length class, in which they comprised ca 20% of the gonads. Testes at stages III to V increased in prevalence with increasing length of fish, comprising ca 22% of the gonads of males in the 250-274 mm length class and ca 90% of those of males in the 300-324 mm length class. The testes of the only male found in the 325-349 mm length class were at stage III. The length at which 50% of male A. forsteri first attained maturity was 272.2 mm, with a 95% confidence interval of 271.3 to 272.6 mm (Fig. 5.7).

Ovaries at stages III to VIII and testes at stages III to V increased in prevalence with increasing age of fish, constituting ca 59 and 32% of the gonads of females and males at the end of their second year of life, respectively, and all of those of fish at the end of their fourth years of life (Fig. 5.7). The ovaries of one female, at the end of its fifth year of life, were at stage V. The age at which 50% of females and males first attained maturity, i.e. the A50, calculated from the parameters of the logistic function fitted to the percentage of gonads at stages III to VIII in each year class, was 2.2 and 2.5 years respectively, with 95% confidence intervals of 2.1 to 2.3 and 2.4 to 2.6 years, respectively (Fig. 5.7).
*Mugil cephalus*

During the spawning period of *M. cephalus* in south-western Australian marine waters, *i.e.* February to September (Chubb *et al.* 1981, Potter *et al.* 2000), the ovaries of all females < 300 mm were at stages I or II (Fig. 5.8). Ovaries at stage III first appeared in the 300-324 mm length class, when they comprised *ca* 7% of all ovaries, while those at stage IV were first found in the 325-349 mm length class, in which they constituted *ca* 11% of all ovaries. The percentage contributions of stages III and IV ovaries in the 350-374 and 375-399 mm length classes were 43 and 67%, respectively. The ovaries of two of the three females in the 400-424 mm length class were at stage IX, *i.e.* resorbing, and the ovaries of the single female in the 450-474 mm length class were at stage III. Testes at stage I were found in males up to 349 mm in length (Fig. 5.8). Stage II testes were first found in males ≥ 300 mm and constituted 100% of all gonads of males >350 mm.

By the end of their second year of life, the ovaries of all females were at stages I or II (Fig. 5.8). Stages III and IV ovaries were first found in females at the end of their third year of life, when they collectively constituted *ca* 16% of all ovaries. Resorbing gonads (stage IX) were found in *ca* 40% of female fish at the end of their fourth year of life and the ovaries of the oldest female *M. cephalus*, which was at the end of its fifth year of life, were at stage III (Fig. 5.8). The testes of all males at the end of their second year of life were at stage I. Stage II testes were present in *ca* 53% of males at the end of their third year of life and were found in one male at the end of the fourth year of life (Fig. 5.8).
Figure 5.8 Percentage frequency of occurrence of sequential stages in the gonadal development in (a) each sequential 25 mm length category and (b) each age class of female and male *Mugil cephalus* caught between April and September, *i.e.* during the spawning period in marine waters. The sample sizes for each length and age class are shown.
5.3.3  Gonadosomatic indices

*Silлагинодес пунката*

The length at which 50% of the *S. punctata* found in Wilson Inlet first reach maturity, given the appropriate conditions, *i.e.* the $L_{50}$, could not be determined for this species due to the paucity of fish in samples with mature gonads. The $L_{50}$ of this species in the coastal marine waters of south-western Australia is 410 mm (Hyndes *et al.* 1998) (Table 5.2). Only four females and three males ≥ 410 mm were caught in Wilson Inlet during the known spawning period of this species in marine waters (see Hyndes *et al.* 1998). The maximum GSI values of such females, caught in the months of June and August of 1988, were 0.29 and 0.39, respectively, while those of the males, also caught in the months of June and August of 1988, were 0.06 and 0.04, respectively.

The mean monthly GSIs of each sex calculated using pooled data for female and male *S. punctata* caught in Wilson Inlet, irrespective of length and age are presented in Fig. 5.9. The mean monthly GSIs of female *S. punctata* ranged between 0.1 and 0.5 and showed no clear tendency to peak at any particular time of the year (Fig. 5.9). The seasonal trends in the mean monthly GSIs of male *S. punctata* were similar to those exhibited by the females (Fig. 5.9). The maximum mean monthly GSIs of females and males, *i.e. ca* 0.4 and 0.1, respectively, were recorded in December 1989 and April 1988, respectively.

*Arrипис георджiana*

The mean monthly GSIs of female *A. georgiana*, using data for those females ≥ the estimated $L_{50}$ at first maturity in Wilson Inlet, if maturing fish had been in an appropriate environment, *i.e. 217 mm*, declined precipitously from a peak of *ca* 5.0 in April and May of
Figure 5.9  Mean monthly gonadosomatic indices \(\pm 1\) s.e. for female and male *Sillaginodes punctata*. Sample sizes are given adjacent to each mean.
Table 5.2  The spawning period, ovarian stages, length at first maturity and size range of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus* caught in Wilson Inlet.

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<thead>
<tr>
<th>Species</th>
<th>Spawning period in south-western Australia</th>
<th>Ovarian stages recorded in Wilson Inlet</th>
<th>( L_{50} ) at first maturity</th>
<th>Length in Wilson Inlet</th>
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</thead>
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<tr>
<td></td>
<td></td>
<td>Females</td>
<td>Males</td>
<td></td>
</tr>
<tr>
<td><em>Sillaginodes punctata</em></td>
<td>June - September(^a)</td>
<td>I - IV</td>
<td>410 mm(^a)</td>
<td>35 - 491 mm</td>
</tr>
<tr>
<td><em>Arripis georgiana</em></td>
<td>April - June(^b)</td>
<td>I - V, VIII, IX</td>
<td>217 mm</td>
<td>121 - 373 mm</td>
</tr>
<tr>
<td><em>Aldrichetta forsteri</em></td>
<td>March - September</td>
<td>I - V, VIII, IX</td>
<td>268 mm</td>
<td>22 - 430 mm</td>
</tr>
<tr>
<td><em>Mugil cephalus</em></td>
<td>February - September</td>
<td>I-IV, IX</td>
<td>&gt; 310 mm(^c) (^d)</td>
<td>27 - 525 mm</td>
</tr>
</tbody>
</table>

\(^a\) From Hyndes *et al.* (1998), \(^b\) from Fairclough *et al.* (2000a), \(^c\) from Kesteven (1942), \(^d\) from Thomson (1951).
1988, to ca 1.2 in June 1988 and remained consistently low, i.e. <1.0, from July 1988 to April 1989 (Fig. 5.10). Following a slight rise to ca 1.3 in May 1989, the mean monthly GSIs decreased to ca 0.4 in June 1989 and remained low, i.e. < 0.5, until April 1990, when they increased to ca 1.6.

The seasonal trends in the mean monthly GSIs of male *A. georgiana* ≥ the *L*₅₀ at first maturity, i.e. 248 mm, were similar to those exhibited by females (Fig. 5.10). The maximum mean monthly GSIs recorded for female and male *A. georgiana* in 1988 were considerably greater than those recorded for both sexes in 1989.

*Aldrichetta forsteri*

The mean monthly GSIs of female *A. forsteri*, using data for female fish ≥ 268 mm, the length at which 50% of females first attain maturity, decreased from a peak of ca 6.6 in April 1988 to < 2.5 in July and August 1988 and remained at low a level, i.e. ≤ 0.7, between September 1988 and February 1989 (Fig. 5.11). Mean monthly GSIs increased from ca 2.2 in April 1989 to reach a peak of ca 7.2 in July, before declining precipitously to ca 1.1 in August 1989 and remaining low, i.e. ≤ 0.5, in December 1989 and January 1990.

The mean monthly GSIs of male *A. forsteri*, using data for male fish ≥ the *L*₅₀ at first maturity, i.e. 272 mm, displayed a far less pronounced seasonal trend than that of females and never exceeded.

*Mugil cephalus*

The length at which 50% of the assemblage of *M. cephalus* would typically have first attained maturity in Wilson Inlet if provided with appropriate conditions, i.e. the *L*₅₀, could
Figure 5.10  Mean monthly gonadosomatic indices ± 1 S.E. for female and male *Arripis georgiana*. Sample sizes are given adjacent to each mean.
Figure 5.11  Mean monthly gonadosomatic indices ± 1 S.E. for female and male *Aldrichetta forsteri*. Sample sizes are given adjacent to each mean.
not be determined for this species due to the paucity of fish in samples with mature gonads. A total of 84 *M. cephalus* were caught in Wilson Inlet with lengths ≥ the *L₅₀* of this species in the coastal marine waters of south-western Australia, *i.e. 310 mm* (Kesteven 1942, Thomson 1951) (Table 5.2), therefore, the GSIs of females and males were estimated using fish ≥ 310 mm (Fig. 5.12). Although the mean monthly GSIs of females and males caught between April 1998 and April 1990 remained low, *i.e. ≤ 0.3* and 0.2, respectively, those of females did show quite pronounced peaks in July 1988 (Fig. 5.12). The maximum GSI value recorded for individual females in Wilson Inlet, *i.e. ca 0.5*, was recorded in April 1990, while that of males, *i.e. 0.2*, occurred in June 1988.

5.3.4 Determination of the spawning period and birth date

*Sillaginodes punctata*

Since *S. punctata* with prespawning, spawning or spent gonads were not caught in Wilson Inlet, there were insufficient gonadal data to estimate accurately when the members of this species in the estuary might have spawned, if provided with appropriate conditions. Furthermore, since the 0+ age class was represented by relatively few individuals (see Chapter 4), it was not possible to estimate the spawning period by extrapolation from the time of first appearance of the small 0+ fish in Wilson Inlet.

Hyndes *et al.* (1998) have shown that *S. punctata* spawns in coastal marine waters on the lower west coast of Australia during the four months from June to September and that the new 0+ age class first appears in nearshore nursery areas in late September. Since small 0+ *S. punctata* were also first found in Wilson Inlet in September, the assemblage of this species in Wilson Inlet is presumed to have been derived from a population that
Figure 5.12  Mean monthly gonadosomatic indices ± 1 s.e. for female and male *Mugil cephalus*. Sample sizes are given adjacent to each mean.
spawned at a similar time. This demonstrates that, for the purposes of ageing and constructing a von Bertalanffy growth curve, the assignment of the same birth date as that previously determined by Hyndes et al. (1998) for *S. punctata* on the lower west coast, *i.e.* 1 August, was appropriate for the assemblage in Wilson Inlet.

*Arripsis georgiana*

Since no *A. georgiana* with gonads at stages VI or VII, *i.e.* spawning and recently spent, were caught in Wilson Inlet, and the small 0+ representatives of this species were apparently absent in the estuary (see Chapter 4), there were no data that could be derived from fish in Wilson Inlet to ascertain the likely spawning period of this species. Thus, in order to assign a birth date to this species, it was necessary to use the results of other studies, which have shown that *A. georgiana* spawns in coastal waters off the lower west coast and eastern south coast of Western Australia between April and June, with most spawning activity occurring in late May and early June (Malcolm 1973, Lenanton 1978, Fairclough et al. 2000a). Since the above spawning period was derived, in part, from fish caught in the coastal region that encompasses Wilson Inlet, a birth date of 1 June was appropriate for the assemblage of *A. georgiana* in Wilson Inlet.

*Aldrichetta forsteri*

Despite the fact that few *A. forsteri* with stage V gonads, *i.e.* prespawning, were found in samples and fish with gonads at stages VI or VII, *i.e.* spawning or recently spent, were not caught in Wilson Inlet, the 0+ year class was sufficiently well represented in monthly samples to obtain a broad estimate of the spawning period of *A. forsteri* by
extrapolating from length-frequency data (see Chapter 4). Based on the assumption of Chubb et al. (1981) that 0+ *A. forsteri* grow at a comparable rate to those of *M. cephalus*, the presence in Wilson Inlet of no 0+ *A. forsteri* greater than 50 mm total length in September 1988 suggests that these fish were derived from spawning that occurred in May of that year. Furthermore, the presence of 0+ fish with lengths less than 25 mm in December (Fig. 4.8) suggests that the spawning period continued through to September 1988. Similarly, the presence of *A. forsteri* less than 40 mm in samples from June to December 1989 suggests that the spawning period extended from March to September 1989.

Since Chubb et al. (1981) found new 0+ recruits with lengths in the range of 20-30 mm in monthly samples obtained from the Swan River Estuary from June and late September 1981, they concluded that *A. forsteri* spawned in inshore marine waters from about March to August. A similar conclusion was derived for the assemblage in the Leschenault Estuary, to the south of the Swan River Estuary (Potter et al. 2000). Since small *A. forsteri* less than 30 mm total length consistently appeared in samples collected from Wilson Inlet between June and December, the spawning period of the *A. forsteri* that gave rise to the fish found in Wilson Inlet would have been similar to that of the populations from which the assemblages in the Swan River Estuary were derived. Therefore, since 0+ fish in Wilson Inlet were assumed to have resulted from spawning seasons that extended from March to September, a birth date of 15 June, which represented the middle of the spawning period, was assigned to the assemblage of *A. forsteri* that gave rise to the members of this species in Wilson Inlet.
*Mugil cephalus*

The absence in Wilson Inlet of *M. cephalus* with gonads at stages V to VII, *i.e.* prespawning, spawning or recently spent, meant that it was necessary to estimate the spawning period of *M. cephalus* by extrapolating from length-frequency data and the time of appearance of small fish (see Chapter 4). Small individuals of *M. cephalus*, ranging in total length from 38 to 45 mm, first appeared in seine net catches in the lower estuary in October 1988 (Fig. 4.11). The larvae of *M. cephalus*, reared under laboratory conditions, achieve a mean length of 17.7 mm in 42 days (Kuo et al. 1973), 18.5 ± 6.7 mm in 52 days (Radtké 1984) and grow at a rate of approximately 15 mm per month during the following three months of life (Anderson 1958). The time when the 0+ age class first appeared in Wilson Inlet in 1988, together with their size, suggests that these fish were derived from spawning that occurred in July of that year. In 1989, small fish of 25-29 mm first appeared in June and were present in August, indicating that spawning was occurring in April and June of 1989. In December 1989, 0+ fish as small as 39 mm were present in the lower estuary, suggesting that spawning may have been occurring as late as September.

The presence of small fish less than 40 mm total length in seine samples collected between June and October in 1988 and between June and December in 1989, as well as the wide range of lengths exhibited by the 1987 cohort of 0+ fish in February 1988, *i.e.* 78-183 mm, indicates that the spawning period of *M. cephalus* is protracted. Furthermore, the length of juveniles of the 1988 year class in February 1989, when two distinct size groups of fish, *i.e.* 70-90 mm and 153-183 mm, belonging to the same year class were present, indicates that this species spawns in pulses.
Since length-frequency data indicates that *M. cephalus* spawned from April to September, a birth date of 1 July, representing the middle of that spawning season, was assigned to this species.

5.4 Discussion

5.4.1 Gonadal development

*Sillaginodes punctata*

During the period when spawning is known to occur in coastal marine waters in south-western Australia, *i.e.* June to September, all females < 225 mm possessed ovaries at stages I or II (Fig. 5.5). The most advanced ovarian stage of *S. punctata* that was found in Wilson Inlet during the spawning period was stage III in 1988 and stage IV in 1989 and 1990. This difference can be attributed to the fact that the *S. punctata* caught in Wilson Inlet during the spawning periods in 1989 and 1990 were generally larger and older than those in 1988.

Furthermore, the maximum GSIs of females and males ≥ 410 mm, *i.e.* the *L50* of this species in marine waters, in Wilson Inlet were *ca* 0.4 and 0.1, respectively, whereas, in the coastal waters of south-eastern Australia where this species spawns, the maximum GSIs of reproductively active female and male *S. punctata* > 300 mm and aged ≥ 3+, were *ca* 9 and 7, respectively, during the spawning period (Fowler *et al.* 1999, 2000). Moreover, relatively few *S. punctata* were caught in Wilson Inlet with gonads at stages III or IV, *i.e.* developing or maturing, and no representatives of this species possessed gonads at stages V, VI or VII, *i.e.* prespawning, spawning or recently spent. These data indicate that *S. punctata* rarely, if ever, reaches maturity in Wilson Inlet. This conclusion is consistent with
the fact that the majority of *S. punctata* caught in Wilson Inlet were less than 400 mm and 4 years old, which are less than the lengths and ages at which the females and males of this species typically first reach maturity in south-western Australian coastal waters (Hyndes *et al.* 1998).

The above strong circumstantial evidence that *S. punctata* does not typically spawn in Wilson Inlet is consistent with the fact that extensive concurrent sampling of the ichthyoplankton of the basin of Wilson Inlet yielded only one larva of *S. punctata* (Neira and Potter 1992a,b) and the small 0+ fish first appeared four months after the time that spawning is known to commence at sea (see Chapter 4, Hyndes *et al.* 1998). Moreover, *S. punctata* is known to spawn in marine waters in different parts of its distribution (Cockrum and Jones 1992, Hyndes *et al.* 1998, Fowler *et al.* 1999, 2000).

In south-western Australia, representatives of *S. punctata* with total lengths of 350-600 mm and ages of 4 to 14 years typically inhabit marine waters > 6 m in depth, which implies that this species moves further offshore and into deeper water, as it increases in size (Hyndes *et al.* 1998). A similar ontogenetic shift in habitat has been described for *S. punctata* in South Australian marine waters where small fish occur inshore and fish of 3 to 17 years in age occur in deeper, offshore waters (Fowler *et al.* 2000). It is thus concluded that the paucity of larger and older fish in Wilson Inlet provides overwhelming evidence that most *S. punctata* have moved out of Wilson Inlet into marine waters by the time they approach *ca* 400 mm at the end of their third year of life and thus prior to their reaching sexual maturity. This conclusion is consistent with the results of Hyndes *et al.* (1998), who found that, as *S. punctata* approached the size and age at which they will
become mature, they migrated out of their nursery areas in marine embayments and estuaries into deeper offshore waters on the lower west coast of Australia.

The absence in Wilson Inlet of fish with stage VII or VIII gonads, i.e. recently spent or recovering spent, demonstrates that this species does not return to this estuary after spawning, a finding consistent with the results of Hyndes et al. (1998), who showed that _S. punctata_ with lengths > 400 mm and possessing spawning and spent gonads congregated in the vicinity of reefs in offshore regions where water depths were 6-50 m.

_Arripis georgiana_

_Arripis georgiana_ spawns in the coastal waters of south-western Australia predominantly in late May and early June (Lenanton 1978, Fairclough et al. 2000a). This would account for the presence of females with stage V ovaries, i.e. prespawning, in Wilson Inlet during April and May of 1988 and 1989, and April of 1990. The proportion of large females and males, i.e. ≥ 275 and 250 mm, respectively, with gonads at stage V in 1988 was greater than in 1989 or 1990, a feature reflected in the fact that peak values for the GSIs were recorded in April and May of 1988, prior to the opening of the mouth of the estuary in that year.

All of the ovaries of female fish in samples collected between May 1988, when stage V ovaries were last present, and September 1988, when stage IX ovaries first appeared, were at stages I to IV. This strongly suggests that fish with ovaries at stage V left the estuary as soon as the sand bar was breached in June 1988. Furthermore, from the macroscopic appearance of stage VIII ovaries, i.e. recovering spent, it is evident that a considerable period of time had elapsed between the completion of spawning at sea and the
time when these fish appeared in Wilson Inlet in September 1988. However, since only a few fish $\geq 275$ mm were caught after November 1988, the larger fish did not show any obvious tendency to re-enter Wilson Inlet after spawning at sea.

