

**Fisheries biology and management of pink
snapper, *Pagrus auratus*, in the inner gulfs of
Shark Bay, Western Australia**

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Thesis presented for the degree of Doctor of Philosophy at Murdoch
University, Western Australia

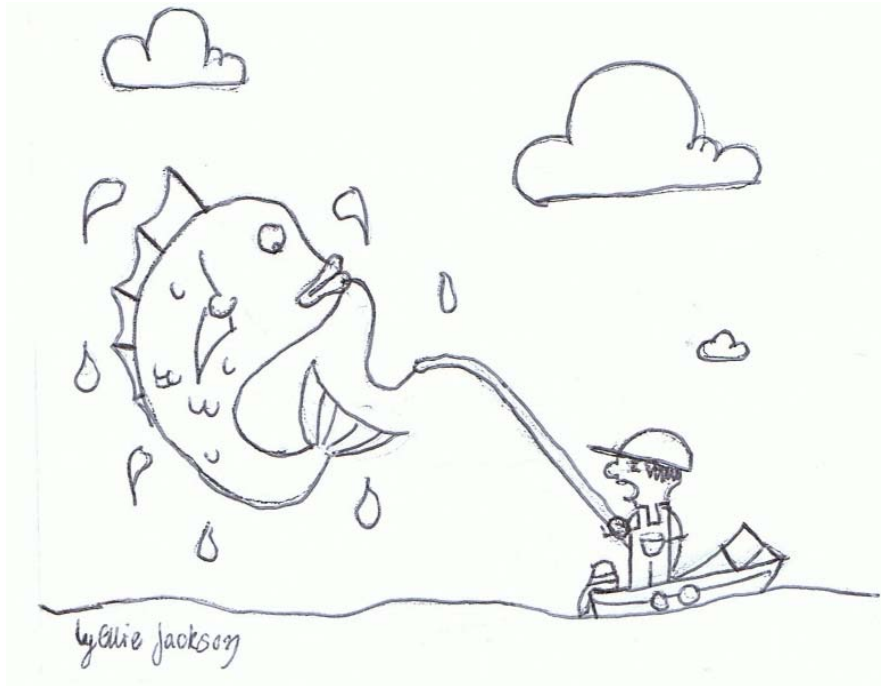
December 2007

Declaration

I declare that the information contained in this thesis is the result of my own research, unless stated otherwise, and contains as its main content, research that has not previously been submitted for a degree at any other tertiary institution.

Gary Jackson

December 2007



‘Snapper fishing in Shark Bay’ by Ellie Jackson, 12 years

Abstract

This study explored an important aspect of the basis for the highly complex population structure of pink snapper (*Pagrus auratus*) within the inner gulfs of Shark Bay, investigated how growth and reproduction differ among these closely-adjacent but separate stocks, and obtained biomass estimates for each stock that are essential for the sustainable management of the regionally-important recreational pink snapper fishery. Using ichthyoplankton data in combination with hydrodynamic modelling, *P. auratus* eggs and larvae were shown to be retained within localized meso-scale eddies that were coincident with the main inner gulf spawning areas. Such hydrodynamic retention, in conjunction with tagging and otolith chemistry data that indicates very limited movement of juvenile and adult fish, explains how separate pink snapper populations can exist in the adjacent waters of the Eastern Gulf, Denham Sound and Freycinet Estuary. The study found significant variation in maximum age, growth, maturity and spawning time at fine spatial scales. Such variation, unusual for a large, potentially mobile fish inhabiting a marine environment with no obvious physical barriers, is linked to the inner gulfs' marked environmental heterogeneity, the low levels of mixing and historic differences in fishing pressure among the three areas. The daily egg production method (DEPM) was used, for the first time with this species in Western Australia, to provide estimates of spawning biomass of the three separate inner gulf *P. auratus* stocks. While relatively imprecise, mostly due to imprecision in estimation of daily egg production, these estimates demonstrated that these stocks are very small (measured in tens of tonnes) compared with *P. auratus* stocks elsewhere in Australia and New Zealand. Biological data and DEPM estimates obtained from this study were incorporated in age-based stock assessment models that have been used to determine the status of inner gulf pink snapper stocks since 2002.

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Having finally finished this thesis, I am starting to look forward to new challenges, and hope that I can continue to repay the faith that some people have had in me over this part of the journey.

Overview of thesis

Pink snapper, *Pagrus auratus*, have been the basis of an important recreational fishery in the inner gulfs of Shark Bay since the 1970s at least. Robust information on the biology and population dynamics of *P. auratus* inside Shark Bay was lacking in 1996-1997 when such information was urgently required by fisheries managers to support proposed drastic management action to protect spawning stocks in the Eastern Gulf. This situation prompted comprehensive research on *P. auratus* in all the main fishing areas in the inner gulfs of Shark Bay that commenced in 1998, much of which forms the basis of this study. The principal objectives were to (i) investigate *P. auratus* stock structure further and, specifically, to test the hypothesis that hydrodynamic conditions in the inner gulfs restrict dispersal of *P. auratus* eggs and larvae among the main spawning areas, (ii) test the hypothesis that key biological characteristics might vary at fine spatial scales given the complexity of *P. auratus* population structure in the region, the Bay's strong environmental gradients and historic differences in fishing pressure, and (iii) provide estimates of *P. auratus* stock biomass and investigate how the respective fishable stocks had responded to exploitation and management through the use, for the first time for this species in Western Australia, of the daily egg production method (DEPM) as a stock assessment tool.

Ichthyoplankton data collected between 1997-2000 and hydrodynamic modelling were used in combination to investigate the dispersal of *P. auratus* eggs and larvae from the main inner gulf spawning areas. Hydrodynamic conditions during the austral winter saw the pelagic eggs and larvae retained within localized meso-scale eddies that were coincident with these locations. Results indicated no spatial

connectivity between the main *P. auratus* spawning areas with the exception of the ! spawning grounds in northern Denham Sound and oceanic waters in the Naturaliste Channel. Hydrodynamic retention therefore provides a mechanism that, in conjunction with tagging data that indicates very limited movement of juvenile and adult fish, explains how separate *P. auratus* populations can exist in such close proximity in the inner gulfs.

Samples of *P. auratus* obtained from the Eastern Gulf, Denham Sound and Freycinet Estuary via fishery-dependent and independent methods were used to investigate spatial variation in life history characteristics. Spawning occurred from late autumn through to mid-spring; fish in the Eastern Gulf and Denham Sound mostly spawned in May-July compared with August-October in the Freycinet Estuary. The longer spawning season in the Freycinet Estuary (~5-6 months) likely represents a risk-spreading strategy presumably to ensure survival of eggs and larvae in the more extreme (salinity ~40-50+) and variable conditions (annual water temperature range ~12-13 °C). Females reach 50% maturity at the smallest size (348 mm FL) and youngest age (3.2 years) in the Eastern Gulf compared with Denham Sound (401 mm FL, 5.5 years) and Freycinet Estuary (420 mm FL, 4.5 years). Batch fecundity is higher for larger females; a fish of 500 mm FL produces ~100,000 eggs per spawning event compared to ~350,000 by a fish of 700 mm FL. *P. auratus* from inner Shark Bay form a single opaque zone in their sagittal otoliths each year with most fish completing their opaque zones in August-November. Opaque zone counts, in combination with month of capture, birth date and increment growth at the otolith edge, can be used to age *P. auratus* from inner Shark Bay. Maximum age observed was 31 years in the Freycinet Estuary, 19 years in Denham Sound and 17 years in the Eastern Gulf. Three-parameter

von Bertalanffy growth models fitted the length-at-age data reasonably well. Growth coefficients were higher in the Eastern Gulf (K , 0.18 and 0.17 year⁻¹, females and males, respectively) and Freycinet Estuary (0.17 year⁻¹ both sexes) compared with Denham Sound (0.14 and 0.18 year⁻¹, respectively). Older fish (*i.e.* 15 years or more) were more prevalent in samples from the Freycinet Estuary where fish of up to 25 years of age were consistently observed in recreational catches up to 2004. Using length-at-age data collected during a 5-year fishing moratorium, natural mortality, M , was directly estimated at 0.22 (95% C.I. 0.09-0.34) year⁻¹ in the Eastern Gulf, significantly higher than the base case value of 0.075 year⁻¹ that is used in *P. auratus* stock assessments in New Zealand.

DEPM ichthyoplankton surveys and sampling of spawning fish were undertaken concurrently during the peak spawning period in each area between 1998-2004. Spawning occurs mostly between mid-afternoon and mid-evening. Large aggregations of spawning fish were observed in the Eastern Gulf and Denham Sound but not in Freycinet Estuary, where fish appear to typically spawn in much smaller groups. There was a strong relationship between lunar cycle and spawning with spawning activity greatest around the new moon and, to a lesser extent, around full moon. The spawning biomasses of *P. auratus* stocks in the inner gulfs are very small (measured in tens of tonnes). The DEPM is a viable assessment tool for *P. auratus* in inner Shark Bay. A more intensive sampling regime within a stratified-systematic design is recommended for future DEPM ichthyoplankton surveys.

Based on information provided by this study (egg and larval dispersal, variation in life history characteristics) and associated stock identification research (tagging,

otolith stable isotopes), in conjunction with existing information (genetics, tagging, !
otolith chemistry), separation between spawning populations in Denham Sound and the
Freycinet Estuary was acknowledged with recognition of three discrete inner gulf *P.*
auratus stocks, *i.e.* Eastern Gulf, Denham Sound and Freycinet Estuary, in 2000.
Biological data for each stock from this study were incorporated into age-based stock
assessment models for the first time in 2002; results of these assessments were used, in
consultations with stakeholders, to consider a range of management options for the
inner gulf snapper fishery for 2003 and onwards. Future research should include:
monitoring of recreational *P. auratus* catches and overall fishing effort; further
investigation into how the respective populations respond following high levels of
exploitation; determination of the extent to which annual recruitment strength varies
between the three areas; and refinement of the genetic relationship between local *P.*
auratus using a DNA-based approach.

Chapter 1: General introduction

1.1 The species

The Sparidae (seabreams or porgies) are a moderately diverse group (approximately 110 species from 33 genera) of predominantly coastal fishes distributed throughout all tropical and temperate seas where they typically support regionally-important nearshore fisheries (Nelson 1984; Carpenter and Johnson 2002; Orrell and Carpenter 2004). Sparid diversity is greatest in southern Africa (Smith and Heemstra 1986) while less so within Australia where the family is represented by only ten species that are found across tropical and temperate regions in estuarine and nearshore marine waters (Hutchins and Swainston 1986; Allen 1997). One of these sparids, *Pagrus auratus* (Bloch and Schneider 1801) (Fig. 1.1), is the focus of this thesis. This species is widely distributed throughout warm temperate and subtropical waters of the western Indo-Pacific, in the northern hemisphere, around Japan, China, Taiwan, the Philippines, Indonesia and off India, and in the southern hemisphere, around Australia and New Zealand (Paulin 1990; Kailola *et al.* 1993). The species is known as snapper in Australia and New Zealand, and locally in Western Australia as pink snapper (FAO name, golden snapper). Throughout its geographic range, the species supports important commercial and recreational fisheries and is the focus of considerable interest to the aquaculture sector (Kailola *et al.* 1993; Fujita *et al.* 1996). Around Australia, *P. auratus* are found in marine embayments and continental shelf waters to depths of ~ 200 m, from approximately Hinchinbrook Island in Queensland (~18° S, 146° E) to Barrow Island in Western Australia (~21 ° S, 115 ° E) (Kailola *et al.* 1993) (Fig. 1.2). Individuals in Australian waters can attain 1.3 m in length and more than 20 kg in weight (Gomon *et al.* 1994).



Figure 1.1 A young-of-the-year (upper, approx. 100 mm FL) and adult (lower, approx. 600 mm FL) *P. auratus* from the inner gulfs of Shark Bay, Western Australia.

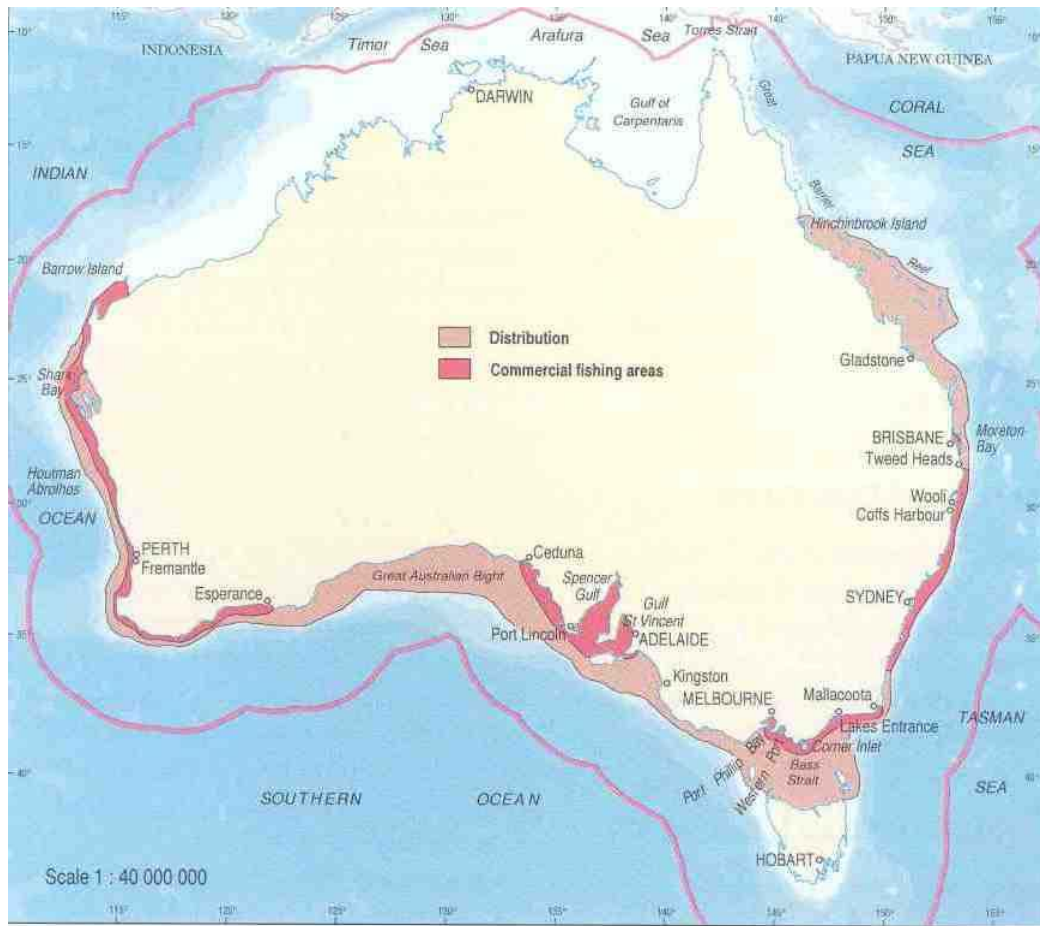


Figure 1.2 Map showing the Australian distribution of *Pagrus auratus* (from Kailola *et al.* 1993)

1.2 Taxonomy

The phylogeny of sparids, and the taxonomy of snapper in particular, has attracted considerable attention. In Australasia, snapper had previously been assigned to the genus *Chrysophrys*, formerly as *Chrysophrys unicolor* and more latterly as *C. auratus* (Paulin 1990). Paulin (1990) determined *Pagrus* to be the senior synonym of *Chrysophrys*, and re-described *C. auratus* as *Pagrus auratus*. In addition, he concluded that the species known as red sea bream in Japan, *i.e.* *Pagrus major*, was a conspecific and should also be re-described as *P. auratus*. Researchers in Japan, however, have not adopted this taxonomy. Tabata and Taniguchi (2000) suggested that the relationship

between *P. auratus* and *P. major* is at the subspecies level, and consequently that ! northern hemisphere populations should be re-described as *P. auratus major* and those in the southern hemisphere as *P. auratus auratus*. In this thesis, snapper are referred to as *P. auratus*¹ following the findings of Paulin (1990) that treats the taxon as a widely distributed western Indo-Pacific species with a number of reproductively-isolated populations throughout a discontinuous range in both northern and southern hemispheres. The common names of snapper and pink snapper are used interchangeably throughout this document.

1.3 The fishery – Australia, Western Australia and Shark Bay

In Australia, *P. auratus* are an important target species for commercial and recreational fishing throughout their range (Kailola *et al.* 1993). Snapper have been held in high regard for their firm white flesh and sport-fishing qualities since European settlement (Ferrell and Sumpton 1998; Coutin *et al.* 2003). The pattern of exploitation has been similar in most Australian mainland states, with an initial period of relatively low commercial fishing effort exploiting seasonally-plentiful snapper stocks followed by steadily increasing fishing activity in the earlier decades of the 1900s (Moran and Jenke 1989; Ferrell and Sumpton 1998; Coutin *et al.* 2003). By the 1960-1970s, participation rates in recreational fishing had markedly increased, concerns about the status of snapper stocks were being raised in most mainland states, and conflicts between the recreational and commercial sectors were increasing. In recent times, concern about the status of *P. auratus* stocks has seen an increase in research to address key management questions to enable snapper resources to be managed in a more

¹ There is a continuing scientific debate, based on genetic evidence presented by Orrell and Carpenter (2004), as to whether *Pagrus* should be abandoned, and *P. auratus* revert to *Chrysophrys auratus* (Gomon *et al.* 2008). However, at the time this thesis was originally written, most researchers in both Australia and New Zealand continued to follow Paulin (1990) and use *P. auratus*.

sustainable and equitable manner. State-managed commercial and recreational fisheries ! in Queensland, New South Wales (Ferrell and Sumpton 1998), Victoria (Coutin *et al.* 2003), South Australia (Fowler *et al.* 2005) and Western Australia (Jackson *et al.* 2005; Moran *et al.* 2005) today contribute to a national *P. auratus* catch of ~3,000 tonnes year⁻¹ (total national recreational catch estimated at ~1,400 tonnes in 2000, Henry and Lyle 2003; total national commercial catch in 2004 reported ~1,600 tonnes, ABARE 2005).

In Western Australia, most of the state's pink snapper catch is taken from waters off the west coast (Fletcher and Head 2006). Until 2004, around 75% of the state's commercial pink snapper catch had historically come from the oceanic *P. auratus* stock (see 1.5 Stock structure of *P. auratus* in the Shark Bay region) in continental shelf waters adjacent to Shark Bay (Moran *et al.* 2005) (Fig. 1.3). Commercial snapper fishing has a long history in the region, dating back to the early 1900s when vessels from Geraldton and Fremantle first sailed northwards to fish oceanic pink snapper spawning aggregations during winter (Cooper 1997, Edwards 2000). Commercial effort in the fishery steadily increased from the 1950s, escalating in the mid 1980s with the catch peaking at around 1,300 tonnes in 1985 (Moran *et al.* 2005). The commercial pink snapper fishery targeting the oceanic *P. auratus* stock in waters outside Shark Bay came under formal management for the first time in 1987 (limited entry, quota-based). Catches remained fairly stable at about 500 tonnes year⁻¹ through the 1990s. More recent research for this fishery identified overfishing of the oceanic spawning stock, in combination with a prolonged period of poor recruitment throughout the 1990s, and resulted in recognition of the need for a significant reduction in commercial quota in 2004 (Jackson 2006).

Pink snapper are also an important target for recreational boat-based fishers in the inner gulfs of Shark Bay (Shaw 2000; Jackson *et al.* 2005). Shark Bay is a popular tourist destination with an estimated 100,000 visitors per year (Francesconi and Clayton 1996). Many of these are recreational fishers, attracted to the sheltered waters of inner Shark Bay by the diversity and high quality of the fishing and the mild sea conditions during late autumn-winter (April-August), which is the most popular visitor period (Francesconi and Clayton 1996). Although recreational fishers catch a variety of species, the main attraction has historically been *P. auratus*, which, until recently, made up more than half the total recreational boat catch by weight in the inner gulfs (Sumner and Malseed 2002).

Commercial fishing for pink snapper in the inner gulfs of Shark Bay dates back to the 1920s at least (Fry 1995), following the demise of the local pearl industry (Edwards 2000). Commercial effort targeted at the species in these waters increased up to the 1950s then steadily declined from the 1960s and 1970s (from the observations of local retired commercial fishers, G. Jackson unpublished data), and progressively shifted to the oceanic waters outside Shark Bay (Moran *et al.* 2005). In contrast, recreational fishing effort in the inner gulfs is thought to have steadily increased from the late 1970s through to the 1990s (Jackson *et al.* 2003). In addition, over the same period, recreational fishing has become more efficient due to improvements in fishing technology (e.g. GPS, colour sounders) and communication between fishers. Most recreational snapper fishing in the inner gulfs was and remains focused on spawning aggregations during winter (May-August), a feature of *P. auratus* reproductive behaviour that makes the species particularly vulnerable to over-exploitation.

By the mid-1990s, some members of the local Shark Bay community had become concerned that recreational snapper catches in the inner gulfs, especially in the Eastern Gulf, had reached unsustainable levels (Prokop 1998; Marshall and Moore 2000). Proposals to introduce more stringent management measures, *e.g.* reduced daily bag limits during the spawning season, were unpopular and not supported politically, as visiting recreational fishers made a significant contribution to the Shark Bay economy. High recreational catches continued through 1994-1996 and heightened concerns that the Eastern Gulf spawning stock was likely to become depleted. In May 1997, the Eastern Gulf snapper fishery was closed. In response to public objections (Marshall and Moore 2000), however, this moratorium was overturned after only two months with the principal objection being the paucity of quantitative information available. It became apparent that estimates of stock size and recreational catches were needed to gain community support for management measures to protect local snapper stocks. The work presented in this thesis represents much of the research undertaken since 1997, which has provided the scientific basis for management of inner gulfs pink snapper stocks from 1998 onwards.

1.4 Shark Bay – its marine environment and World Heritage status

Shark Bay, on the mid-west coast of Western Australia (approximately 24° 30' to 26° 30' S and 113° to 114° E) was formed following marine inundation of mainly Pleistocene coastal dunes approximately 7,000-8,000 years ago (Logan and Cebulski 1970; Hagan and Logan 1974). The flooding created a large, generally shallow (average depth 9 m, maximum depth 29 m), semi-enclosed marine embayment covering approximately 14,000 km². This embayment is comprised of open, deeper waters to the north and two shallower gulfs, known locally as the Western (waters of Denham Sound

and Freycinet Estuary combined) and Eastern Gulf (collectively referred to as the inner gulfs), separated by the Peron Peninsula, to the south (Fig. 1.3). To the west, a chain of three large islands (Bernier Island, Dorre Island and Dirk Hartog Island) acts as a barrier that restricts tidal exchange with oceanic waters and limits water circulation inside Shark Bay (Burling *et al.* 2003).

The region's climate is arid (average rainfall 200-220 mm year⁻¹) with minimal terrestrial runoff (Logan and Cebulski 1970). The limited tidal exchange combined with persistent winds and the resultant high evaporation rates (average 2000–2200 mm year⁻¹) has led to a key feature of inner Shark Bay, *i.e.* its elevated salinities and strong environmental gradients (Fig. 1.4) (Logan and Cebulski 1970; Burling *et al.* 2003; Nahas *et al.* 2005). Salinities in the inner gulfs consistently exceed the oceanic level (35²) with metahaline conditions maintained in the Eastern Gulf and southern Denham Sound (38-48) and Freycinet Estuary (45-48), and hypersaline conditions (50-65+) in Hamelin Pool (Logan and Cebulski 1970) (Fig. 1.5).

The combined effects of the physical and biological processes operating in Shark Bay have shaped its unique marine environment (Wyatt *et al.* 2005). Extensive sea grass beds covering ~4,000 km² (Walker 1990) combined with low tidal exchange and increased sedimentation have led to a series of banks and sills thereby further limiting water circulation and, in conjunction with the high evaporation levels, producing the meta- and hypersaline environments and associated diverse biological phenomena (Logan and Cebulski 1970; Walker 1990). Shark Bay's unique natural heritage, in particular the high conservation value of its marine environment, was

² Practical Salinity Scale is used here, where salinity is defined as a pure ratio, and is therefore dimensionless.

recognised in 1991 when the region was inscribed on the World Heritage List and the Shark Bay World Heritage Property was created (Francesconi and Clayton 1996). The region is one of the few natural heritage areas to meet all four UNESCO (1972) criteria in relation to outstanding natural values. Key features of the Shark Bay marine environment that have been assessed as of World Heritage value include (i) three distinct biological zones caused by the salinity gradients, (ii) a number of highly restricted marine communities adapted to the hypersaline conditions, (iii) significant genetic variability in some marine taxa (*e.g.* *P. auratus*, see below), high species diversity and density of bivalves, and (iv) an abundance of marine fauna and seagrass-based ecosystems (Environment Australia 1999).

The Shark Bay region is an ecological transition zone between the northern limits of temperate marine fauna and the southern limit of the tropical Indo-West Pacific Biotic Province, and as a consequence has high species diversity (Wyatt *et al.* 2005). The inner gulf waters contain a higher proportion of temperate fish species while the more exposed oceanic waters are dominated by tropical taxa (Black *et al.* 1990; Hutchins 1990, 1994). A commercial seine net fishery for whiting, mullet, tailor and yellowfin bream (*Sillago* spp., *Mugil cephalus*, *Pomatomus saltatrix*, *Acanthopagrus latus*) operates throughout the inner gulfs (Shaw 2000) while limited commercial trawling for prawns (*Penaeus latisulcatus*, *P. esculentus*, *Metapenaeus* spp.) and scallops (*Amusium balloti*) is permitted within only a portion of the waters of Denham Sound.

1.5 Stock structure of *P. auratus* in Shark Bay region

Marine fish rarely exhibit complete panmixia, *i.e.* random inter-breeding of individuals, throughout their entire geographic range (Pawson and Jennings 1996). Spawning is more usually confined to groups of fish that maintain some level of spatial and temporal integrity so as to be considered self-sustaining units. This is the basis of the ‘stock’ concept in fisheries (Waldman 2005). Understanding stock structure, *i.e.* the relationship between coherent units of individual conspecifics that have some level of discreteness in time and space, is fundamental to fisheries management and a prerequisite of any stock assessment (Begg *et al.* 1999; Cadrin *et al.* 2005). The fishery concept of a stock involves more than a simple recognition of genetic or phenotypic differences between fish. Determining stock structure in marine fishes is a complex task with no single method capable of determining stock relationships (Waples 1998). The use of multiple techniques to examine a range of traits *e.g.* genetic, morphological, meristic, and phenotypic, referred to as the ‘holistic’ or ‘comparative’ approach (Begg and Waldman 1999, Waldman 2005), is now recommended for stock identification. Failure to recognise the existence of local sub-populations that are adapted to local environments, and the inappropriate harvest levels that may result, can lead to changes in biological attributes, reduced productivity and loss of genetic diversity (Larkin 1977; Smith *et al.* 1991; Walters and Martell 2005).

Shark Bay is near the northern limit of the geographic range of *P. auratus* on the west coast of Australia. Potential differences in the biological characteristics of snapper from different locations within the Shark Bay region initially became apparent in the results of a health-related study of mercury levels in fish flesh (Department of Primary Industry 1979). MacDonald (1980), using allozyme electrophoresis and *P. auratus*

samples collected from eight locations between Moreton Bay (Qld) and Shark Bay ! (WA), found no significant genetic differentiation across approximately 4,500 km of the species' Australian distribution with the only exception being the samples collected from Shark Bay, which were thought to represent a distinct population. Since this research, numerous stock identification studies using both genetic and alternative techniques undertaken over more than 20 years indicate that the population structure of *P. auratus* in the Shark Bay region is unusually complex.

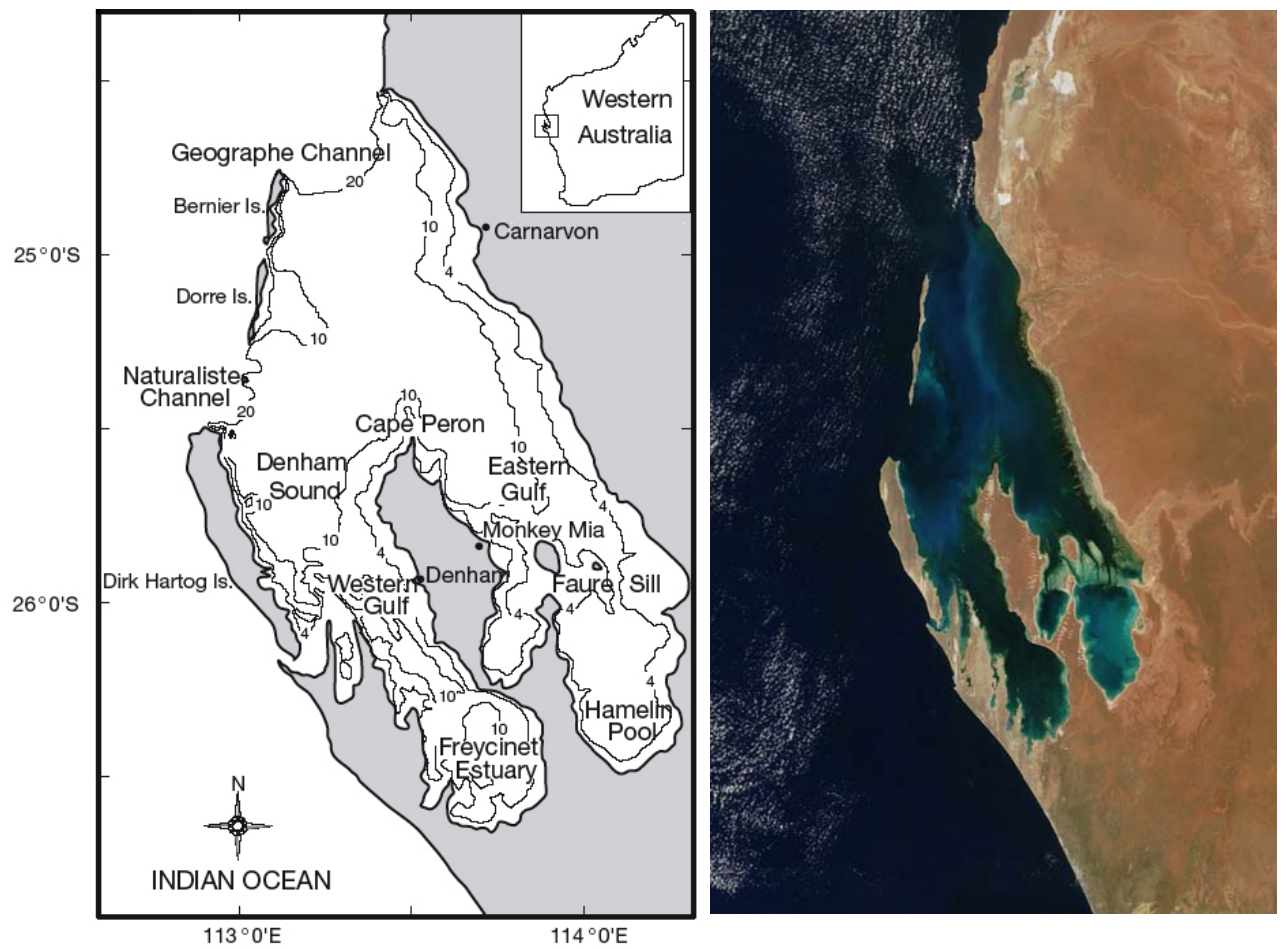


Figure 1.3 Map of Shark Bay showing bathymetry (depths in m) and names of localities referred to in text (left) and satellite image of region (right, image courtesy of Western Australian Department of Environment and Conservation).

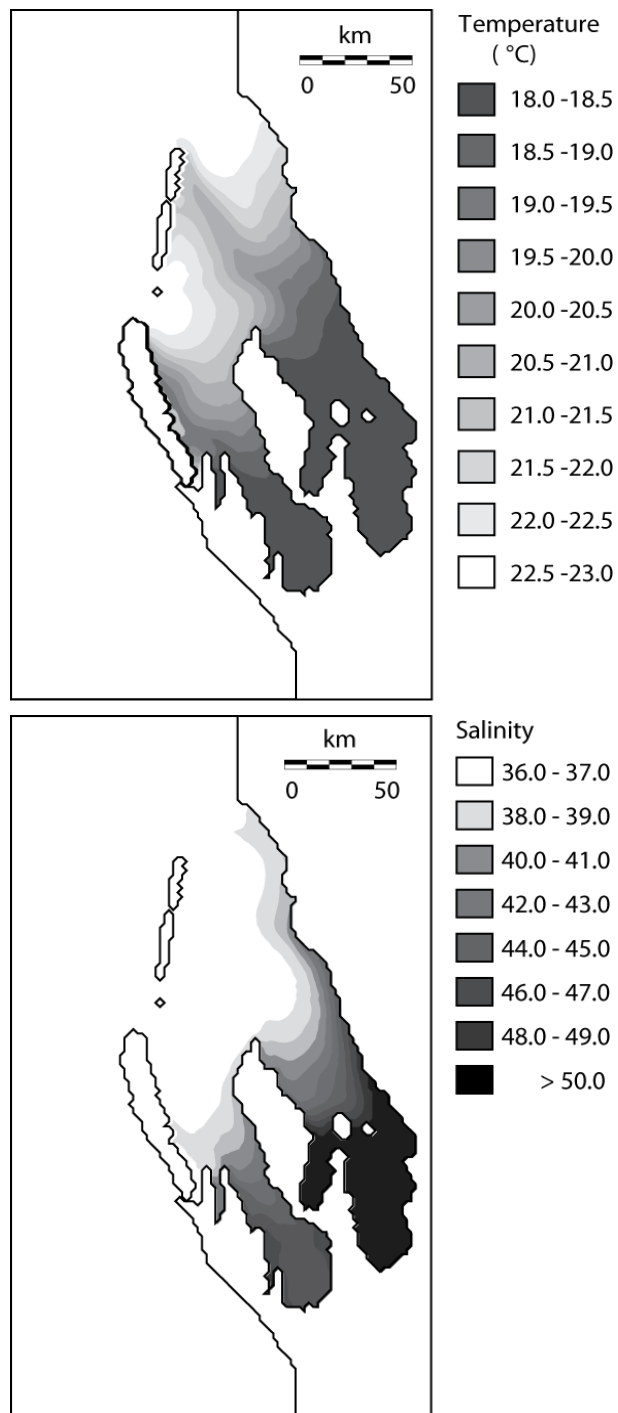


Figure 1.4 Typical temperature (upper) and salinity (lower) distributions for surface waters in inner Shark Bay during winter (from Nahas *et al.* 2005, reproduced by permission from C. Pattiaratchi).

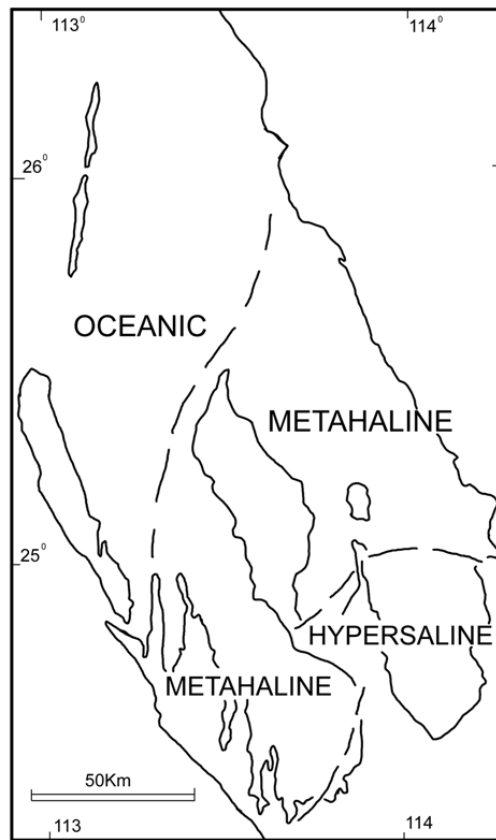


Figure 1.5 Schematic representation showing the separate salinity regimes of Shark Bay (after Logan and Cebulski 1970).

Following MacDonald (1980), several other independent allozyme-based genetic studies have been conducted and have yielded essentially consistent results and confirmed significant *P. auratus* population subdivision in the Shark Bay region. Johnson *et al.* (1986) found genetic differences between snapper from oceanic waters outside Shark Bay, the Eastern Gulf (around Faure Island) and the Freycinet Estuary, and concluded that fish in each area represented a separate breeding population. More than a decade later, Whitaker and Johnson (1998) again looked at *P. auratus* in the Western Gulf and, as with Johnson *et al.* (1986), found fish in the Freycinet Estuary to be genetically distinct from those in oceanic waters. Although the results were more ambivalent, Whitaker and Johnson (1998) suggested that partial isolation existed between fish from these areas and *P. auratus* from Denham Sound (and Useless Inlet).

In a study that complemented Whitaker and Johnson (1998), Baudains (1999) found no ! further stock subdivision in the Eastern Gulf beyond that previously shown by Johnson *et al.* (1986). However, while snapper are known to live and spawn within Hamelin Pool (commercially fished until 1995, licensed fisherman caught spawning fish in months July-September, R. Yukich pers. comm.), no samples of fish from this region have ever been included in any of the genetic studies above. It is possible that these fish may represent a further sub-population (now completely protected from all fishing as Hamelin Pool is a Class A Marine Reserve).

Physical barriers may impose limits on genetic exchange even with highly mobile fish species (Aulsebrook 1994; Palumbi 1994). Johnson *et al.* (1986) had originally proposed that the extreme range of salinities and limited water movement within the inner gulfs of Shark Bay might impede movement of adults and dispersal of the pelagic eggs and larvae and thereby restrict genetic exchange within Shark Bay. To address the questions of levels of mixing within the Bay, the genetic studies described above have been complemented by two major tagging studies and several otolith chemistry studies (see below).

A comprehensive tagging study was undertaken between 1982-1984 (Moran *et al.* 2003) to complement the Johnson *et al.* (1986) genetic study and investigate pink snapper movement in the Shark Bay region, both between the inner Bay and oceanic waters and within each inner gulf. More than 16,000 fish were tagged at locations in the inner gulfs (size range 220–500 mm fork length FL) and oceanic waters (size range 350–630 mm FL). Overall, results indicated no mixing of pink snapper between the ocean and the inner gulfs nor between each inner gulf, thereby strongly supporting the

conclusions of Johnson *et al.* (1986) and the notion that genetically different *P. auratus* 'stocks could exist in close geographic proximity. More recently, further tagging was conducted between 1998-2002 to investigate *P. auratus* movement in the inner gulfs at a finer spatial scale (G. Jackson unpublished data). More than 2,000 snapper (size range 176-770 mm FL) were tagged and released at locations in Eastern Gulf, Denham Sound and Freycinet Estuary. No tagged fish were recaptured outside the inner gulfs, and no movement was observed between each inner gulf or, importantly, between Denham Sound and the Freycinet Estuary. Results were consistent with those from the tagging study of Moran *et al.* (2003) and indicate very limited movement of sub-adult and adult snapper in the inner gulfs.

Edmonds *et al.* (1989) used analysis (inductively coupled plasma atomic emission spectrometry, ICP-AES) of nine trace elements in *P. auratus* sagittal otoliths to investigate the technique's potential to distinguish between the trace element composition of otoliths of fish collected from various locations along the west coast of Western Australia. Shark Bay samples from two oceanic locations (Koks Island, Cape Inscription) and a single inner gulf location (Freycinet Estuary) were included in the study. Results showed the greatest separation for snapper from the Freycinet Estuary, followed by Koks Island and Cape Inscription. These findings were interpreted as consistent with results of the Moran *et al.* (2003) tagging study, indicating minimal levels of mixing between adjacent locations in the Shark Bay region. Edmonds *et al.* (1999), utilizing knowledge gained from previous stock identification studies, used trace element analysis (ICP-AES) and evaluated the use of stable isotope analysis (isotope ratio-mass spectrometry, IR-MS) of teleost otolith carbonate as a stock discrimination technique and compared data for a more mobile species, tailor

(*Pomatomus saltatrix*) with data for the less mobile *P. auratus*. Samples of both species ! were collected from a range of locations between the south coast of Western Australia (Wilson's Inlet) to Shark Bay and further north (NW Shelf). Because the elevated salinities inside Shark Bay were expected to influence otolith isotopic composition, the *P. auratus* analysed included samples from several inner gulf (Hamelin Pool, Freycinet Estuary) and oceanic locations (Koks Island, Cape Inscription). Results indicated that *P. auratus* were highly location-specific, particularly in the inner gulfs of Shark Bay where, as expected, the higher salinities generated strong isotopic characteristics. Carbonate isotopes suggested that *P. auratus* from oceanic waters had not spent any time in areas of elevated salinity, *i.e.* inner gulfs, nor vice versa, while the oxygen isotopes were related to local water temperatures.

More recently, Bastow *et al.* (2002) examined the isotopic composition of otolith carbonate (using IR-MS) in *P. auratus* collected from inner gulf waters, over a broad range of salinities to investigate isotopic differences at a finer spatial scale and to provide further information on levels of mixing to complement the 1998-2002 tagging study). Results indicated that fish had remained resident in the respective locations sampled with the greater part of the otolith carbonate deposited in a spatially distinct environment with its own characteristic water chemistry. In addition, similarity in the oxygen isotopic signatures of otolith carbonate from juvenile and adult snapper from the Freycinet Estuary indicated a lifetime spent in the same environment. Gaughan *et al.* (2003) compared trace element composition (using laser ablation - inductively coupled mass spectrometry) and isotopic composition (using IR-MS) of otoliths of juvenile *P. auratus* (71-127 mm FL) from Denham Sound and Freycinet Estuary, and related the findings to the chemical composition of otolith cores of larger fish collected from the same areas (range 301-705 mm FL). They concluded that juveniles recruit to separate

nursery areas and then undertake only very limited movement and that the adults retain ! a high degree of site fidelity.

The results of the otolith chemistry studies are therefore consistent with the considerable body of evidence relating to the highly complex nature of snapper stock structure in the inner gulfs of Shark Bay that indicates minimal or nil post-settlement mixing of *P. auratus* at very fine spatial scales (tens of kilometres). However, a question still remains in relation to the level of exchange of eggs and larvae between separate regions within the inner gulfs, and with adjacent oceanic waters.

1.6 Previous research on *P. auratus*

Compared with many exploited species, considerable research has been undertaken on *Pagrus auratus* and its conspecific *P. major*. There is an extensive literature dealing with the reproductive biology of *P. auratus* in New Zealand (Cassie 1956; Crossland 1977 a, b; Francis and Pankhurst 1988; Scott and Pankhurst 1992; Scott *et al.* 1993) and of *P. major* in Japan (Matsuyama *et al.* 1987 a, b, 1988 a, b). However, until recently, relatively little had been published on the reproductive biology of the species in Australian waters (Ferrell and Sumpton 1998; Sumpton 2002; McGlennon 2003; Coutin *et al.* 2003).

Age and growth of *P. auratus* have been extensively studied in New Zealand (Paul 1992; Francis R.I.C.C. *et al.* 1992; Francis M.P. *et al.* 1992, 1993; Francis M.P. 1994; Walsh 1997; Millar *et al.* 1999; Davies *et al.* 2003) and Australia (Saunders and Powell 1979; Jones 1984; Thomas 1985; Francis and Winstanley 1989; Bell *et al.* 1991; Ferrell *et al.* 1992; Ferrell and Sumpton 1998; McGlennon *et al.* 2000; Sumpton 2002;

Ferrell 2004; Fowler *et al.* 2004; Moran *et al.* 2005). While annual growth increments ! on scales were used to age individuals of the species in earlier studies (MacDonald 1982; Jones 1984; Thomas 1985; Paul 1992), they have been shown to underestimate age in older snapper (Paul 1976; McGlennon *et al.* 2000). The interpretation of alternating opaque and translucent zones in sectioned sagittal otoliths is now routinely used for ageing *P. auratus* both in New Zealand and Australia (Francis R.I.C.C. *et al.* 1992; Ferrell and Morison 1994; McGlennon *et al.* 2000; Coutin 2003; Fowler *et al.* 2004; Moran *et al.* 2005). Annulus formation has been validated as annual for 0+ and 1+ fish in eastern Australia (Ferrell *et al.* 1992) and for fish up to 30 years in New Zealand (Francis R.I.C.C. *et al.* 1992).

Other areas of previous *P. auratus* research in Australia include juvenile growth, mortality and recruitment variation (Lenanton 1974; Francis 1993; Francis M.P. *et al.* 1995; Fowler and Jennings 2003; Hamer and Jenkins 2004; Sumpton and Jackson 2005), and use of tagging and otolith chemistry to investigate stock structure (Saunders 1974; Gillanders 2002; Sumpton *et al.* 2003; Hamer *et al.* 2005; Fowler *et al.* 2005).

Prior to this study, there have been no published studies of the biology of *P. auratus* in the inner gulfs of Shark Bay.

1.7 Objectives and thesis structure

In contrast to *P. auratus* in oceanic waters outside Shark Bay, which support an important commercial fishery and which have been extensively studied (Moran *et al.* 2005; Wakefield 2006), information on the biology and population dynamics of *P. auratus* inside Shark Bay, which nowadays support a mostly recreational fishery, was

lacking at the time of the snapper ‘crisis’ in the mid-1990s (Marshall and Moore 2000; Jackson *et al.* 2005). This thesis describes aspects of research on *P. auratus* in the inner gulfs of Shark Bay, which has provided the basis for the management of the regionally-important recreational fishery since 1998 (Jackson and Stephenson 2002; Stephenson and Jackson 2005; Jackson *et al.* 2005). The thesis is structured as follows.

Chapter 2 investigates the hypothesis that the potential for mixing between inner gulf *P. auratus* spawning populations is constrained by hydrodynamic dispersal of the eggs and larvae originating from proximate spawning areas. Previous genetic and alternative stock identification studies to investigate *P. auratus* stock structure within the Shark Bay region had been based only on the later life history stages, *i.e.* sub-adult and adult snapper. Johnson *et al.* (1986) suggested that gene flow between *P. auratus* within inner Shark Bay might be limited in part because hydrodynamic conditions could restrict widespread dispersal of the pelagic eggs and larvae. Hydrodynamic numerical modelling and field survey data were used in combination to test the hypothesis that *P. auratus* eggs and larvae were retained in close proximity to the main spawning grounds, and thereby to determine the degree of connectivity between adjacent *P. auratus* spawning populations.

Chapters 3 and 4 investigate the hypothesis that the key *P. auratus* biological characteristics, *e.g.* timing of spawning, size and age at maturity, longevity and growth, might vary at a spatial scale of tens of kilometres inside Shark Bay given the complexity of local *P. auratus* population structure, the region’s strong environmental gradients and historic differences in fishing pressure among these locations. If differences in the life-history characteristics of the different *P. auratus* stocks exist at this spatial scale, the

finding would have implications for other exploited fish species for which complex ! stock structures exist.

Chapter 5 investigates how the spawning biomass of *P. auratus* in the respective areas of the inner gulfs has responded to exploitation and management since 1998. In 1996/97, when anecdotal evidence suggested that, following several years of over-exploitation of spawning aggregations, the *P. auratus* spawning stock in the Eastern Gulf was depleted, quantitative information on stock size was not available. Zeldis (1993) had previously proposed that the daily egg production method (DEPM, Lasker 1985; Alheit 1993), used for batch spawning species with pelagic eggs, had potential for estimating spawning biomass of *P. auratus* in New Zealand based on particular biological characteristics. At the time of the snapper ‘crisis’, when urgent stock assessments were called for, the DEPM was considered to have potential for a relatively rapid assessment of the size of *P. auratus* stocks in the inner gulfs of Shark Bay.

Chapter 6 concludes the thesis with a general discussion of the research presented in the preceding chapters. Importantly, this chapter describes how information derived from the research has been used directly in management of the *P. auratus* fishery since 1998. Attempts to manage many Australian marine finfish fisheries with a large recreational component are often compromised by an absence of information on stock size and recreational catches. In contrast, based on outcomes of the research described in this thesis, it has been possible to establish the status of the *P. auratus* stocks in the inner gulfs of Shark Bay with some confidence. This chapter also includes a brief description of management approaches used with the *P. auratus* fishery in the inner gulfs, some of which may have application to similar fisheries elsewhere.

Chapter 2: The influence of hydrodynamic processes on *P. auratus* egg and larval dispersal in the inner gulfs of Shark Bay and potential implications for stock structure

This chapter represents a collaborative study that I undertook with a number of co-investigators from the Centre for Water Research, University of Western Australia, that has previously been published as:

Nahas, E.L., Jackson, G., Pattiaratchi, C.B., and Ivey, G.N. (2003). Hydrodynamic modelling of snapper (*Pagrus auratus*) egg and larval dispersal in Shark Bay, Western Australia: reproductive isolation at a fine spatial scale. *Marine Ecology Progress Series* 265, 213-226.

*The original concept for this study was developed by myself in conjunction with Dr M. Moran (previously of the Department of Fisheries, Western Australia). The research proposal was further refined in discussions that I subsequently had with Prof. Pattiaratchi (University of Western Australia). I was solely responsible for the underlying biological/ecological concepts and the associated research framework and field surveys in addition to analysis and interpretation of the results and their implications for the stock structure of *P. auratus* in the inner gulfs of Shark Bay. The oceanographic component including the numerical modelling was undertaken by Elizabeth Nahas as part of a MSc thesis under the supervision of Profs C. B. Pattiaratchi and G. N. Ivey. As a consequence, E. Nahas was assigned primary authorship to satisfy the requirements of the UWA MSc programme.*

*For the purposes of my thesis, I have excluded some portions of the published paper here for a number of reasons. They include information (e.g. descriptions of the physical environment of Shark Bay, background on *P. auratus* in Shark Bay, *P. auratus* biology, etc.) that has been reported elsewhere in the thesis and (ii) the more technical sections of the paper relating to the numerical modelling written by E. Nahas.*

2.1 Introduction

Across their geographic range, many marine species are divided into reproductively-isolated, self-recruiting populations. Understanding the population structure of exploited species and the spatial distribution of individual harvested stocks is fundamental to stock assessment and the implementation of effective fisheries management (Ryman and Utter 1987; Clark 1990; Begg *et al.* 1999). Critical here is the degree of connectedness between local populations, *i.e.* whether they are primarily sustained by recruitment from local production (and therefore relatively closed) or substantially from external sources (and therefore relatively open) (Warner and Cowen

2002). Because many marine fish species have bipartite life cycles, the spatial distribution of individual stocks is determined by the dispersal of eggs and larvae, and the vagility of post-settlement stages (Harden Jones 1968; Sinclair 1988; Bakun 1996; Bradbury and Snelgrove 2001). There is mounting evidence that some larvae use a range of behaviours in response to oceanographic conditions that can influence their dispersal (Bakun 1996; Jenkins *et al.* 1999; Kingsford *et al.* 2002; Sponaugle *et al.* 2002). However, it is likely that, for many species, dispersal of eggs and younger larvae is essentially passive (Okubo 1994; Bradbury and Snelgrove 2001). The spatio-temporal distribution of these earliest stages is therefore dependent upon local hydrodynamic processes at the time and place of spawning and initial development (Alvarez *et al.* 2001).

For marine fishes with pelagic formative stages, widespread hydrodynamic dispersal can result in genetic homogeneity over large geographic distances (Bagley *et al.* 1999; Dudgeon *et al.* 2000; Kloppmann *et al.* 2001). However, hydrodynamic retention of eggs and larvae, particularly in combination with spawning site fidelity, may provide barriers to gene flow that help explain stock subdivision within fish populations existing in apparently ‘open’ environments (Bailey *et al.* 1997; Ruzzante *et al.* 1999; Stepien *et al.* 2000; Pogson *et al.* 2001; Skogen *et al.* 2001; Gold and Turner 2002; Smedbol *et al.* 2002). Some knowledge of the hydrodynamics of the water body inhabited during the planktonic, pre-settlement stages can provide useful insights into population structure, the geographic distribution of individual stocks, and recruitment dynamics of marine species.

Because of the logistical difficulties in determining dispersal directly, numerical ! modelling has become an important tool for understanding how hydrodynamic processes influence the transport of marine ichthyoplankton (Bartsch and Coombs 1997; Jenkins *et al.* 1997, 1999, 2000; van der Veer *et al.* 1998; Cowen *et al.* 2000; Fowler *et al.* 2000). Selection of an adequate model requires prior knowledge of the local hydrodynamics and behavior of the species under study. Both two- and three-dimensional schemes have been successfully used to model the dispersal of passive particles in marine systems. If currents act uniformly throughout the water column, any vertical movement of planktonic organisms will not significantly influence their horizontal transport. Conversely, marked differences between surface currents and those at depth combined with vertical movement of larvae can affect their horizontal movement.

As noted previously (Chapter 1 – General introduction), salinities inside Shark Bay are consistently above oceanic levels (35) and, at the southern head of the inner gulfs, Hamelin Pool and the Freycinet Estuary, regularly exceed 60 (Logan and Cebulski 1970; Burling *et al.* 1999). Hamelin Pool exhibits higher salinities than the Freycinet Estuary due to the effect of Faure Sill, the general shallowness of its waters, and its geographic isolation from deeper waters to the north. Tidal mixing creates a state of equilibrium between the mixed and stratified regions of the Bay, the transitions between which constitute density fronts (Logan and Cebulski 1970; Smith and Atkinson 1983; Burling *et al.* 1999). The two primary fronts, a semi-circular intrusion around Naturaliste Channel, and a transition running southwest to northeast from Denham Sound to Carnarvon, effectively divide Shark Bay into its deeper, northern, and shallower, southern sections. Sea Surface Temperature (SST) satellite images indicate

that the system has remained stable for more than three decades. !

The physical and biological oceanography of waters offshore from Shark Bay is dominated by the Leeuwin Current, a major eastern boundary current, that flows southwards off the west coast of Australia (Lenanton *et al.* 1991). Recruitment to many commercially-important Western Australian fisheries is affected by inter-annual variations in current strength and water temperature (Lenanton *et al.* 1991; Caputi *et al.* 1996) resulting mainly from El Niño/Southern Oscillation (ENSO) fluctuations (Pearce and Phillips 1988, 1994). Shark Bay also experiences large seasonal variations in wind strength and direction. Strong southerlies (average 10 m s^{-1}) dominate during the austral summer (December-February) while weaker (average 3 m s^{-1}) and more variable winds (usually south-southeast) occur during the austral winter (June-August).

The genetic and phenotypic evidence for the existence of several reproductively-isolated populations of *P. auratus* in the inner gulfs of Shark Bay (see Chapter 1 – General introduction) has resulted from studies involving mainly sub-adults and adults, *i.e.* fish older than 2 or 3 years of age. The potential for any mixing between these populations, via the hydrodynamic dispersal of eggs and larvae originating from proximate (but possibly separate) spawning populations/natal areas, has not been studied previously. Hydrodynamic retention of the ichthyoplankton in the vicinity of the main spawning areas would provide a mechanism that would significantly limit mixing between adjacent populations prior to settlement.

P. auratus in inner Shark Bay aggregate to spawn between late autumn and mid-spring (see Chapter 3 – Reproduction). Spawning is generally localized and

appears to occur at the same key spawning sites each year (see Chapter 5 – Daily egg production method). Spawning mostly takes place in the afternoon to early evening ~ 3-5 m below the surface in waters of 10-14 m average depth. The eggs, which are positively buoyant immediately post-fertilization, have been shown elsewhere to become more neutrally buoyant during development (Kitajima *et al.* 1993). Hatching in Shark Bay occurs after ~20-30 hours (Norriss and Jackson 2002) and is followed by a pelagic larval phase of ~20-25 days prior to metamorphosis (Tapp 2003) and settlement, and commencement of the demersal juvenile phase.

The objective of this study was to test the hypothesis that eggs and larvae were retained in close proximity to the main *P. auratus* spawning grounds in inner Shark Bay. Using ichthyoplankton data collected between 1997 and 2000³, we identified a number of discrete egg and larval distributions that were taken to represent the main *P. auratus* spawning grounds. We then examined the observed distributions for any spatial overlap, over the planktonic development period (~20-30 days), to test the null hypothesis of no (geographic) connectivity between the main spawning populations/natal areas. Hydrodynamic conditions and the consequent dispersal of planktonic particles were simulated using numerical modelling to provide some explanation for the observed patterns in egg/larval distributions, and to determine the degree of connectivity between the spawning populations.

