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TEMPORAL AND SPATIAL VARIABILITY OF THE LIFE HISTORY CHARACTERISTICS OF SAND FLATHEAD, *PLATYCEPHALUS BASSENSIS*.

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SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR

THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF TASMANIA

OCTOBER 2005

DECLARATION OF ORIGINALITY

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ABSTRACT

Spatial and temporal variability in life history characteristics of sand flathead *Platycephalus bassensis*, were explored in the context of energy tradeoffs between growth and reproduction. Given the similarity in environmental conditions and somatic condition of individuals and the populations, this study was able to examine whether and to what extent spatial variability in dynamics of recreationally fished populations was associated with variation in life history characteristics. This was achieved through intensive sampling at three locations (Georges Bay, Coles Bay, and the Tamar River) describing variability in demographic parameters, variability in reproductive life history characteristics, and the patterns of energy allocation to growth and reproduction.

Demography of sand flathead populations varied significantly among the three locations around the coastal waters of Tasmania. The proportion of older and larger fish was greater in Coles Bay, compared with the Georges Bay and the Tamar River populations. The absence of old (> 4 years) individuals in the Tamar Estuary was attributed to the movement of older fish out of the estuary. In contrast, less older and larger individuals in Georges Bay was hypothesised to be a function of greater mortality rates of fast-growing individuals. Similarity in growth rates of all examined populations during the first two years of life, before they suffer fishing pressure, suggests that environmental conditions at least for younger fish, were similar in all three locations.

Reproductive potential and spawning strategy of *P. bassensis* populations also differed spatially. Very low attainment of maturity in the Tamar River population during the spawning season, together with minimal gonad weight and lack of seasonal changes in gonad development, as well as the absence of older fish suggests

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that the Tamar Estuary is most probably not part of the spawning grounds for *P. bassensis*. Duration of spawning activity in the Coles Bay population (October-March) was longer than for the Georges Bay population (September-November), suggesting a greater chance to spawn more batches of eggs during the spawning period in Coles Bay. Additionally, the Coles Bay population showed greater reproductive investment during the spawning season, compared to Georges Bay. As a result, the Coles Bay population, which consisted of relatively more larger individuals was expected to have a greater reproductive output compared with Georges Bay, which had predominantly smaller individuals.

For both mature and immature individuals differences in somatic and liver condition among the populations were relative small compared to the differences in life history parameters of growth and reproduction. Changes in liver lipid and water content of Coles Bay and Georges Bay individuals with reproductive state indicated that sand flathead used liver lipid for reproduction. No changes in muscle water content of mature individuals suggested that muscle is not a primary energy source for reproduction.

A comparison of the patterns of energy allocation and the condition of individuals from different populations indicated that variability in the life history traits can not be explained in the context of energy allocation. Absence of spatial variability in somatic condition and energy allocation suggests that significant spatial variability in *P. bassensis* life history traits may be a result of population responses to exogenous factors, e.g. fishing. Such a response can override other contributing factors in the life history variability and consequently drive population structure and dynamics.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1. POPULATION STRUCTURE

The structure of a fish population is determined by the balance between lifehistory processes of reproduction, growth, and mortality (Sissenwine, 1984; Beverton & Holt, 1993) (Fig 1.1). Growth and reproduction as two major components of the life history traits are interconnected, energy channelled into the gonads detracts from growth (Roff, 1984). There is thus a direct trade-off between growth and reproduction. The extent of such trade-off in driving population dynamics and the implication of fish condition, at the whole animal level, in quantifying variation in the differential allocation of energy yet to be addressed for fish. This study explore variability in the life history characteristics of sand flathead, *Platycephalus bassensis*, in the context of energy tradeoffs between growth and reproduction. Understanding of energy tradeoffs develops our knowledge in identifying contributing factors responsible for variation of sub-populations.

Given that populations of marine organisms with dispersive larvae recruit into different environments, life history characteristics such as reproduction, growth, and mortality are likely to vary temporally and among sub-populations. Such changes in life history traits will drive the variability in the structure of fish populations (Ihssen *et al.*, 1981). Changes in population structure, in turn, may alter life history traits (Elliott, 1987; Clutton-Brock *et al.*, 1997; Rodd & Reznick, 1997). Despite the general recognition that life history traits are the fundamental component of population dynamics (Cole, 1954; Sinclair, 1995), few studies have assessed the relationship between life history traits and population response (Begg *et al.*, 1999; Leips & Travis, 1999). Of those that do study the relationship between life history traits and population dynamics, almost none assess the variability among populations

over the time and the possible consequence of such variation in population structure. The rarity of studies that examine variability in population structure of a species limits our ability to identify general mechanism(s) underlying changes in population structure.

Apart from influences of reproduction, growth, and mortality, behavioural process such as migration or movement of fish between areas may drive changes in population structure (Jennings & Kaiser, 1998). Such variations in population structure are often unpredictable and cause uncertainty for the fisheries scientist.



Figure 1.1. Schematic of population formation and contributing parameters in this process.

Population growth is a result of recruitment of new animals to the population and the growth of individuals already in the population (Beverton & Holt, 1993; Haddon, 2001). Since individuals of similar size can have vastly different ages, the size structure of a population alone is generally unable to reveal underlying processes of population growth. However, size-at-age data that can be used to describe patterns of growth and to estimate growth rates of individuals revealing the process of increase in stock biomass (Kirkpatrick, 1993; Haddon, 2001). Additionally, estimates of growth rate, together with size/age structure and longevity, are needed to estimate rates of population turnover and their resilience to different mortality regimes (Choat *et al.*, 2003). Apart from growth, reproduction is central to the capacity of a population to increase in size. In unfished populations, variability in reproductive potential may indicate local adaptation, either through genetically isolated demes or through responses to a broad range of physical and biological conditions (Jennings & Beverton, 1991; see review in Stearns, 1992).

Although the implications of growth and reproduction in population structure and its variability among populations is unquestionable, these two parameters are tightly interconnected (Wootton, 1979; Roff, 1984). Energy channelled to reproduction potentially affects growth and survival. For fish in general, a 'growth cost' of reproduction is evident in the asymptotic growth curve where growth slows after maturation (Roff, 1984; Kozlowski & Teriokhin, 1999). If energy is limiting, such trade-off is certainly reasonable (Roff, 1992; Stearns, 1992). Alternatively, it is possible that energy is not limiting and growth rate is not limited by input (Roff, 1992), thereby trade-off may not occur. Theories on resource allocation between growth and reproduction remain almost untested in practice for most animals (Heino & Kaitala, 1999), because separating the effect of exogenous factors on life history

traits is difficult. For fishes our understanding of trade-off between reproduction and growth is far from complete and limited to a few studies (Roff, 1982; Reznick, 1983). As a result, spatial variability in growth and reproduction in the context of energy allocation has not been explored. Theoretically, spatial differences in the pattern of energy allocation may be seen in spatial variation in growth rates, especially where differences in the level of reproductive investment are also evident. Such variation in growth rate and reproductive output can drive population dynamics. Therefore, examination of spatial variability in somatic condition highlights the implication of energy allocation in driving growth and reproduction processes.

The body size of a fish species determines much of its ecology, life history, and vulnerability to the exploitation (Charnov, 1993; Pope et al., 1994; Kerr & Dickie, 2001). Life history traits such as fecundity, size/age at maturity, and maximum size/age are strongly correlated to body size (Reynolds et al., 2001; Hutchings, 2002). There is a significant correlation between the life history traits of size/age at first reproduction, mortality, and growth rates in local populations (Roff, 1984). Life history theory predicts that populations with high adult mortality rates will select for individuals that mature earlier in their lifetime, thereby increasing reproductive effort in younger age classes (Schaffer, 1979; Stearns, 1983; Charlesworth, 1994). However, as fecundity is proportional to the size/age of fish (Bagenal, 1966; Kjesbu et al., 1998) small individuals would not be able to invest significantly in egg The trade-off between current and future reproduction (Roff, 1992; production. Stearns, 1992; Rochet et al., 2000) suggests that the lower fecundity at lower size/age maturity, would be compensated through a higher fecundity at larger size/age. Maturating at a greater age/size results in lower mortality (Roff, 1981;

Rochet *et al.*, 2000) and because of higher fecundity of larger individuals, recruitment of new animals to the population is expected to be higher. Variation in life history traits has the potential to drive population dynamics, therefore investigations of such variability is central to understanding the mechanisms underlying such dynamics.

Life history traits such as growth, fecundity, and size/age at maturity may vary among populations as a result of variations in the environment that an animal lives (Vollestad & Labee-Lund, 1990; Jennings & Beverton, 1991). For example, growth rates of fish will typically increase with temperature (Atkinson, 1994), with faster growth rates decreasing the age at maturity (Trippel, 1995; Poortenaar *et al.*, 2001). Fish growth is also highly sensitive to resource availability, and at low densities where intraspecific competition is expected to be reduced fish growth rate can be high (Borisov; 1978; Frank & Leggett, 1994; Rijnsdorp, 1994). Because of the positive relationship between fecundity and fish size (Bagenal, 1966; Kjesbu *et al.*, 1998), any environmental factor that influence growth rate and body size may indirectly effect fecundity and reproductive potential (Reiss, 1989).

The size and age structure of a population can also be the result of size selective fishing mortality (Rothschild, 1986). Spatial variability in mortality regimes of different size/age classes can cause variations in the size and age structure of populations (Law & Rowell, 1993; Bertschy & Fox, 1999). Greater rates of mortality of larger and older individuals, which are generally part of the spawning stock, directly affects the reproductive potential of a population (Garrod & Horwood, 1984; Rijnsdorp *et al.*, 1991; Begg & Marteinsdottir, 2003). Determination of variability in fish population dynamics is important and necessary to fisheries management for the development of optimal harvest and monitoring strategies

(Smith *et al.*, 1990; Law, 2000). Many studies have documented differences in population parameters among species (Turchin & Taylor, 1992; Clutton-Brock *et al.*, 1997), but relatively few have examined spatial differences in exploited populations of a single species (Trippel, 1995), or populations in distinct habitat types (Leips & Travis, 1999). This study examines population dynamics of a fish species at different locations where recreational fishing pressure occurs in all locations.

Although over the last few decades, recreational fisheries has grown in coastal waters all over the world (Radomski et al., 2001; Post et al., 2002), it is still regulated without specific management plans (Pereira & Hansen, 2003). Even if a recreational fisheries management plan exists it does not usually consider temporal and spatial variability in population structure. Almost all fisheries management is based on assumption that populations of a fish species are uniform at least in the regional scale. Such management, together with a common view on self-sustaining of recreationally fished stocks or underestimated impact of recreational fishing, may fail to prevent long-term effects of recreational fishing and can end to an invisible collapse (Post et al., 2002; Radomski, 2003). Responses of different populations to exogenous factors (e.g. fishing pressure, patterns of fish movement, and environmental conditions) and their resilience to such factors is now a concern of fisheries managers, but poorly documented. Quantifying the nature and magnitude of differences in life history parameters of sand flathead, Platycephalus bassensis, as an example of a fish species that is under recreational fishing pressure (Kailola et al., 1993; Lyle & Campbell, 1999), allows potential mechanisms of plasticity in population to be identified. This study will quantify variability in demographic parameters and reproductive potential among sub-populations, and therefore determine the condition of each population. Such information is required to progress

spatial and temporal management of the recreational fishery for this species and will assist the application of these approaches to other species.

1.2. GENERAL OBJECTIVES

The general aim of this study was to examine spatial and temporal variation in life history characteristics of the sand flathead, *Platycephalus bassensis*. This was achieved through intensive field sampling and an *in vitro* experiment with particular emphasis on identifying the spatial and temporal variability in growth, reproduction, and condition of adult population.

1.3. CHAPTER SCOPES

This thesis consists of four data chapters; each one comprising a stand-alone manuscript for publication, therefore there may be areas in the text that are slightly repetitive.

Chapter 2: Spatial and temporal variation in population dynamics of sand flathead, *Platycephalus bassensis*.

Through two years of sampling this chapter's primary aim was to quantify spatial differences in the population structure of sand flathead. Size/age composition, patterns and rates of growth and mortality rates were quantified for each population. The growth rate in the first year of life was also assessed using the mean radius of the otolith first increment. A snapshot of monthly changes in water temperature and salinity was used as an index for environmental conditions in each location.

Chapter 3: Reproductive biology of sand flathead, Platycephalus bassensis.

Histological analysis of ovary and testis was used to quantify reproductive characteristics of sand flathead. With the combination of acquired information from field sampling and results from an *in vitro* experiment this study aimed to investigate the dynamics of spawning of sand flathead and differences in reproductive strategy. Lunar and diel spawning periodicity and spawning frequency were determined based on the presence of postovulatory follicles in the ovary. Additionally, the presence and extent of atresia in the ovary was used to quantify the proportion of spawning in different length classes during the spawning period.

Chapter 4: Spatial and temporal variability in reproductive ecology of sand flathead, *Platycephalus bassensis*.