From the monthly length-frequency data (see Chapter 4), it is evident that the size compositions of the assemblage of *A. georgiana* in Wilson Inlet during the 1988 and 1989 spawning periods were very different. Thus, for example, in contrast to the situation in 1988, few female and male *A. georgiana*, with total lengths greater than the $L_{50}$ at first maturity, were caught in Wilson Inlet during the 1989 spawning season which accounts for the low prevalence of fish with gonads at stages IV and V in that year. This situation is reflected in the very low mean monthly GSIs found for both sexes, *i.e.* $< 2$, in all months during 1989.

Although fewer fish with gonads beyond stage IV were captured in 1989, the last fish with stage V gonads appeared before the sand bar was breached in July 1989 and fish with gonads at stage VIII were first caught in August, a similar situation to that which occurred in 1988.

While *A. georgiana* with ovaries and testes at stages III and IV were first found in the coastal marine waters of south-western Australia in March and were no longer present after May (Fairclough *et al.* 2000a), females and males with stage III and IV ovaries and testes were caught in Wilson Inlet for up to two months after the completion of spawning activity in marine waters. Although the times when stage V gonads were first found in fish in Wilson Inlet and in south-western marine waters were similar, the gonads that were at stages III and IV in fish in marine waters continued to mature through to stage VI, *i.e.* spawning, whereas those of many fish in Wilson Inlet did not appear to mature beyond
stage IV, despite the fact that the estuary mouth remained open throughout the 1988 spawning season and the lengths of the majority of these fish were greater than the $L_{50}$. The decline in the relative abundance of fish with stage III and IV gonads coincided with the appearance of stage IX fish. The fact that stage IX gonads, \textit{i.e.} resorbing, are not found in fish in marine waters (Fairclough \textit{et al.} 2000a), suggests that gonads which were undergoing resorption during late spring and early summer were those which had previously reached stages III and IV. Since vitellogenesis commences in stage III ovaries (Fairclough \textit{et al.} 2000a), this resorption is presumably the result of pre-ovulatory atresia.

From the above, it appears that, even when there was no physical barrier to prevent a seaward spawning migration, a few \textit{A. georgiana} with gonads at stages III and IV remained in Wilson Inlet until after the period after peak spawning, and later resorbed their gonads. This conclusion agrees with Lenanton's (1977) observation that these members of this species, which enter estuaries, may remain there without rejoining the inshore spawning population and resorb their gonads as they develop. Furthermore, the gonads of \textit{A. georgiana} in Wilson Inlet do not progress beyond stage V and are subsequently resorbed when Wilson Inlet remains closed during the months when spawning occurred in marine waters (D. Fairclough pers comm.)

The absence of fish with stage VI or VII gonads, \textit{i.e.} spawning or recently spent, in Wilson Inlet and the absence of eggs and larvae of \textit{A. georgiana} in Wilson Inlet in plankton samples collected during a concurrent study of ichthyoplankton (Neira and Potter 1992a, b) is consistent with the above overwhelming circumstantial evidence that \textit{A. georgiana} does not spawn in Wilson Inlet. It is also consistent with the fact that 0+ fish first appeared in
Wilson Inlet several months after the time that spawning had been completed in marine waters (Malcolm 1973, Lenanton 1978, Fairclough et al. 2000a).

*Aldrichetta forsteri*

The elevated mean monthly GSIs for female *A. forsteri* in Wilson Inlet in April and June in 1988 and between May and July in 1989 reflected an increase in the relative abundance of females with ovaries at stage V, *i.e.* prespawning, in those months. Moreover, stage V gonads, which was the most advanced stage of development observed in the ovaries of females, were present during the five months between April and August in 1988. This finding is consistent with that of Thomson (1957b), who stated that female *A. forsteri* with gonads at an advanced stage of development, although not running ripe, were present in south-western Australian estuaries between April and mid-September. The presence of fish with stage V ovaries over a lengthy period in Wilson Inlet presumably reflects the protracted duration of the spawning period of *A. forsteri* and the fact that individual fish mature at different rates during the spawning season (Thomson 1951, 1957d, Chubb et al. 1981). The appearance in October 1988 and August and October in 1989 of spent females with ovaries in an advanced stage of recovery, indicates that these *A. forsteri* were entering Wilson Inlet after spawning at sea.

In June 1988 and August 1989, when the mouth of the estuary was open to the sea, the gonads of most large *A. forsteri*, *i.e.* > 275 mm total length, were at stages IV and V. The monthly length-frequency data show that the relative abundance of these larger fish decreased in the months immediately following the opening of the estuary mouth, which
indicates that these maturing *A. forsteri* were emigrating out of the system, presumably to spawn at sea.

The following data provide overwhelming evidence that *A. forsteri* does not spawn within the estuary. (I) No *A. forsteri* were found in Wilson Inlet with gonads at stages VI or VII, *i.e.* spawning or recently spent. (II) The few "post-spawning" fish caught in the estuary all possessed gonads in an advanced state of recovery, *i.e.* they were at stage VIII. (III) Neither ova nor larvae of *A. forsteri* were found in plankton samples collected during a concurrent study of the ichthyoplankton in Wilson Inlet (Neira and Potter 1992b). (IV) The new 0+ recruits first appeared three months after the time when *A. forsteri* is known to exhibit peak spawning activity. Although *A. forsteri* with pre-spawning gonads have been found in other south-western Australian estuaries (Thomson 1957b, d, Lenanton 1977, Chubb et al. 1981), there is overwhelming circumstantial evidence that the assemblages of *A. forsteri* in those estuaries spawn at sea (Lenanton 1977, Chubb et al. 1981, Lenanton 1982). Indeed, the results of many studies indicate that, while hormonal treatments and manipulation of environmental factors can induce ovulation and spermiation in the gonads of mugilids in captivity (Kuo 1974, Lee and Menu 1981, James et al. 1983, Bok and Jongbloed 1987, Alvarez-Lajonchere et al. 1988, Cataudella et al. 1988, Kuo 1995, De Monbrison et al. 1997), the final stages of gonadal maturation of nearly all non-captive mugilid species, with the possible exception of *Rhinomugil corsula* (Kurian 1975), can only be completed in marine conditions (Blaber 1987, Brusle 1981a, Kuo 1995).

*Mugil cephalus*
None of the *M. cephalus* caught in Wilson Inlet possessed gonads at stages V to VIII during the period that this species spawns in marine waters and no *M. cephalus* ova and larvae were found in plankton samples collected during a concurrent study of the ichthyoplankton in this estuary (Neira and Potter 1992b). This strong circumstantial evidence that *M. cephalus* does not spawn in Wilson Inlet is consistent with the fact that small 0+ fish first appeared in the estuary some months after the time of peak spawning activity at sea (see Chubb et al. 1981). Although the gonads of *M. cephalus* can develop to an advanced stage in estuaries and rivers (Webb 1973a, Wallace 1975, Chubb et al. 1981, Halliday 1998), all of the available evidence suggests that this species spawns at sea (Arnold and Thomson 1958, Thomson 1963, Fitch 1972, Chubb et al. 1981, Blaber 1987, Greeley et al. 1987).

The absence of sexually mature female and male *Mugil cephalus* in Wilson Inlet is reflected in the maximum values for the GSIs, *i.e.* 1.3 and 0.2, respectively, these values being recorded for fish with total lengths of 478 mm and 422 mm, respectively, whereas the mean monthly GSIs of sexually mature females in eastern Australia, *i.e.* > 300 mm, typically peak at values ≥ 20 (Kesteven 1942, Grant and Spain, 1975). The ovaries of female *M. cephalus* caught in Wilson Inlet were never found to progress beyond stage IV and gonads at stage IX, *i.e.* resorbing, were found in female *M. cephalus* caught in Wilson Inlet as late as December in 1988, months after the peak spawning of this species. Thus, the data suggests that the ovarian resorption observed in female *M. cephalus* is the result of pre-ovulatory atresia and these findings agree with those of previous workers who found that, when migration to the sea is prevented or interrupted, the maturation of the gonads of
female *M. cephalus* is arrested and the ovaries are resorbed prior to the onset of spawning (Abraham et al. 1966, Zhitenev et al. 1974, Wallace 1975, Bok 1979).

In both 1988 and 1989, Wilson Inlet was connected to the sea for lengthy periods during the spawning period of *M. cephalus*. However, despite the fact that most *M. cephalus* in Wilson Inlet were $\geq$ the $L_{50}$ at first maturity recorded in other studies, *i.e.* 310 mm (see Kesteven 1942, Thomson 1951, Grant and Spain 1975), no fish possessed gonads at stages V to VIII. Females with gonads at stage IX, *i.e.* in a state of pre-ovulatory atresia, were caught at sites in both the upper and lower estuary of Wilson Inlet in months when the estuary was open to the sea and in months when the estuary mouth was closed. The absence of males with resorbing gonads agrees with the observations of Abraham et al. (1966) that resorbing gonads are rarely found in those male *M. cephalus* that fail to undertake seaward spawning migrations.

The above findings strongly indicate that, during the spawning period, the maturation of the gonads of *M. cephalus* in Wilson Inlet is arrested during an early stage of development and that the gonads are subsequently resorbed, even during those periods when there is no physical barrier to prevent a seaward spawning migration.

5.4.2 *Pre-ovulatory atresia in Arripis georgiana and Mugil cephalus*

Factors such as captivity, starvation, environmental pollutants and changes in salinity and acidity have all been shown to initiate pre-ovulatory atresia in a range of freshwater and marine teleost species (June 1977, Kling 1981, Goodall et al. 1987, McCormick et al. 1987, Horwood 1989, Agarwal and Singh 1990, Guraya 1993). In the case of *M. cephalus*, the onset of vitellogenesis and the triggering of migratory behaviour
are dependent on the secretion of high levels of gonadotropin (Abraham 1974, 1975, de Vlaming 1983). However, stress caused by captivity and abnormal fluctuations in photoperiod and water temperature have been shown to reduce significantly the levels of pituitary gonadotropin in teleosts, thereby inhibiting vitellogenesis and causing pre-ovulatory atresia (Tanascichuk and Ware 1987, Jafri 1989, Clearwater and Pankhurst 1997, Coward et al. 1997).

The presence in Wilson Inlet of *M. cephalus* and *A. georgiana* with resorbing gonads suggests that these fish are not receiving the environmental cues necessary for the secretion of the sufficiently high levels of gonadotropin required for full sexual maturation (see Eckstein 1975, Guraya 1993). Large *A. georgiana* with gonads that appear hardened and non-functional have been caught in the nearby Normalup-Walpole Estuary (R. Lenanton pers. comm.), but *M. cephalus* with resorbing gonads have not been recorded in other south-west estuarine systems during a number of comprehensive sampling programs (Lenanton 1977, Chubb et al. 1981, Lenanton et al. 1984, Potter and Hyndes 1994).

The occurrence of pre-ovulatory atresia in the gonads of other mugilid species, that were prevented from undertaking a seawards migration, has been recorded by Abraham (1963), Abraham et al. (1966), Eckstein (1975), Wallace (1975) and Bok (1979). It is interesting to note that pre-ovulatory atresia also occurs in large proportions of the adult populations of other teleosts which do not participate in annual spawning migrations, such as yellowfin bream *Acanthopagrus australis* (Pollock 1984) and barramundi *Lates calcarifer* (Moore and Reynolds 1982), these non-migratory fish remaining in estuaries and rivers during the spawning season, despite the fact that there is no barrier preventing them from reaching the sea.
5.4.3 *Length and age at first maturity*

*Sillaginodes punctata*

Since the gonads of only a few of the *S. punctata* caught in Wilson Inlet reached even stages III to IV, no attempt was made to estimate the $L_{50}$ and $A_{50}$ of the assemblage of *S. punctata* in this estuary. However, since the growth parameters of the estuarine assemblage is similar to that of the marine assemblage (see Chapter 4), it seems likely that the length and age at which 50% of female and male *S. punctata* in Wilson Inlet would first attain maturity, when they left the estuary, is similar to that reported by Hyndes *et al.* (1998) for fish in south-western Australian marine waters, *i.e.* ca 410 mm and ca 3.4 years of age (Table 5.2).

*Arripsis georgiana*

The age at which 50% of female *A. georgiana* attain first maturity in Wilson Inlet would have first attained maturity, if they had entered the sea, lies within the 95% confidence limits of the $A_{50}$ recorded by Fairclough *et al.* (2000a) for the females of this species in marine waters in south-western Australia. However, the growth rate of females is considerably greater in estuaries than in marine waters (see Chapter 4) which could account for the fact that the estimate of the $L_{50}$ for the females in Wilson Inlet, *i.e.* 217 mm (Table 5.2), is greater than that reported for females in marine waters, *i.e.* 197 mm (Fairclough *et al.* 2000a).

The $L_{50}$ and $A_{50}$ for male *A. georgiana* in Wilson Inlet, *i.e.* 248 mm and 3.9 years, were considerably greater than the 179 mm and 1.4 years calculated by Fairclough *et al.*

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(2000a) for males in marine waters. These differences may be attributed to the paucity of small males in the estuary and to the fact that *A. georgiana* in Wilson Inlet grow to a larger size and are considerably longer lived than males in marine waters (see Chapter 4).

*Aldrichetta forsteri*

Using data from estuaries on the lower west coast and south coast of Western Australia, Thomson (1957b, c) found that female and male *A. forsteri* matured at the end of their third year of life when, on average, the total lengths were 267 mm and 240 mm, respectively. Harris (1968) reported that female and male *A. forsteri* in South Australia matured during their third year of life at total lengths of 230 mm and 220 mm, respectively. The presence, during the spawning season, of gonads at stages III, IV, V or VIII in *ca* 61% of females and 30% of males aged 2+ demonstrates that a substantial proportion of female *A. forsteri* in Wilson Inlet and a lesser proportion of males were capable of reaching maturity at the end of their third year life. Thus, the gonads of *A. forsteri* in Wilson Inlet mature when fish are of an equivalent age to those in other estuaries in Western Australia and South Australia. However, the most advanced gonadal stage observed in *A. forsteri* in Wilson Inlet, *i.e.* stage V, first appeared in females and males with lengths of 291 mm and 270 mm, respectively, which are greater than the lengths at first maturity recorded either by Thomson (1957b, c) or Harris (1968), a difference that may be due to a faster growth rate of *A. forsteri* in Wilson Inlet (see Chapter 4).

*Mugil cephalus*
The ovaries of all 2+ females were at stages I or II, which demonstrates that female
*M. cephalus* in Wilson Inlet had not achieved maturity by the end of the third year of life.
Stage III and IV ovaries were present in fish aged between 3+ and 5+, which suggests that
some female *M. cephalus* may have reached maturity by the end of the fourth year of life.
Although few male *M. cephalus* were caught in the estuary, the gonads of all males aged
between 2+ and 4+ were at stages I or II, indicating that these fish had not reached maturity
at the end of the fifth year of life. It is generally accepted that female and male *M. cephalus*
reach maturity at the end of their third year of life at a size of 310-350 mm (Kesteven 1942,
Thomson 1951) (Table 5.2). These above findings suggest that, compared to assemblages
of this species in other estuaries and coastal waters of south-western Australia, the onset of
sexual maturity in *M. cephalus* in Wilson Inlet is considerably delayed.
Chapter 6

Trophic relationships between Sillaginodes punctata, Arripis georgiana, Aldrichetta forsteri and Mugil cephalus in Wilson Inlet

6.1 Introduction

6.1.1 Resource partitioning

Competition for resources and behavioural interactions, recruitment patterns, predation and stochastic events all influence the structure of communities (Nilsson 1967, Pianka 1969, Schoener 1974, Macan 1977, Toft 1985, Lima and Dill 1990, Levin et al. 1997). Resource partitioning, defined as “any substantial difference in resource use between coexisting species” (Ross 1986), is particularly important in structuring animal populations (Schoener 1974). The co-existence of different species in the same environment is facilitated by partitioning along three major resource axes, namely food, habitat and time (Schoener 1983, Ross 1986, Piet et al. 1999). Trophic segregation reduces interspecific competition for food resources in many sympatric teleost communities (Pianka 1981) and is often more important than spatial or temporal partitioning in determining the structure of fish assemblages in coastal marine waters and estuaries (Ross 1986).

The low levels of dietary overlap between many sympatric populations of teleost fishes (e.g. Keast 1978, Robertson and Lassig 1980, Keast 1985, Gibson and Ezzi 1987, Hall et al. 1990), even when the species belong to the same family or genus (Chao and Musick 1977, Paine et al. 1982, Prince et al. 1982, Humphries and Potter 1993, Castillo-

Overlap in resource use by two or more species can be used as evidence to support or reject the existence of competition between those species, depending on whether the resource under consideration is scarce or abundant (Colwell and Futuyma 1971). In some circumstances, sympatric fish species demonstrate high levels of dietary overlap, but this is not necessarily symptomatic of competition for food resources if the shared prey taxa are abundant (Keast 1977, Evans 1983, Moreira et al. 1992, Pen et al. 1993, Gaughan and Potter 1997, Hoines and Bergstad 1999, Hostens and Mees 1999). Resource partitioning, as a means for reducing competition, only becomes crucial when food resources are scarce (Pianka 1981), in which case high levels of dietary overlap between sympatric fish species can result in competition, and thus affect the size of the populations of those competing species (Le Mao 1986, Persson 1986, 1987).
6.1.2 Resource partitioning in estuarine teleost assemblages

The different populations of fish in estuaries typically display a high level of spatial and temporal overlap (Knox 1986, Kennish 1990). Furthermore, the relatively low diversity of prey taxa, that is typically available in estuarine environments, restricts the scope for trophic specialisation by teleosts (Day 1981, Kennish 1990). However, the potential for the partitioning of food resources among populations, and thus of reducing dietary overlap, may be facilitated by differences in morphological adaptations for feeding, and consequently in diets, and ontogenetic shifts in diet and habitat (Stickney et al. 1974).

The majority of studies on the food resources used by estuarine fish are confined either to an examination of age/size differences of a single species or to groups of species that are relatively closely related, i.e. at a conspecific or confamilial level (Ross 1986). Many of these studies are limited to descriptions of the stomach contents of each individual species within the estuarine fish assemblage (e.g. Sarojini 1954, Thomson 1957a, 1959, Webb 1973b, Diener et al. 1974, Whitfield and Blaber 1978a, b, Henderson et al. 1992, Blay 1995, Schlacher and Wooldridge 1996, Salini et al. 1998). Relatively few studies of the trophic relationships of teleosts in estuaries have examined interspecific interactions between sympatric populations of taxonomically-diverse fish species in estuarine systems and, of these, only a few have included indices of niche breadth or niche overlap (see Marais 1984, Huh and Kitting 1985, Whitfield 1985, Le Mao 1986, Moreira et al. 1992, Thiel et al. 1996, Gaughan and Potter 1997, Hostens and Mees 1999). This is despite the fact that intraspecific or intraguild competition for food resources has been identified as a
major factor in structuring relationships between possible competitors (Werner and Gilliam 1984, Wissinger 1992, Piet et al. 1999).

6.1.3 *Fish and potential food sources in Wilson Inlet*

Estuarine teleost communities typically have a high biomass but low species richness. Thus, they are usually dominated numerically by only a few species and generally contain only one or two species of each of the families in that community (Day 1981, Kennish 1990). Twenty four of the 28 teleost families that occur in Wilson Inlet are represented either by one or less frequently two species, and only the Atherinidae, Gobiidae and Sparidae are represented by more than two species (Potter et al. 1993, Potter and Hyndes 1994).