³ Further surveys have been conducted in these waters since 2000. See Chapter 5 – Daily egg production method.

2.2 Materials and Methods

2.2.1 Ichthyoplankton surveys

Ichthyoplankton surveys were undertaken in both inner gulfs during winter (June – August) each year between 1997-2000 with oblique tows of double bongo-nets (each net mouth 60 cm diameter, net mesh 500 μm) made at pre-determined locations in a grid-like pattern (see Chapter 5 – Daily egg production method). A General Oceanics flowmeter was fitted in the mouth of one net to allow the volume of water sampled at each tow location to be calculated. Ichthyoplankton samples were fixed at sea in 5% buffered formaldehyde.

These samples were subsequently sorted in the laboratory with *P. auratus* eggs identified, counted and classified into development stages based on their internal morphology (Norriss and Jackson 2002). Eggs were attributed a median age (hours) based on their development stage and environmental conditions (water temperature, salinity) at the time of sampling (Norriss and Jackson 2002). For ichthyoplankton samples collected in 2000 only, *P. auratus* larvae were identified and counted with reference to published descriptions (Cassie 1956; Neira *et al.* 1998). Egg and larval abundances were corrected for the volume of water filtered and expressed as the number of individuals 100 m^{-3} .

The geographic distributions of *P. auratus* eggs and larvae (samples from 2000 only) were summarized by mapping their centroids of distribution under the assumption that the data followed bivariate normal distributions in latitude and longitude. Centroids and the respective variance-covariance matrices (Kendall and Picquelle 1990) were computed for; (i) eggs < 2 hours old, (ii) eggs > 24 hours old and (iii) all larvae. 95% confidence regions were calculated and represented graphically by drawing ellipsoids

around each centroid. Spatial displacement and directional movement of the centroids were modeled using ‘ribbon formulae’ (National Mapping Council of Australia 1972; Cheng and Chubb 1998; http://en.wikipedia.org/wiki/Frenet-Serret_formulas). Hotelling’s T^2 test (Seber 1983) was used to test for centroid movement between (i) eggs < 2 hours old and > 24 hours old, (ii) eggs < 2 hours old and all larvae and (iii) eggs > 24 hours old and all larvae, assuming unequal dispersion matrices.

2.2.2 Hydrodynamic surveys

A conductivity-temperature-density probe (CTD) was employed during the ichthyoplankton surveys conducted in 2000 (see Fozdar 1983 and Fozdar *et al.* 1985 for details of probe and sensors). The CTD was deployed vertically and recorded data at a rate of 1 Hz as it descended at 1 m s⁻¹ to the sea floor. Deployments of the CTD were undertaken at a subset of the ichthyoplankton survey sites (Eastern Gulf, Denham Sound and Useless Inlet only) (Fig. 2.1). Additional CTD data were obtained from previous hydrodynamic surveys conducted in these waters in 1995 by Burling (1998). Salinity was calculated using the Practical Salinity Scale 1978 (PSS78) (Lewis 1980; Pickard and Emery 1990).

2.2.3 Numerical modelling

P. auratus eggs and larvae were considered passive particles distributed within the surface layer. This simplified, 2-dimensional approach (barotropic) was deemed appropriate as CTD casts indicated homogeneity throughout the water column, implying a uniform flow regime across all depths. Note that the effect of wind will alter these conditions, resulting in higher velocities at the surface. Particle tracking was based on a simple Lagrangian framework with displacements driven by the following equations:

$$\frac{dx}{dt} = U + u' \quad \text{Eqn 2.1}$$

$$\frac{dy}{dt} = V + v' \quad \text{Eqn 2.2}$$

where U and V represent the corresponding x and y advective velocities. Similarly, u' and v' represent turbulent velocity fluctuations in x and y .

Advective velocities were generated using the Hamburg Shelf Ocean Model (HAMSOM) in barotropic mode. HAMSOM is a 3-dimensional primitive equation model initially developed by Backhaus (1985) for simulations of the North Sea and uses semi-implicit and finite-difference schemes (Backhaus 1985; Stronach *et al.* 1993). HAMSOM has been applied successfully to coastal and estuarine systems worldwide (Backhaus 1985; Stronach *et al.* 1993; Pattiaratchi *et al.* 1996; van der Veer *et al.* 1998; Ranasinghe and Pattiaratchi 1999) and was modified for Shark Bay by Burling *et al.* (2003).

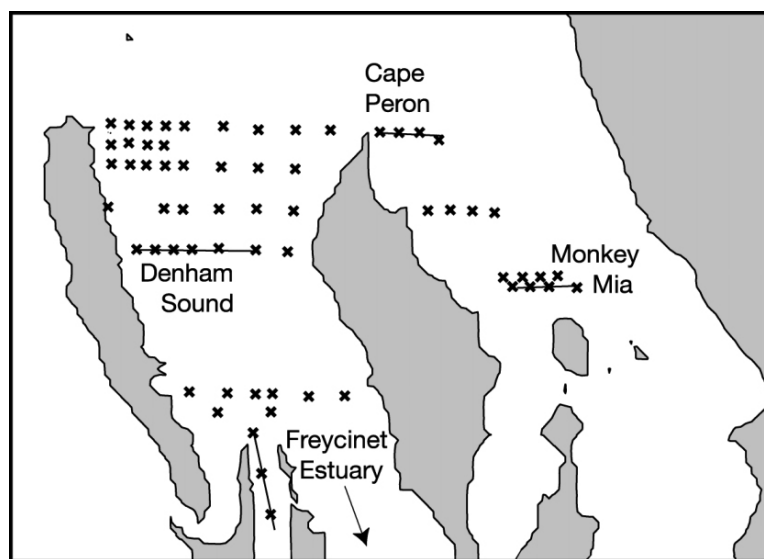
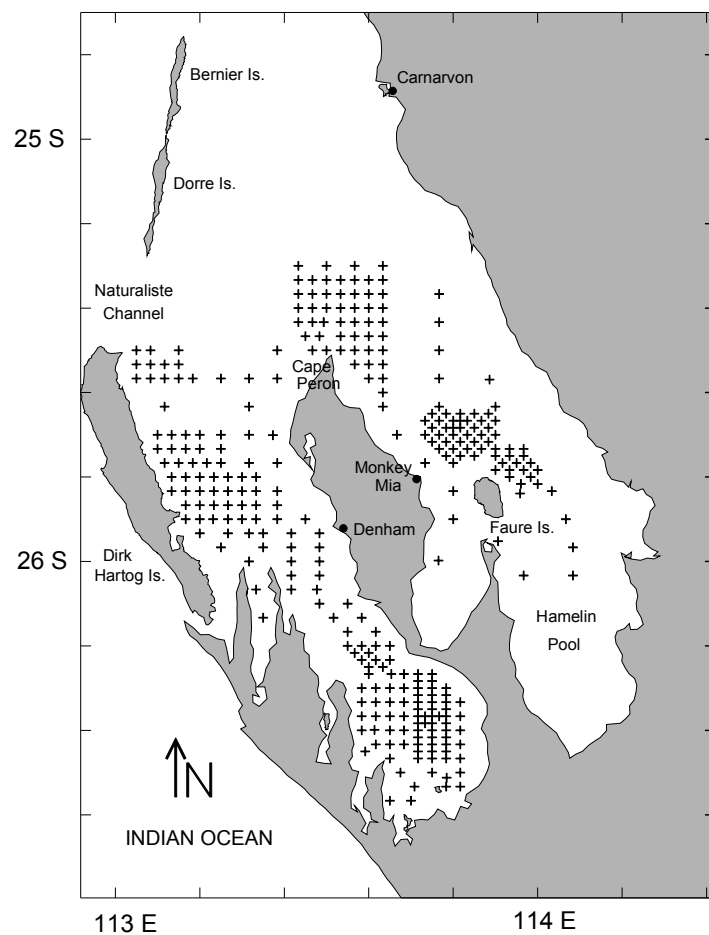


Figure 2.1 Upper - locations of ichthyoplankton tows conducted in 2000. Lower – locations where CTD casts were conducted during the same surveys. CTD transects are labelled as in the temperature-salinity diagram (Fig. 2.4).

Using the numerical (barotropic) framework described, seven different hydrodynamic scenarios were simulated, each using a 30-day model run-time. A single particle was released from four separate release points each hour during the simulation to allow for temporal variation in tidal conditions. The locations of these release points were the approximate centres of the four principal *P. auratus* spawning areas in the inner gulfs, each of which contained a number of individual spawning sites. The locations of the spawning sites were determined by the higher densities (> 50 eggs 100 m^{-3}) of the youngest eggs (*i.e.* < 2 hour old), collected during ichthyoplankton surveys between 1997 and 2000 (Fig. 2.2). The spawning areas are referred to as Cape Peron, Monkey Mia, Denham Sound and Freycinet Estuary (a, b, c, d, respectively, in Fig. 2.2). Although the foci of this study were the inner gulf spawning populations, an important spawning area for the oceanic *P. auratus* stock is known to exist at the northern end of Dirk Hartog Island in the Naturaliste Channel (see 2.3 Results).

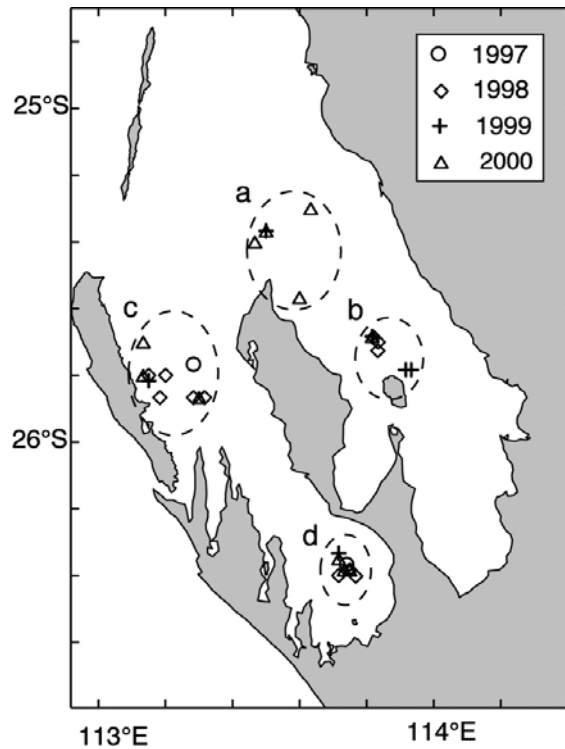


Figure 2.2. Model domain for particle tracking as determined by locations at which the highest densities of eggs < 2 hr old were collected during surveys conducted each year 1997-2000. Hatched ellipses: the four main *P. auratus* spawning areas: a) Cape Peron, b) Monkey Mia, c) Denham Sound and d) Freycinet Estuary. Modelling particle-release points were located within each of these four areas.

Forcing inputs to the model included a range of actual and idealized conditions (Table 2.1). The first three simulations isolated the major hydrodynamic forces including idealized wind conditions, for a controlled comparison. The remaining simulations included all the major hydrodynamic forces and observed wind data. In three model runs, we used data typical for months when the ichthyoplankton surveys were carried out, *i.e.* June, July and August, while in the fourth run we used data typical for January for seasonal comparison. Wind data from the Carnarvon meteorological station were used as the data from Denham were consistently lower in magnitude, probably due to sheltering effects of the local topography, and thus potentially biased.

Comparisons of wind rosettes (not presented here) for the period 1997 to 2000 showed good monthly correlation between years.

Table 2.1. Summary of model runs. All simulations included tidal forcing; those with additional forcing from Leeuwin Current and wind are described. ni: not included.

Model run	Leeuwin Current	Wind
t06	ni	ni
lc07	0.10 m s ⁻¹	ni
w05	0.10 m s ⁻¹	5 m s ⁻¹ southerly
jun08	0.10 m s ⁻¹	June 1998 data
jul09	0.10 m s ⁻¹	July 1999 data
aug10	0.10 m s ⁻¹	August 2000 data
run11	0.10 m s ⁻¹	January 2000 data

2.3 Results

2.3.1 Ichthyoplankton surveys

Although only the results from 2000 are presented here, the patterns of *P. auratus* egg distributions were broadly similar to those found in previous years (1997 to 1999, see Chapter 5 – Daily egg production method). In 2000, a total of 305 plankton tows were carried out between June and August across both inner gulfs. The highest densities of the youngest *P. auratus* eggs were found in close proximity to the known spawning sites, the locations of which were confirmed in most cases by the concomitant capture of actively spawning fish. These spawning sites were located within the four broad spawning areas described previously, *i.e.* off Cape Peron, northeast of Monkey Mia, in Denham Sound, and in the Freycinet Estuary (Figs 2.1 and 2.3). Older *P. auratus* eggs and larvae were still found within these broad spawning areas but, to some extent, had dispersed away from the actual spawning sites. Concentrations of eggs and larvae were also found adjacent to the northern tip of Dirk Hartog Island (Fig. 2.1), known to be an important spawning area for oceanic *P. auratus* that is regularly targeted by commercial operators during winter. This clearly indicated some overlap in the

distribution of eggs and larvae derived from the oceanic and Denham Sound spawning populations. The centroids of distribution representing the four main spawning areas all showed statistically significant movement with development of the eggs/larvae (Table 2.2) with the exception of older eggs and larvae in the spawning area off Cape Peron. However, given that the distances moved by each centroid were mostly less than 10 km, the results were interpreted as biologically insignificant in the context of this study. These results indicated no spatial connectivity between the main spawning areas with the exception of the spawning grounds in Denham Sound and oceanic waters in the Naturaliste Channel, where there appeared to be some spatial overlap.

Table 2.2 Distance and direction of movement of centroids representing each spawning area. Probabilities associated with Hotelling's T^2 - test statistics in bold are significant ($P < 0.05$).

Spawning area	Egg age (hours)	Distance moved by centroid (km)		Direction of movement (°)		Probabilities for T^2 statistic	
		Eggs > 24 hour	Larvae	Eggs > 24 hour	Larvae	Eggs > 24 hour	Larvae
Cape Peron	< 2	12.44	12.72	231	227	0.00	0.00
	> 24		0.97		151		0.15
Monkey Mia	< 2	4.89	2.65	284	136	0.00	0.00
	> 24		7.25		114		0.00
Denham Sound	< 2	4.51	6.50	106	356	0.00	0.00
	> 24		9.16		326		0.00
Freycinet Estuary	< 2	3.53	4.18	159	190	0.00	0.00
	> 24		1.96		248		0.00

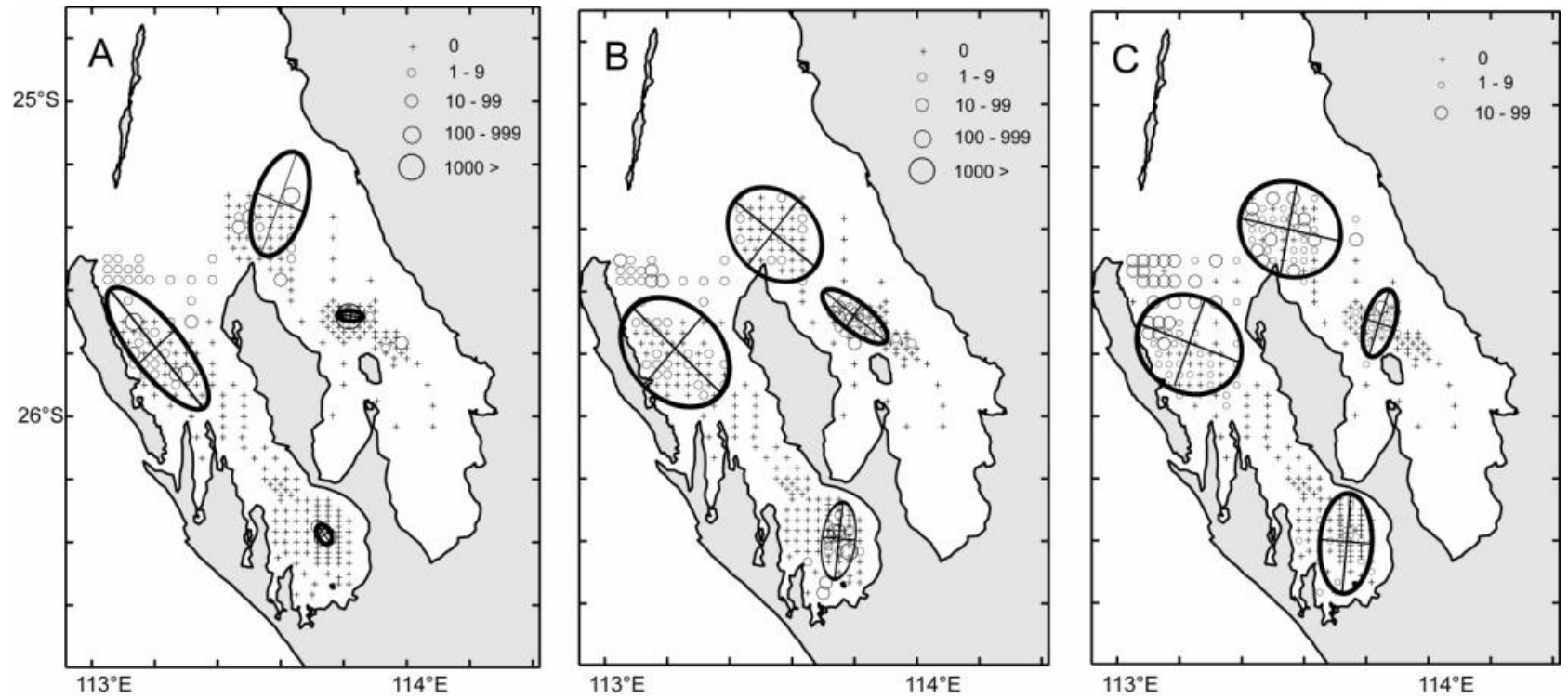


Figure 2.3. *P. auratus* egg and larval distributions from ichthyoplankton surveys in 2000. (A) eggs < 2 hours old; (B) eggs > 24 hours old; (C) all larvae. Units are numbers 100 m⁻³. Ellipsoids represent 95% confidence intervals from rotated axes of the centroids of distribution for spawning areas defined in Fig. 2.2.

2.3.2 Hydrodynamic surveys

There were marked differences in water temperature and salinity characteristics between the four areas in Shark Bay (Fig. 2.4). Hydrodynamic surveys were not conducted in the Freycinet Estuary in 2000; conditions found along the most southerly transects in Denham Sound (Fig. 2.1) were assumed to be representative of those further south. Overall, the system exhibited differences in temperature of almost 6° C and in salinity of more than 6. Sampling sites in Denham Sound and the Freycinet Estuary data were approximately 35 km apart and data showed a difference in temperature of almost 6° C, and in salinity, of almost 5. Cape Peron and Monkey Mia sites were approximately 30 km apart and exhibited similar temperatures but a salinity difference of 4.

Waters were generally vertically mixed, with some stratification apparent to the north of Denham Sound, in the vicinity of the Naturaliste Channel frontal system. Conditions in the inner gulfs were probably dominated by diffusive-mixing processes such as those known to occur across Faure Sill (Burling *et al.* 1999). This implies that, irrespective of where *P. auratus* eggs and larvae were distributed within the water column, they would be subject to the same hydrodynamics, and therefore similar advection. Thus, the 2-dimensional barotropic model used here adequately represented the local hydrodynamic conditions.

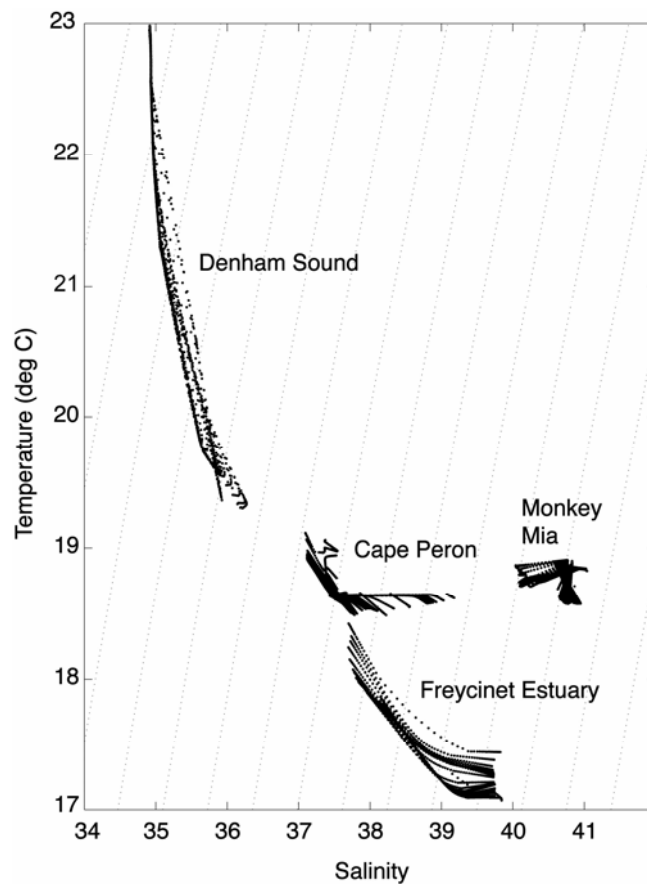


Figure 2.4. Temperature-salinity signatures for inner Shark Bay indicating unique (non-overlapping) water bodies in the four regions of interest.

2.3.3 Numerical Modelling

2.3.3.1 Surface residual flows

The predicted residual⁴ currents were initially analysed at the local scale in the areas of higher egg and larval abundance. For tide-only runs, 30-day tidal residual velocity plots were overlaid with ichthyoplankton data to relate velocity structure to the observed patterns of egg and larval distributions. A series of circulatory flows with stagnant cores (eddies), probably reflecting the influence of the complex local topography, were identified in all four areas of interest.

⁴ 'residual' refers to the net water movement over the full tidal cycle (*i.e.* effect of tides removed)

Around Cape Peron there was strong flow convergence, accelerated by the topography, with water moving northwards out of each gulf to either side of the Peron Peninsula (Fig. 2.5A). North of Cape Peron, the residual flow decreased and separated into an eastern eddy and a northwestern current. The model results indicate that eggs and larvae are advected from the Eastern Gulf, northwards through a convergent zone, towards a stagnant eastern region, with the possible loss of some eggs and larvae to waters to the northwest under certain conditions. In the Monkey Mia region (Fig. 2.5B), the southerly portion of the same velocity path initially headed westwards and then turned northwards towards Cape Peron, representing a possible hydrodynamic link between these two areas. With maximal residual velocities of $\sim 5 \text{ cm s}^{-1}$, passive advection from Monkey Mia to Cape Peron (approximately 50 km apart), via this pathway, would take a minimum of 12 days. To the southeast, flow accelerated across Faure Sill, diverged around Faure Island, and converged again to form the main eddy in the Monkey Mia region.

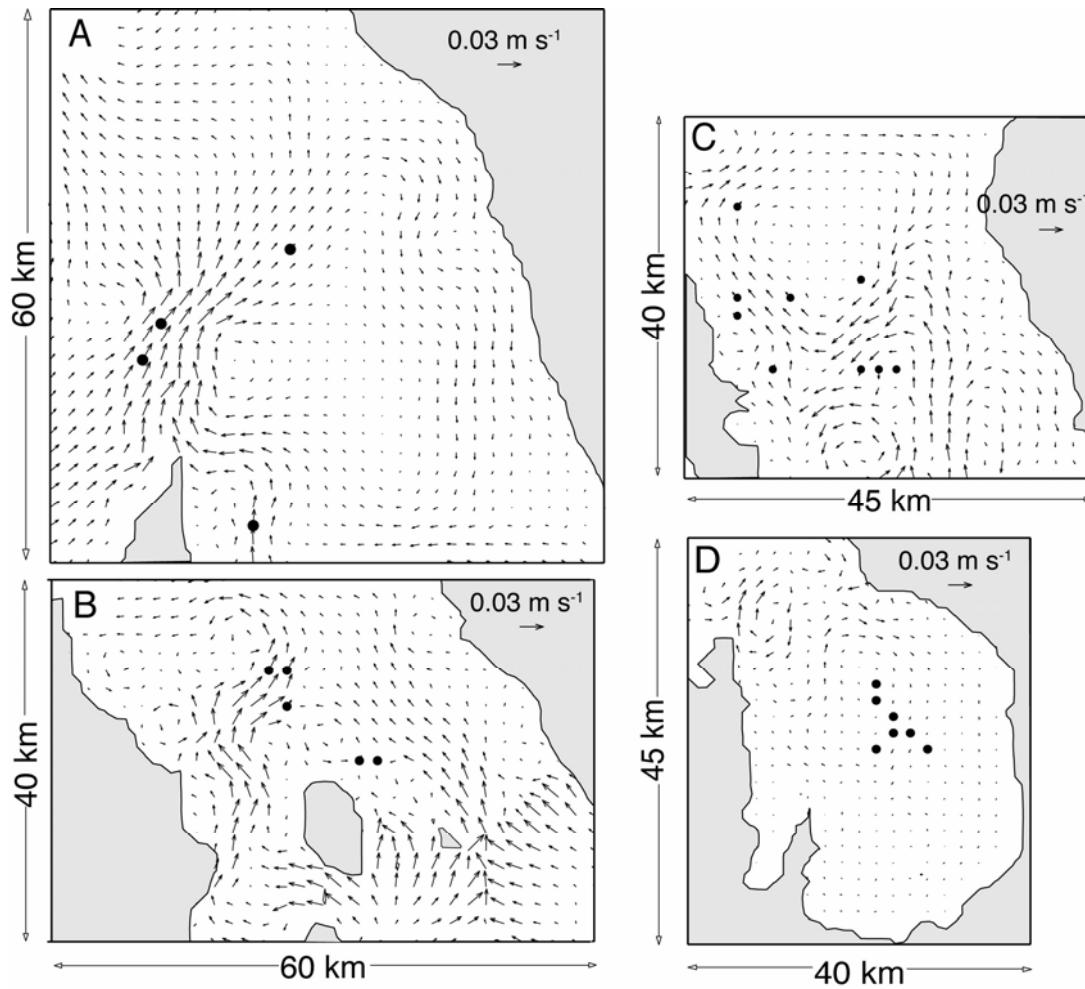


Figure 2.5 Predicted surface residual currents plotted for the four regions of interest (i.e. local scale). (A) Cape Peron; (B) Monkey Mia; (C) Denham Sound; (D) Freycinet Estuary. (●) locations at which the highest densities of younger *P. auratus* eggs were found.

In Denham Sound, eggs and larvae were concentrated in the modeled regions of peripheral, high velocity flow (Fig. 2.5C). Reproductive output originating to the southeast would be moved northwest, via two counter-rotating systems, before slowing at the northern margin of an eddy. The Freycinet Estuary likewise contained a circular flow encompassing the locations of higher egg and larval abundance (Fig. 2.5D). However, velocities were generally low, suggesting that the entire southern section of the Western Gulf was mostly free of residual transport.

From the broader scale (all Shark Bay) residual current plots, the tide-only model run (Fig. 2.6A) showed low residual flows in the inner gulfs and stronger flows through the Naturaliste Channel, along the inside of Bernier and Dorre Islands, and off Cape Peron. Addition of the Leeuwin Current (Fig. 2.6B) appeared to have minimal effect in the inner gulfs, although it did dampen residual flows in northern waters, possibly providing a retention mechanism for eggs and larvae north of Cape Peron. This dampening affect was moderated by the addition of a southerly wind that altered conditions in northern Shark Bay from tidally-driven to wind-driven (Fig. 2.6C). Hydrodynamic conditions in southern Shark Bay were only minimally altered by wind although flow velocities increased along the shores of both Hamelin Pool and the Freycinet Estuary. This opened possible advection pathways between Hamelin Pool and north of Cape Peron. Water in Denham Sound also appeared to flow northward along the eastern shore, again indicating possible wind-driven connectivity with Cape Peron. Overall, the hydrodynamic systems in both inner gulfs were tidally-dominated.

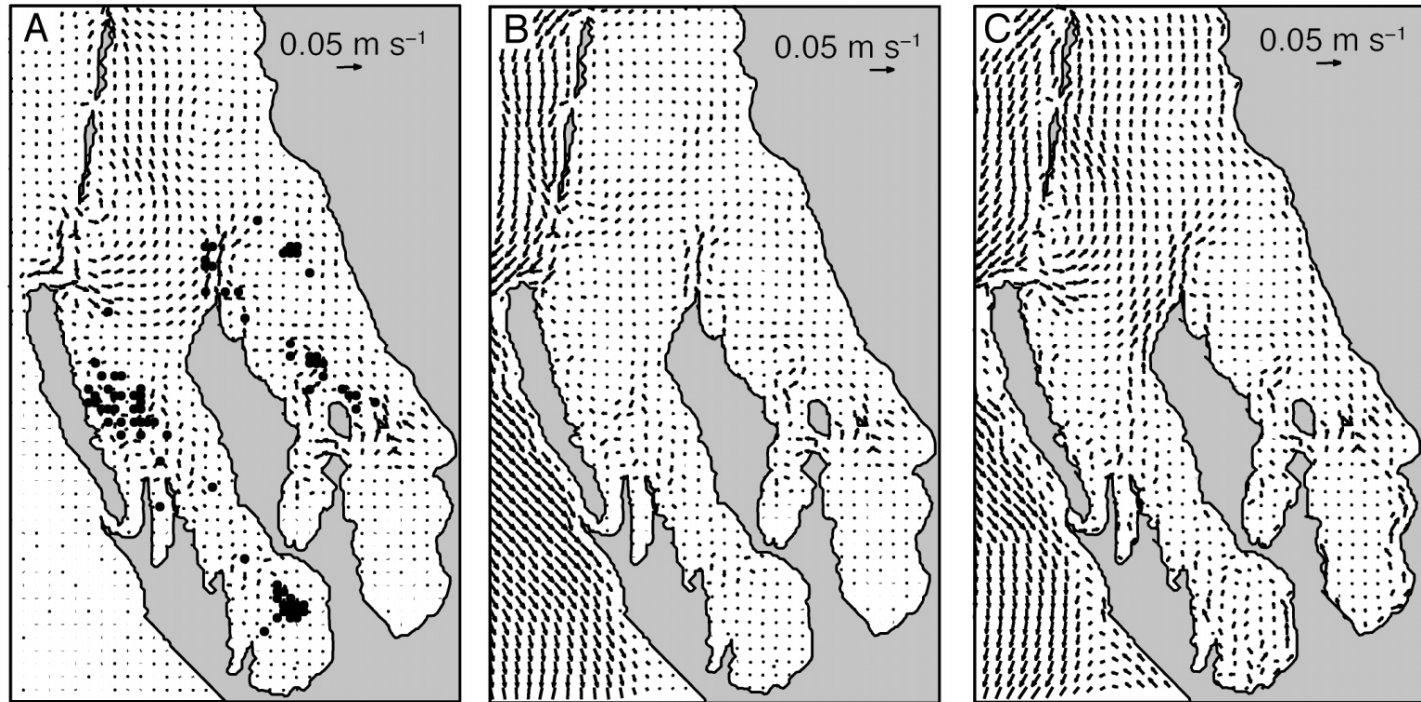


Figure 2.6. Predicted surface residual currents for the whole of Shark Bay (*i.e.* broader scale) under varying hydrodynamic conditions. (A) residual currents from the model run including tidal forcing only (run t06), including locations of highest densities of younger eggs (●); (B) residual currents from the run including tidal forcing and additional forcing from the Leeuwin Current (run lc07); and (C) residuals currents from the run including all forces combined (run w05).

2.3.3.2 Particle tracking

Particles released in each of the simulations verified the behaviour predicted by the surface residual currents. Under conditions of tide-only, particles in all areas except Cape Peron remained inside the localised areas of cyclic residual flow (Fig. 2.7A). Although some particles released at Cape Peron were entrained in an eddy to the east, they were not retained to the same extent as particles released at locations to the south in the inner gulfs (Fig. 2.7B). Introduction of the Leeuwin Current had very little influence on particles in the regions of Monkey Mia, Denham Sound, and the Freycinet Estuary (Fig. 2.7C). However, it dampened the northerly residuals off Cape Peron, with the same propagation into the eastern eddy, but greatly decreased advection northwards. A constant 5 m s^{-1} wind from the south advected particles from Denham Sound up the eastern shore via a northerly-flowing path (Fig. 2.7D). The Freycinet Estuary remained isolated despite an increase in local velocities. Particles from Monkey Mia were advected further eastwards, but did not reach the northerly flow along the eastern shore as in the residual plot.

Model runs using observed wind data showed the same retention patterns as with the generic model. Throughout the winter (June – August), the four particle release locations in the inner gulfs exhibited very little interaction with northern Shark Bay (Fig. 2.8C). Cape Peron particles responded to the dampening effect of the Leeuwin Current in June and July but, with increased winds in August, moved northwards into the high residual regions to the east of Bernier and Dorre Islands (Fig. 2.8C). Similarly, in June and July, a clockwise-eddy was maintained in Denham Sound, while in August the increased wind caused some entrainment along the eastern shoreline, advecting particles towards Cape Peron. During summer (January), particles

from each location followed the advection pathways seen in the residual-current plots (Fig. 2.8D) with the exception of Freycinet Estuary, which again remained isolated.

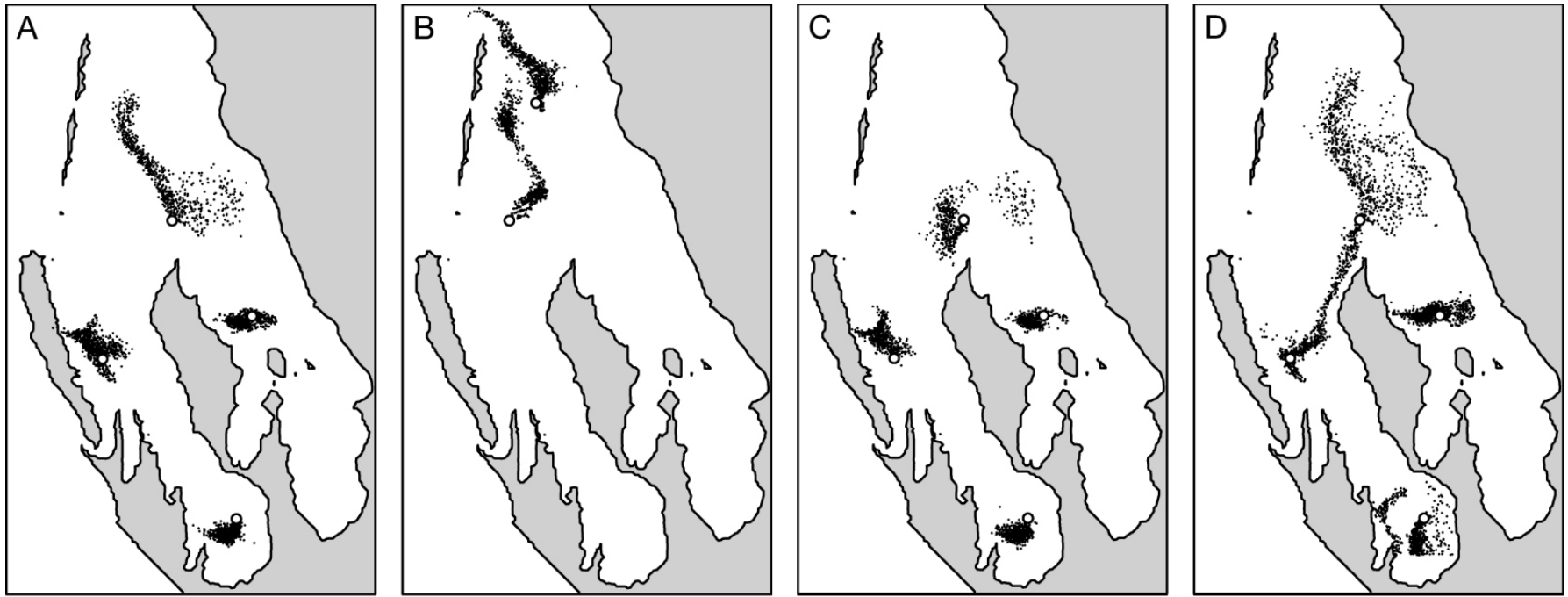


Figure 2.7. Particle-tracking results for the model run of 30-days duration and one particle released each hour. (o) indicate particle release points. (A) the model results from the tidal forcing only run (run t06) in areas where youngest *P. auratus* eggs were found; (B) the same model run with particles released farther north in higher residual-flow paths; (C) the same release points as (A) but including Leeuwin Current (run lc07); and (D) the same release points and including a combination of tide, Leeuwin Current and wind (run w05).

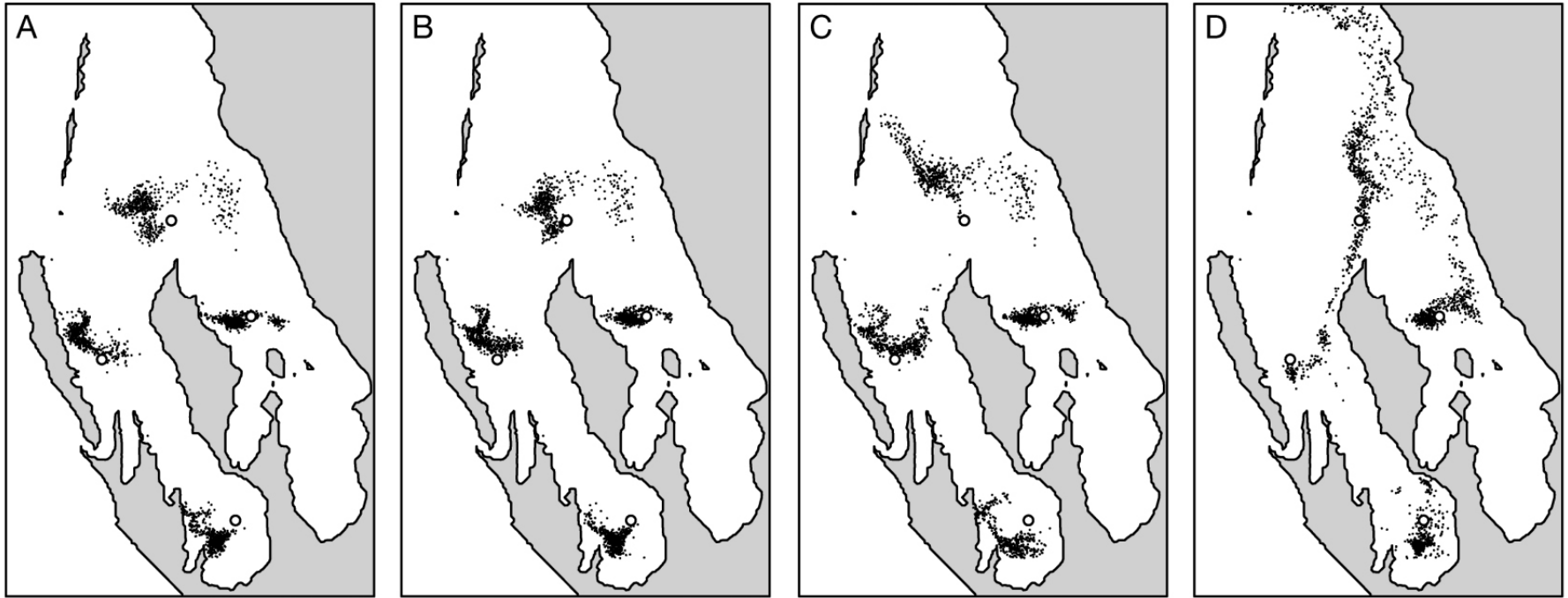


Figure 2.8. Additional particle-tracking results with different forcing conditions incorporating wind data from (A) June 1998, (B) July 1999, (C) August 2000 and (D) January 2000.

2.4 Discussion

This study investigated the potential for hydrodynamic dispersal of *P. auratus* eggs and larvae in the inner gulfs of Shark Bay, to provide some insight into dispersal of the early life-history stages prior to settlement. Low levels of mixing between apparently separate *P. auratus* populations living in adjacent waters bodies have been inferred from previous genetic and phenotypic studies (Johnson *et al.* 1986; Edmonds *et al.* 1989, 1999; Moran *et al.* 1998, 2003; Whitaker and Johnson 1998; Baudains 1999; Bastow *et al.* 2002), mainly involving sub-adult and adult fish. Although direct measures of larval dispersal do not necessarily indicate successful mixing between fish populations (Bailey *et al.* 1997), highly localized retention of eggs and larvae, originating from discrete natal areas, would strengthen support for the prevailing hypothesis that several reproductively-isolated populations exist in these waters. From the management perspective, it is important to determine whether these proximate *P. auratus* populations are self-recruiting or sustained by external production.

Ichthyoplankton surveys conducted during the winter spawning season over a four-year period (1997-2000) consistently found the highest densities of the youngest *P. auratus* eggs within several well-defined spawning areas. Within each of these, those sites at which eggs less than 2-hour old were collected in higher abundance were taken to represent individual spawning sites, on the basis that the 2-hour old eggs were unlikely to have been transported any great distance. With the exception of the region between the spawning grounds in Denham Sound and oceanic waters in the Naturaliste Channel off the northern tip of Dirk Hartog Island, where there is likely to be some spatial overlap of egg and larval distributions, no connectivity was found between the spawning areas. This implies that the Cape Peron, Monkey Mia and Freycinet Estuary

populations are reproductively isolated and thus likely to be self-recruiting, while the Denham Sound population is less so. !

Hydrodynamic surveys found waters in the vicinity of the four spawning areas to possess unique temperature-salinity signatures, thereby identifying water masses with distinct characteristics, and implying minimal horizontal mixing. Previous studies identified tide to be the primary transport mechanism in Shark Bay's inner gulfs (Logan and Cebulski 1970; Burling *et al.* 2003). The modelling here corroborates this and suggests that tidal flows interact with local topography (Zimmerman 1978; Wolanski and Hamner 1988) to form localised areas of convergence. These residual eddies are coincident with the main *P. auratus* spawning grounds and provide a mechanism that would retain eggs and larvae within each natal area. The distributions of *P. auratus* ichthyoplankton observed from field surveys were consistent with this, indicating that local hydrodynamics significantly limit mixing of eggs and larvae between the spawning areas. Although at larger scales than in Shark Bay, larval retention resulting from interaction between coastal complexity and flow has been linked with population structure in marine fishes elsewhere, *e.g.* Atlantic cod off Newfoundland (Ruzzante *et al.* 1999) and Pacific Ocean perch off British Columbia (Withler *et al.* 2001).

Although the strength of the Leeuwin Current has been linked previously to recruitment variation in major fisheries off Western Australia (Lenanton *et al.* 1991; Pearce and Phillips 1988, 1994; Caputi *et al.* 1996), its influence on recruitment in the inner gulf *P. auratus* populations appears negligible. Model simulations showed minimal penetration of the Current into the shallower inner gulfs with the exception of

the waters off Cape Peron, where years of weaker current strength may be reflected in lower retention of eggs and larvae. The results of this study suggest that there is a strong correlation between the seasonality of *P. auratus* spawning, wind and hydrodynamic retention. Although the effect of the wind was likely exaggerated here, because surface particle-tracking was used in the simulations, the seasonal transitions of the system from wind-driven to tide-driven highlight patterns that could potentially affect spawning success. *P. auratus* in the northern waters of each inner gulf (Cape Peron, Monkey Mia, Denham Sound) spawn during months of minimum wind, *i.e.* June and July. Unseasonably high winds in these months would see eggs and larvae transported away from the main natal areas, thereby reducing local recruitment. In contrast, in the Freycinet Estuary where spawning mostly occurs in August and September when winds have increased, recruitment is probably not affected, as local waters still experience low residual flows because of their geographic isolation from the deeper waters to the north.

The role of larval dispersal in determining whether local marine populations are open and consequently dependent on exogenous recruitment, or relatively closed and sustained by endogenous recruitment, remains an important ecological question (Cowen *et al.* 2000; Swearer *et al.* 2002) that is largely dependent on scale (Strathman *et al.* 2002; Warner and Cowen 2002). Based on the results of this study, which was very much at the local scale, and of tagging (Moran *et al.* 2003; G. Jackson unpublished data), *P. auratus* populations off Cape Peron, Monkey Mia and in the Freycinet Estuary appear essentially closed, and are likely to be dependent on recruitment from local spawning. In contrast, the Denham Sound population may receive some recruitment from oceanic spawning and is therefore more open; however, the question as to the

degree to which oceanic snapper may act as a recruitment source for the Denham Sound population and how any contribution may vary between years remains to be answered. Preliminary studies indicate that snapper recruitment in both inner gulfs, currently measured by the relative abundance of 0+ fish caught during annual trawl surveys, is highly variable (Moran and Kangas 2003).

P. auratus inside Shark Bay demonstrate many characteristics that are likely to increase the probability of self-recruitment (Swearer *et al.* 2002) with spawning taking place at the times (winter) and locations most favourable for retention, rapid egg development (approximately one day), and a relatively short larval duration (less than 30 days). The latter two factors equate to a relatively short planktonic larval duration, the most cited biological variable potentially affecting self-recruitment (Sponaugle *et al.* 2002). Why inner gulf *P. auratus* spawn just where they do remains unclear with no obvious habitat feature common to all spawning sites other than the hydrodynamic characteristics identified in this study. Site selection may be some adaptation to maximize larval feeding potential as the localized areas of convergence coincident with the spawning grounds are probably waters of relatively higher productivity within a marine environment that, in general, receives limited nutrient input (Atkinson 1987). Evidence suggests that *P. auratus* spawning activity is greatest during the periods of larger tides, and therefore maximum retention, *i.e.* around the new moon and to some extent full moon (G. Jackson unpublished data). Overall, the behaviour demonstrated by *P. auratus* adds support to the view proposed by Strathman *et al.* (2002) that selection in non-migratory species may favour recruitment to the same environment as that inhabited by the adults.

This study provides further support for the existence of a number of proximate but discrete spawning populations of *P. auratus* in the inner gulfs of Shark Bay. The mechanism shown here, *i.e.* hydrodynamic retention, partly explains existing data on local *P. auratus* stock structure. The information obtained has relevance in the management of the recreational fishery in the inner gulfs, where large numbers of visiting fishers target known snapper spawning aggregations during winter, when fishing mortality can be high and highly localized. Populations with extensive larval retention are more vulnerable to recruitment overfishing (Strathman *et al.* 2002). Results of this study underline the need to continue to monitor and manage inner gulf *P. auratus* populations at an unusually fine spatial scale compared with the scale appropriate for management of many other marine fish stocks in Western Australian waters.

Chapter 3: Reproductive biology of *P. auratus* in the inner gulfs of Shark Bay

3.1 Introduction

Information on the reproductive biology of an exploited fish species, *e.g.* sexual pattern (*i.e.* whether a gonochorist or hermaphrodite), size and age at maturity, and temporal and spatial patterns of spawning, are essential for understanding the life history of the species and for fisheries management purposes. Knowledge of spawning behaviour may identify species at higher risk of over-exploitation, *e.g.* species that form spawning aggregations that are predictable both in time and space (Domeier and Colin 1997; Rhodes and Sadovy 2002). An understanding of temporal (seasonal) and spatial patterns in spawning activity may be required where fishery closures, *e.g.* closed areas and/or closed seasons, are identified as potentially useful forms of management control (Jackson *et al.* 2005). Data collected during the peak spawning period are necessary for determining size and age at maturity, the former typically being used in setting minimum legal sizes (Hill 1992). Also, identifying the reproductive strategy of a species, *i.e.* whether individuals change sex, and obtaining robust estimates of fecundity, is dependent upon the collection of representative biological samples during the spawning season. Fecundity data are used in egg-per-recruit models to determine appropriate minimum legal sizes (Haddon 2001) and to assess the impacts of fishing on the reproductive potential of fish stocks (*e.g.* spawning potential ratio, Goodyear 1993). Weight-specific fecundity data are a required input with egg production-based methods used for estimating spawning biomass (Gunderson 1993; Stratoudakis *et al.* 2006). Finally, otolith-based age determination requires knowledge of birth date so that ages can be assigned to individual fish accurately and reliable population growth curves can therefore be obtained.

Compared with many exploited species found in Australian waters, considerable research has been undertaken on the reproductive biology of *Pagrus auratus* and its conspecific *P. major*. There is an extensive literature dealing with reproductive biology of *P. auratus* in New Zealand (Cassie 1956; Crossland 1977a,b; Francis and Pankhurst 1988; Scott and Pankhurst 1992; Scott *et al.* 1993) and of *P. major* in Japan (Matsuyama *et al.* 1987a,b, 1988a,b). However, until relatively recently, very little had been published on the reproductive biology of *P. auratus* in Australian waters (*e.g.* Ferrell and Sumpton 1998; Sumpton 2002; McGlennon 2003; Coutin *et al.* 2003). Importantly, no such information for the Shark Bay region or more generally for Western Australian waters has been published in the primary literature.

Many forms of sexuality have been reported in sparids (Buxton and Garratt 1990). Francis and Pankhurst (1988) showed *P. auratus* in New Zealand to be functional gonochorists with protogynous sex inversion occurring in some individuals prior to the onset of sexual maturity. In this study, they found that juveniles first developed as females with functional males developing from a proportion of fish which underwent sex inversion around the 3rd or 4th year while functional females developed directly from juvenile females. This pattern of sexual behaviour resulted in an approximate 1:1 sex ratio among the adult population. Based on a preliminary study of juvenile *P. auratus* from Shark Bay (G. Jackson unpublished data), and no evidence to the contrary from elsewhere in Australia, a similar pattern of sexuality as shown by Francis and Pankhurst (1988) was therefore assumed with *P. auratus* in Shark Bay.

Other studies in New Zealand have shown that *P. auratus* have an annual reproductive cycle and are batch spawners that display asynchronous gonadal

development and indeterminate fecundity (Crossland 1977a,b; Scott and Pankhurst 1992). In New Zealand, *P. auratus* spawn from October (mid-spring) through to February (late summer) (Crossland 1977a; Scott and Pankhurst 1992) with an increase in spring water temperatures being the presumed environmental trigger. Scott and Pankhurst (1992) found annual variation in both the onset and conclusion of spawning due to inter-annual differences in water temperature patterns. Spawning in New Zealand has been shown to occur on a daily basis with most spawning occurring in the late afternoon to early evening (Scott *et al.* 1993). In Australia, *P. auratus* spawn between November and January (late spring to mid-summer) in South Australia (McGlennon 2003) and Victoria (Coutin *et al.* 2003) but earlier in the year, during winter, in Queensland (Ferrell and Sumpton 1998). In Western Australia, commercial and recreational fishers in the Shark Bay region have targeted known *P. auratus* spawning aggregations during winter for many decades (Bowen 1961; Jackson and Cheng 2001). Fishing of spawning aggregations is a feature of other *P. auratus* fisheries around Australia, *e.g.* in Cockburn Sound, Western Australia (Wakefield 2006; Wise *et al.* 2007), in northern Spencer Gulf, South Australia (McGlennon 2003) and in western Port Philip Bay, Victoria (Coutin *et al.* 2003) and, if allowed to continue unmanaged, can increase the vulnerability of the spawning stock to over-exploitation.

The overall objective of this component of the study was to investigate the reproductive characteristics and seasonal spawning patterns of *P. auratus* in the Eastern Gulf, Denham Sound and Freycinet Estuary areas of inner Shark Bay. Given that Shark Bay is located towards the northern limit of the geographic range of the species on the west coast of Australia, reproductive characteristics (*e.g.* timing of spawning) would be expected to be more similar to those of *P. auratus* populations at the northern limit of

distribution on the east coast compared with populations located at higher latitudes in ! more temperate regions (Sumpton 2002). Given the complex nature of *P. auratus* population structure in inner Shark Bay, the high level of environmental heterogeneity (see Chapter 1 – General introduction) and historic differences in levels of exploitation in the different areas of inner Shark Bay, it was hypothesised that differences in reproductive characteristics, such as timing of spawning and size and age at maturity with *P. auratus* among the three main localities (Eastern Gulf, Denham Sound and Freycinet Estuary) were likely to exist.

The daily egg production method (DEPM) was developed as a method of assessing stock size for fish species with planktonic eggs and indeterminate annual fecundity, *i.e.* multiple or ‘batch’ spawners (Lasker 1985). The technique estimates spawning biomass as the ratio of daily egg production and weight-specific daily fecundity (number of eggs spawned each day by a female of average weight, *i.e.* batch fecundity). Critical to application of this technique with *P. auratus* in inner Shark Bay (see Chapter 5 – Daily egg production method) were estimates of mean batch fecundity for *P. auratus* in the Eastern Gulf, Denham Sound and Freycinet Estuary.

The aims of the research described in this chapter therefore were 1) to determine the duration and timing of the *P. auratus* spawning season in the Eastern Gulf, Denham Sound and the Freycinet Estuary, 2) to compare the lengths and ages at which individuals of both sexes attain sexual maturity, and 3) to estimate batch fecundity for *P. auratus* from the three localities, to determine the relationship between batch fecundity and individual fish length, and to test for differences in these relationships among years and locations.

3.2 Materials and Methods

Pagrus auratus were sampled from the Eastern Gulf, Denham Sound and Freycinet Estuary areas of Shark Bay (Fig. 1.3, Chapter 1 – General introduction) on an approximately monthly basis between 1997-2004, principally using rod and line fishing. The samples were mostly obtained by Western Australian Department of Fisheries research staff and volunteer recreational boat-fishers during fishery-independent surveys conducted mainly between March-September. These samples were occasionally supplemented with filleted carcasses of fish donated by recreational boat fishers (line-fishing, all months, size limits applied). Smaller fish were collected during research trawl (twin otter trawls, 45 mm cod-end mesh, Moran and Kangas 2003) and trap surveys (Antillean-Z fish traps, 12 mm mesh, Jackson *et al.* 2006). All fish were measured (fork length, FL) to the nearest mm. A randomly-selected sub-sample were weighed (whole wet weight) to the nearest 10 g. These data were logarithmically (natural) transformed and used to derive an allometric length:weight relationship for each area, which, after adjustment for log-bias (Quinn and Deriso 1999) was used to estimate the weights of all unweighed fish from that locality. Differences in the length:weight relationships among the localities were tested using a t-test; where differences were non-significant, the corresponding data were pooled. No difference in length:weight relationships for females and males was assumed in this study based on previous research on the species from elsewhere in Australia (Sumpton 2002; Coutin *et al.* 2003).

3.2.1 Gonad staging

In the field, the paired gonads of each fish were sexed and staged macroscopically using, for females, a six-stage classification system (1 = immature, 2 = resting, 3 = developing, 4 = developed, 5 = spawning, 6 = spent (Table 3.1) and for males, a five-stage classification system (1 = immature, 2 = resting, 3 = developed, 4 = spawning, 5 = spent) similar to the categories used by Scott and Pankhurst (1992, based on the descriptive scale of Crossland 1977a). The gonads were then weighed to the nearest 0.01 g. A random selection of female gonads was fixed in 10% formalin with seawater for subsequent histological examination. In the laboratory, a sub-sample of approximately 3 mm thickness taken from the mid-region of one ovarian lobe from each of these gonad samples was embedded in paraffin wax, cut into 7-8 mm transverse sections and stained using Harris's haematoxylin and eosin. The sections were examined microscopically and the ovaries re-staged on the basis of their histological characteristics (Table 3.1).

The terminology used to describe oocyte development stages observed in *P. auratus* ovary sections followed that adopted by Wallace and Selman (1981) and West (1990): (1) chromatin-nucleolus stage, (2) perinucleolus stage, (3) cortical alveoli (yolk vesicle) stage, (4) vitellogenic (yolk globule) stage, (5) migratory nucleus/hydration stage. Post-ovulatory follicles (POFs, Hunter and Macewicz 1985) were categorised based on their appearance as either 'new' (*i.e.* POF is relatively large, granulosa cells form a loose, convoluted layer inside thecal cell layer, nuclei of the granulosa cells are large and orderly arranged, and central lumen is distinct) or 'old' (*i.e.* POF is small and compact, outer thecal cell layer is angular in shape, granulosa cells are difficult to define

and may no longer form an unbroken layer). The amount of atresia observed in each ! ovary sample was recorded. The main criterion for classification of ovaries as stage 6 (spent) was that >50% of vitellogenic oocytes were atretic (Table 3.1).