Based on the reproductive biology of sand flathead, this chapter describes spatial and temporal differences in reproductive life history characteristics. This study highlighted the variability in gonad weight and its correlation to body size that was considered a determinant of the reproductive output of each population. Size and age at maturity, as one of the most essential components for understanding of life history strategy, was also estimated for each population.

Chapter 5: Spatial variation in condition and patterns of repro-somatic investment in sand flathead, *Platycephalus bassensis*.

To understand the process and patterns of resource allocation between reproduction and other competing needs such as maintenance and growth, somatic, reproductive, and liver conditions were assessed for mature and immature individuals separately. For mature fish, condition was examined in the context of

reproductive state; pre-spawning, spawning, and post-spawning. Proximal analysis was also carried out for further investigation on process of energy partitioning. Lipid and water contents of liver and muscle water content was measured for mature and immature individuals separately.

CHAPTER TWO

SPATIAL AND TEMPORAL VARIATION IN AGE, GROWTH, AND MORTALITY OF SAND FLATHEAD, *PLATYCEPHALUS BASSENSIS*.

Spatial and temporal variation in age, growth, and mortality of sand flathead, *Platycephalus bassensis*.

2.1. INTRODUCTION

Estimates of demographic parameters, such as age and size structure, growth rates, longevity, and mortality, are essential for understanding the population dynamics of a species and the extent to which these vary due to exploitation and geographic location. The magnitude of spatial and temporal differences in population parameters may have important implications for fisheries management strategies based on population responses to both environmental conditions and fishing mortality impact. Generally, it is difficult to determine the effect of fishing and other causative factors on demographic variables, especially when combined with spatial variations. However, this study which quantifies the population dynamics of sand flathead will provide information about the processes responsible for the variability in demographic parameters. It is important to quantify demographic parameters of populations under (recreational) exploitation over a range of spatial and temporal scales, to determine the scales at which the parameters vary the most in order to highlight the appropriate scales for assessment and management purposes.

A combination of fishing pressure, movement patterns of fish, and environmental conditions can often influence demographic parameters such as: growth rates, mean size/age, longevity, and mortality rates (Rochet, 1998; Choat *et al.*, 2003). The growth of sand flathead, like other ectotherms, would be adjusted by exogenous factors, e.g. temperature, food, and salinity, imposed by the environment (Donald *et al.*, 1980; Wootton, 1998). Behavioural process such as migration or movement of fish between areas may also drive changes in population structure (Jennings &

Kaiser, 1998). Fishing, on the other hand, may influence growth trajectory of a fish species (Beverton et al., 1984). Such influence may result from density-dependent processes. Growth rates of fish may decrease when densities increase due to competition for resources (Gust et al., 2002). Nevertheless, growth during the juvenile phase is unlikely to be influenced by (recreational) fishing and therefore growth variability during this phase may help understanding of variability in the phase at which fish recruit to the adult fishery (Van der Veer et al., 1994). For some fish species, it has been proven that growth during the first year of life influences subsequent growth (Brophy & Danilowicz, 2003). Final maximum and mean sizes and ages will be normally greater for populations that experienced higher growth rate as juvenile (Wydoski & Wydoski, 2002). In contrast, removal of individuals through fishing may reduce the mean and maximum sizes of the population (Ricker, 1981; Halpern & Warner, 2002). As size is normally related to age, fishing would also reduce maximum and mean ages in target species (Choat et al., 2003). In general, there are fewer larger and older individuals in a population than smaller and younger ones due to natural and fishing mortality. However, intensive fishing may be responsible for increased mortality rates (Jennings et al., 2001). Moreover, climatic phenomena like El Nino have been accounted for specific age structure of some fish populations by means of episodic recruitment (Meekan, 2001).

Sand flathead, *Platycephalus bassensis*, is one of the most widespread and abundant of the 13 Platycephalid species found in the estuarine, coastal and continental shelf waters of temperate Australia (Keenan, 1991; Gomon, 1994). Sand flathead are present from the central coast of New South Wales, throughout southern Australia (including Tasmania), as far west as Lancelin in Western Australia (Kailola *et al.*, 1993). While the species is recreationally and commercially important, the

recreational catch in Port Philip Bay, Victoria, is ca. 240 tonnes year⁻¹ (Koopman et al., 2004), which is about 10 times greater than the commercial fishery (MacDonald & Hall, 1987). In Tasmania, catches of sand flathead represent over 60% of the total recreational catch (Kailola et al., 1993; Lyle & Campbell, 1999). Therefore, sand flathead is an example of a species that is under recreational fishing pressure and for which information is required on the spatial and temporal variation in life history characteristics to assist the development of management controls. Recreational fishing of sand flathead in Tasmania is currently controlled through daily bag limits and minimum size limits. Such management regulations assume that the demography of sand flathead as a target species does not vary significantly around the state and all sand flathead populations represent a single, uniform stock. However, because of fishing effects, fish movement, and different environmental conditions demography of sand flathead may vary from one region or area to another.

Previous studies of sand flathead population parameters in Tasmania has largely been undertaken in the cooler waters in the south of the State (Jordan, 2001). Comparison of sand flathead population dynamics between Tasmania (Jordan, 2001) and Port Philip Bay in Victoria, Australia (Brown, 1978; Koopman *et al.*, 2004) reveal differences in demographic parameters between the two locations, suggesting that exogenous factors and locality may be important in determining demographic responses. Therefore, a focus on populations in northern and eastern Tasmania is likely to reveal demographic variability. With regard to the spatial scale of this study, one estuarine site in north Tasmania and two embayment sites in north-east and east coasts of Tasmania that vary in size, *P. bassensis* may experience a wide range of habitat and fishing pressure. Hence, populations of *P. bassensis* would be

expected to reflect these different conditions in variability in demographic parameters. As all selected locations are subject to recreational fishing, variations in demographic parameters are assumed to be a function of the combined influence of fishing activity, movement patterns of fish, and environment.

This study examined the spatial and temporal variability in sand flathead demography in order to understand more about population responses to causative mechanism(s). Sampling of recreationally fished sand flathead populations over two years in three locations in northern and eastern Tasmania aimed to examine interpopulation variation of life-history characteristics.

2.2. MATERIALS AND METHODS

2.2.1. Study sites and sampling

Fish were sampled from three locations (Tamar River, Georges Bay, and Coles Bay) around the north, north-eastern, and east coasts of Tasmania, Australia (Fig 2.1). Georges Bay (GB) is an estuarine embayment in the northeast, linked to the Tasman Sea by a narrow entrance. Coles Bay (CB) on the east coast is a marine dominated embayment site, linked to the Tasman Sea through Great Oyster Bay. The Tamar River (TR) is an estuary situated on the north coast and linked to Bass Strait, with all sampling occurring in the lower reaches of the river.



Figure 2.1. Map showing sampling locations for sand flathead.

Platycephalus bassensis individuals were collected at all three locations during two periods of sampling, 2001/02 and 2002/03, using hook and line (Table 2.1).

Hook and line method is a less size-selective collection method compared to demersal trawls and gill nets, which typically under represents small fish (King, 1995), and is also the dominant recreational fishing method used in Tasmania. All fish were caught in inshore shallow habitats in water depths of 5-25 m. To obtain a representative sample of the *P. bassensis* population at each location, fishing was carried out at 4-6 sites selected haphazardly depending on weather conditions and accessibility of fish at each location. All fish were sexed, measured to the nearest millimetre total length, and weighed to the nearest gram. Sagittal otoliths were removed and stored dry.

Salinity and water temperature near the bottom were recorded at the time of sampling between April 2002 and May 2003.

Location	Date of sampling	Surface area (km ²)	No. of occasions	Total no. caught	Catch per hook hour
Coles Bay	March 2001-February 2002 & October 2002- May 2003	· 362	9	552	0.53
Georges Bay	May 2001-February 2002 & September 2002- January 2003	18	7	323	0.46
Tamar River	March 2001-January 2002 & September 2002	54	9	368	0.50

Table 2.1. Collection details of *Platycephalus bassensis* at each location.

2.2.2. Age determination

Age estimates were determined by counting annual rings in the transverse plane of sagittal otoliths. Otoliths were prepared using the burn and crack technique

(Williams & Bedford, 1974). Each otolith was heated over a flame until brown, and then broken in half with a scalpel across the short lateral axis, as close to the nucleus as possible. The surface of a transverse section of the prepared otoliths was covered with a drop of emersion oil on the surface and examined under a dissecting microscope using reflected light.

An increment was considered complete when a translucent zone at the side of a distinct opaque zone was visible across the proximal face of the otolith transverse section. Increments have previously been validated as annuli for this species from transverse sagittal sections for the 1^+ to 8^+ individual cohorts and $9-17^+$ cohorts combined (Jordan, 1998). The inner region adjacent to the primordium revealed an opaque region with no obvious increment structure that was found not to be an annuli (Jordan, 1998). In this study, this opaque zone were characterised by being fainter than outer opaque zones and not being continuous around the distal face of the otolith and was not included in the age estimates.

To assess the precision of ring counts from otoliths prepared using the burn and crack technique, the age of a sub-sample of 100 flathead was estimated by the same reader, from one otolith prepared using the burn and crack method and the second otolith prepared from a thin-section (Campana, 2001). The average percent error (APE) between the ring counts using the two techniques was calculated using the following formulae Beamish & Fournier (1981).

$$APE = \frac{100}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{R} \frac{|Xij - Xj|}{Xj} \right]$$

Where N is the number of fish aged in the sub sample, R is the number of times fish are aged, X_{ij} is the *i*th determination for the *j*th fish, and X_j is the average estimated

age of the *j*th fish. A paired sample T-test was used to determine if there was a difference between the age estimated using the two techniques.

The repeatability of ring counts from otoliths prepared using the burn and crack technique, was determined from counts on two different occasions within 2 months of each other. The first reading was done using a stereomicroscope with reflected light. On the second occasion, images of sagittae were precisely examined to validate the first reading. A video camera (DXC-107P) mounted to a light microscope and integrated with a PC was used to capture images of each transverse otolith section. Image capture software [Vid-Cap 32] and Adobe Premiere 5.1 was used to collect the images. Following image capture, the increments were counted from the otolith images on the screen. If the two age estimates were not exactly the same, then a third reading was done from the image on another occasion to verify which of two previous readings was correct. Approximately 6% otoliths were discarded as unreadable due indistinct annual ring formation. All otoliths were read blind without reference to fish size.

2.2.3. Analysis

Chi-square test of independence was used to examine differences in length and age frequency distributions between years and locations. Data from four seasons were pooled for length and age frequency distribution comparison among locations. Standardized residuals, under normal distribution, were used to determine where observed frequencies differed from expected frequencies. Observed frequencies were calculated based on the null hypothesis that the size and age frequency distributions were independent of year and location. As sampling time differ between years, comparisons of the length and age frequency distributions between years restricted to the months where there was overlap between years.

Growth curves were fitted to size-at-age data for each location and for two sampling years separately and combined (in cases of no difference). Linear, logarithmic, power, Von Bertalanffy, and exponential equations were tested to acquire the best fit of size-at-age data for each location and for two sampling years. Linear and Von Bertalanffy growth relationships were selected to describe the sizeat-age relationships, based on a visual examination of the residuals and the coefficient of determination (r^2). The highest value of r^2 with the smallest residuals was considered for determining the best fitting curve. Comparison of linear growth descriptions were made using ANCOVA, and a comparison of Von Bertalanffy growth curves was done using an analysis of the residual sum of squares (ARSS) (Chen *et al.*, 1992). To compare growth rates of fish < 5 years old, data were transformed (logarithmic) to linearise the data.

Total mortality rates (Z) were estimated using age-based catch curves (Beverton & Holt, 1993). This method assumes that annual recruitment rates remain consistent at each location and is obtained from a plot of the natural logarithm of the number of fish caught from each age class against their corresponding age. The slope of the descending regression line estimates the mortality rate. Year classes to the left of the modal age were excluded from the analysis as the sampling procedure may have under-sampled smaller fishes (Ricker, 1957). Mortality rates of the Tamar River population could not be estimated because of the absence of fish older than 4 years in the population. To evaluate the effect of any weighting of the rarer, older year classes on the regression, comparison of Coles Bay regressions were done both with

the complete data set, and without the large year classes. ANCOVA was used to compare the slope of the regression lines according to the procedure of Zar (1999).

2.3. RESULTS

2.3.1. Environmental conditions

Differences of monthly water temperature in benthos were not considerable among the 3 locations (Fig 2.2). Water temperature in all three locations showed a distinct seasonal cycle, with temperatures highest between December and March and lowest in August-September. In contrast, mean salinity along the Tamar estuary varied markedly across the months and was consistently lower than the other two locations.



Figure 2.2. The average of monthly water temperature and salinity near the benthos for each location.