The trophic relationships of atherinids and gobies in the nearshore shallows of Wilson Inlet have been described by Humphries and Potter (1993) and the extent of the dietary overlaps between the larvae of gobids, blenniids and sygnathids in that seasonally-closed estuary have been analysed by Gaughan and Potter (1997). However, detailed quantitative data on the diets of commercially and recreationally important species of fish in Wilson Inlet are restricted to those for the platycephalid *Platycephalus specularis*, together with the degree to which the diets of that species overlapped those of four cormorant species (Humphries et al. 1992), and to a description of the stomach contents of juveniles and adults of the plotosid *Cnidoglanis macrocephalus* (Laurenson 1992). Information on the diets of the four other commercially and recreationally important species, that are found in Wilson Inlet, *i.e.* *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus*, is limited to the brief descriptions of their stomach
contents given by Thomson (1957a), based on samples collected from a range of estuaries in south-western Australia. Furthermore, no attempt was made in that study to identify whether there were size-related changes in diet or interspecific dietary overlap.

Results from several other studies conducted in other estuaries and coastal marine waters of south-western Australia show that adults of *S. punctata*, *A. georgiana* and *A. forsteri* feed on macroinfauna, while *M. cephalus* is predominantly a detritivore (Thomson 1951, 1954b, 1957b, Wallace 1976, Lenanton *et al.* 1982, Hyndes *et al.* 1997). Studies in Australian coastal marine waters have established that the diet of *S. punctata* consists primarily of crustaceans when it is a juvenile (Robertson 1977, Jenkins *et al.* 1996, Hyndes *et al.* 1997) and that it changes with increasing body size (Hyndes *et al.* 1997). In estuaries elsewhere in the world, juvenile *M. cephalus* feed mainly on plankton and crustaceans (*Zismann et al.* 1975, Blaber and Whitfield 1977, De Silva and Wijeyaratne 1977, De Silva 1980, Loftus *et al.* 1983, Whitfield 1985) and the composition of the diet changes with increasing body size (Eggold and Motta 1992). No previous studies have examined the degree to which the diets of either *A. georgiana* or *A. forsteri* might change with body size.

Due to the absence of a salinity gradient throughout the basin of Wilson Inlet for much of the year, the hydrological environment of Wilson Inlet is relatively homogenous (Hodgkin and Clark 1988, Potter *et al.* 1993). The composition of the benthic macroinvertebrate community throughout the long basin of Wilson Inlet is relatively uniform and the invertebrate fauna is dominated by a few species of polychaetes and molluscs (Platell and Potter 1996). The presence of reduced salinities, a restricted tidal exchange with the sea (even when the estuary mouth is open), a sand bar which periodically

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prevents recruitment from the sea and relatively constant sediment composition all contribute to the low species diversity of the benthic macroinvertebrate community throughout the basin of Wilson Inlet (Platell and Potter 1996).

*Silloginodes punctata, A. georgiana, A. forsteri* and *M. cephalus* are amongst the most abundant teleosts in the deeper waters of Wilson Inlet and are sympatric throughout the basin of the estuary (Potter *et al.* 1993). Juveniles of these four species utilise the estuary as a nursery ground and the adults can remain in the system for lengthy periods (see Chapter 4). Previous studies have established that *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* prey upon benthic macroinvertebrates at various stages of their life cycles (e.g. Thomson 1957a, Eggold and Motta 1992, Edgar and Shaw 1995, Hyndes *et al.* 1997). Thus, the low diversity of the benthic macroinvertebrate community in Wilson Inlet limits the scope for partitioning the available food resources and thereby increases the potential for significant levels of dietary overlap between these co-existing teleost species, which all presumably feed to some extent on benthic macroinvertebrates.

6.1.4 *Aims of this study*

Although *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* are abundant in south-western Australian estuaries (Potter and Hyndes 1999), there is little information on the trophic interrelationships of these species or on the relationships with potential food resources in these environments. The aim of this component of the thesis was therefore to determine the types of food ingested by each of the above four species and thereby elucidate the extent of any intra- and interspecific differences in the dietary compositions of these species at different life-history stages and thus the extent to which there was a
potential for intra- and interspecific competition for food resources. Emphasis was thus placed on describing the dietary compositions of the full size range of each of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in Wilson Inlet and the degree to which each of those change with body size. To facilitate the above aims, the dietary data were subjected to a series of multivariate analyses, including classification and ordination, which are particularly well suited to analysing dietary data (Platell et al. 1998).

6.2 Materials and methods

6.2.1 Study locality and sampling regime

The sampling methodology and the location of the sampling sites in Wilson Inlet are described in Chapter 2.

6.2.2 Dietary analysis

Individuals in subsamples of the catches of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus*, that were collected by seine netting and gill netting at each site in Wilson Inlet in each season, were measured to the nearest 1 mm and their stomachs removed and preserved in 70% alcohol. The gut, *i.e.* oesophagus, stomach and intestine, of each fish in each subsample was removed soon after capture and stored in 70% alcohol. When available, 10 randomly-selected individuals of each species, caught in each of the four seasons and in each region of the estuary, *i.e.* the lower (sites 1, 2 and 3), middle (sites 4, 5 and 6) and upper (sites 7, 8 and 9) basin, were used for dietary analyses. In the laboratory, the gut was blotted dry and the stomach cut away from the other organs and weighed to the nearest 0.01g. The contents of the stomach
were removed and the empty stomach re-weighed, thereby enabling the wet weight of the stomach contents to be calculated. The stomach contents were examined under a dissecting microscope and the dietary items identified to the lowest possible taxon. In most cases, each animal taxa could be identified to species, except when digestion was very advanced, in which cases the item was assigned to a higher taxonomic group. Henceforth, the term dietary category is used to refer to food items classified either to species or to a higher taxonomic level when the species could not be identified. Sediment (including particulate organic material), macroalgae, plant detritus and diatoms were also recognised as separate dietary categories. All dietary categories, except unidentifiable species and unidentifiable organic matter, were used in subsequent analyses. The number, total weight to the nearest 0.01 g, and total volume of each dietary category were recorded, the latter being measured to the nearest 0.05 ml by recording the amount of water that was displaced in a partially filled 10 ml graduated cylinder. When present, diatoms were counted by mixing the stomach contents with a known volume of water, i.e. 5 ml, and then examining a drop of the solution under a microscope. The counts of diatoms in three replicate samples were averaged and extrapolated to the known volume, using a technique adapted from Odum (1970).

Since no single method of quantifying the dietary characteristics of fish gives a complete indication of dietary importance of the different food types (Hyslop 1980), five different indices were used to describe and compare the diets of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus*. The percentage by number (%N), percentage by volume (%V), percentage by weight (%W) and percentage frequency of occurrence (%FO) were calculated for each dietary category (see Windell 1971, Hyslop 1980). The numerical,
volumetric and gravimetric percentages were combined to produce the Index of Relative Importance (%IRI), a single value which reflects the relative contribution of each dietary category to the diet of each species (Pinkas et al. 1971, Eggleston and Bochenek 1989). The %N, and thus also the %IRI, could not be calculated for dietary categories that could not be enumerated, i.e. sediment, macroalgae, plant detritus and unidentifiable organic material. Empty stomachs were excluded from all calculations.

Each of the numerical, gravimetric and volumetric data sets were used to describe size-related differences in dietary composition of each species, however, since the fact that percentage by volume data is considered to provide the most representative quantitative measure of the contribution made by all components of the diet (Windell and Bowen 1978, Hyslop 1980), and is the best measure for calculating dietary overlap indices (Wallace 1981), the volumetric data were used to analyze the extent of any size-related changes in diets and whether there were overall interspecific or intraspecific differences in diet. Since preliminary analyses showed that dietary compositions of different length classes of each of the four species were influenced neither by season nor region of the estuary, all analyses were based on the mean percentage volumetric contribution of each dietary category, which was calculated using pooled data for all seasons and regions, in each sequential 50 mm length class of each species, i.e. 25-74, 75-124 mm etc. The species diversity of dietary categories, corresponding to dietary breadth (see Scrimgeour and Winterbourn 1987, Harmelin-Vivien et al. 1989), was calculated for each successive 50 mm length class of each species using the Shannon-Wiener Index (Pielou 1966). The values for intra- and interspecific dietary overlap between length classes were calculated using Schoener’s Index (Schoener 1970). This index provides values that range from zero, i.e. no overlap, to 1,
both species consume the dietary item in the same proportions, with a value greater than or equal to 0.6 being considered to represent "biologically significant" overlap (Harmelin-Vivien et al. 1989).

The percentage volume of each dietary category in the diets of each length class of *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* were subjected to classification and ordination using PRIMER Version 4.0 software (Clarke and Warwick, 1994). These analyses used only those mean dietary compositions of a given length class of each species that were based on at least five stomachs. The Bray-Curtis similarity coefficient was applied to root-transformed data and a similarity matrix constructed. Classification of the similarity matrix was accomplished using hierarchical agglomerative cluster analysis with group-average linking and ordination of the similarity matrix was performed using non-metric multidimensional scaling (MDS). One-way analysis of similarities (ANOSIM) (Clarke 1993) was used to test for pair wise differences between the dietary compositions of the length classes for each of the four species. Similarity percentages (SIMPER) was used to determine which dietary categories characterised the different length classes of each species and contributed most to any dissimilarities between species (Clarke 1993).

6.3 Results

6.3.1 Overall dietary composition

*Sillaginodes punctata*

Food was found in 136 (61.5%) of the 221 stomachs of *Sillaginodes punctata*. Of the major taxa, polychaetes made the greatest overall contribution to the diet in terms of numbers, weight and volume, occurring in 64% of those stomachs that contained food
(Table 6.1) and producing the highest index of relative importance of all taxonomic groups consumed by this species. In particular, the large-bodied polychaete *Neanthes vaalii* was the dietary item most frequently ingested by *S. punctata*, occurring in more than 30% of the stomachs examined and contributing more than 20% to each of the total weight and volume of the stomach contents. The small polychaete *Capitella capitata* was by far the most numerous of the polychaetes ingested (38.1%), but accounted for less than 4% of the weight and volume of the diet. Molluscs were the second most important major taxon consumed by *S. punctata*. Molluse siphons, which almost certainly belonged to *Tellina deltoidalis* (M. Platell, pers. comm.), occurred in approximately 14% of the stomachs and accounted for more than 12% of the diet in terms of both weight and volume. Although the gastropod *Philine* sp. occurred in low numbers (<3%), it contributed nearly 16% to each of the total weight and total volume of the stomach contents (Table 6.1).

Crustaceans occurred in more than 19% of the stomachs examined, of which *Palaemonetes australis* was the most frequently ingested, contributing nearly 14% by number and more than 7% by each of weight and volume to the stomach contents (Table 6.1). *Sillaginodes punctata* was the only one of the four species of teleosts to ingest appreciable quantities of nemerteans.

*Arripis georgiana*

A total of 138 (45.5%) of the 303 stomachs of *Arripis georgiana* contained food. Crustaceans, and particularly *P. australis*, were by far the most important of all dietary taxa, dominating the stomach contents by number, weight and volume and occurring in over 60% of the stomachs examined (Table 6.2). Teleosts, including the engraulid
Table 6.1  Percentage contribution by frequency of occurrence (%FO), number (%N), weight (%W), volume (%V) and index of relative importance (%IRI) of each major taxa and dietary category to the overall diet of *Sillaginodes punctata* in Wilson Inlet. The number of stomachs that contained food are given in parentheses. * Asterisks denote the dietary categories that were used for subsequent intra- and interspecific comparisons.

<table>
<thead>
<tr>
<th>MAJOR TAXA</th>
<th>DIETARY ITEMS</th>
<th>Sillaginodes punctata (136)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%FO</td>
<td>%N</td>
</tr>
<tr>
<td>*NEMERTINEA</td>
<td>Unidentifiable spp.</td>
<td>8.09</td>
</tr>
<tr>
<td>POLYCHAETA</td>
<td>64.00</td>
<td>69.30</td>
</tr>
<tr>
<td>*Errant (Nereididae)</td>
<td>Neanthes vaalii</td>
<td>31.62</td>
</tr>
<tr>
<td></td>
<td>*Ceratonereis spp.</td>
<td>15.44</td>
</tr>
<tr>
<td></td>
<td>Other nereids</td>
<td>10.29</td>
</tr>
<tr>
<td>Sedentary</td>
<td>*Scoloplos simplex</td>
<td>6.62</td>
</tr>
<tr>
<td></td>
<td>*Capitella 'capitata'</td>
<td>2.94</td>
</tr>
<tr>
<td>MOLLUSCA</td>
<td>25.74</td>
<td>14.52</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>*Liloa brevis</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>*Philine sp.</td>
<td>6.62</td>
</tr>
<tr>
<td></td>
<td>*Nassarius burchardi</td>
<td>2.21</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>0.74</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>*Mytilus edulis</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>*Arthritica semen</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Xenostrous sp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Bivalve siphons</td>
<td>13.97</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>1.47</td>
</tr>
<tr>
<td>CRUSTACEA</td>
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<td>10.96</td>
</tr>
<tr>
<td>*Cladocera</td>
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<td>-</td>
</tr>
<tr>
<td>*Copepoda</td>
<td>-</td>
<td>-</td>
</tr>
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</tr>
<tr>
<td></td>
<td>*Other decapods</td>
<td>2.94</td>
</tr>
<tr>
<td>INSECTA</td>
<td>0.74</td>
<td>0.14</td>
</tr>
<tr>
<td>*Collembola</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>*Hymenoptera</td>
<td>0.74</td>
<td>0.14</td>
</tr>
<tr>
<td>CHORDATA</td>
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<td>0.14</td>
</tr>
<tr>
<td>*Petromyzontiformes</td>
<td>Geotria australis (young adults)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Engraulis australis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Atherinid spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Gobid spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
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</tr>
<tr>
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</tr>
<tr>
<td></td>
<td>*Sediment</td>
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<td>*Macroalgae</td>
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<td></td>
<td>*Plant detritus</td>
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</tr>
<tr>
<td></td>
<td>*Diatoms</td>
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<td>Unidentifiable organic matter</td>
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Table 6.2  Percentage contribution by frequency of occurrence (%FO), number (%N), weight (%W), volume (%V) and index of relative importance (%IRI) of each major taxa and dietary category to the overall diet of *Arrpis georgiana* in Wilson Inlet. The number of stomachs that contained food are given in parentheses. * Asterisks denote the dietary categories that were used for subsequent intra- and interspecific comparisons.

<table>
<thead>
<tr>
<th>MAJOR TAXA</th>
<th>DIETARY ITEMS</th>
<th><em>Arrpis georgiana</em> (138)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%FO</td>
<td>%N</td>
</tr>
<tr>
<td><strong>NEMERTINEA</strong></td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td><strong>POLYCHAETA</strong></td>
<td>25.36</td>
<td>24.77</td>
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<tr>
<td><em>Errant (Nereididae)</em></td>
<td>14.49</td>
<td>3.42</td>
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<td><em>Ceratonereis spp.</em></td>
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<td>18.64</td>
</tr>
<tr>
<td><em>Other nereids</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SEDENTARY</td>
<td>1.45</td>
<td>0.26</td>
</tr>
<tr>
<td><em>Scoloplos simplex</em></td>
<td>0.73</td>
<td>2.46</td>
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<td>2.90</td>
<td>0.71</td>
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<tr>
<td><em>Gastropoda</em></td>
<td><em>Lioa brevis</em></td>
<td>-</td>
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<tr>
<td><em>Philine sp.</em></td>
<td>2.17</td>
<td>0.66</td>
</tr>
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<td><em>Nassarius burchardi</em></td>
<td>0.73</td>
<td>0.02</td>
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<td><em>Unidentifiable spp.</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Bivalvia</em></td>
<td><em>Mytilus edulis</em></td>
<td>-</td>
</tr>
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<td><em>Arthritica semen</em></td>
<td>0.73</td>
<td>0.02</td>
</tr>
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<td><em>Xenosirobus sp.</em></td>
<td><em>Bivalve siphons</em></td>
<td>-</td>
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<td><em>Unidentifiable spp.</em></td>
<td>-</td>
<td>-</td>
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<td><strong>CRUSTACEA</strong></td>
<td>63.04</td>
<td>68.05</td>
</tr>
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<td><em>Cladocera</em></td>
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<td><em>Copepoda</em></td>
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<td>-</td>
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<td>3.52</td>
</tr>
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<td><em>Collembola</em></td>
<td>-</td>
<td>-</td>
</tr>
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<td><em>Hymenoptera</em></td>
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<td>2.95</td>
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<td><em>Petromyzontiformes</em></td>
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<td><em>Teleosts</em></td>
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<td>8.70</td>
<td>1.30</td>
</tr>
<tr>
<td><em>Gobiid spp.</em></td>
<td>14.49</td>
<td>0.57</td>
</tr>
<tr>
<td><em>Unidentifiable spp.</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>OTHER</strong></td>
<td>3.62</td>
<td>1.30</td>
</tr>
<tr>
<td><em>Sediment</em></td>
<td>0.73</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Macrophytes</em></td>
<td>0.73</td>
<td>1.27</td>
</tr>
<tr>
<td><em>Plant detritus</em></td>
<td>5.60</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Diatoms</em></td>
<td>Unidentifiable organic matter</td>
<td>0.73</td>
</tr>
</tbody>
</table>

146
*Engraulis australis* and two species of gobiid (*Favonigobius lateralis* and *Pseudogobius olorum*), were found in over 40% of all stomachs and, although consumed in low numbers, contributed approximately 37% to both the total volume and weight of the stomach contents. Although nereid polychaetes were frequently ingested, the nereid *Neanthes vaalii* was consumed in only low numbers and accounted for less than 5% of both the weight and volume of the stomach contents, while other nereids (*Ceratonereis* spp.), contributed ca 19% to the total numbers, but only slightly more than 8% to both the total weight and volume of all dietary items consumed by *A. georgiana* (Table 6.2).

**Aldrichetta forsteri**

Less than 40% (116) of the 298 stomachs of *Aldrichetta forsteri* contained food. The decapod *P. australis* was the single most important dietary item (Table 6.3) and, although occurring in very low numbers (< 1%), contributed ca 42% to both the overall weight and volume of the stomach contents. Diatoms, which were presumably consumed in association with sediment and plant detritus (see Odum 1970), were present in large numbers, but comprised only a very small proportion of the overall weight and volume. Polychaetes were present in more than 25% of the stomachs of *A. forsteri*, with *C. 'capitata'* being the most frequently consumed species, contributing ca 19% to both the overall weight and volume (Table 6.3).

**Mugil cephalus**

Of the 236 stomachs of *Mugil cephalus* examined, more than 65% (154) were empty or contained no identifiable dietary items, except gill raker filaments (Table 6.4). Since the
Table 6.3  Percentage contribution by frequency of occurrence (%FO), number (%N), weight (%W), volume (%V) and index of relative importance (%IRI) of each major taxa and dietary category to the overall diet of *Aldrichetta forsteri* in Wilson Inlet. The number of stomachs that contained food are given in parentheses. * Asterisks denote the dietary categories that were used for subsequent intra- and interspecific comparisons.