3.2.2 Timing and duration of spawning season

Mean monthly gonadosomatic indices (GSI) for fish with lengths of the estimated length at which 50% of fish attain maturity (*i.e.* L_{50}) or greater (see 3.2.3 Length and age at sexual maturity) were determined for each sex within each of the three sampling localities using the following,

$$GSI = 100 \times W_g / (WW - W_g) \quad \text{Eqn 3.1}$$

where WW = whole wet weight of fish and W_g = weight of gonads. The monthly percentage frequency of each gonad maturity stage was calculated for females and males with lengths equal to or greater than the estimated L_{50} and plotted as frequency histograms to determine the seasonal pattern of gonad development. Reproductive data were pooled by month across years for the Eastern Gulf, Denham Sound and the Freycinet Estuary separately.

3.2.3 Length and age at sexual maturity

Logistic regression analysis was used to determine the parameters α and β of the logistic relationship between the probability, p , that an individual is mature and the individual's fork length, L , *i.e.*

$$p = \{1 + \exp[-(\alpha + \beta L)]\}^{-1} \quad \text{Eqn 3.2}$$

Individual fish from each locality were classified as mature if, during the peak spawning ! period (see 3.3 Results), they possessed gonads categorised as Stage 4-6 for females and Stage 3-5 for males. Estimates of the length at which 50 and 95% of individuals were expected to be mature were calculated as $L_{50} = -\alpha / \beta$ and $L_{95} = \{\log_e(19) - \alpha\} / \beta$, respectively, and were calculated separately for each sex in each area. The analysis was repeated using each of 1000 sets of re-sampled data with the 95% confidence intervals for values of L_{50} and L_{95} estimated as the 2.5 and 97.5 percentiles of the resulting parameter estimates.

The ages (see Chapter 4 - Age and growth for details of ageing methods) at which 50 (A_{50}) and 95% (A_{95}) of males and females in each area were expected to be mature were estimated directly using a similar approach based on a subset of individuals for which both gonad development stage and otolith-based estimates of age were available. The 95% confidence intervals for values of A_{50} and A_{95} were similarly estimated using the bootstrapping technique described above.

Length at maturity (L_{50}) and age (A_{50}) at maturity for females and males were compared among the three localities, with the null hypothesis of no difference in the logistic regression curves fitted to the length or age at maturity data, using a likelihood-ratio test (Kimura 1980; Cerrato 1990) with the significance level adjusted for multiple comparisons using the Bonferroni method (Quinn and Keough 2003, p 49).

Table 3.1. Macroscopic and histological characteristics used to determine the developmental stages of *P. auratus* gonads from the inner gulfs of Shark Bay. Terminology for oocyte development follows Wallace and Selman (1981) and West (1990). CAS = cortical alveoli stage; CNS = chromatin nucleolus stage; MNS = migratory nucleus stage; POFs = post-ovulatory follicles; PNS = perinucleolus stage; YGS = yolk globule stage.

Stage	Macroscopic characteristics	Histological characteristics
<i>Juvenile</i>	Tiny, translucent. Sex indistinguishable.	Germ tissue rudimentary and comprised of undifferentiated gonia.
<i>Females</i>		
1. Immature !	Ovary small, firm, pale or translucent pink. No oocytes visible. Difficult to distinguish late Stage 1 from Stage 2 ovaries.	Ovary compact, lamellae generally more orderly and straighter than those in mature ovaries. Tunica tight. CNS and PNS oocytes present. No evidence of prior spawning (see Stage 6).
2. Resting	Ovary larger and more rounded than Stage 1, translucent pink or reddish in colour, and $\frac{1}{4}$ - $\frac{1}{3}$ length of body cavity. May appear flaccid and bloodshot. Individual oocytes not distinguishable.	Lamellae generally more branched than in Stage 1 ovaries and may contain evidence of spawning (see Stage 6). CNS and PNS oocytes present.
3. Developing !	Ovary pale orange or pink in colour and $\frac{1}{3}$ - $\frac{2}{3}$ length of body cavity. Small, semi-opaque oocytes visible.	CAS oocytes are the most advanced stage. Lamellae usually full and tightly packed.
4. Developed !	Ovary enlarged and orange, apricot or yellow in colour with prominent blood vessels. May be flaccid and bloody after spawning. Opaque oocytes clearly distinguishable.	Tunica expanded and thin. YGS oocytes are the most advanced stage. Lamellae full and tightly packed but become disorganised and empty towards end of spawning season.
5a. Pre-spawning !	Ovary at maximum size, pale orange or apricot in colour with a speckled appearance. Large, translucent hydrated oocytes visible in lamellae. Blood vessels prominent.	MNS or hydrated oocytes are the most advanced stage within the lamellae. Both old and new POFs may be present.
5b. Spawning / Running ripe	As above except eggs are in the lumen and extruding from gonoduct.	Ovulated hydrated oocytes (eggs) present in lumen. New POFs in the lamellae, usually near the perimeter. Old POFs may also be present.
5c. Post-spawning	Similar to Stage 4. Areas of the ovary may appear watery.	Old or new POFs present. No MNS or hydrated oocytes.
6. Spent	Ovary flaccid and bloody. Often confused with other stages.	> 50 % of vitellogenic oocytes atretic. Evidence of prior spawning includes loose tunica, disordered lamellae, yellow-brown bodies, much vascular and connective tissue.
<i>Males</i>		
1. Immature	Testis small, ribbon-like, translucent white.	-
2. Resting	Testis larger than Stage 1 and greyish.	-
3. Developed	Testis large, opaque and creamy white. Some milt may be squeezed from central sperm sinus.	-
4. Spawning	Testis large, firm, creamy white. Milt released with/without slight pressure.	-
5. Spent	Testis flaccid and reduced in size, whitish grey and bloody	-

3.2.4 Batch fecundity

Crossland (1997b) showed *P. auratus* from New Zealand waters to be of indeterminate fecundity based on seasonal change in the distribution of oocyte diameters within ovary samples. In such species, the total number of eggs produced and spawned each year, *i.e.* annual fecundity, is not fixed prior to the onset of the spawning season, rather unyolked oocytes continue to be produced and mature into yolked oocytes during the course of the spawning season (Hunter *et al.* 1985). Batch fecundity, *i.e.* the number of eggs released during a single spawning event, can be estimated by counting the number of hydrated oocytes present in the ovary prior to that spawning event (Hunter *et al.* 1985).

Batch fecundity for *P. auratus* from inner Shark Bay was estimated gravimetrically using the hydrated-oocyte method (Hunter *et al.* 1985) using formalin-preserved ovarian samples collected during the peak spawning season. These samples were obtained from the Eastern Gulf, Denham Sound, and the Freycinet Estuary during daily egg production method surveys carried out each year between 1998 and 2003 (see Chapter 5 – Daily egg production method). To reduce potential bias in the estimation of batch fecundity, only ovaries from females determined by histological examination to be in pre-spawning condition (*i.e.* with gonads at Stage 5a, Table 3.1) and thus were fully hydrated, *i.e.* no early hydrated oocytes still present, were used in the analysis. Ovaries that are not fully hydrated tend to result in over-estimates of batch fecundity (Mackie *et al.* 2005). In addition, to avoid under-estimating batch fecundity, samples which contained ‘new’ POFs, indicating that spawning had commenced prior to capture, were also excluded from the analyses.

Zeldis and Francis (1998) showed that estimates of batch fecundity for *P. auratus* from Hauraki Gulf, New Zealand, did not differ significantly among samples taken from the mid, posterior and anterior regions of individual ovaries, *i.e.* hydrated oocytes were distributed uniformly along the length of each lobe. McGlennon (2003) similarly found no difference in the distribution of hydrated oocytes within *P. auratus* ovaries from Spencer Gulf, South Australia in a 1994 study. In view of this, no further testing for homogeneity in hydrated oocyte distribution within ovaries was undertaken in this study of *P. auratus* from inner Shark Bay. Three transverse sections that typically weighed 30-70 mg each were randomly taken from around the mid-region from either lobe of each ovary sample, and weighed wet to the nearest 0.1 mg. Each section was placed on a microscope slide and covered in glycerine. The oocytes were loosened after 10-15 minutes by tapping the tissue section gently with the blunt tip of a pair of forceps, after which 3-4 more drops of glycerin were added, and the sample spread over the microscope slide. Hydrated oocytes (diameter range 370 - 740 μm , mean 555 μm , Mackie *et al.* 2008) were counted in each section using a dissecting microscope (magnification $\times 10$). Batch fecundity for each female was calculated by multiplying the mean number of hydrated oocytes per gram of ovary section by the total weight of both ovaries.

Crossland (1977b) showed the relationship between female body length and fecundity in *P. auratus* to be positive and non-linear. Because most of the *P. auratus* samples from the inner gulfs of Shark Bay were not weighed, individual values of batch fecundity (F) were plotted against fork length (FL) in this study. The relationships between F and FL for females from each sampling area and survey year between 1998 and 2003 were then described using a nonlinear model of the form,

$$F = a FL^b \quad \text{Eqn 3.3}$$

where a and b are parameters to be estimated. Initially, the resultant regression curves ! were compared within areas among years (‘Year’ effect) using the following model,

$$F_{ij} = a_i FL^{b_{i1} + b_{i2}I(j=2) + \dots + b_{in_j}I(j=n_j)} \quad \text{Eqn 3.4}$$

Here F_{ij} is the fecundity of a female in area i and year j ; FL_{ij} is the fork length of a female in area i and year j ; $I()$ is the identity function that is 1 if the condition is true (e.g. $j = 2$) and 0 otherwise; n_j is the number of year comparisons for area i and a_i , $b_{i1}, \dots, b_{in_j}$ are parameters to be estimated. Year comparisons were designed so that one year (i.e., $j = 1$) was considered the control (chosen to be the first year sampled for that area, i.e. 1998) and all remaining years were then compared to that year. In effect, b_{ij} represents the difference between the first year of sampling and the $(j+1)$ th year for area i and b_{i1} is the effect for the year taken to be the control. With this approach, if resulting estimates of $b_{i2}, \dots, b_{in_j}$ are found not to differ significantly from 0, then year effects are considered to be statistically insignificant. A similar approach was then employed, using pooled data, to compare the relationship among the areas, thereby testing for an ‘Area’ affect.

3.3 Results

3.3.1 Length-weight relationship

There was no difference between the relationships of natural log-transformed weight (WW , g) against length (FL , mm) for *P. auratus* from the Eastern Gulf and Denham Sound (no weights were available for Freycinet Estuary fish) (t-test, $df = 315$, between slopes $P = 0.608$, between intercepts $P = 0.732$). After data for these two areas were pooled, the relationship $\log WW = 2.6703(\log FL) - 8.817$ ($r^2 = 0.99$) was derived, which, after adjustment for log bias resulted in the non-linear relationship, $WW =$

$0.000148FL^{2.6703}$ (subsequently used to estimate the weight[mass] of each unweighed fish).

3.3.2 Timing and duration of spawning season

Gonadosomatic indices

The mean monthly GSIs of female *P. auratus* $\geq$ the L_{50} (see 3.3.3 Length and age at sexual maturity) rose sharply from around 0.8 in April in both the Eastern Gulf and Denham Sound to reach a peak of around 5.0 in the Eastern Gulf in May and at a lower level around 2.4 in Denham Sound in July (Fig. 3.1). In both these areas female GSIs declined to a base level of around 1 or less between August and September. In contrast, in the Freycinet Estuary, female GSIs rose slightly later in the year, from around 0.8 in May, reached a peak in August-September at around 4.3-4.8 and declined sharply to less than 1 in November. Female mean monthly GSIs were elevated for a longer period in the Freycinet Estuary, *i.e.* June-October, than they were in both the Eastern Gulf and Denham Sound (May-July). Mean monthly GSIs of male *P. auratus* $\geq$ the L_{50} followed essentially the same patterns as females in all three areas (Fig. 3.1). In the Eastern Gulf, male GSIs rose sharply and peaked at a similar level to females in the same month, *i.e.* May. In Denham Sound, however, while male GSIs peaked at a similar level to females in that area, they did so two months earlier, *i.e.* in May. In the Freycinet Estuary, male GSIs peaked at around the same time as with females but did so at a significantly lower level at around 2.7-2.8 compared with 4.8. During the spawning season, both female and male mean GSI values for the Eastern Gulf and Freycinet Estuary were larger by a factor of ~ 2 than values for Denham Sound.

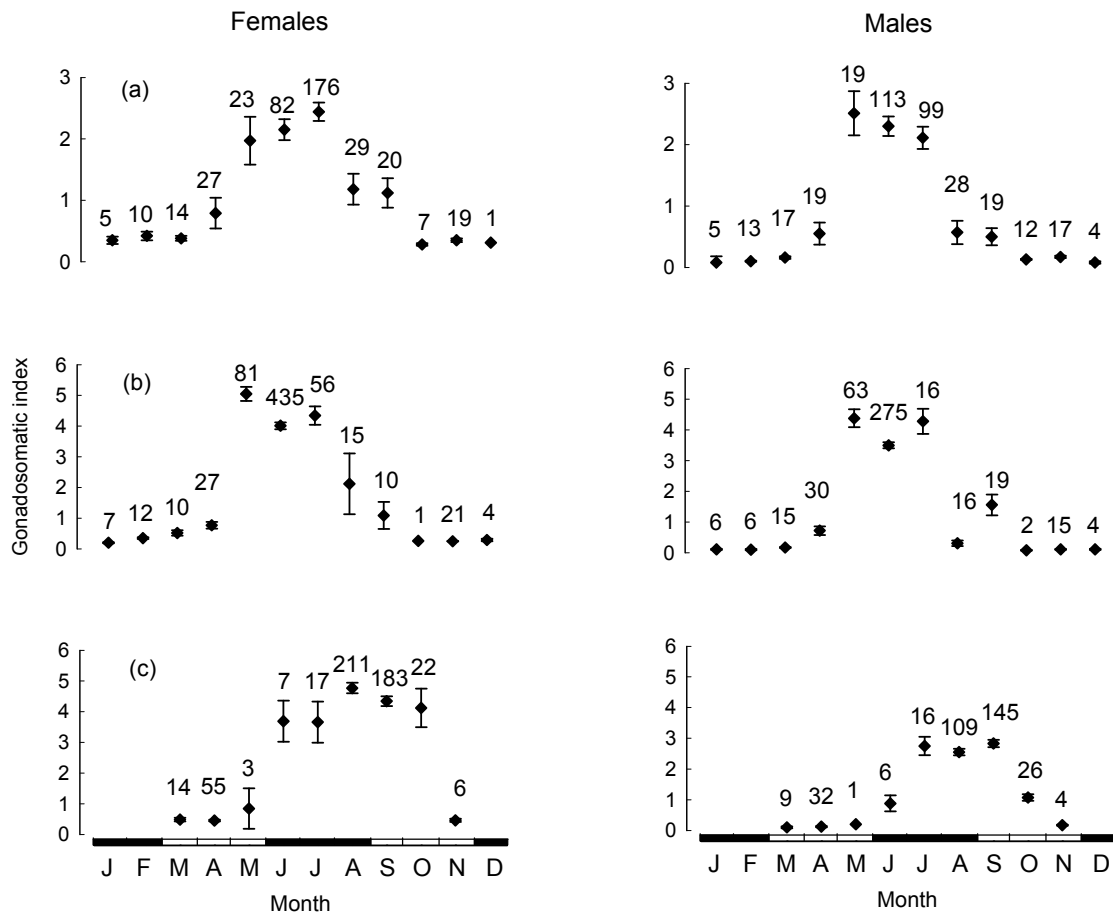


Figure 3.1 Mean monthly gonadosomatic indices ± 1 se for female and male *P. auratus* in (a) Denham Sound, (b) Eastern Gulf and (c) Freycinet Estuary, based on fish $\geq$ the estimated L_{50} . Data for corresponding months from 1997-2004 were pooled. Sample size for each month is shown. Closed rectangles on x-axis represent winter and summer months, open rectangles, spring and autumn months.

Monthly sequential development of gonads

Most of the female *P. auratus* with fork lengths $\geq$ the L_{50} possessed resting ovaries, *i.e.* Stage 2, in samples collected between October and February in the Eastern Gulf and Denham Sound, and in both November and March in the Freycinet Estuary (no samples were obtained for the period December-February) (Fig. 3.2). Females with developing ovaries, *i.e.* Stage 3, were recorded substantially for the first time in March in all three areas (one developing female was obtained from the Eastern Gulf in

February). Developed ovaries, *i.e.* Stage 4, appeared for the first time in samples in April in all three areas. In the Eastern Gulf, females in spawning condition, *i.e.* Stage 5, were recorded between May and September but were dominant in May-July. Females in Denham Sound followed a similar pattern to those in the Eastern Gulf but with a tendency for relatively more Stage 5 ovaries to be present in August-September (Fig. 3.2). In contrast, in the Freycinet Estuary, Stage 5 ovaries were not recorded until June, and were most dominant between August and October (Fig. 3.2). Very few spent stage, *i.e.* Stage 6, females were recorded but those that were observed appeared between June and October in the Eastern Gulf, June and September in Denham Sound and between August and November in the Freycinet Estuary. Similar trends were exhibited by the gonadal stages of male *P. auratus* with fork lengths $\geq$ the L_{50} in all three areas (data not presented).

The trends described above show that in the inner gulfs of Shark Bay *P. auratus* spawn over an extended spawning season of 5-6 months duration from approximately late autumn through to mid-spring, *i.e.* May to October. Based on months when the majority of females sampled possessed Stage 5 ovaries, spawning activity peaked earliest in the Eastern Gulf in May-June, around June-July in Denham Sound, and later in the Freycinet Estuary in August-September.

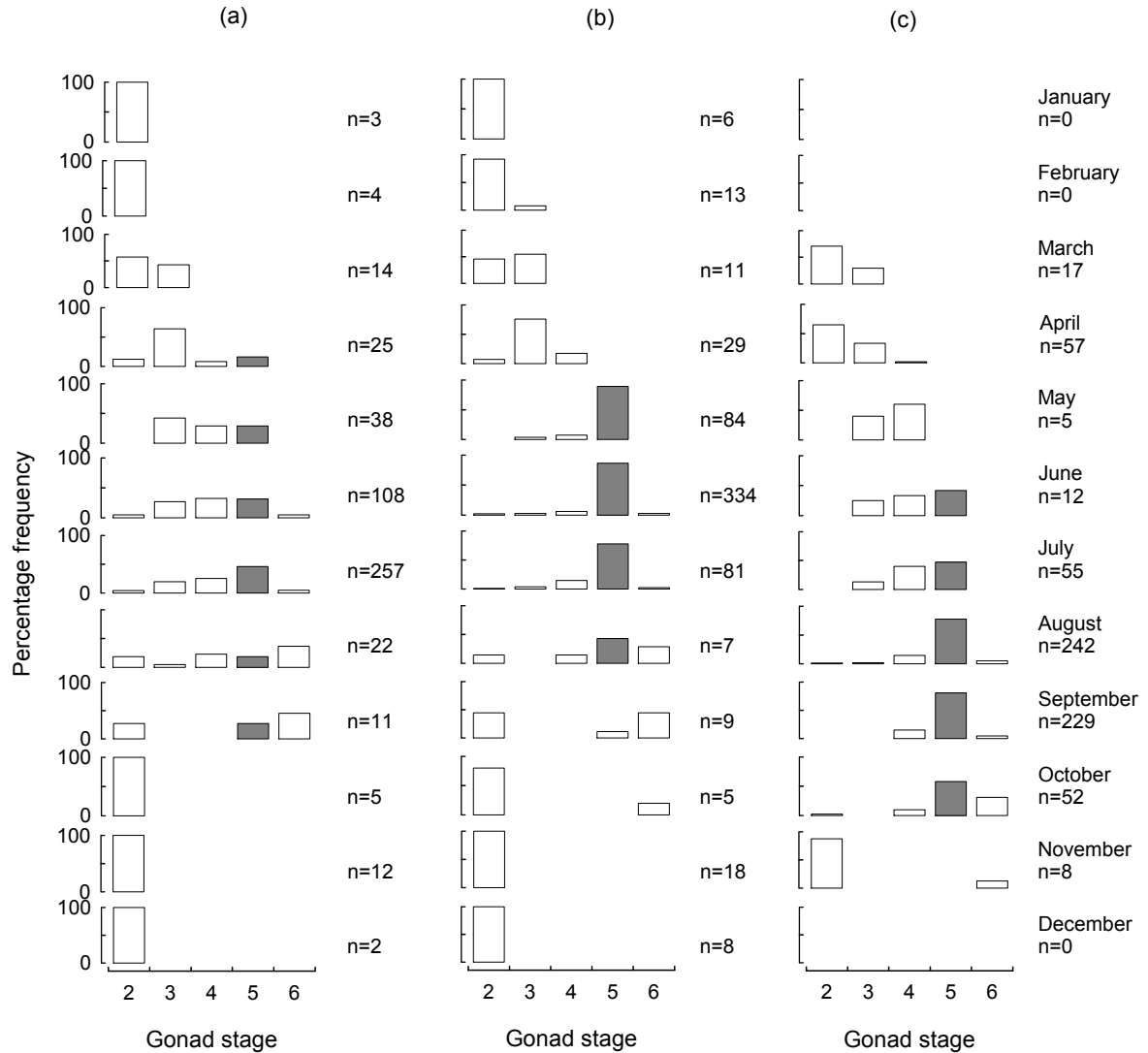


Figure 3.2 Monthly percentage frequency histograms showing sequential development of gonads of female and male *P. auratus* from (a) Denham Sound, (b) Eastern Gulf and (c) Freycinet Estuary based on fish with fork lengths $\geq$ the estimated L_{50} . Data for corresponding months from 1997-2004 were pooled. Sample sizes for each month are shown.

3.3.3 Length and age at sexual maturity

From the trends in GSIs and sequential development of gonads, the months taken to represent the peak period in each area, the data for which could be used to determine the lengths and ages at sexual maturity, were May-June in the Eastern Gulf,

June-July in Denham Sound and August-September in the Freycinet Estuary. In Denham Sound, mature females were first recorded at 241 mm and males at 245 mm, compared with 193 and 186 mm, respectively, in the Eastern Gulf, and 165 and 203 mm, respectively, in the Freycinet Estuary (Fig. 3.3).

Females matured at a larger size and older age than males in each area. The mean lengths at which 50 and 95% of females reached sexual maturity were 401 and 601 mm in Denham Sound, 348 and 484 mm, respectively, in the Eastern Gulf and 420 and 566 mm, respectively, in the Freycinet Estuary (Table 3.2, Fig 3.3). The mean lengths at which 50 and 95% of males reached maturity were 276 and 397 mm, respectively, in Denham Sound, 243 and 403 mm, respectively, in the Eastern Gulf, and 330 and 465 mm, respectively, in the Freycinet Estuary. The mean ages at which 50 and 95% of females and males reached maturity were 5.5 and 9.9 years, and 2.7 and 7.1 years, respectively, in Denham Sound, 3.2 and 5.6 years, and 1.6 and 4.2 years, respectively, in the Eastern Gulf, and 4.5 and 8.4 years, and 2.7 and 5.9 years, respectively, in the Freycinet Estuary (Table 3.2).

The results of likelihood-ratio tests showed that mean lengths at maturity for both females and males differed significantly among the three areas. Pairwise testing indicated that female length at maturity in the Eastern Gulf was significantly different to that in Denham Sound ($P<0.001$) and Freycinet Estuary ($P<0.001$) while differences between Denham Sound and Freycinet females were not significant. Male length at maturity in the Eastern Gulf was not significantly different to that in Denham Sound but it was with that in Freycinet Estuary ($P<0.001$) while differences between Denham Sound and Freycinet males were also significant ($P<0.001$). Mean ages at maturity for

both sexes also differed significantly among the three localities. Female age at maturity ! in the Eastern Gulf was significantly different to that in Denham Sound ($P<0.001$) and Freycinet Estuary ($P<0.001$) while differences between Denham Sound and Freycinet females were not significant (but almost significant). Male age at maturity in the Eastern Gulf was significantly different to that in Denham Sound and Freycinet Estuary ($P<0.001$) and between the latter two areas ($P<0.001$).

Table 3.2 Mean lengths (FL mm) and ages (years) at which 50 (L_{50} , A_{50}) and 95% (L_{95} , A_{95}) of individual female and male *P. auratus* from inner Shark Bay are expected to be mature, estimated from samples collected during the peak spawning period. Values in parentheses are bootstrapped 95% C.I.s. n = sample size

		L_{50} (mm)	L_{95} (mm)	n	A_{50} (years)	A_{95} (years)	n
Denham Sound	females	401 (384-417)	601 (572-629)	482	5.5 (4.9-6.1)	9.9 (8.4-11.8)	202
	males	276 (259-295)	397 (369-423)	380	2.7 (1.6-3.3)	7.1 (5.5-8.9)	139
Eastern Gulf	females	348 (330-365)	484 (464-500)	689	3.2 (2.7-3.5)	5.6 (5.0-6.0)	309
	males	243 (218-267)	403 (374-429)	599	1.6 (1.0-2.2)	4.2 (3.1-5.2)	225
Freycinet Estuary	females	420 (392-452)	566 (542-587)	580	4.5 (3.8-5.1)	8.4 (7.4-9.2)	213
	males	330 (301-352)	465 (436-489)	522	2.7 (2.0-3.3)	5.9 (4.4-7.5)	178

n = sample size

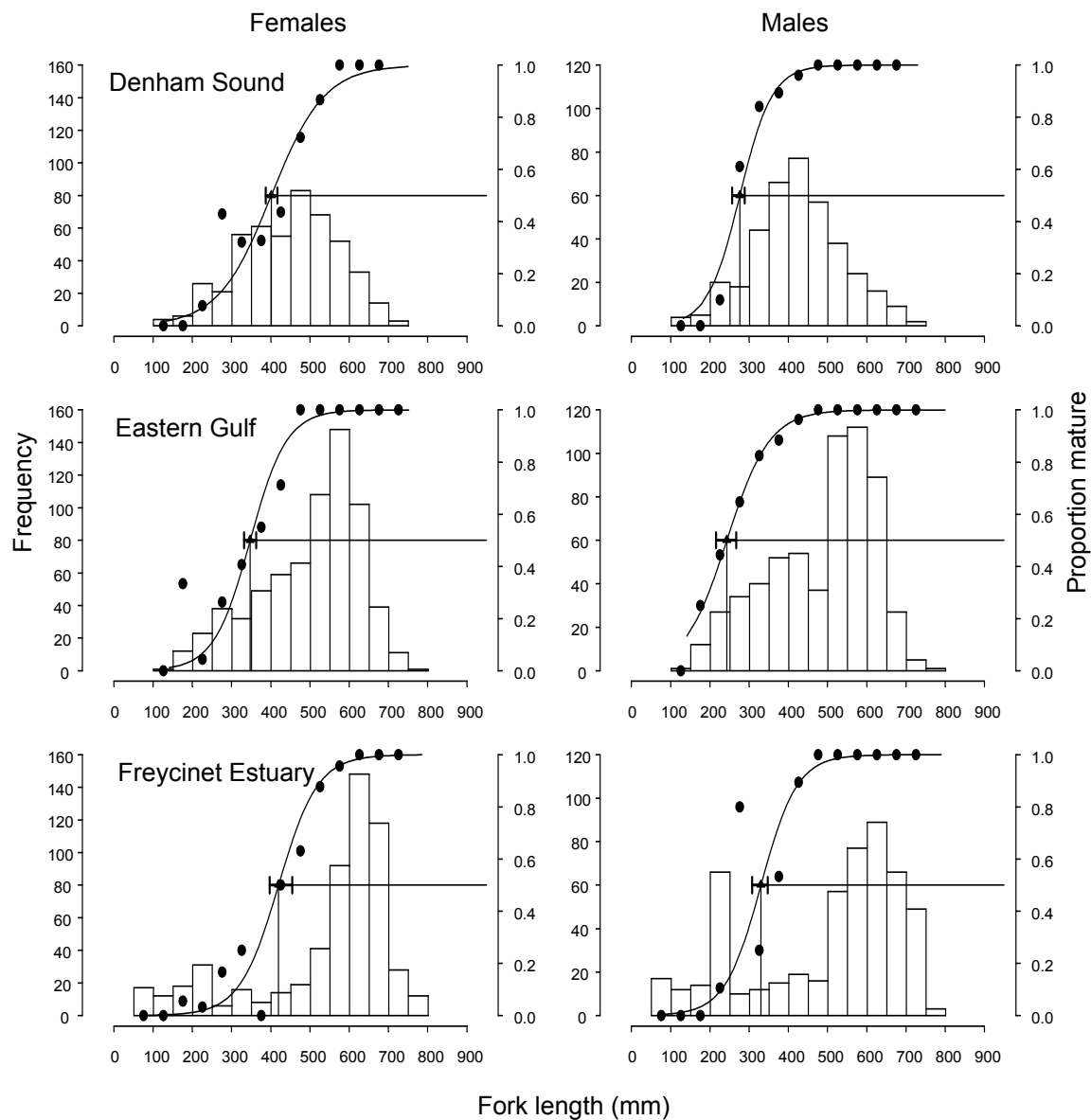


Figure 3.3 The proportions of mature female and male *P. auratus* (•, right y-axis) in each 50 mm length class during the peak spawning period in each area (June-July in Denham Sound; May-June in the Eastern Gulf; August-September in Freycinet Estuary). The numbers of samples within each length class are indicated by the vertical bars and the left y-axis. Values of $L_{50} \pm 95\%$ C.I. are indicated by horizontal bars on the logistic curves.

3.3.4 Batch fecundity

Batch fecundity estimates ranged from 1,510 hydrated oocytes for a 195-mm-FL female to 530,752 hydrated oocytes for a 650-mm-FL female in the Eastern Gulf, from 2,358 hydrated oocytes for a 387-mm-FL female to 473,465 hydrated oocytes for a 615-mm-FL female in Denham Sound and from 4,230 hydrated oocytes for a 195-mm-FL female to 653,261 hydrated oocytes for a 710-mm-FL female in the Freycinet Estuary (Table 3.3). Batch fecundity (F) was positively related to female fork length (FL) in all cases (Fig. 3.4).

Table 3.3 Estimates of batch fecundity (F) for *P. auratus* from inner Shark Bay from samples collected during the peak spawning period 1998-2003.

Area	Year	n	FL range (mm)	F range (eggs $\times 10^3$)
Eastern Gulf	1998	91	172 - 696	3 - 429
	1999	45	348 - 714	23 - 531
	2000	41	284 - 706	18 - 424
	2001	-	-	-
	2002	14	396 - 710	22 - 293
	2003	45	193 - 636	2 - 331
Denham Sound	1998	22	241 - 638	2 - 277
	1999	-	-	-
	2000	27	341 - 619	4 - 474
	2001	-	-	-
	2002	-	-	-
	2003	22	437 - 701	21 - 416
Freycinet Estuary	1998	37	473 - 741	15 - 653
	1999	18	343 - 685	8 - 543
	2000	14	195 - 670	4 - 265
	2001	-	-	-
	2002	32	432 - 725	32 - 660
	2003	-	-	-

n = sample size; FL = fork length

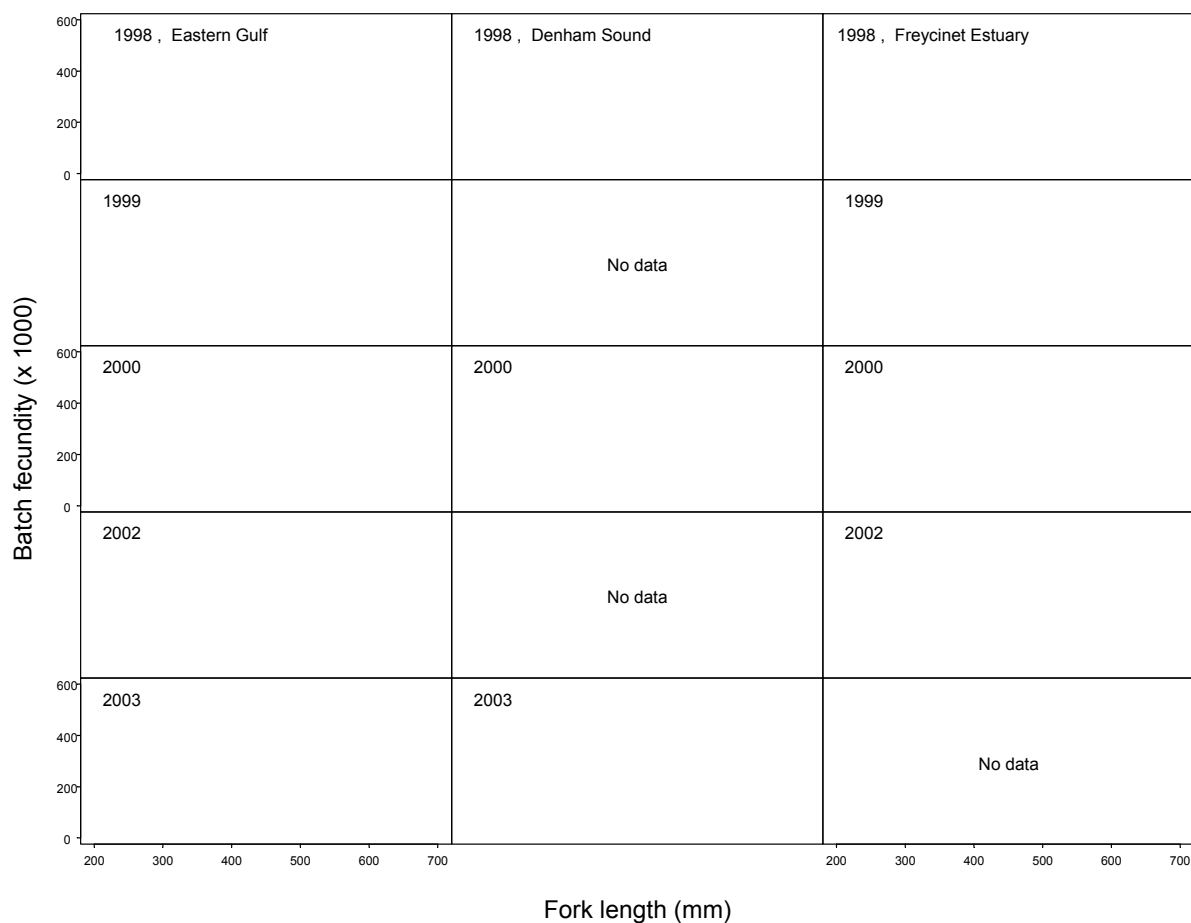


Figure 3.4 Batch fecundity (●) against fork length for *P. auratus* from the Eastern Gulf, ! Denham Sound and Freycinet Estuary estimated from female samples obtained between 1998-2003. Solid line in each case is the common non-linear curve fitted to all data pooled (see Results and Fig. 3.5). Empty panels represent years when Stage 5a ovary samples were not obtained. !

Comparison of non-linear regressions within each area among sample years ('Year' effect) showed no significant difference in nearly all cases (Table 3.4). When the data were pooled within areas and the resultant regressions compared, there was no significant difference between Eastern Gulf and Denham Sound (coefficient = -0.01669, s.e. = 0.01149, $P = 0.147$) and between Eastern Gulf and Freycinet Estuary (coefficient = 0.01402, s.e. = 7.360, $P = 0.058$). Examination of these results and the data in Fig. 3.4 suggested that it was appropriate to pool batch fecundity data from all areas and years (Fig 3.5). A common non-linear model based on the pooled data (all areas, years) was derived as follows:

$$F = 9.436 \times 10^{-5} FL^{3.359}$$

For the above, values of the 95% C.I. of the parameters a and b were 1.32×10^{-4} to 3.2×10^{-4} and 3.34 to 3.38, respectively.

Table 3.4 Significance levels from pairwise comparisons of batch fecundity:fork length non-linear curves to determine effect of ‘Year’ within areas. nd, no data. Values in bold were significant at $P = 0.05$.

Area	Base year	1998	1999	2000	2001	2002	2003
Eastern Gulf	1998	-	0.066	0.480	nd	0.082	0.887
Denham Sound	1998	-	nd	0.046	nd	nd	0.007
Freycinet Estuary	1998	-	0.185	0.308	nd	0.681	nd

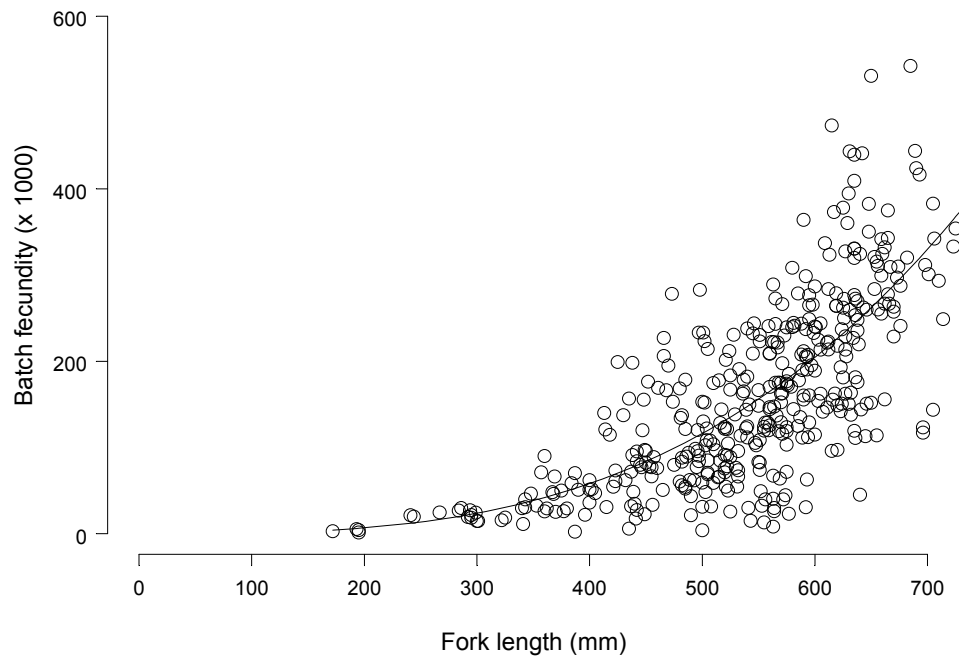


Figure 3.5 Batch fecundity against fork length for Eastern Gulf, Denham Sound and Freycinet pooled for years 1998-2003. Solid line is common non-linear regression curve (see Results).

3.4 Discussion

This study confirms that *P. auratus* inhabiting the inner gulfs of Shark Bay have an annual reproductive cycle with an overall spawning period of 5-6 months duration between May and October (late autumn to mid-spring). The trends exhibited by the mean monthly GSIs and monthly development of the gonads (based on fish with fork lengths $> L_{50}$) identified differences both in the onset of the spawning season, and the timing and duration of the peak spawning period, among the three areas of interest. Spawning in the Eastern Gulf and Denham Sound commenced around May (late autumn) and continued through to September (early spring) with the peak in spawning activity around May-July. In contrast, further to the south, in the Freycinet Estuary, spawning commenced approximately one month later in June (early winter) and continued into October (mid-spring) at least (few samples were obtained for November) with peak spawning around August-September. The production of eggs and larvae over an extended spawning season, as with *P. auratus* here in Shark Bay, is presumably an example of 'bet hedging' (Lambert and Ware 1984), a reproductive strategy of risk-spreading to maximise the survival of eggs/larvae under conditions of environmental variability, and is common in sparids from tropical through to cold temperate environments (Scott and Pankhurst 1992). The longer duration of the spawning season in the Freycinet Estuary may indicate an even greater degree of environmental variability there compared with that experienced in the Eastern Gulf and Denham Sound.

During the periods of spawning activity, the mean monthly GSI values for both females and males from the Eastern Gulf and Freycinet Estuary were approximately double the GSI values for fish in Denham Sound. In addition, the proportion of females

with gonads in spawning condition (Stage 5) was less in Denham Sound in any month ! than in the other two areas. To explore whether the observed differences were related to differences in size composition among the areas, individual GSIs were plotted against fork length for the peak month of spawning in each area (June in Eastern Gulf; July in Denham Sound; August in Freycinet). From this, the range of fish lengths and maximum values of GSI were found to be broadly similar (Eastern Gulf females, 400-700 mm FL, max. GSIs 12-14; Denham Sound females, 400-700 mm FL, max. GSIs 10-11; Freycinet Estuary females 450-750 mm FL, max. GSIs 10-12). When mean monthly GSIs were re-estimated based only on fish $> L_{95}$ (and thus likely to be independent of length), both the magnitude of the GSI maxima and overall seasonal pattern remained unchanged from those based on fish of $> L_{50}$.

In latitudes such as Shark Bay, seasonal changes in water temperature are likely to be the principal environmental trigger for *P. auratus* gonad development and subsequent spawning activity, as with other teleosts (Lam 1983; Bye 1990). In New Zealand, the initiation and conclusion of spawning with the same species occurs in late spring to early summer and is associated with sea surface temperatures (SST) of 15-16 and 19-21°C, respectively (Scott and Pankhurst 1992). While environmental data were not collected during this study, monthly SST data for Shark Bay's inner gulfs from other previous studies indicate less seasonal variation in Denham Sound (annual range ~19-26°C), compared with the Freycinet Estuary (~15-27°C) and the Eastern Gulf (~16-26°C) (Tapp 2003; Fairclough 2005). Optimum temperature conditions for *P. auratus* spawning (16-21°C) exist for around 5-6 months in the Freycinet Estuary compared with 3-4 months in Denham Sound and Eastern Gulf, hence the more protracted spawning season in the former area. While variations in the timing of peak

spawning among the inner Shark Bay locations would, in theory, allow settlement and ! juvenile recruitment to occur at different times, thereby reducing potential for habitat-limited intra-specific competition, this would seem not to be the case here where *P. auratus* eggs and larvae have been shown to be hydrodynamically retained within discrete spawning areas as discussed in Chapter 2 (Nahas *et al.* 2003).

While the duration of the *P. auratus* spawning season in Shark Bay at 5-6 months is similar to that in found in New Zealand (Scott and Pankhurst 1992) and elsewhere in Australia (*e.g.* in South Australia, McGlennon 2003), there are marked differences in the timing of the spawning season between latitudes across the geographic range of the species. Seasonal spawning patterns in Shark Bay are similar to those in other lower latitude populations *e.g.* southern Queensland and northern NSW (Ferrell and Sumpton 1998) and are in contrast with higher latitude populations *e.g.* South Australia, Victoria and New Zealand, where spawning occurs in late spring to late summer (Scott and Pankhurst 1992; Fowler 2002; Coutin *et al.* 2003).

There were significant differences in the mean size and age at 50% maturity between female and male *P. auratus* in the three localities in Shark Bay; females were consistently larger (L_{50}), by ~90-120 mm, and older (A_{50}), by 1.6–2.8 years than males. Sex-based differences in size and age at maturity are characteristic of protogynous species such as *P. auratus* (Francis and Pankhurst 1988) and some other sparids (Pajuelo and Lorenzo 1996). Females reached 50% maturity at the smallest size (348 mm) and youngest age (3.2 years) in the Eastern Gulf, the greatest size (420 mm) in Freycinet but oldest age (5.5 years) in Denham Sound. The relatively high proportions of mature fish observed at the smaller sizes (200–300 mm FL) in all three areas are

likely to be due to the fact that sampling effort was not uniform throughout the year but rather was focussed during the peak spawning period and often in the vicinity of spawning aggregation sites. Smaller fish of both sexes found in association with the larger spawners are likely to be more precocious compared with smaller fish in the company of other immature individuals of similar size. Female sizes at first maturity found here in the Eastern Gulf (193 mm FL) and the Freycinet Estuary (165 mm FL) are much lower than the 270 mm FL reported for Port Phillip Bay, Victoria (Coutin *et al.* 2003). Overall, lengths at 50% maturity estimated for *P. auratus* in the inner gulfs of Shark Bay were similar to those found in Port Phillip Bay, Victoria (363 mm FL, Coutin *et al.* 2003) but considerably greater than those reported for northern Spencer Gulf, South Australia (220-240 mm FL, McGlennon 2003) and Moreton Bay, Queensland (230 mm FL, Sumpton 2002).

Based on the reproductive data pooled between years, both sexes matured at significantly smaller sizes and younger ages in the Eastern Gulf compared with Denham Sound and the Freycinet Estuary. This most likely reflects a phenotypic compensatory response to a significant decline in population size (Trippel 1995) in the Eastern Gulf. While there is no evidence of any major variation in environmental conditions (*e.g.* water temperature and salinity) peculiar to the Eastern Gulf over the study period here, significant recruitment overfishing is acknowledged to have occurred there during the early to mid 1990s when recreational vessels caught large numbers of spawning fish in the vicinity of the main spawning aggregation off Monkey Mia (Stephenson and Jackson 2005). An egg production based survey (Jackson and Cheng 2001) and age-based stock assessment modelling (Jackson *et al.* 2005) both indicate that by around 1997-1999, spawning biomass in the Eastern Gulf had declined to possibly as low as

10% of its unexploited level. Following the introduction of a moratorium on catching *P. auratus* in the Eastern Gulf in June 1998, which remained in place to March 2003, spawning biomass was estimated to have recovered to around 60% of unexploited level by 2005 (Jackson *et al.* 2005).

It should be noted that the mean sizes and ages at 50% maturity reported here are based on the pooled data collected over an 8-year period (*i.e.* 1997-2004). The smaller sizes and younger ages at maturity in the Eastern Gulf may be related to some genotypic change resulting from heavy exploitation of the older, larger spawners. Baudains (1999) reported that a number of rare alleles that were present in Eastern Gulf *P. auratus* samples collected in 1984 (some 10 years before period of serious recruitment overfishing), as part of an earlier allozyme-based study (Johnson *et al.* 1986), were absent in samples collected in 1997 (some 12-13 years later, and several years after the period of recruitment overfishing). Reasons for the loss of these alleles were unclear, however evidence of loss of genetic diversity with another overexploited *P. auratus* population has been shown in New Zealand (Hauser *et al.* 2002).

Because the proven hydrated-oocyte method (Hunter *et al.* 1985) was used here, and the hydrated oocytes were so clearly identifiable in the Shark Bay ovary samples, as was the case with *P. auratus* in New Zealand (Scott 1991), there is a high level of confidence in the accuracy of the batch fecundity estimates for Shark Bay females. Batch fecundity was taken to represent the number of eggs released during each spawning event (*i.e.* daily, see Chapter 5 – Daily egg production method). While fork length was shown to be a good predictor of batch fecundity, and the regression curves fitted the data well in all cases, the Shark Bay females showed a large amount of

variation in batch fecundity with respect to individual length. Based on pooled data for 10 years 1998-2003 and the three areas combined, the mean batch fecundity for 500-700 mm FL females from inner Shark Bay ranged between 106 and 329 thousand hydrated oocytes. While broadly consistent with estimates for a similar size range of female *P. auratus* from Port Phillip Bay, Victoria (131 to 652 thousand hydrated oocytes, Coutin *et al.* 2003) and northern Spencer Gulf, South Australia (171 to 361 thousand hydrated oocytes, estimated from linear regression reported in Fowler 2002), the apparent differences are likely due to the highly conservative approach used in the Shark Bay study, *i.e.* ovaries with early hydrated oocytes and/or 'new' POFs were excluded from the analyses.

Annual variation in fecundity due to variability in environmental conditions is often proposed. However, no significant difference in the relationship between batch fecundity and fish size (fork length) for *P. auratus* among years and localities over a study period of 5 years was found with the exception of Denham Sound in 2003. This is useful in relation to application of the daily egg production method to estimate *P. auratus* spawning biomass, where a common relationship based on a large number of data can therefore be used to predict batch fecundity (see Chapter 5 – Daily egg production method). Interestingly, Fowler *et al.* (1999) found significant spatial variation in the relationship between batch fecundity and fish size between sites separated by < 100 km for King George whiting, *Sillaginodes punctata*, in South Australia. DeMartini (1991) found only minor variation in batch fecundity in four out of five study years with queenfish (*Seriphus politus*), however, in one year, batch fecundity was significantly lower and possibly linked to a major El Nino event.

Chapter 4: Age and growth of *P. auratus* in the inner gulfs of Shark Bay

4.1 Introduction

A comprehensive understanding of the biology of a fish species requires knowledge of the rates of growth and mortality and the ages at which individuals first become sexually mature. Such information is essential for sustainable management of exploited fish stocks. The development of growth models, estimates of mortality rates and determination of stock productivity using age-based stock assessment models are dependent upon accurate estimates of fish age (Hilborn and Walters 1992; Quinn and Deriso 1999). Fish have been aged by counting growth increments observed in a range of calcified structures, *e.g.* scales, dorsal spines, vertebrae and opercula, however, otoliths are the body part most widely used for age determination (Campana 2001). Validating the relationship between otolith growth and fish age ('age validation') is crucial to establishing the reliability of the age determination process and requires (i) a visible increment structure, (ii) knowledge of the periodicity of increment formation and (iii) knowledge of the timing of increment formation. Ageing of fish using otoliths involves the interpretation of growth zones (increments) on a micro (daily) or macro (annual) scale; annual growth increments are usually observed as alternate opaque and translucent zones (termed annuli, Kalish *et al.* 1995). Marginal increment analysis is a technique commonly used for age validation (Campana 2001) and is based on the assumption that, if annual growth increments are laid down once per year, there should be a clear and measurable periodic pattern of growth at the otolith edge. In contrast to the difficulties that accompany marginal increment analysis, chemical marking of otoliths in wild fish can provide one of the most unequivocal methods of age validation (Campana 2001).

Age and growth of *P. auratus* have been extensively studied in New Zealand ! (see Paul 1992 for review of research 1921-1990; Francis R.I.C.C. *et al.* 1992; Francis M.P. *et al.* 1992, 1993; Francis M.P. 1994; Walsh 1997; Millar *et al.* 1999; Davies *et al.* 2003) and Australia (Jones 1984; Ferrell *et al.* 1992; McGlennon *et al.* 2000; Sumpton 2002; Ferrell 2004; Fowler *et al.* 2004; Moran *et al.* 2005). While annual growth increments on scales were used to age individuals of the species in earlier studies (MacDonald 1982; Jones 1984; Thomas 1985; Paul 1992), they have been shown to underestimate age in older fish (Paul 1976; McGlennon *et al.* 2000). The interpretation of alternating opaque and translucent zones in sectioned sagittal otoliths is now routinely used for ageing *P. auratus* both in New Zealand and Australia (Francis R.I.C.C. *et al.* 1992; Ferrell and Morison 1993; McGlennon *et al.* 2000; Coutin 2003; Fowler *et al.* 2004; Moran *et al.* 2005). Annulus formation has been validated as annual for 0+ and 1+ fish in eastern Australia (Ferrell *et al.* 1992) and for fish up to 30 years in New Zealand (Francis R.I.C.C. *et al.* 1992). There are, however, currently no published studies in the primary literature on age and growth of *P. auratus* in the Shark Bay region or more generally for Western Australian waters.

Given the complex nature of *P. auratus* population structure in inner Shark Bay and the strong environmental gradients that are a key feature of the marine environment (see Chapter 1 – General introduction), it was hypothesised *a priori* that differences in the growth characteristics of *P. auratus* inhabiting the three main localities (Eastern Gulf, Denham Sound and Freycinet Estuary) were likely to exist. In addition, there is evidence that *P. auratus* in these respective areas have historically been subjected to different levels of exploitation, the consequences of which would be reflected in differences in population age structures between the Eastern Gulf, Denham Sound and

the Freycinet Estuary. The aims of the research described in this chapter were 1) to validate that growth increments (opaque zones) in sagittal otoliths of *P. auratus* from the inner gulfs of Shark Bay are formed annually, 2) to fit growth models to lengths at age and compare growth between females and males and among the three sampling localities, 3) to determine and compare *P. auratus* age structures in the Eastern Gulf, Denham Sound and Freycinet Estuary and, 4) to take advantage of a five year moratorium on fishing for *P. auratus* in the Eastern Gulf (June 1998-March 2003) to directly estimate the instantaneous rate of natural mortality, M , for the species.

4.2 Materials and Methods

Details of the collection of *P. auratus* samples are described in Chapter 3 (Reproductive biology).

4.2.1 Otolith preparation

Both sagittal otoliths were removed from each fish, cleaned, dried and stored in paper envelopes. One randomly-selected otolith from each pair was embedded in clear polyester resin and a single transverse section (0.3–0.5 mm thickness) taken through the primordium with a low-speed diamond-blade saw. Sections were mounted on slides and examined microscopically under reflected light against a black background using a video camera linked to an Apple-MacIntosh computer. Section images were analysed and marginal increments measured using ImageJ software (National Institutes of Health, USA, <http://rsb.info.nih.gov/ij/Java>).

For each section, completed opaque zones between the primordium and the proximal edge were counted along a common axis at the ventral margin of the *sulcus*

acusticus (terminology as per Kalish *et al.* 1995, Fig. 4.1). The outer edge of each ! section was categorised as either (i) opaque, (ii) narrow translucent, *i.e.* less than 50% of the previous translucent zone or (iii) wide translucent, *i.e.* more than 50% of previous translucent zone.

4.2.2 Precision and bias

Each section was read twice, and in cases where opaque zone counts differed, on a third occasion, by a single experienced reader, without knowledge of date of capture, fish length or the result of any previous reading. Otoliths were included in the analysis (*i.e.* opaque zone counts were accepted) only in cases where there was agreement between any two readings (either the 1st and 2nd or 1st and 3rd). The precision in opaque zone counts between the 1st and 2nd readings of the primary reader was estimated using an index of average percent error (IAPE, Campana *et al.* 1995 *sensu* Beamish and Fournier 1981). A second experienced reader independently read a random sub-sample of sections from a representative size range of fish to investigate between-reader bias using an age-bias plot (Campana *et al.* 1995).

4.2.3 Validation

Marginal increment analysis (Campana 2001) was used to determine whether the opaque zones were formed annually. Each marginal increment was measured (to the nearest 0.01 mm) as the distance from the outer edge of the ultimate opaque zone to the proximal edge of the section along the common axis and expressed as (i) a proportion of the distance between the primordium and the outer edge of the opaque zone (where only one opaque zone was present) or (ii) as a proportion of the distance between the outer edges of the ultimate and penultimate opaque zones (where more than two opaque zones

were present). Marginal increments for otoliths with the same number of completed ! opaque zones were pooled over years and plotted against month of collection. Marginal increment data for the Eastern Gulf, Denham Sound and the Freycinet Estuary samples were pooled for purposes of age validation.

Chemically-marked otoliths recovered from *P. auratus* that had been tagged and released and subsequently recaptured as part of a study investigating fine-scale movement patterns in the inner gulfs (G. Jackson unpublished data) were also used to validate the periodicity of opaque zone formation. Between 1998-2002, a total of 2,105 fish were tagged between the pterygiophores approximately 1-2 cm below the dorsal fin with either anchor (FloyTag model FT-94, length 80 mm) or dart tags (FloyTag model FT-1-97, length 105 mm). Fish were also injected in the gut cavity with either oxytetracycline (OTC, dosage rate 25 mg kg⁻¹ body weight) or calcein (dosage rate 10 mg kg⁻¹ body weight) prior to release at various locations throughout both gulfs (G. Jackson unpublished data) (Fig. 4.2). Otoliths that were subsequently recovered from a total of 26 tagged fish with a range of times at liberty were sectioned and viewed (magnification x 30) under ultra-violet light. For sections where the chemical mark was visible (n = 12), colour photographs taken of the region containing the mark and the proximal edge ventral to the sulcus were digitised and then superimposed on corresponding white light images of the same sections using Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA). Without knowledge of the times at liberty, the images were examined to determine, where possible, whether the chemical mark was located within an opaque or translucent zone and the number and type of zone(s) to the outside of the chemical mark. The widths of each translucent and opaque zone between the primordium and proximal edge were measured and plotted relative to the chemical

mark and the known dates of release and recapture. !