2.3.2. Precision of age estimates and otolith examination

Clear and distinctive annuli rings were seen using reflected light in sagittal otolioths prepared by the burn-crack technique. Counts of rings in otoliths prepared using the two techniques were very similar; in 82% of the fish where the otoliths were prepared using the two techniques, the number of rings counted was the same (Fig 2.3). The average percent error (APE) was very low (0.79%), suggesting no bias between the thin section and burn and crack techniques of preparation. An APE of less than 5% is indicative of consistent interpretation of ages (Morison *et al.*, 1998). Therefore, the burn-crack method was used to prepare otoliths in this study as this is faster. There was no significant difference between counts taken on two occasions (t=-0.39, df 198, P=0.69). Therefore age estimates from the burn and crack prepared otoliths were repeatable.



Figure 2.3. The frequency distribution of the differences in the age of P. bassensis estimated using thin-section and burn and crack techniques, n=100.
2.3.3. Size and age composition

The proportion of individuals in each length class was dependent on the location $(\chi^2=586.5, df 18, P<0.001)$. A greater proportion of fish in the larger size classes (28-52 cm) were present in Coles Bay, compared with two other locations (Fig 2.4). On the other hand, the proportion of fish in size classes between 19-27 cm was less than the expected proportion at Coles Bay. The most abundant size class at Georges Bay was individuals with 22-27 cm total length. Similarly, around 70% of the Tamar River population was made up of fish with sizes smaller than 24 cm, creating peaks at 19-24 cm total length. Individuals ≥ 31 cm were less frequent than expected in the Tamar River and Georges Bay. Only 3% of all captured fish in the Tamar River and Georges Bay were larger than 30 cm, which is the current legal size for sand flathead in Tasmania. In contrast, 55% of caught fish from Coles Bay were > 30 cm.

The length frequency distribution was the same in the two years of sampling in Coles Bay (χ^2 =7.7, df 7, P=0.359). In contrast, Georges Bay and the Tamar River had significant differences in size composition between the years sampled (GB χ^2 =10.1, df 4, P=0.038; TR χ^2 =28.9, df 5, P<0.001). In the Tamar River, the proportion of 19-21 cm fish was smaller and greater than expected proportions in 2001/02 and 2002/03, respectively (Fig 2.5). In Georges Bay, the frequency of the 19-21 cm size class was significantly higher and lower than the expected frequency in 2001/02 and 2002/03 respectively. Size composition was almost identical between sexes in the Tamar River (χ^2 =3.7, df 8, P=0.879) and Georges Bay (χ^2 =11.7, df 6, P=0.069). However, Coles Bay males with total length 37-39 cm were found at a lower frequency than expected (χ^2 =26.5, df 8, P<0.001).



Figure 2.4. Length-frequency distribution of *P. bassensis* in three locations. Arrows indicate the direction in which the observed frequencies differed from expected frequencies, generated under the assumption that size class was independent of location.





Age frequency distribution differed among the locations (χ^2 =783.9, df 14, P<0.001). This was largely due to the higher proportion of individuals \geq 6 years at Coles Bay, in comparison to the other two locations (Fig 2.6). The most abundant year class in Georges Bay was 4-5 year old individuals, while individuals older than seven years were rarely seen in Georges Bay. The number of individuals younger than three years was less than expected at both Georges Bay and Coles Bay. Furthermore, 60% of sand flathead caught in Georges Bay was <5 years, while around 25% of Coles Bay's catch were < 4 years. In the Tamar River more than 50% of caught fish were two years old. Interestingly, despite using the same fishing gear for all three locations, fish > 4 years old were not caught in the Tamar River.

There was also evidence of differences in the age frequency distributions between the two years of sampling for each location (TR χ^2 =13.7, df 3, P=0.003; GB χ^2 =31.3, df 7, P<0.001; CB χ^2 =18.3, df 7, P=0.010). Nevertheless these differences were limited to particular age classes in each location (Fig 2.7). In Georges Bay, the proportion of 6-year-old fish was smaller and greater than expected proportions in 2001/02 and 2002/03, respectively. In Coles Bay, 8⁺-year-old individuals showed a greater proportion in 2002/03 compared to 2001/02. In the Tamar River, only, the proportion of 2-year-old individuals was less than expected in 2001/02, compared to 2002/03. Males and females had similar age-frequency distributions in Georges Bay (χ^2 =5.4, df 8, P=0.714) and the Tamar River (χ^2 =0.4, df 3, P=0.932), but not in Coles Bay (χ^2 =33.1, df 10, P<0.001). The Coles Bay population had a higher proportion of males in the 8 and 11-20 year classes, while females showed a lower proportion in these two age classes.



Figure 2.6. Age frequency distributions of *P. bassensis* at three locations. Arrows indicate the direction in which the observed frequencies differed from expected frequencies, generated under the assumption that age class was independent of location.



Figure 2.7. Age frequency distribution of P. bassensis at each location for 2001/02 and 2002/03 sampling years. Arrows indicate the direction in which the observed frequencies differed from expected frequencies generated, under the assumption that age class was independent of year of sampling.

The average age of sand flathead among the locations were significantly different (F=259.47, df 2, 1130, P<0.001). The average age of Coles Bay individuals was more than twice that of Tamar River individuals (Fig 2.8a). The Georges Bay population showed an average age of 49% older and 17% younger than the Tamar River and Coles Bay populations, respectively. Sand flathead displayed the different pattern of differences in average length than average age among populations. There was no significant difference (F=351.48, df 2, 1149, P<0.001) in average length between the Georges Bay and Tamar River populations (Fig 2.8b), but Coles Bay individuals were 1.3 times bigger than at the other two locations.



Figure 2.8. The mean age (a) and length (b) of *Platycephalus bassensis* for each location. Means with different letters above the bars represent groups that are statistically different. Values above letters represent the sample size.

2.3.4. Growth

Individuals in the populations at the Tamar River and Georges Bay did not reach an asymptotic size, because all individuals were less than 5 years old in the Tamar River and most were less than 8 years old in Georges Bay (Fig 2.9). The size-at-age relationship was linear for both the Tamar River (F=283, df 1, 2, P<0.005) and Georges Bay (F=275, df 1, 7, P<0.001). No significant interaction of location*sex*year of sampling was detected in size-at-age for the Georges Bay or the Tamar River populations (F=0.24, df 1, 669, P=0.622). However, there was a significant location*year interaction in size-at-age for these two populations (F=6.91, df 1, 669, P=0.009). Therefore, a separate growth curve for each year was fitted for each of these two locations (Fig 2.9). Tamar River individuals were found to be growing 2.1 and 3.2 times faster than Georges Bay individuals in 2001/02 and 2002/03, respectively. Slope of size-age regression lines were the same for the two years in Georges Bay, while growth of Tamar River individuals in 2001/02 was 1.5 times slower than in 2002/03.



Figure 2.9. The relationship between age and total length of *Platycephalus* bassensis in Georges Bay and the Tamar River at each sampling year. Values in parentheses are standard errors for the slope and intercept.

Playcephalus bassensis showed an asymptotic growth pattern in Coles Bay; therefore Von Bertalanffy growth function was fitted to the individual length-age data. Generating a single growth curve for sexes and years together provided a poorer fit of the data than a growth curve for each group separately (F=9.43, df 9, 446, P<0.001). Males and females had similar growth rates in 2001/02 (F=0.86, df 3, 191, P=0.462). Variation in growth among individuals in 2002/03 was a function of gender (F=13.28, df 3, 255, P<0.001) (Fig 2.10). Furthermore, Coles Bay males showed different growth rate between years (F=23.73, df 3, 186, P<0.001), which was not observed in females (F=0.36, df 3, 260, P=0.781). The plots of 95% confidence limits (Fig 2.11) show that Coles Bay females, compared to males, approached higher asymptotic length, with slower rate in the second year. There were overlapping values of K and L infinity for both sexes captured in 2001/02 and females captured in two different years, indicated similar growth trajectories. Males had a higher K value in 2002/03 than in 2001/02, which indicates that they converge on their asymptotic lengths more rapidly (but not necessarily grow more rapidly) than in 2001/02. However, the mean asymptotic length was higher in 2001/02, compared to 2002/03.

Size-at-age plots also provided estimates of the maximum size achieved in each population (Figs 2.9 & 10). The maximum obtained size, all of which belonged to females, for Coles Bay (TL=51.5 cm) was greater than for the Tamar River (TL=36.8 cm) and Georges Bay (TL=35 cm). The largest recorded size for a Coles Bay male (31.2 cm TL) was around 20 cm smaller than for females. In Georges Bay and the Tamar River, the maximum size recorded for males was 30 and 31.2 cm TL respectively.



Figure 2.10. Von Bertalanffy growth curves for Coles Bay *Platycephalus bassensis* for each year of sampling and each sex. See Table 2.2 for estimates parameters for the four growth curves.



Figure 2.11. Approximate 95% confidence ellipses of the parameter estimates K (growth coefficient) and L infinity (mean asymptotic total length) of Von Bertalanffy growth curve for sand flathead caught from Coles Bay, following (Kimura, 1980).

Table 2.2.	Von Bertalanffy gro	wth parameters for P.	bassensis for each	h sampling
year and each s	sex from Coles Bay.	Values in parentheses	are standard error	s.

	n	$L_{\infty}(cm)$	K (y ⁻¹)	t ₀ (y)	r ²
2001/02		1. 7. 1			
Female	108	39.01 (3.39)	0.25 (0.08)	-1.57 (0.76)	0.66
Male	89	37.43 (1.47)	0.21 (0.04)	-1.76 (0.54)	0.82
<u>2002/03</u>					
Female	158	45.35 (3.41)	0.15 (0.04)	-2.53 (0.88)	0.64
Male	103	34.40 (0.61)	0.39 (0.05)	-0.51 (0.39)	0.72

Given the very different age range of fish from the three locations, it was not possible to make comparisons of growth rates across the total range of ages among the locations. Therefore, growth rates were compared for fish < 5 years old. For these age classes, an interaction between location*year*sex was not found in size at age (F=1.62, df 2, 761, P=0.199). Variation in size-at-age was found to be a function

of location (F=11.08, df 2, 761, P<0.001). Individuals from Coles Bay and Tamar River grew 2.4 and 1.8 times faster respectively than Georges Bay individuals (Table 2.3), while there was no difference in growth rates between Coles Bay and the Tamar River (Fig 2.12a). A divergence in growth rates between Georges Bay and the other locations was evident in individuals > 2 years old (Fig 2.12b).

Table 2.3.Summery of age-length linear regression, associated with statistics, forP. bassensis < 5 years old.</td>Asymmetric CLs resulted from back transformation oflogarithmic values.

Location	n	Slope	95%	C.L.	r ²	df	F	Р
			Lower	Upper				
Georges Bay	-188	0.17	0.12	0.24	0.15	187	34.19	0.000
Coles Bay	219	0.41	0.35	0.46	0.48	218	214.61	0.000
Tamar River	355	0.35	0.31	0.38	0.42	354	263.34	0.000



Figure 2.12. (a) Comparison of slope of linear age-length relationship (+/- 95% Confidence Limit) and, (b) linear fit of this relationship among locations for P. bassensis < 5 years old. Coles Bay (solid line), Tamar River (dotted line), and Georges Bay (broken line). Asymmetric CLs resulted from back transformation of logarithmic values.

2.3.5. Longevity and mortality

Individuals from Coles Bay attained much greater maximum age than those in other locations (Figs 2.9 & 10). The maximum recorded life span for *P. bassensis* caught in Coles Bay was 20 years. Coles Bay males had higher maximum age compared with females in both year of sampling. For Tamar River and Georges Bay the greatest age recorded was 4 and 11 years, respectively. Mortality rates were

estimated from catch curves for populations sampled in Coles Bay and Georges Bay (Fig 2.13). Mortality rates were 2.1 times greater in the Georges Bay population compared with Coles Bay (F=7.26, df 1, 22, P=0.015). Additionally, removal of large year classes (17-20 year) had almost no effect on the outcome of Coles Bay's catch curve analysis (b=-0.28, a=5.25, r^2 =0.85).



Figure 2.13. Age-based catch curve and estimates of *P. bassensis* mortality in the two populations. Mortality estimates per each year are; Coles Bay, 0.28 and Georges Bay, 0.59. Values in parentheses are standard errors for the slope and intercept.

2.4. DISCUSSION

There were striking differences in the demography of *P. bassensis* populations caught from different geographical regions around Tasmania. With the exception of some similarities in growth rate of the first four years of sand flathead between the Tamar River and Coles Bay, and size structure of Georges Bay and the Tamar River populations, all estimated parameters were substantially different among the locations (Table 2.4). Coles Bay and Georges Bay populations consistently showed the greatest difference for each demographic parameter, despite their relative proximity as embayment sites.

Table 2.4. Estimates of numbers of demographic parameters of Platycephalusbassensis from the 3 locations.