<table>
<thead>
<tr>
<th>MAJOR TAXA</th>
<th>DIETARY ITEMS</th>
<th>Aldrichetta forsteri (116)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%FO</td>
<td>%N</td>
</tr>
<tr>
<td><em>NEMERTINEA</em></td>
<td>Unidentifiable spp.</td>
<td>0.86</td>
</tr>
<tr>
<td>POLYCHAETA</td>
<td>*Errant (Nereididae)</td>
<td>25.86</td>
</tr>
<tr>
<td></td>
<td>Neanthes vaalti</td>
<td>14.66</td>
</tr>
<tr>
<td></td>
<td>Ceratonereis spp.</td>
<td>1.72</td>
</tr>
<tr>
<td></td>
<td>Other nereids</td>
<td>1.72</td>
</tr>
<tr>
<td>Sedentary</td>
<td>*Scoloplos simplex</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Capitella 'capitata'</td>
<td>11.21</td>
</tr>
<tr>
<td>MOLLUSCA</td>
<td>Gastropoda</td>
<td>12.07</td>
</tr>
<tr>
<td></td>
<td>*Liloa brevis</td>
<td>2.59</td>
</tr>
<tr>
<td></td>
<td>*Philine sp.</td>
<td>6.03</td>
</tr>
<tr>
<td></td>
<td>*Nassarius burchardi</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Mytilus edulis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Arthritica semen</td>
<td>3.45</td>
</tr>
<tr>
<td></td>
<td>*Xenostrobus spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Bivalve siphons</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td>CRUSTACEA</td>
<td>41.38</td>
<td>4.62</td>
</tr>
<tr>
<td>*Cladocera</td>
<td>2.59</td>
<td>0.61</td>
</tr>
<tr>
<td>*Copepoda</td>
<td>6.03</td>
<td>3.33</td>
</tr>
<tr>
<td>*Amphipoda</td>
<td>0.86</td>
<td>0.23</td>
</tr>
<tr>
<td>Mysidaea</td>
<td>*Gastroscus sp.</td>
<td>-</td>
</tr>
<tr>
<td>Decapoda</td>
<td>*Palaeomonetes australis</td>
<td>31.90</td>
</tr>
<tr>
<td></td>
<td>*Other decapods</td>
<td>-</td>
</tr>
<tr>
<td>INSECTA</td>
<td>1.04</td>
<td>1.33</td>
</tr>
<tr>
<td>*Collembola</td>
<td>4.31</td>
<td>1.23</td>
</tr>
<tr>
<td>*Hymenoptera</td>
<td>8.62</td>
<td>0.10</td>
</tr>
<tr>
<td>CHORDATA</td>
<td>0.86</td>
<td>0.01</td>
</tr>
<tr>
<td>*Petromyzontiformes</td>
<td>Geotria australis</td>
<td>(young adults)</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>*Teleosts</td>
<td>Engraulis australis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Athrinid spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Gobid spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>0.86</td>
</tr>
<tr>
<td>OTHER</td>
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<td>61.40</td>
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<tr>
<td>*Sediment</td>
<td>8.62</td>
<td>1.46</td>
</tr>
<tr>
<td>*Macroalgae</td>
<td>7.76</td>
<td>7.74</td>
</tr>
<tr>
<td>*Plant detritus</td>
<td>23.28</td>
<td>15.13</td>
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<tr>
<td>*Diatoms</td>
<td>3.45</td>
<td>61.40</td>
</tr>
<tr>
<td>Unidentifiable organic matter</td>
<td>7.76</td>
<td>2.43</td>
</tr>
</tbody>
</table>

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Table 6.4  Percentage contribution by frequency of occurrence (%FO), number (%N), weight (%W), volume (%V) and index of relative importance (%IRI) of each major taxa and dietary category to the overall diet of *Mugil cephalus* in Wilson Inlet. The number of stomachs that contained food are given in parentheses. * Asterisks denote the dietary categories that were used for subsequent intra- and interspecific comparisons.

<table>
<thead>
<tr>
<th>MAJOR TAXA</th>
<th>DIETARY ITEMS</th>
<th><em>Mugil cephalus</em> (82)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%FO</td>
<td>%N</td>
</tr>
<tr>
<td>*NEMERTINEA</td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td>POLYCHAETA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Errant (Nereididae)</td>
<td>*Neanthes vaalii</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Ceratoneireis spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Other nereids</td>
<td>-</td>
</tr>
<tr>
<td>Sedentary</td>
<td>*Scoloplos simplex</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Capitella 'capitata'</td>
<td>-</td>
</tr>
<tr>
<td>MOLLUSCA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>*Liola brevis</td>
<td>6.10</td>
</tr>
<tr>
<td></td>
<td>*Philine sp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Nassarius burchardi</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>*Mytilus edulis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Arhritica semen</td>
<td>6.10</td>
</tr>
<tr>
<td></td>
<td>*Xenostrobus spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Bivalve siphons</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td>CRUSTACEA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Cladocera</td>
<td>12.20</td>
<td>4.9</td>
</tr>
<tr>
<td>*Copepoda</td>
<td>12.20</td>
<td>1.56</td>
</tr>
<tr>
<td>*Amphipoda</td>
<td>12.20</td>
<td>3.34</td>
</tr>
<tr>
<td>Mysidacea</td>
<td>*Gastroscus sp.</td>
<td>-</td>
</tr>
<tr>
<td>Decapoda</td>
<td>*Palaeomonetes australis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Other decapods</td>
<td>-</td>
</tr>
<tr>
<td>INSECTA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Collembola</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>*Hymenoptera</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CHORDATA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Petromyzontiformes</td>
<td>Geotria australis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>(young adults)</td>
<td>-</td>
</tr>
<tr>
<td>*Teleosts</td>
<td>*Engraulis australis</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Atherinid spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Gobiid spp.</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable spp.</td>
<td>-</td>
</tr>
<tr>
<td>OTHER</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>*Sediment</td>
<td>87.80</td>
</tr>
<tr>
<td></td>
<td>*Macroalge</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>*Plant detritus</td>
<td>63.42</td>
</tr>
<tr>
<td></td>
<td>*Diatoms</td>
<td>92.68</td>
</tr>
<tr>
<td></td>
<td>Unidentifiable organic matter</td>
<td>6.10</td>
</tr>
</tbody>
</table>
presence of these filaments in the stomachs of this species is usually a result of the
regurgitation of food, following capture in gill nets (Blaber 1975), those stomach samples
containing numerous gill rakers were excluded from dietary analysis. In terms of numbers,
the diet of *M. cephalus* was dominated by diatoms (*ca* 95%), but this taxon contributed less
than 1% to each of the total weight and volume (Table 6.4). Sediment, which included
particular organic material, was found in the majority of stomachs (*ca* 88%) and contributed
*ca* 89% to both the total weight and volume of the diet. Cladocerans and copepods were the
only crustacean taxa ingested and each occurred in less than 15 (*ca* 12%) of the stomachs
examined. The very small bivalve *Arthritis semen*, which was probably incidentally
ingested with sediment, comprised only a very small proportion of the diet (Table 6.4).

6.3.2 *Ontogenetic differences in diets*

*Sillaginodes punctata*

Polychaetes made the greatest percentage contribution to the overall numbers,
weight and volume of food ingested by all length classes of *S. punctata*. Indeed, the diet of
the 75-124 mm length class consisted exclusively of nereid polychaetes (Fig 6.1). The
smallest representatives of *S. punctata*, *i.e.* those of the 25-74 mm length class, were the
only fish to consume appreciable quantities of amphipods. Nemertians, bivalves and
decapods were found only in the stomachs of fish greater than 125 mm in length, while
gastropods were ingested only by fish greater than 275 mm in length (Fig. 6.1).
Figure 6.1 Percentage composition by number, weight and volume of each major dietary group in successive 50 mm length classes of *Sillaginodes punctata* and *Arrips georgiana*. Sample sizes are given in parentheses.
NB Sediment, detritus, diatoms and macroalgae are not included in the numerical analyses.
*Arripis georgiana*

Decapods, *i.e.* *P. australis*, comprised a large proportion of the total number, weight and volume of the dietary categories consumed by all length classes of *A. georgiana*, with the diet of the smallest length class consisting exclusively of *P. australis* (Fig 6.1). Although *A. georgiana* was the only one of the four fish species to ingest mysids, these prey were found mainly in the stomachs of fish in the 125-174 mm length class, where they comprised *ca* 70% of both the weight and volume of the diet. Terrestrial insects occurred only in the stomachs of the 175-224 mm length class. Between 77 and 90% of the diets of fish greater than 175 mm in length consisted of teleosts and decapods, together with a smaller contribution of polychaetes (Fig. 6.2).

*Aldrichetta forsteri*

Copepods were found only in the stomachs of the smallest length class of *A. forsteri* and, although they made a particularly large contribution in terms of numbers, *i.e.* *ca* 95%, their contribution to the overall weight and volume of this length class was far less important (Fig 6.2). Terrestrial insects and diatoms each made large contributions to the weight and volume to the diets of smaller fish, but were not found in the stomachs of those greater than 125 mm in length. Amphipods were ingested only by fish in the 75-124 mm length class and gastropods were found only in the stomachs of the 275-324 mm length class. Polychaetes were consumed by all length classes of *A. forsteri* greater than 75 mm and dominated the diets of the largest size group. While decapods comprised the largest proportion of the diets of fish between 225 and 324 mm, they contributed less than 2% in
Figure 6.2  Percentage composition by number, weight and volume of each major dietary group in successive 50 mm length classes of *Aldrichetta forsteri* and *Mugil cephalus*. Sample sizes are given in parentheses.

NB Sediment, detritus, diatoms and macroalgae are not included in the numerical analyses.
terms of numbers, weight and volume to the diet of fish greater than 325 mm in length (Fig. 6.2).

*Mugil cephalus*

The diet of the smallest representatives of *M. cephalus* comprised cladocerans, copepods, diatoms and sediment (Fig. 6.2). However, sediment and detritus comprised more than 90% of the weight and volume of the stomach contents of all fish greater than 75 mm in length (Fig 6.2).

6.3.3 Dietary breadth

The mean dietary breadths of the different length classes of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* varied markedly (Table 6.5). The dietary breadths of *S. punctata* ranged from 0 to 0.79 and, in the case of individuals greater than 175 mm in length, tended to increase with increasing body size. The mean dietary breadths of *A. georgiana* increased progressively from 0 in fish of 75-124 mm to 0.52 in the 225-274 mm length class, before subsequently decreasing to 0.40 in the largest length class, *i.e.* 325-374 mm. The mean dietary breadths of the different length classes of *A. forsteri* showed no conspicuous tendency to increase or decrease with increasing body size, with the largest size class of this species recording the lowest dietary breadth. The mean dietary breadth of *M. cephalus* was greatest in the smallest length class, *i.e.* 25-74 mm. Fish between 75 and 274 mm had similar dietary breadths, with mean values ranging between 0.12 and 0.15, while fish between 275 and 375 mm in length had the lowest dietary breadth, *i.e.* 0.06. The mean dietary breadths of *M. cephalus* greater than 74 mm in length were thus
<table>
<thead>
<tr>
<th>Length class (mm)</th>
<th>Sillaginodes punctata (136)</th>
<th>Arripis georgiana (138)</th>
<th>Aldrichetta forsteri (116)</th>
<th>Mugil cephalus (82)</th>
</tr>
</thead>
<tbody>
<tr>
<td>25-74</td>
<td>0.21 ± 0.04</td>
<td>-</td>
<td>0.40 ± 0.06</td>
<td>0.63 ± 0.04</td>
</tr>
<tr>
<td>75-124</td>
<td>0.00</td>
<td>0.00</td>
<td>0.74 ± 0.03</td>
<td>0.12 ± 0.02</td>
</tr>
<tr>
<td>125-174</td>
<td>0.57 ± 0.06</td>
<td>0.27 ± 0.04</td>
<td>0.76 ± 0.06</td>
<td>0.14 ± 0.03</td>
</tr>
<tr>
<td>175-224</td>
<td>0.42 ± 0.06</td>
<td>0.43 ± 0.05</td>
<td>0.34 ± 0.06</td>
<td>0.15 ± 0.03</td>
</tr>
<tr>
<td>225-274</td>
<td>0.62 ± 0.06</td>
<td>0.52 ± 0.06</td>
<td>0.57 ± 0.07</td>
<td>0.14 ± 0.03</td>
</tr>
<tr>
<td>275-324</td>
<td>0.76 ± 0.05</td>
<td>0.48 ± 0.06</td>
<td>0.77 ± 0.04</td>
<td>0.06 ± 0.01</td>
</tr>
<tr>
<td>325-374</td>
<td>0.79 ± 0.05</td>
<td>0.40 ± 0.06</td>
<td>0.31 ± 0.04</td>
<td>0.06 ± 0.02</td>
</tr>
</tbody>
</table>
far lower than in all length classes of *A. forsteri*. In addition, the mean dietary breadth of *M. cephalus* was always considerably less than those of *S. punctata* and *A. georgiana* in the case of fish greater than 124 mm in length (Table 6.5).

6.3.4 *Intraspecific dietary overlap*

Values for Schoener’s overlap index for successive length classes of *S. punctata* ranged from 0.135 to 0.811 (Table 6.6). Intraspecific dietary overlap was \( \geq 0.6 \) in five cases, *i.e.* with the 25-74 vs 75-124, 125-174 vs 225-274 and 275-324, 225-274 vs 275-324 and 325-374 mm length classes.

Intraspecific dietary overlap values between the four largest length classes of *A. georgiana* ranged between 0.613 and 0.853 (Table 6.6) and were thus considered biologically significant. Dietary overlap values between more disparate length classes were \( \geq 0.6 \) in two cases, *i.e.* 75-124 vs 175-224 and 75-124 vs 325-374 mm. The dietary overlap of only one length class, *i.e.* 125-174 mm, did not overlap with those of any other length class.

Dietary overlap values between successive length classes of *A. forsteri* were all less than 0.6, except between the 225-274 mm length class and 275-324 mm length class, where it was 0.625 (Table 6.6).

*Mugil cephalus* showed the highest levels of intraspecific overlap of any of the four fish species (Table 6.6). With the exception of the smallest length class, *i.e.* 25-74 mm, intraspecific dietary overlap values between all length classes of *M. cephalus* ranged between 0.908 and 0.992. Values between the 25-74 mm length class and all other length classes were less than 0.6.
Table 6.6  Intraspecific Schoener’s overlap indices between the diets of different length classes of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cepalus*. NB Values ≥ 0.6 are highlighted in bold.

<table>
<thead>
<tr>
<th>Length class (mm)</th>
<th>25-74</th>
<th>75-124</th>
<th>125-174</th>
<th>175-224</th>
<th>225-274</th>
<th>275-324</th>
<th>325-374</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sillaginodes punctata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 - 74</td>
<td>-</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>75 - 124</td>
<td>0.811</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>125 - 174</td>
<td>0.438</td>
<td>0.438</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>175 - 224</td>
<td>0.021</td>
<td>0.021</td>
<td>0.341</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>225 - 274</td>
<td>0.377</td>
<td>0.377</td>
<td>0.641</td>
<td>0.135</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>275 - 324</td>
<td>0.430</td>
<td>0.430</td>
<td>0.735</td>
<td>0.251</td>
<td>0.658</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>325 - 374</td>
<td>0.302</td>
<td>0.302</td>
<td>0.568</td>
<td>0.079</td>
<td>0.641</td>
<td>0.523</td>
<td>-</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Length class (mm)</th>
<th>25-74</th>
<th>75-124</th>
<th>125-174</th>
<th>175-224</th>
<th>225-274</th>
<th>275-324</th>
<th>325-374</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aldrichetta forsteri</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 - 74</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>75 - 124</td>
<td>-</td>
<td>0.068</td>
<td></td>
<td></td>
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<td>0.908</td>
<td>0.916</td>
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</table>
6.3.5  *Interspecific dietary overlap*

There were no cases of significant interspecific overlap (Table 6.7). Interspecific values for Schoener's overlap index between the different length classes of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* were always less than 0.6, with most values being less than 0.4.

6.3.6  *Classification and ordination*

Classification separated the dietary categories that constituted the different length classes of each of the four species into two distinct clusters (Fig 6.3). The larger cluster, *i.e.* group A, contained all of the dietary samples of *S. punctata* and *A. georgiana*, and all of those of *A. forsteri* greater than 75 mm. The smaller cluster, *i.e.* group B, contained all of the samples of *M. cephalus* and that of the smallest length class of *A. forsteri*. Group A contained three distinct subdivisions, *i.e.* with Group C comprising all of the samples of *A. georgiana* and the 175-224 mm length class of *S. punctata*, Group D comprising all of the remaining length classes of *S. punctata* and Group E comprising the dietary samples of the six largest length classes of *A. forsteri*. Group B consisted of two subgroups, namely those containing the samples of the two smallest length classes of *M. cephalus* and *A. forsteri*, *i.e.* Group F, and those comprising the six largest length classes of *M. cephalus*, *i.e.* Group G.

The results produced by ordination paralleled those of classification (*cf.* Figs 6.3, 6.4). The dietary samples of *S. punctata* and *A. georgiana* formed a broad vertical band on the left-hand side of the plot, with all but one of the samples for the various length classes of
Figure 6.3  Classification of the mean volumetric percentage contribution for the different dietary categories of successive 50 mm length classes of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus*.
Figure 6.4  Two dimensional solution produced by MDS of the mean volumetric percentage composition for the different dietary categories of successive 50 mm length classes of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus*.
Table 6.7  Interspecific Schoener’s overlap indices between the diets of different length classes of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus*. NB Values ≥ 0.6 are highlighted in bold.

<table>
<thead>
<tr>
<th>Length class (mm)</th>
<th><em>Sillaginodes punctata</em></th>
<th><em>Arripis georgiana</em></th>
<th><em>Aldrichetta forsteri</em></th>
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<td>325-374</td>
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S. punctata lying directly below all of those of A. georgiana (Fig 6.4). The samples of the six largest length classes of A. forsteri formed a vertical group in the middle of the plot, to the right of those of S. punctata and A. georgiana and to the left of those of M. cephalus. The sample of the smallest length class of M. cephalus lay in the top right hand corner of the plot, below but near that of the smallest size class of A. forsteri, and above the tight and discrete group formed by all other length classes of M. cephalus (Fig. 6.4).

ANOSIM showed that the composition of the diets of the different length classes of the four species were significantly different from each other (P < 0.001). SIMPER demonstrated that the taxon which typified the diets of Sillaginodes punctata was nereid polychaetes, while the carid decapod Paleomonetes australis was characteristic of the diet of Arripis georgiana, detritus and Capitella 'capitata' typified the diet of A. forsteri and sediment, including particulate, inorganic material, dominated the diet of Mugil cephalus.

6.4 Discussion

This study showed that Sillaginodes punctata, Arripis georgiana and Aldrichetta forsteri, which are abundant in Wilson Inlet, consumed a wide variety of epibenthic and benthic prey, with carid shrimps and nereid polychaetes each being consumed in large quantities by these three species. However, while small polychaetes, i.e. Capitella 'capitata', were frequently ingested by A. forsteri, they were consumed in only small quantities by S. punctata and A. georgiana. Furthermore, although teleosts made a substantial contribution to the diet of A. georgiana, they contributed less than 1% to the dietary volume of S. punctata and A. forsteri. Bivalve siphons were found in the stomachs of 14% of S. punctata, but were not consumed by any other species. While the smallest
size class of *Mugil cephalus* was distinctive in its ingestion of large volumes of plankton, all other size class of this species ingested predominantly sediment, including particulate organic material, and detritus.