4.2.4 First opaque zone

The position of the first opaque zone in *P. auratus* sections was determined using a distinct inflection point in the sagitta-subcupular meshwork fibre zone (SMF), a feature radiating from the primordium to the ventral otolith margin (Fig. 4.1) that appears as a light band under reflected light, widely recognised as a useful marker in *P. auratus* and other sparids (Francis M.P. *et al.* 1992; Ferrell and Morison 1993; Morison *et al.* 1998). The age at which the first opaque zone became delineated was validated by plotting measurements of the distance between the primordium and the section proximal edge against month of collection for sections without a completed opaque zone.

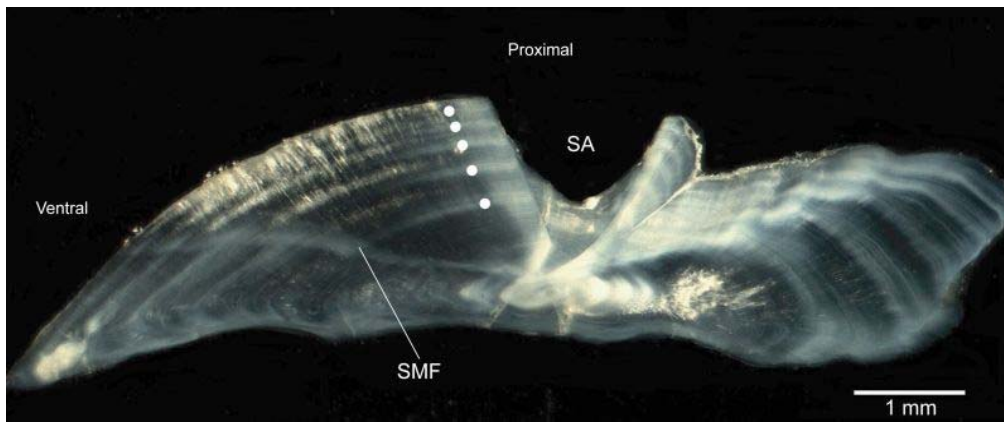


Figure 4.1 Transverse section of sagittal otolith from a 5-year-old (532 mm FL) *P. auratus* from the inner gulfs of Shark Bay viewed under reflected light showing opaque zones (●) along a common axis ventral to the *sulcus acusticus* (SA) and the inflection point in the sagitta-subcupular meshwork fibre zone (SMF).



Figure 4.2 Injecting a tagged *P. auratus* in Denham Sound, Shark Bay, with oxytetracycline. Note two red FloyTag dart tags just visible below dorsal fin.

4.2.5 Growth

Birth dates were determined from the approximate times of peak spawning as identified by trends in the gonadosomatic indices and monthly progression of gonad maturity stages (see Chapter 3 - Reproductive biology). Ages (decimal years) were assigned to individual *P. auratus* using opaque zone counts that were adjusted to take

account of the month of capture, birth date and increment growth at the otolith edge. !
 von Bertalanffy growth (vBG) curves were fitted to the lengths (FL) at age (i) for individual females and males separately and (ii) all individuals combined, for each area, using non-linear regression in S-PLUS (Insightful Corp., Seattle, WA, USA). The von Bertalanffy growth equation is

$$L_t = L_{\infty} \{1 - \exp[-K(t - t_0)]\} \quad \text{Eqn 4.1}$$

where L_t = mean length of fish (mm, FL) at age t (year);

L_{∞} = mean asymptotic length (mm, FL);

K = the growth coefficient (year^{-1});

t = age of fish (year);

t_0 = hypothetical age (year) at which mean length is zero if fish had always grown at the rate described by the equation.

Juvenile *P. auratus* for which sex could not be determined were randomly assigned to either the male or female sets of length-at-age data. Adequacy of fit for all cases was investigated by plotting standardised residuals against the observed ages. The growth curves for females and males were compared both within and among areas using a likelihood-ratio test (Kimura 1980) under the assumption that the residual variances differed (Cerrato 1990) and with the significance level for multiple comparisons adjusted using the Bonferroni method (Quinn and Keough 2003).

4.2.6 Age structure

Catches of *P. auratus* landed by recreational fishers at the Denham and Nanga boat ramps during recreational fishing surveys conducted by the Department of Fisheries WA in 1998 and all years 2000-2003 (no survey undertaken in 1999) were randomly selected and then measured (mm, total length, TL) (Sumner and Malseed

2001, 2002; Sumner *et al.* 2002). Although these length frequency data were biased as a result of legal length regulations in place at the time the surveys were conducted, the data were taken to be representative of the retained proportion of the ‘fished’ populations in Denham Sound and Freycinet Estuary in each year, *i.e.* the proportion of fish vulnerable to the gear (hook and line) and landed by fishers.

Total lengths were converted to fork lengths (mm, FL) using

$$FL = 0.3 + 0.846TL \text{ (n = 244, } r^2 = 0.99 \text{) (Moran and Burton 1990).}$$

Length frequencies from each year were converted to age frequencies using age-length keys (Ricker 1975; Quinn and Deriso 1999). Because it was not possible to obtain adequate numbers of otoliths directly from recreational catches of *P. auratus*, age-length keys were determined using length-at-age data for comparable years derived from otolith samples collected during fishery-independent research surveys. For years when the numbers of fish that were directly aged were inadequate, lengths at age for that year and the year immediately prior (same locality) were pooled. While it is recognised that such an approach produces biased estimates (Quinn and Deriso 1999), it was nonetheless considered a useful exercise in the context of the objectives of this study, *i.e.* to provide some insights to age structure of populations in the three study areas. Due to the low sample numbers of older fish, fish of 10 years and older from Denham Sound, and 17 years and older from the Freycinet Estuary, were allocated to the 10+ and 17+ age groups, respectively.

In the Eastern Gulf, where *P. auratus* were protected for most of the period of this study by a fishing moratorium (June 1998 to March 2003), length frequency data obtained from fishery-independent research surveys were supplemented by logbook

data provided by a limited number of participating volunteer recreational boat fishers. ! These people were asked to fish for *P. auratus*, using their local knowledge, as they would if no moratorium had been in place (research-exemptions were provided to the vessels' skippers) and record the fork lengths of all *P. auratus* caught and subsequently released (as required by the regulations) between 1998 and 2003. Length frequency data for fish of the minimum legal size and above, as applied in the other areas (Denham Sound, Freycinet Estuary) for each year 1998-2002, were converted to age-frequencies using age-length keys in a similar manner as previously described. Due to the low sample numbers of older fish, fish of 12 years and older from the Eastern Gulf were allocated to the 12+ age group.

Age structures for all three localities were plotted as frequency histograms to determine the contributions made by each age class in each year. Multiple pair-wise comparisons using a Kolmogorov-Smirnov test were used to compare age frequencies within each locality among years and for each year among the three localities (Zar 1984).

4.2.7 Estimating natural mortality

During the *P. auratus* moratorium period, commercial and recreational fishing for other species was permitted in the Eastern Gulf. Abundance-at-age data for *P. auratus* obtained from fishery-independent research surveys conducted during the moratorium were used to estimate the instantaneous rate of natural mortality, M , for the species under the assumption that fishing mortality (in the Eastern Gulf) had been effectively reduced to nil. This assumption was predicated on (i) a high level of recreational compliance with the fishing moratorium and (ii) high survival rates of

snapper caught and returned while fishing for other species (related to robust nature of the species and the shallowness of the Eastern Gulf). Length frequency data (research surveys, recreational logbooks) for the Eastern Gulf for the period 1998-2003 were converted to age-frequencies using age-length keys as previously described (see 4.2.6 Age structure).

Catches at age within each year were converted to catches per unit of effort (cpue) at age by dividing each catch by fishing effort (boat fishing days) to eliminate bias due to differences in sampling intensity among years. It was assumed that, from an age of t_c , catchability was age-independent and remained constant over time. The age t_c was taken as the age at which *P. auratus* of each year class became fully vulnerable to the sampling gear (rod and line). Recognising the limited number of ages for which relative abundance data for each year class were available and the noise in those data, t_c was determined as the youngest age for which the relative abundance-at-age data exceeded 70% of the value at the peak of the catch curve formed when abundance-at-age data for that year class were plotted against year by year class. The analysis used only data from those year classes in which there were three or more values of relative abundance at age, *i.e.* year classes 1990 to 1997.

The cpue of each year class of fish of age t_c or older that was present in 1998 or subsequently attained age t_c was denoted by $n_{0,y}$, where y identifies the year-class. The cpue of each year class was tracked through subsequent samples, becoming $n_{1,y}$, then $n_{2,y}$, etc., where the first subscript refers to the number of years that had elapsed since 1998 or since the fully-vulnerable fish in the year-class first became available in

the research samples as a fish of age t_c , during which period they experienced only natural mortality. It was assumed that the values of cpue were indices of *P. auratus* abundance, $n_{j,y}^*$, with a log-normally distributed error, *i.e.* $n_{j,y} = n_{j,y}^* \exp(\varepsilon_{j,y})$, where $\varepsilon_{j,y}$ is a random variate drawn from a normal distribution with mean of zero and common variance σ^2 , *i.e.* $\varepsilon_{j,y} \sim N(0, \sigma^2)$.

As the number of fish within each of these year classes and years after entering the vulnerable proportion of the stock was subject only to natural mortality,

$$n_{j,y}^* = n_{j-1,y}^* \exp(-M) = n_{0,y}^* \exp(-jM). \quad \text{Eqn 4.2}$$

Accordingly,

$$\log_e(n_{j,y}) = \log_e(n_{0,y}^*) - jM + \varepsilon_{j,y}. \quad \text{Eqn 4.3}$$

Logarithms of the observed cpue thus had a linear relationship with the number of years that had elapsed since the fish first began to experience only natural mortality. Hence, natural mortality may be estimated as the negative value of the slope of the linear regression, *i.e.* traditional catch curve analysis applied to a year class tracked through successive years.

The data from the various year classes were combined to obtain a single estimate of the instantaneous rate of natural mortality rather than separate estimates of M for each year-class. Data were analysed using the general linear model (GLM) procedure in SPSS (SPSS Inc., Chicago, IL, USA), using an implicit model of the form

$$Y_i = \sum_{j=1}^m \beta_j X_j + \gamma Z_i + \eta_i \quad \text{Eqn 4.4}$$

where the dependent variable Y represents $\log_e(n_{j,y})$, the dummy variables X_j that are set to 0 or 1 and identify to which of the m year classes the record pertains, the covariate Z is the number of years of natural mortality experienced by the year class since 1992 or when it first became fully vulnerable to research sampling, the values of β and γ are coefficients estimated by the procedure, and η is a normally-distributed random variate. This model is equivalent to that described by Equation 4.3, with the additional assumption that each year-class experiences a common level of natural mortality.

Following the GLM analysis, natural mortality was taken as the value $-\gamma$ and estimates of the 95% confidence limits for γ , calculated by the GLM procedure, were negated to provide estimates of the corresponding confidence limits for M . The lower confidence interval of M was taken as the maximum of this estimate of the lower confidence bound and zero.

4.3 Results

4.3.1 Precision and bias

Between 1997 and 2004, otolith samples were obtained from a total of 2,560 individual *P. auratus* and were subsequently successfully aged; 908 from the Eastern Gulf (length range 63-752 mm, FL), 681 from Denham Sound (length range 58–750 mm, FL), and 791 from the Freycinet Estuary (length range 47–800 mm, FL). The opaque zones, which appeared as thin white bands or lines on the otolith sections when viewed under reflected light, were relatively clear in most cases (Figure 4.3). The number of completed opaque zones ranged from 1 to 31. No systematic bias was evident from the sub-sample of sections read independently by two readers ($n = 336$,

Fig. 4.4). The level of precision between the 1st and 2nd readings for the primary reader was high overall (IAPE = 5.4%). Otolith readability varied with location with precision highest for sections from the Eastern Gulf (IAPE = 2.3%) compared with the Freycinet Estuary (IAPE = 4.4%) and Denham Sound (IAPE = 6.2%).

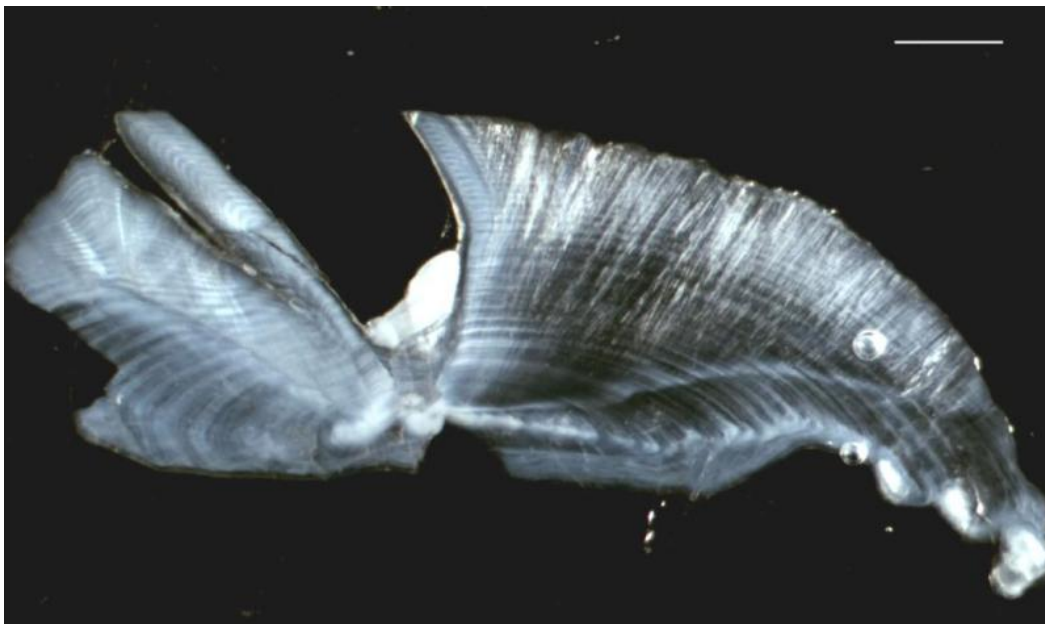
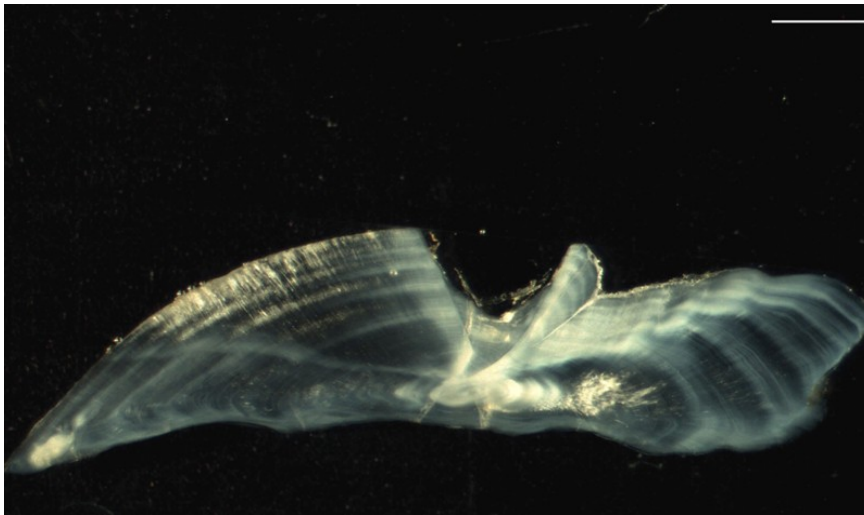
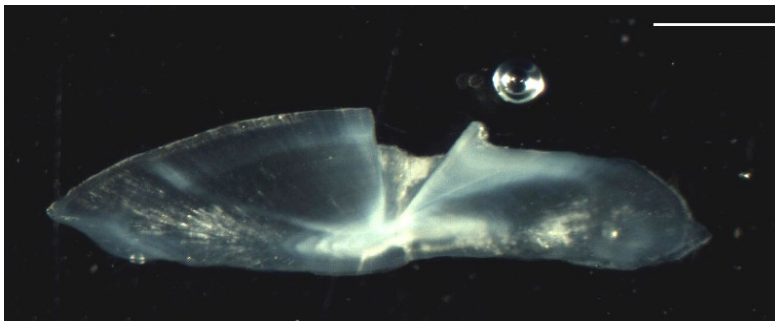


Figure 4.3 Sectioned *P. auratus* otoliths from the inner gulfs of Shark Bay as seen under reflected light, (top) a 193 mm FL fish with one completed opaque zone, (middle) a 523 mm FL fish with five completed opaque zones and (bottom) a 711 mm FL fish with 28 completed opaque zones. Scale bars = 1 mm.

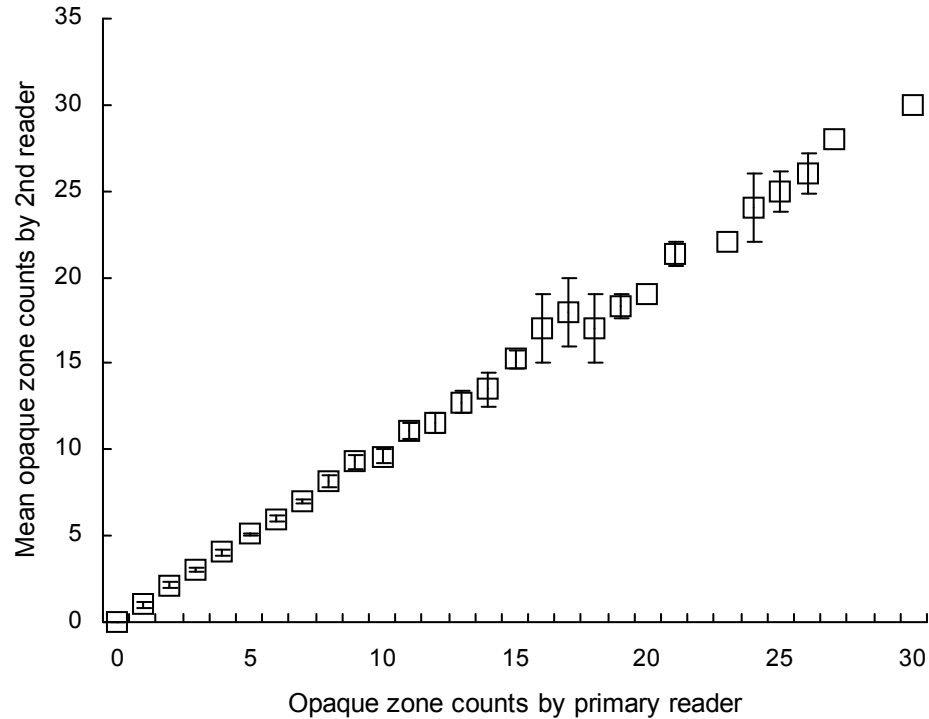


Figure 4.4 Between reader bias in opaque zone counts from a sub-sample ($n = 336$) of *P. auratus* otolith sections from inner Shark Bay. The counts of opaque zones (☐) are mean values assigned by the primary reader and a second reader for sections initially assigned a single value by primary reader, plotted against a 1:1 line of equivalence (solid line). Error bars represent ± 2 s.e.; lack of bars in some cases indicates insufficient data for some count groups.

4.3.2 Validation

Mean marginal increments (data for sections with both opaque and translucent edges combined) from sectioned *P. auratus* otoliths plotted against month in the conventional manner showed some seasonal pattern (solid lines in Figure 4.5). However, when increment data for sections with translucent edges (both narrow and wide categories) were plotted against month separately from those with opaque edges, a much clearer pattern emerged and identified that opaque zones were both formed and delineated (completed) over a six to seven month period. The pattern of increase and decrease in the mean monthly marginal increments was consistent across all count

groups and confirmed that a single opaque zone is laid down each year in *P. auratus* ' otoliths in inner Shark Bay (Fig. 4.5).

While translucent edges were apparent in all months of the year, sections only had translucent edges between January and April. Mean monthly marginal increments on sections (all edge-types combined) with more than one opaque zone were lowest in January at between 0.23 (sections with 9 or more opaque zones) and 0.39 (sections with 2-3 opaque zones) and increased steadily through to April when they reached between 0.50 (sections with 6-8 opaque zones) and 0.58 (sections with 4-5 opaque zones). Opaque edges first appeared in May and were present through to December, implying that the timing of the onset of opaque zone formation was highly variable between individuals. Marginal increments for sections with opaque edges reached maxima (0.68-0.78) between June-December and minima for sections with translucent edges (0.17-0.36) between August-October. From the consistent departure in trends of mean marginal increments for sections with opaque edges compared with translucent edges, the period of opaque zone delineation was taken to typically peak over an extended period between August and November, *i.e.* late winter to late spring.

While otoliths with a single completed opaque zone were not sampled in all months, and samples sizes were low when they were obtained, trends in the mean marginal increments were consistent with those observed in otoliths with more than one opaque zone. Measurements of the radial distance from the otolith core to the outer edge for sections with no completed opaque zones (fish between 47 and 111 mm FL obtained from trawl surveys), showed the first opaque zone appearing at the otolith edge for the first time around May-June (Fig. 4.5). This pattern was similar to that observed

for older fish and, although samples were not collected during months August–October, the appearance of sections with translucent edges and smaller radii to the otolith edge were consistent with trends for fish with one or more completed opaque zones. From this it was determined that the first opaque zone became delineated between August–November when, in the Eastern Gulf and Denham Sound juveniles would be around 14–17 months of age (based on an assumed birth date of June 1, see Growth) and, in the Freycinet Estuary, around 12–15 months of age (assumed birth date of August 1, see 4.3.3 Growth).

Sections of the chemically-marked otoliths recovered from tagged fish on which the mark was visible (Figs 4.6 and 4.7) further validated that opaque zones were laid down annually. Most of these fish were tagged and released around June–July, *i.e.* winter, with the chemical marks subsequently found to be located at the outermost region of a translucent zone immediately adjacent to the next opaque zone in all cases except one (Table 4.1). Eight of the recaptured fish had been at liberty for more than 300 days, *i.e.* approximately 1 year, and had formed at least one complete opaque zone during that time, while only one fish, at liberty for more than 700 days, *i.e.* approximately 2 years, had formed two complete opaque zones over this period.

Both marginal increment analysis and the chemically-marked otoliths showed that counts of opaque zones, in combination with month of capture, birth date and increment growth at the otolith edge during the defined period of opaque zone delineation can be used to age *P. auratus* from the inner gulfs of Shark Bay.

Table 4.1 Details of otoliths from tagged *P. auratus* injected with OTC or calcein and subsequently recaptured (trans = translucent zone). *FL* = fork length (mm, FL) at release.

Fish id #	<i>FL</i> (mm)	Days at liberty	Mark location	Number opaque zones outside of mark	Otolith edge	Number of opaque zones
nw990630-01	456	369	trans	1	trans	5
nw990703-01	397	372	trans	2	opaque	6
eg000705-2	464	733	trans	2	trans	4
nw991122-01	392	237	trans	1	trans	5
ui000702-3	354	460	trans	2	opaque	4
sw000813-01	492	136	trans	1	trans	5
eg010712-1	434	402	trans	2	opaque	5
eg010416-7	?	315	trans	1	trans	6
nw010603-1	323	334	opaque	1	opaque	5
nw010530-7	475	330	trans	1	trans	5
nw011210-01	342	95	trans	1	opaque	5
nw011211-01	340	61	trans	1	opaque	5

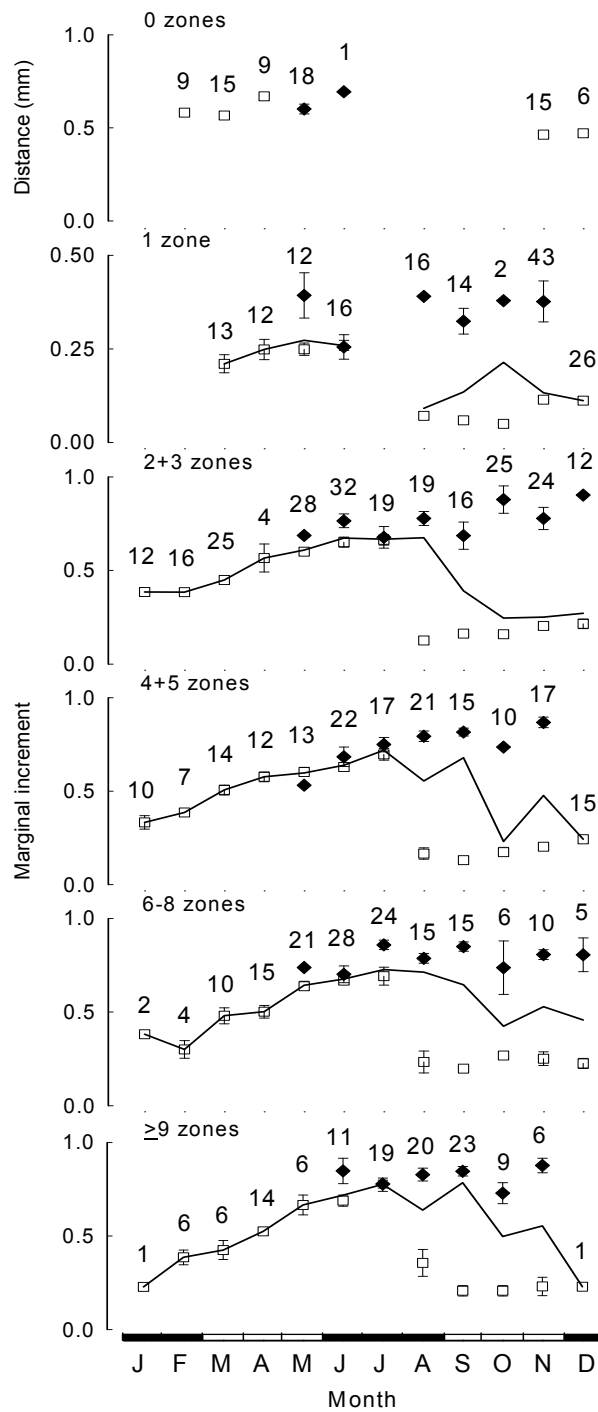


Figure 4.5 Mean monthly marginal increments ± 1 s.e. on sectioned otoliths of *P. auratus* from the inner gulfs of Shark Bay. Data for sections with translucent (◆) and opaque (□) edges are plotted separately in each case; solid lines represents mean monthly values for all otolith edge types combined. Sample size for each month is shown. Note, in the upper figure (0 opaque zones), the y-axis represents the radial distance (mm) measured between primordium and proximal edge.

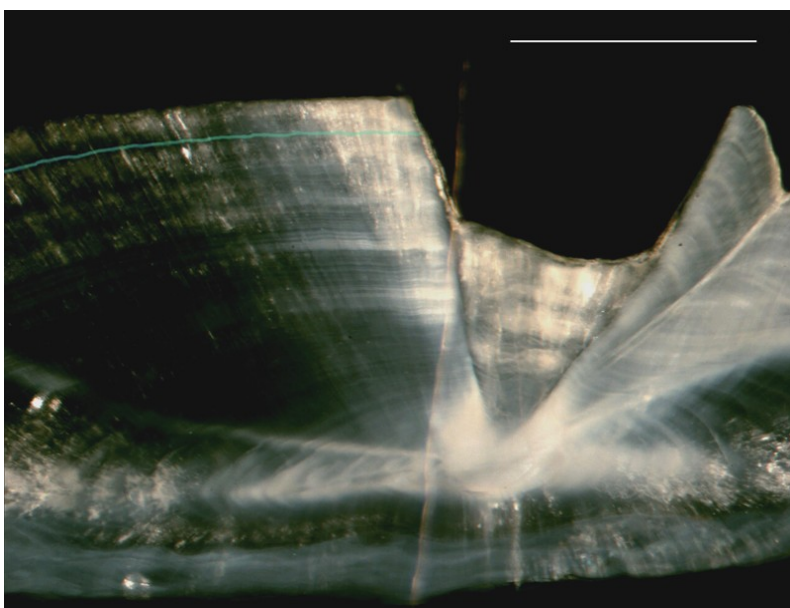


Figure 4.6 Sample nw990630-1, at liberty for 369 days following chemical-marking, (top) white (reflected) light image of whole section, (middle) ultra-violet image showing chemical mark (OTC in this case) and (bottom) composite image showing OTC mark in translucent zone with one completed opaque zone to outside of chemical mark. Scale bars = 1 mm.

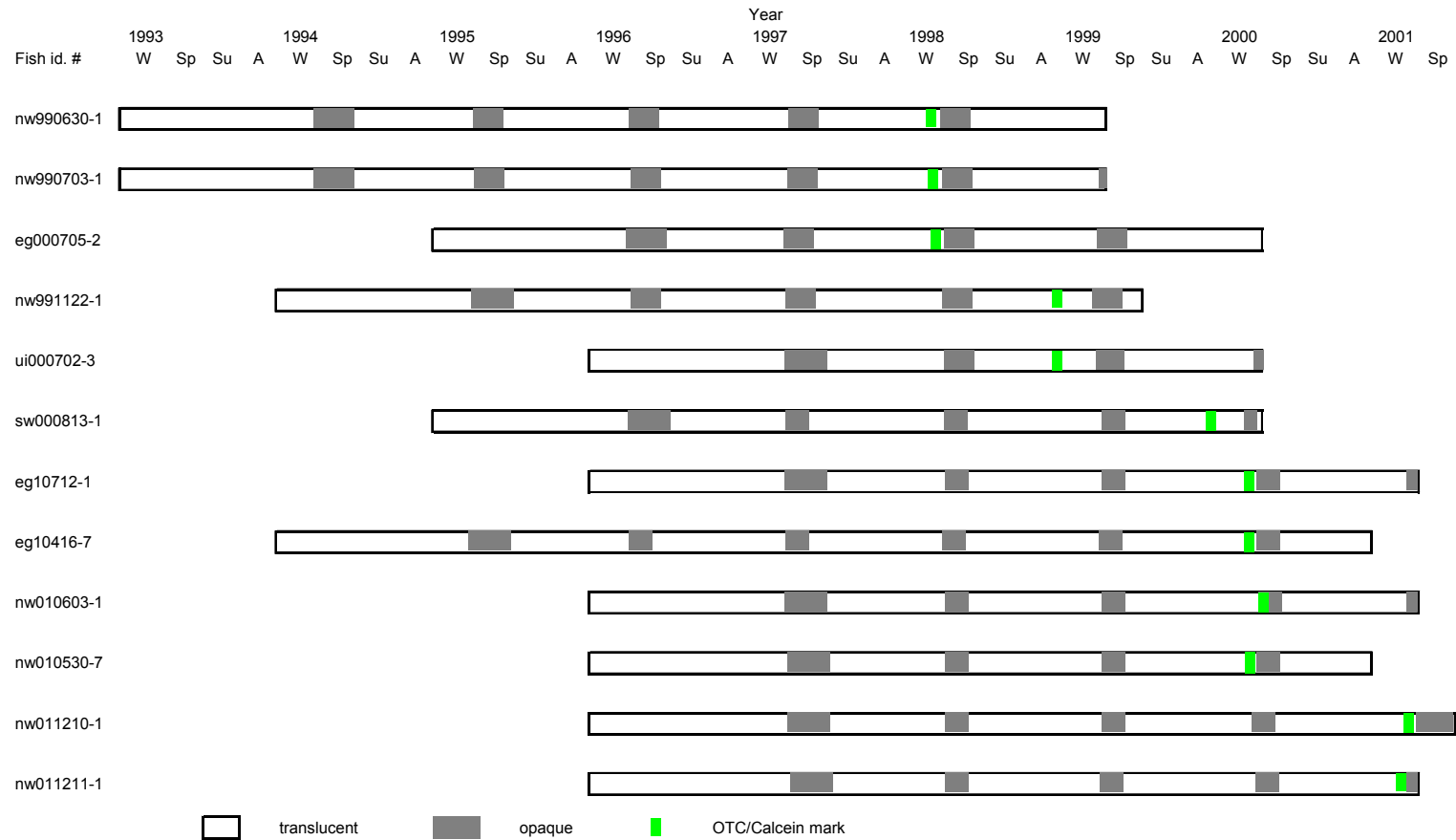


Figure 4.7 Diagrammatic (stylistic) representation of growth increments measured on chemically-marked sagittal otolith sections recovered from tagged *P. auratus* relative to time at initial capture and release and subsequent recapture. The location of the chemical mark (oxytetracycline or calcein) observed on each section was interpreted as indicated. W = Winter; Sp = Spring; Su = Summer, A = Autumn

4.3.3 Growth

From the peaks in spawning activity (see Chapter 3 – Reproductive biology), a mean birth date of June 1 was assigned to *P. auratus* from the Eastern Gulf and Denham Sound and August 1 for *P. auratus* from the Freycinet Estuary.

Ages (in decimal years) were determined on the basis of number of opaque zones plus the number of months from the assumed birth date for Eastern Gulf and Denham Sound samples collected in January-May (Freycinet Estuary samples, January-July), irrespective of marginal increment and section edge, and for samples collected June-December (Freycinet Estuary, August-December) when the marginal increment was < 60% of the previous increment and/or the section edge was categorised as ‘narrow translucent’. For fish collected in June-December from the Eastern Gulf and Denham Sound, and August-December from the Freycinet Estuary, when the marginal increment was $\geq 60\%$ and/or the section edge was categorised as ‘opaque’ or ‘wide translucent’, ages were assigned on the basis of opaque zone count plus the number of months from the assumed birth date plus one year.

von Bertalanffy growth curves were fitted to the resulting length-at-age data for individual *P. auratus* of each sex within each of the three localities (Fig. 4.8). The coefficients of determination for these growth curves were generally high (range 0.84 - 0.95) and the mean extrapolated ages at zero length (t_0) were in most cases, close to zero (range -0.055 to 0.125) (Table 4.2). Although examination of the standardised residuals from each analysis indicated no systematic bias for samples from the Eastern Gulf and Denham Sound, some deviation was apparent with the younger (0-5 years) and older (15 years and greater) age classes for both sexes from the Freycinet Estuary.

However, the overall lengths at age, particularly over the size range taken by the recreational fishery, were generally well described by the respective growth curves for each locality. Fish from all areas generally exhibited a pattern of rapid, almost linear growth up to approximately five years of age after which growth slowed to around 10–15 years of age before becoming asymptotic. The maximum ages observed for females and males were 17.2 and 15.2 years in the Eastern Gulf, respectively, 19.1 and 17.1 years in Denham Sound, respectively, and 29.7 and 31.1 years in the Freycinet Estuary, respectively.

The likelihood-ratio tests indicated no significant difference in growth curves between females and males in the Eastern Gulf and Freycinet Estuary but highly significant differences between females and males from Denham Sound ($P < 0.01$, Table 4.3, Fig. 4.9). When both sexes were compared separately among the three localities, growth for both females and males was not significantly different between Eastern Gulf and Freycinet Estuary but for both sexes differed significantly between these localities and Denham Sound.

Growth in the earliest years of life was broadly similar in all three localities. However, after approximately 3 years, growth of both females and males in Denham Sound was slower compared with the Eastern Gulf and the Freycinet Estuary. Overall, growth appeared to asymptote for both sexes at approximately the same age in all areas. By ages 1–5 years, *P. auratus* in the Eastern Gulf had attained mean lengths at age of 107, 215, 298, 373, and 460 mm FL; in Denham Sound, 113, 186, 256, 341 and 401 mm FL; and in the Freycinet Estuary, 102, 179, 252, 298 and 448 mm FL, respectively. By 10 and 15 years, fish had on average reached 624 and 712 mm FL, in the Eastern Gulf,

570 and 637 mm FL, in Denham Sound, and 635 and 704 mm FL, in the Freycinet Estuary. Fish of 20 years or greater were only observed in the Freycinet Estuary (mean length at age of 725 mm FL for 20 year olds) where individuals up to around 30 years of age were sampled in most years during this study. *P. auratus* reached the minimum legal size of 500 mm TL (426 mm FL) on average at 4-5 years of age in the Eastern Gulf, at 5 years in Denham Sound and at 5-6 years in the Freycinet Estuary.

Table 4.2 von Bertalanffy growth parameters (and 95% C.I.) derived from lengths (mm FL) at age for female and male *P. auratus* from inner Shark Bay.

		t_0 (year)	K (year ⁻¹)	L_∞ (mm FL)	r^2	n
Denham Sound						
females		-0.032	0.142	762	0.85	384
	lower	-0.170	0.129	728		
	upper	0.108	0.157	795		
males		-0.055	0.181	660	0.84	297
	lower	-0.189	0.151	615		
	upper	0.091	0.209	722		
sexes combined		-0.084	0.151	728	0.85	681
	lower	-0.171	0.139	694		
	upper	0.020	0.166	762		
Eastern Gulf						
females		0.035	0.178	755	0.91	523
	lower	-0.049	0.165	732		
	upper	0.146	0.192	782		
males		-0.071	0.172	751	0.93	385
	lower	-0.133	0.158	724		
	upper	0.009	0.187	784		
sexes combined		-0.022	0.174	755	0.92	908
	lower	-0.071	0.165	735		
	upper	0.040	0.185	774		
Freycinet Estuary						
females		0.125	0.166	773	0.94	392
	lower	0.044	0.156	759		
	upper	0.205	0.176	791		
males		0.075	0.173	766	0.95	399
	lower	0.009	0.164	756		
	upper	0.146	0.182	780		
sexes combined		0.100	0.169	770	0.95	791
	lower	0.047	0.162	761		
	upper	0.156	0.176	781		

t_0 = hypothetical age at zero length; K = growth coefficient; L_∞ = mean asymptotic length; r^2 = coefficient of determination; n = sample size

Table 4.3 Significance level of differences between von Bertalanffy growth curves for female and male *P. auratus* from inner Shark Bay using the likelihood-ratio test. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ns = not significant at Bonferroni adjusted level, n = number of samples in each case.

	All parameters	n
<i>Differences between sexes:</i>		
Denham Sound	**	681
Eastern Gulf	ns	908
Freycinet Estuary	ns	791
<i>Differences among areas:</i>		
<i>(i) Females</i>		
Eastern Gulf x Denham Sound	***	1,589
Eastern Gulf x Freycinet Estuary	ns	1,679
Denham Sound x Freycinet Estuary	***	1,472
All areas	***	
<i>(ii) Males</i>		
Eastern Gulf x Denham Sound	***	1,589
Eastern Gulf x Freycinet Estuary	ns	1,679
Denham Sound x Freycinet Estuary	***	1,472
All areas	***	

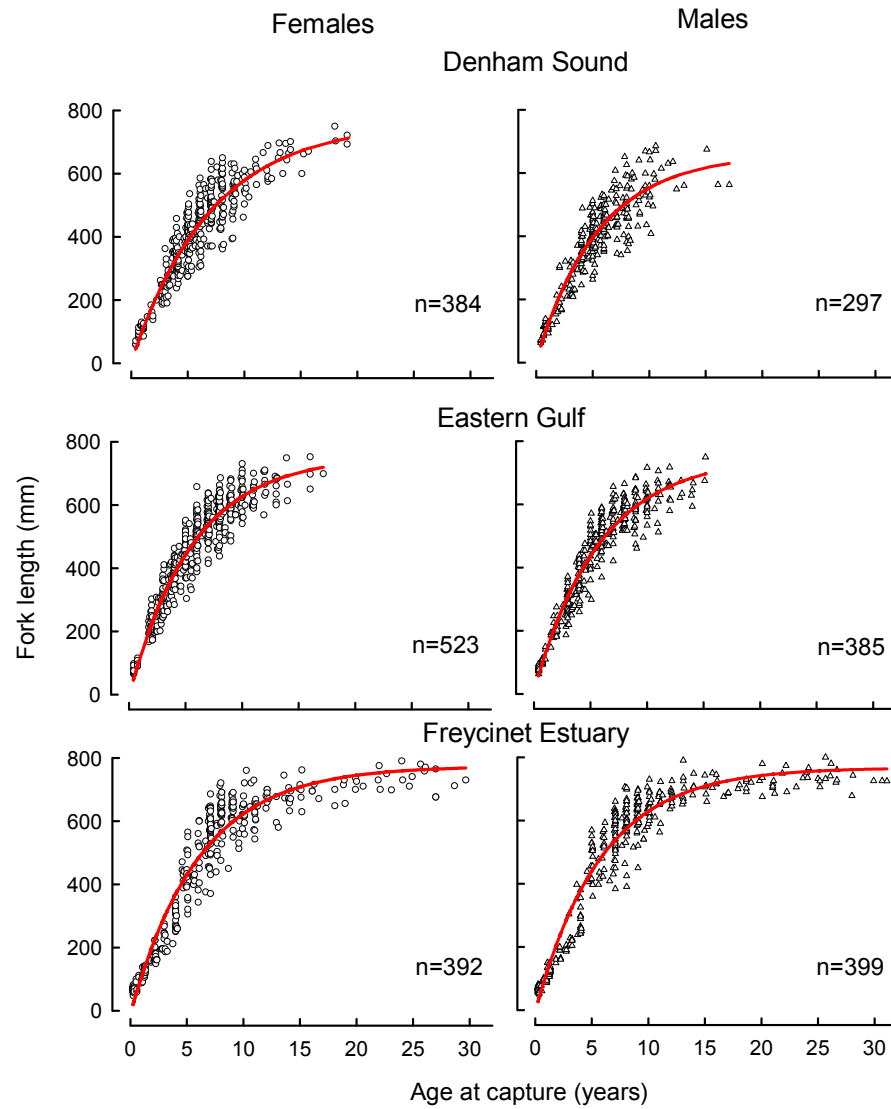


Figure 4.8 von Bertalanffy growth curves fitted to lengths at age of female (●) and male (△) *P. auratus* from the inner gulfs of Shark Bay. Sample sizes as indicated.

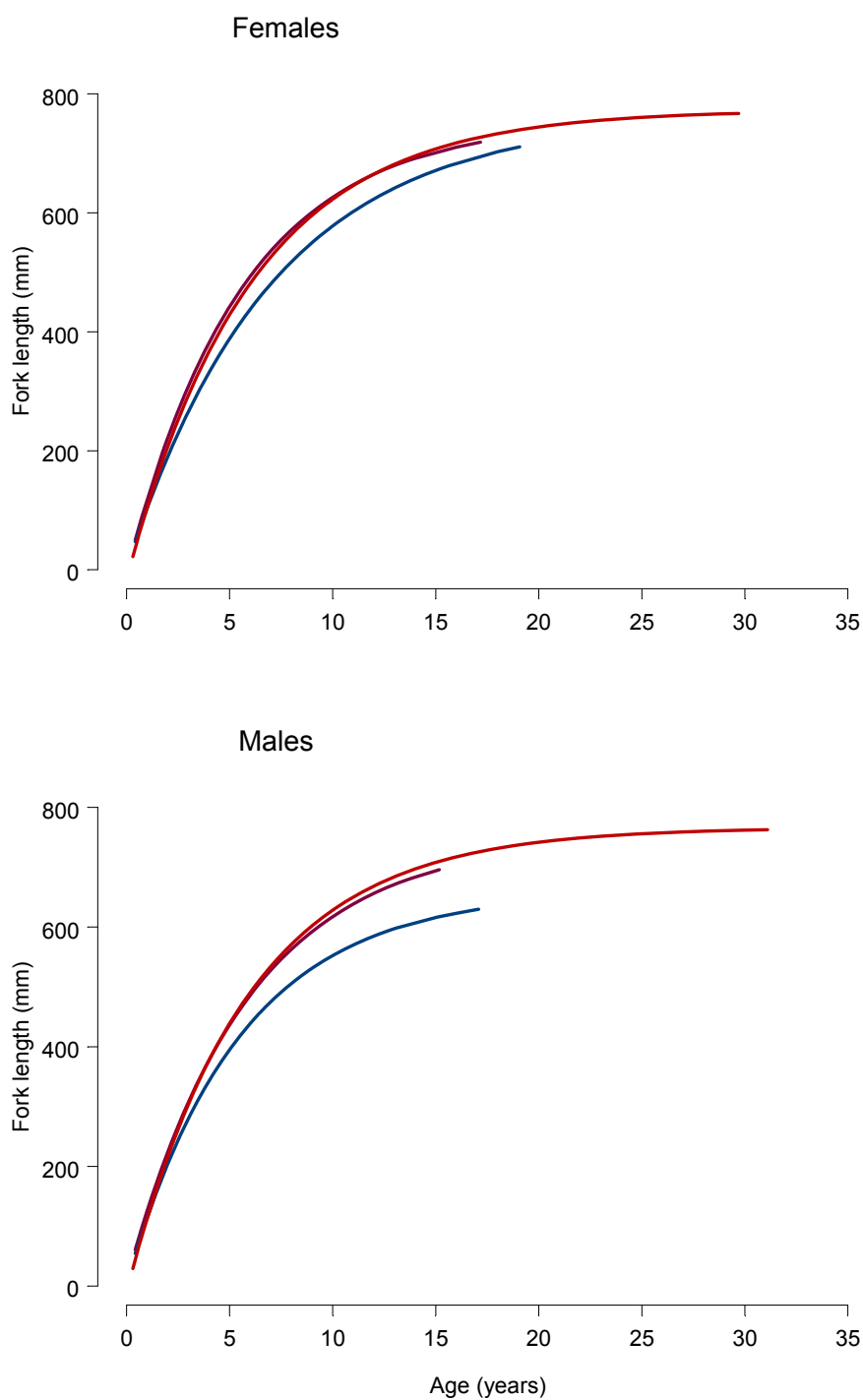


Figure 4.9 von Bertalanffy growth curves for female (upper) and male (lower) *P. auratus* from Denham Sound (blue), the Eastern Gulf (purple) and Freycinet Estuary (red).

4.3.4 Age structure

While numbers of *P. auratus* landed by recreational boat fishers and measured during recreational fishing surveys in Denham Sound and the Freycinet Estuary were

relatively low (Table 4.4), they represented approximately 3-5% of the estimated catch in terms of the total numbers of fish landed by recreational boat fishers in each year (Sumner and Malseed 2002). Numbers of fish measured during research surveys in the Eastern Gulf, in contrast, were considerably higher in all years. Because the numbers of otoliths collected and subsequently aged were inadequate to develop age-length keys on their own in most years, lengths at age for the year in question and the year immediately prior were pooled as indicated in Table 4.4. In Denham Sound and the Freycinet Estuary, *P. auratus* first appeared in recreational catches at 3 or 4 years of age and appeared to be fully recruited by 5 years of age (Fig. 4.10, 4.11).

Table 4.4 Information used to generate age-length keys and determine *P. auratus* age structure in inner Shark Bay 1998-2002. n_{len} = number of snapper landed by recreational fishers (Denham Sound, Freycinet Estuary) or from research samples (Eastern Gulf) measured in each year; n_{age} = numbers of otoliths read and used to develop age-length keys (sampling years as indicated).

Area	1998	1999	2000	2001	2002
Denham Sound					
n_{len}	184	-	102	136	151
% of catch	3%	-	2%	5%	3%
n_{age}	216 (1997,1998)	-	252 (2000)	319 (2000,2001)	319 (2000,2001)
Freycinet Estuary					
n_{len}	230	-	170	199	169
% of catch	4%	-	5%	4%	3%
n_{age}	151 (1997,1998)	-	294 (1999,2000)	193 (2000,2001)	107 (2001,2002)
Eastern Gulf					
n_{len}	540	216	438	465	239
n_{age}	194 (1998,1999)	194 (1998,1999)	265 (2000)	369 (2000,2001)	207 (2001,2002)

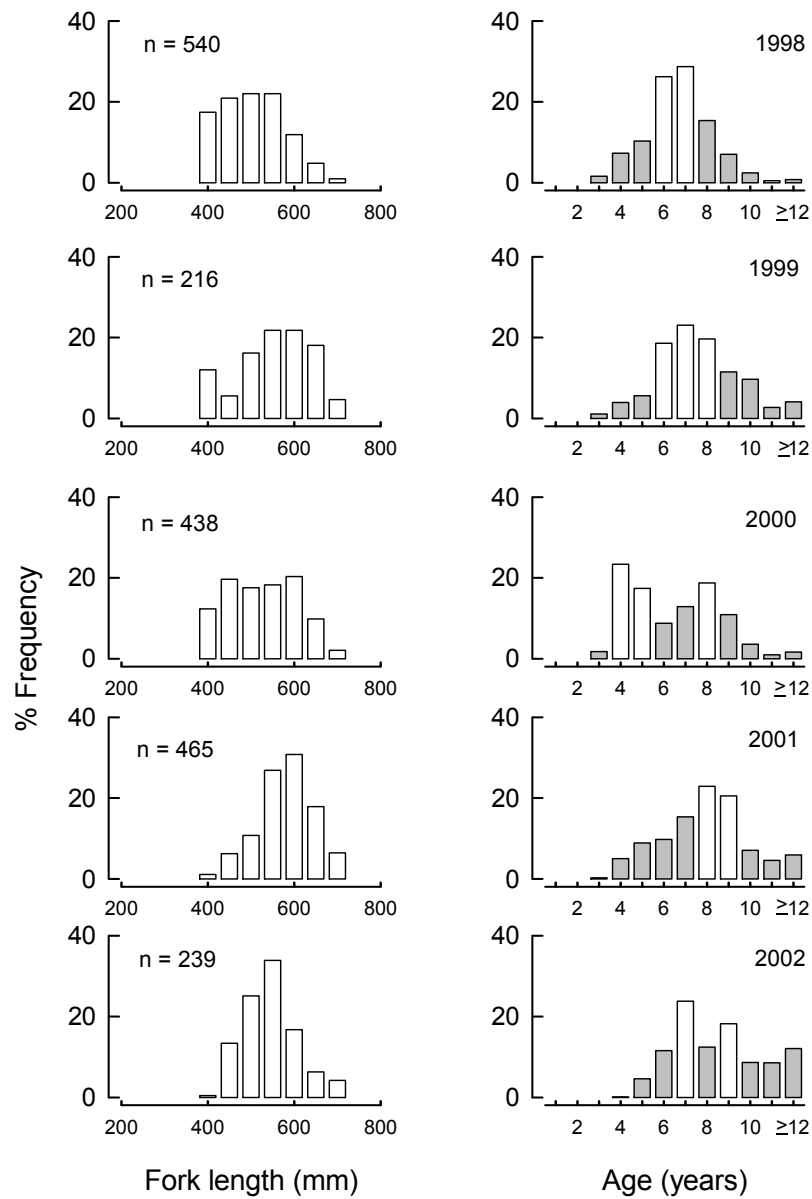


Figure 4.10 Length (class interval = 50 mm) and age frequency distributions of *P. auratus* from the Eastern Gulf 1998-2002 during which period the species were completely protected by a moratorium on their capture by recreational and commercial fishers. Sample sizes are numbers of fish measured in each year. Fish of 12 years and older were pooled. The number of otoliths read in each year are given in Table 4.4.

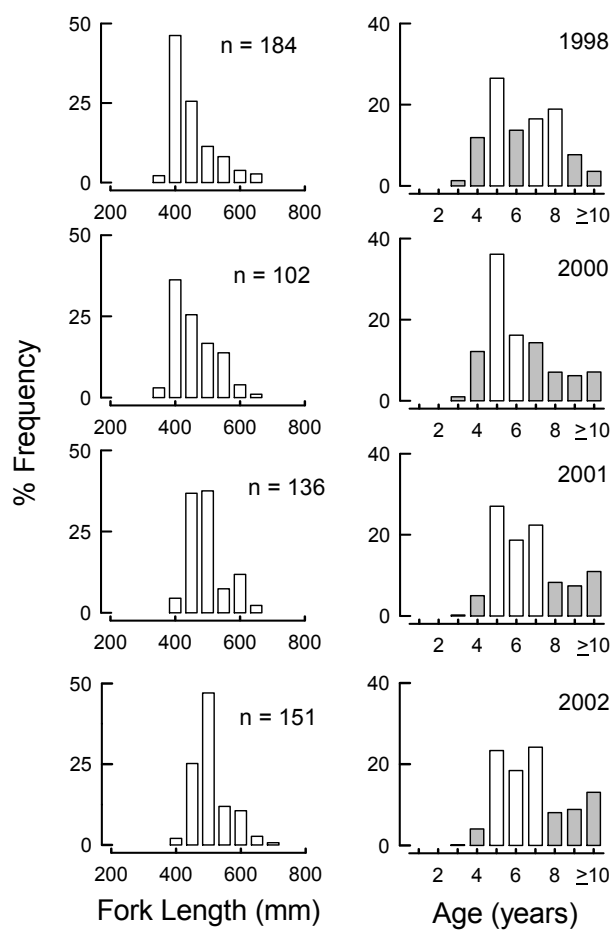


Figure 4.11 Length (class interval = 50 mm) and age frequency distributions of *P. auratus* from Denham Sound 1998-2002. Sample sizes are numbers of fish measured in each year. No data are available for 1999. Fish of 10 years and older were pooled. The number of otoliths read in each year are given in Table 4.4.

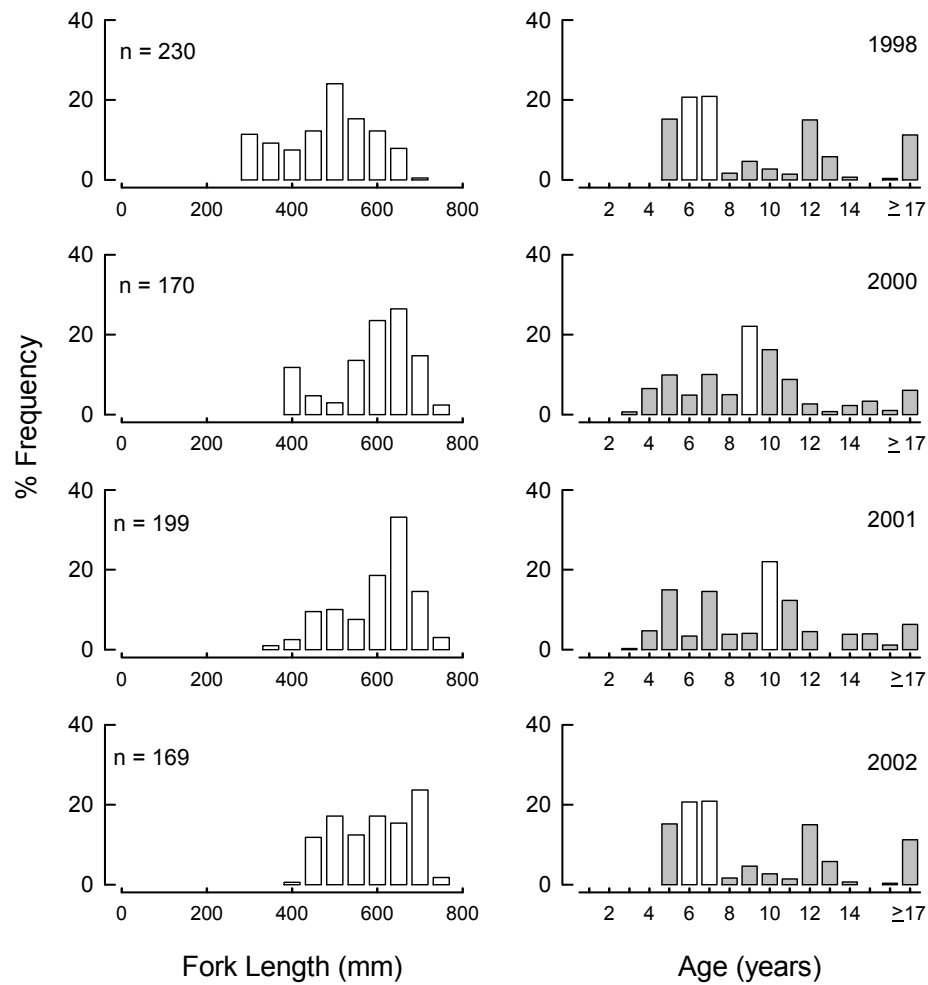


Figure 4.12 Length (class interval = 50 mm) and age frequency distributions of *P. auratus* from the Freycinet Estuary 1998-2002. Sample sizes are numbers of fish measured in each year. No data are available for 1999. Fish of 17 years and older were pooled. The number of otoliths read in each year are given in Table 4.4.