	Max.	Max.	N	Mean size-at-age (cm)			Mortality	
Location	length (cm TL)	age (years)	Age 1	Age 2	Age 3	Age 4	rate	
Coles Bay	51.5	20	17.6	21.8	25.7	29.2	0.28	
Georges Bay	. 35	11	17.8	21.1	21.6	23.2	0.59	
Tamar River	36.8	4	18.9	22.2	25.8	28.2	-	

Age and size structures of *P. bassensis* showed the possible impacts of habitat shift and fishing pressure on populations. The absence of individuals > 4 years old in the Tamar River is either due to movement of fish out of the River and/or very heavy fishing pressure on individuals as they enter the legal size class. With reference to the average age of Tamar River individuals with legal size (30 cm), which is around 3.3 years, it is possible that individuals \geq 4 years suffer very high mortality rates as a function of recreational fishers. However, although a dramatic decline in the abundance of older fish, due to very heavy commercial fishing, is reported (Hutchings & Myers, 1994; Morison & Rowling, 2001), removal of all sand flathead

stock in this age group only by recreational fishing is unlikely. Number of samples (n=368) and duration of sampling (2 years) in the Tamar River ensured that the sand flathead collected, represented the actual population of this fish in the Tamar River. Additionally, broad range of age classes (1-20 years) acquired from different locations in the present study, showed the capability of hook and line method for flathead fishing. Unpublished data collected in 1995-97 in the Tamar River (Jordan, Marine Research Laboratories, University of Tasmania), shows similar age composition for sand flathead (all fish \leq 5 years old) using beam trawl and gill-net.

There is almost no information on the movement of *P. bassensis*. However, as sand flathead 3-6 years old are in a transitional stage, from immaturity to maturity (Jordan, 1998), the absence of older fish in the Tamar estuary may be related to habitat changes from feeding/nursery to the spawning ground. Such movements are seen in marine species like striped mullet, *Mugil cephalus*, (Haedrich, 1983) and flatfishes (Gibson, 1997). Low abundance of sand flathead larvae in the Tamar estuary (Lara & Neira, 2003), suggests that the Tamar estuary is not an important spawning ground and most probably they enter to this estuary as juveniles. This is consistent with the age structure of sand flathead in the Tamar estuary in both sampling years. Therefore, it is more likely that the age structure of *P. bassensis* in the Tamar estuary resulted from movement of older, mature fish out of the estuary. Relationship between demographic variables and reproduction is explored in more detail in Chapter 4.

Lack of older and larger individuals is clearly seen in the Georges Bay population, where individuals > 7 years and > 30 cm are rarely caught. In contrast, in Coles Bay, the presence of larger and older individuals suggests that loss of these individuals through movement and/or fishing mortality is not as great. Previous studies

demonstrated some evidence of seasonal movements of sand flathead between inshore and offshore in east and south-eastern Tasmania (Jordan, 1998). As our sampling was conducted throughout all seasons, the size and age structure at each location cannot be result of seasonal movement. However, since Coles Bay is linked through a relatively open and wide passage to the continental shelf, it is likely that fish move more openly both in and out of the shelf in this area. In contrast, Georges Bay is a relatively small bay linked to the Tasman Sea by a narrow passage. Given the same abundance of sand flathead and the same number of recreational fishers per square kilometre in these two locations, the effect of fishing may even be greater in Georges Bay, compared to Coles Bay. Lack of older and larger individuals in Georges Bay, may occur as a combination of less movement of fish between inshore and offshore and recreational fishing pressure in inshore region. This is consistent with the low proportion of legally catchable size fish (>30 cm) in Georges Bay. In Coles Bay, the absence of a clear mode in age frequency distribution and its relative consistency in 2001/02 and 2002/03 may have occurred due to the removal of 3-5 years old individuals. Alternatively, this may reflect the occurrence of very weak recruitment of year-classes in Coles Bay during 1996-1998. This is unlikely as large fluctuations in recruitment are normally associated with climatic changes, like El Nino (Cushing, 1990). An El Nino-Southern Oscillation (ENSO) was evident across Australia in 1997/98 (Kane, 1999), however, relatively high proportion of 4-5 years old individuals in Georges Bay in both 2001/02 and 2002/03 is strong evidence that ENSO has little influence on sand flathead recruitment. This is also supported by the fact that low year-class strength was not evident in all regions which would be expected if large-scale oceanic processes such as ENSO was important. The low proportion of six year old individuals in Georges Bay in 2001/02 compared to

2002/03 may have resulted from weak recruitment back to the hatching year. These, however, are combined with fishing impact on size and age composition, as Georges Bay six year old individuals enter the fishers.

The maximum and mean age and size achieved in Coles Bay was significantly higher than other two locations. Differences in maximum and mean age or size within species are considerable for those populations distributed across a significant latitudinal gradient, mostly due to the influence of temperature on fish growth (Atkinson & Sibly, 1997). However, 2° latitudinal differences along the sampling locations in the present study could not create significant temperature differences among locations, especially when there is a mixture of cold sub Antarctic waters with a warm East Australian Current on the eastern shelf of Tasmania (Prince, 2001). Such a huge mixture of water mass, apart from interannual and seasonal variations, has an absolute influence on homogeneity of environmental conditions experienced by P. bassensis populations on the eastern coast of Tasmania, including Coles Bay and Georges Bay. This is consistent with our temperature and salinity data, indicating no considerable differences among the locations. This indicates that the observed differences in maximum and mean size or age among the locations were not simply, or only, related to the environmental differences between the locations. Decreases in maximum age and size, and consequently reductions in mean age and size of target fishes, are one of the most widely reported and quickly observed changes when fishing effort increases (Russ, 1991). There is no specific information regarding the scale of fishing pressure on sand flathead populations around Tasmania. However, differences in maximum and mean age or size highlighted the possible impacts of fishing on each population and/or movement of specific size/age of fish out of the bay.

Given similar environmental conditions and equal fishing pressure, populations of a fish species should grow at similar pattern throughout life (Beverton, 1992). Changes in exogenous factors will result in changes in growth of individuals in the population (Donald *et al.*, 1980). Growth rate of individuals over the first four years of the life of *P. bassensis*, highlighted differences in growth rates among the three populations. Individuals had similar growth rates during their first two years in all three locations. A divergence in growth rate appeared afterwards, with lower growth rates for Georges Bay in comparison to the other two locations. This revealed that conditions for growth, at least for younger fish, are the same in all three locations.

Estuarine habitats are considered to be 'nutrient traps' that support high primary, and subsequently secondary, productivity (Nixon *et al.*, 1986). They promote the biomass of fish, through better growth rates and higher recruitment (Houde & Rutherford, 1993). Although there is no specific information on the productivity of the Tamar estuary or other two locations, the growth rate of *P. bassensis* was comparable between the Tamar River and Coles Bay. Fish populations with lowdensity are characterised by increased growth rate, due to lack of competition for food (Beentjes & Jellyman, 2003; Pierce *et al.*, 2003). While we did not estimate the absolute abundance of *P. bassensis* populations, catch per hook hour can be considered as a proxy of relative abundance of fish populations (Jennings *et al.*, 2001) indicating that the abundance of sand flathead was slightly lower in the Tamer River than Coles Bay. Moreover, absence of older individuals in the Tamar River may be interpreted to the lack of food competition between younger and older individuals, particularly when major dietary components of different size class of *P. bassensis* are similar (Edgar & Shaw, 1995).

A possible source of bias in the estimated growth rates of the Georges Bay population may be due to the removal of faster growing fish entering the fishable component of the population. If it is supposed that caught individuals from Georges Bay are slow-growing individuals and fishermen have already removed fastergrowing individuals, the growth rate in the first year of life in Georges Bay, could be slower than other two locations. This is the case as previous studies show the influence of growth during the first year of life on the subsequent growth of fish (Brophy & Danilowicz, 2003). However, there was no difference in growth rates among locations in the first two years of life. Under these circumstances the observed weak growth rate of the Georges Bay population could be a result of the combination of fishing pressure on fish with different growth rates and movement of older fish out of the bay.

Asymptotic growth pattern for the Coles Bay population mainly derived from the rapid growth of individuals for the first four years of their life and the presence of older individuals. Females attained larger size than males at corresponding ages in Coles Bay. A larger female size appears to be a life history strategy to increase reproductive potential, through increased fecundity in larger fish (Roff, 1984). Thus, this may be the possible explanation for the shorter lifespan for females in comparison to males in Coles Bay. Observed variations in growth trajectory of males between years is harder to explain and can be attributed to the broader age classes in 2002/03.

The age-based catch curves revealed significantly higher total mortality for Georges Bay compared with Coles Bay, as a result of very few individuals >7 years in Georges Bay. However, mortality results should be treated with caution, because of the potential for variable recruitment in different years (Pauly, 1984) and

movement of, mostly older, fish away from an area. Theoretical and experimental studies suggest that in fish populations where older or adult individuals undergo high mortality, there is strong selection for very rapid asymptotic size and maturation at young ages (Bertschy & Fox, 1999; Meekan *et al.*, 2001). However, Georges Bay individuals did not reach the asymptotic size. Furthermore, if fishing led to a low-density population in Georges Bay, remaining individuals would be characterized by increased growth rate. Georges Bay individuals did not show such an increase in growth rate. Therefore, the existing demography in Georges Bay was not simply due to high total mortality of older fish and other factors like higher emigration rates of older/larger, fully mature fish may be involved.

Our observations of the demography of P. bassensis, demonstrated the extent of spatial and temporal variability in population dynamic of a species. Two years of sampling in a significant geographical region provided a comprehensive picture of demography of P. bassensis and somewhat hypothesized mechanisms for variability in demographic parameters. However, continued monitoring of the populations may be required, to determine the stability of the observed patterns. In addition, comparative stock structure studies of examined locations with an untouched or reserve area are required, to understand more effectively the causative mechanism(s) of demographic patterns. Spatial and temporal variations in demographic parameters indicate that there is significant structuring, within what has previously been considered, and still is being considered, as a single stock of *P. bassensis*. This shows that even where the fishing effort as a whole is managed at a presumed to be sustainable level, there is higher potential of vulnerability in less productive populations to be fished or dangerously overfished. Furthermore, as fish use different habitats or locations for different purposes, like P. bassensis usage of the

Tamar estuary as nursery/feeding ground, further protection for some locations is warranted. This study highlights a more general need for the use of multiscale sampling and analysis of fish populations, for better understanding of the magnitude and mechanisms of processes affecting demographic parameters. This rationalizes the necessity of temporal and spatial management, even for recreational fisheries, based on population responses.

CHAPTER THREE

Reproductive biology of sand flathead, *Platycephalus*

BASSENSIS.

Reproductive biology of sand flathead, *Platycephalus bassensis*.

3.1. INTRODUCTION

Reproduction is an essential component of the life history of fish and survival of any species or population of a species depends on successful reproduction. Fish can be defined as either single spawners where all oocytes develop synchronously and released at once, or multiple spawners where a number of oocyte batches at different times during the spawning season (Wallace et al., 1987; Pankhurst, 1998). The study of reproductive biology and reproduction effects on population dynamics is not as complex for single spawners as multiple spawners. Thus, aspects of reproductive biology required in the study of a multiple spawning species include batch fecundity and spawning frequency (DeVlaming, 1983). The multiple spawning pattern of these fishes affect their life history in a number of ways. Firstly, recruitment of cohorts into the population during the typically extended spawning season, in conjunction with the plasticity in fish growth, ensures a large range of size-at-age. This variation will affect the population reproductive parameters when fish mature, with individuals of fish possibly maturing at different years and may have different reproductive investment strategy according to their sizes (Luo & Musick, 1991). Secondly, it affects the age at which fish reach a minimum size limit, which may cause differential adult survivorship (Law & Grey, 1989). All these factors affect the size and age of the breeding population and potentially drive the evolution of the population.

Sand flathead spawn in Tasmania for up to six months, between October and March (Jordan, 2001), suggesting that sand flathead is a serial spawner. However, a protracted spawning season does not always indicate serial spawning, as many fish

have extended spawning seasons with different individuals breeding at different times (Bye, 1984). To determine the actual dynamics of spawning it is essential to observe gonadal development patterns and examine gonad histologically (Hunter & Macewicz, 1985a). For serial spawners, the standing stock of advanced oocytes gives no indication of reproductive potential, because new spawning batches are recruited from unyolked oocytes during the spawning season (DeVlaming, 1983). As a consequence of such continuous recruitment of oocytes throughout the season, the number of spawning events within a season cannot be inferred from modes in the oocyte size frequency distribution (Hunter & Goldberg, 1980). Thus, age estimation of postovulatory follicle (POF) is essential for determining spawning frequency and time of spawning (DeMartini & Fountain, 1981; Hunter & Macewicz, 1985a), as POF does not fragment and pass out of the ovary with the oocyte, but retains its integrity.

One of the other complexities with protracted spawning is that not all the standing stocks of oocytes are spawned throughout the spawning season and some oocytes undergo resorption, a process known as atresia (Hunter & Goldberg, 1980). In many fish species, the incidence of atresia varies during and close to the end of the spawning season (Kurita *et al.*, 2003). Incidence of atresia, apart from its influences on oocyte losses and reduction in reproductive output (Hunter *et al.*, 1992), it is a marker for the cessation of spawning and can be used to separate immature females from those in post-spawning condition (Marshall *et al.*, 1993; DeMartini *et al.*, 2000). A general knowledge of atresia is also required to age POF accurately, without confusion with some stages of atresia.