6.4.1 *A description of the diet of each species*

*Sillaginodes punctata*

The protrusable upper and lower jaws and tube-like mouth of *S. punctata* enables this species to feed on those benthic macroinvertebrate prey that occur in, on, or just above the substrate (Gunn and Milward 1985, McKay 1985, Hyndes et al. 1997). Nereid polychaetes, carid shrimps and the siphons of tellinid molluscs made by far the greatest contribution to the diet of *S. punctata*. The consumption of these prey is consistent with the results of Thomson (1957a), who described the diet of *S. punctata* in Wilson Inlet as broadly consisting of polychaetes, shrimps and molluscs. The very large contribution made by errant polychaetes and decapods to the diet of *S. punctata* in Wilson Inlet parallels the situation recorded for this species in marine waters (Hyndes et al. 1997). The concentration by *S. punctata* on the carid shrimp *Palaemonetes australis* reflects the large numbers of this species of decapod in Wilson Inlet (see Hodgkin and Clark 1988). Amphipods and copepods are consumed to a greater extent by *S. punctata* in the marine environment than in Wilson Inlet (cf Results and Hyndes et al. 1997).

*Arrpis georgiana*

The composition of the diet of *A. georgiana* suggests that this species is an opportunistic carnivore, feeding predominantly on prey that occur on the substrate or in the
water column. The very large contribution made by carid shrimps and teleosts to the diet of *A. georgiana* parallels the situation with the large individuals of this species in other estuaries of south-western Australia (see Thomson 1957a, Wallace 1976).

The consumption by *A. georgiana* of decapods, nereid polychaetes and teleosts, and in particular the anchovy *Engraulis australis*, is similar to the situation found with the congeric *Arripis trutta* and *Arripes truttaceus* in marine waters (see Malcolm 1973, Baker 1971, Webb 1973b, Stanley 1980, Edgar and Shaw 1995). This suggests that these three members of the family Arripididae consume similar prey items in both estuarine and marine environments. The decapod *P. australis* made a greater contribution to the diet of *Arripis georgiana* than has been recorded for other arripidids (Hoedt and Dimmlisch 1994, Edgar and Shaw 1995). This decapod is also an important component of the diets of other teleost species in the study area (Humphries *et al.* 1992), reflecting the abundance of this prey type in Wilson Inlet (see Hodgkin and Clark 1988, Potter *et al.* 1993).

*Aldrichetta forsteri*

In Wilson Inlet, *A. forsteri* fed predominantly on the decapod *P. australis*, errant and sedentary polychaetes, gastropods, insects and plant detritus, indicating that this species consumed a variety of invertebrate prey that occur throughout the water column and both in and on the substrate. The proportion of sediment in stomach samples was low, indicating that they were ingested incidentally during the capture of macroinvertebrate prey, which suggests that, unlike *M. cephalus*, this mugilid species does not typically utilise sediment and its associated particulate organic material as a food resource. Although mugilids have protrusible mouths, prey such as crustaceans and molluscs are ingested only by a few
species of this family, such as *A. forsteri* that also have well-developed oral and pharyngeal teeth (Thomson 1954a,b). The results of this study indicate that, as with other mugilids, such as *Liza macrolepis* and *Valamugil cunnesius*, that occur in waters off the Indian coast, *A. forsteri* is a substrate browser (Wijeyaratne and Costa 1987, 1988). The diet of *A. forsteri* in Wilson Inlet broadly parallels the situation recorded for this species in other estuarine and marine environments (Thomson 1957a, b, Webb 1973b, Wallace 1976, Edgar and Shaw 1995). However, whereas chironomids and the bivalve *Arhritica semen* comprise a large proportion of the diet of adult *A. forsteri* in other south-western estuaries (Thomson 1957a, b, Wallace 1976), they make little or no contribution to the diet of this species, despite their relative abundance in the basin of Wilson Inlet (Platell and Potter 1996).

*Mugil cephalus*

While the teeth of *Mugil* species are extremely weak and poorly developed, the upper jaws of these species move forward when the mouth is protruded, whereas in other Australian mugilids the maxilla moves only slightly, if at all (Thomson 1954b). The protrusibility of the jaws presumably aids *M. cephalus* in “sucking up” the uppermost layer of sediment which is then filtered in the pharynx (Thomson 1951, Odum 1970). *Mugil cephalus* possesses a highly complex pharyngobranchial structure, which filters and rejects coarse particles in the sediment while enabling this species to retain and ingest diatoms, plant detritus, macroalgae, bacteria and particulate organic matter as well as the smaller inorganic particles in the sediment, which are relatively richer in absorbed organic material, protozoans and other microorganisms (Odum 1968, Moriarty 1976, Marais and Erasmus 1977).

### 6.4.2 Relationship between diet and body size

*Sillaginodes punctata*

The smallest individuals of *S. punctata* in Wilson Inlet ingest large volumes of amphipods, as is also the case with the juveniles of this species in the marine environment (Robertson 1977, Jenkins *et al.* 1996, Hyndes *et al.* 1997). Although copepods are extremely abundant in Wilson Inlet (Gaugham and Potter 1995) and comprised the bulk of the diet of small individuals of *M. cephalus* in Wilson Inlet, they were not consumed by *S. punctata*. The absence of copepods in the diet of *S. punctata* in Wilson Inlet contrasts with the situation in coastal marine waters where the juveniles of many sillaginid species, including *S. punctata*, ingest large quantities of harpacticoid copepods (see Robertson 1977, Coull *et al.* 1995, Hyndes *et al* 1997).
As *S. punctata* increases in size, the diet undergoes a conspicuous change, reflected in an increased consumption firstly of decapods and nemerteans and then of bivalve siphons and gastropods. The dietary breadths of fish greater than 125 mm in length were relatively high, which indicates that larger *S. punctata* occupy considerably wider trophic niches than those of the smaller members of this species. A shift towards the consumption of larger prey with increasing body size also occurs with *S. punctata* in marine waters (Hyndes *et al*. 1997). The marked ontogenetic changes that occur in the diet of *S. punctata* as this species increases in size, minimises the occurrence of dietary overlap between the size classes and thus reduces the potential for competition between the small and large representatives of this species.

The significant dietary overlaps, *i.e.* with values for Schoener’s index $\geq 0.6$, that were recorded for four of the larger length classes, can be attributed to the consumption of similar quantities of errant polychaetes, sedentary polychaetes, nemerteans and bivalves. Since these prey items are relatively abundant in the basin of Wilson Inlet (Platell and Potter 1996), it is unlikely that high levels of dietary overlap between large *S. punctata* in Wilson Inlet are indicative of competition for food resources.

*Arippis georgiana*

The smallest *A. georgiana*, *i.e.* 75-124 mm, had the narrowest dietary breadth, due to their ingestion exclusively of *P. australis*. This contrasts with the situation in nearshore marine waters, where the small representatives of this species feed on amphipods, bivalves and brachyuran crabs (Lenanton *et al*. 1982). Whilst *P. australis* was consumed by all length classes of *A. georgiana*, prey such as errant polychaetes and teleosts were ingested
only by the larger fish. The larger \textit{A. georgiana} consumed a wider variety of prey species, resulting in higher values for dietary breadth than those recorded for the smaller size classes. Although significant levels of dietary overlap occur between some of the smaller and all of the larger size classes, the shared prey taxa in every case were abundant in the system (Hodgkin and Clark 1988, Potter \textit{et al.} 1993). It is therefore assumed that intraspecific competition for food resources is limited.

\textit{Aldrichetta forsteri}

The composition of the diet of \textit{A. forsteri} in Wilson Inlet indicates that this species is an omnivore that consumes prey taxa occurring in, on or above the substrate. In the marine environment, the volume of the diet of small \textit{A. forsteri}, \textit{i.e.} < 52 mm total length, is dominated by amphipods and harpacticoid copepods (Lenanton \textit{et al.} 1982). In contrast, the volume of the diet of the smallest individuals of \textit{A. forsteri} in Wilson Inlet was dominated by diatoms and terrestrial insects, with copepods contributing \textit{ca} 8\% to the total volume of the diet of fish < 75 mm. Benthic macroinvertebrates were found only in the stomach contents of fish \( \geq 75 \) mm. The proportion of benthic macroinvertebrates in the diet tended to increase with size and sediment were found only in the stomach contents of animals larger than 125 mm, which suggests that the prevalence of benthic foraging behaviour increased as fish increased in body size. The absence of significant dietary overlap between the different length classes of this species indicates a complete ontogenetic shift in the diet with increasing body size and suggests that there is little intraspecific competition for food resources between the largest and smallest fish.
*Mugil cephalus*

Assuming that single large bivalve found in the dietary samples of this species was the result of incidental ingestion, living organic matter was only ingested by the smallest length class of *M. cephalus*. This group feeds principally on phytoplankton and zooplankton, while the larger size classes of this species ingest mainly sediment and its associated particulate organic material and plant detritus. A rapid ontogenetic shift from a planktivorous to an iliophagous diet has previously been recorded for this species by many researchers (Vallet *et al.* 1970, Cain and Dean 1976, De Silva and Wijeyaratne 1977, Pisarevskaya and Aksenova 1991, Oozeki *et al.* 1992) and has been attributed to a change in feeding behaviour rather than to a modification in any morphology (Eggold and Motta 1992). It is widely acknowledged that postlarval mugilids initially feed predominantly on planktonic invertebrates, principally harpacticoid copepods (Hickling 1970, Odum 1970, Zismann *et al.* 1975, De Silva 1980) and that the animal component of the diet decreases with increasing body length (De Silva and Wijeyaratne 1977). Post-larvae and small juveniles of *M. cephalus* feed selectively on zooplankton and phytoplankton (see Odum 1968, 1970, Zismann *et al.* 1975, Blaber and Whitfield 1977, De Silva and Wijeyaratne 1977, De Silva 1980) and the proportion of sediment in the diet increases with increasing body size until fish reach a length of 55 mm, when they adopt the exclusive iliophagous diet of the adults (De Silva and Wijeyaratne 1977). This increasing contribution of sediment and its associated organic material and plant detritus to the diet of *M. cephalus* with increasing body size has been recorded in both estuarine and coastal marine environments (Thomson 1951, 1954b, 1963, 1966, Odum 1968, 1970, Vallet *et al.* 1970, Moore 1974, Marais and Erasmus 1977).
There was consistent and substantial dietary overlap between the six largest size classes of *M. cephalus*, as a result of the very high consumption of sediment and particulate organic material by fish in these groups. The bottom substrate in the deeper waters of Wilson Inlet is rich in particulate organic material (Platell and Potter 1996) and is not considered to be a limiting resource. The ability to ingest and utilise diatoms, protozoans, macroalgae, organic material and associated micro-organisms in sediment ensures that the larger representatives of *M. cephalus* have access to a constant food resource (Odum 1970).

6.4.3 **Interspecific dietary comparisons**

*Sillaginodes punctata, A. georgiana, A. forsteri* and *M. cephalus* commonly consume polychaetes, molluscs and/or crustaceans at some, if not all, stages in their life cycles. The smallest length class of *M. cephalus* was the only group of this species to consume fauna, *i.e.* copeods and cladocerans, with all other size classes of this species ingesting exclusively sediment, benthos and diatoms. Although the diets of *S. punctata, A. georgiana* and *A. forsteri* all included large proportions of errant and sedentary polychaetes and decapods, significant interspecific dietary overlap did not occur between any length class of the four species examined in this study.

The fact that, on the ordination plot, the points for the dietary samples of all size classes of *S. punctata* and *A. georgiana* and the six largest size classes of *A. forsteri* were essentially discrete, demonstrated that the dietary compositions of each of these species were different. This conclusion was supported by the results of ANOSIM tests. While the diets of the smallest length classes of *A. forsteri* and *M. cephalus* both included a large proportion of copepods, the contributions made by other dietary categories to the diets of
small representatives of these species suggest that the diets of these two species were sufficiently diverse to prevent any significant dietary overlap from occurring.

6.4.4 Partitioning of food resources

The composition of the potential food resource, i.e benthic macroinvertebrates, zooplankton and ichthyofauna, in Wilson Inlet does not differ greatly between the regions of the basin of this system (Potter et al. 1993, Gaughan and Potter 1995, Platell and Potter 1996), which suggests that S. punctata, A. georgiana, A. forsteri and M. cephalus co-exist in an environment that provides little scope for the partitioning of food resources by the occupation of different regions. However, the diets of these four species were significantly different from each other. The absence of significant interspecific dietary overlap is attributable through a combination of small-scale partitioning and ontogenetic shifts in diet by each of these species. Thus, in general terms, S. punctata is a benthic macroinvertevore feeding principally on errant polychaetes and nemerteans. The small representatives of A. georgiana are benthic macroinvertevores, ingesting decapods and mysids but, with increasing size, this species incorporates teleosts into its diet and becomes a benthic macroinvertevore/piscivore. Aldrichetta forsteri remains an omnivore throughout its life, while M. cephalus switches from an omnivorous to an iliophagous diet with increasing body size.

Although the species diversity of the benthic macroinvertebrate and zooplankton assemblages of Wilson Inlet are both low, some of these species are capable of attaining very high densities in this protected estuarine environment (Gaughan and Potter 1995, Platell and Potter 1996). The major prey taxa found in the diets of S. punctata,
*A. georgiana* and *A. forsteri*, *i.e.* capitellid and nereid polychaetes, tellinid molluscs, the carid shrimp *Paleomonetes australis*, and the small pelagic teleost *Engraulis australis*, are all very abundant in the system (Hodgkin and Clark 1988, Potter *et al.* 1993, Platell and Potter 1996), which suggests that the coexistence of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in the estuary is not conditional on the partitioning of shared resources. Furthermore, in those cases where intraspecific dietary overlap occurs between different length classes of these three teleost species, it can be attributed to the common consumption of prey taxa that are abundant in Wilson Inlet, which suggests that the effects of competition between the small and larger representatives of the same species is limited.

In summary, there is no evidence that competition for food resources occurs between or within *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in Wilson Inlet. Each species occupies a separate feeding niche or jointly exploits non-limiting food resources and also undergo ontogenetic changes in diet. These features thereby facilitate the co-existence of large populations of these four species in the same estuary. This lack of competition for food resources between four of the most abundant and commercially significant teleosts should help contribute to a long-term stability of both the fishery and the estuarine resources.
Chapter 7

Selectivity of Sillaginodes punctata, Arripis georgiana,

Aldrichetta forsteri and Mugil cephalus retained in
gill nets by gilling and wedging

7.1 Introduction

Gill nets are used extensively in commercial fisheries, particularly for catching
those species that occur in low densities in small water bodies such as reservoirs, lakes
and estuaries (Hamley 1975). Gill netting is also traditionally used to sample fish
populations in order to obtain information that is vital for effective fisheries
management. However, since gill nets are one of the most selective types of gear used
in fishing, they are highly species and size selective and thus do not sample the
population randomly (Gulland 1985, Laevastu and Favorite 1988). Consequently, the
size composition of the catch of a species obtained by gill nets is largely determined by
the selectivity characteristics of the net rather than the size composition of the
population.

The bias introduced by net selectivity can affect all of those estimates of
population parameters that assume that sampling is random (Kipling 1957). Thus,
measures of size composition and abundance, that are crucial for the effective
management of gill-net fisheries, must be corrected in order to account for the effect of
gear selectivity. It is also important to determine the selectivity of particular mesh sizes
so that the mesh sizes used in the commercial gillnet fishery are appropriate for
optimising yield from the stock (Armstrong et al. 1990, Madenjian and Ryan 1995).

The various models that have been developed for determining the relative selectivity of gill nets have been comprehensively reviewed by Regier and Robson (1966), Hamley (1975) and Millar and Fryer (1999).

7.1.1 Factors affecting selectivity in gill nets

The selectivity of gill nets is determined by a wide range of factors including the environmental conditions and the way in which the nets are deployed (Pope et al. 1975, Hansson and Rudstam 1995), the behaviour of fish when encountering the net (Hunter and Wisby 1964, Glass et al. 1993, Sannomiya and Matuda 1993), mesh size (Baranov 1914, 1948, Engås and Løkkeborg 1994), the type of material used in the manufacture of the net (Baranov 1914, Jester 1973, Steinberg 1964), the type of net construction (Margetts 1954, Wilson and Andrew 1987) and the method of fishing (Kennedy 1951, Pope et al. 1975).

7.1.2 Direct and Indirect methods of estimating the selectivity of gill nets

The various methods used for estimating the selectivity of gill nets have been comprehensively reviewed by Regier and Robson (1966), Hamley (1975) and Pope et al. (1975). Absolute selectivity can only be determined in those special cases where the size distribution of the fished population is known. Due to the difficulty and expense of carrying out such studies, such data are relatively sparse and those that have been recorded have generally been restricted to those developed from mark and recapture studies or acoustic surveys (Cucin and Regier 1966, Hamley and Regier 1973,

In practice, the majority of studies of gill net selectivity are conducted using indirect methods to estimate relative selectivity. Relative selectivity is usually estimated by the use of experimental gill nets comprising a series of different mesh sizes that sample a wide range of size classes simultaneously and, in most cases, with equal effort (Regier and Robson 1966, Hamley 1975, Pope et al. 1975).

Indirect methods do not require information on the size composition of the fish population being investigated. Instead, indirect methods rely on mathematical assumptions about the shape of the selectivity curves and their relationships to mesh size and commonly use "type A" or "type B" curves to estimate selectivity in gill nets (Hamley 1975, Millar 2000). Type B curves are estimated by comparing the catches of a particular length class across nets of several different mesh sizes, resulting in the representation of selectivity as the probability of capture of a single size class in a range of mesh sizes (Regier and Robson, 1966). Type A curves model selectivity as the probability of capture of a fish in one mesh size to a range of size classes of fish. In most cases, Type B curves are easier to estimate and, in practice, are usually used as intermediates to calculate corresponding Type A selectivities (Regier and Robson 1966, Millar 2000).

More recently, gill net selectivity data have been analysed using the general statistical model that was first proposed by Kirkwood and Walker (1986). The general statistical model fits an assumed selectivity function directly to catch data, while simultaneously estimating the parameters of the selectivity function across a range of mesh sizes and length classes. The flexibility and robustness of the general statistical
model and its application to all gear types such as towed gears, traps and hooks, as well as gear nets, have contributed to the general acceptance and increased use of this new methodology (Millar and Fryer 1999).

7.1.3  *Gill net selectivity as a function of body morphology*

The body shape of a fish is important in determining its capture in gill nets (Margetts 1954, McCombie and Berst 1969, Marais 1985, Hickford and Schiel 1996). Selectivity models incorporating information on the body dimensions of fish were initially proposed by Sechin (1969) and Kawamura (1972). These models assume that the capture of fish in gill nets is a mechanical process dependent on the relationship between the size of the fish and the size of the mesh (Baranov 1914, 1948).

Sechin’s (1969) model estimates probabilities of fish retention in gill nets as a function of head girth and maximum girth, as well as incorporating coefficients allowing for compression of the body in the mesh, the stretching of netting material and variability in girths for fish of a given length (Hamley 1975). This model has been successfully used to estimate the selection characteristics of smooth-bodied, fusiform fish that are predominantly caught in gill nets by wedging and gilling (Clarke and King 1986, Ehrhardt and Die 1988). However, Sechin’s (1969) model does not account for fish that are tangled by spines, teeth or other protuberances, or those that are wedged on the head in front of the operculum.