The results of the Kolmogorov-Smirnov tests indicated highly significant differences in age structure between years in the Eastern Gulf and Freycinet Estuary but not for Denham Sound in most cases; differences between areas in each year were very highly significant in all cases. Age distributions in the Freycinet Estuary were consistently positively skewed compared with Denham Sound due to the greater representation by fish of more than 10 years of age in recreational catches (Fig. 4.12). In Denham Sound, 5–8 yr olds made up around 75% or more of the recreational catch between 1998 and 2002 with the proportion of fish aged 10 years or more approximately 4% in 1998, after which year, with increased protection of fish > 700 mm, the proportion increased progressively to 7% in 2000, 11% in 2001 and 13% in 2002. In the Freycinet Estuary, older fish were more prevalent compared with Denham Sound, with fish of 25-30 years of age consistently represented in recreational catches. Here 7-10 yr olds made up 60% of catch in 1998 and 50% in 2000, however the proportion fell to 45% in 2001 and to 30% in 2002. The contribution made by fish of 10 yr or more was 24% in 1998 and 2000, increased to over 30% in 2001 and 37% in 2002. In the Eastern Gulf, where the *P. auratus* fishery was closed during the period of this study, age frequency data showed a clear shift in age structure towards older fish as would be expected under such levels of protection. While 5–8 year olds made up around 80% or more of the population in 1998, this fell to 67% in 1999, 60% in 2000 and 2001 and to 50% in 2002. Over the same period, fish of 12 years or more, which made up less than 1% of the population in 1998, increased to more than 12% by 2002.

4.3.5 Natural mortality

The age at recruitment was typically 3 years but, for the 1994 and 1997 year classes, was 4 years. The relative abundances (ln cpue) of the 1990 to 1997 year classes

were followed for up to 5 subsequent years (Fig. 4.13). The estimate of the coefficient ! of the number of years over which *P. auratus* were exposed to natural mortality was significant ($P < 0.01$), and the resulting estimate of instantaneous rate of natural mortality, M , was 0.22 (95% C.I. 0.09-0.34) year⁻¹.

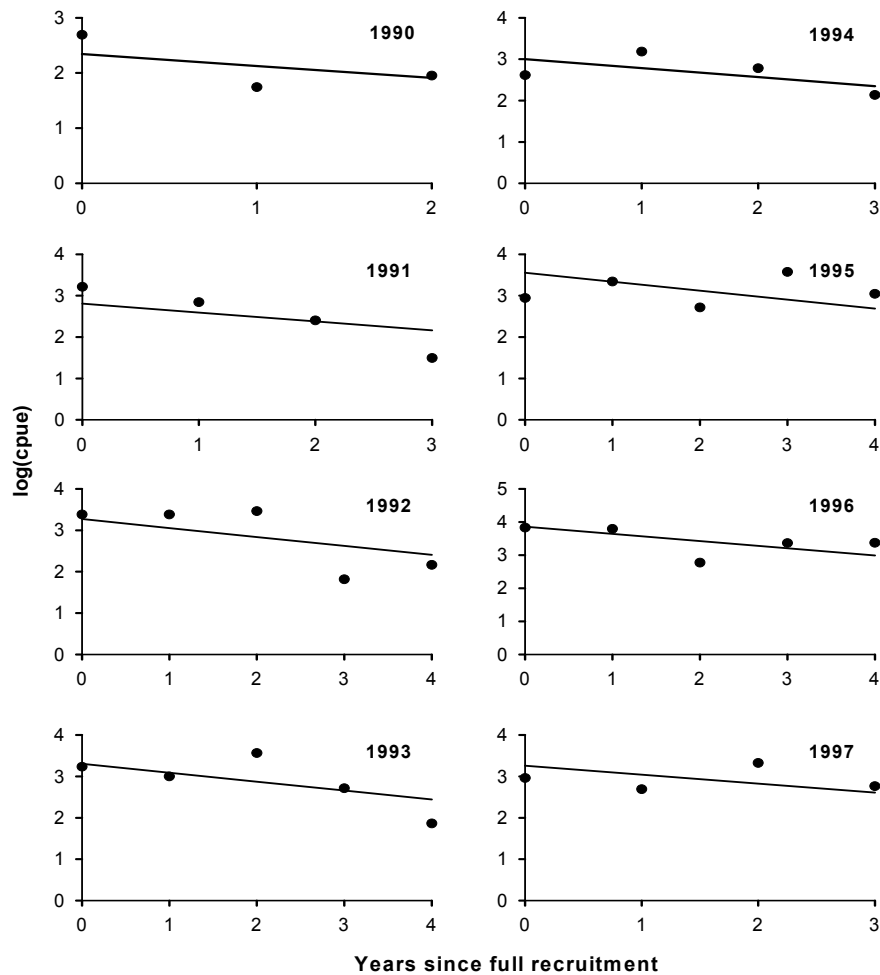


Figure 4.13 Catch curves for the 1990, 1991, 1992, 1993, 1994, 1995, 1996 and 1997 year classes used to estimate natural mortality for *P. auratus* in the Eastern Gulf. Measures of abundance are natural log (cpue).

4.4 Discussion

4.4.1 Validation

Determining the ages of individual fish by counting visible growth increments, *e.g.* opaque zones, observed in their otoliths is well established (Secor *et al.* 1995) as is the importance of validating the periodicity of increment formation (Campana 2001). In addition, accurate otolith-based ageing requires information on the average (population) birth date, which, in turn, is dependent upon knowledge of the peak spawning period. The age-structured assessment models that now underpin the management of the three *P. auratus* stocks in inner Shark Bay (Stephenson and Jackson 2005) incorporate information on the age-composition of recreational catches.

The results of this study, based on two validation methods, *i.e.* marginal increment analysis and chemically-marked otoliths, demonstrate that *P. auratus* in inner Shark Bay form one opaque zone per year, thereby confirming that opaque zone counts on sagittal otolith sections can be used to age the species with adequate confidence. Although the annual period of opaque zone formation in *P. auratus* has been validated previously elsewhere in Australia (Ferrell *et al.* 1992) and New Zealand (Francis R.I.C.C. *et al.* 1992), it was considered important to undertake further validation in this study given difficulties previously experienced with the interpretation of *P. auratus* otolith structure in samples from the oceanic waters off Shark Bay (Moran *et al.* 2005; C Wakefield unpublished data) and given the fact that Shark Bay is located at the northern limit of the species' distribution on the west coast of Australia.

In general, opaque zones in *P.auratus* sections from inner Shark Bay, from approximately the fourth or fifth zone onwards, were observed to be consistently much

thinner than the corresponding translucent zones. A similar pattern has been found in another important Australian sparid, *Acanthopagrus butcheri* (Morison *et al.* 1998; Sarre and Potter 2000), and other sparids from South Africa (Buxton and Clarke 1989, 1991; Radebe *et al.* 2002) and the Arabian Gulf (Grandcourt *et al.* 2004), and is characteristic of Perciforme otoliths from warmer environments (Beckman and Wilson 1995; Fowler *et al.* 2004). In most *P. auratus* sections from inner Shark Bay, the first 3 or 4 opaque zones, moving from the otolith core to the proximal edge, were wider and more diffuse than subsequent opaque zones, possibly due to the more rapid growth of juveniles. The abrupt change in the subcupular meshwork fibrezone (SMF or ‘Francis line’, Ferrell and Morison 1993), first identified in *P. auratus* otoliths by Francis M.P. *et al.* (1992), proved to be an extremely useful marker for the first opaque zone in our study.

The marginal increment technique used here, where mean monthly increments for sections with translucent and opaque edges were plotted separately against month, assisted in interpretation of the data and demonstrated that a single opaque zone is formed annually across all age groups. Sections with opaque edges were apparent over a period of 6-7 months, from late autumn to early summer, implying that the timing of opaque zone formation was highly variable among individuals. Opaque zone delineation, *i.e.* when the opaque zone is completed, was also variable and appeared to peak from late winter to mid-spring, consistent with results of a preliminary study of *P. auratus* from oceanic waters outside of Shark Bay (M. Moran unpublished data). Ferrell *et al.* (1992) found both interannual and individual variation in the timing of opaque zone formation in *P. auratus* otoliths from New South Wales. Marginal increment data in this Shark Bay study were pooled across areas and years. While sample sizes were low in some months in some years, when the effect of year was

investigated (unpublished data), the extended period of opaque zone formation was ! consistent across years and suggests that variation in timing was due to individual variation. Francis R.I.C.C. *et al.* (1992), highlighted a problem common to all otolith-based validation studies, *i.e.* the importance of the reader's ability to differentiate between the time of year when the opaque zone becomes delineated, as opposed to when it first becomes apparent, *i.e.* when sufficient additional (translucent) material has been laid down on the proximal edge. It is acknowledged that the extension of the period of opaque zone formation to November and December here may result from difficulties in accurately determining the outer edge of the ultimate opaque zone in some sections in those months when sample sizes were generally lower than those earlier in the year. By using additional information on increment growth at the otolith margin when determining the age of individual fish, a more accurate estimate of age is obtained when the delineation of the opaque zone appears to occur over an extended period.

Results from this ageing study of *P. auratus* from inner Shark Bay are broadly consistent with previous studies elsewhere in Australia and in New Zealand where opaque zone formation has been recorded between July and February (Francis R.I.C.C. *et al.* 1992; Ferrell *et al.* 1992; Ferrell and Sumpton 1998). Francis R.I.C.C. *et al.* (1992) proposed that opaque zones were formed in winter in New Zealand, as was also found by Ferrell *et al.* (1992) in New South Wales, but could not readily be observed until after additional material was laid down in late spring-summer. A recent study of *P. auratus* from Spencer Gulf, South Australia (Fowler *et al.* 2004), showed that opaque zone delineation peaked around November-December, *i.e.* late spring–early summer, consistent with results of an earlier study in South Australia by McGlennon *et al.*

(2000). Importantly, Fowler *et al.* (2004) also found the timing of opaque zone formation to be highly variable with opaque edges recorded over a period of six months from September-February, *i.e.* early spring to mid-summer.

Opaque zone formation in *P. auratus* in inner Shark may be related to both spawning and lower water temperatures. Mann-Lang and Buxton (1996) investigated the relationship between individual growth and otolith structure in South African sparids and showed that opaque zones reflected slower growth and translucent zones faster growth, and suggested that slow growth in mature fish was related more to spawning than environmental factors *e.g.* water temperature minima. In Australia, most researchers accept the paradigm that wider translucent zones in fish otoliths represents faster seasonal growth and are formed in austral late spring-summer-autumn while the narrower opaque zones reflect slower growth and are formed during winter-early spring (*e.g.* Sarre and Potter 2000; Newman and Dunk 2002, 2003; Smith and Deguara 2003).

4.4.2 Precision

Ageing precision in this study was high with the overall IAPE (5.4%) around the benchmark of 5% proposed by Campana (2001) for routine ageing of species of moderate longevity and otolith complexity. Sections from the Eastern Gulf and Freycinet Estuary were easier to interpret than those of fish from Denham Sound, possibly reflecting environmental differences among the locations. Monthly SST data for Shark Bay's inner gulfs indicate less seasonal variation in Denham Sound (annual range ~19-26° C), compared with the Eastern Gulf (~16-26° C) and Freycinet Estuary (~15-27° C) (Tapp 2003; Fairclough 2005). *P. auratus* otoliths from oceanic waters outside Shark Bay, where environmental conditions are more similar to those in

Denham Sound, are generally more difficult to interpret (Moran *et al.* 2005). Ferrell ! and Sumpton (1998) found *P. auratus* otoliths from waters off the east coast of Australia increasingly more difficult to interpret with decreasing latitude moving northwards from Sydney (34 ° S) to Fraser Island (26°S, *i.e.* the same latitude as Shark Bay). This pattern of increasing difficulty in the interpretation of otolith macrostructure with decreasing latitude has been shown for other teleost species in the southern hemisphere (*e.g.* Smith and Deguara 2003).

4.4.3 Growth

Fish used for age determination from all three localities in this study were mostly obtained via fishery-independent sampling using a range of gear-types, *i.e.* rod and line, trawls and baited fish traps, each with their own selectivity. Because the sampling methods were diverse and the sampling locations were consistent between study years, otoliths for ageing were obtained from both fast and slow growing individuals from the respective areas. Length-at-age data are therefore assumed to be representative and reflect *P.auratus* growth in the respective areas. The von Bertalanffy growth curves fitted the length-at-age in each area reasonably well apart from the youngest fish (particularly in the Freycinet Estuary), as has been the case with sparids elsewhere (Pajuelo and Lorenzo 2002). Linear models fitted just as well as von Bertalanffy growth curves for fish of ages 1 to 5 years in all three areas, with on average approximately more than 88% of the variation in length explained by age. An *a posteriori* analysis indicated that length-at-age data were fitted better by a Schnute and Richards (1990) five-parameter growth model compared with the three-parameter von Bertalanffy growth model ($P<0.001$). However, a key objective here was to allow statistical comparison of growth between the three localities and to provide growth

parameters for stock assessment modelling (see Chapter 6 – General discussion). In addition, it was considered useful to compare results of this study with growth curves fitted to length-at-age data for this species from elsewhere.

P. auratus in inner Shark Bay are moderately long-lived with a maximum age of at least 31 years, *i.e.* similar longevity to that found in *P. auratus* from South Australia (McGlennon *et al.* 2000) and Victoria (Coutin *et al.* 2003). Results of the likelihood-ratio tests in the Shark Bay study indicated sex-based differences in growth among the localities on the basis of a significant difference between growth curves for females and males in Denham Sound only. Differences in growth between sexes in both the Eastern Gulf and Freycinet Estuary were not significant. The absence of sex-based differences in growth is typical of many sparids (Sarre and Potter 2000; Grandcourt *et al.* 2004). The comparison among localities indicated that, for both females and males, growth in Denham Sound differed from that in both the Eastern Gulf and Freycinet Estuary.

The observed differences in growth for *P. auratus* in Denham Sound may be explained by geographic variation in a number of density-dependent factors. For example, intra-specific competition may have varied due to differences in stock sizes in the respective areas; Denham Sound spawning biomass was estimated to be greater in relation to the unexploited level for most of period of this study, in contrast with the other two areas where spawning biomass was conversely significantly lower (*i.e.* more resources available per individual) (Jackson *et al.* 2005). Environmental conditions (water temperature, salinity) in the Eastern Gulf and Freycinet Estuary are more similar than they are to those in Denham Sound. There is no evidence of differences in productivity among the study areas; Shark Bay is rich in *P. auratus* prey species

including crustaceans, echinoderms, bivalve molluscs and fish species (Kangas *et al.* 2007). However, major commercial trawl fisheries for scallops (*Amusium balloti*) and prawns (*Penaeus latisulcatus*, *P. esculentus* and *Metapenaeopsis* spp.) operate in the Denham Sound area only, and have, in theory, the capacity to remove large quantities of *P. auratus* prey biomass and thereby potentially limit individual growth there compared with the Eastern Gulf and Freycinet Estuary where no commercial trawling has been allowed. In comparison with published von Bertalanffy growth parameters for *P. auratus* elsewhere in Australia and New Zealand, values of K in inner Shark Bay are higher, with the exception of southern Spencer Gulf in South Australia (Table 4.5), where environmental conditions (water temperature, salinity, bathymetry, available prey species) are very similar to those in Shark Bay.

Table 4.5 Comparison of von Bertalanffy growth parameters for *P. auratus* from Australia and New Zealand estimated from lengths-at-age based on sectioned otoliths. Values are for both sexes combined.

Location	L_{∞} (mm)	K (year ⁻¹)	t_0 (year)	Source
<i>Western Australia</i>				
Shark Bay, Eastern Gulf	755	0.174	-0.022	This study,
Shark Bay, Denham Sound	728	0.151	-0.084	
Shark Bay, Freycinet Estuary	770	0.169	0.100	
<i>South Australia</i>				
Spencer Gulf, northern	984	0.124	-0.347	Fowler <i>et al.</i> (2004),
Spencer Gulf, southern	632	0.210	-0.108	
Gulf St Vincent, northern	907	0.159	-0.082	
Gulf St Vincent, southern	895	0.131	-0.062	
<i>Victoria</i>				
Port Phillip Bay	857	0.119	na	Coutin <i>et al.</i> (2003)
<i>New South Wales</i>				
various	574	0.138	-2.29	Ferrell (2004)
<i>Queensland</i>				
various	792	0.082	-2.45	Sumpton (2002)
<i>New Zealand</i>				
various	720	0.106	-0.75	Francis R.I.C.C. <i>et al.</i> (1992)
Hauraki Gulf	588	0.102	-1.11	Gilbert and Sullivan (1994)
West Coast	667	0.16	-0.11	Gilbert and Sullivan (1994)
East Northland	462	0.128	-1.4	N. Davies (unpublished data)

4.4.4 Age structure

The most obvious and consistent feature when age structures in the three localities are compared is the low representation of older fish in the Eastern Gulf and Denham Sound, compared with the Freycinet Estuary where fish of 25+ years of age were regularly sampled from recreational catches during this study. High levels of annual variation in juvenile *P. auratus* recruitment have been shown in the Freycinet Estuary (G. Jackson unpublished data) and in oceanic waters off Shark Bay (Moran *et al.* 2005) and are a feature common to *P. auratus* populations elsewhere in Australia and New Zealand (Francis M.P. *et al.* 1995; McGlennon *et al.* 2000; Fowler and Jennings 2003; Hamer and Jenkins 2004). While inner gulf *P. auratus* populations appear to be mostly self-recruiting (Chapter 2; Nahas *et al.* 2003), and differences in recruitment strength among the three areas, within years, cannot be discounted, it is more likely that the differences in longevity and age structure shown in this study reflect different levels of fishing mortality over the last 20-30 years.

Complete catch histories and CPUE time series are not available for the period prior to the late 1990s because the inner gulf *P. auratus* fishery has been primarily a recreational fishery for many years (Stephenson and Jackson 2005). Anecdotal information obtained by interviews with experienced commercial and recreational fishers (G. Jackson unpublished data) indicated a decline in commercial snapper fishing effort in inner Shark Bay over the last 20-30 years in parallel with a steady increase in recreational effort since the late 1970s (Jackson *et al.* 2003). Most of this effort was historically focussed in waters of Denham Sound (the site of the only human settlement of any significant size on the shores of the inner gulfs) rather than the Eastern Gulf and the Freycinet Estuary. Recreational snapper catches are believed to have increased gradually from the late 1970s to early 1980s and then increased rapidly from the mid

1990s – as a result of improved vehicle access to the region and increased fishing efficiency (*e.g.* introduction of new fish finding technology) - until the start of implementation of adequate management around 1998 (Jackson *et al.* 2005).

Moderately long-lived species such as *P. auratus* are capable of having 20-25 year classes coexisting, *e.g.* in northern Spencer Gulf, South Australia (Fowler 2005). In inner Shark Bay, only in the Freycinet Estuary does the age structure approach this. Given the estimate of $M = 0.22 \text{ year}^{-1}$ obtained for the Eastern Gulf, a higher maximum observed age would be expected in that area. The lower maximum age and general absence of older fish in both the Eastern Gulf and Denham Sound samples reflect the effects of fishing. Age composition data for the Eastern Gulf show a clear shift in age structure towards older fish between 1998 and 2002 under protection of the moratorium as would be expected. There is a discrepancy between the regular occurrence of older (20 years and greater) fish in recreational catches landed from the Freycinet Estuary and the lower level of spawning biomass (and still declining, see Chapter 5 – Daily egg production method) in that area compared with Denham Sound and Eastern Gulf. This may be a result of a sustained period of lower recruitment in Freycinet where annual trawl surveys indicate only one good recruitment year (as measured by abundances of 0+ fish, Moran and Kangas 2003). The hypothesis might be that Freycinet Estuary represents a more marginal environment for *P. auratus* compared with the Eastern Gulf and Denham Sound, and years of poor recruitment (possibly to due to lower survival rates of early life history stages) are reflected in missing age classes in the population age structure.

4.4.5 Natural mortality

Although the estimate of $M = 0.22$ (95 C.I. 0.09-0.34) year^{-1} is imprecise due to limited contrast in the data (as it was only possible to follow some cohorts for a maximum of 5 years, *i.e.* the period of fishery closure) it represents, to our knowledge, the first direct estimate of this important parameter for *P. auratus* from Australian waters. Indirect estimates of M obtained using the empirical equations of Pauly (1980, assuming a mean water temperature of 23°C), Ralston (1987) and Hoenig (1983, assumed $Z = M$) were 0.51, 0.38 and 0.12 year^{-1} , respectively (using a common maximum age of 35 years). The value of 0.075 year^{-1} used in *P. auratus* stock assessments in New Zealand (Gilbert *et al.* 2000), where individuals of the species live to 55-60 years of age (Francis R.I.C.C. *et al.* 1992) compared with around 30 years in Shark Bay, lies below the lower 95% confidence limit of our direct estimate of M . This estimate of M is slightly greater than the range of $0.08 - 0.19\text{ year}^{-1}$ assumed for the age-based stock assessment that is currently used for management of *P. auratus* stocks in inner Shark Bay (Stephenson and Jackson 2005), although the latter range falls almost completely within the 95% confidence interval for the estimate of M from this study. While the range of values assumed in this assessment will need to be expanded to explore the full range of the 95% confidence interval, it should be noted that, by adopting more conservative estimates of M and hence of the productivity of the stock, the management decisions flowing from those assessments would have been likely to be more robust to the uncertainty that is invariably associated with the estimate of natural mortality.

Chapter 5: Estimating spawning biomass of *P. auratus* populations in inner Shark Bay using the daily egg production method (DEPM)

5.1 Introduction

In the management of fisheries, there are occasions when urgent assessments are required for stocks for which there is little or no prior quantitative information on stock abundance or rates of exploitation. The demand for such information, which is essential for sustainable resource management, has increased dramatically in recent years (Gunderson 1993), particularly in the management of marine recreational fisheries (Cox *et al.* 2002; McPhee *et al.* 2002; Post *et al.* 2002). In the absence of survey indices of abundance or a time series of catch and fishing effort (CPUE) data that can be used to derive indices of abundance, traditionally used with established commercial fisheries, recreational fishery managers often have inadequate information on which to develop management strategies (Smith and Pollard 1996). As a consequence, fishery management agencies are unable to respond to the need for timely management based on sound assessment advice. Even if the precautionary principle is applied and the necessary management action taken to protect the stock(s) in question, quantitative information on stock status will be required shortly thereafter both to confirm the appropriateness of that action and subsequently to monitor its effectiveness.

Such a situation arose with the management of *P. auratus* stocks in inner Shark Bay around the mid-1990s, when concerns were raised principally in relation to the sustainability of recreational fishing in the Eastern Gulf, with the removal of large numbers of larger and assumed older fish from spawning aggregations off Monkey Mia (Marshall and Moore 2002; Jackson *et al.* 2005). No information on the size of the *P. auratus* spawning stock in the Eastern Gulf, or in the other inner gulf areas of Denham

Sound and Freycinet Estuary, or on the magnitude of recreational catches was available ! at that time (Stephenson and Jackson 2005). In addition, data that could be used for stock assessment purposes *e.g.* catch rates or age structure of catches, were similarly not available. Estimates of stock size were urgently required to determine the extent to which the spawning stock in Eastern Gulf was depleted, and to assess the status of the stocks in Denham Sound and the Freycinet Estuary. The challenge at the time was to identify a stock assessment technique that would be able to provide useful quantitative data promptly for this principally recreational-only fishery, given the relatively limited research resources that were available.

Mark-recapture techniques, such as tagging, although subject to bias (Zeldis 1993), have routinely been used in assessments of *P. auratus* stocks in New Zealand where adequate numbers for tag-and-release are caught using commercial trawl-fishing methods with significant industry participation (Maunder and Starr 2001). Such an approach was not applicable in inner Shark Bay where there is no history of trawling for adult *P. auratus* and much of the bottom-habitat is unsuited to this method of fishing. There were also concerns at the time of potential bias in estimating tag recovery rates due to under-reporting of tagged fish by recreational fishers (M. Moran, Department of Fisheries WA, pers. comm.). Regulatory actions by fishery management agencies have been implicated in the low co-operation in reporting tag recaptures with recreational fisheries elsewhere (Fable 1990; Patterson *et al.* 2001)

The idea that the biomass of a fish stock can be directly estimated from the abundance of its eggs and larvae has a long history (Saville 1964; Hunter and Lo 1993). Egg production methods are widely used to provide fishery-independent estimates of biomass (Gunderson 1993) and are based on the underlying principle that abundance of

the earliest life-history stages can be used to estimate reproductive output of a stock ! over time (Hunter and Lo 1993). Such methods involve estimating egg production over the area of spawning and estimating adult stock size by back-calculation using adult reproductive parameters including fecundity and sex ratio (Hunter and Lo 1993).

The daily egg production method (DEPM) was originally developed in California in the late 1970s for small, schooling pelagic species (*Engraulis*, *Sardinops*) with planktonic eggs and indeterminate annual fecundity (Lasker 1985; Alheit 1993; Stratoukadis *et al.* 2006). The DEPM estimates spawning biomass as the ratio of daily egg production (= eggs produced each day per unit area), over the entire area of spawning, and the weight-specific daily fecundity ('batch fecundity' = number of eggs spawned each day by a female of average weight). The DEPM requires that ichthyoplankton surveys and sampling of spawning fish are undertaken concurrently during the peak spawning period. The relevant parameters are estimated from a single survey and can thereby provide a rapid, fishery-independent estimate of biomass (Bunn *et al.* 2000). Empirical evidence from more than 120 different surveys over 25 years suggests that appropriate application of the DEPM provides unbiased but usually imprecise (coefficients of variation generally > 30%) estimates of spawning biomass (Stratoukadis *et al.* 2006).

Zeldis (1993) proposed that the DEPM had potential for use with three commercially-important demersal species in New Zealand, including *P. auratus*, based on particular biological characteristics of the species that included (i) multiple spawning with indeterminate fecundity, (ii) a well-defined daily pattern of ovulation and spawning with a high spawning frequency and (iii) well-described planktonic (pelagic)

eggs (*i.e.* readily identifiable in ichthyoplankton samples). Since the publication of ! Zeldis (1993), DEPM-based assessments have been undertaken successfully with *P. auratus* populations in South Australia (McGlennon 2003) and New Zealand (Zeldis and Francis 1998).

At the time of the Shark Bay pink snapper ‘crisis’ around 1995-1996, when urgent stock assessments were being called for, the DEPM was considered to have potential for assessment of the size of *P. auratus* stocks in the inner gulfs of Shark Bay. However, the following potential problems were foreseen:

- detailed information on life history of *P. auratus* in the inner gulfs was lacking, in particular temporal spawning patterns were unknown;
- detailed information on the spatial distribution of spawning was unavailable;
- whether adequate numbers of spawning adults could be caught in the required time frame (*i.e.* within the duration of a DEPM ichthyoplankton survey) in the absence of a significant commercial *P. auratus* fishery inside Shark Bay;
- whether egg production could be estimated with an acceptable level of precision.

Despite these uncertainties and in the absence of any alternative method of rapid stock assessment, a series of pilot DEPM surveys were conducted between June and September 1997. Following this preliminary research, more comprehensive surveys were undertaken each year from 1998 onwards. During each of these years, modifications were made to refine the sampling design and analytical methods.

The main objectives of the research described in this chapter were (i) to undertake ichthyoplankton surveys each year at the peak *P. auratus* spawning times in

the Eastern Gulf, Denham Sound and Freycinet Estuary to estimate the necessary egg production parameters, (ii) to concomitantly sample adult spawning populations to estimate the necessary adult reproductive parameters, and (iii) to provide estimates of spawning biomass for each *P. auratus* population over a number of years to enable an assessment of the effectiveness of the various management measures introduced over the period (see Chapter 6 – General discussion) to recover and maintain *P. auratus* stocks. In addition to the key objectives, to address other underlying objectives, it was also necessary (i) to determine the spatial extent of spawning in each survey area and identify the main spawning locations, (ii) to improve understanding of the reproductive biology and behaviour of *P. auratus* and, in particular, the temporal (diel) spawning patterns, (iii) to determine the optimum sampling approach for the ichthyoplankton surveys to allow estimation of egg production with reasonable precision, and (iv) to provide an evaluation of the application of the DEPM for use in on-going stock assessment of inner Shark Bay *P. auratus* stocks. This chapter describes in detail the research associated with DEPM surveys undertaken by WA Department of Fisheries Research Division, and led by the author of this thesis, during the period 1998-2004.

5.2 Materials and Methods

The method of estimating spawning biomass (B , tonnes) used in this study followed the DEPM model described by Parker (1985):

$$B = P A k W / R F S \quad \text{Eqn 5.1}$$

where,

P = daily egg production per unit area of sea surface (eggs m⁻² dy⁻¹)

A = spawning area (km²)

W = average weight of mature females (g)

R = sex ratio of mature females to mature fish (by weight) !

F = batch fecundity (= number of eggs spawned by a female of average weight)

S = spawning fraction (= proportion of females spawning each day, by weight)

k = conversion factor (m^2 to km^2 , g to t)

The methods for estimating the respective egg production and adult reproductive parameters are described in detail in the following sections.

5.2.1 Egg production

A series of DEPM surveys were conducted in inner Shark Bay for the first time in the winter of 1997. The principal objective was to obtain the necessary data to estimate *P. auratus* spawning biomass in each area, with the Eastern Gulf being the highest priority. Because the exact timing of the spawning season and peak spawning period of *P. auratus* in the inner gulfs had, at that time, not been determined, pilot surveys were initially scheduled based on knowledge of the spawning season of *P. auratus* from the oceanic waters adjacent to Shark Bay (*i.e.* winter, Moran *et al.* 2003). Given that spatial patterns of spawning activity inside Shark Bay were also unknown, ichthyoplankton survey design was based on a systematic approach with sampling stations arranged in a 4 x 4 nautical mile (nm) grid pattern (Fig. 5.1, 5.2 and 5.3). Surveys were conducted during daylight hours only (approximately 0800 - 1800 hours).

An ichthyoplankton survey was conducted in the waters of Denham Sound and Freycinet Estuary initially in June; *P. auratus* eggs were found at locations in mid Denham Sound but nowhere in the Freycinet Estuary (Fig. 5.1). No ichthyoplankton

survey was conducted in the Eastern Gulf in June, as no adults in spawning condition were observed in recreational catches landed at Monkey Mia during that month. A second survey was carried out in July in Denham Sound and the Freycinet Estuary with eggs again found in the former but not in the latter (Fig. 5.2). No samples of spawning fish were obtained from Denham Sound or the Freycinet Estuary either in June or July. In July, however, samples of spawning fish were obtained and an ichthyoplankton survey was undertaken in the Eastern Gulf; *P. auratus* eggs were collected for the first time at locations to the north and northeast of Faure Island (Fig. 5.2). Large numbers of spawning fish were observed for the first time in recreational catches landed at Nanga (the main launching point for recreational snapper boats in the Freycinet Estuary) in late August 1997. A further ichthyoplankton survey was subsequently carried out (Freycinet Estuary only) in early September; *P. auratus* eggs were present at many sites and in particularly high abundance at one site north of White Island (Fig. 5.3). Further surveys in the Eastern Gulf and Denham Sound in September, to complement those conducted in June and July, were not possible due to limitations on research resources at that time.

Important outcomes from the 1997 pilot surveys included (i) evidence of variation in temporal spawning patterns between areas, (ii) emerging spatial patterns in spawning activity from egg distributions and (iii) confirmation that egg distributions, in particular for youngest eggs, were highly patchy (lots of zero counts and occasional very high counts). Information gained from these pilot surveys provided an important basis for modifications to the ichthyoplankton survey design in 1998, and during subsequent years. Considerable effort was focused on ways to reduce variance around estimates of egg production.

5.2.1.1 Field survey design

DEPM surveys in 1998 were planned to better coincide with peak spawning in each inner gulf based on improved understanding of the timing of spawning obtained from the 1997 pilot surveys. To confirm temporal differences in peak spawning between the three localities, surveys were repeated in consecutive months in both the Eastern Gulf (early June and early July) and Denham Sound (late June and late July). A single survey only was conducted in the Freycinet Estuary (late August). In an attempt to reduce the variance around estimates of egg production, a stratified systematic sampling approach was adopted in 1998 with sampling stations arranged in a combination 2 x 2 and 4 x 2 nm grid pattern with finer-scale stratification in the vicinity of the main spawning locations identified from the 1997 pilot surveys. In addition, in areas of significant egg abundance observed whilst at sea, 'real-time' additional tows were made in the immediate vicinity, as part of an adaptive sampling approach (Thompson and Seber 1996; Hunter and Lo 1997; Lo *et al.* 1997). Surveys were again conducted primarily during daylight hours (approximately 0800 - 1800 hours) with the exception of a single night in the Freycinet Estuary where adaptive sampling was undertaken in an area of particularly high egg abundance identified during earlier daytime sampling, to investigate the extent of night-time spawning activity. No account was taken of lunar cycles in relation to the timing of DEPM surveys in 1998.

Details of the adaptive sampling approach used in 1998 are given in Jackson and Cheng (2001) but are not presented here (see 5.4 Discussion). Key outcomes from the 1998 surveys were (i) further confirmation of spatial spawning patterns with key spawning locations identified off Monkey Mia (at a location known locally as The Patch), north east of Faure Is. and to the north of Cape Peron in the Eastern Gulf, off

mid Dirk Hartog Is. in Denham Sound and just to the north of White Island in the Freycinet Estuary; (ii) improved understanding of seasonal spawning patterns in the Eastern Gulf and Denham Sound with peak spawning in the former in June but spawning at similar levels in Denham Sound in both months; (iii) continuing high levels of variability in egg abundances in the ichthyoplankton samples remained, and (iv) occurrence of low numbers of the younger eggs in some surveys (*e.g.* Eastern Gulf in both June and July and in Freycinet), possibly due to the effect of the time of day of spawning or the distribution of eggs of different ages with respect to depth.

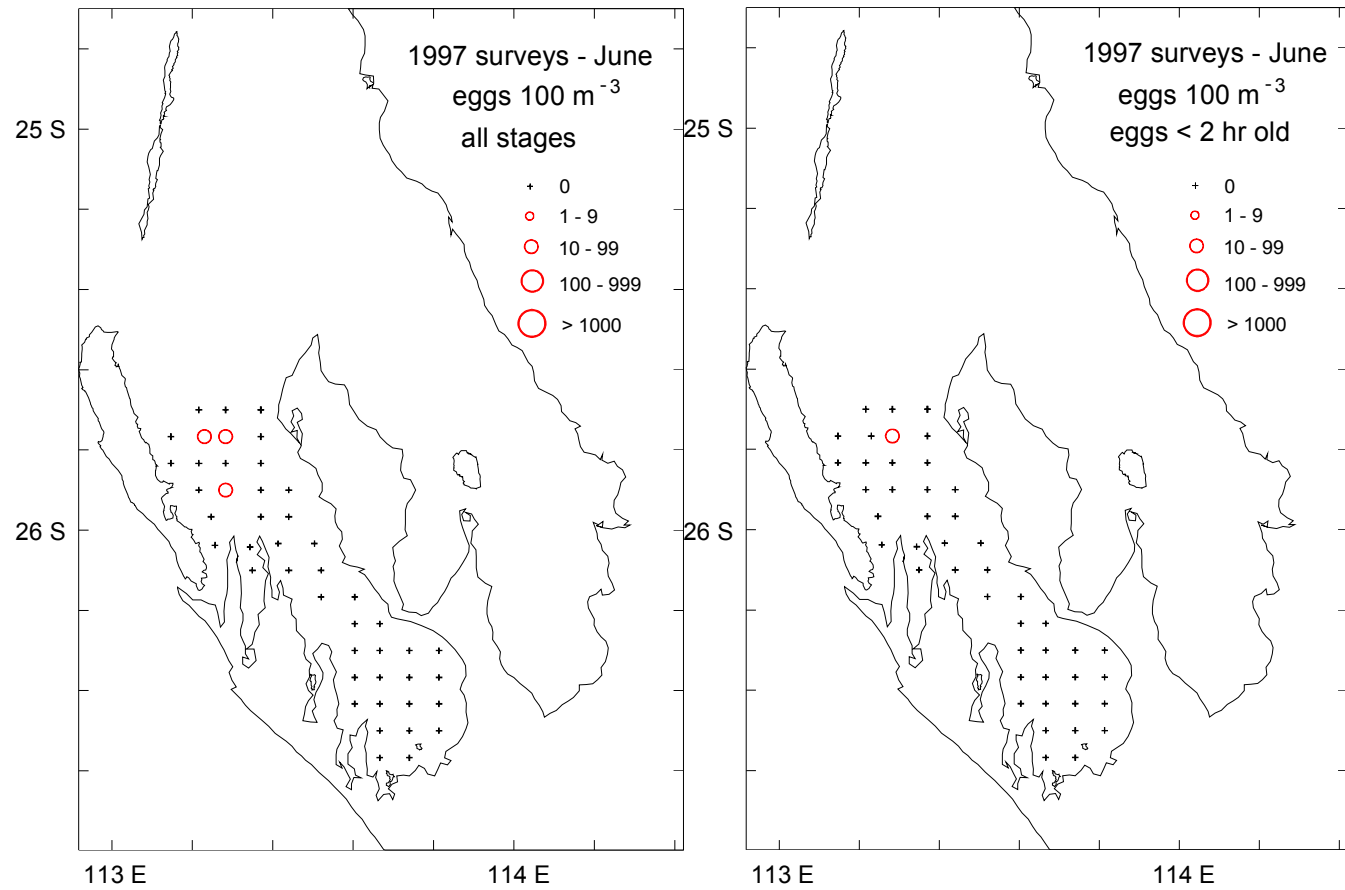


Figure 5.1 Distribution of *P. auratus* eggs from pilot DEPM surveys undertaken in inner Shark Bay in June 1997, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m⁻³

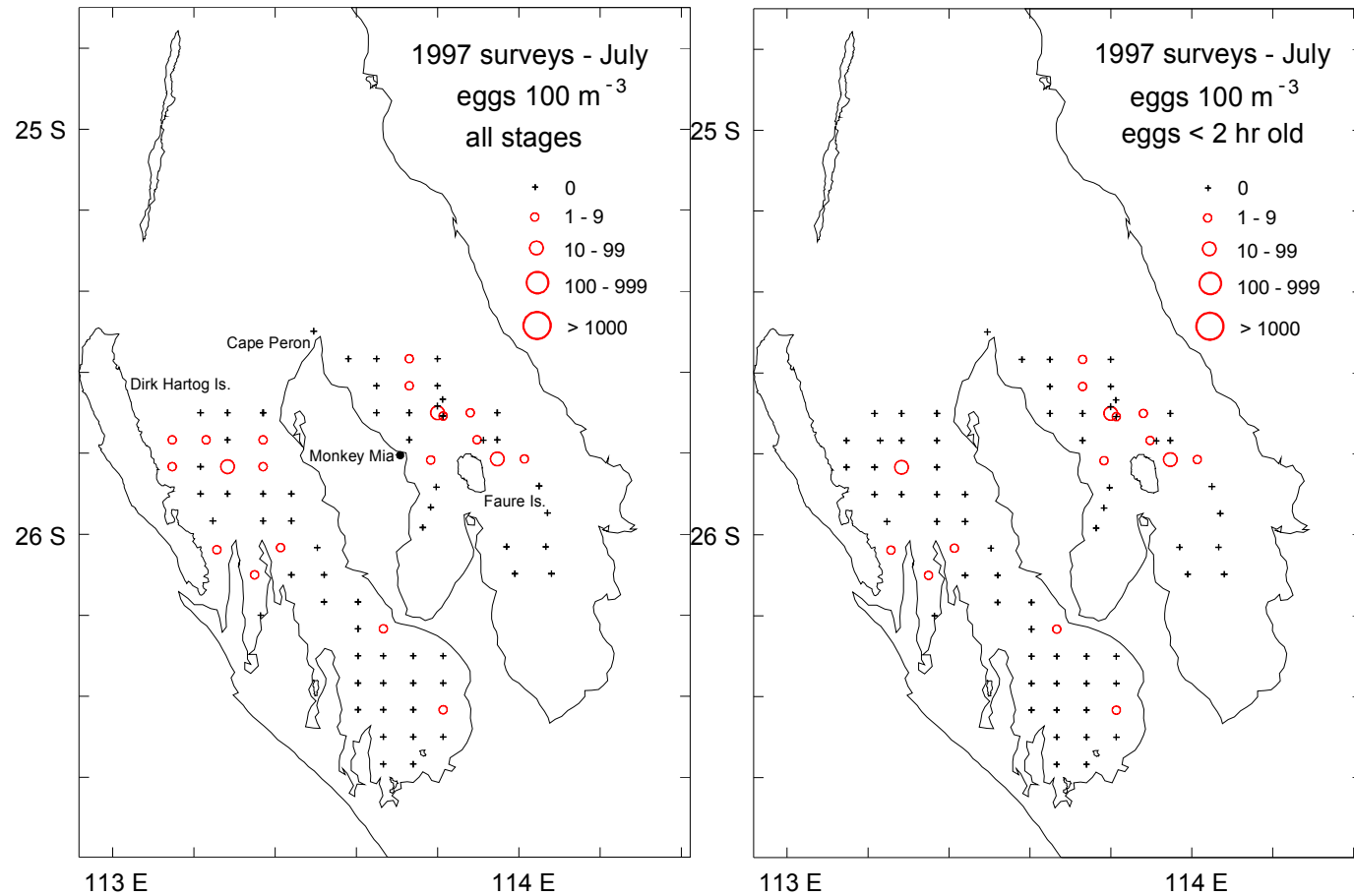


Figure 5.2 Distribution of *P. auratus* eggs from pilot DEPM surveys undertaken in inner Shark Bay in July 1997, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m⁻³.

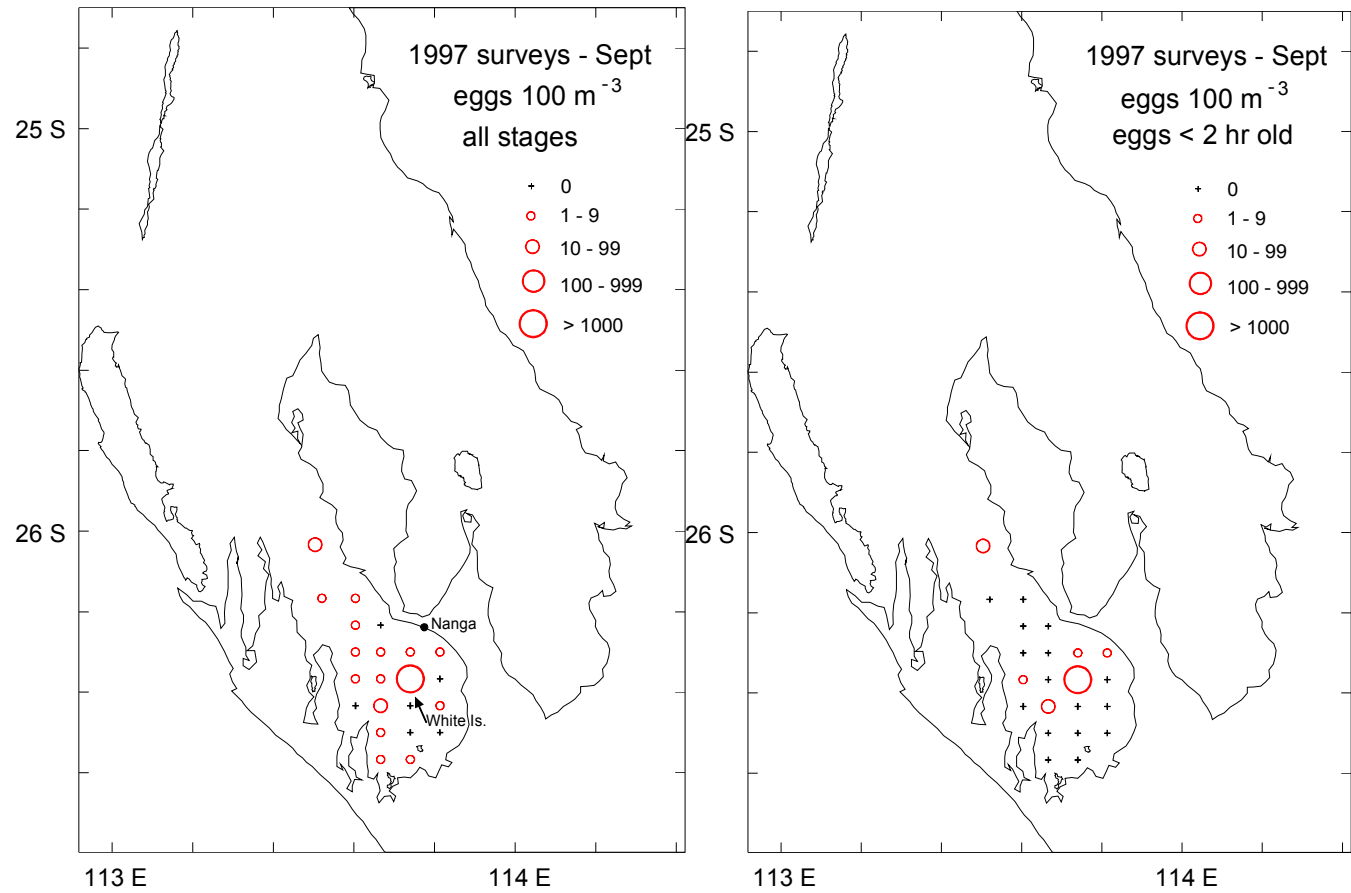


Figure 5.3 Distribution of *P. auratus* eggs from pilot DEPM surveys undertaken in inner Shark Bay in September 1997, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m⁻³.

In 1999, a single DEPM survey only was undertaken in each area (Eastern Gulf in June; Denham Sound in July; Freycinet Estuary in late August). The ichthyoplankton surveys incorporated a further level of stratification with sampling stations arranged in a combination 1 x 1, 2 x 2 and 4 x 2 nm grid pattern. As in 1998, again in an attempt to reduce the variance around estimates of mean egg production, 'adaptive' sampling was also undertaken in close proximity to the suspected spawning areas where recreational boats were catching spawning fish (Eastern Gulf and Denham Sound only). Again, as in 1998, no account was taken of lunar cycles in relation to the timing of DEPM surveys in 1999.

However, based on the results of DEPM surveys in 1998 and 1999, it was apparent that lunar cycle had a significant effect on the levels of spawning activity within the peak spawning period and therefore it was important to take lunar phase into account when scheduling future DEPM surveys. For example, the DEPM survey in the Eastern Gulf in 1999 was, by chance, coincident with the new moon; early stage eggs were sampled in high abundances at some stations and the proportion of females actively spawning was also very high (80-90%, see 5.3 Results). In contrast, the DEPM survey in Denham Sound in the same year took place around the full moon; much lower numbers of youngest eggs were sampled and the proportion of females actively spawning was lower (approximately 60-70%). Thus, in 2000, DEPM surveys were standardised around moon phase in each area for the first time, with each survey commencing two days prior to the new moon. A similar stratified-systematic approach was used for the ichthyoplankton surveys with combination 1 x 1, 2 x 2 and 4 x 2 nm grid pattern again with some 'adaptive' sampling undertaken in the vicinity of spawning locations. The DEPM surveys conducted between 2001-2004 were similar in design to

that described for 2000 with the exception that ‘adaptive’ sampling was discontinued. No DEPM surveys were undertaken in the Freycinet Estuary in 2003, or in Denham Sound in 2004. A summary of the various sampling strategies used between 1997 and 2004 is presented in Table 5.1.

Table 5.1 Summary of sampling strategies used with *Pagrus auratus* DEPM surveys in inner gulfs of Shark Bay between 1997-2004.

	1997	1998	1999	Year/Month 2000	2001	2002	2003	2004
Area	J J A S	J J A S	J J A S	J J A S	J J A S	J J A S	J J A S	J J A S
Eastern Gulf pilot full survey	- Y - -	Y _{A,S} Y _S - -	Y _{A,S} - - -	Y _{A,S,O} - - -	Y _{S,O} - - -	Y _{S,O} - - -	Y _{S,O} - - -	Y _{S,O} - - -
Denham Sound pilot full survey	Y Y - -	Y _S Y _S - -	- Y _{A,S} - -	- Y _{A,S,O} - -	- Y _{S,O} - -	- Y _{S,O} - -	- Y _{S,O} - -	- - - -
Freycinet Estuary pilot full survey	Y Y -Y	- - Y _{A,S} -	- - - Y _S	- - - Y _{A,S,O}	- - Y _{S,O} -	- - - Y _{S,O}	- - - -	- - - Y _{S,O}

J J A S = June, July, August, September; Y = yes, survey conducted; _A = adaptive sampling included; _S = stratified sampling; _O = survey scheduled around new moon

5.2.1.2 Ichthyoplankton sampling

In all years, the ichthyoplankton surveys employed oblique tows of a double bongo-net (each net mouth 60 cm diameter, net mesh 500 μm , Fig. 5.4) of 3 minutes duration at each sampling station. These surveys were conducted from either Department of Fisheries WA vessels *RV Snipe* (~7 m overall length) or *PV John Brockman* (~9 m) with net tow-speeds maintained at ~1.5-2 knots to avoid problems with back-wash. A single flowmeter (General Oceanics model 2030R) was fitted in the mouth of one net to monitor the volume of water filtered. The length of rope deployed during each tow was approximately 2.5 times the water depth at each station. At the conclusion of each tow, the retrieved bongo-net was washed thoroughly with seawater via a deck hose, from net mouth downwards, towards both cod ends.



Figure 5.4 Retrieving the bongo-net from portside of *RV Snipe* during DEPM ichthyoplankton survey in Denham Sound, Shark Bay. Note flowmeter clearly visible in the mouth of the net (right).

Cod ends were then removed, washed-out with seawater and the ichthyoplankton sample rinsed into either a 250 or 500 ml plastic jar (labelled). Samples were fixed with 5% formalin and seawater buffered with borax powder

(approximately 1 g L^{-1}). Note: during DEPM surveys in 1998 and 1999, to maximise the numbers of *P. auratus* eggs collected, both cod end samples at each station were retained; from 2000 onwards, to reduce sample processing time (sampling had been so successful in 1999 that very large numbers of eggs were collected at some sites), a single cod-end sample only was retained (net mouth with flowmeter). Sea surface temperature, salinity (measured using hand-held model WTW Condi 315i) and depth (taken from survey vessel colour-sounder) were recorded at each station.

5.2.1.3 Laboratory procedures

Central to the estimation of spawning biomass (B) using the DEPM is the estimation of daily egg production (P) and corresponding daily mortality rate (Z) based on the relative abundances of eggs of the different stages of development collected during the ichthyoplankton survey(s). Both P and Z are usually estimated by fitting a mortality curve (also termed the egg production curve) to the abundance of sampled eggs classified into age classes (Bernal *et al.* 2001). Daily egg production (P) is typically estimated as the y-intercept of the mortality curve, *i.e.* number of eggs of age 0 hr (just spawned) produced per day while daily egg mortality (Z) is estimated from the slope of the fitted curve. The DEPM requires that eggs of the target species can be clearly identified, classified into development stages (usually based on morphological characteristics) and ages assigned to each egg stage. Typically some form of development model, often based on incubation experiments, is used to determine the age of the individual development stages (Stratoukadis *et al.* 2006). The period of egg development (*i.e.* time to hatching) for marine fishes generally decreases with increasing ambient water temperature (Pepin 1991). Knowledge of the environmental

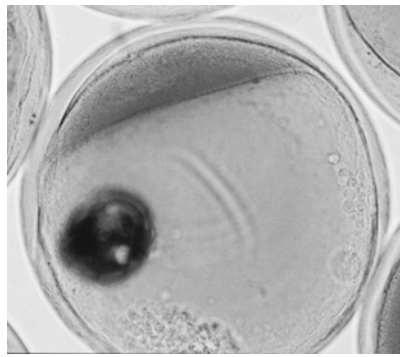
conditions at the time of the DEPM ichthyoplankton survey is therefore critical to !
determining the rate of egg development.

5.2.1.4 Egg stages

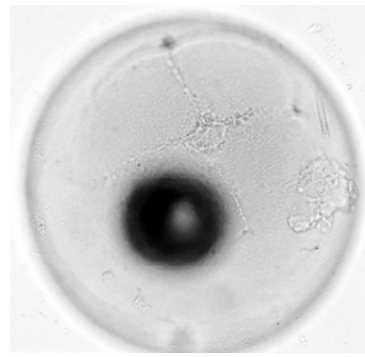
Ichthyoplankton samples from Shark Bay were systematically sorted in the laboratory using a dissecting microscope (magnification 10-20x). The *P. auratus* eggs were identified using characteristics including overall egg diameter (~0.8-1.0 mm), yolk sac diameter (~0.7 mm) and oil globule diameter (~0.2 mm) and classified into 19 development stages based on their internal morphology (Norriss and Jackson 2002, Table 5.2, Fig. 5.5).

Table 5.2 Egg stage key for classifying preserved eggs of *P. auratus* (from Norriss and Jackson 2002)

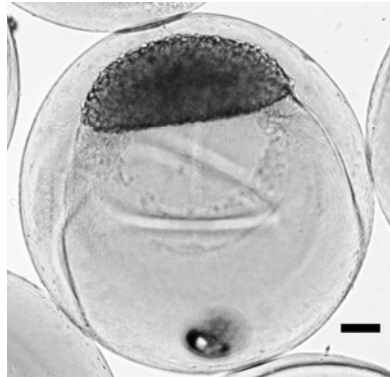
Egg characteristic	Stage
Embryo absent	
Single celled protoplasm	1
2 cells	2
4 cells	3
8 cells	4
16 cells	5
> 16 cells individually visible at magnification of 30 x	6
> 16 cells not individually visible at magnification of 30 x	7
Blastoderm larger than original germinal disc	
Blastoderm not extending past equator	8
Blastoderm at the equator	9
Blastoderm extending past equator	10
Embryo present, without somites	
Embryonic streak only, head and tail undefined	11
Head distinct, tail undefined	12
Head with optic lobes	13
Somites present	
Tail margin not distinct	14
Tail margin distinct, flush with yolk sac	15
Tail raised as a bulge above yolk sac	16
Tail partly separated from yolk sac	17
Width of tail fin less than width of caudal peduncle	18
Width of tail fin greater than width of caudal peduncle	19



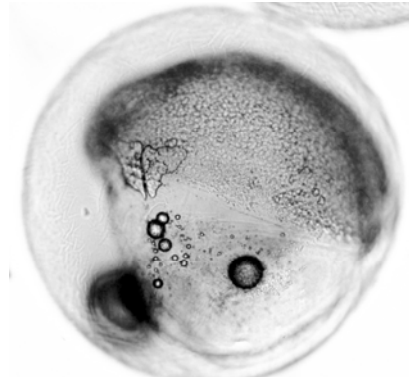
Stage 1 !



Stage 3



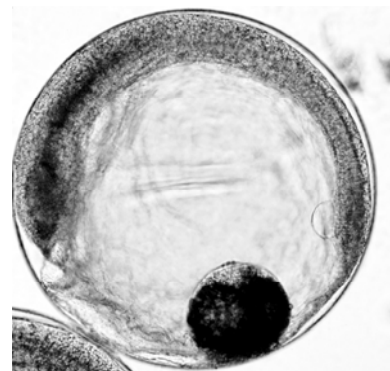
Stage 7 !