Fish species exhibit considerable diversity in temporal patterns of reproduction at a range of scales; seasonal, lunar, and diel (Johannes, 1978). Duration and initiation

of spawning season may differ among populations of a species (Brown-Peterson et al., 2001). Among species that reproduce repeatedly within a spawning season, some display a lunar, semi-lunar or high frequency (i.e. daily) periodicity in reproduction (Taylor & DiMichele, 1980; Scott et al., 1993), whereas no such patterns are found in others (Robertson et al., 1990). Most hypotheses concerning the adaptive nature of lunar cycles consider the effects of the tidal regimes or moon light on planktonic eggs or larvae (Robertson et al., 1990). Hypotheses for lunar reproductive cycles include dispersal of planktonic larvae away from predators either due to water current (Robertson, 1983) or photopositive attraction of eggs toward the water's surface because of moon light (Allen, 1972), and reduction in food competition among temporal spacing of cohorts of young larvae (Lambert & Ware, 1984) are addressed as the most probable reasons. Within a daily time scale, spawning often takes place during a restricted time of the day (24 h), mostly towards night, while some marine fish spawn throughout the daylight period (Ferraro, 1980). The diel periodicity in fish spawning may occur to reduce predation of eggs (Robertson, 1991), minimise the cost of parental care (Doherty, 1983), optimise time of hatching (Thresher, 1984), or to minimise the risk of feeding loss due to time spent in reproduction (Conover & Kynard, 1984). In most studies, timing of spawning is determined by monitoring female reproductive activity. However, in a few studies, time of spawning is estimated by observing monthly or daily development of the spermatogenesis process (Pankhurst & Kime, 1991). Timing in reproduction may maximize the reproduction output or recruitment, and therefore has applications for the temporal management of fisheries.

Sand flathead, *Platycephalus bassensis*, is one of the most abundant of the 13 platycephalid species found in coastal regions of the temperate waters of Australia

(Keenan, 1991; Gomon, 1994). Flathead are an important component of recreational and commercial fishery in Tasmania (Lyle & Campbell, 1999) and mainland Australia (Kailola *et al.*, 1993). Although some general information on the reproduction and early life history of sand flathead is available (Jordan, 2001), the reproductive biology of this species for fisheries management is still far from complete. Furthermore, little is still known on reproductive biology of platycephalids as a whole, with only limited information available on *Neoplatycephalus richardsoni* (Fairbridge, 1951; Jordan, 1997), *P. fuscus, P. speculator*, and *P. bassensis* (Brown, 1978), and *P. speculator* (Hyndes *et al.*, 1992).

Selective fishing can have potentially detrimental consequences for the reproductive capacity of fish populations (Coleman et al., 1996). This is because of shifts in size and age distributions of populations, particularly the loss of bigger and older individuals results in the capacity for population growth being limited to smaller, less fecund individuals (Barbieri et al., 1994; Adams et al., 2000). Sand flathead populations from different geographical regions around Tasmania showed variability in demographic parameters, possibly due to movement pattern, fishing effects, and different environmental conditions (Chapter 2). This may cause differentiation in reproductive biology of this species, based on locality. Therefore, knowledge on reproductive biology of sand flathead can help us to understand the mechanisms of spatial and temporal variability in reproduction, which is essential for the implementation and refinement of fisheries management strategies. Thus, the general aim of this chapter is to investigate aspects of reproductive biology of sand flathead. The specific objectives of this chapter are: to determine the dynamics of spawning, evaluate the occurrence of atresia, determine diel and lunar periodicity in spawning and estimate spawning frequency.

3.2. MATERIALS AND METHODS

3.2.1. Field sampling

To determine spatial differences in the patterns of maturation and spawning of *P. bassensis* sampling was undertaken throughout 2001 and 2002 in two locations around Tasmania (Chapter 2); Coles Bay (east coast) and Georges Bay (north east coast). Sand flathead were sampled seasonally from the inshore regions of two locations between March 2001 and February 2002, using hook and line (Table 3.1). To better describe changes early in the spawning season, further intensive sampling was undertaken in Georges Bay within spawning season in the early and late spring 2002 (Table 3.1).

To determine spawning frequency and lunar or diel periodicity in spawning, sampling was undertaken over 24 hours, weekly, and monthly in Coles Bay between October 2002 and May 2003. Fish were sampled in the morning (5:30- 10:00), midday (10:00-15:00), and afternoon (15:00- 21:00) on 2nd, 10th, 17th, and 24th October 2002. Due to difficulties in collecting animals, sampling was done in Spring Bay (55 km south of Coles Bay) and North-West Bay (130 km south of Coles Bay) only, on the 10th and 24th October, respectively. Fish could not be caught between dusk and dawn using either gill-net or hook and line, therefore no night-time samples were obtained. On two occasions, both gill-net and hook and line methods were used to obtain a broad range of reproductively active fish.

Table 3.1. The sampling regime and the exact date and time of *Platycephalus* bassensis collection in Georges Bay (GB), Coles Bay (CB), North-West Bay (NWB), and Spring Bay (SB).

		<u>.</u>		
Year	Location	Sampling regime	Date & Time	Objective(s) of sampling
2001/02	CP	Seconally	May-Jul-Nov-	Pattern of gonad
	GB	Seasonally	Feb	development.
	CD	Casconally	Mar-Jun-Oct-	Pattern of gonad
	CB	Seasonally	Feb	development.
2002/03				Further investigation for
				determination of
			Can Mary Day	spawning time,
	GB	Monthly	Sep-Nov-Dec	spawning frequency,
				and occurrence of
				atresia.
	CB	Weekly & 24 h	2 nd & 3 rd Oct-	
		·	12:00, 17:30, &	
			6:00	
	SB	Weekly & 24 h	10 th & 11 th	
		,	Oct- 13:00,	
			19:00, & 5:30	
	CB	Weekly & 24 h	17 th Oct- 12:00	Determination of diel and lunar spawning
		Wester & OAL	ath a acth	periodicity, spawning
	NWB	weekiy & 24 n	24 & 25	frequency, and
			18.20 + 6.20	occurrence of atresia.
	,		18:50, & 0:50	
	СВ	Monthly	18 th Nov- 9:00	
	CB	Monthly	17 th Dec- 7:30	
	CB	Monthly	17 th Jan- 12:00	
	CB	Monthly	4 th Feb- 16:00	
	· CB	Monthly	6 th Mar- 13:00	
	CB	Monthly	6 th May- 13:30	

* Mid-point of sampling time.

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3.2.2. Laboratory processing and histological analysis

To prevent rapid degeneration of postovulatory follicles (POFs), fish were dissected either on board or within three hours after capture. Gonads were removed, weighed, macroscopically staged according to the criteria (Tables 3.2 & 3.3) modified from Pankhurst *et al.* (1987) and Jordan (2001), and preserved in formalin acetic-acid calcium-chloride (FAACC). All fish were classified as male, female or immature, measured to the nearest millimetre total length, and weighed to the nearest gram.

Histological analysis was used to verify macroscopic staging, determine age of POFs, and occurrence of atresia in ovaries. Preserved gonads were dehydrated in an ethanol series, embedded in paraffin, and sectioned at 6μ m, before staining with Mayer's Haematoxylin and Eosin. Many studies have found no significant differences in maturation and oocyte frequency distribution between right and left ovaries (Laroche & Richardson, 1980; DeMartini & Fountain, 1981; West, 1990); therefore, in this study, the left ovary was used for all histological analysis. Possible variation in the developmental stage of oocytes due to their position in the ovary was minimized by transversally sectioning the ovary from the medial portion (e.g. Forberg, 1982; Gooley *et al.*, 1995). A longitudinal section and 6-8 transverse sections from left ovary were used for histology (as per. Hunter & Macewicz, 1985a).

The size frequency distribution of oocytes within the intact ovaries of 10 females in each stage of maturity was determined macroscopically. Sections 1-2 mm thick were cut from the middle of left ovary, the oocytes teased apart with needle, and further separated by immersion in an ultrasound bath for 3-5 mins (as per. Lowerre-Barbieri & Barbieri, 1993). The maximum diameter of around 300 randomly-

selected oocytes was measured under a stereomicroscope using transmitted light and bright-field illumination. Stage of whole-oocyte development was assessed though appearance (Table 3.2) of each oocyte (Davis & West, 1993).

Macroscopic staging scale was validated histologically, in which ovaries were classified based on the presence of the most advanced type of oocyte (Wallace et al., 1987; West, 1990). Histological classification (Table 3.2) was assigned, based on terminology defined by Yamamoto (1956) and staging criteria from West (1990). The presence of postovulatory follicles, hydrated oocytes, and migratory nucleus oocytes was used to identify females that had begun to spawn (Hunter & Macewicz, In contrast, cessation of spawning activity was identified by lack of 1985a). hydrated oocytes and postovulatory follicles together with high levels of the atretic vitellogenic oocytes (Hunter & Macewicz, 1985b; Marshall et al., 1993). Ovaries were classified based on the presence of different types of atretic oocytes (Table 3.4), by following the method of Hunter and Macewicz (1985b). As structure of the delta (δ) stage of attretic oocytes was almost indistinguishable from highly degenerated POFs in sand flathead, the presence of alpha (α), beta (β), and gamma (γ) stages of atretic oocytes in ovaries was examined. The percentage of total of the three stages of atretic oocytes in each ovary was determined by counting 100 randomly-selected oocytes from ovarian tissue.

A longitudinal section $(5\mu m)$ of each testis near the posterior tip and a transverse section of the mid-section of the testis was used to determine the presence of spermatozoa in lobules and determine the gonadal stage of males. The relative proportion of gamete stages in each testis was calculated by scoring the stage present under intersections of an ocular grid with 100 intersections. In the transverse section, three grids were placed from the outer edge to the centre of the testis, while

another two grids were haphazardly placed on the longitudinal section. The histological stage of testis maturation was determined using the criteria described in Table 3.3, outlined in Pankhurst *et al.* (1987) and Takashima & Hibiya (1995).

Table 3.2. Microscopic, macroscopic and histological staging criteria used for sand flathead ovaries.

Maturity stage	Category	Microscopic histology*	Macroscopic ovary#	Macroscopic whole oocyte ¹
1	Immature	Chromatin nucleolar: Very small oocytes. Clear, spherical nucleus surrounded by a thin layer of purple-stained cytoplasm. No nucleolus visible.	Small trap with rounded edge, pale pinkish colour.	Unyolked: Spherical transparent bodies.
2	Maturing	<i>Perinucleolar:</i> Oocyte size increases because of thick cytoplasm around a light nucleus, containing few to many peripheral nucleoli.	Ovaries reddish-pink and translucent. Virgin: Ovary wall thin and transparent. Recovering: Ovaries flaccid and ovary wall thick and opaque.	Unyolked: Spherical transparent bodies. Nucleus clear and brownish in colour.
3	Developing	<i>Cortical alveoli:</i> Appearance of yolk vesicles in cytoplasm, thick &pink-stained zona radiata distinguishable.	Almost length of body cavity. Ova not visible.	Partially yolked: Some yolk granules appear, becoming darker with increased
4	Late developing	Vitellogenic yolk: Marked increase in oocyte size. Cytoplasm filled with yolk granules, oil vesicles and yolk vesicles. Peripheral nucleolus around the nuclear membrane.	Full length of body cavity. Ova visible.	<i>Yolked:</i> Oocytes completely opaque except for the translucent perivitelline border.
5	Ripe	<i>Nuclear migration:</i> Migration of nucleus to periphery of cytoplasm, fusion of oil vesicle into the oil droplet, coalescence of yolk granules to form uniform plate.	Ovaries occupy all available space of body cavity, transparent oocytes visible.	Nuclear migration: Parts of oocytes become translucent as yolk coalesced.
6	Running ripe	<i>Hydration:</i> Yolk granules fused into a few plates. Thecal cells appear like a string.	Large hydrated oocytes easily expressed with slight pressure. Ovaries pinkish and granular.	Hydration: Whole oocytes is translucent, expect for the oil droplet.
7	Spent	Spent: Postovulatory follicles present.	Ovaries flaccid and bloodshot with thick wall.	

* Adapted from West (1990).
Adapted from Jordan (2001).
¶ Adapted from Davis and West (1993).

	•	,	
Maturity stage	Category	Microscopic Histology [#]	Macroscopic testis [*]
- 1	Immature	Immature: Abundance of spermatogonia, some primary spermatocytes.	Small, white and threadlike testis, occupy ¹ / ₄ length of body cavity.
2	Early developing	<i>Early spermatogenic:</i> Primary spermatocytes predominate, presence of secondary spermatocytes and spermatids.	Flattened white tube, occupy more than ¼ length of body cavity.
3	Developing	Spermatogenic: Increasing number of secondary spermatocytes, presence of spermatids and spermatozoa.	Becoming large. No sperm expelled when testis cut.
4	Late developing	Partially spermiated: Predominance of spermatids and spermatozoa.	Almost length of body cavity and large. Some sperm expelled when testis cut.
5	Ripe	Fully spermiated: Spermatozoa predominate, ripe sperm present in spermatic ducts.	Full length of body cavity and swollen. Sperm runs freely with slight pressure on belly.
6	Spent	Spent: Residual spermatozoa. Spermatogonia present towards testis margin.	Testis broad, flaccid and bloodshot. No milt expressible.