The aim of the present study was to estimate the gill net selectivities of *Sillaginodes punctata, Arriris georgiana, Aldrichetta forsteri* and *Mugil cephalus* in Wilson Inlet. It was necessary to estimate the selectivity of these species using indirect methods since the true size structure of the assemblages of *S. punctata, A. georgiana,*
*A. forsteri* and *M. cephalus* in Wilson Inlet is unknown and, in any case, the size composition of these species can exhibit considerable inter-annual variation (see Chapter 4).

A new methodology, hereafter referred to as the “integrated model”, describing selectivity both as a function of body morphology and the length distribution of the catch in a range of mesh sizes, was developed specifically for this purpose by Dr N. Hall of the Fisheries Department of Western Australia. The selectivity estimates of this new model were compared with those determined using the conventional models of Kirkwood and Walker (1986) and Sechin (1969).

7.2 Materials and Method

Gill net selectivity studies were conducted in Wilson Inlet between April 1988 and April 1990. The sampling sites in Wilson Inlet and the methods used to catch *S. punctata, A. georgiana, A. forsteri* and *M. cephalus* in gill nets are described in Chapter 2. Catches were not standardized since the series of panels of different mesh sizes that comprised the gill net were assumed to fish with equal effort on each sampling occasion. After hauling, nets were placed in bins, with the fish still entangled in the mesh and transported to the laboratory. As each fish was removed from each mesh size, its total length (TL) was measured to the nearest 1 mm and a record made of the way in which the fish was retained in the mesh. Fish caught by mesh encircling the head behind the operculum were considered to be “gilled”, whereas those that were trapped by mesh encircling the body behind the posterior edge of the operculum were regarded as “wedged” and those retained in the mesh by snagging of the maxilla, preoperculum,
fins, or spines were considered to be "tangled". Damaged fish and those lying free in the bins were excluded from further analyses of gillnet selectivity.

On each sampling occasion, the opercular girth, maximum girth and retention girth of a random sample of up to five fish of each species caught in each mesh size were measured to the nearest 1 mm, using a loop of nylon filament. The head girths of all fish were measured in a perpendicular plane from the posterior edge of the operculum. The maximum body girths of *S. punctata* and *A. georgiana* were determined by the circumference, measured in a perpendicular plane, incorporating the origin of the first dorsal fin, while those of *A. forsteri* and *M. cephalus* were measured in a perpendicular plane, incorporating the origin of the ventral fin. Retention girth was measured at the mesh mark. Care was taken to prevent constriction of the head and body when measuring girths.

The mean stretched mesh size of each mesh was determined from measurements that were made of the inside perimeter of a random sample of 100 meshes from each panel of the soaked gill net. The measurements were obtained using vernier callipers and recorded to the nearest 0.01 mm.

The distribution of the girths should represent the whole of the fish assemblage not just that of fish retained in gill nets (Reis and Pawson 1992). Thus, in order to obtain unbiased estimates of the girth/length relationships of each species, measurements of the total length, opercular girth and maximum girth of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* caught in Wilson Inlet using alternative capture techniques were also recorded and pooled with those of fish caught in multifilament gill nets. These additional fish were obtained from a concurrent beach seining sampling program (see Potter *et al.* 1993), and from professional fishers using
monofilament gill nets in Wilson Inlet between April 1988 and April 1989, and a purse
seine in January 1989. In addition, recreational anglers fishing in Wilson Inlet between
September 1988 and March 1989 supplied over one hundred A. georgiana. Note that
the measurements of these fish were only used in the estimation of the relationships
between head girth, maximum girth and total length used in the Sechin and integrated
models, and since they were not caught in multifilament gill nets, their numbers were
not included with the catch data used in the Kirkwood and Walker model.

Regression analysis of the girth and length data was carried out using the REG

Although the commercial fishery primarily targets the estuarine catfish
Cnidoglanis macrocephalus (Laurenson et al. 1993a), catches of S. punctata,
A. georgiana, A. forsteri and M. cephalus were occasionally abundant. A monthly
survey of commercial gill net catches provided information on the length-frequency
distributions of the four latter species.

7.2.1 Sechin’s model

Sechin’s (1969) model estimates the probability of retention as a function of the
relationship between mesh size and body morphology. The model assumes that
selection by body girth is knife-edged, i.e. fish with a maximum opercular girth greater
than the mesh perimeter will not be able to penetrate the mesh and will not thus be
cought, while fish with a maximum body girth less than the mesh perimeter will be able
to pass through the mesh and thereby escape. The model is only suitable for fish caug
in gill nets by wedging and gilling and incorporates coefficients to account for the
compression of the fish's body at retention points and variability in fish and mesh size.
The model assumes that all fish are fully selected when their head girth is smaller than the mesh diameter and that the girths of fish in any length class are normally distributed with a common variance. The selection probability \( P \) for the length distribution of fish small enough to enter a mesh beyond the operculum is given by

\[
P\{G_{e,j} \leq 2m_i\} = \Phi \left( \frac{2m_i - K_{e,i}G_{e,j}}{\sqrt{\sigma_{e,j}^2 + \sigma_i^2}} \right)
\]

and for fish too large to pass through the mesh by

\[
P\{G_{\text{max,}j} \geq 2m_i\} = 1 - \Phi \left( \frac{2m_i - K_{\text{max,}i}G_{\text{max,}j}}{\sqrt{\sigma_{\text{max,}j}^2 + \sigma_i^2}} \right)
\]

where -

- \( G_{e,j} \) = mean opercular girth of fish of size class \( j \);

- \( \sigma_{e,j}^2 \) = variance of \( G_{e,j} \),

- \( K_{e,i} \) = a factor combining the elasticity of the netting material and body tissue at the point of opercular girth for mesh size \( i \);

- \( G_{\text{max,}j} \) = mean maximum girth of fish of size class \( j \);
\[ \sigma_{\text{max},j}^2 = \text{variance of } G_{\text{max},j}, \]

\[ K_{\text{max},i} = \text{a factor combining the elasticity of the netting material and body tissue at the point of maximum girth for mesh size } i; \]

\[ 2m_i = \text{inside mesh perimeter of mesh size } i; \]

\[ \sigma_i^2 = \text{variance of mesh perimeter of mesh size } i; \]

\[ \Phi = \text{the cumulative distribution function of the standard normal distribution such that } \Phi(x) \text{ is the cumulative probability of a standard normal variate less than or equal to } x. \]

The length distribution of fish retained by mesh \( i \) is given by the following expression -

\[ S_{i,j} = \Phi \left( \frac{2m_i - K_{e,i} G_{e,j}}{\sigma_{e,j}^2 + \sigma_i^2} \right) \left[ 1 - \Phi \left( \frac{2m_i - K_{\text{max},i} G_{\text{max},j}}{\sigma_{\text{max},j}^2 + \sigma_i^2} \right) \right] \]

where-

\[ S_{i,j} = \text{probability of retention of fish of size class } j \text{ in mesh size } i; \]
The optimum selectivity of each mesh size $i$, was obtained from the length class corresponding to maximum selectivity of each species in each mesh. An estimate of the relative frequency of each length class ($\mu_j$) in the assemblage of each species in Wilson Inlet was obtained by

$$\mu_j = \frac{\sum_{i=1}^{l} n_{i,j}}{\sum_{i=1}^{l} S_{i,j}}$$

where $n_{i,j}$ is the total catch of each length class in mesh size $i$, in the series of $l$ mesh panels. This equation results in an estimation of the relative length frequency distribution of the population of the species under consideration. The population profile of each species was compared with the pooled length frequency distribution of catches in commercial gill nets. For ease of comparison, both length frequency distributions were scaled to give a maximum catch of 100 fish.

7.2.2 The Kirkwood and Walker model

Kirkwood and Walker's (1986) approach fits a chosen selectivity function to catch data using a non-linear maximum likelihood estimation procedure. Since selectivity curves are frequently skewed to the right (Hamley, 1975), the model simultaneously fits catch data across mesh sizes and length classes using a flexible gamma distribution model with two parameters that can accommodate varying amounts of skew. The model requires no knowledge of the underlying processes influencing fish capture and results in a selectivity curve that gives the closest fit to the catch data.
In brief, the model is based on the assumption that catches \( n_{i,j} \), in each net \( i \) and of length class \( j \) are independent observations from a Poisson distribution with mean \( \mu_j S_{i,j} \). This is expressed as

\[
Pr(N_{i,j} = n_{i,j}) = \frac{e^{-\mu_j S_{i,j}} (\mu_j S_{i,j})^{n_{i,j}}}{n_{i,j}!}.
\]

The maximum likelihood estimate of \( \mu_j = \frac{\sum_{i=1}^{I} n_{i,j}}{\sum_{i=1}^{I} S_{i,j}} \).

Ignoring constants, the log-likelihood of the catch data in all mesh sizes \( I \) and all length classes \( J \), is given by

\[
L = \sum_{i=1}^{I} \sum_{j=1}^{J} \left[ n_{i,j} \ln(\mu_j S_{i,j}) - \mu_j S_{i,j} \right].
\]

Relative selectivity \( S_{i,j} \), expressed as a function of fish body length, \( l_j \), is estimated using a gamma distribution model which incorporates a scalar factor to give a modal value for \( S_{i,j} \) of one, according to the following equation

\[
S_{i,j} = \left( \frac{l_j}{\alpha \beta} \right)^{\alpha} \exp\left( \alpha - \frac{l_j}{\beta} \right)
\]
Both $\alpha$ and $\beta$ are expressed in terms of mesh size and length class and are parameters of a gamma distribution with mode $\alpha \beta$ and variance $(\alpha+1)\beta^2$. In effect, $\alpha$ controls the degree of skew and influences optimum length, while $\beta$ influences optimum length and selection range (Kenchington 1993).

The model also includes the following assumptions-

i) the length at maximum selectivity for panel $i$, *i.e.* the optimal selectivity of each panel, is proportional to mesh size, so that $\alpha \beta = \theta_i m_i$;

ii) the variance is a constant $\theta_2$ for each mesh panel;

iii) fish capture in each mesh panel is a random process over time and the experiment; samples the entire population;

iv) all panels have equal fishing power;

v) mean selectivity for fish in each length class is approximated from the continuous function as a discrete variable $S_{ii}$ at the mid-point of each length class.

The first two assumptions result in a positive $\beta$ in the form of the quadratic equation

$$\beta = -0.5 \left[ \theta_i m_i - (\theta_i^2 m_i^2 + 4 \theta_2)^{0.5} \right]$$

The overall log-likelihood was maximised using the SOLVER routine supplied within Microsoft EXCEL to estimate the parameters $\theta_i$ and $\theta_2$. Despite the fact that this model makes no assumptions regarding the mode of capture of fish in gill nets, in this study, selectivity was estimated only for fish caught by gilling or wedging in order

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to facilitate the comparison of the results of this model with the results of Sechin’s model and the integrated model.

7.2.3 The Integrated model

While Sechin’s method is based on the actual process by which fish become enmeshed, the Kirkwood and Walker (1986) method assumes an empirical form, the gamma distribution, for the selection curve. Thus, based on different assumptions, it is not surprising that the results from the two methods will differ. There would be an advantage if analysis of the various data sets applied a consistent set of assumptions thereby producing the best available estimate of the selection curve using all available data.

It has been assumed that, for the fish that encounter the gill nets and are enmeshed, the assumptions made for the Sechin approach will apply. Equations for the calculation of the log-likelihood of each data set are presented, and then combined to provide an estimate of the log-likelihood of the combined data sets.

7.2.3.1 Head girth data

The set of data comprises $n_c$ observations of the total length, $L_{c,k}$, and opercular girth, $G_{c,k}$, where the $k$th fish is caught within mesh, $m_k$. It is assumed that there is a linear relationship between the opercular girth and fish length, such that

$$\hat{G}_{c,k} = a_c + b_c L_{c,k}$$
The observed length is assumed to be observed with error, where the error is an independent and identically distributed random variate from a normal distribution with mean of zero and variance, $\sigma^2$. Thus,

$$G_{c,k} = \hat{G}_{c,k} + e_{c,k}$$

The value of the normal probability distribution function corresponding to the observed girth is therefore calculated as $\pi(G_{c,k}, \hat{G}_{c,k}, \sigma^2)$, where the probability of a normally distributed variate $x$, where $x \sim N(\mu, \sigma^2)$, is given by

$$\pi(x, \mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(x - \mu)^2}{2\sigma^2}\right)$$

Many of the fish within the sample were caught within gill nets, thus the opercular girth was constrained to lie below the circumference of the mesh in which they were captured. Thus, the sample of fish was not random, but biased, for gillnet-caught fish. The likelihood of observation of a fish with opercular girth $G_{c,k}$ given a length of $L_{c,k}$ was therefore calculated as

$$P(G_{c,k}) = P(G_{c,k} \leq m_k) \pi(G_{c,k}, \hat{G}_{c,k}, \sigma^2)$$

while the likelihood of other fish in the sample that were caught by alternative methods was calculated as
\[ P\{G_{c,k}\} = \pi(G_{c,k}, \tilde{G}_{c,k}, \sigma_c^2) \]

It should be noted that the correction for the bias associated with the opercular girth and capture by gill nets assumed that the bias was independent of the body girth of the fish. It should also be noted that the Sechin formulae have been slightly modified to adjust the variance of the opercular girth by the compressibility factor to reflect the variance of the compressed girth, that is

\[ P\{G_{c,k} \leq 2m_k\} = \Phi\left( \frac{2m_k - K_{c,k}G_{c,k}}{\sqrt{K_{c,k}^2\sigma_{c,k}^2 + \sigma_k^2}} \right) \]

where, for each species, the values for \( K_{c,k} \) and \( \sigma_{c,k}^2 \) were assumed to be constant over all fish.

The log-likelihood of the data set of opercular girth and fish length was therefore calculated as

\[ \lambda_e = \sum_{k=1}^{n_c} \left[ \log(P\{G_{c,k}\}) \right] \]

This log-likelihood is dependent on the three parameters, \( a_c \), \( b_c \) and \( \sigma_c \).
7.2.3.2 Body Girth Data

The set of data comprises $n_{\text{max}}$ observations of the total length, $L_{\text{max},k}$, and body girth, $G_{\text{max},k}$, where the $k$th fish is caught within mesh, $m_k$. It is assumed that there is a linear relationship between the body girth and fish length, such that

$$\hat{G}_{\text{max},k} = a_{\text{max}} + b_{\text{max}} L_{\text{max},k}$$

The observed length is assumed to be observed with error, where the error is an independent and identically distributed random variate from a normal distribution with mean of zero and variance, $\sigma^2_{\text{max}}$. Thus,

$$G_{\text{max},k} = \hat{G}_{\text{max},k} + \epsilon_{\text{max},k}$$

The value of the normal probability distribution function corresponding to the observed girth is therefore calculated as $\pi\left(G_{\text{max},k}, \hat{G}_{\text{max},k}, \sigma^2_{\text{max}}\right)$.

Many of the fish within the sample were caught within gill nets, thus the body girth was constrained to lie above the circumference of the mesh in which they were captured. Thus, the sample of fish was not random, but biased for gillnet-caught fish. The likelihood of observation of such fish was therefore calculated as

$$P\{G_{\text{max},k}\} = P\{G_{\text{max},k} \geq 2m_k\}\pi\left(G_{\text{max},k}, \hat{G}_{\text{max},k}, \sigma^2_{\text{max}}\right)$$
while the likelihood of other fish in the sample that were caught by alternative methods was calculated as

$$P \{ G_{\text{max},k} \} = \pi(G_{\text{max},k}, G_{\text{max},k}, \sigma_{\text{max}}^2)$$

It should be noted that the correction for the bias assumed that the bias associated with fish caught in gill nets was independent of the opercular girth of the fish. It should also be noted that the Sechin formulae have been slightly modified to adjust the variance of the body girth by the compressibility factor to reflect the variance of the compressed girth, that is

$$P \{ G_{\text{max},k} \geq 2m_k \} = 1 - \Phi \left( \frac{2m_k - K_{\text{max},k} G_{\text{max},k}}{\sqrt{K_{\text{max},k}}^2 \sigma_{\text{max},k}^2 + \sigma_k^2} \right)$$

where, for each species, the values for $K_{\text{max},k}$ and $\sigma_{\text{max},k}^2$ were assumed to be constant over all fish.

The log-likelihood of the data set of body girth and fish length was therefore calculated as

$$\lambda_{\text{max}} = \sum_{k=1}^{n_{\text{obs}}} \log(P \{ G_{\text{max},k} \})$$

This log-likelihood is dependent on the three parameters, $a_{\text{max}}$, $b_{\text{max}}$ and $\sigma_{\text{max}}$.

7.2.3.3 Catch Data

The third set of data comprises the length compositions of the catches within the various gillnets, when the nets are fished simultaneously. Calculation of the log-
likelihood for these data is as described when discussing the Kirkwood and Walker method, with the exception that the selectivity associated with the fish within each length class, \( j \), is now determined in accordance with the Sechin method as

\[
S_{i,j} = P\{G_{c,j} \leq 2m_i\}P\{G_{\text{max},j} \geq 2m_i\}
\]

The corrections for the variance to reflect the variance of the compressed girth, as discussed in the sections above, have been included in this calculation. The log-likelihood arising from this calculation will be denoted as \( \lambda_{\text{Catch}} \), rather than \( L \), to distinguish it from the value calculated using the gamma distribution. The log-likelihood of the catch data is dependent on the parameters \( a_c, b_c, \sigma_c, a_{\text{max}}, b_{\text{max}} \) and \( \sigma_{\text{max}} \).

7.2.3.4 Combining the data sets

Estimation of the six parameters, \( a_c, b_c, \sigma_c, a_{\text{max}}, b_{\text{max}} \) and \( \sigma_{\text{max}} \), is carried out simultaneously, by writing the overall likelihood of the combined data as

\[
\lambda = W_c \lambda_c + W_{\text{max}} \lambda_{\text{max}} + W_{\text{Catch}} \lambda_{\text{Catch}}
\]

where \( W_c, W_{\text{max}} \) and \( W_{\text{Catch}} \) are subjective weights applied to the log-likelihoods of the opercular girth, body girth and catch data, respectively. These weights reflect the relative weight to be given to each data set, reflecting the relative precision and accuracy of each data set.
The overall log-likelihood is maximised using the SOLVER routine supplied within Microsoft EXCEL to estimate the six parameters.

7.2.4 *Comparison of selectivity models*

The goodness of fit for the Kirkwood and Walker model and integrated model was evaluated by comparing observed and predicted catches and by inspection of the residual plots for each species in the different mesh sizes. Note that since there were differences in the types of data used by both models to estimate selectivity, caution must be exercised when comparing the residuals of the Kirkwood and Walker model with those of the integrated model.

Since the Sechin model does not include count data in the form of observed catches in its estimation of selectivity, it was not appropriate to evaluate the goodness of fit of this model by comparison of observed and predicted catches. The “fit” of the Sechin model was interpreted from an examination of the relationship between observed catches and the estimated selectivity in each length class.

7.3 *Results*

The data were not analysed separately by sex since there is no evidence to suggest that males of \textit{S. punctata}, \textit{A. georgiana}, \textit{A. forsteri} or \textit{M. cephalus} have different allometric growth from that of females of the same species. The proportion of each species in each 10 mm length class caught by gilling/wedging or tangling in each mesh are presented in Figures 7.1 to 7.4. The problem of net saturation was not encountered in this study as the number of fish caught in each mesh size, on each sampling occasion, rarely exceeded 20.
The mesh size and the variance of each of the six panels in the gill net are presented in Table 7.1. There were some discrepancies between manufacturer-specified mesh sizes and actual mesh sizes.