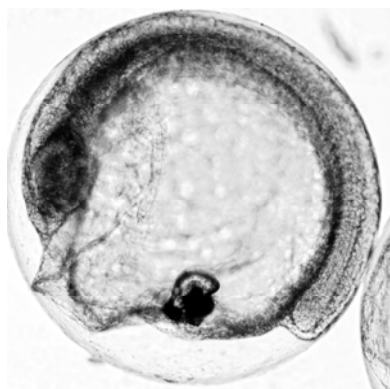
Stage 9



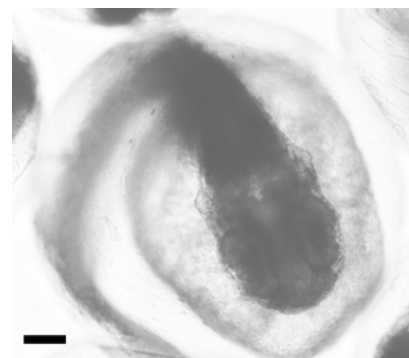
Stage 13



Stage 15 !



Stage 16



Stage 19 !

Figure 5.5 Photo-images of a selection of development stages of preserved *P. auratus* eggs from Shark Bay. Scale bars = 100 μ m. From Norriss and Jackson (2002).

5.2.1.5 Egg ages

Time to hatching, conventionally estimated as the time at which 50% of eggs hatch, was estimated separately for each DEPM survey using a set of empirical relationships determined for *P. auratus* eggs by McGlennon (2003) based on incubation experiments and a range of water temperature (18-24 °C) and salinity (36-48) conditions. Although McGlennon (2003) found that the effect of salinity on the incubation period was not statistically significant, there was a consistent (small) increase in hatch time of 1-1.5 hours within each temperature condition with increasing salinity. For *P. auratus* eggs from inner Shark Bay in this study therefore, time to hatching (H_t , hours) for a range of temperature (t , °C) and salinity conditions observed during DEPM surveys was estimated using the following equations (D. McGlennon unpublished data):

$$\text{At salinity 36: } H_t = -2.417t + 74.83$$

$$\text{At salinity 40: } H_t = -2.33 t + 73.5$$

$$\text{At salinity 44: } H_t = -2.5 t + 77.58$$

$$\text{At salinity 48: } H_t = -2.417 t + 76.25$$

For each DEPM survey and corresponding estimated time to hatching, mean-age-at-stage for each of the 19 egg development stages was then estimated using a non-linear development model derived by Wakefield (2006, see Results) that was based on an incubation experiment and by following cohorts of ‘wild’ *P. auratus* eggs contained in ichthyoplankton samples collected from Cockburn Sound.

5.2.1.6 Spawning times

Patterns in daily spawning activity were determined by back-calculation of the time of spawning using egg ages and collection time. Thus, the time of spawning of each batch of eggs, *i.e.* eggs of a similar stage (independent of the number of eggs in

any sample), was estimated by subtracting the mean-age-at-stage from the known time ! of collection for each sample. Spawning times for all batches of eggs collected during each DEPM survey were plotted as frequency histograms to identify temporal (diel) patterns in *P. auratus* spawning activity. In addition, patterns in spawning activity from histological examination of female *P. auratus* gonads of known time of capture were investigated and used, where possible, to corroborate patterns inferred from back-calculated spawning times. Here, frequency histograms of the proportions of females either with Stage 5a ('pre-spawning'), 5b ('spawning') or 5c ('post-spawning') gonads (see Chapter 3 – Reproductive biology) in the samples were plotted against time of collection where the 24-hour cycle was divided into 3-hour blocks *e.g.* 0900-1200, 1201-1500, 1501-1800, and so on.

5.2.1.7 Estimation of daily egg production (*P*)

The methods used in this study followed those described by Picquelle and Stauffer (1985). Here estimates of the daily production of eggs are derived by regressing counts of eggs observed in samples on their estimated age using an exponential mortality model. This approach assumes a constant mortality rate across the survey area and over the duration of the survey (Picquelle and Stauffer 1985; Bunn *et al.* 2000; Stratoukadis *et al.* 2006).

The numbers of eggs of each stage sampled at each station were corrected⁵ for the volume (*v*) of water filtered based on the observed flow meter readings as follows,

$$v = A (f^{0.026873}) \quad \text{Eqn 5.2}$$

where *A* = surface area of mouth of net ($A = \pi r^2$, where *r* = 0.3 m when one cod-end only retained; $A = 2(\pi r^2)$ if both cod-ends retained) and *f* = flow meter count. Where

tow duration at any station deviated from the 3 minute standard time, corrections were ! made to the volume of water sampled *e.g.* if tow time = 4 minutes, v was multiplied by 4/3, if tow time = 5 minutes, v was multiplied by 5/3 and so on.

The number of eggs of each stage at each station (N_t) was converted to density (termed ‘unweighted egg density’) of eggs m^{-2} of sea surface (P_t) as follows,

$$P_t = (N_t d) / v \quad \text{Eqn 5.3}$$

where d = depth of water (m) at station.

Following each survey, the total area surveyed was divided into a series of contiguous polygons approximately centred on each sampling station. The area of spawning (A , km^2) was estimated from the summation of area represented by each station at which *P. auratus* eggs were collected (termed ‘positive’ egg stations) during the survey. Where multiple samples were taken at the same station or close by but still within the representative polygon (as part of the adaptive sampling), a mean (‘unweighted’) egg density for each stage was estimated from the pooled samples. These mean (‘unweighted’) egg densities were used in subsequent analyses. Egg densities were weighted (‘weighted egg density’) in proportion to the area represented by each station with the sum of weighting factors equal to the total number of stations within A (see Picquelle and Stauffer 1985, p 8).

Instantaneous daily egg mortality (Z) is usually expressed as follows,

$$N_t / N_0 = \exp [-Zt] \quad \text{Eqn 5.4}$$

where N_t = number of eggs at time $t > 0$ and N_0 = number of eggs spawned (*i.e.* $t = 0$).

⁵ 0.026873 = standard speed rotor constant for Model 2030 Series flowmeter, General Oceanics Inc., Miami, Florida, US.

Daily egg production (P) was estimated for each survey by fitting a non-linear least squares regression (with errors assumed to be normally distributed, Jackson and Cheng 2001) to the weighted mean egg densities of all 19 egg stages (P_t) against egg age (t , days),

$$P = P_t e^{Zt} + \varepsilon \quad \varepsilon \sim N(0, \sigma^2) \quad \text{Eqn 5.5}$$

However, because the error structure was in reality unknown, balanced non-parametric bootstrapping was used to calculate 95% confidence intervals for the estimates of P (Jackson and Cheng 2001). This approach is distribution free and provides satisfactory results in small samples that compare favourably with other large-sample methods in larger samples (Fisher 1993). Balanced re-sampling is a more effective way of random re-sampling with replacement (Fisher 1993). For each estimate of P , the analysis was repeated using each of 1000 sets of re-sampled data with the 95% confidence intervals for values of P estimated as the 2.5 and 97.5 percentiles of the resulting parameter estimates.

5.2.2 Adult reproductive parameters

Samples of mature *P. auratus* were collected concomitantly with the DEPM ichthyoplankton surveys in each year. These fish were obtained by Department of Fisheries WA research staff with the assistance of local volunteer recreational fishers rod and line fishing from small recreational vessels mostly in the vicinity of the known spawning grounds. On capture, all *P. auratus* were bled and placed in an ice slurry. Where possible, the time of capture of individual fish was recorded on a label that was then placed in the mouth cavity/gills of each fish. Onshore, all fish were measured (FL,

mm) and, using the paired gonads, were sexed and staged macroscopically (see Chapter ! 3 – Reproductive biology). Female gonads were weighed to the nearest g and fixed in 10% formalin with seawater for subsequent histological examination and the estimation of batch fecundity (see Chapter 3 – Reproductive biology).

Individual *P. auratus* were not routinely weighed during this study. Rather, whole weight (WW , g) of individual fish was estimated from fork length (FL , mm) using a length-weight relationship where $WW = 0.000148FL^{2.6703}$ (see Chapter 3 – Reproductive biology). The adult reproductive parameters W , R , S and F were estimated separately based on the samples of mature fish collected during each DEPM survey, as follows.

Average female weight (W)

Average female weight (W) was estimated as the mean of the weights (whole) of all mature females sampled, *i.e.* fish possessing Stage 4–6 gonads.

Sex ratio (R)

Sex ratio (R) was estimated from the summation of the weights of all mature females divided by the summation of the weights of all mature fish sampled, *i.e.* the total weight of mature males (*i.e.* fish possessing Stage 3-5 gonads), plus the total weight of mature females.

Spawning fraction (S)

Spawning fraction (S) was estimated from the summation of the weights of females with ovaries determined by histological examination to be in spawning

condition, *i.e.* females possessing Stages 5a, 5b or 5c gonads, divided by the sum of the ! weights of all the mature females sampled.

Batch fecundity (F)

Of the female gonad samples collected from each DEPM survey, only the ovaries determined histologically to be in pre-spawning condition (Stage 5a) were employed to estimate batch fecundity using the standard gravimetric method as described in detail in Chapter 3 (Reproductive biology). Mean batch fecundity (F) for all the mature females sampled in each separate DEPM survey (*i.e.* mean batch fecundity for the female spawning population) were estimated using a common non-linear relationship between FL (mm) and F based on the pooled batch fecundity data (all areas/years) obtained during 1998-2004 as follows,

$$F = 9.436 \times 10^{-5} FL^{3.359}$$

(see Chapter 3 -Reproductive biology).

As with the estimation of egg production, because the error structure was in reality unknown, balanced non-parametric bootstrapping was used to calculate 95% confidence intervals for the estimates of the mean adult parameters W , R , S and F (Jackson and Cheng 2001). For each estimate of W , R , S and F , the analysis was repeated using each of 1000 sets of re-sampled data with the 95% confidence intervals estimated as the 2.5 and 97.5 percentiles of the resulting parameter estimates. Differences among the means for the four adult parameters were compared among years within areas using ANOVA (Zar 1984).

5.2.3 Estimation of spawning biomass (B)

Spawning biomass, B , was estimated independently for each survey using Equation 5.1 (p 147). Balanced non-parametric bootstrapping was used to calculate 95% confidence intervals for the estimates of B (Jackson and Cheng 2001). For each estimate of B , the analysis was repeated using each of 1000 sets of re-sampled data with the 95% confidence intervals estimated as the 2.5 and 97.5 percentiles of the resulting parameter estimates.

5.3 Results

5.3.1 Ichthyoplankton surveys

Between 1998 and 2004, a total of 21 separate DEPM surveys were carried out; eight in the Eastern Gulf, seven in Denham Sound, and six in the Freycinet Estuary (Tables 5.3, 5.4 and 5.5). These surveys involved a total of 2,432 plankton tows; 1,032 in the Eastern Gulf, 663 in Denham Sound and 737 in the Freycinet Estuary. The proportion of tows that contained *P. auratus* eggs varied between surveys and ranged from 24% (July 1998) to 64% (1999) in the Eastern Gulf, 41% (2001) to 78% (2000) in Denham Sound, and 34% (2004) to 73% (2000) in the Freycinet Estuary. Overall these tows yielded a total of 91,754 *P. auratus* eggs of which 60,148 were collected from the Eastern Gulf, 6,684 from Denham Sound and 24,922 from the Freycinet Estuary. While most samples with eggs ('positive' samples) contained only low numbers, *i.e.* < 10 , occasionally samples, usually those taken in the vicinity of spawning fish, yielded very high numbers of eggs. For example, a single tow in the Eastern Gulf in 2000, taken at 1540 hr in the vicinity of a major spawning aggregation, contained 9,224 early stage eggs (Stages 1-6).

Table 5.3 DEPM survey details and parameter estimates for the Eastern Gulf, 1998-2000. Values in parentheses are bootstrapped 95% C.I.s. Note, all estimates of spawning biomass were determined using $Z = 0.49 \text{ day}^{-1}$.

Eastern Gulf: Parameter	Year			
	1998		1999	2000
	June	July	June	May/June
No. males	62	28	67	65
No. females	86	71	97	86
Average female weight W (g)	2840(2606-3094)	2429(2197-2688)	3338(3113-3543)	3226(2971-3506)
Sex ratio R	0.61(0.51-0.67)	0.72(0.55-0.84)	0.59(0.52-0.67)	0.59(0.48-0.65)
Spawning fraction S	0.98(0.93-1.0)	0.85(0.76-0.93)	0.9(0.83-0.95)	0.89(0.79-0.95)
Batch fecundity F	141488(127461-155879)	118922(104486-130190)	169102(156445-182379)	163164(147164-177201)
Date of survey	2/6 to 6/6/98	2/7 to 5/7/98	9/6 to 13/6/99	31/5 to 4/6/00
Area surveyed (km^2)	1731	1380	2130	2339
no. of plankton tows	110	82	131	205
% stations with eggs	41	24	64	56
Area of spawning A (km^2)	707	386	947	1032
Daily egg mortality Z (day^{-1})	0.51	0.98	-0.39	-1.59
Z used to estimate B (day^{-1})	0.49	0.49	0.49	0.49
Daily egg production P (eggs $\text{m}^{-2} \text{day}^{-1}$)	1.06(0.64-2.17)	2.62(2.09-4.4)	1.68(1.12-2.63)	5.91(3.87-8.99)
Spawning biomass B (tonnes)	25(12-45)	34(23-52)	59(35-89)	232(139-354)

Table 5.3 contd DEPM survey details and parameter estimates for the Eastern Gulf, 2001-2004. Values in parentheses are bootstrapped 95% C.I.s. Note, all estimates of spawning biomass were determined using $Z = 0.49 \text{ day}^{-1}$.

Eastern Gulf (contd):	Year			
	2001	2002	2003	2004
Parameter	June	June	May/June	June
No. males	41	61	78	67
No. females	45	57	86	46
Average female weight W (g)	3601(3163-3939)	3081(2828-3472)	2403(2115-2770)	3412(3079-3727)
Sex ratio R	0.53(0.41-0.64)	0.56(0.46-0.65)	0.59(0.48-0.67)	0.45(0.35-0.55)
Spawning fraction S	0.88(0.76-0.95)	0.99(0.96-1.00)	0.9(0.79-0.96)	0.71(0.53-0.83)
Batch fecundity F	184827(162081-205389)	154663(140268-173610)	119038(102647-135372)	173166(156419-191984)
Date of survey	21/6 to 25/6/01	9/6 to 13/6/02	30/5 to 1/6/03	17/6 to 20/6/04
Area surveyed (km^2)	2360	2373	1921	1962
no. of plankton tows	161	129	101	113
% stations with eggs	62	48	46	35
Area of spawning A (km^2)	1118	957	827	700
Daily egg mortality Z (day^{-1})	-0.11	0.09	-0.31	-0.73
Z used to estimate B (day^{-1})	0.49	0.49	0.49	0.49
Daily egg production P (eggs $\text{m}^{-2} \text{day}^{-1}$)	2.04(1.26-4.56)	1.79(0.90-4.54)	5.73(2.59-12.91)	1.35(0.98-1.84)
Spawning biomass B (tonnes)	96(46-176)	62(22-121)	181(59-377)	59(38-92)

Table 5.4 DEPM survey details and parameter estimates for Denham Sound 1998-2000. Values in parentheses are bootstrapped 95% CIs. Note, all estimates of spawning biomass were determined using $Z = 0.49 \text{ day}^{-1}$.

Denham Sound: Parameter	Year			
	1998		1999	2000
	June	July	July	June/July
No. males	21	9	38	75
No. females	41	17	61	76
Average female weight W (g)	1611(1375-1894)	2779(2282-3240)	2926(2595-3249)	2565(2369-2747)
Sex ratio R	0.64(0.49-0.77)	0.68(0.50-0.84)	0.68(0.58-0.78)	0.58(0.49-0.67)
Spawning fraction S	0.46(0.29-0.66)	0.81(0.52-0.94)	0.74(0.60-0.83)	0.59(0.48-0.70)
Batch fecundity F	67522(57462-78709)	123470(98347-146059)	131674(115754-147609)	112598(103982-121822)
Date of survey	23/6 to 25/6/98	21/7 to 24/7/98	21/7 to 24/7/99	30/6 to 3/7/00
Area surveyed (km^2)	1129	1064	849	1386
no. of plankton tows	79	77	95	120
% stations with eggs	53	58	78	71
Area of spawning A (km^2)	593	583	511	872
Daily egg mortality Z (day^{-1})	-1.34	-0.46	-0.23	0.12
Z used to estimate B (day^{-1})	0.49	0.49	0.49	0.49
Daily egg production P (eggs $\text{m}^{-2} \text{day}^{-1}$)	3.69(0.84-10.12)	0.77(0.47-1.83)	0.45(0.37-0.66)	3.15(1.78-8.33)
Spawning biomass B (tonnes)	176(30-455)	18(8-39)	10(7-15)	184(79-370)

Table 5.4 contd DEPM survey details and parameter estimates for Denham Sound 2001-2003. Values in parentheses are bootstrapped 95% CIs. Note, all estimates of spawning biomass were determined using $Z = 0.49 \text{ day}^{-1}$.

Denham Sound (contd): Parameter	Year		
	2001	2002*	2003
	July	July	June/July
No. males	23	85	62
No. females	20	74	54
Average female weight W (g)	2986(2096-3843)	2993(2627-3329)	2996(2677-3404)
Sex ratio R	0.60(0.42-0.77)	0.57(0.49-0.66)	0.56(0.45-0.65)
Spawning fraction S	0.85(0.55-0.96)	0.77(0.65-0.85)	0.74(0.62-0.84)
Batch fecundity F	136940(97068-179234)	135336(118057-153950)	134742(118293)
Date of survey	19/7 to 24/7/01	9/7 to 11/7/02	28/6 to 1/7/03
Area surveyed (km^2)	1816	1816	1816
no. of plankton tows	126	83	83
% stations with eggs	41	51	61
Area of spawning A (km^2)	732	933	1041
Daily egg mortality Z (day^{-1})	-1.96	-0.32	0.72
Z used to estimate B (day^{-1})	0.49	0.49	0.49
Daily egg production P (eggs $\text{m}^{-2} \text{day}^{-1}$)	2.24(1.43-4.33)	2.65(1.77-4.24)	1.63(1.22-2.17)
Spawning biomass B (tonnes)	70(32-151)	125(70-205)	92(60-137)

Table 5.5 DEPM survey details and parameter estimates for Freycinet Estuary 1998-2001. Values in parentheses are bootstrapped 95% CIs. Note, all estimates of spawning biomass were determined using $Z = 0.49 \text{ day}^{-1}$.

Parameter	Year			
	1998	1999	2000	2001
	Aug	Aug/Sept	Aug/Sept	Aug
No. males	67	88	66	17
No. females	87	119	69	17
Average female weight W (g)	4505(4297-4769)	4362(4140-4586)	3011(2622-3418)	4263(3469-4958)
Sex ratio R	0.57(0.48-0.64)	0.6(0.53-0.67)	0.47(0.36-0.56)	0.62(0.42-0.78)
Spawning fraction S	0.91(0.83-0.96)	0.72(0.62-0.8)	0.81(0.66-0.89)	0.75(0.51-0.93)
Batch fecundity F	261603(246915-275921)	252836(238973-266575)	170364(146172-194517)	247674(196742-295176)
Date of survey	24/8 to 27/8/98	31/8 to 5/9/99	28/8 to 4/9/00	18/8 to 20/8/01
Area surveyed (km ²)	1002	933	1056	1068
no. of plankton tows	123	119	138	119
% stations with eggs	49	71	73	40
Area of spawning A (km ²)	513	625	699	401
Daily egg mortality Z (day ⁻¹)	0.72	-0.46	-0.67	-0.92
Z used to estimate B (day ⁻¹)	0.49	0.49	0.49	0.49
Daily egg production P (eggs m ⁻² day ⁻¹)	11.39(2.74-47.15)	1.28(0.83-1.91)	2.65(2.07-3.89)	0.95(0.74-1.26)
Spawning biomass B (tonnes)	195(37-528)	32(21-50)	87(56-137)	14(8-27)

Table 5.5 contd DEPM survey details and parameter estimates for Freycinet Estuary 2002-2004. Values in parentheses are bootstrapped 95% CIs. Note, all estimates of spawning biomass were determined using $Z = 0.49 \text{ day}^{-1}$.

Freycinet Estuary (contd):	Year		
	2002	2003	2004
Parameter	Sept		Sept
No. males	37		48
No. females	32		49
Average female weight W (g)	4452(3999-4877)		4069(3619-4398)
Sex ratio R	0.45(0.34-0.57)		0.53(0.43-0.64)
Spawning fraction S	0.84(0.64-0.95)	no survey	0.85(0.72-0.93)
Batch fecundity F	258816(229802-289657)		234668(208177-256431)
Date of survey	6/9 to 8/9/02		12/9 to 16/9/04
Area surveyed (km^2)	1105		1105
no. of plankton tows	118		120
% stations with eggs	64		34
Area of spawning A (km^2)	711		344
Daily egg mortality Z (day^{-1})	-0.8		-0.12
Z used to estimate B (day^{-1})	0.49		0.49
Daily egg production P (eggs $\text{m}^{-2} \text{day}^{-1}$)	1.69(1.19-3.03)		0.71(0.54-0.99)
Spawning biomass B (tonnes)	27(14-49)		9(6-14)

5.3.2 Egg distributions

The distribution of *P. auratus* eggs was broadly similar between years in the three survey areas (Figs 5.6 to 5.13). In the Eastern Gulf, eggs (all stages) were found throughout waters to the north of Faure Island but not to the south. Loci of higher abundance (all stages) were consistently observed around Cape Peron, to the northeast of Monkey Mia, in the vicinity of a large spawning aggregation known locally as ‘The Patch’, and to the northeast of Faure Island. Concentrations of the youngest eggs, *i.e.* < 2 hours old (Stages 1-6), were located within these same three areas and were taken to be indicative of the main spawning sites in the Eastern Gulf.

In Denham Sound, eggs (all stages) were mostly found throughout waters off the eastern shore of Dirk Hartog Island and in mid Denham Sound rather than further to the east (western shore of Peron Peninsula) or south (due west of Denham). Loci of higher abundances (all stages) were generally found adjacent to Dirk Hartog Island, in particular to just east and north of Quoin Bluff and northwards to the northern limit of the survey area (see Discussion). In most years, the highest abundances of eggs <2 hours old were found within this region to the north of Quoin Bluff. Note: The reduced extent of the survey area in 1999 resulted from the ichthyoplankton survey being abandoned prematurely due to mechanical problems with the survey vessel.

In the Freycinet Estuary, in most years, eggs (all stages) were found throughout all waters surveyed. Loci of higher abundances (all stages) were located

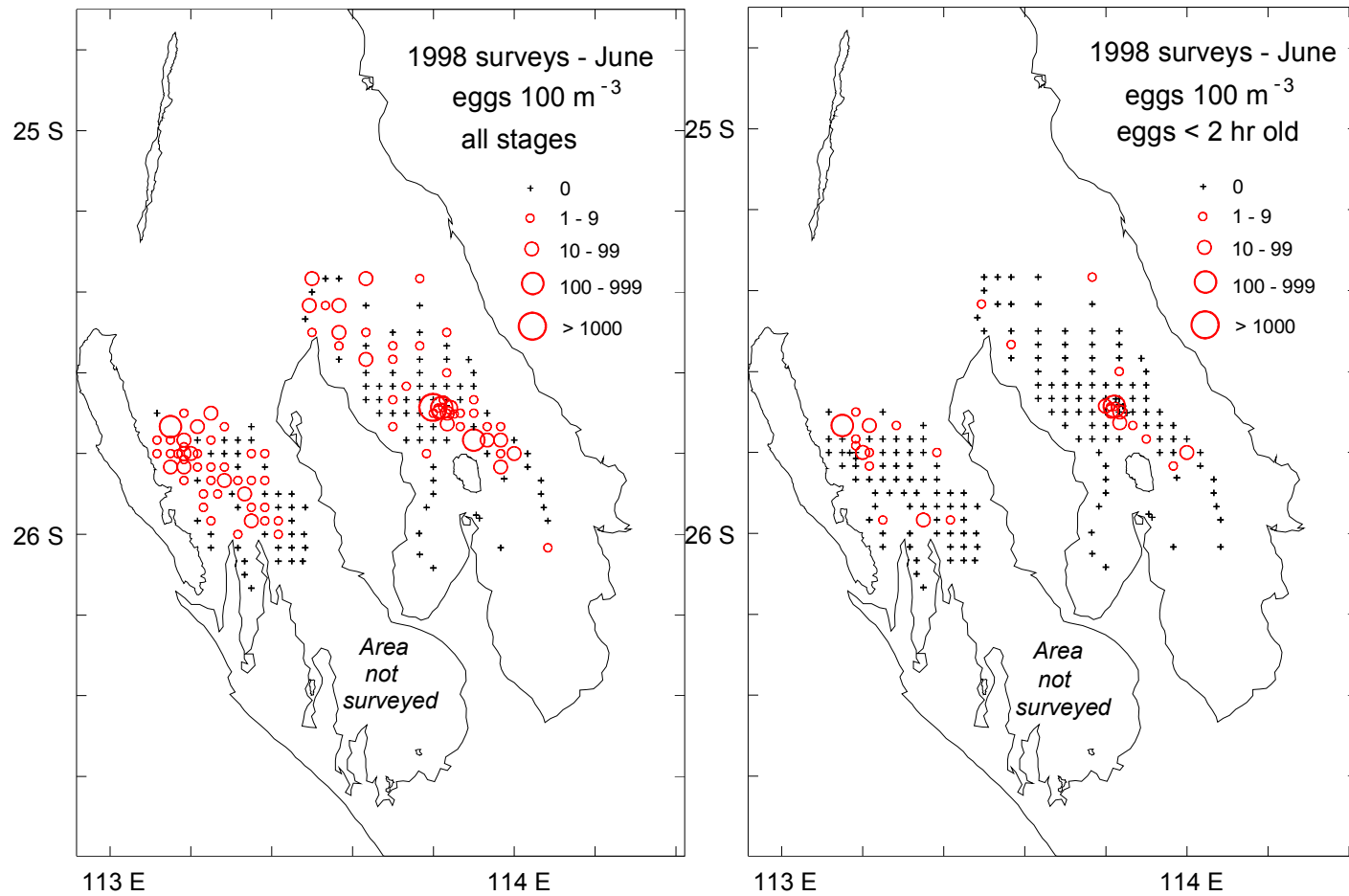


Figure 5.6 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in June 1998, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m^{-3} . Note stratification compared with surveys in 1997.

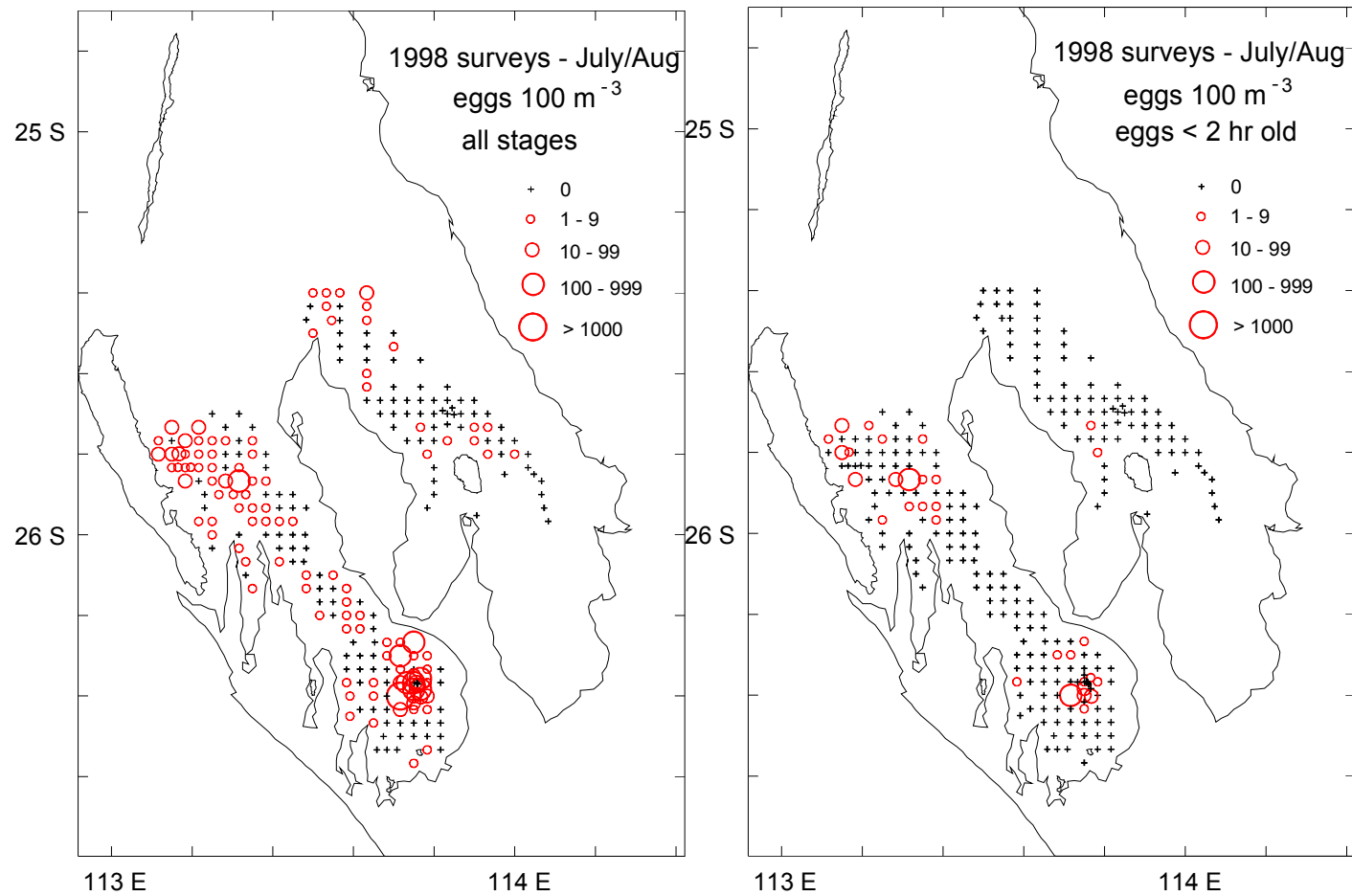


Figure 5.7 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in July-August 1998, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m^{-3} . Note stratification compared with surveys in 1997.

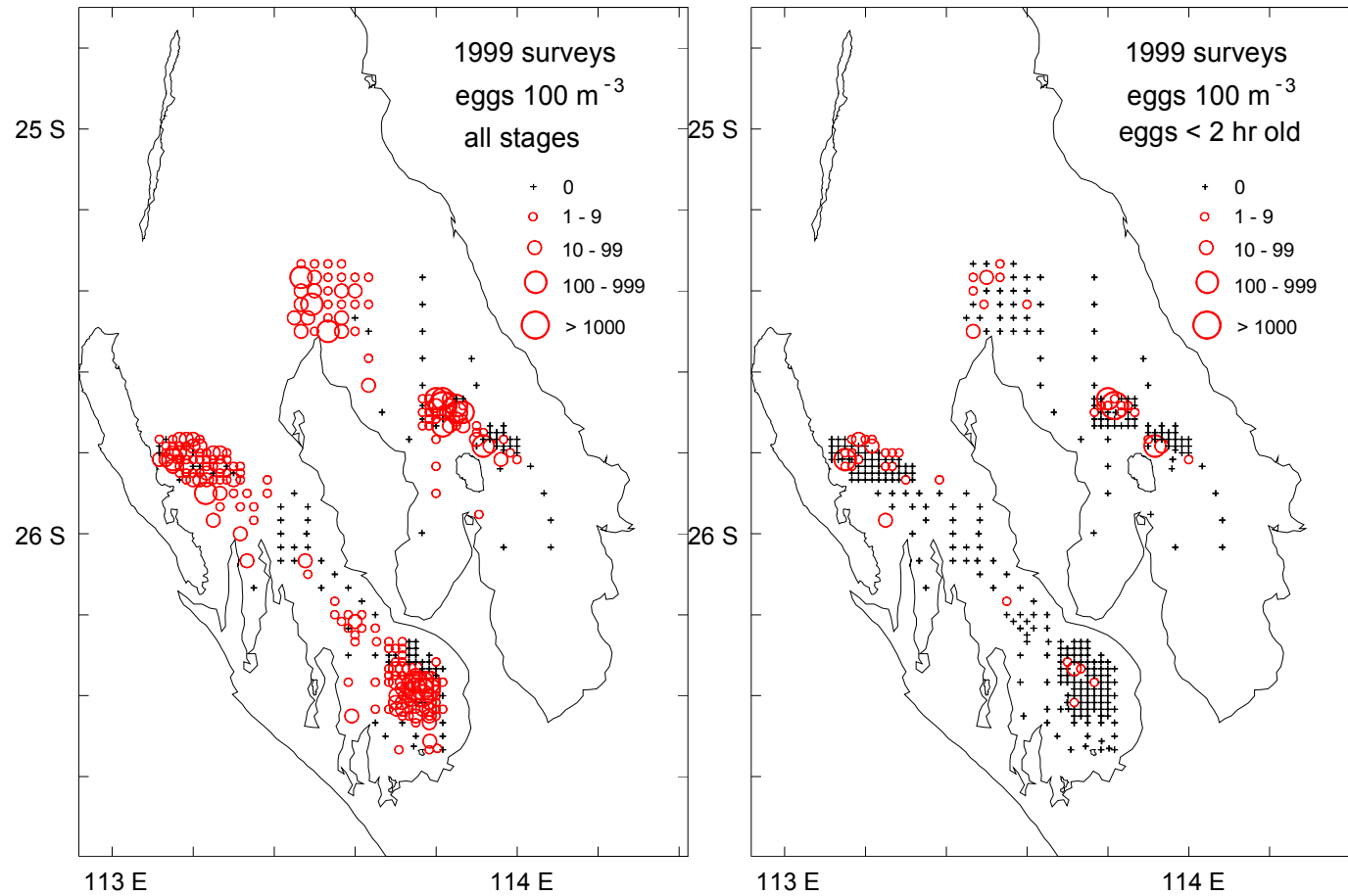


Figure 5.8 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in 1999, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m⁻³. Note increased stratification around main spawning locations compared with 1998.

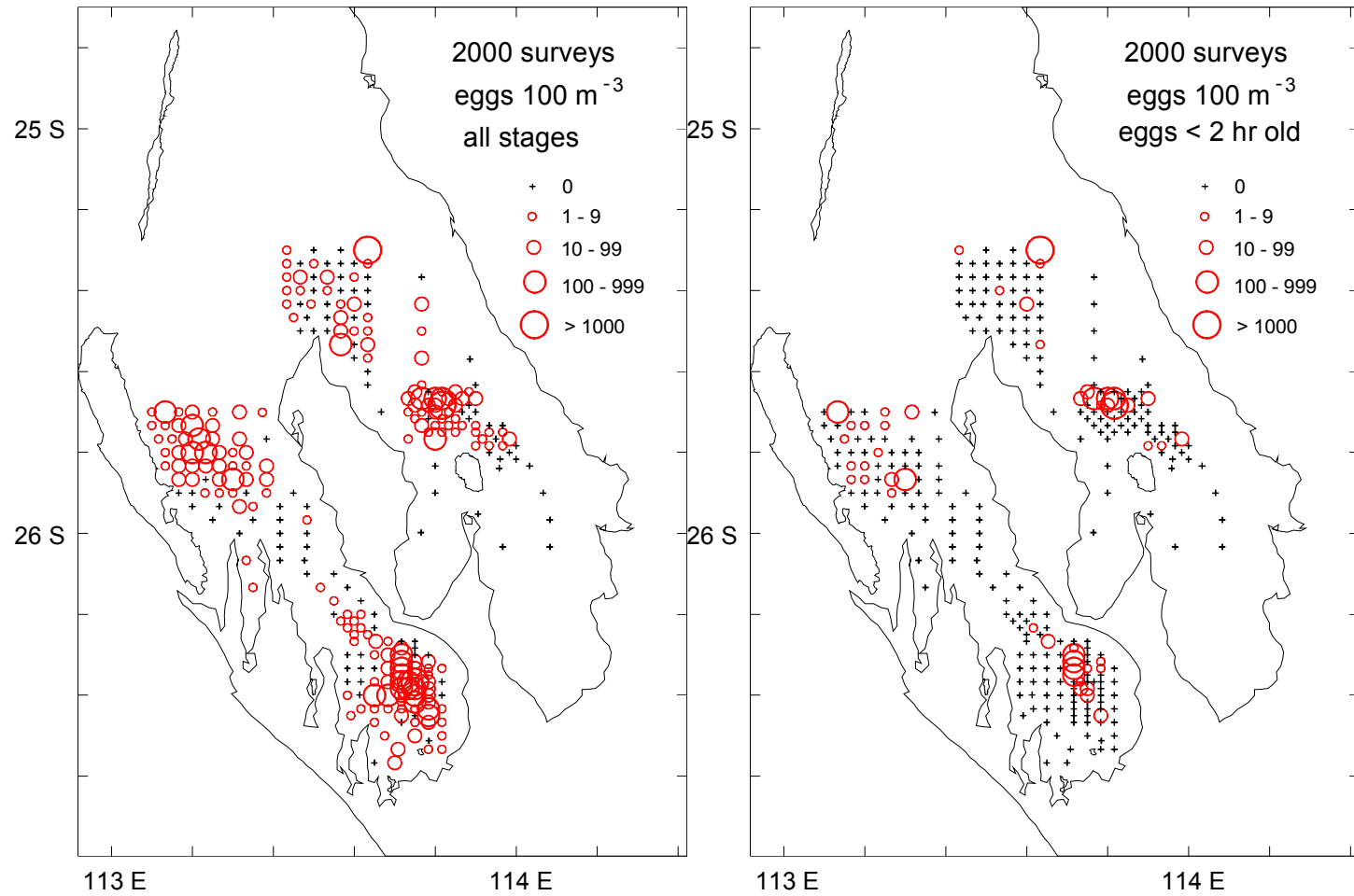


Figure 5.9 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in 2000, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m⁻³.

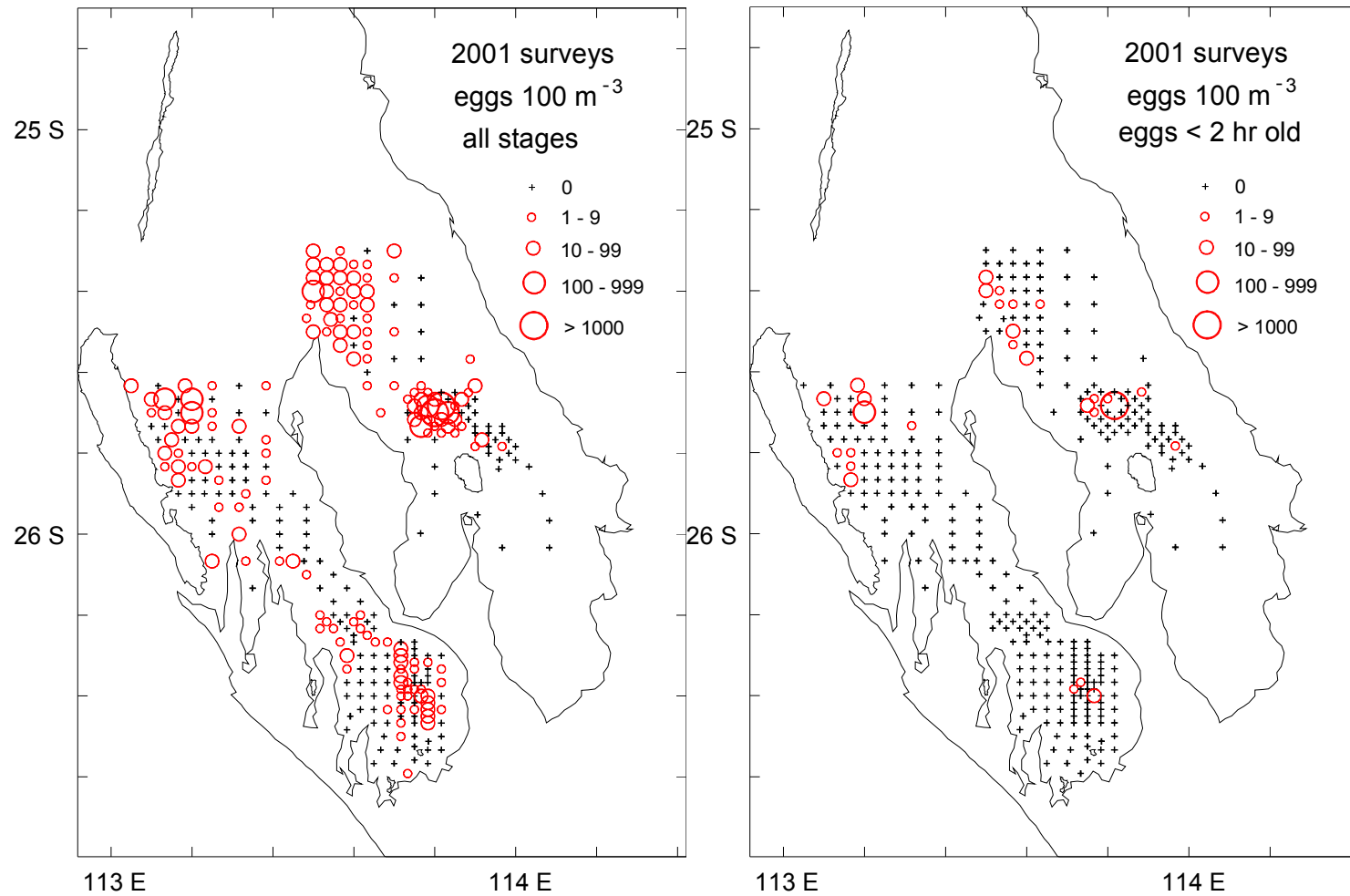


Figure 5.10 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in 2001, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100^{-3} .

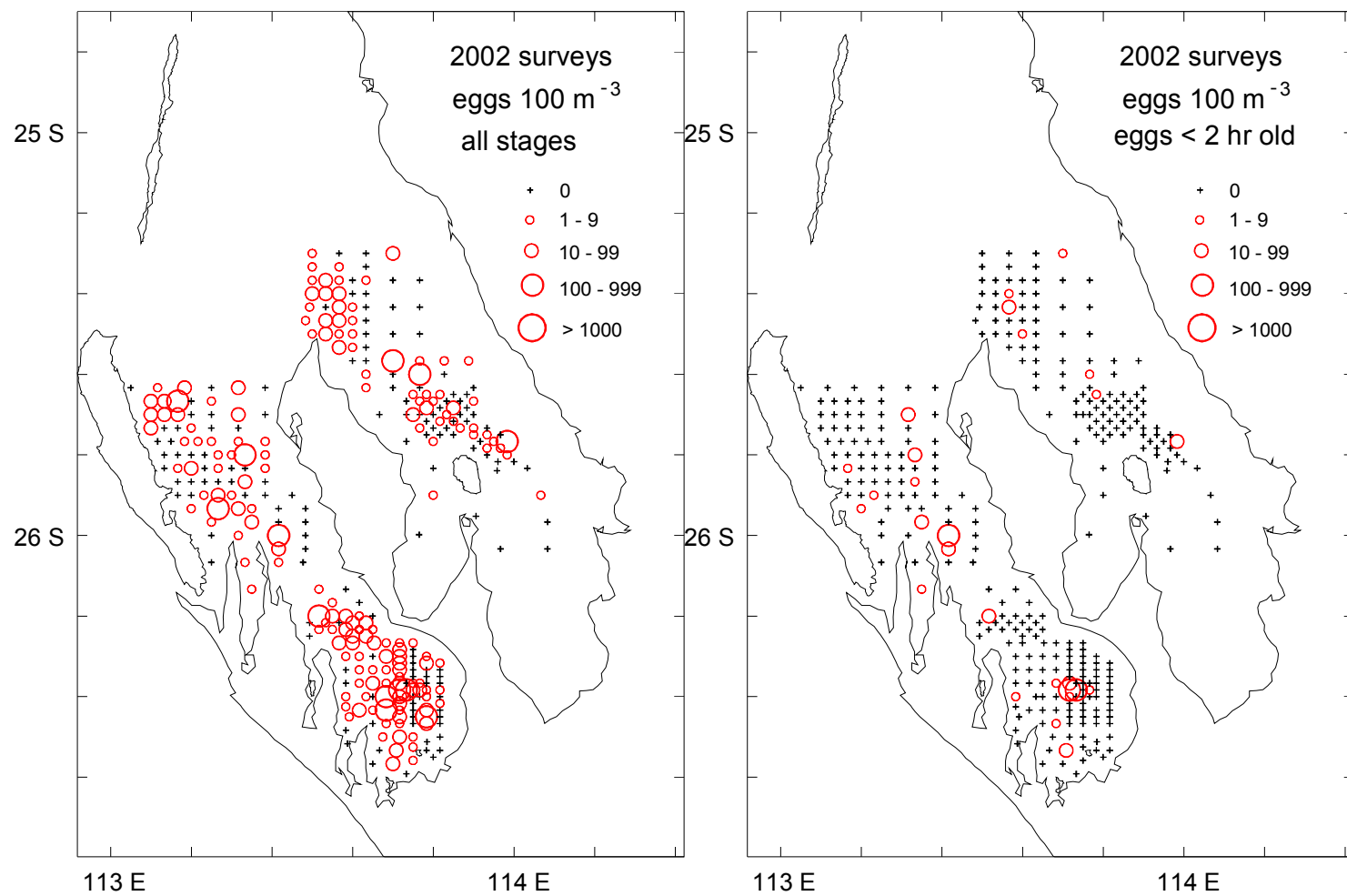


Figure 5.11 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in 2002, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m⁻³.

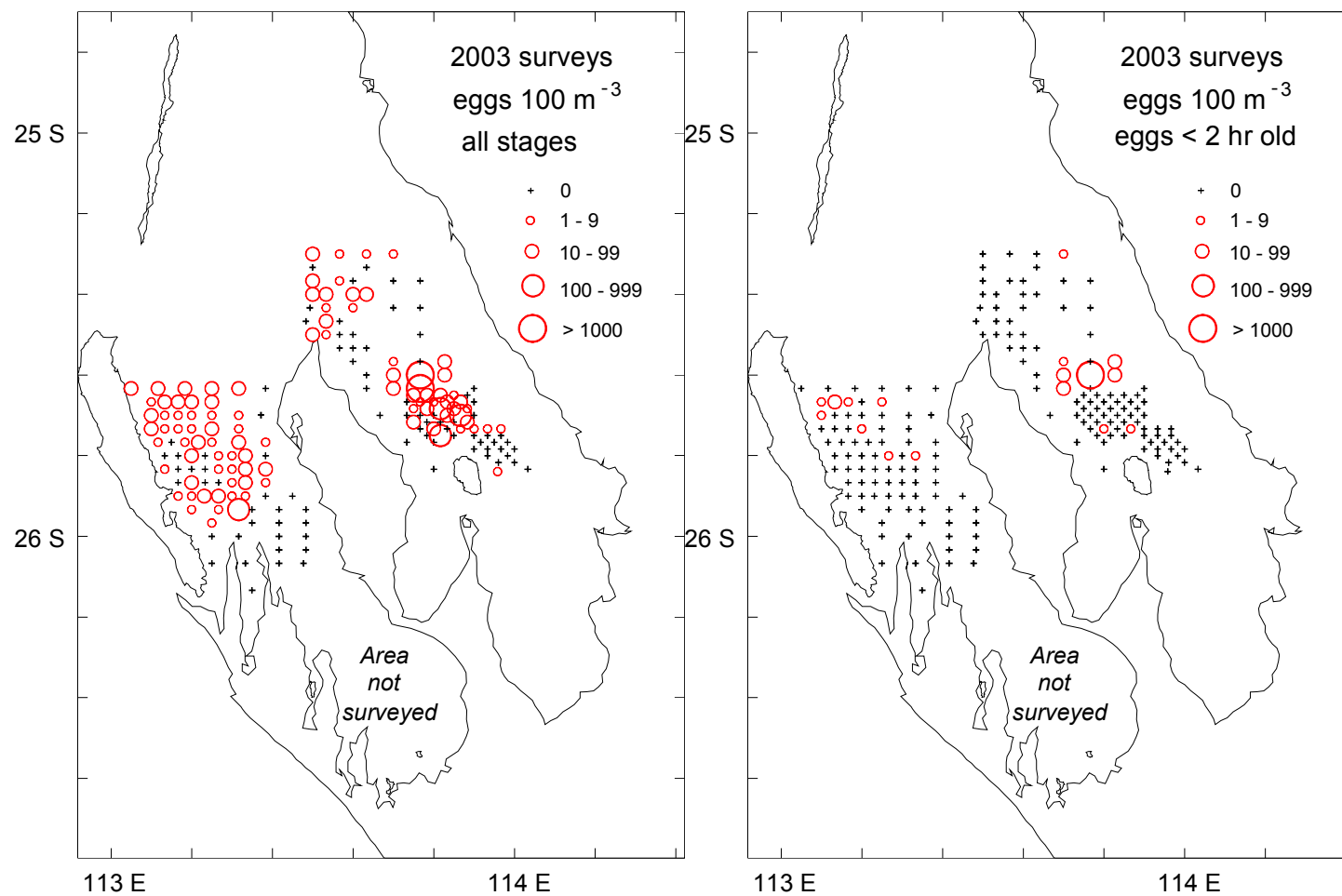


Figure 5.12 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in 2003, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m^{-3} .

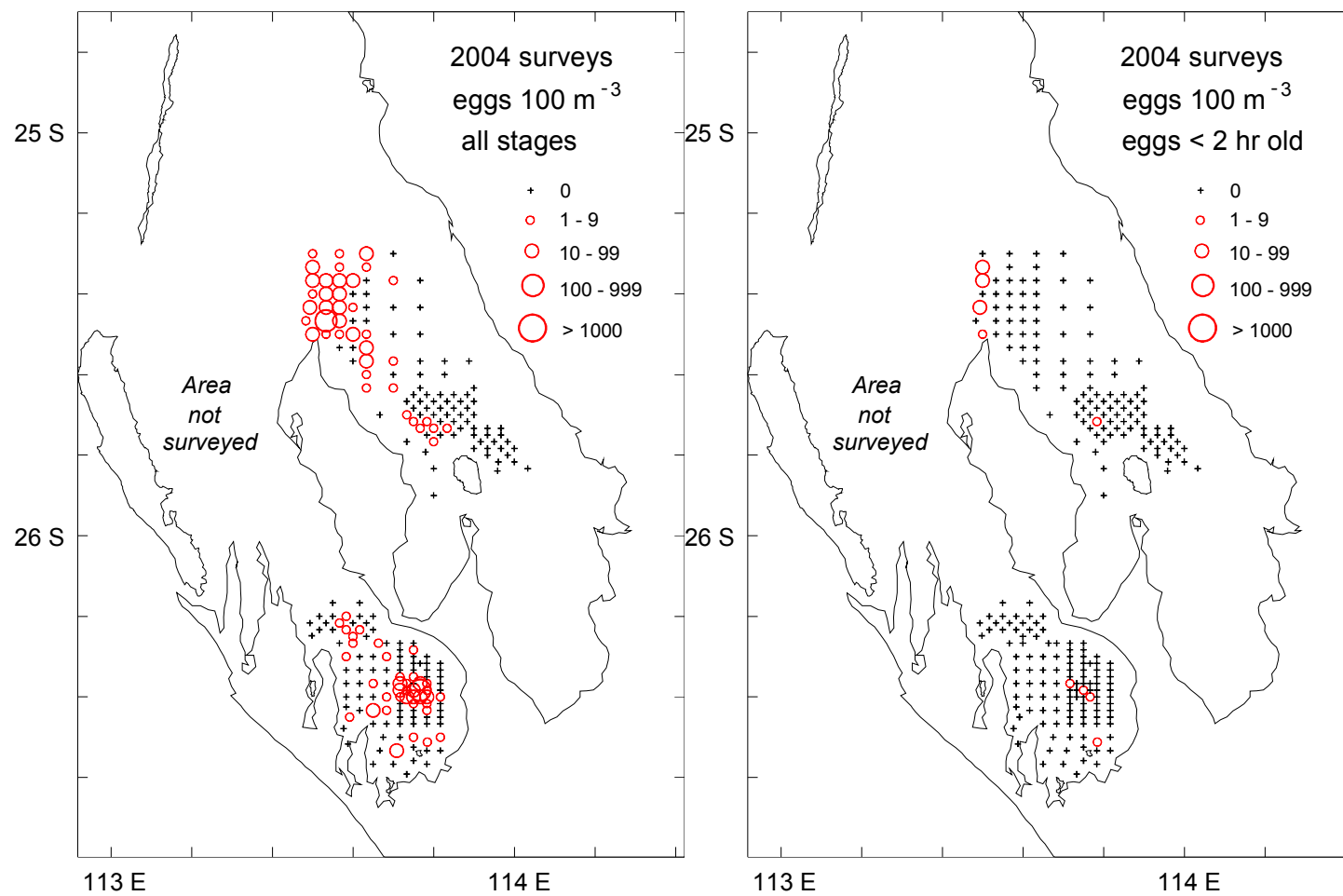


Figure 5.13 Distribution of *P. auratus* eggs from DEPM surveys undertaken in inner Shark Bay in 2004, (left) all egg stages (right) youngest eggs (< 2 hours old). Units are eggs 100 m^{-3} .

in the central region, particularly just north of White Island, and in more southern waters. Higher abundances of the youngest eggs (<2 hours old) were consistently found in an area just north of White Island.

5.3.3 Area of spawning

From the area represented by stations where the samples collected contained eggs ('positive' stations), the area of spawning A in the Eastern Gulf was estimated at 700 km² or greater for every survey (mean = 900 km²) with the exception of that in July 1998 (Tables 5.3, 5.4 and 5.5). Surveys conducted in consecutive months, *i.e.* in June and July, in the Eastern Gulf indicated a significant contraction in spawning area between the months. In Denham Sound, the area of spawning was estimated at 700 km² or greater (years 2000-2003, mean = 890 km²) for years after the survey area was standardised to include only waters below a line from Withnell Point eastwards to the Peron Peninsula (see Discussion). In the Freycinet Estuary, even though area surveyed was standardised to include only waters below a line from Goulet Bluff westwards to Heirisson Prong, the area of spawning calculated following each survey varied more than in the other two areas and ranged between 344 km² (2004) and 711 km² (2003).

5.3.4 Spawning times

While there was some minor variation between years, in general most batches of eggs collected during individual surveys were spawned between early-mid afternoon (approximately 1400-1500 hours) and mid evening (approximately 2000-2200 hours)(Fig. 5.14, only data for surveys conducted in 2000 presented). Either nil or very low levels of spawning occurred between midnight and midday in most cases. The ages of batches of eggs collected during night sampling, *i.e.* in the Freycinet Estuary in 1998, were consistent with patterns observed from daytime sampling; while a few Stage 1

eggs were present (from spawning around 0100 hr), most eggs were Stage 7 (approximately 7 hours old) from spawning around 1700 hours the previous evening. Despite low sample sizes during hours of darkness, evidence from the relative proportions of females at different stages of spawning were in general agreement with egg batch data from samples collected during the day (Fig. 5.15, only data for Eastern Gulf 1999 and Freycinet 2000 presented).