Table 3.3. Macroscopic and histological staging criteria used for sand flathead testis.

* Adapted from Jordan (2001). # Adapted from Pankhurst et al. (1987) and Takashima & Hibiya (1995).

Atretic states	Histological characteristics	Atresia stages *
0	Absence of α stage of atresia. Possible present of insignificant β stage of atretic yolked oocytes.	<u>Alpha stage</u> : Granular, dark, and basophilic staining of cytoplasm. Disintegrated nucleus. Slightly dissolved zona radiata accompanied by loss of striation and uneven diameter. <u>Beta stage</u> : Much smaller than the
1	Less than 50% of yolked oocytes are affected by atresia.	original oocyte. Numerous disorganized granulosa cells. One or more large intracellular vacuoles. <u>Gamma stage</u> : Extra or intercellular flocculent materials encapsulated by a layer of granulosa and thecal cells.
2	More than 50% of yolked oocytes are atretic. y atretic oocytes may be present.	In sand flathead elongated with one or two vacuoles.

Table 3.4. Histological staging criteria of atresia in sand flathead ovary.

3	Almost all (yolked) oocytes			
	affected by atresia.	β stage is		
	dominant.			

* Adapted from Hunter & Macewicz (1985b).

3.2.3. Spawning frequency and hormone treatment

To estimate age of POFs for assessing spawning frequency, a series of distinct histological stages of the deterioration and resorptive process of the follicles was prepared from the ovaries of fish for which the time of ovulation and egg release was known. To obtain ovaries containing known age POF, 10 sexually mature females were captured by hook and line from Coles Bay in late October. Females were immediately anaesthetized with benzocaine (50 mg/L), then three females were injected intraperitoneally with luteinizing hormone releasing hormone analogue (LHRH_a; 50 μ g/kg body weight) and seven females with human chorionic
gonadotropin (hCG; 500 u/kg body weight), fin clipped, and placed into the holding tank. Hormone treated females and two males were placed into a 300-L fibreglass tank with oxygenation until transportation to the aquatic centre within three hours, where they were placed in 1000 L, temperature-controlled tanks supplied with recirculating seawater. Water temperature was maintained at 15 °C, the water temperature in Coles Bay at time of sampling.

Twelve hours after hormone injection, females were anaesthetized, examined, and ovulated fish were fully stripped using light abdominal pressure. Successfully stripped fish were killed in specific times post stripping (< 6, 12, 24, 36, 48, and 72 hours). Two females were killed at each time point, except at 12 and 36 hours after stripping in which only one fish was killed. Ovaries from sacrificed fish were removed for histological examination and description of postovulatory follicle structure. This provided a comprehensive description of POF deterioration over 72 hours. We estimated age of POF based on: 1) size and appearance of the follicles (from large and folded to small and V-shaped); 2) alignment of granulosa cells (from continuous arrangement to collapsed features); and 3) lumen shape (from open to not discernible) (Hunter & Goldberg, 1980).

Spawning frequency (percentage of mature females spawning per day) at each location was estimated through the percentage of mature females with POFs less than 48 h old, as described by Hunter & Macewicz (1985a). To avoid confusion of POFs with other structures, such as atretic oocytes, only POFs < 48 hour were used to assess spawning frequency. The percentage of mature female with ovaries containing POFs was calculated for each location. Spawning frequency was then determined by dividing 100 (representing the total population of females) by the percentage of females with POFs in the ovaries (DeMartini & Fountain, 1981).

To determine the spawning activity of males during different times of the day, in one occasion at spawning peak, sexual condition was assessed on board by the application of gentle pressure to the abdomen at different times between dawn and dusk. Fish were classified as non-spermiated (no milt expressible), partially spermiated (viscous milt expressible), or fully spermiated (fluid milt easily expressible).

3.3. RESULTS

3.3.1. Gonad development

Ovaries at stage 1 and 2 did not contain vitellogenic oocytes, by stage 3 some oocytes had increased in size (approx. 0.2 mm) and were producing yolk vesicles (Fig 3.1). Stage 4 was marked by the appearance of yolk granules in the oocyte cytoplasm. This was accompanied by increase in the thickness of the zona radiata. Migration of nucleus towards the periphery in stage 5 signalled the final oocyte maturation, where the yolk and lipid material in the oocyte cytoplasm coalesced during hydration (stage 6). Spent (stage 7) ovaries contained chromatin nucleolar and perinucleolar oocytes, alongside some atretic oocytes, but all other oocyte types were absent.

The size-frequency distribution of oocytes in ovaries displays the developmental sequence of maturation (Fig 3.2). The size distribution of oocyte diameters were polymodal in the late stage of ovary development, with considerable overlap between stages. In stage 2 and 3 females, all oocyte diameters were < 0.26 mm. Oocyte diameters increased to a maximum size of 0.54 and 0.59 mm in stage 4 and 5, respectively. There was significant overlap in size of vitellogenic oocytes and oocytes with migrated nucleus in stage 5 ovaries, despite their different appearance (Fig 3.3). Hydration was accompanied by enlargement of oocytes (ca. 0.9 mm diameter). Smaller, mostly vitellogenic oocytes were present in all females with hydrated ovaries (stage 6). The presence of a range of oocytes stages (Figs 3.1c & 3.3) in ovulated females (stage \geq 4), together with mode of size-frequency distribution of oocytes, suggests asynchronous oocyte development.



Figure 3.1. Histological section of ovary showing oocytes development (stage 2-6). (A) Stage 2: A dark, dense and thick cytoplasm (cy) around a light nucleus (nu) of pre-vitellogenic oocytes (po); nucleoli (n) at periphery of nucleus. (B) Stage 3: Appearance of yolk vesicles (yv) in cytoplasm of primary vitellogenic oocyte (pvo). (C) Stage 4: Marked increase in secondary vitellogenic oocyte (svo) size. Cytoplasm bounded by the zona radiata (zr), filled with yolk granules (yg) and oil vesicles. (D) Stage 5: Two nucleus (nu) migrated oocytes. (E) Stage 6: Onset of hydration (h), yolk granules coalesced to form yolk plates (yp). (F) Post-spawning: Folded postovulatory follicles (POF). Scale bars 0.1 mm.



Figure 3.2. Oocyte size frequency distribution in sand flathead at different stages of gonadal maturation. Due to the lack of more than 50% of oocyte types in stages 2 and 3, frequency of oocyte could not be statistically compared among stages.



Figure 3.3. Photomicrograph of whole oocytes of sand flathead representing unyolked (U), partially yolked (PY), yolked (Y), nucleus migrated (NM), and hydrated (H) oocytes. Translucent strip of perivitelline (arrows) in yolked oocyte changed, to a transparent cap in nucleus migrated oocyte. Scale bar 0.5 mm.

Changes in macroscopic state of testes was characterised by significant changes in proportions of gamete type (χ^2 =255.2, df 12, P<0.001). Immature testes contained significantly more spermatogonia (SPG) than any other testis stage (Fig 3.4). A few primary (SC1) and secondary (SC2) spermatocytes were also present, but no spermatids (SPD) or spermatozoa (SPZ) were recorded in immature testes. Testes undergoing spermatogenesis contained all gamete types, but the proportion of SC1 was higher than expected (Figs 3.4 & 3.5a). Spermatids were more common in partially spermiated testes than in any other testis stage. Fully spermiated testes were characterised by high proportions of SPZ in the tubule lumens (Fig 3.5b). The presence of all gamete types in spermiated testes (partially and fully) indicates continuous gamete maturation.



Figure 3.4. Frequency of different gamete stages in histological sections from each macroscopic testicular stage of sand flathead. The arrows indicate the direction in which the observed frequencies differed from expected frequencies, generated under the assumption that gamete type is independent of testis stage. n = number of individuals, with 500 observation per testis of each individual.



Figure 3.5. Photomicrographs of (A) spermatogenic and (B) spermiated testes from sand flathead, showing spermatogonia (SPG), primary and secondary spermatocytes (SC1 and SC2), spermatids (SPD), and spermatozoa (SPZ). Scale bars 100 μ m.

3.3.2. Reproduction and spawning strategy

Mature females (stages 3-6, Table 3.2) were first seen in the size class 24-25.9 cm in Coles Bay (Table 3.5). The proportion of reproductively active females increased with length until a length of about 28 cm, when all females were mature in October, which is the start of spawning season in Coles Bay. For larger size classes (\geq 28 cm) females were reproductively active till March, although some Coles Bay females (\geq 32 cm) remained reproductively active as late as May. In contrast, spawning activity ceased in smaller individuals (< 28 cm) by January, suggesting a shorter spawning activity for smaller individuals. In Georges Bay, spawning activity was first seen in females \geq 22 cm in September (Table 3.6), and females \geq 30 cm were all mature in September. The proportion of reproductively active females in Georges Bay decreased for all length classes in November, compared with September. No evidence of spawning activity was seen in Georges Bay females by January. Ovaries of some small females (< 28 cm) contained a considerable proportion (> 50%) of alpha and beta (Fig 3.6) stages of atresia in Coles Bay during October (Table 3.5). In contrast, for larger females (\geq 28 cm), no state 2 and/or 3 atresia was evident from October to December. All reproductively active females in Coles Bay exhibited atresia in January. Surprisingly, during March, all Coles Bay females \geq 28cm were mature, with no evidence of occurrence of atresia, although by May, atresia was common (66-87%) in reproductively active females in Coles Bay. In Georges Bay, atresia did not occur for any length classes during September (Table 3.6), suggesting very efficient spawning activity. Females within the length class < 26 cm showed atresia in November. By January, all ovaries were regressed and for some length classes around 50% of females were classified in states 2 and 3 of atresia.

Table 3.5. Percentage of mature female sand flathead in each size category during the spawning season in Coles Bay. Percentage of atresia includes ovaries that are classified in states 2 and 3 of atresia. n = sample size for each size class.

	Month					
Length class (cm TL)	Oct	Nov	Dec	Jan	Mar	May
< 24 (% Mature)	· 0			0	0	
% Atresia	0	-	-	0	0	-
n	13	-	-	3	4	-
24-25.9 (% Mature)	67	-	-	-	0	-
% Atresia	10	-	-	-	0	•
n	6	-	-	-	4	•
26-27.9 (% Mature)	83	-	-	0	0	0
% Atresia	8	-	-	0	0	0
n	12	-	-	3	4	3
28-29.9 (% Mature)	100	-	_	25	100	0
% Atresia	0	•	-	12	0	100
n	12	_	-	4	3	2
30-31.9 (% Mature)	100	100	100	33	100	0
% Atresia	0	0	0	67	0	50
'n	5	4	5	6	6	2
32-33.9 (% Mature)	100	100	100	70	100	25
% Atresia	0 ·	0	0	30	0	87
n	5	9	9	20	3	8
≥ 34 (% Mature)	100	100	100	93	100	7.7
% Atresia	0 ·	0	0	[·] 6.7	0	66
<u>n</u>	3	17	16	15	4	13

Table 3.6. Percentage of mature female sand flathead in each size category during the spawning season in Georges Bay. Percentage of atresia includes ovaries that are classified in states 2 and 3 of atresia. n = sample size for each size class.

·	Month			
Length class (cm TL)	Sep	Nov	Jan	
< 22 (% Mature)	0	0	-	
% Atresia	0	25	-	
n	6	18	-	
22-23.9 (% Mature)	42	9	0	
% Atresia	0	34	50	
n	12	11	4	
24-25.9 (% Mature)	50	33	0	
% Atresia	0	33	0	
n	6	9	3	
26-27.9 (% Mature)	80	33	0	
% Atresia	0	0	· 0	
n	5	3	2	
28-29.9 (% Mature)	50	25	0	
% Atresia	0	0	-50	
n	2	4	4	
\geq 30 (% Mature)	100	-	0	
% Atresia	0	-	0	
n .	7	-	2	



Figure 3.6. States of atresia in sand flathead ovaries described in Table 3.4. (A) State 1: A small proportions of yolked oocytes are affected by atresia. An alpha (α) stage of atretic oocyte beside two intact vitellogenic oocytes. (B) State 2: Predominance of atretic oocytes, here beta (β) stage, in ovary. (C) State 3: α , β , and gamma (y) stages of atresia influenced in all oocytes. Scale bars 0.1 mm. Ovaries in stage 2 (maturing) and 6 (hydration) had few atretic oocytes (ca. 20-30% of unyolked oocytes) during the spawning season; therefore, they were not classified as either state 2 or 3 of atresia. In developing ovaries, atresia was more common early in the spawning season (October) in Coles Bay, whereas ripe and spent ovaries exhibited high levels of atresia in January and May (Table 3.7). In Georges Bay, however, atresia did not occur in any gonad developmental stage in September (Table 3.8), but by November, both ripe and spent ovaries were affected by atresia.