<table>
<thead>
<tr>
<th>Manufacturer’s mesh size (mm)</th>
<th>Mean mesh size (mm)</th>
<th>Variance of mesh size</th>
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</tr>
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</tr>
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<td>103.77</td>
<td>1.15</td>
</tr>
</tbody>
</table>

Table 7.1. The mean and variance of the stretched mesh in each panel of gill net

7.3.1 Mode of capture

The length-frequency distributions of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* caught in Wilson Inlet show that different sized meshes caught different numbers of fish from a range of different length classes (Figs 7.1 to 7.4). Most fish were retained in gill nets by gilling or wedging.

*Sillaginodes punctata*

The proportion of fish caught by tangling tended to increase with increasing mesh size (Fig. 7.1). The majority of the catch of this species was caught by gilling or wedging in the 38 mm and 51 mm mesh. The number of fish gilled/wedged and tangled was approximately equal in the 63 mm mesh and the relatively few individuals that were caught in the larger mesh sizes were caught predominantly by tangling.
Figure 7.1  Percentage frequency of each 10 mm length class of *Sillaginodes punctata* caught by gilling and wedging or tangling in each mesh size. The sample sizes for each length class are shown. The pie charts represent the same data expressed as a percentage of the total catch in each mesh caught by gilling and wedging or tangling in each mesh.
In mesh sizes of 38 mm, 51 mm and 63 mm, the modal length of fish increased with mesh size. The smallest and the largest representatives of this species were both caught by tangling in the 63 mm mesh.

*Arripis georgiana*

With the exception of the 38 mm mesh, the modal length of fish caught in each panel increased with mesh size. Although all length classes were represented in the 38mm mesh, most fish were caught by tangling and only one small representative of this species was caught by gilling/wedging in this mesh size (Fig. 7.2). The paucity of small *A. georgiana* in 38 mm mesh is attributed to the fact that most representatives of this species recruit to Wilson Inlet after the second year of life at lengths > 200 mm. The majority of the catch of this species in gill nets was caught by gilling/wedging in the 51 mm, 63 mm and 76 mm mesh. Of the few fish caught in larger mesh sizes, most caught in the 89 mm mesh were wedged/gilled and all of those caught in 102 mm mesh were tangled.

*Aldrichetta forsteri*

The modal length of fish retained in each panel increased with mesh size. The proportion of fish caught by tangling increased with mesh size (Fig. 7.3). The majority of the total catch of this species was retained by gilling or wedging in the 38 mm, 51 mm, 63 mm and 76 mm mesh sizes. Catches in the 89 mm and 102 mm panels were low and all fish in these meshes were caught by tangling. Fish in the smallest and largest length classes were caught by tangling in the 38 mm and 76 mm meshes, respectively.
Figure 7.2 Percentage frequency of each 10 mm length class of *Arripsis georgiana* caught by gilling and wedging or tangling in each mesh size. The sample sizes for each length class are shown. The pie charts represent the same data expressed as a percentage of the total catch in each mesh caught by gilling and wedging or tangling in each mesh.
Figure 7.3  Percentage frequency of each 10 mm length class of *Aldrichetta forsteri* caught by gilling and wedging or tangling in each mesh size. The sample sizes for each length class are shown. The pie charts represent the same data expressed as a percentage of the total catch in each mesh caught by gilling and wedging or tangling in each mesh.
*Mugil cephalus*

The modal length of fish retained in each panel increased with increasing mesh size (Fig. 7.4). Catches of this species were relatively small and there was no consistent pattern relating the mode of capture to mesh size. Slightly more than half of the fish retained in the 38 mm mesh were gilled/wedged. The majority of fish caught in the 51 mm mesh were tangled while all of those in the 63 mm mesh were gilled/wedged. In the 76 mm mesh the number of fish caught by each mode were approximately equal and in the larger mesh sizes the proportion of fish caught by gilling or wedging decreased with increasing mesh size.

The smallest length class was represented by a single fish caught by tangling in the 38 mm mesh. Fish in the largest length class were caught by tangling in the 89 mm and 102 mm mesh.

7.3.2 *Selectivity – the Sechin model*

At the outset, it is necessary to recognise that the selectivity curves estimated in this study are retention curves, *i.e.* for each mesh size, the selectivity curve quantifies the relative probability of retaining fish in each length class given that the fish came into contact with the fishing gear (Millar and Fryer 1999).

Before applying the Sechin (1969) estimation procedure, it is necessary to examine the form of the observed catches and relate these to assumptions inherent in the model.

Sechin’s model assumes that fish are retained only by gilling or wedging in gill nets. In this study, fish were retained by gilling, wedging and tangling, however, since tangled fish represented a relatively small proportion of the total catch of each species, it
Figure 7.4  Percentage frequency of each 10 mm length class of *Mugil cephalus* caught by gilling and wedging or tangling in each mesh size. The sample sizes for each length class are shown. The pie charts represent the same data expressed as a percentage of the total catch in each mesh caught by gilling and wedging or tangling in each mesh.
was considered appropriate to use Sechin’s approach to estimate the selectivity for
*S. punctata, A. georgiana, A. forsteri* and *M. cephalus.*

The equality of the girth variances in each data set (Table 7.2) was tested using
Bartlett’s test and, for each species, the variances of head girth in each length class and
those of body girth in each length class were not found to be significantly different
\( (P < 0.01) \). Therefore, variances were pooled to give variance estimates of head girth
\( (\sigma^2_h) \) and maximum girth \( (\sigma^2_{max}) \) for each species (Table 7.3).

For all species, head girth and maximum girth were linearly increasing functions
of the length of fish (Fig. 7.5). The strength of these relationships is evidenced by the
high values of the coefficients of determination \( (r^2) \) recorded for each species. An
interspecific pairwise comparison, using the *F* statistic (Sokal and Rohlf 1981),
indicated a significant difference \( (P < 0.01) \) between the parameter estimates of slopes
of the regression lines of both head girths and maximum girths with lengths for all
species pairs, with the exception of slopes of the regression lines of the head girths of
*A. georgiana* and *M. cephalus* which were not significantly different \( (P < 0.01) \)
(Fig. 7.6). The mean maximum girths of *A. georgiana, A. forsteri* and *M. cephalus*
exceeded mean head girths in all length classes, whereas the mean maximum girths of
*S. punctata* exceeded mean head girths only for fish \( \geq 170 \) mm in length (Table 7.2).
An intraspecific comparison indicated that the parameter estimates of the slope of the
regression lines of maximum girths for all species were significantly greater \( (P < 0.01) \)
than those of head girths (Fig 7.7), *i.e.* the maximum girths of each species increased
with length at a significantly faster rate than did the respective head girths.

The compressibility factors \( K_{c,i} \) and \( K_{max,i} \) for each species in each mesh size are
presented in Table 7.4. In general, mean values estimated for \( K_{c,i} \) were higher than
Fig 7.5  Relationships between (a) head girths at length and (b) maximum girths at length of *Sillaginodes punctata*, *Arrips georgiana*, *Aldrichetta forsteri* and *Mugil cephalus* caught in Wilson Inlet by seine nets (diamonds), multifilament gill nets (closed circles), professional fishers using monofilament gill nets (open circles), professional fishers using purse seines (triangles) and recreational fishers using hooks and lines (squares).

The linear regression equation for each length (x) and girth (y) relationship, coefficient of determination ($r^2$) and the sample size (n) for each species are shown.
Figure 7.6 A comparison of the regression lines of the relationships between head girth at length and maximum girth at length for Sillaginodes punctata, Arripes georgianus, Aldrichetta forsteri and Mugil cephalus.
Figure 7.7  A comparison of the regression lines for head girth at length (solid line) and maximum girth at length (dashed line) for *Sillaginodes punctata, Arripis georgiana, Aldrichetta forsteri* and *Mugil cephalus.*
<table>
<thead>
<tr>
<th>Length class j (mm)</th>
<th>Sillaginodes punctata</th>
<th>Arripsis georgiana</th>
<th>Aldrichetta forsteri</th>
<th>Mugil cephalus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Head Girth (mm)</td>
<td>Mean Head Var (mm²)</td>
<td>Mean Max Girth (mm)</td>
<td>Mean Max Var (mm²)</td>
</tr>
<tr>
<td>100-109</td>
<td>40.1</td>
<td>0.31</td>
<td>40.80</td>
<td>2.37</td>
</tr>
<tr>
<td>120-129</td>
<td>48.9</td>
<td>0.29</td>
<td>51.00</td>
<td>0.04</td>
</tr>
<tr>
<td>140-149</td>
<td>57.7</td>
<td>0.25</td>
<td>61.20</td>
<td>2.37</td>
</tr>
<tr>
<td>160-169</td>
<td>66.5</td>
<td>0.73</td>
<td>71.40</td>
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</tr>
<tr>
<td>180-189</td>
<td>76.2</td>
<td>0.84</td>
<td>86.50</td>
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</tr>
<tr>
<td>200-209</td>
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<td>0.86</td>
<td>86.70</td>
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<tr>
<td>220-229</td>
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<td>1.00</td>
<td>98.50</td>
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<td>240-249</td>
<td>101.7</td>
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<td>2.06</td>
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<td>2.85</td>
<td>216.00</td>
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<td>3.65</td>
<td>241.80</td>
<td>3.98</td>
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<td>400-409</td>
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<td>158.9</td>
<td>6.05</td>
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Table 7.2  Mean head girths, mean maximum girths and their associated variances in each 10mm length class for Sillaginodes punctata, Arripsis georgiana, Aldrichetta forsteri and Mugil cephalus.
<table>
<thead>
<tr>
<th>Species</th>
<th>Variance of Head Girth (mm²)</th>
<th>Variance of Max. Girth (mm²)</th>
</tr>
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<tr>
<td>Sillaginodes punctata</td>
<td>0.5181</td>
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<tr>
<td>Arripis georgiana</td>
<td>0.3187</td>
<td>1.8704</td>
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<td>Aldrichetta forsteru</td>
<td>0.1470</td>
<td>0.3026</td>
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<td>Mugil cephalus</td>
<td>0.3390</td>
<td>0.7181</td>
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</table>

Table 7.3  Pooled variance estimates for head girth ($\sigma^2$) and maximum girth ($\sigma^2_{max}$) for each species.
<table>
<thead>
<tr>
<th>Species</th>
<th>Mesh size $i$</th>
<th>$K_{c,i}$</th>
<th>$\sigma^2_{K_{c,i}}$</th>
<th>$K_{\text{max},i}$</th>
<th>$\sigma^2_{K_{\text{max},i}}$</th>
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</thead>
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<tr>
<td></td>
<td>(mm)</td>
<td></td>
<td>(mm²)</td>
<td></td>
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<td></td>
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<td>1.0000</td>
<td>0.0000</td>
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<td><em>Arripis georgiana</em></td>
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<tr>
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<td><em>Aldrichetta forsteri</em></td>
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<td>0.8896</td>
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</tr>
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<td>51</td>
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<td>0.0000</td>
</tr>
<tr>
<td><em>Mugil cepalus</em></td>
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<td>0.8567</td>
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</tbody>
</table>

Table 7.4 Values of the compressibility factors $K_{c,i}$ and $K_{\text{max},i}$ and their associated variances for each species in each mesh size.
those of $K_{\text{max}}$, since the bony structure of the head is less compressible than the softer retention regions of the body. In the case of small sample sizes, \textit{i.e.} total catch < 3 fish, the compressibility factor was assumed to be 1 with a variance of 0.

The selectivity curves estimated using Sechin's model and the frequency distributions of the lengths of each species caught by gilling and wedging (not tangling) in each mesh size are presented in Figures 7.8 to 7.11.

\textit{Sillaginodes punctata}

The size of the modal length class increased with increasing mesh size (Fig 7.8). Length frequencies of this species in each mesh size were within the range of the probability of retention as indicated by the selection curve for the 38 mm and 51 mm meshes. The shift of catches towards the left of the selectivity curve for 63 mm mesh may be attributed to the paucity in Wilson Inlet of \textit{S. punctata} with lengths > 400 mm (see Chapter 4). The absence of large \textit{S. punctata} in the system also accounts for the fact that no fish were caught in mesh sizes > 63 mm.

\textit{Arripsis georgiana}

The size of the modal length class increased with increasing mesh size (Fig 7.9). Length frequencies of this species in each mesh size were within the range of the probability of retention as indicated by the selection curve in each mesh. The considerable overlap in the ranges of the selection curves in each of the mesh sizes is reflected in the overlapping length distributions in the contiguous mesh sizes. The lack of fish in the 38 mm mesh may be attributed to the fact that this species typically recruits into Wilson Inlet during the second year of life at lengths > 200 mm. The poor
Figure 7.8 Selection curves (solid line) from the Sechin selectivity model and length frequencies (shaded histogram) for *Sillaginodes punctata* gilled or wedged in each mesh size.
Figure 7.9 Selection curves (solid line) from the Sechin selectivity model and length frequencies (shaded histogram) for *Arripsis georgiana* gilled or wedged in each mesh size.
catches in 89 mm and 102 mm mesh sizes may be attributed to a decrease in the abundance of large representatives of this species, as females and males approach their asymptotic lengths of 385 and 317 mm, respectively (see Chapter 4).

*Aldrichetta forsteri*

The size of the modal length class increased with increasing mesh size (Fig 7.10). Length frequencies of this species in each mesh size were within the range of the probability of retention as indicated by the selection curve in each mesh. The poor catches in 89 mm and 102 mm mesh sizes may be attributed to a decrease in the abundance of large representatives of this species, as females and males approach their asymptotic lengths of 428 and 357 mm, respectively (see Chapter 4).

*Mugil cephalus*

The size of the modal length class increased with increasing mesh size (Fig 7.11). The selectivity curves for all mesh sizes matched the distribution of the observed catches.

7.3.3 *Selectivity – the Kirkwood and Walker model*

The Kirkwood and Walker (1986) model makes no assumptions regarding the mode of capture of fish in gill nets, however, this model was only used to estimate the selectivity of fish caught in gill nets by gilling or wedging, thus facilitating the comparison of the results from this model with those of the Sechin and integrated models.
Figure 7.10  Selection curves (solid line) from the Sechin selectivity model and length frequencies (shaded histogram) for *Aldrichetta forsteri* gilled or wedged in each mesh size.
Figure 7.11 Selection curves (solid line) from the Sechin selectivity model and length frequencies (shaded histogram) for *Mugil cephalus* gilled or wedged in each mesh size.
Before applying the estimation procedure to the data it is necessary to examine the assumptions of Kirkwood and Walker’s model. As noted by McLoughlin and Stevens (1994), Kirkwood and Walker’s (1986) assumption that length at maximum selectivity in each mesh is proportional to mesh size is reasonable if there is a strong relationship between lengths and girths. All four species of *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* recorded high coefficients of determination for the linear relationships between length and head girth and length and maximum girth (Fig. 7.5) thus the data support this assumption.

Maximum girth increased faster than head girth for all species and such a relationship has been shown to result in an increase of both the selection range and peak efficiency with mesh size as the two cumulative distribution functions $P \{ G_{c,j} \leq 2m_i \}$ and $P \{ G_{\text{max},j} \geq 2m_i \}$ cross each other at a higher cumulative probability, (Clarke and King 1986, Ehrhardt and Die 1988). Thus, the girth information indicates that Kirkwood and Walker’s (1986) assumption of constant variance and equal peak efficiency for all mesh sizes is violated for *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in Wilson Inlet.

The assumption that all panels have equal fishing power is difficult to assess directly (Kirkwood and Walker 1986, McLoughlin and Stevens 1994). The large differences in catch rates between panels of adjacent mesh sizes, observed for all species in this study, may indicate considerable differences in the fishing powers of the different panels (Hovgård 1996). The assumption that fish behave independently may be violated since *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* all exhibit schooling behaviour (Thomson 1955, Chubb *et al.* 1981, Anon 1988, Hyndes *et al.* 1996).
The selectivity estimates from Kirkwood and Walker’s (1986) model were used to predict catches in each mesh size. A comparison of the predicted catches with observed catches in each mesh size is presented in Figures 7.12 to 7.15.

_Sillaginodes punctata_

The residuals are small indicating that the Kirkwood and Walker model provides a good fit to the data. There are systematic trends in the residuals (Fig 7.12).

_Arripis georgiana_

There are systematic trends in the residuals which also indicate a lack of fit, particularly in the smaller length classes caught in 51 mm and 63 mm mesh (Fig 7.13). The model underestimates catches of the majority of length classes caught in 76 mm mesh.

_Aldrichetta forsteri_

The residuals indicate a good fit for all length classes caught in 38 mm mesh. There are systematic trends in the residuals. Large residuals corresponding to peak catches in the 51 mm and 63 mm mesh indicate poor estimation of peak selectivity in these mesh sizes (Fig 7.14). The model underestimates catches of the majority of length classes caught in 76 mm mesh.

_Mugil cephalus_

Interpretation of the fit of this model is hampered by the small sample sizes in all meshes (Fig 7.15). The exceptionally low catch in the 51 mm mesh suggests that the
Figure 7.12  Observed (solid line) and predicted (dashed line) length-frequencies from the Kirkwood and Walker selectivity model for *Sillaginodes punctata* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
Figure 7.13  Observed (solid line) and predicted (dashed line) length-frequencies from the Kirkwood and Walker selectivity model for *Arripis georgiana* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
Figure 7.14  Observed (solid line) and predicted (dashed line) length-frequencies from the Kirkwood and Walker selectivity model for *Aldrichetta forsteri* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
Figure 7.15  Observed (solid line) and predicted (dashed line) length-frequencies from the Kirkwood and Walker selectivity model for *Mugil cephalus* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
fishing power of this panel was particularly low for this species. In general, the residuals indicate a good fit for most length classes of this species, with the exception of peak catches in the 51 mm, 63 mm, 76 mm and 89 mm mesh sizes.

7.3.4. The Integrated model

The integrated model assumes that head girth and maximum girth are linearly increasing functions of body length. The values predicted by the integrated model for head girth and maximum girth for each species showed good agreement with the observed values for these parameters (Fig. 7.16), therefore this assumption is considered to hold true for all species.

The subjective weights $W_c$, $W_{\text{max}}$, and $W_{\text{Catch}}$ were assigned values of 40, 15 and 1, respectively. The selectivity estimates from the integrated model were used to predict catches in each mesh size. A comparison of the predicted catches with observed catches in each mesh size is presented in Figures 7.17 to 7.20. The residual plots show similar trends to those of the Kirkwood and Walker model.

*Sillaginodes punctata*

The residuals show systematic trends. The model provides a good fit to the catch data in 38 mm mesh but the residuals show that the model provides a poorer fit to the smaller length classes in 51 mm mesh (Fig 7.17).

*Arrhipis georgiana*

The residuals show marked systematic trends and indicate a general lack of fit (Fig 7.18).
Fig 7.16  Relationship between observed and predicted (a) head girths and (b) maximum girths of *Sillaginodes punctata, Arripis georgiana, Aldrichetta forsteri* and *Mugil cephalus* caught in Wilson Inlet by seine nets (diamonds), professional fishers using multifilament gill nets (closed circles), professional fishers using monofilament gill nets (open circles), professional fishers using purse seines (triangles) and recreational fishers using hooks and lines (squares). The dashed line shows equivalent values of observed and predicted girths.
Figure 7.17  Observed (solid line) and predicted (dashed line) length-frequencies from the Integrated selectivity model for *Sillaginodes punctata* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
Figure 7.18  Observed (solid line) and predicted (dashed line) length-frequencies from the Integrated selectivity model for *Arripis georgiana* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
*Aldrichetta forsteri*

The residuals indicate a good fit for all length classes in all meshes with the exception of the 260-269 mm class, which exhibited relatively large residuals in 51 mm and 63 mm mesh (Fig 7.19).