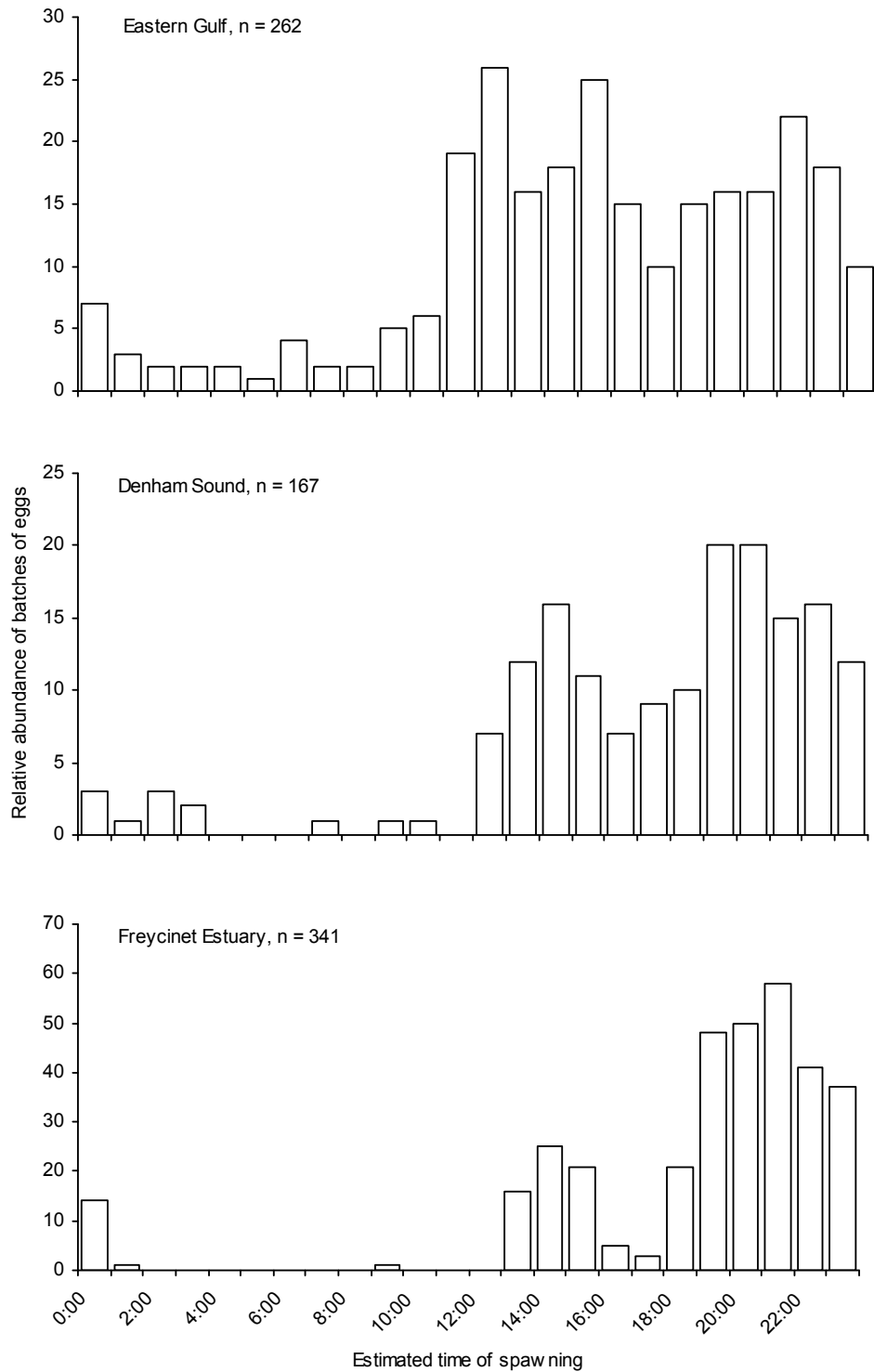


Figure 5.14 Back-calculated spawning times (24-hour clock) from ages of batches of *P. auratus* eggs collected during DEPM surveys conducted in 2000. n = number of batches of eggs.

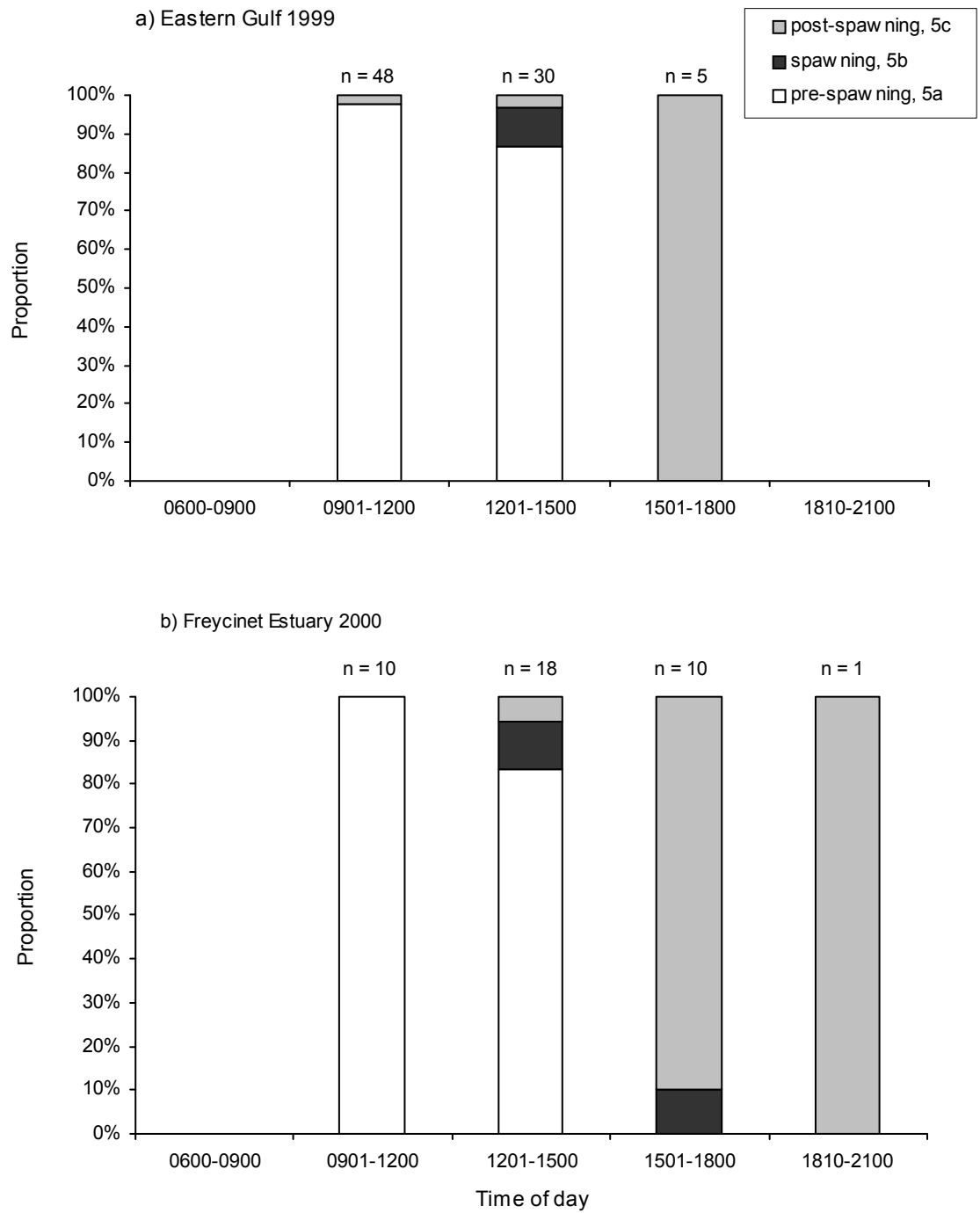


Figure 5.15 Estimated spawning times of *P. auratus* in a) Eastern Gulf in 1999 and b) Freycinet Estuary in 2000, inferred from proportions of female gonads in spawning condition collected during DEPM surveys. Spawning condition of females from histological examination as indicated. n = number of samples in each 3-hour block of 24-hour cycle.

5.3.5 Environmental conditions and times to hatching

From environmental data recorded during the DEPM surveys, water temperatures were generally warmest in the Eastern Gulf and coolest in the Freycinet Estuary, where waters were also the most saline. During the period 1998-2004, mean SST ranged between 18.3-22.4 °C in the Eastern Gulf, 18.5-21.1 °C in Denham Sound and 17.2-18.9 °C in the Freycinet Estuary (Table 5.6). Based on estimated mean SST and salinity over the period of the study, time to hatching for *P. auratus* eggs was estimated to range between 21 and 34 hours (Fig. 5.16, Table 5.6).

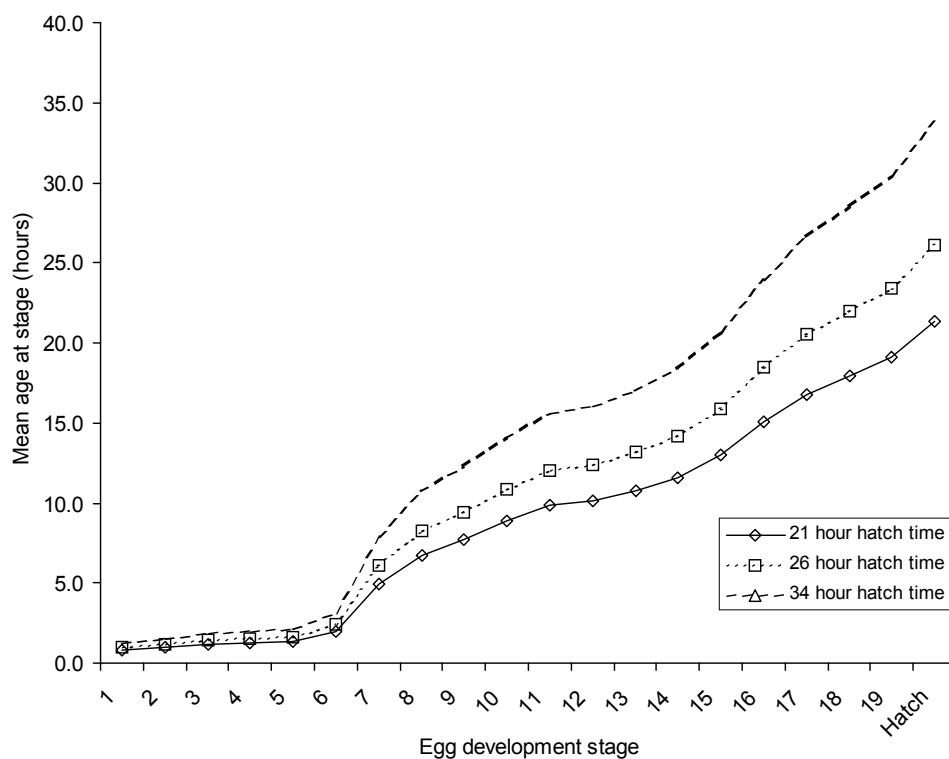


Figure 5.16 Development models for *P. auratus* eggs from inner Shark Bay. The three curves represent the estimated rates of development for a range of hatch times (21, 26 and 34 hours) as indicated. Hatch times were estimated using empirical data from incubation experiments of McGlennon (2003) and mean-age-at-stage from development model of Wakefield (2006).

Following page. Table 5.6 Mean SST and salinity recorded during DEPM surveys in inner gulfs of Shark Bay 1998-2004. Hatch times were estimated using empirical data from McGlennon (unpublished data) and mean-age-at-stage for 19 egg stages estimated using the development model of Wakefield (2006).

Area/Year	Mean SST (°C)	Mean salinity	Mean age at stage (hour)																			Hatch time (hour)	
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
Eastern Gulf:																							
1998, June	22.4	41	0.8	1	1.2	1.3	1.3	2	5	6.8	7.7	8.9	9.8	10	11	12	13	15	17	18	19		21
1998, July	18.3	42	1.2	1.5	1.8	1.9	2	2.9	7.4	10	12	13	15	15	16	17	19	23	25	27	29		31
1999	19.6	38	1	1.3	1.6	1.7	1.8	2.7	6.7	9.1	10	12	13	14	14	16	18	20	23	24	26		28
2000	19.2	38	1	1.3	1.6	1.7	1.8	2.7	6.7	9.1	10	12	13	14	14	16	18	20	23	24	26		28
2001	18.7	38	1.1	1.4	1.7	1.8	1.9	2.8	7	9.5	11	12	14	14	15	16	18	21	24	25	27		30
2002	20.2	41	1	1.2	1.5	1.6	1.7	2.4	6.2	8.4	9.6	11	12	13	13	14	16	19	21	22	24		26
2003	21.8	38	0.8	1.1	1.3	1.4	1.5	2.1	5.4	7.4	8.4	9.6	11	11	12	13	14	16	18	20	21		22
2004	21.6	38	0.8	1.1	1.3	1.4	1.5	2.1	5.4	7.4	8.4	9.6	11	11	12	13	14	16	18	20	21		22
Denham Sound:																							
1998, June	20.2	36	0.9	1.2	1.5	1.5	1.6	2.4	6.1	8.3	9.4	11	12	12	13	14	16	18	20	22	23		26
1998, July	18.5	36	1.1	1.4	1.7	1.8	1.9	2.8	7	9.6	11	13	14	14	15	16	18	21	24	25	27		30
1999	19.9	35	1	1.2	1.5	1.6	1.7	2.5	6.3	8.6	9.8	11	12	13	14	15	16	19	21	23	24		27
2000	19.8	36	1	1.2	1.5	1.6	1.7	2.5	6.3	8.6	9.8	11	12	13	14	15	16	19	21	23	24		27
2001	20.7	35	0.9	1.1	1.4	1.5	1.6	2.3	5.8	7.9	9	10	11	12	12	14	15	18	20	21	22		25
2002	21.1	38	0.9	1.1	1.3	1.4	1.5	2.2	5.6	7.6	8.6	9.9	11	11	12	13	15	17	19	20	21		24
2003	19.7	35	1	1.3	1.5	1.6	1.7	2.5	6.3	8.6	9.9	11	13	13	14	15	17	19	21	23	24		27
2004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-
Freycinet Estuary:																							
1998	18.8	43	1.1	1.4	1.7	1.8	1.9	2.8	7.1	9.7	11	13	14	14	15	17	19	22	24	26	27		31
1999	18.4	43	1.1	1.5	1.8	1.9	2	2.9	7.4	10	11	13	15	15	16	17	19	22	25	27	28		32
2000	17.5	45	1.2	1.6	1.9	2	2.1	3.1	7.9	11	12	14	16	16	17	18	21	24	27	28	30		34
2001	17.2	42	1.2	1.5	1.9	2	2.1	3.1	7.8	11	12	14	15	16	17	18	20	24	26	28	30		34
2002	18.9	43	1.1	1.4	1.7	1.8	1.9	2.8	7.1	9.6	11	13	14	14	15	17	18	21	24	26	27		30
2003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-
2004	18	44	1.2	1.5	1.8	1.9	2.1	3	7.6	10	12	14	15	15	16	18	20	23	26	27	29		32

5.3.6 Daily egg mortality

The range of egg ages collected in each area showed considerable variation between surveys that was likely due to annual variation in diel spawning patterns relative to actual timing of ichthyoplankton sampling in any year. Plots of egg density against egg age indicated that the youngest eggs (*i.e.* Stages 1-6) were generally under-sampled (Figs 5.17-5.23). However, there were some notable exceptions when sampling in the vicinity of the main spawning sites coincidentally took place when fish were actively spawning and the youngest eggs (*i.e.* Stage 1) were correspondingly collected in very high abundance *e.g.* Eastern Gulf in 2000 and 2001 and Freycinet Estuary in 2000 (Figs 5.17, 5.18 and 5.22). Under-representation of younger eggs combined with very high abundances of older eggs (*i.e.* Stages 15-17) presented problems in fitting the exponential mortality curve and estimation of daily egg mortality (Z) separately for each DEPM survey with no significant slope or even positive slopes in some cases. Initially when this was done, the independent estimates of Z were highly variable between surveys and ranged between -1.59 and 0.73 day^{-1} in the Eastern Gulf, -1.96 and 0.72 day^{-1} in Denham Sound, and -0.92 and 0.72 day^{-1} in the Freycinet Estuary (Table 5.3, 5.4 and 5.5). To overcome the inability to estimate Z precisely for each DEPM survey, the decision was made to pool the available egg data and thereby assume Z to be constant over all years. Here, based on egg density data (all 19 stages) for each area 1998-2004 pooled, a mean Z was estimated for each area separately as follows: Eastern Gulf = 0.52 day^{-1} (s.e. 0.13), Denham Sound = 0.42 day^{-1} (s.e. 0.13), Freycinet Estuary = 0.41 day^{-1} (s.e. 0.13). Because these values of Z were not markedly different, egg density data were again pooled (all years and areas) and Z re-estimated at 0.49 day^{-1} (s.e. 0.07). Egg production curves were then fitted to weighted egg density

data for each survey with Z fixed at 0.49 day^{-1} in all cases, *i.e.* assumed to be constant for all years and areas.

5.3.7 Daily egg production

Estimates of mean daily egg production (P) varied considerably between surveys even with Z assumed constant at 0.49 day^{-1} . Estimates ranged from 1.06 (95% C.I. 0.64-2.17) to 5.91 eggs $\text{m}^{-2} \text{ day}^{-1}$ (95% C.I. 3.87-8.9) in the Eastern Gulf, from 0.45 (95% C.I. 0.37-0.66) to 3.69 eggs $\text{m}^{-2} \text{ day}^{-1}$ (95% C.I. 0.84-10.12) in Denham Sound, and from 0.71 (95% C.I. 0.54-0.99) to 11.39 eggs $\text{m}^{-2} \text{ day}^{-1}$ (95% C.I. 2.74-47.15) in the Freycinet Estuary (Table 5.3, 5.4, 5.5). When samples of particularly high egg density in some years where large uncertainty around P existed, were subsequently excluded, the corresponding estimates of P were significantly reduced. For example, Eastern Gulf in 2000, when a single batch of Stage 1 eggs was excluded, the estimate of P reduced from 5.91 eggs $\text{m}^{-2} \text{ day}^{-1}$ to 5.26 eggs $\text{m}^{-2} \text{ day}^{-1}$ (an 11% decrease); Eastern Gulf in 2003, when a single batch of Stage 4 eggs was excluded, the estimate of P reduced from 5.73 to 3.77 eggs $\text{m}^{-2} \text{ day}^{-1}$ (a 34% decrease).

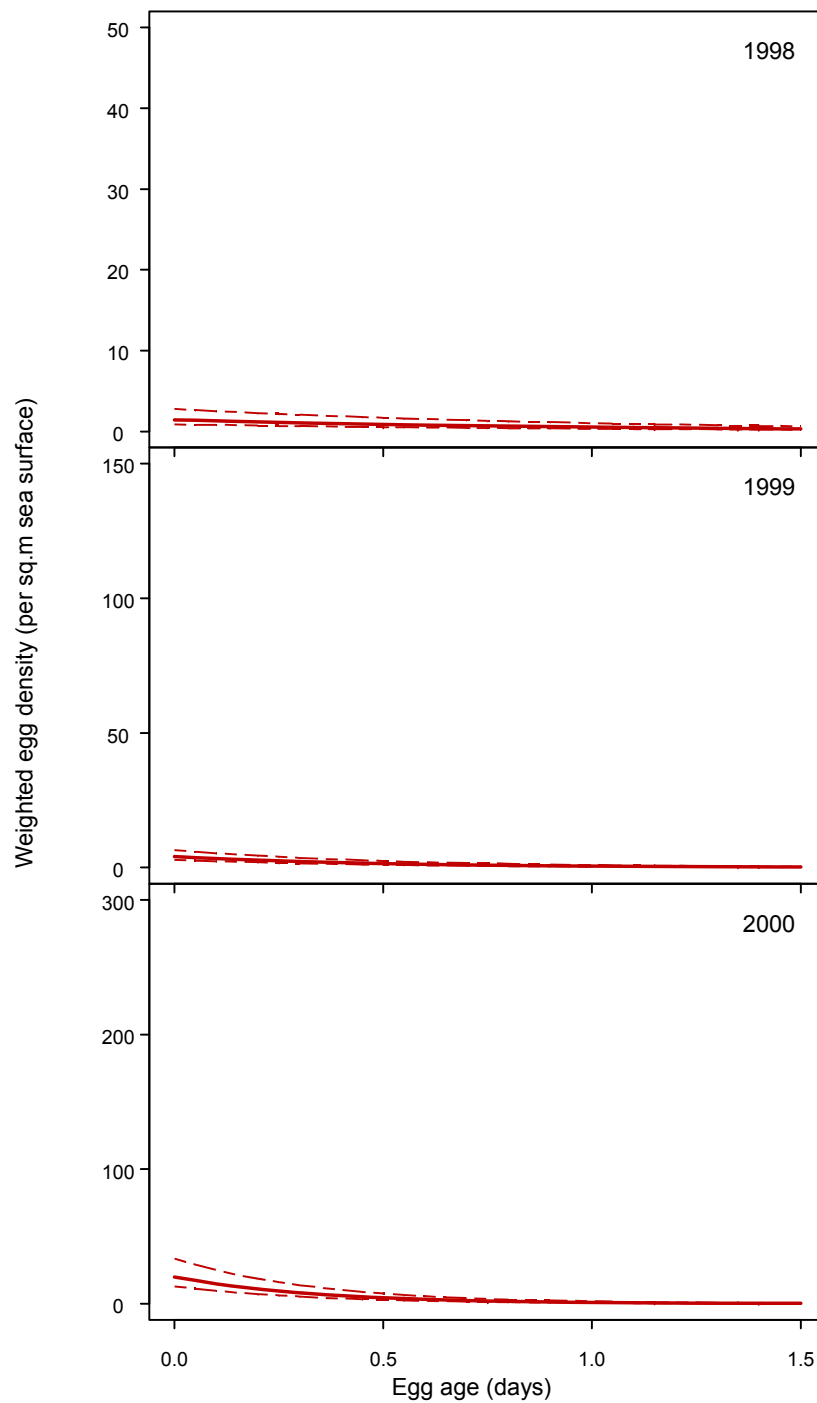


Figure 5.17 Egg production curves for the Eastern Gulf DEPM surveys in 1998 (June survey), 1999 and 2000. Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in ichthyoplankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} in all years, hatched red line represents bootstrapped 95% C.I. Note, different scale of y-axis values.

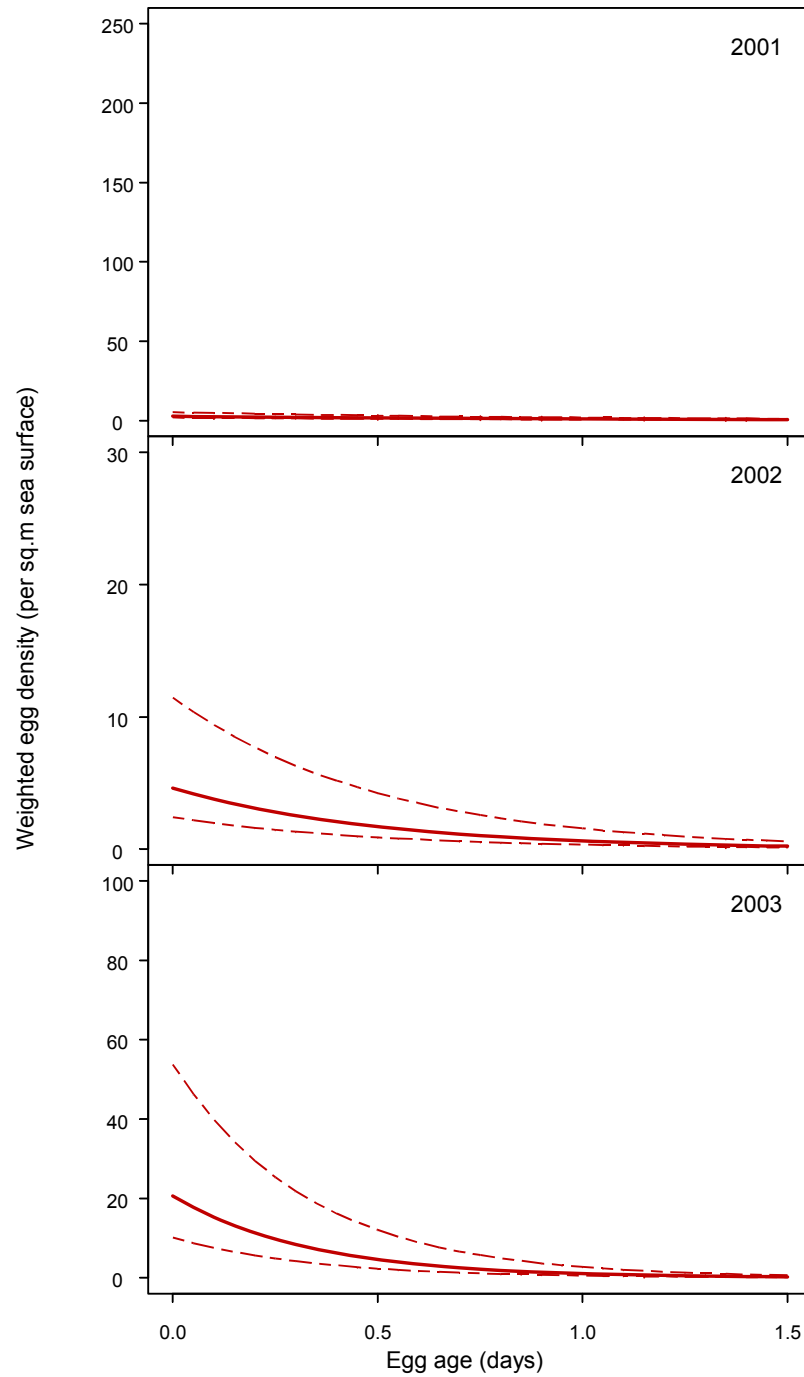


Figure 5.18 Egg production curves for the Eastern Gulf DEPM surveys in 2001, 2002 and 2003. Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in ichthyoplankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} in all years, hatched red line represents bootstrapped 95% C.I. Note, different scale of y-axis values.

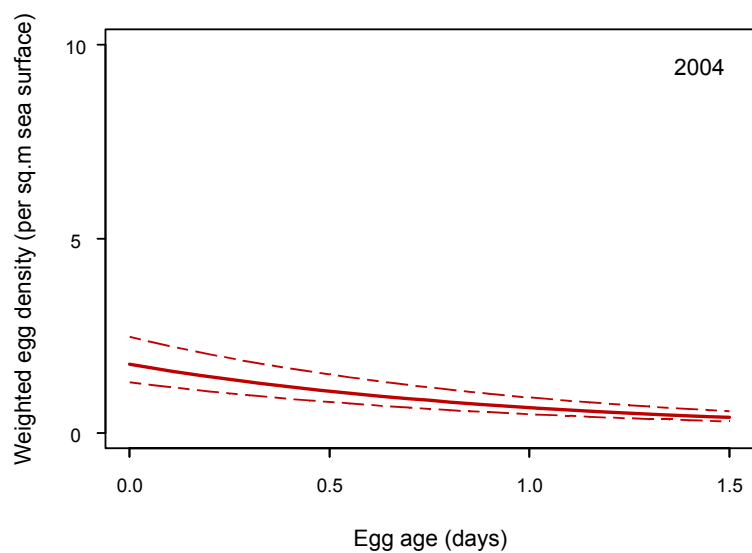


Figure 5.19 Egg production curve for the Eastern Gulf DEPM survey in 2004. Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in ichthyoplankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} , hatched red line represents bootstrapped 95% C.I.

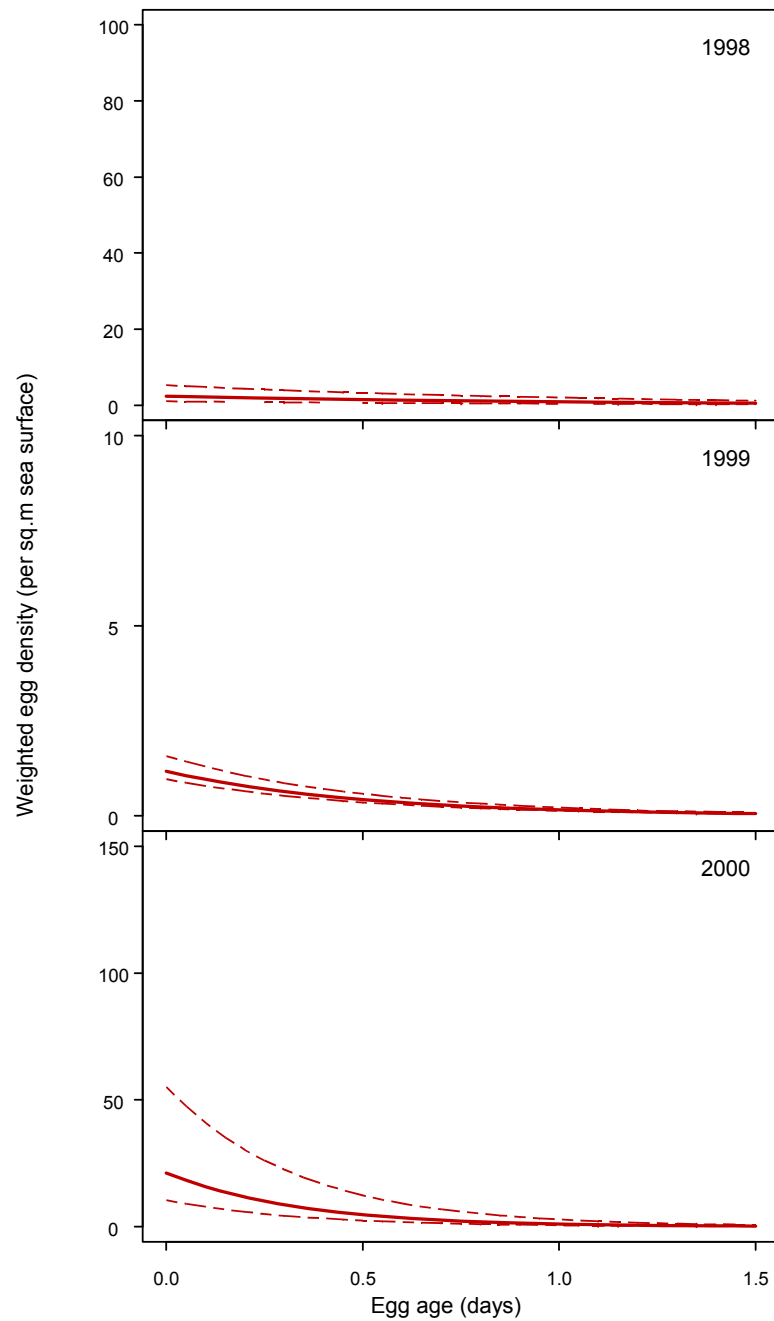


Figure 5.20 Egg production curves for the Denham Sound DEPM surveys in 1998 (July survey), 1999 and 2000. Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in ichthyoplankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} in all years, hatched red line represents bootstrapped 95% C.I. Note, different scale of y-axis values.

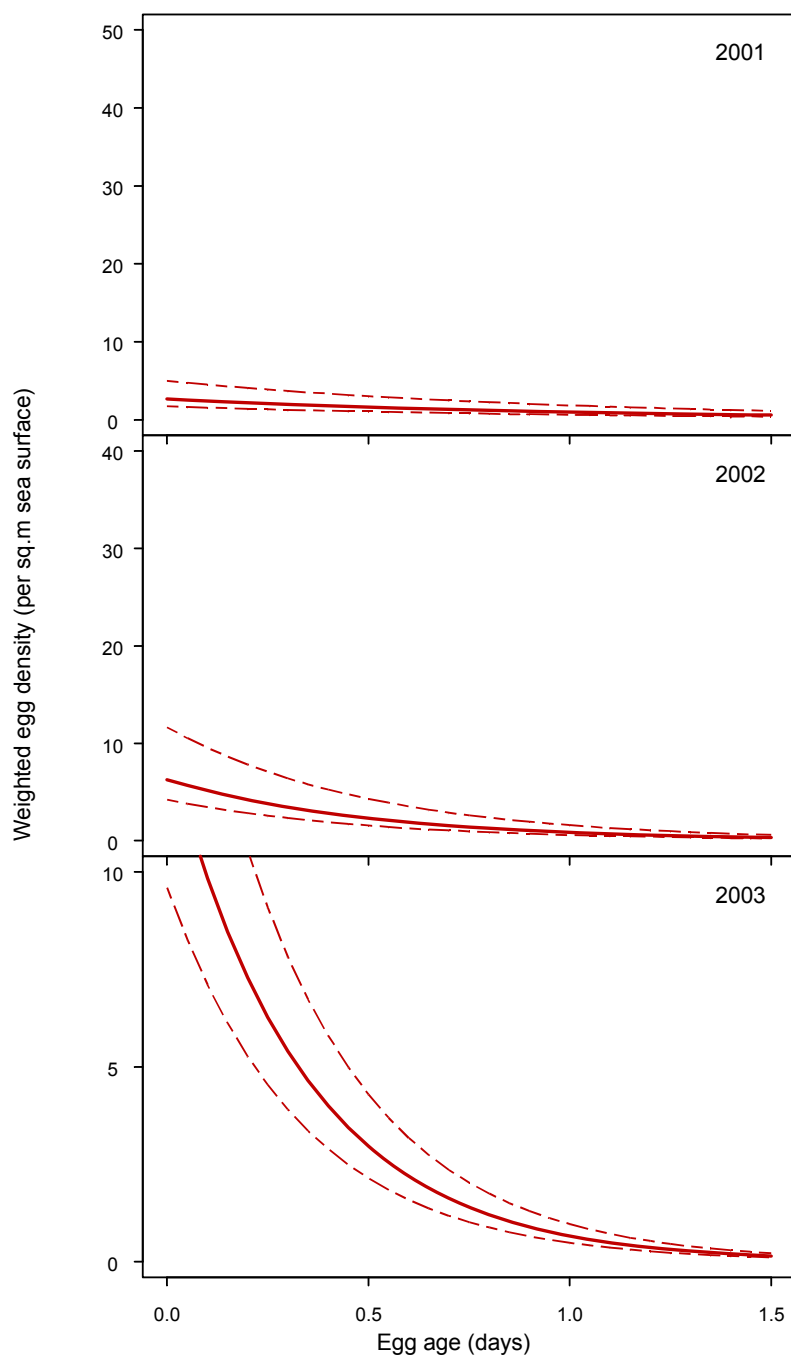


Figure 5.21 Egg production curves for the Denham Sound DEPM surveys in 2001, 2002 and 2003 (no survey in 2004). Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in ichthyoplankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} in all years, hatched red line represents bootstrapped 95% C.I. Note, different scale of y-axis values.

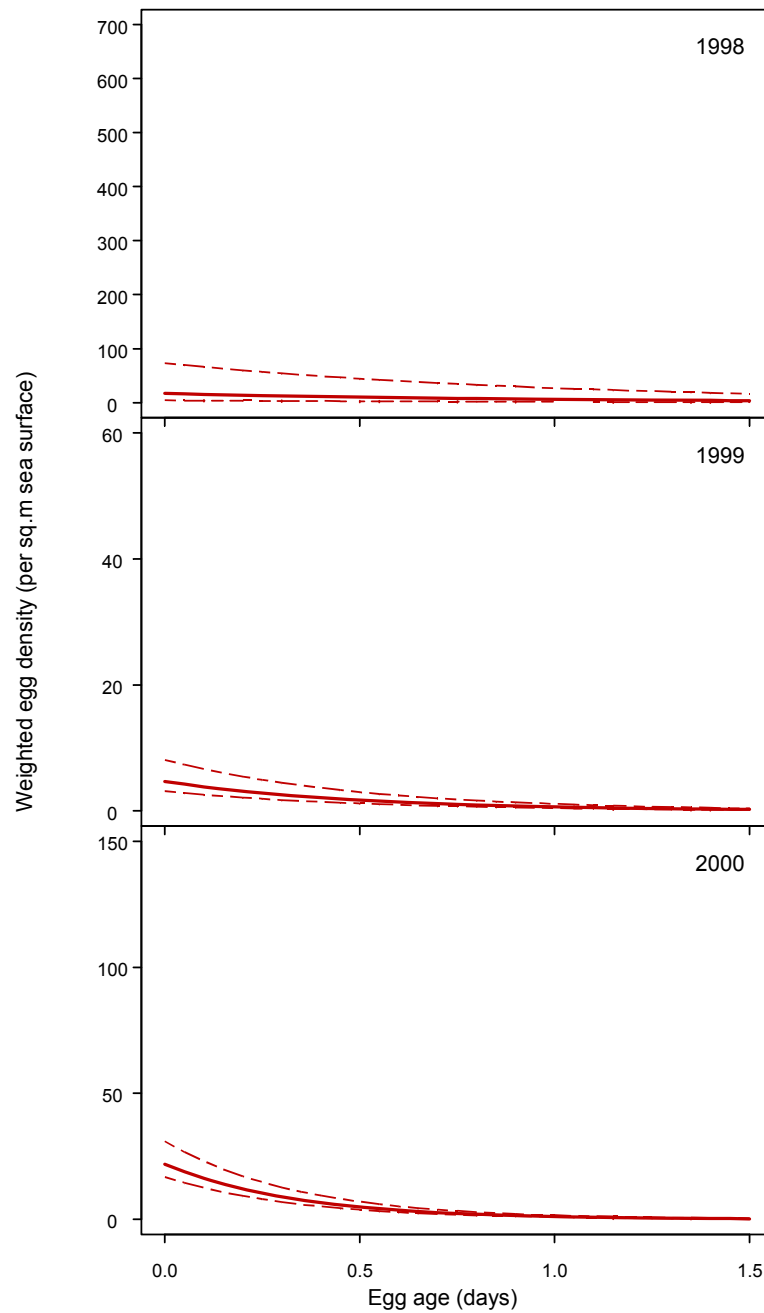


Figure 5.22 Egg production curves for the Freycinet Estuary DEPM surveys in 1998, 1999 and 2000. Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in ichthyoplankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} in all years, hatched red line represents bootstrapped 95% C.I. Note, different scale of y-axis values.

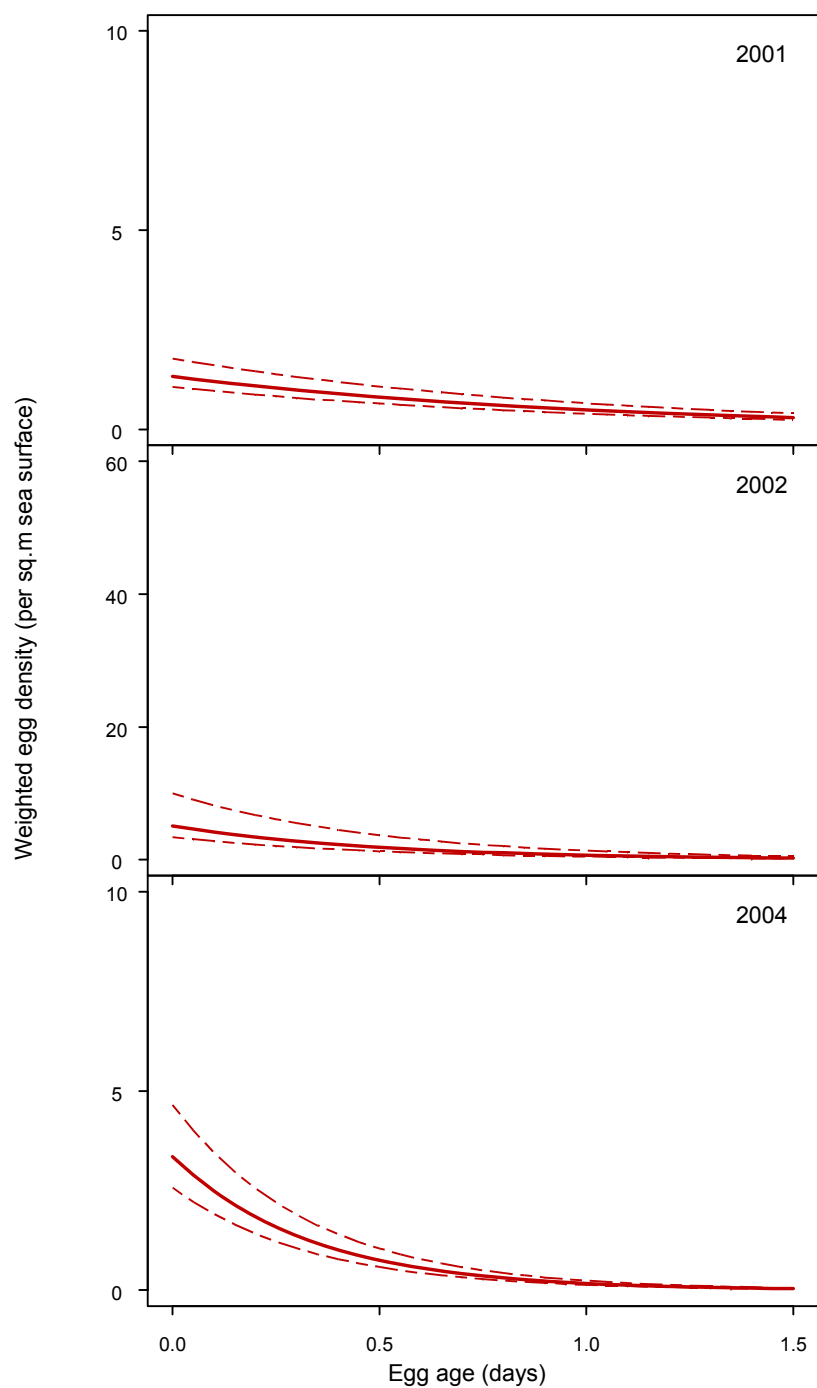


Figure 5.23 Egg production curves for the Freycinet Estuary DEPM surveys in 2001, 2002 and 2004 (no survey in 2003). Open circles represent abundance of *P. auratus* eggs of each of 19 development stages present in plankton samples collected in respective years. Solid red line represents non-linear curve fitted to each data set, Z fixed at 0.49 day^{-1} in all years, hatched red line represents bootstrapped 95% C.I. Note, different scale of y-axis values.

5.3.8 Adult parameters

While the numbers of adult *P. auratus* sampled were inadequate in some DEPM surveys *e.g.* Denham Sound in July 1998 and 2001, Freycinet Estuary in 2001, the fish collected were considered to be representative of the spawning population in each case, and the reproductive parameters estimated with acceptable precision (Table 5.3, 5.4, 5.5).

Average weight, W

Mature females were on average smallest in Denham Sound and largest in Freycinet Estuary. In the Eastern Gulf, female average weight ranged between 2,403 and 3,601 g. In Denham Sound, female average weight ranged between 1,611 and 2,996 g. In the Freycinet Estuary, female average weight ranged between 3,011 and 4,505 g.

Sex ratio, R

Sex ratios were generally close to 50% (1:1) by number but slightly higher by weight. Mean sex ratio was 0.53 by number and 0.56 by weight in the Eastern Gulf, 0.54 and 0.61, respectively, in Denham Sound, and 0.53 and 0.55, respectively, in the Freycinet Estuary.

Batch fecundity, F

Mean batch fecundity was significantly higher in the Freycinet Estuary where spawning females were generally larger than in the other two areas. While numbers of individuals with gonads at Stage 5a, *i.e.* which could be used for estimation of batch fecundity, were low in some surveys, use of the relationship between fork length and

batch fecundity based on pooled data (all years, areas) allowed mean batch fecundity for each DEPM survey to be estimated with confidence.

Spawning fraction, S

The proportion of females actively spawning during the respective DEPM surveys was generally high and ranged between 0.71-0.99 in the Eastern Gulf, 0.46-0.85 in Denham Sound and 0.72-0.91 in the Freycinet Estuary.

There was no significant difference in mean values of S and R between years within each area while differences in mean W and F were highly significant (Table 5.7).

Table 5.7 Results of the ANOVA comparison of DEPM adult reproductive parameters, average female weight, W , mean batch fecundity, F , female sex ratio, R , spawning fraction, S , between areas and years. df = degrees of freedom, SS = Type III Sum of Squares.

Parameter	df	SS	Mean S	F	P
W					
Within areas	2	120016360	60008180	33.50203	<0.001
Between years	6	89663524	14943921	8.34306	<0.001
residuals	1012	18126743373	1791180		
F					
Within areas	2	165.8862	82.94310	142.9796	<0.01
Between years	6	25.9181	4.31968	7.4464	<0.01
residuals	1099	637.5347	0.58010		
R					
Within areas	2	0.002032344	0.001016172	1.446105	>0.05
Between years	6	0.007214437	0.001202406	1.711133	>0.05
residuals	9	0.006324262	0.000702696		
S					
Within areas	2	0.00702927	0.003514634	2.944803	>0.05
Between years	6	0.00583999	0.000973331	0.815524	>0.05
residuals	9	0.01074153	0.001193504		

5.3.9 Spawning biomass

The DEPM estimates of spawning biomass for the three *P. auratus* stocks appeared biologically realistic, and although imprecise, indicated that the mature populations in each area were very small in each case and generally measured in tens of tonnes only (Tables 5.3, 5.4, 5.5). The increasing trajectory of estimated spawning biomass for the Eastern Gulf (Fig. 5.24) appeared to be consistent with that expected, at

least between 1998 and 2000, in response to management action where the *P. auratus* ' fishery was closed 1998-2003. Similarly, in the Freycinet Estuary, where no serious management action was taken until 2000 (when a six week spawning closure was introduced for the first time), the spawning biomass was estimated to have declined sharply since 1998. Sensitivity analysis indicated that the relatively low precision of biomass estimates from some surveys was principally related to high variances around estimates of egg production. When samples of higher egg density deemed as 'outliers' from particular surveys where large uncertainty around *P* existed were excluded, the corresponding estimates of *P* and *B* were significantly reduced as follows; Eastern Gulf biomass estimate decreased by 11% in 2000 and 34% in 2003, Denham Sound biomass estimate decreased by 76% in July 1998 and 37% in 2000 and Freycinet Estuary biomass estimate decreased by 73% in 1998. There was high congruence in biomass estimates in 1998 from surveys in consecutive months (June and July) for the Eastern Gulf and Denham Sound.

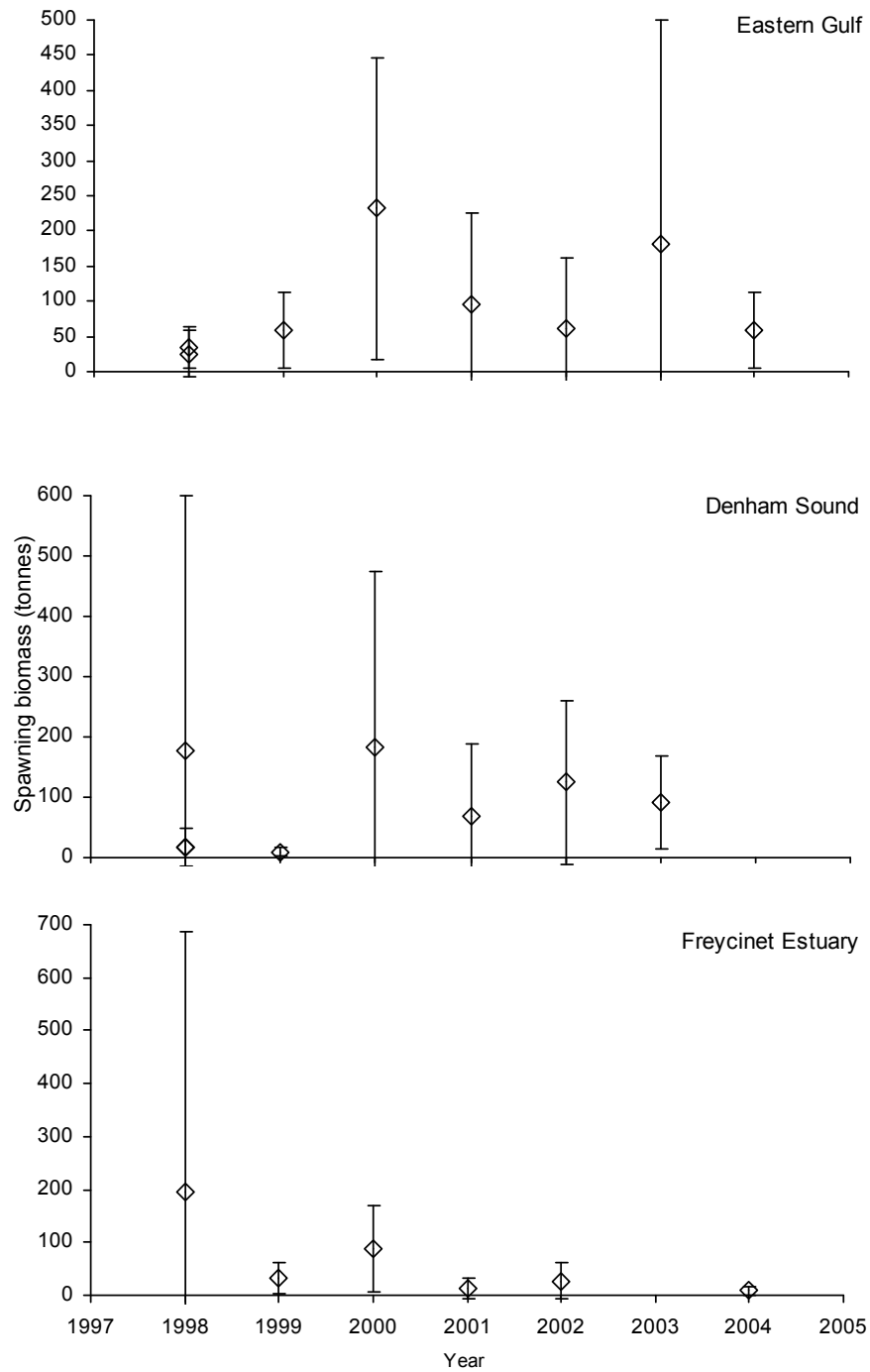


Figure 5.24 Mean estimates of spawning biomass for Eastern Gulf, Denham Sound and Freycinet Estuary *P. auratus* stocks determined from DEPM surveys 1998-2004. Error bars are bootstrapped 95% C.I. Two data points in 1998 for Eastern Gulf and Denham Sound represent biomass estimates for June and July surveys. Note different y-axis scales.

5.4 Discussion

This study was the first to use the DEPM to estimate spawning biomass of a long-lived, demersal species in Western Australian waters and, when the first Shark Bay surveys commenced in 1997, only the third-ever attempt to use the method for *P. auratus* stocks in Australia and New Zealand (Zeldis and Francis 1998; McGlennon 2003). The study has provided, for the first time, estimates of mature biomass for the three separate *P. auratus* stocks inhabiting the inner gulfs of Shark Bay. Importantly, these stocks have been shown to be very small in each case. The results have been used directly by fisheries managers to develop management strategies for the recreational *P. auratus* fishery since 1998 (Jackson *et al.* 2005). The fishery-independent estimates of *P. auratus* spawning biomass in the Eastern Gulf made it possible to track the recovery, over the first three or so years, of the breeding stock in that area following introduction of the fishing moratorium in June 1998. The data were incorporated in age-based stock assessment models that were used to determine the status of these stocks, and to inform discussions of different management scenarios with stakeholders prior to re-opening of the Eastern Gulf to fishing for *P. auratus* in 2003 (Jackson *et al.* 2005; Stephenson and Jackson 2005).

The research has provided valuable, previously unavailable, detailed information on the reproductive biology of *P. auratus* in the inner gulfs. Egg distributions from DEPM ichthyoplankton surveys have provided fine-scale spatial information on spawning patterns in all three areas and, combined with results of histological examination of female gonads, have improved our understanding of diel spawning patterns. Information on the timing of spawning and location of the main spawning grounds formed the basis for investigation of the influence of hydrodynamic processes

on *P. auratus* egg and larval dispersal (described in detail in Chapter 2) which in turn ! has provided further understanding of possible mechanisms that give rise to the unusually complex stock structure of *P. auratus* inside Shark Bay.

The early years of the Shark Bay DEPM study gave rise to two important methodological developments which were subsequently recognised by an ICES DEPM working group, (i) the trialling of an adaptive sampling approach to improve precision around egg production estimation and (ii) the use of non-parametric bootstrapping to estimate variance around all DEPM parameters (Stratoukadis *et al.* 2006). The study has highlighted key issues associated with application of the DEPM in the context of this type of fishery and developed the most effective survey design and associated cost-structure for future monitoring of *P. auratus* stocks in inner Shark Bay (Jackson *et al.* 2005). While acknowledging that confidence intervals around estimates of spawning biomass were not well estimated in many cases, it is important to recognise that (i) there were no alternative data to estimate *P. auratus* stock size available at the time the study commenced, (ii) the DEPM typically provides imprecise biomass estimates (Stratoukadis *et al.* 2006) and (iii) all DEPM parameters estimated for Shark Bay *P. auratus* (with the exception of *B*) were within the range of values estimated for DEPM-based studies with the species elsewhere (Zeldis and Francis 1998; McGlennon 2003, Table 5.8). Note also that the precision of fishery model-based estimates of stock biomass are often of much lower precision particularly when based on limited fishery and biological data as is often the case.

5.4.1 Spatial and temporal spawning patterns

P. auratus egg distributions in the three areas were highly congruent between years. The key spawning locations were identified from the loci of higher egg

abundance and concentrations of the youngest eggs. In the Eastern Gulf, these principally comprised areas to the northeast of Monkey Mia, north east of Faure Island and to the north of Cape Peron; in Denham Sound, a number of areas off mid Dirk Hartog Island; and in the Freycinet Estuary, an area just to north of White Island. Further evidence of the significance of these spawning sites is provided by estimates of the female spawning fraction that ranged from ~0.7-0.9 from samples taken by recreational vessels fishing in and around these locations. Commercial and recreational fishers have known about winter *P. auratus* spawning aggregations both inside and in oceanic waters outside Shark Bay for decades (Moran and Jenke 1989; Jackson *et al.* 2005). In the inner gulfs, large aggregations of spawning fish were routinely observed using vessel colour sounders during the course of this study in the Eastern Gulf (in the vicinity of The Patch) and Denham Sound (just to north of Quoin Bluff)(Fig 5.25). Spawning behaviour in the Freycinet Estuary, however, appears somewhat different with no large aggregations observed during this study. Fish in that area typically spawn in much smaller groups (as few as several dozen in some cases, P. Somerville pers. observation). Throughout the inner gulfs, *P. auratus* spawning sites have been shown to relate to hydrodynamic features rather than topographic or habitat characteristics (Nahas *et al.* 2003).



Figure 5.25 Photo image of the colour sounder on *RV Snipe* taken June 2001 at approx. 1600 hrs showing large spawning aggregation *P. auratus* and actively spawning fish. Note dark red band = main aggregation on bottom with small groups of fish breaking away and swimming to surface to spawn. Samples of females with Stage 5b ovaries were collected by recreational vessels fishing at this location at the same time.

From the back-calculated spawning times, spawning appears to take place mostly between mid-afternoon and mid-evening which is broadly similar to the daily pattern found with *P. auratus* in South Australia (McGlennon 2003) and New Zealand (Scott *et al.* 1993). Spawning appears to take place just below the surface (no fish were ever observed actually spawning at the surface during this study) in waters of ~10-14 m average depth. While more research is required, there is clearly a significant relationship between lunar cycle and *P. auratus* spawning activity in inner Shark Bay. Spawning with many marine species is strongly correlated with lunar and tidal cycles, particularly batch-spawners (Jackson *et al.* 2006). The levels of spawning activity observed in this study appeared to be greatest around the new moon and to a lesser extent around full moon, and much reduced at the first and last quarter moons. Broadcast spawners tend to spawn more around full/new moon when tidal activity is at

a maximum, such reproductive behaviour is assumed to be an adaptation to maximise ! egg and larval dispersal (Ross 1983; Davis and West 1993). Wakefield (2006) found daily spawning patterns linked to lunar phase and tides with *P. auratus* in Cockburn Sound, Western Australia.

5.4.2 Estimates of spawning biomass

This study provides the first direct estimates of *P. auratus* spawning biomass in the inner gulfs of Shark Bay, as previously noted. These *P. auratus* stocks are clearly very small in comparison with the oceanic *P. auratus* stock (Moran *et al.* 2005) and *P. auratus* stocks elsewhere in Australia and New Zealand (Zeldis and Francis 1998; McGlennon 2003) (Table 5.8). While the estimates of spawning biomass in Shark Bay were imprecise in most cases, the overall biomass estimates have provided a useful guide for managers to compare against levels of commercial and recreational catch, and develop stock recovery strategies each year since 1998. While the large confidence intervals around biomass estimates derive from uncertainty in all parameter estimates, the primary source of imprecision was the uncertainty associated with estimates of daily egg production, a common problem with the DEPM (Borchers *et al.* 1997; Hunter and Lo 1997; Zeldis and Francis 1998; Stratoukadis *et al.* 2006).