Table 3.7. Percentage of atresia (sum of states 2 and 3) calculated for each gonad stage for sand flathead caught in Coles Bay. n = sample size for each gonad stage.

	Month					
Gonad stage	Oct	Nov	Dec	Jan	Mar	May
Developing (3 & 4)	14	0	0	0	0	_
n	7	1	3 ·	4	2	· _
Ripe (5)	0	0	0	17	0	67
n	32	29	26	23	13	3
Spent (7)	-	-	-	70	-	71
n	-	-		10		21

Table 3.8. Percentage of atresia (sum of states 2 and 3) calculated for each gonad stage for sand flathead caught in Georges Bay. n = sample size for each gonad stage.

	Month			
Gonad stage	Sep	Nov	Jan	
Developing (3 & 4)	0			
n n	5	-	-	
Ripe (5)	0	33	-	
n	10	3	-	
Spent (7)	-	100	66	
n	- . ·	2	9	

3.3.3. Spawning periodicity

In sand flathead up to 48 h post-spawning, POFs could be accurately distinguished without confusion with late stages of atresia. After spawning, newly collapsed POF (age-0 day) appeared as a form of folded loops (Fig 3.7a). The nucleus was located at the apex of the cuboidal or columnar granulosa cells, which were arranged in an orderly way along the edge of the lumen. Twenty-four hours post-spawning POFs had fewer folds and granulosa cells did not show alignment (Fig 3.7b). Vacuoles were seen in the nucleus of some granulosa cells. The underlying thecal cells were present, although less distinct than in 0-day age POFs. A POF 48 h old was recognized by a closed lumen and defused thecal cells layer into the granulosa cells layer (Fig 3.7c). It was difficult to distinguish POFs beyond 48 h, due to collapse of POF structure and degeneration of nucleus of granulosa cells (pyknotic) and thecal layer (Fig 3.7d).



Figure 3.7. Deterioration of sand flathead POF following release of eggs. (A) Newly (< 6 h post-spawning) collapsed follicle with distinct granulosa (g) and theca (t) cells. Changes of POF structure at 24 h (B), 48 h (C), and 72 h (D) post-spawning. 1=lumen. Scale bars 0.05 mm.

A clear pattern of lunar periodicity in spawning was apparent from the proportion of females with POF (χ^2 =8.6, df 3, P=0.035), but the proportion of females with hydrated oocytes did not vary at different moon phases (χ^2 =6.4, df 3, P=0.091). Mature females had a higher proportion of POFs in their ovaries in the new moon during the spawning season (Fig 3.8).



Figure 3.8. Proportion of mature female *Platycephalus bassensis* with early (structure similar to 24 h age POF or younger) or late-stage (structure similar to 36 h age POF or older) POF at different moon phase in October and December. Values above points are number of mature females.

The proportion of mature females with newly collapsed POFs (< 6 h) in samples taken at different times throughout the day was significantly different (χ^2 =6.3, df 2, P=0.043), indicating a diel cycle in spawning activity. In contrast, the proportion of mature females with or without hydrated oocytes did not differ (Table 3.9) at different times during daylight hours (χ^2 =1.6, df 2, P=0.442). The proportion of females with POF was highest between 10:00 and 15:00 h (Fig 3.9). Males, however, had fully spermiated testis at different times of the day, ranging from 66% (before 10:00 h) to a maximum of 80% (between 10:00 and 15:00). As a consequence, they did not show a clear diel cycle (χ^2 =0.9, df 2, P=0.639) and were ready to spawn throughout the day during the spawning season.

		Percentage mature females		
Collection time (hour)	n	With hydrated oocytes	Without hydrated oocytes	
<10:00	52	1.9	98.1	
10:00-15:00	72	6.9	93.1	
>15:00	37	5.4	94.6	



Figure 3.9. Proportion of mature female *Platycephalus bassensis* with new POF (< 6 h) at different times of the day during spawning season. Values above bars are numbers of mature females.

During the spawning season, an average of 16.7 and 20.3% of the mature females had POFs in their ovaries in Georges Bay and Coles Bay respectively. Therefore, it appears that females spawn approximately every six days in Georges Bay and every 4.9 days in Coles Bay. Chi-square analysis showed no significant difference in spawning frequency estimates for the two locations (χ^2 =0.1, df 1, P=0.763). If we assume that Coles Bay females spawn every six days during October-March, then they spawn at least 36 times each year. Whereas Georges Bay females with 1-2

Table 3.9. Percentage of mature females *Platycephalus bassensis* with and without hydrated oocytes in their ovaries at different times of the day.

month spawning activity (September and October), may spawn only 5-10 times each year.

3.4. DISCUSSION

Platycephalus bassensis were shown to display multiple group synchronous oocyte development. The pattern of changes in size-frequency distribution of oocytes and proportions of oocyte stages during ovarian development suggests continuous development of batches of oocytes. The presence of all developmental stages of oocytes in the ovaries of mature females indicated a capacity for multiple spawning of individuals within a reproductive season. Male *P. bassensis* exhibited multiple group synchronous gamete development, since the pattern of gamete development shown by males is generally similar to females of the same species (Pankhurst, 1998). The presence of all gamete stages in partially and fully spermiated males, suggests recruitment and subsequent maturation of immature gamete types for multiple spawning episodes. These evidences confirm that *P. bassensis* is a serial spawner, which is capable of spawning multiple times during the spawning season.

Although the duration of the spawning period of *P. bassensis* throughout eastern and southern Tasmania was estimated to be six months (Jordan, 2001), this study indicate that fish of different sizes display a different spawning period duration. In Coles Bay and Georges Bay, smaller fish revealed a shorter reproductive activity compared to their larger individuals. This indicates that smaller individuals, who have recently reached maturity, may release advanced yolked oocyte batches for a shorter period. In contrast, larger and older individuals release oocyte batches over a longer duration, resulting in an extended spawning season. Recruitment of partially yolked oocytes to a new batch of advance yolked oocytes has been shown to occur over a longer period in larger females of some multiple spawner species, like Atlantic croaker (Barbieri *et al.*, 1994) and bluefin tuna (Farley & Davis, 1998), compared to smaller females. Reproductive activity of *P. bassensis* probably ceases after November in Georges Bay, as neither small nor big reproductively mature females were seen in January. In Coles Bay in contrast, although there were no small (< 28 cm) reproductively active female in January, larger females appeared to be reproductively active until May. Differences in spawning duration of different sizes of fish can be generally related to the strategy of resource allocation to reproduction (Schultz *et al.*, 1991). Further investigation of conditions and energy allocation will explain differences in reproductive strategy.

The occurrence of atresia of Coles Bay's small females (< 28 cm) in October was mostly related to the presence of alpha and beta atresia of unyolked oocytes. Absence of atretic unyolked oocytes in the second half of the spawning period confirms that spawning activity for these individuals ceased before January, as for many teleosts the presence of atresia has been typically used to identify regressing ovaries (Hunter *et al.*, 1986; Lowerre-Barbieri *et al.*, 1996). For larger individuals (\geq 28 cm) from Coles Bay, atresia did not occur in March, therefore, the occurrence of atresia in January may be related to variable or unfavourable environmental conditions in January. Hay and Brett (1988) showed a similar occurrence of atresia for Pacific herring (*Clupea harengus pallasi*) in some months that is attributable to environmental factors, rather than a female's physiological ability. Reabsorption of residual oocytes after spawning eliminates unwanted materials (Macer, 1974). However, the reason for deterioration of some oocytes during the spawning season is

not well understood and may be related to environmental and dietary factors (Hunter & Macewicz, 1985b; Hay & Brett, 1988).

One other possible explanation for the presence of atresia in January is that the spawning activity of some females is finished or close to finishing. This is supported by the high frequency of atresia for ripe (stage 5) and spent (stage 7) females in January, as it is unlikely that they have made a significant contribution to spawning activity. It can be assumed that there is no likelihood of spawning for individuals that had high levels of atresia i.e. states 2 and 3 (Hunter & Macewicz, 1985a). Therefore, given the small percentage of mature females and a high level of atresia in May, it is likely that almost all females were reproductively inactive by that time. In Georges Bay, the absence of atresia in developing and ripe females caught in September suggests a high spawning success during the early portion of spawning period, and it may suggest suitable and stable environmental conditions in this region. An increased number of atretic females during November is an indicator of lower efficacy of spawning, through atretic losses. The presence of atresia, together with decline in percentage of mature females in November, could be evidence of spawning cessation in Georges Bay, especially as no atresia was found in any size classes in January.

As postovulatory follicles of *P. bassensis* were still fully distinguishable two days after spawning, they were used to estimate spawning frequency. In contrast, POFs of temperate species can be rapidly reabsorbed and are often difficult to identify one to two days after spawning (Hunter & Goldberg, 1980; Schaefer, 1996). Such slow deterioration of POFs in *P. bassensis* may reflect the use of POFs of both hormone induced fish and fish caught from wild in this study, while almost in all previous studies POF age only is estimated from a series of samples taken at regular intervals

from wild. The proportion of two day old POFs in mature females, indicated lunar periodicity in the spawning activity of *P.bassensis*. Such periodicity in spawning was not found when the proportion of females with hydrated oocytes was used as a basis for the spawning periodicity estimation. In fish that spawn multiple times during the spawning season, the processes of hydration and spawning usually occur within a matter of hours (Hunter & Macewicz, 1985a; Brown-Peterson *et al.*, 1988), therefore our estimation of spawning periodicity based on the presence of hydrated oocytes may be biased by the effects of the time of day of sampling. In contrast, as POFs persisted for more than two days in *P. bassensis* (at 15° C), their detection was not dependent on the time of day of sampling, and therefore estimating spawning periodicity using POFs is more reliable.

The greatest spawning activity in *P. bassensis* was on and around the new moon. Lunar periodicity in spawning activity is common for many teleosts (Robertson *et al.*, 1990; Davis & West, 1993; McIlwain, 2002), and different hypotheses were proposed to explain why lunar reproductive cycles have developed in fishes (Johannes, 1978; Robertson, 1991). Spawning in *P. bassensis* is likely to be linked to the lunar tidal cycle rather than moonlight, as it occurred during the daytime hours. The majority of teleosts known to have lunar periodicity, spawn on or around the new or full moon (Johannes, 1978), possibly in order to take advantage of spring tides (Davis & West, 1993). Spawning of *P. bassensis* in the spring tide would therefore disperse the spawned eggs alongside the inshore regions.

Based on the results from this study the peak spawning activity of *P. bassensis* appears to be between midday and dusk. However, as no fish could be caught at night it was not possible to completely discount the probability of night-time spawning. It seems unusual that *P. bassensis* spawns during the day, as most fishes

with diel spawning patterns typically spawn around dusk (Ferraro, 1980; Colin & Clavijo, 1988), to reduce predation on the eggs (Robertson, 1991). However spawning during daylight hours may be preferable, in the case that released eggs on a single day, but throughout much of the daylight period, hatch during the same evening (Goulet, 1995; Asoh & Yoshikawa, 2002). In this case, incubation period (time from fertilization to hatching) is relatively long and fertilized eggs develop until they attain competence for hatching at darkness. Male *P. bassensis* are probably capable of spawning throughout the day as percentage of males with partially or fully spermiated testes did not different during the daylight hours. This agrees with less timely restricted spawning activity of males of other fish species (Grier & Taylor, 1998; Yoneda *et al.*, 1998).

The estimated spawning frequency of *P. bassensis* is approximately 5-6 days, which is very similar to other platycephalid species. Militelli and Macchi (2001) found that Brazilian flathead, *Percophis brasiliensis*, spawn once every six days during spawning season. Despite a wealth of information about spawning frequency of different multiple spawner species, only a few studies have addressed spatial variability in spawning frequency (Brown-Peterson *et al.*, 2001). However, spawning frequency can affect egg production potential through increasing or decreasing the quantity of released egg batches during the reproductive season. Although the difference in spawning frequency of *P. bassensis* between Coles Bay and Georges Bay populations was not big, the magnitude of such small differences could be high for a protracted spawning season. Given equal spawning season duration, populations with less frequent spawning have less potential for egg production. Similarly, decreased egg production can also occur due to a shorter spawning period.

As few females with hydrated oocytes were collected during this study, batch fecundity could not be estimated for *P. bassensis*. The proportion of sand flathead females with hydrated oocytes in samples caught with trawl and gill-nets (Unpublished data, Jordan, Marine Research Laboratories, University of Tasmania) was almost similar to the proportion of hook and line catches. This may indicate that a small proportion of the population in every occasion undergo hydration of oocytes, reducing the likelihood of them being caught, particularly if the process of hydration occurs within a matter of hours. However, knowing the spawning frequency and approximate time of spawning peak may help to explore sand flathead total fecundity, which is important for stock management.