*Mugil cephalus*

It is difficult to determine the fit of this model since sample sizes in all meshes were very small (Fig 7.20). There was no difference recorded between predicted and observed catches in 38 mm mesh. The residuals indicate a lack of fit in those length classes corresponding to peak catches in the 51 mm, 63 mm, 76 mm and 89 mm mesh sizes.

7.3.5. *Optimal selectivities*

The theoretical optimum selection length, *i.e.* the length of each species that is retained with maximum efficiency in each mesh size, was calculated for each species (Fig 7.21). Optimal selection lengths of all species increased with increasing mesh size and each of the models provided similar estimates of optimal lengths for each species in each mesh size. The Kirkwood and Walker (1986) model uses an assumption that results in an exact linear relationship between optimal lengths and mesh size. Mesh specific parameters of mesh variances and the mesh specific compressibility/elasticity factors $K_{C,i}$ and $K_{max,i}$ are included in the estimation of optimal selectivities by the Sechín and integrated models, thus the optimal selectivities for each species estimated by these two models exhibited departures from an exact linear relationship.
Figure 7.19  Observed (solid line) and predicted (dashed line) length-frequencies from the Integrated selectivity model for *Aldrichetta forsteri* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
Figure 7.20  Observed (solid line) and predicted (dashed line) length-frequencies from the Integrated selectivity model for *Mugil cephalus* caught in gill nets in Wilson Inlet. Residuals are shown for each mesh size.
Figure 7.21 Optimal selectivities of *Sillaginodes punctata*, *Arripis georgiana*, *Aldrichetta forsteri* and *Mugil cephalus* in each mesh size, estimated using the Sechin model, the Kirkwood and Walker model and the Integrated model.
In each mesh size, the differences between the optimal lengths of each species in each mesh size reflected their respective morphological characteristics. The elongate head and slender body of *S. punctata* result in higher optimal lengths than those recorded for the relatively stouter species of *A. georgiana, A. forsteri* and *M. cephalus*. The similarity of the girth-to-length relationships of the otherwise morphologically dissimilar species of *A. georgiana* and *M. cephalus* (see 7.3.2) resulted in similar estimates for optimum selection lengths for these two species.

7.3.6. Relative population profiles

The selectivity curves of the Sechin, Kirkwood and Walker and integrated models are presented in Figures 7.22 to 7.25. Selectivity curves of each model, in all mesh sizes, showed considerable overlap, indicating that the particular range of mesh sizes used in this study were effective in sampling a wide range of length classes. Despite differences in the range and amplitude of their respective selection curves, the estimated population length-frequency distributions for *S. punctata, A. georgiana* and *A. forsteri* were essentially the same for each of the models (Figs. 7.26 to 7.28). The relative population profile of *M. cephalus* estimated using the Kirkwood and Walker showed an abundance of large fish that were absent from the relative population profiles estimated using Sechin’s (1969) model and the integrated model (Fig. 7.29).

It is interesting to compare the relative length distributions of the populations with those of commercial catches (Figures 7.26 to 7.29). The length frequency distributions of the population estimates and commercial catches have both been scaled to a maximum catch of 100 (see 7.2.1), thus, the relative abundance of the population cannot be directly compared with that of commercial catches and these figures are only
Figure 7.22 The selection curves for each mesh size estimated for *Sillaginodes punctata* in Wilson Inlet using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.23 The selection curves for each mesh size estimated for *Arripis georgiana* in Wilson Inlet using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.24 The selection curves for each mesh size estimated for *Aldrichetta forsteri* in Wilson Inlet using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.25 The selection curves for each mesh size estimated for *Mugil cephalus* in Wilson Inlet using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.26 The length frequencies of the commercial gill net catch (crosses) and the relative length frequency distribution of the population (solid line) for *Sillaginodes punctata* in Wilson Inlet estimated using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.27 The length frequencies of the commercial gill net catch (crosses) and the relative length frequency distribution of the population (solid line) for *Arripsis georgiana* in Wilson Inlet estimated using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.28  The length frequencies of the commercial gill net catch (crosses) and the relative length frequency distribution of the population (solid line) for *Aldrichetta forsteri* in Wilson Inlet estimated using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
Figure 7.29  The length frequencies of the commercial gill net catch (crosses) and the relative length frequency distribution of the population (solid line) for *Mugil cephalus* in Wilson Inlet estimated using a) the Sechin model, b) the Kirkwood and Walker model and c) the integrated model.
intended as a comparison between the range of length-classes represented in the population with those present in commercial catches.

At the time of this study, the minimum legal mesh size for gill nets in Wilson Inlet was 57 mm and the minimum legal sizes of *S. punctata*, *A. forsteri* and *M. cephalus* were 250, 230 and 240 mm, respectively, with no minimum legal size set for *A. georgiana*. The length frequency distributions show that the commercial catch is comprised of larger, older *S. punctata*, *A. forsteri* and *M. cephalus* that are comparatively poorly represented in their respective populations. In contrast, all length classes of *A. georgiana* in the population are represented in commercial catches.

### 7.4 Discussion

The integrated method provides a realistic model of the catch processes determining the retention of fish in gill nets. By incorporating catch data with information on girth-length relationships and the physical dimensions of gill nets, the integrated model provides a new and cohesive approach to the estimation of relative selectivity.

The integrated model may be constrained to the Sechin approach by including the length/girth components of the data and setting the weight of the catch data component of the log-likelihood to zero. Similarly, the integrated model may be constrained to the Kirkwood and Walker approach by including only the length composition data for the different meshes, by setting the weight of the length-girth component of the log-likelihood to zero.

A major advantage of the integrated model over other girth-based selectivity models, such as Sechin’s model, is the inclusion of catch data to produce estimates of
predicted catches in each length class. Thus, the goodness-of-fit of the integrated model can be investigated by comparison of observed with predicted catches and inspection of the residuals. Previously, researchers using Sechin's model have interpreted the fit of the model through the comparison of selectivity estimates with observed catches in each length class in each mesh size (Ehrhardt and Die 1988, Clarke and King, Reis and Pawson 1992, 1993, Hansen et al. 1997). However, at best, catch curves can only be an approximation to selectivity curves since observed catches reflect the underlying local abundance of length classes in the fished population (Millar and Fryer 1999, Millar 2000), therefore, the usefulness of direct comparisons of selection curves with observed catches in each mesh size is limited. Factors such as under-representation of large length classes due to decreased abundance of older fish approaching their terminal age and length contribute to lack of agreement between catch curves and selectivity curves (Clarke and King 1986, Ehrhardt and Die 1988).

Dimensional characteristics are an important factor in determining the selectivity of fish in gill nets (Kipling 1957, Regier 1969, Kawamura 1972, Marais 1985). The Kirkwood and Walker (1986) model estimates gill net selectivity using only the size composition of catches. It does not include information on girth/length relationships thereby ignoring the mechanisms by which fish are retained in gill nets. To compensate, the Kirkwood and Walker model makes a series of assumptions regarding the size and shape of the selection curves however, in the case of S. punctata, A. georgiana, A. forsteri and M. cephalus, increasing divergence between the slopes of the regression lines of the girth-length relationships causes a violation of these fundamental assumptions.
The residuals of the Kirkwood and Walker model generally show good agreement between predicted and observed catches, as would be expected of a model that uses only catch data in the estimation of selection parameters. The model performed well in estimating catches of *S. punctata* in 38 mm, 51 mm and 63 mm mesh. The residuals exhibited systematic trends and a general lack-of-fit between observed and predicted catches for *A. georgiana*, *A. forsteri* and *M. cephalus*. It is possible that the non-random distribution of these species with respect to the nets contributed to the poor fit of the model (McLoughlin and Nelder 1994). It is theoretically possible to correct for the effect of schooling using an overdispersed Poisson parameter in the model, however this has little effect on the actual selectivity parameter estimates (Millar 1992, Millar and Fryer 1999).

Another factor contributing to the lack of fit of this model for these species may be unequal fishing power of the panels (McLoughlin and Nelder 1994), however, in this study, it was not possible to distinguish variations in fishing power from the effect of other selection processes. No attempt was made to quantify fishing power since robust estimates of fishing power and selectivity are difficult to determine simultaneously (Kirkwood and Walker 1986) and Hovgård *et al.* (1999) advise that fishing power can only be determined by separate, specifically designed experiments.

The residuals of the integrated model showed that it fitted the data at least as well as the Kirkwood and Walker model. Both the Kirkwood and Walker model and the integrated model provided the best fit for *S. punctata*. Catches of *A. georgiana*, *A. forsteri* and *M. cephalus* were considerably smaller than those of *S. punctata*, consequently increased variation in the parameter estimates may have contributed to lack-of-fit of the model for the three former species. It is recommended that future
experiments using the integrated model are designed to maximise catches in each length
class with the purpose of reducing variance in girth measurements.

Other researchers have concluded that a large proportion of the difference
between observed catches and those estimated from selectivity models may be caused
by patchiness in fish distribution (Hansson and Rudstam 1995). Gill nets are a passive
fishing gear and catches are dependent on fish activity, where such activity is size-
dependent and subject to a number of seasonal variations (Hamley 1975, Rudstam et al.
1984). In this study, catches taken over a two year period were pooled in an attempt to
reduce any annual differences in the relative abundance of year classes. In addition,
sampling was conducted throughout the whole of the basin of the estuary and its
tributaries in an effort to minimise any spatial segregation of fish species or age classes.
However, fluctuations in recruitment and emigration processes caused by seasonal
differences in the timing of the opening and closing of the sand bar at the mouth of
Wilson Inlet have been shown to influence the size composition of the assemblages of
*S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in Wilson Inlet (see Chapter 4).
It is therefore recommended that future testing of the integrated model involves fish
species with relatively stable population structures.

As noted by Ehrhardt and Die (1988), seasonal changes in the reproductive
status of fish can have important ramifications on head girth/length and maximum girth
length relationships which can result in changes in the selection range and optimal
selectivity of mesh sizes. Most *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus*
leave Wilson Inlet prior to attaining sexual maturity and those mature *A. georgiana* and
*M. cephalus* that remain in the estuary during the spawning period exhibit exceptionally
low GSIs (see Chapter 5). Thus, it is considered that estimates of the selectivity of these species are not affected by seasonal changes in their girth/length relationships.

The optimum lengths estimated for *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* in each mesh size may prove useful in selection of future management controls of commercial and recreational netting in Wilson Inlet. However, it is necessary to recognise that the selectivity experiments were conducted in a manner that standardised the deployment of the fishing gear and ensured that the hanging coefficients of the nets were as similar as possible on each sampling occasion. In contrast, commercial fishermen alter the hanging coefficients of their nets and deploy their fishing gear in different ways in an attempt to modify the selection characteristics of their nets and target particular species or fish of a particular size.

It is necessary to note that the relative size composition of the population refers only to fish retained in gill nets (Millar and Fryer 1999). Wilson Inlet provides a nursery area for marine-estuarine opportunists such as *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* for protracted periods (see Chapter 4, Potter and Hyndes 1999). Large numbers of these species recruit into Wilson Inlet at sizes too small for physical retention in gill nets (Chapter 4, Potter *et al.* 1993). If encounter rates (Rudstam *et al.* 1984), avoidance behaviour and the availability for capture of fish are size dependent then it is necessary to apply correction factors to the estimates of the relative size distribution of the population in order to produce the true stock size distribution (Hovgård *et al.* 1999, Millar 2000).

There was a marked similarity in the relative size compositions of the respective populations of *S. punctata*, *A. georgiana*, and *A. forsteri* estimated by all three models, and that of *M. cephalus* estimated by the Sechin and integrated models. This suggests
that the total selectivity estimates of each species are relatively independent of the choice of selectivity model, a finding which agrees with that of Hovgård et al. (1999).

The length compositions of the relative populations of *S. punctata*, *A. georgiana* and *A. forsteri* show that smaller, younger fish are more abundant in Wilson Inlet than larger and older fish. Since *S. punctata*, *A. georgiana*, *A. forsteri* and *M. cephalus* predominantly utilise Wilson Inlet as a nursery area (Potter et al. 1993), the population profiles estimated by each of the models for the former three species appear to be reasonable. The population profile for *M. cephalus* estimated by the Kirkwood and Walker model appears less realistic than either of those estimated by the Sechin or integrated models. It shows a large modal group of fish in the 330-339 mm length class, but it is unlikely that older and larger *M. cephalus* in Wilson Inlet are relatively more abundant than the juveniles of this species. The small sample size used for the fitting procedure may be responsible for the less realistic population profile estimated for *M. cephalus* by the Kirkwood and Walker model.

The length composition of the commercial catches of *S. punctata*, *A. forsteri* and *M. cephalus* show that the minimum mesh and size limit regulations are effective in preventing exploitation of the juvenile and sub-adults of these species. With no minimum size length, all length-classes of *A. georgiana* in Wilson Inlet are exploited in similar proportions to their abundance in the population. However, this cannot be considered to constitute a risk to the stock from over-fishing since the assemblage of *A. georgiana* in Wilson Inlet includes neither juveniles aged < 1+ nor spawning adults and the assemblage of this species in Wilson Inlet represents only a small proportion of the total population of *A. georgiana* in the estuaries and marine waters of Western Australia.
The fit of the integrated model may perhaps be improved by changing the subjective weightings. In this study the weightings reduced the influence of the size composition data, thus ensuring adherence to the assumption that fish are caught only if the opercular girth is less than the mesh perimeter and maximum girth is greater than the mesh perimeter. In its present form, the integrated model estimates the selectivity of fish caught only by wedging or gilling yet, due to the flexibility of the model, it is a simple matter to increase the weighting of the size composition component of the data and decrease that of the girth/length component in order to estimate the selectivity of fish caught by retention mechanisms such as tangling or enmeshing by teeth or spines. This is an important consideration if the integrated model is to realistically estimate the selectivities of a wide range of species (Høvård et al. 1999).

The fit of the model may also benefit from decreasing the variability in the data and future experiments should focus on increasing the size of catches in each length class of fish in order to provide better estimates of mean girths, girth variances and body compressibility.

It seems evident that the integrated model provides a more complete description of the retention processes affecting the selectivity of fish in gill nets than models based only on girth information, such as Sechin's (1969) model or those based only on catch information, such as Kirkwood and Walker (1986) model. The flexibility of the model is such that by modifying the weightings applied to the components of the model relating to catch data and girth data, the model can estimate the selectivity of any species based on assumptions regarding the retention processes of that species in gill nets.
Chapter 8

Conclusions

Since the results of each of the components of this thesis have been discussed in detail in the relevant chapters, this final chapter focuses just on the main conclusions that can be drawn from the individual studies conducted in Wilson Inlet.

1. The study of various aspects of the biology of *Sillaginodes punctata, Arripis georgiana, Aldrichetta forsteri* and *Mugil cephalus* was undertaken between April 1988 and April 1990. The estuary mouth was open between June 1988 and May 1989 and between July 1989 and February 1990, which were much shorter periods than in the previous two years. The differences between the time of opening in the different years apparently accounted for differences in the patterns of immigration and emigration in the two years (see later).

2. Monthly trends exhibited by the marginal increment on the hard structures of the above four species demonstrated that it was valid to use the number of annuli on scales to age *S. punctata, A. forsteri* and *M. cephalus* and the number of annuli on the otoliths to age *A. georgiana.*
3. The von Bertalanffy growth curves for males and females were significantly different in the case of *A. georgiana* and *A. forsteri* but not with *S. punctata* and *M. cephalus*. These differences are apparently related to the fact that the first two species are represented by a greater number of older fish and which had therefore reached the size at first maturity.

4. The vast majority of *S. punctata*, *A. forsteri* and *M. cephalus* were less than 3½ years old while most *A. georgiana* were over 2½ and a few were even over 8 years old.

5. The 0+ age class of each of the four species was represented at best by small numbers of individuals, presumably reflecting the considerable distance between Wilson Inlet and the lower west coast of Western Australia where these species are believed mainly to spawn.

6. The closure of the estuary mouth for all but a short period between January 1987 and June 1988 accounts for the fact that the 1987 year class of *S. punctata* and *M. cephalus* were not recruited at all during their first years of life.

7. *Sillaginodes punctata* almost invariably left Wilson Inlet before reaching first maturity and there was no evidence that this species returned to this estuary after spawning at sea. In contrast, there was evidence that some *A. georgiana* returned to Wilson Inlet after spawning at sea.
8. The use of classification and ordination, allied with associated tests, demonstrated that the dietary compositions of each of the four species were significantly different. Thus, while *S. punctata* and *A. georgiana* fed mainly on benthic macroinvertebrates, all but the smallest *M. cephalus* ingested predominantly detritus and *A. forsteri* was an omnivore. Furthermore, the diet of *S. punctata* consisted mainly of errant polychaetes and nemerteans, while that of *A. georgiana* comprised predominantly decapods and mysids and, in the case of larger fish, other teleosts.

9. The diets of each species underwent ontogenetic (size-related) changes. Thus for example, *A. forsteri* switched progressively from feeding mainly on copepods and insects when small to ingesting predominantly sedentary polychaetes when large.

10. The differences between the dietary compositions of the four species and the ontogenetic changes undergone by each species would reduce the potential for both inter- and intraspecific competition for food resources if those resources were in limited abundance.

11. The new integrated model, constructed to determine the mesh selectivity of the four species, has the advantage that, unlike previous selectivity models, it takes into account both the girths of the fish and the number of fish caught in each of the different gill meshes.
References


Anon. (1988). The Australian Herring. Fishing WA 3. Fisheries Department of Western Australia


Caton, A.E. (1966). Preliminary synopsis of biological data on the Australian (spotted or King George) whiting (Sillaginodes punctatus) (Cuv. and Val.) 1929. CSIRO Technical Session, Department of Fisheries and Fauna Conservation, Agenda item No. 5.


Gysels, E., Janssens de Bisthoven, L., de Vos, L. and Ollevier, F. (1997). Food and habitat of four *Xenotilapia* species (Teleostei, Cichlidae) in a sandy bay of northern Lake Tanganyika (Burundi). *Journal of Fish Biology* 50, 254-266.


abundances of Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). *Canadian Journal of Fisheries and Aquatic Sciences 52*, 75-83.


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Appendix 1  Likelihood ratio statistics comparing von Bertalanffy growth models for females of *Arrips georgiana* caught in Wilson Inlet (F est) and marine coastal waters of south-western Australia (F sea). Length-at-age data of *A. georgiana* in marine waters used with the kind permission of D. Fairclough. The model with the lowest level of complexity that adequately describes the data is highlighted in bold. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

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<th>Hypothesis</th>
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<th>$t_\infty$ (F est)</th>
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Appendix 2  Likelihood ratio statistics comparing von Bertalanffy growth models for females of *Arripis georgiana* caught in Wilson Inlet (M est) and marine coastal waters of south-western Australia (M sea). Length-at-age data of *A. georgiana* in marine waters used with the kind permission of D. Fairclough. The model with the lowest level of complexity that adequately describes the data is highlighted in bold. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

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<th>$K$</th>
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