Imprecision in the estimation of egg production can arise from a number of sources including high intrinsic variability or low sample size. The highly contagious distribution of *P. auratus* eggs in Shark Bay's inner gulfs, in particular for the youngest eggs, reflects the very patchy distribution of the spawning adults. The decline in patchiness with increasing egg age, as eggs disperse to some extent away from point locations where they were spawned, can be clearly seen when egg distributions for all

19 egg stages and those for eggs < 2 hours old only are compared. The probability that ! an early stage egg is encountered is significantly lower than that for the older egg stages. The contagion increases the minimum number of 'positive' egg samples required to estimate egg production with an adequate level of precision (Hunter and Lo 1997). For example, Lo (1997) estimated a minimum of 600 plankton tows were required to achieve a CV of 30% for anchovy egg production in waters off California while Zeldis (1993) estimated that 300 tows would be needed to obtain a CV of 15% for *P. auratus* egg production in Hauraki Gulf, New Zealand. The total survey area in Hauraki Gulf was approximately equal to a single one of the three areas surveyed in inner Shark Bay. The average numbers of tows per survey in this study were significantly lower; 110 in the Eastern Gulf of which on average 47% contained eggs (*i.e.* 52 'positive' samples), 82 in Denham Sound of which on average 59% contained eggs (*i.e.* 48 'positive' samples) and 108 in the Freycinet Estuary of which on average 57% contained eggs (*i.e.* 62 positive samples). The conclusion is that the numbers of tows undertaken in each Shark Bay survey were well below that required to achieve optimal precision.

The short egg development times (generally < 1 day) in Shark Bay, located in the sub-tropics towards the northern limit of the geographic range of *P. auratus* on the west coast of Australia, 'reduces' the potentially available data points in the *P. auratus* egg abundance data sets. The ichthyoplankton surveys were limited to daytime sampling only, which imposed a further limitation on availability of some egg stages (ages). Zeldis and Francis (1998) suggested it was important to investigate possible depth-stratification of egg distributions in Hauraki Gulf, New Zealand, following the apparent under-sampling of the youngest *P. auratus* eggs during a DEPM survey there. The oblique tow method used in inner Shark Bay appears to have adequately sampled

eggs of all ages, likely because inner gulf waters are shallow (mean depth ~10 m) and ! well mixed by wind during the winter months (Nahas *et al.* 2005) in contrast to Hauraki Gulf (much deeper on average, >25 m). It should be noted that vertical towing (of the same ichthyoplankton nets) was trialled during the pilot surveys in 1997 but was subsequently discontinued in preference to the oblique tow method due the shallow depths at many sampling sites.

The very high abundances of eggs sampled occasionally presented problems in the estimation of egg production. Sensitivity analyses involving re-estimation of egg production for some cases where estimates of spawning biomass were very high (and biologically unrealistic) and imprecise showed the significant influence such data points can have on P (and thereby on B). Data from this study were inadequate to test the assumption that mortality rate Z and egg production P did not vary during any survey or in case of the former, between years. Bernal *et al.* (2001) suggested that, for species with fast-developing eggs, using information from all egg development stages would increase precision around the egg production estimates. McGarvey and Kinloch (2001) found spawning biomass estimates to be relatively insensitive to variation in egg mortality with a 10-fold increase in Z (from 0.1-1.0) resulting in doubling of the spawning biomass estimate. It should be noted that the imprecision of the estimate of $Z = 0.49 \text{ year}^{-1}$ was not subsequently taken into account when estimating spawning biomass in this study. The assumption that daily egg mortality is constant during the entire egg phase is likely to be unrealistic especially in highly localised areas (McGarvey and Kinloch 2001). Zeldis and Francis (1998) estimated mortality of *P. auratus* eggs (between spawning and hatching) to be ~ 83% in Hauraki Gulf, New Zealand, mostly due to predation. It is likely that egg mortality in Shark Bay is similarly high as the main predator groups *e.g.* chaetognaths, hydromedusae and

crustaceans (copepods, decapods) (Zeldis and Francis 1998) were routinely observed in ! high abundance in the ichthyoplankton samples.

Conventionally, DEPM egg abundance-at-age data are log-transformed and Z and P estimated using linear regression methods, where the error structure is additive in the transformed expression (and by implication, a multiplicative error structure is assumed for the non-linear model) (Picquelle and Stauffer 1985; Bunn *et al.* 2000). In this study, egg production was estimated in each case by fitting a non-linear mortality curve with constant Z and additive error structure to the untransformed abundance data for all 19 egg development stages. While it is possible that the true error structure is multiplicative, the use of bootstrapped confidence intervals in this study takes the uncertainty associated with this assumption into account. The approach used is ‘conservative’ in that it tends to under-estimate egg production and, in turn, therefore under-estimates spawning biomass. However, given the limitations of the egg abundance data and the fishery management context within which the biomass estimates were to be used, *i.e.* very small biomass of separate (and unique) *P. auratus* stocks and high conservation status of region (a World Heritage Property), a conservative approach was considered highly appropriate at the time.

While an adaptive sampling approach was applied in the early years of this study (1998-2000) in an effort to reduce variance in egg production, it was discontinued in later years because it was not possible to meet most of the specific requirements identified by Lo *et al.* (1997), particularly in relation to ability to accurately count *P. auratus* eggs while at sea due to limitations of vessel size and numbers of field staff. Rather, a highly-stratified sampling design with fine-scale (1 x 1 and 0.5 x 0.5 nm in some cases) sampling in the vicinity of the main spawning locations, as identified from

highest densities of youngest egg stages, was employed from 2001 onwards. This ! approach was taken in an effort to overcome limitations imposed by cost/resources while maintaining reasonable precision in all estimates obtained.

Sensitivity analysis confirmed DEPM spawning biomass estimates to be relatively insensitive to variation in the adult reproductive parameters compared with variation in estimates of daily egg production. Adult parameters estimated for *P. auratus* for the study were taken to be representative of the spawning populations. No sampling bias was evident, with both sexes observed in approximately equal proportions in the samples. There appeared to be no sex-based or size-based (with respect to sexual maturity) selectivity issues with the rod and line sampling gear. DEPM-based estimates of spawning biomass of small pelagic species are highly sensitive to variation in spawning fraction (Hunter and Lo 1997). Estimates of spawning fraction in *P. auratus* here in Shark Bay showed relatively low variation at between 0.71-0.99 and were similar to estimates for the species from elsewhere (Spencer Gulf, South Australia, 0.69-1.0, McGlennon 2003; Hauraki Gulf, New Zealand, 0.76, Zeldis and Francis 1998) (Table 5.8). Batch fecundities were estimated with confidence using a common batch fecundity:fork length relationship based on the large (pooled) sample of females.

5.4.3 Evaluation of DEPM as assessment tool for *P. auratus* stocks

Researchers who have applied the DEPM to *P. auratus* elsewhere both concluded that the method is a viable assessment tool for the species (Zeldis and Francis 1998; McGlennon 2003). Experience indicates that the DEPM may be easier and cheaper to apply to non-pelagic species, *i.e.* demersal fishes (Stratoukadis *et al.* 2006).

Stratoukadis *et al.* (2006) suggests that the DEPM will never become a very precise method. Concern about the high ‘spikes’, *i.e.* large spawning biomass estimates with associated large variance, resulting from some surveys in some years needs to be viewed in light of the fact that egg production surveys elsewhere have been shown to be biased towards over-estimating egg production and thereby spawning biomass (Bunn *et al.* 2000). It is important therefore, that DEPM estimates are used in combination with other sources of information to determine stock status, rather than as stand alone estimates (*e.g.* Punt *et al.* 2001). This is the case with *P. auratus* stocks in inner Shark Bay where stock status has been determined using DEPM estimates in conjunction with age-structured models since 2002 (Stephenson and Jackson 2005; Jackson *et al.* 2005).

Table 5.8 DEPM parameter estimates for *P. auratus* in inner gulfs of Shark Bay from this study compared with estimates for the species in Spencer Gulf, South Australia (McGlennon 2003) and Hauraki Gulf, New Zealand (Zeldis and Francis 1998). Estimates are mean values (95 % C.I.). Note large differences in size of spawning biomass, particularly in New Zealand.

Parameter	Eastern Gulf, Shark Bay	Denham Sound, Shark Bay	Freycinet Estuary, Shark Bay	Spencer Gulf, South Australia	Hauraki Gulf, New Zealand
Average female weight, W (kg)	2.4-3.6 (2.2-3.9)	1.6-2.9 (1.4-3.8)	3.0-4.5 (2.6-4.9)	2.2-3.2 (1.8-3.8)	0.73 (0.05)
Sex ratio, R	0.45-0.72 (0.35-0.84)	0.56-0.68 (0.42-0.84)	0.45-0.62 (0.34-0.78)	0.58-0.66 (0.28-1.00)	0.43 (0.03)
Batch fecundity, F	118,922-184,827 (102,647-205,389)	67,522-136,940 (57,462-179,234)	170,364-261,603 (146,172-295,176)	99,798-137,797 (71,602-192,557)	63,152 (0.05)
Spawning fraction, S	0.71-0.99 (0.53-1.0)	0.46-0.81 (0.29-0.96)	0.72-0.91 (0.62-0.96)	0.58-0.96 (0.06-1.00)	0.76 (0.07)
Area of spawning, A (km ²)	386-1032	511-1041	344-699	1,968-4,948	
Daily egg mortality, Z (day ⁻¹)	-1.59-0.98	-1.96-0.72	-0.92-0.72	0.21-0.66 (0.0-1.32)	0.5-1.4
Daily egg production, P (eggs m ⁻² dy ⁻¹)	1.06-5.91 (0.64-8.99)	0.45-3.69 (0.37-10.12)	0.71-11.39 (0.54-47.12)	1.19-4.17 (0.84-7.44)	13-871
Total daily egg production (x 10 ⁸ eggs dy ⁻¹)	7.5-61.0	2.3-27.0	2.4-58.0	59.0-259 (42-267)	4,500 (3,500-8,600)
Spawning biomass (tonnes)	25-232 (12-354)	10-184 (7-455)	9-195 (6-528)	302-1,318 (134-2,880)	24,499 (17,995-48,650)

Chapter 6: General discussion

6.1 Key findings

This study has provided new insights into the complex nature of *P. auratus* stock structure in the inner gulfs of Shark Bay. Based on an improved understanding of the very low levels of exchange across all life stages among *P. auratus* living in closely-adjacent waters inside Shark Bay, groupings that are now recognized as belonging to three discrete management-units ('fishable stocks'), the study has been able to provide biological information at the appropriate scale for management of the species in this region of high conservation value (World Heritage). In addition, the study has applied a new method for this species within Western Australian waters to obtain previously unavailable estimates of stock biomass that subsequently have been used (since 1998) in the management of inner Shark Bay *P. auratus* stocks and the associated recreational fishery.

6.1.1 Stock structure

The study provided evidence of a mechanism, *i.e.* hydrodynamic retention, that potentially retains *P. auratus* eggs and larvae within the main, discrete spawning areas in the inner gulfs during the winter spawning season (Chapter 2). These spawning locations are separated by as little as tens of kilometres in some cases. Previous *P. auratus* stock identification studies in the Shark Bay region based on genetics, tagging, morphometrics, and otolith chemistry (see review in Chapter 1) involved sub-adult and adult fish only. In one of these studies, Johnson *et al.* (1986) suggested that gene flow within inner Shark Bay might be limited, in part, by hydrodynamic conditions restricting broadscale dispersal of the pelagic eggs and larvae. The results of this study indicate that *P. auratus* spawning populations off Monkey Mia and Cape Peron and in the Freycinet Estuary are reproductively isolated. These spawning stocks therefore are

likely to be self-recruiting, *i.e.* dependent on recruitment from local spawning. !
However, the spawning population in Denham Sound, particularly in northern waters close to Naturaliste Channel, may receive some recruitment from spawning of *P. auratus* at oceanic locations off Cape Inscription. The management implications of this are discussed in ‘Contributions to management’.

6.1.2 Biological characteristics

Consistent with the findings described above, the study found significant variation in *P. auratus* life-history characteristics at a spatial scale that is unusual for a large, potentially mobile fish inhabiting a marine environment with no obvious physical barriers (Chapter 3). Differences in life-history characteristics have long been used to identify separate fish stocks (Begg 2005). Spawning in inner Shark Bay occurred from late autumn through to mid-spring; fish in the Eastern Gulf and Denham Sound mostly spawned in May-July, while most fish in the Freycinet Estuary spawned later between August-October. Optimum water temperatures for *P. auratus* spawning (16-21° C, Scott and Pankhurst 1992) exist for ~5-6 months in the Freycinet Estuary compared with ~3-4 months in Denham Sound and the Eastern Gulf. The longer spawning season in the Freycinet Estuary likely reflects both this and the greater overall environmental variability there; the Estuary’s waters are more saline (~40-50+) and thermally variable (annual range ~12°C) than in the other two areas (Table 6.1). The production of eggs and larvae over an extended spawning season is a reproductive strategy of risk-spreading to ensure progeny survival in highly variable environments and is common in sparids (Scott and Pankhurst 1992). *P. auratus* are a warm-temperate marine species and while clearly ‘environmentally plastic’, there are likely reproductive consequences

of living in meta and hypersaline conditions, as here in Shark Bay, which are still not ! well understood. !

Females were estimated to reach 50% maturity at the smallest size (348 mm FL) and youngest age (3.2 years) in the Eastern Gulf compared with Denham Sound (401 mm FL, 5.5 years) and Freycinet Estuary (420 mm FL, 4.5 years) (Table 6.1) based on pooled data collected over an 8-year study period. Smaller size and younger age at maturity for both males and females in the Eastern Gulf may reflect a compensatory response to stock decline (Trippel 1995) believed to have occurred in the early-mid 1990s due to over-exploitation by recreational fishers (Jackson *et al.* 2005). The study confirms that larger (and assumed older) females are responsible for a disproportionately greater proportion of the egg production: a female of 500 mm FL produces ~110,000 eggs per spawning event compared to ~ 340,000 by a fish of 700 mm FL. That the power term of the relationship between batch fecundity and female fork length was greater (3.359) than the power term of the length-weight relationship (2.6703) indicates the greater contribution of larger females and the strength of the relationship between fecundity and weight determined in this study. Research elsewhere has shown that older/larger female marine fish enhance recruitment success through the production of larger larvae that have higher survival rates (Cardinale and Arrhenius 2000). Management of moderately long-lived species such as *P. auratus* (maximum ages of 20-30 years) should focus more on maintaining 'longer-tailed' population age structures to dampen recruitment variability (Hsieh *et al.* 2006) rather than solely focus on maximizing stock production (*e.g.* Hilborn 2002 in reference to management of *P. auratus* stocks in New Zealand).

Growth increments in sagittal otolith sections were characterised by alternating thin opaque and wider translucent zones and were clear and relatively easy to interpret in most cases (Chapter 4). Sections from the Eastern Gulf (IAPE = 2.3) and Freycinet Estuary (IAPE = 4.4) were easier to read than those from Denham Sound (IAPE = 6.2). *P. auratus* otoliths from oceanic waters outside Shark Bay, where environmental conditions are more similar to those in Denham Sound (*i.e.* lower seasonal variation in water temperatures than in the Eastern Gulf and Freycinet), are typically more difficult to interpret (IAPE ~ 8, Moran *et al.* 2005; Wakefield 2006). *P. auratus* from the inner gulfs of Shark Bay form a single opaque zone in their sagittal otoliths each year. While opaque zones were being formed over 6-7 months of the year, most fish were completing their opaque zones between August and November. Similar high variability in the timing of opaque zone formation has been found with *P. auratus* in northern Spencer Gulf, South Australia (Fowler *et al.* 2004), where environmental conditions (*e.g.* water temperatures, salinity, bathymetry, habitat-types) are very similar to those in Shark Bay. Opaque zone formation may be related to spawning activity and seasonal water temperature minima (Beckman and Wilson 1985). Opaque zone counts, in combination with month of capture, birth date and increment growth at the otolith edge can be used to age *P. auratus* from inner Shark Bay with confidence, as with the species elsewhere (Francis R.I.C.C. *et al.* 1992; McGlennon *et al.* 2000). Maximum age was 31 years in the Freycinet Estuary, 19 years in Denham Sound and 17 years in the Eastern Gulf (Table 6.1). A three-parameter von Bertalanffy growth model fitted the length-at-age data from each area reasonably well, allowing direct comparisons with growth parameters for the species from elsewhere (Table 4.5).

Growth coefficients for *P. auratus* in inner Shark Bay were higher in the Eastern Gulf (0.18 and 0.17 year⁻¹, females and males, respectively) and Freycinet Estuary (0.17 year⁻¹, both sexes) compared with Denham Sound (0.14 and 0.18 year⁻¹, respectively). Mean asymptotic length was highest for both females and males in Freycinet (773 and 766 mm FL) and lowest for females in the Eastern Gulf (755 mm FL) and for males in Denham Sound (660 mm FL). Wakefield (2006) estimated growth coefficients for *P. auratus* from oceanic waters off Shark Bay (Carnarvon) to be higher again at 0.23 and 0.28 year⁻¹ for females and males, respectively, while Wise *et al.* (2007) reported values of *K* at between 0.09 and 0.22 year⁻¹ for *P. auratus* off the west coast between Kalbarri and Augusta.

Growth rates in this study were lower for both sexes in Denham Sound compared with the other two areas. Differences in growth rates among separate stocks of *P. auratus* in New Zealand (West Coast, Hauraki Gulf, Bay of Plenty, East Northland - Walsh 1997) have been attributed to water temperature, food availability and genetic diversity (Francis M.P. 1994). Sarre and Potter (2000) found variation in growth rates with the closely-related sparid, *Acanthopagrus butcheri*, among estuaries along the lower west coast of Western Australia that was attributed to differences in environmental conditions, diet and stock density. Research with juveniles in Shark Bay (30-200 mm FL, Tapp 2003) and mature fish in South Australia (W. Hutchinson, South Australian Research and Development Institute, pers. comm.) found that *P. auratus* growth was unaffected at salinities of between 35-36 and 42-44 but became significantly reduced at salinities of 48 or greater. While salinities can exceed 50 in waters at the southern margins of the Freycinet Estuary, most fish would probably reside in waters of salinities ~40-46 (G. Jackson unpublished data). That growth rates

were higher in the Freycinet Estuary and Eastern Gulf (compared with Denham Sound) ! suggests that the differences in growth inside Shark Bay are not explained by environmental factors alone. Whilst there are genetic differences among fish from the three areas (Johnson *et al.* 1986; Whittaker and Johnson 1998; Baudains 1999), differences in growth may be linked to density-dependent factors *e.g.* food availability or competition. The lower growth rates for both sexes in Denham Sound fish may reflect reduced prey biomass (linked with commercial trawl fisheries for scallops and prawns that operate in the Denham Sound area only) and/or higher stock densities in Denham Sound over the period of this study compared to other two areas (Table 6.1, Jackson *et al.* 2005). Growth coefficients at between 0.14 and 0.18 year⁻¹ in Shark Bay were higher than those reported for *P. auratus* elsewhere in Australia (with the exception of the value reported for fish in southern Spencer Gulf, South Australia of 0.21 year⁻¹, Fowler *et al.* 2004) or New Zealand (0.10-0.16 year⁻¹, Francis R.I.C.C. *et al.* 1992; Gilbert and Sullivan 1994) where water temperatures are generally cooler.

There was clear truncation of the population age structure in the Eastern Gulf and Denham Sound that probably reflects the historic differences in fishing pressure. For a fish of maximum age ~30 years, age structures as observed through samples collected in this study reflect recruitment events and levels of fishing mortality that occurred between the late 1970s and early 1990s. As discussed in Chapter 1, the information available suggests that significant exploitation of snapper in inner Shark Bay occurred firstly in Denham Sound with recreational activity increasing from the late 1970s there and in the Freycinet Estuary and Eastern Gulf where overexploitation occurred later, in early to mid-1990s.

The relative abundances of 0+ *P. auratus* (surveys in October, ~50-100 mm FL; ' surveys in February, ~70-120 mm FL) from annual trawl surveys conducted in the inner gulfs since 1996 indicate significant variation in annual recruitment (Moran and Kangas 2003). This has also been shown to be the case with the oceanic *P. auratus* stock in waters outside Shark Bay (Moran *et al.* 2005) and *P. auratus* stocks elsewhere (Francis M.P. 1993; Fowler and Jennings 2003; Hamer and Jenkins 2004). The available data for the Freycinet Estuary indicate only one strong recruitment year (in 2000, Moran and Kangas 2003) in 12 years of trawl surveys (G. Jackson unpublished data). Poor recruitment in the Freycinet Estuary is more likely related to environmental factors affecting survival of the earliest life history stages rather than markedly lower egg production. While the larger proportions of older fish in the Freycinet population may suggest the latter via senescence, this is discounted as no instances of decreased or arrested gonadal development were observed among older fish during the study. Pankhurst *et al.* (1991) assessed *P. auratus* larvae, which are relatively small and poorly developed at hatching, to be highly vulnerable to starvation in turbid sea conditions or during periods of low prey availability. In New Zealand, small variations in mean sea surface temperature have been shown to hugely affect year class strength (Francis 1993; Francis *et al.* 1997). This suggests that more extreme conditions in the shallower Freycinet Estuary represents a more marginal environment for the species, particularly during the earliest life history stages, compared with Denham Sound and the Eastern Gulf. The Freycinet population however appears to have adapted (*e.g.* longer spawning season, different spawning behaviour) to survive in the most extreme and variable environments in inner Shark Bay, to compensate for reduced area of spawning, lower average egg production and poor recruitment generally (Table 6.1).

Older fish (*i.e.* 15 years or more) were more prevalent in samples from the Freycinet Estuary where fish of up to 25 years of age were consistently observed in recreational catches up to 2004. This represents an apparent inconsistency with results of DEPM surveys that indicate spawning biomass in the Freycinet Estuary has declined sharply since surveys commenced in 1998, and continued to decline since 2003 when serious management measures were introduced to rebuild the spawning population in this area (see Contributions to management). Alternative hypotheses to explain the apparent prevalence of older fish in a stock that is significantly depleted include (a) that a few bigger/older fish (i) seasonally move into the Freycinet area to spawn during the winter-spring period when most recreational fishing occurs (however, results of tagging and otolith chemistry studies discount this) (ii) become available to capture in Freycinet during this spawning period or (b) that catchability of the older fish is significantly lower here compared with the Eastern Gulf and Denham Sound. Experienced recreational fishers who operate out of Nanga each year have observed that larger spawning fish do not aggregate in large numbers in the Freycinet Estuary during the winter-early spring spawning season in the same manner they do elsewhere, and that quite different fishing techniques are required to consistently catch the bigger/older fish (*e.g.* very lightly weighted baits are fished up to 300-400 m away from the vessel) in the Freycinet Estuary compared with the Eastern Gulf or Denham Sound. The presence of the older fish in Freycinet reflects the greater survival of these fish when they first became recruited to the fishery (at ages 3-4 years, when levels of exploitation were lower in 1970s) and/or pulses of better than average recruitment during the previous 20-30 years. Natural mortality, M , was directly estimated at 0.22 (95% C.I. 0.09-0.34) year⁻¹ in the Eastern Gulf, significantly higher than the base case 0.075 year⁻¹ used in *P. auratus* stock assessments in New Zealand (Maunder and Starr 2001). Fish grow faster

in Shark Bay but do not live as long as in New Zealand where fish are smaller at age ! *e.g.* a 15 year old from Hauraki Gulf would be 280-600 mm (Walsh 1997) compared with ~600-700 mm in inner Shark Bay (this study). Natural mortality may be higher in Shark Bay possibly due to higher densities of natural predators (*e.g.* sharks, dolphins).

6.1.3 Biomass estimation

From the DEPM ichthyoplankton surveys, key spawning locations were identified in the Eastern Gulf (to the northeast of Monkey Mia, north east of Faure Island and to the north of Cape Peron); in Denham Sound (north of Quoin Bluff off the middle of Dirk Hartog Island); and in the Freycinet Estuary (to north of White Island) (Chapter 5). Spawning occurs mostly between mid-afternoon and mid-evening, similar to the pattern found elsewhere in Australia and New Zealand (Scott *et al.* 1993; McGlennon 2003). Large aggregations of spawning fish were observed in the Eastern Gulf and Denham Sound but not in Freycinet Estuary, where fish appear to spawn typically in much smaller groups. This behaviour in the Freycinet Estuary is unlikely to be simply a response to the current low level of stock size as it has been observed by recreational fishers over several decades at least. Different groups of fish spawning at different times over the 5-6 month spawning season may again be a risk-spreading strategy, reflecting the more extreme and variable nature of the spawning environment in the Freycinet Estuary. The study found a strong relationship between lunar cycle and spawning with spawning activity greatest around the new moon and to a lesser extent around full moon. Spawning with many marine species is strongly correlated with lunar and tidal cycles, particularly batch-spawners (Jackson *et al.* 2006; Wakefield 2006). It was not possible to estimate daily egg mortality (Z) precisely for each DEPM survey due to the high variability in egg abundance of the various stages of development. Egg

production curves were fitted to weighted egg density data for each survey with Z fixed at 0.49 day^{-1} in all cases (based on pooled egg data), *i.e.* assumed to be constant for all years and areas. This pooled value of Z lies in the middle of the range estimated for *P. auratus* in northern Spencer Gulf, South Australia ($0.21\text{-}0.66 \text{ day}^{-1}$, McGlennon 2003) but at the lowest end of the range for *P. auratus* in Hauraki Gulf, New Zealand ($0.5\text{-}1.4 \text{ day}^{-1}$, Zeldis and Francis 1998). The imprecision in estimation of daily egg production reflects the highly patchy distribution of *P. auratus* eggs and low sample sizes relative to the variability (Hunter and Lo 1997; Lo 1997; Zeldis 1993). In addition to conducting more intense ichthyoplankton surveys, improvements to the estimation of egg mortality and egg production for inner Shark Bay *P. auratus* may be possible using alternative analytical techniques *e.g.* delta-lognormal or similar model (Pennington 1996; Field *et al.* 2007) and Bayesian techniques (Lo *et al.* in press).

DEPM biomass estimates indicated recovery of the Eastern Gulf stock (at least between 1998 and 2000-2001) and Denham Sound and a decline in biomass in the Freycinet Estuary between 1998-2002. The spawning biomasses of *P. auratus* stocks in the inner gulfs are very small (measured in tens of tonnes) in comparison with biomasses of the oceanic *P. auratus* stock (1,000s of tonnes, Moran *et al.* 2005) and *P. auratus* stocks elsewhere in Australia (1,000s of tonnes, McGlennon 2003) and New Zealand (10,000s of tonnes, Zeldis and Francis 1998) (Table 6.1). The DEPM is a viable assessment tool for monitoring changes in biomass *P. auratus* in inner Shark Bay as has been shown with the species elsewhere (Zeldis and Francis 1998; McGlennon 2003). A more intensive stratified-systematic sampling design is recommended for future DEPM surveys in inner Shark Bay.

6.2 Contributions to management

The outcomes of the research described in this study have provided a fundamental contribution to the management of *P. auratus* in the inner gulfs of Shark Bay as follows:

6.2.1 Stock structure

The Shark Bay *P. auratus* stock structure paradigm at the time this study commenced, based on genetics (Johnson *et al.* 1986) and complementary techniques (tagging, Moran *et al.* 2003; head morphology, Moran *et al.* 1999; otolith microchemistry, Edmonds *et al.* 1989, 1999) was that three discrete stocks existed in the Shark Bay region, *i.e.* an oceanic stock (found in northern and continental shelf waters) and separate Eastern Gulf and Western Gulf stocks (found in the inner gulfs) ('Three stock model'). Management boundaries (Fig. 6.1) delineating the approximate extent of the two inner gulf stocks had already been drawn up by the Department of Fisheries (in 1997, following some consultation with local fishermen, J. Penn pers. comm.) before this study commenced. With little biological information available at that time, these boundaries were based on the approximate location of a salinocline that separates oceanic waters from metahaline waters (Logan and Cebulski 1970) under the expectation that the inner gulf populations had adapted to the elevated salinities (as discussed by Johnson *et al.* 1986).

Based on the information provided by this study (egg and larval dispersal, Chapter 2, Nahas *et al.* 2003; variation in life history characteristics, Chapters 3 and 4) and associated stock identification research (tagging, G. Jackson unpublished data; otolith stable isotopes, Bastow *et al.* 2002), in conjunction with the findings of Gaughan *et al.* (2003) and pre-existing information (see Chapter 1), the distinction between

spawning populations in Denham Sound and the Freycinet Estuary was confirmed. The existence of three discrete inner gulf *P. auratus* stocks, *i.e.* Eastern Gulf, Denham Sound and Freycinet Estuary (in addition to an oceanic stock -> 'Four stock model'), was formally recognized for the first time by fisheries managers in 2000.

Information on the spatial extent of spawning, derived from egg distributions from the DEPM ichthyoplankton surveys (Chapter 5), were used to identify the northern limit of the Freycinet Estuary population and to draw a new boundary line (westwards from Goulett Bluff, Fig. 6.2) between waters inhabited by these fish and those by the Denham Sound population. The geographic boundaries between the oceanic, Eastern and Denham Sound stocks are difficult to define precisely. While there is clearly some overlap in spawning grounds used by Denham Sound and oceanic fish, and therefore the sources of recruitment (see discussion in Chapter 2), there is sufficient evidence that juvenile (0+) fish inside Shark Bay are relatively sedentary and that separate nursery areas exist in Denham Sound and Freycinet Estuary (Gaughan *et al.* 2003). Genetic evidence also suggests that fish in Useless Inlet/Denham Sound are partially genetically isolated from those in the Freycinet Estuary and in oceanic waters (Whitaker and Johnson 1998). The possibility of further stock structure cannot be entirely discounted. For example, some experienced recreational fishers at Nanga strongly believe a number of separate sub-populations are found in the Freycinet Estuary based on fish colour, body shape and seasonal movement patterns (P. Somerville pers. comm., recreational fisher).

At first glance, it is tempting to conclude that *P. auratus* in Shark Bay demonstrate metapopulation structure. However, based on one of the criteria originally

proposed by Levins (1970), *i.e.* the presence of a number of discrete local breeding ! populations connected via the exchange of individuals, *P. auratus* in the inner gulfs do not conform to the metapopulation model with the possible exception of the Denham Sound population that may exchange individuals with a larger, oceanic population. Smedbol *et al.* (2002) suggested that scientists and managers should refrain from injudiciously using the metapopulation concept when making decisions about exploited fisheries; all identified subpopulations should be managed as distinct management units or fishable stocks until metapopulation structure has been tested empirically.

6.2.2 Biology and stock assessments

A wide range of management measures aimed at rebuilding and maintaining inner gulf *P. auratus* stocks have been introduced since 1998 (Appendix 1), the first year that any scientific assessment of stock status became available. While there had been attempts to take management action to protect local *P. auratus* stocks from 1996, community support for more drastic measures (*e.g.* closure of the Eastern Gulf in 1997) was generally absent, in part due to the lack of available data (Marshall and Moore 2000; Stephenson and Jackson 2005). Following the pilot DEPM surveys in 1997 (Chapter 5), which indicated that the spawning biomass in the Eastern Gulf was depleted (possibly to as low as 10% of its unexploited level), a moratorium on the taking of all *P. auratus* in that area was introduced in June 1998. While both commercial and recreational fishing for other species continued in the Eastern Gulf during the moratorium, the breeding stock was further protected through a total fishing exclusion zone in the vicinity of the key spawning ground off Monkey Mia (Fig. 6.1), a localized spatial closure which remained in place until 2003. During the initial years of the moratorium (until March 2003), the Eastern Gulf spawning stock was shown to

recover by the results of the annual DEPM surveys (~25-35 tonnes in 1998, ~60 tonnes ! in 1999, ~200 tonnes in 2000, see Chapter 5).

In contrast, in Denham Sound and the Freycinet Estuary, a wide range of measures had only limited effect in constraining recreational snapper catches (Sumner and Malseed 2002). These included: (i) increases in the minimum legal size (introduced in 2000, from 450 mm to 500 mm TL, where this increase was based on maturity data from this study, Chapter 3), (ii) protection of larger fish (also in 2000, where a maximum size limit of 700 mm TL was based principally on batch fecundity analyses that showed that larger females contribute significantly more to total egg production, Chapter 3), (iii) reduced bag limits and, (iv) a six week spawning closure (also in 2000, mid-August to end of September, where this period of closure was selected on the basis of GSI and gonadal development data from this study, Chapter 3).

A review of the research conducted between 1997-2001 was undertaken in 2002 (Jackson and Stephenson 2002) and presented to a Ministerial Working Group that was convened to discuss when and how the Eastern Gulf should be re-opened to fishing for snapper. Various biological data (Chapter 3 and 4), estimates of spawning biomass (obtained from the DEPM surveys, Chapter 5) and estimates of recreational catches (from recreational fishing surveys conducted by Department of Fisheries 1998-2001, Sumner *et al.* 2002; Sumner and Malseed 2001, 2002) were incorporated in age-based stock assessment models for the first time. These models are dependent upon the ability to accurately age fish (Chapter 4) and were used to determine the status of the three inner gulf stocks (Jackson *et al.* 2005; Stephenson and Jackson 2005, details of model given in this paper in Appendix 1). The determination of the necessary biological data required for these stock assessment models is one of the most significant contributions

from this study. !

At the time (2002), these model-based assessments allowed visual representations of probable stock levels under different catch scenarios and proved to be a valuable tool assisting managers and stakeholders in the decision-making process, prior to re-opening of the Eastern Gulf to *P. auratus* fishing in 2003. These assessments were used to explore different catch scenarios and thereby determine appropriate levels of Total Allowable Catch (TAC) and catch allocations (between the commercial and recreational sectors) for each stock for the period 2003–2005, the first time this had been done with a principally recreational fishery in Australia (Stephenson and Jackson 2005; Jackson *et al.* 2005). In mid-2005, an FRDC-funded project, which evaluated TAC-based management of inner gulf snapper, including the first ever use of a lottery-based system⁶ of allocating a limited number of management-tags to constrain the recreational catch in Freycinet Estuary to <25% of the historical level (Jackson *et al.* 2005) was completed. The results of this project and those of the updated (model-based) stock assessments were presented to the Ministerial Working Group (June 2005). These formed the basis for determining management arrangements for inner gulf snapper for the next 3-year period (2006–2008). The importance of the research described in this thesis, and its contribution to the Department of Fisheries' success in the management of inner gulf *P. auratus* stocks between 1997 and 2007 was publicly recognised in November 2007, when the project won the Premier's Overall Award for Excellence in the Public Service (Appendix 2).

⁶ A full description of the lottery-based allocation of management-tags in the recreational snapper fishery in the Freycinet Estuary are given in Jackson *et al.* 2005.

Table 6.1 Summary of environmental differences, *P. auratus* biological characteristics and management history for the three areas in this study. ¹ mean values for surveys 1998-2004 (see Chapter 5).

	Denham Sound	Eastern Gulf	Freycinet Estuary
<i>Environment:</i>			
Depth (m)	Max. ~20	Max. ~16	Max. ~12
Annual range SST (°C)	~19-26	~16-26	~15-27
Salinity	35 to 38	38 to 44	40 to 50+
<i>Reproduction:</i>			
Peak spawning	May-July	May-July	August-October
Spawning behaviour	Larger aggregations	Larger aggregations	Smaller groups
Female L_{50} (mm)	401	348	420
Female L_{max} (mm)	750	752	785
Female A_{50} (years)	5.5	3.2	4.5
Female A_{max} (years)	19	17	29
Male L_{50} (mm)	276	243	330
Male L_{max} (mm)	730	599	790
Male A_{50} (years)	2.7	1.6	2.7
Male A_{max} (years)	17	15	31
Sex ratio	~1:1	~1:1	~1:1
Fecundity	$F=9.44 \times 10^{-5} FL^{3.36}$	$F=9.44 \times 10^{-5} FL^{3.36}$	$F=9.44 \times 10^{-5} FL^{3.36}$
Mean ¹ spawning area (km ²)	750	830	550
Mean ¹ daily egg production	1.9	1.7	1.5
<i>Growth:</i>			
Females			
t_0 (years)	-0.03	0.04	0.13
K (year ⁻¹)	0.14	0.18	0.17
L_{∞} (mm)	762	755	773
Males			
t_0 (years)	-0.06	-0.07	0.08
K (year ⁻¹)	0.18	0.17	0.17
L_{∞} (mm)	660	751	766
<i>Status spawning stock</i>	some increase	at very low levels in 1998,	declined since 1998,
<i>Based on DEPM estimates:</i>	between 1998 and 2000, some variability since	increased sig. by 2000- 2001 under moratorium some variability since	still at low levels despite very limited catches since 2003
<i>Juvenile recruitment:</i>	variable?	variable?	highly variable
<i>History of fishing:</i>	fished longest, since 1920-1930s, initially commercial, mostly recreational since 1980s	some commercial fishing, heavy exploitation by recreational boats in early to mid 1990s	less commercial activity overall, seriously targeted by recreational fishers since 1970s
<i>Current management:</i>	daily bag & slot limits only	daily bag & slot limits plus spawning closure (3 months)	bag limit, slot limits, plus spawning closure (6 weeks), plus limited management-tags

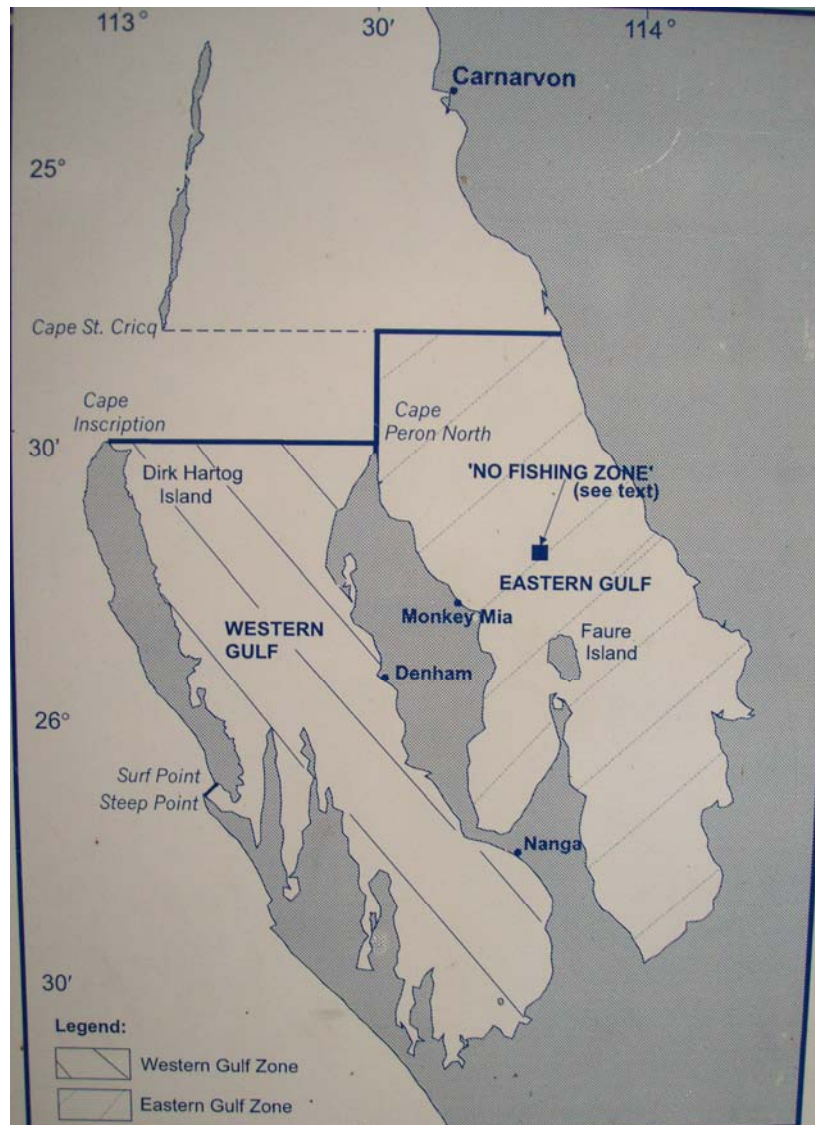


Figure 6.1 Photograph of map on Departmental of Fisheries WA sign showing recreational fishing areas in inner gulfs of Shark Bay as at June 1998. Note map shows only two zones 'Eastern Gulf' and 'Western Gulf' reflects the understanding of *P. auratus* stock structure at that time (compare with Fig. 6.2). 'No Fishing Zone' in the Eastern Gulf refers to a fishing exclusion zone around the main *P. auratus* spawning ground off Monkey Mia that was introduced in 1998 (and remained in place until 2003) to protect spawning fish.

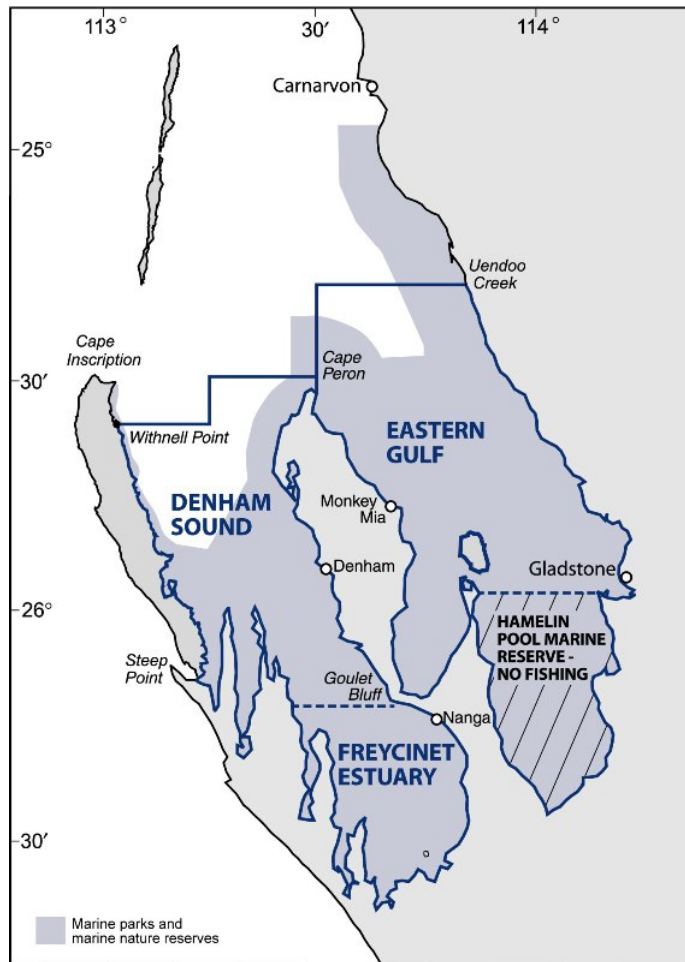


Figure 6.2 Commercial and recreational fishing areas of inner Shark Bay that have been used since 2003. The three management zones (Eastern Gulf, Denham Sound, Freycinet Estuary) reflect the understanding of *P. auratus* stock structure that has been formally recognized since 2000. *P. auratus* in waters outside of these zones are assumed to be part of the larger, oceanic stock (and managed separately). No fishing is permitted in Hamelin Pool (Class A Marine Reserve).

6.3 Future research

The combination of Shark Bay's environmental characteristics, its unique *P. auratus* populations, and the complex history of exploitation, including the adaptive approach adopted for the management of the recreational fishery, have provided research opportunities rarely available to fishery biologists. In addition, that the research has been conducted over a longer timeframe (~7-8 years and longer) than is typically the case with such species/fisheries (very small stocks, low levels of annual

catch, recreational-focused) has made it possible to investigate biological response(s) to ! management actions *e.g.* the Eastern Gulf moratorium and re-opening of the fishery. Some suggestions for future research are discussed below.

From a management perspective, the Department of Fisheries will need to consider what level of scientific advice is required for the ongoing future management of the *P. auratus* fishery. With catch levels (both recreational and commercial) in the three management areas under tight control (TAC-based management), and two of the three stocks above the management target level of spawning biomass (Jackson 2006), the need for detailed research is no longer as critically urgent as it was a decade ago (from 1997). However, given the importance of the fishery to the region's economy and its World Heritage status, it is recommended that the Department of Fisheries continues to periodically monitor recreational catches and fishing effort, and to undertake at approximately 5-year intervals fishery-independent stock assessments using DEPM surveys or tagging (see Jackson *et al.* 2005 for discussion of merits/costs of each method).

From the broader scientific perspective, many exciting research opportunities remain due to the ecological plasticity of this species that has proved to be highly successful in Shark Bay, a region at the northern extent of its Australian range on the west coast. The apparent differences in how each of the respective populations responded following high levels of exploitation require further investigation. For example, the Eastern Gulf spawning stock appeared to recover relatively quickly under the protection of the moratorium. In contrast, the spawning stock in the Freycinet Estuary appears not be recovering as rapidly since the introduction of the management-

tag system in 2003 (Jackson *et al.* 2005) even though catches have been reduced by ! >80% compared with levels in 1998 (Sumner *et al.* 2002).

While some attempts have been made to investigate juvenile recruitment through use of annual research trawl (1996-present, Moran and Kangas 2003) and trap surveys (1998-2000, Jackson *et al.* 2007), it is important to continue this research, to determine the extent to which annual recruitment strength varies between the three areas. There is very little information on the diet of *P. auratus* in the inner gulfs; such information would improve understanding of inter-specific competition among the key recreational target species. Allozyme-based genetic techniques are recognized as providing only indirect indicators of genetic variation and often yield results that are difficult to interpret in a fisheries management context (Ward 2000, Hellberg *et al.* 2002). Future research could be focussed on more adequately determining the genetic relationship between local *P. auratus* populations using a DNA-based approach (Carvalho and Hauser 1994).

6.4 Concluding comments

While the importance of understanding stock structure has been long recognised, stock identification is now receiving greater attention at smaller geographic scales for a variety of reasons including increased emphasis on biodiversity and a shift towards more cautious management (Stephenson 1999). Fisheries management has typically assumed population homogeneity over large geographic scales with potentially highly mobile marine fish. However, there is increasing evidence of population structuring with marine species occurring at scales of hundreds of kilometres and less, *e.g.* red snapper (*Lutjanus campechanus*, Saillant and Gold 2006), key demersal species on west

coast of Western Australia (Lenanton *et al.* 2008). Differences in life history characteristics such as growth and size and age at maturity are being used to support the management of fish populations at the finer spatial scale, *e.g.* orange roughy (*Hoplostethus atlanticus*) in the eastern Tasman Sea off New Zealand (Smith *et al.* 2002), red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico (Fischer *et al.* 2004), canary drum (*Umbrina canariensis*) (Hutchings *et al.* 2006) and carpenter (*Argyrozona argyrozona*) (Brouwer and Griffiths 2005) off South Africa, snapper (*P. auratus*) and dhufish (*Glaucosoma herbraicum*) on west coast of Western Australia (Wise *et al.* 2007). The knowledge of spatial differences in biological characteristics in combination with environmental information is essential in helping to achieve a better understanding of the ecological processes that shape such distinctive fish stocks.

Appendix 1.

Chronology of research and management of *P. auratus* (pink snapper) fishery in the inner gulfs of Shark Bay. DoF = Department of Fisheries WA; RRFAC = Regional Recreational Fishing Advisory Committee; RFAC = Recreational Fishing Advisory Committee; DEPM = daily egg production method; TAC = Total Allowable Catch. All size limits are total lengths, t = tonnes.

1950s – 1980s	Size limit 38 cm, no bag limits.
1983	First Shark Bay recreational fishing survey estimated catch ~ 45 t pink snapper for entire Gascoyne (south of Quobba); Eastern Gulf ~7 t, Denham Sound ~12 t, Freycinet Estuary ~17 t (DoF unpublished data).
1984 onwards	Tagging, genetics, otolith chemistry, morphometrics indicate three separate pink snapper stocks; oceanic, Eastern Gulf, Western Gulf ('Three stock model').
1986	Size limit increased to 41 cm, daily bag limit of 10 'reef fish' per person (includes pink snapper) introduced (statewide).
1991	Bag limit reduced to 8 fish per day (statewide).
May 1995	Community concern about high catches of spawning pink snapper out of Monkey Mia, from observations at boat ramp (DoF unpublished data) estimated that ~100 t taken in Eastern Gulf in total in 1995 (thought not to be sustainable).
September 1995	Denham RRFAC recommends introduction of daily bag limit of 6 'prize fish', overall possession limit, and daily bag limit of 4 pink snapper during spawning season only (May-July).
March 1996	State RFAC recommends minimum size of 45 cm, slot limit of 2 fish > 70 cm, daily bag limit of 4.
May 1996	Regulation changes delayed until 1997.
June 1996	Denham RRFAC expressed disappointment, recommends slot limit of 2 pink snapper > 70 cm, 6 other fish < 70 cm.
November 1996	Eastern Gulf, daily bag limit reduced to 4, minimum size limit increased to 45 cm. Denham Sound/Freycinet Estuary, no change to regulations. Limited creel survey conducted at Monkey Mia ramp, juvenile recruitment (0+) trawl surveys commence.
February 1997	Juvenile trawl surveys indicate poor recruitment in Eastern Gulf compared with Freycinet.
May 1997	Eastern Gulf pink snapper fishery closed. Denham Sound/Freycinet Estuary, minimum size limit increased to 45 cm, slot limit of 2 fish > 70 cm, daily bag limit reduced to 4.
July 1997	Eastern Gulf pink snapper fishery reopens, slot size limit 50-70 cm introduced, daily bag limit reduced to 2.
June 1998	Based on 1997 pilot DEPM results, estimated that ~5-20 t of spawning biomass in Eastern Gulf, pink snapper fishery closed (again). Gascoyne Recreational survey underway (started in March 1998).
1999	Results of Gascoyne recreational fishing survey, estimated catch of pink snapper in 1998; Denham 12 t, Freycinet 26 t. No recreational survey conducted in 1999, DEPM surveys conducted in all three areas.
August 2000	Eastern Gulf fishery remains closed. Based on further research (genetics, tagging, otolith chemistry, egg/larval dispersal), management recognizes separation between Denham Sound and Freycinet pink snapper stocks. Denham Sound, daily bag limit reduced to 2, minimum size limit increased to 50 cm, slot limit with only 1 fish > 70 cm. Freycinet, same

	as Denham plus 6 week spawning season closure (15/8 to 31/10) introduced. Recreational survey and DEPM surveys in all three areas.
2001	No changes to regulations. Recreational survey, DEPM surveys in all three areas.
July 2002	Ministerial Working Group, review of pink snapper research and management, results of preliminary model-based stock assessments, considered management options for period 2003-2006, set TACs for each stock. Recreational survey, DEPM surveys in all three areas.
2003	Eastern Gulf re-opened in March, TAC 15 t (12 t allocated to recreational sector, 3 t to commercial), daily bag limit 1 snapper, slot limit >50<70 cm, spawning closure April-July. Denham Sound, TAC 10 t (8 t recreational, 2 t commercial), daily bag limit 1 snapper, slot limit >50<70 cm. Freycinet, TAC of 5 t (3.8 t recreational, 1.2 t commercial), slot limit >50<70 cm, 6 week spawning season closure, plus 900 'management-tags' only available to recreational fishers (300 to commercial sector), allocated via lottery system. Catches monitored with boat ramp survey, DEPM surveys in Eastern Gulf, Denham Sound only.
2004	Same management arrangements as in 2003. Catches monitored with boat ramp survey, DEPM survey in Eastern Gulf, Freycinet only. FRDC-funded tagging study in Eastern Gulf.
2005	Same management arrangements as 2003,2004. Catches monitored with boat ramp survey, no DEPM surveys conducted. Research and management reviewed in mid-2005, TACs and regulations set for period 2006-2008.
2006	Eastern Gulf, TAC 15 t, daily bag limit 1 snapper, slot limit >50<70 cm, spawning closure reduced by one month to May-July. Denham Sound, TAC increased by 5 t to 15 t, bag limit 1 snapper, slot limit >50<70 cm. Freycinet, TAC 5 t, slot limit >50<70 cm, 6 week spawning season closure, number of 'management-tags' available increased to 1,050 for recreational fishers (350 for commercial sector), allocated via lottery system. Catches monitored with ramp survey, DEPM survey in Freycinet only.
2007	Same management arrangements as in 2006 (and for 2008). Catches monitored with ramp survey, DEPM survey in Freycinet only. Research and management to be reviewed in mid-2008, to set TACs and regulations for period 2009-2011.

Appendix 2. Department of Fisheries win Premiers Award for Excellence in Public Sector Management, November 2006

FOREWORD



I am very pleased to present the finalists for the 2006 Premier's Awards for Excellence in Public Sector Management.

Now in its eleventh year, the Premier's Awards are attracting a high calibre of

submissions. We received a total of 68 submissions for the five categories from Government departments, statutory authorities, local governments and hospitals.

The level of interest by agencies nominating their initiatives remains solid and the diversity and quality of submissions compared with other years has certainly been maintained.

The aim of the Awards is to motivate and inspire agencies to strive for sustainable excellence, innovation and creativity in meeting the community's needs. They also serve as a primary vehicle to recognise and celebrate world-class achievements by those involved in the delivery of public services.

Thank you to all agencies that submitted projects and programs for this year's Awards. I trust the process of developing the submission was a

valuable experience, providing individuals and work teams with an opportunity to undertake assessment and reflection on the outcomes of these initiatives.

I also extend a special thank you to the Peak Judging Panel that comprised eminent persons from academia, industry, the private sector and the Western Australian community.

Throughout this publication there are many examples of responsive management, leadership and collaboration that have resulted in better services to the community of Western Australia. I highly recommend all Directors General and Chief Executive Officers circulate these finalist profiles amongst their staff as a testament to agency enterprise and innovation.

I congratulate all agencies and work teams recognised for their outstanding contributions to the 2006 Premier's Awards for Excellence in Public Sector Management.

ALAN CARPENTER MLA
PREMIER, MINISTER FOR PUBLIC SECTOR MANAGEMENT



OVERALL WINNER

2006 PREMIER'S AWARD FOR EXCELLENCE IN PUBLIC SECTOR MANAGEMENT

Department of Fisheries

Recovery of Shark Bay's Inner Gulf Pink Snapper Populations 1995-2006

The Peak Judging Panel's role of selecting an overall winner for such a prominent award is certainly a challenging one. Nevertheless, rigorous evaluation produced clear and unanimous agreement that the Department of Fisheries' *Recovery of Shark Bay's Inner Gulf Pink Snapper Populations 1995-2006* was the most outstanding and deserving submission of this high accolade.

Three unique and vulnerable pink snapper populations located in the Shark Bay inner gulfs would have been devastated if the Department of Fisheries had not developed and implemented an innovative and engaging research and management program spanning the last decade - a world first for the management of finfish fisheries where recreational fishing dominates.

In response to community concern, research was undertaken in 1995 that indicated that better coastal access and advanced fishing technology had led to coastal fish stocks across the remote northern regions being exposed to unprecedented levels of pressure from recreational fishers.

To combat the over-exploitation committed planning, strategies, operations and the use of effective communication, innovation, monitoring and measurement were coordinated by the Department of Fisheries. This integrated approach resulted in enthusiastic and dedicated stakeholder support that has helped to turn around the decline of the pink snapper fishery in the region and place this popular fish species firmly back on a sustainable footing.

Panel consensus indicated that the *Recovery of Shark Bay's Inner Gulf Pink Snapper Populations 1995-2006* project impressively addressed all Award category criteria, particularly, modelling the way through community partnership and collaboration, agency goal achievement through high innovation and sustainability, and the enhancement of the Western Australian lifestyle through the protection and conservation of our natural and built environment.

The ten year journey of discovery has made a significant contribution to many of the key issues associated with managing human impacts on wild fish populations for the benefit of the local community, fishing and tourism industries, the Western Australian economy and broader global environment. Signs are encouraging that this world heritage area, and other marine conservation areas, can co-exist with recreational fishing if good information, good science, good regulation and good collaboration are in place to support sustainable fishing.

The Department of Fisheries is to be congratulated for its leadership in this groundbreaking long-term recovery project, which has ensured the long term viability of one of Western Australia's valuable social, environmental and economic resources.

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