This study describes the details of sand flathead reproductive biology, which is essential for further investigation on temporal and spatial variability in reproduction. Fundamental reproductive characteristics such as dynamics of spawning, spawning periodicity and occurrence of atresia are required to examine the reproductive output and its variability in a spatial and temporal scale. This is especially the case when our results have shown that sand flathead are able to have a variable reproductive strategy. Such a capability, together with demographic variability, warrants further investigation in reproductive variability which may influence fisheries management options to optimise reproductive capacity and recruitment of sand flathead.

CHAPTER FOUR

SPATIAL AND TEMPORAL VARIABILITY IN REPRODUCTIVE

ECOLOGY OF SAND FLATHEAD, *PLATYCEPHALUS BASSENSIS*.

Spatial and temporal variability in reproductive ecology of sand flathead, *Platycephalus bassensis*.

4.1. INTRODUCTION

One of the major challenges in ecology is to understand the processes that shape populations and are responsible for variability in population dynamics. In highly fecund species like fishes, variability in population structure is believed to be in part determined by reproductive potential of that population (Einum *et al.*, 2003), i.e. the ability of a fish population to produce viable offspring that may recruit to the adult population or fishery (Marshall *et al.*, 1999; Trippel, 1999). Spatial and temporal variation in fundamental elements of reproductive characteristics (e.g. size/age at maturity, gonad weight, fecundity, spawning strategy), maybe the result of biotic and abiotic conditions (Stearns, 1992). Such factors can potentially alter the reproductive potential of a fish population (Stearns & Crandall, 1984; Marshall *et al.*, 1998), which in turn influences population growth and abundance. Despite the general recognition that reproductive life history characteristics have a significant influence on population dynamics, little is still known about the magnitude of the influence (Trippel *et al.*, 1997; Marshall *et al.*, 1998).

The quantity of produced eggs or reproductive investment of spawners is a factor that may affect population dynamics, because strong recruitment events can be associated with egg production (Jennings *et al.*, 2001; Zheng & Kruse, 2003). Although, in most studies, fecundity is usually taken as an indication of egg production (Horwood *et al.*, 1986; Koslow *et al.*, 1995; Yoneda *et al.*, 2002), with variability in egg production being reflected in variations in gonad weight during the spawning season (Rijnsdorp *et al.*, 1991; Bell *et al.*, 1992). Given the positive correlation between fecundity and fish size (Magalhaes *et al.*, 2003; Yoneda &

Wright, 2004), a larger fish with greater gonad volume is expected to make a greater contribution to population egg production than its smaller counterpart.

In temperate marine fish species, gonad investment changes seasonally, with extensive gonad growth and investment to reproduction during the spawning season (DeVlaming *et al.*, 1982; Sumpter, 1990). However, the length or duration of the spawning season may vary among populations of a species (Wilk *et al.*, 1990; Brown-Peterson *et al.*, 2001), as well as interannual variability in the start and duration of the spawning season within the population (Yamahira, 2001; Kupschus, 2004). In serial spawners, yolked oocytes are repeatedly recruited from unyolked oocytes over the spawning season (DeVlaming, 1983; Taylor *et al.*, 1998), therefore, a longer spawning period will result in more batches of spawned eggs compared to shorter spawning period. The result of such variability in egg production may result in the capacity for variations in population growth.

For animals with indeterminate growth (e.g. reptilians, amphibians, and fish) age and size of first reproduction is a key point in the life history (Charnov & Berrigan, 1991; Roff, 1992). As fecundity is so tightly coupled to body size in fishes, a precociously maturing small individual is limited by body size in the level of investment in egg production. If early maturation compromises growth, the resulting smaller individuals may be more vulnerable to predation (Wootton, 1998). However, early maturation may ensure a longer reproductive life, and if larger fish have a greater fishing mortality risk it guarantees some egg production for population stability (Roff, 1992). Moreover, initial low investment (fecundity) would be compensated with later greater egg production with increasing age/size (Rochet, 1998), provided that older/larger individuals remained in the population. In contrast, individuals attaining maturity at older/larger age/size are more fecund. However, if

large individuals suffered a greater risk of mortality (e.g. fishing), it is possible that individuals that delay maturation would never have the chance to produce eggs (Rochet, 2000). Therefore, estimates of size/age at maturity, together with the size/age composition of population is essential to identifying which parts of the population are involved in egg production (Goodyear, 1993). Such knowledge is also beneficial in determination and refinement of size limits in fisheries management.

Platycephalus bassensis showed temporal and spatial variations in demographic parameters around Tasmanian coastal waters (Chapter 2). The reproductive biology of this species (Chapter 3) has also revealed potential for flexibility in reproductive life history characteristics. The combination of demographic variability and potential for flexibility can potentially cause spatial and temporal variability in reproductive output of sand flathead. In spite of the potential of such variability, present fishing regulations for this species are based on similarity in reproductive output and uniformity of population structure for all P. bassensis stocks around As demographic variability causes differences in reproductive output Tasmania. (LePage & Cury, 1997; Jennings & Kaiser, 1998), there is concern that under present fishing regulations, sustainability of less productive stocks could be in jeopardy. While P. bassensis is the species most heavily targeted by recreational fishers in Tasmania (Lyle & Campbell, 1999), knowledge about this species' fundamental reproductive traits and their variability in temporal and spatial scales, remain basic (Jordan, 2001).

This study examines the variability in reproduction of P. bassensis in order to develop a set of recommendations for recreational fisheries management. Our specific objectives were, 1) to quantify the spatial and temporal variation in

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reproductive investment to assess the possible influence of egg production on population growth, 2) to examine the duration of spawning period and its implication in egg production, and 3) to estimate size/age at maturity to identify the part of the population that contributes in egg production.

4.2. MATERIALS AND METHODS

4.2.1. Study sites and sampling

Fish were sampled from three inshore coastal locations in the north and east of Tasmania (Chapter 2); Coles Bay (east coast), Georges Bay (north east coast), and Tamar River estuary (north coast). Sand flathead were collected seasonally during 2001/02 and 2002/03 using hook and line. Additionally, to further resolve changes on a monthly basis in the Tamar River, monthly sampling occurred during spring and summer 2001/02, while in Coles Bay monthly sampling was done from October 2002 to May 2003. Fish were also caught in the Tamar River and Georges Bay during early (September) and late (November) spring 2002. To minimize bias in reproductive information, fishing was carried out at 4-5 haphazard selected sites at each location. Animals were stored on ice until dissection later on the day of collection.

4.2.2. Laboratory processing

All fish were sexed (male, female, or immature), measured to the nearest millimetre total length, and weighed to the nearest gram. Sagittal otoliths were removed from all specimens and used to determine the age of each individual, using the burn and crack technique (Williams & Bedford, 1974, Chapter 2). Gonads of

each fish were removed and weighed to the nearest 0.1 mg and staged macroscopically and histologically using criteria described in Chapter 3.

4.2.3. Size and age at maturity

Size and age at maturity (L_{50}) were estimated as the smallest length or age at which 50% of the fish collected over the spawning season (October to March for Coles Bay and September to November for Georges Bay) were sexually mature. Individuals were considered sexually mature if they were in stage 3 (developing) or higher. To avoid classifying resting (reproductively inactive) or early developing fish as immature, only fish collected at the peak of the spawning season (October to December for Coles Bay and September to November for Georges Bay) were used for this analysis. The proportion of mature fish per 1-cm total length (TL) class and 1-year interval was calculated for males and females separately using a binary logistic regression. Percent maturity was then fitted to age/length class for males and females separately.

4.2.4. Analysis

Differences in gonad weight were analysed using a 3-way analysis of covariance (ANCOVA) with location, sex, and season as factors of interest and somatic weight (body weight minus visceral weight) as the covariate, followed by a comparison of adjusted means taking the covariate into account (Quinn & Keough, 2002). During the spawning season monthly changes in gonad weight adjusted for somatic weight was also analysed using a 3-way ANCOVA with location, sex, and month as factors of interest. Variations in gonad weight were analysed only for mature fish. Reproductively mature fish were defined by size at maturity for Coles Bay and

Georges Bay. In the Tamar River, males > 22cm and females > 25cm were conservatively selected as mature individuals based on the smallest mature size records.

To explore the trends in maturity stages for each location throughout the year and among locations, the frequency of individuals at each maturity stage between the months sampled and in different locations, was analysed using a Chi-square test of independence for males and females separately. Standardized residuals, under normal distribution, were used to determine where observed frequencies differed from expected frequencies.

Sex ratio (female as fraction of total) was estimated in different locations and in different months, and monthly differences at each location were analysed using a Chi-square test of independence.

4.3. RESULTS

4.3.1. Changes in gonad development

Changes in gonad (both ovary and testis) weight with somatic weight was dependent upon the combination of location and season ($F_{location*season}=72.52$, df 6, 713, P<0.001), with similar patterns seen for both sexes. Thus, a significant 3-way interaction between location, season, and sex was not detected. The Coles Bay mature population showed increased gonad weight during spring and summer, which then decreased in autumn (Fig 4.1). In Georges Bay, the increase in gonad weight occurred in spring, then declined in summer and remained low (Fig 4.1). Interestingly the increase in gonad weight was detected during the winter in the Georges Bay population, but not in the Coles Bay population. However, Coles Bay

individuals had 52 and 84% higher gonad weight than Georges Bay in spring and summer, respectively. Unlike the two other locations, the adjusted mean weight of gonads in the Tamar River population was consistently < 1gr throughout the year.



Figure 4.1. Mean gonad weight $(gr \pm SE)$ adjusted for somatic weight of *P.* bassensis at each location and in each season. Means sharing the same letter are not significantly different. Asymmetric SEs resulted from back transformation of logarithmic values. Values in parentheses are sample size.

During the spawning season, monthly variation in gonad weight with somatic weight was a function of an interaction between location and month $(F_{location*month}=5.31, df 5, 613, P<0.001)$. Highest gonad weight was recorded in Coles Bay in December, which dropped to its lowest level in March (Fig 4.2). In comparison, the heaviest gonad weight was approximately 50% less in Georges Bay and occurred three months earlier in September. Mean gonad weight was small between September and January in the Tamar River.



Figure 4.2. Monthly changes in mean gonad weight $(gr \pm SE)$ adjusted for somatic weight of *P. bassensis* in three locations. Means sharing the same letter are not significantly different. Asymmetrical SEs resulted from back transformation of logarithmic values. Values in parentheses are sample size.

The proportion of mature females at different stages of maturity (Fig 4.3) differed among the three locations across all times (χ^2 =199.4, df 10, P<0.001). Additionally, in Coles Bay and Georges Bay, the proportion of mature females in each gonad stage depended upon the month of sampling (CB χ^2 =349.7, df 50, P<0.001; GB χ^2 =134.3, df 26, P<0.001). This was not the case for the Tamar (χ^2 =8.2, df 14, P=0.726), where only two fish had developing ovaries (Fig 4.3a) and the remained were reproductively immature.

The appearance of hydrated oocytes in the ovaries was approximately three months earlier in females from Georges Bay compared to females from Coles Bay. In 2001/02, Georges Bay females with developing ovaries (stages 3 & 4) first appeared in July 2001 and by November 2001 59% of females were spent (stage 7) (Fig 4.3b). During 2002/03 females with hydrated oocytes (stage 6) were caught in September, but were absent from the population by November with 25% of females

caught in November were spent. From January to July all females in Georges Bay had regressed ovaries.

In Coles Bay, developing (stage 4) and ripe (stage 5) oocytes were present in the ovary in females caught in October (Fig 4.3c). The presence of females with ripe oocytes in October and with hydrated oocytes in the ovary until March suggested an extended spawning activity in Coles Bay. As postovulatory follicles (POF) were present in ovaries of females from Coles Bay from October to March, absence of hydrated oocytes in fish during some months is more related to the time of sampling and/or sample numbers. Interannual variation in reproductive activity was seen in Coles Bay. In the 2000/01 spawning season by March 84% of females were either in stage 7 (spent) or stage 2. In contrast in the 20002/03 spawning season none of the 23 females caught in March were spent; the greatest percentage of spent individuals were seen in May.

The number of mature males at each maturity stage depended on location across all times ($\chi^2 = 143.8$, df 8, P<0.001). While stage 5 individuals (ripe) dominated the Coles Bay population, stage 2 fish (immature) were predominant in the Tamar River (Fig 4.4). In each location, the proportion of males in each testis stage depended upon month of sampling (GB $\chi^2=132.7$, df 24, P<0.001; CB $\chi^2=329.2$, df 32, P<0.001; TR $\chi^2=23.7$, df 14, P<0.05). Except for six developing males (stages 3 & 4), no fully spermiated males were found in the Tamar River (Fig 4.4a). A considerable proportion of males in Georges Bay were fully spermiated between September and November (Fig 4.4b), but by January approximately 72% of male were reproductively inactive. In Coles Bay, regressed (spent) males were first sampled in March and, between October 2002 and March 2003, >60% of males were fully spermiated (Fig 4.4c).



Figure 4.3. Changes in the proportion of mature-sized females in each reproductive stage caught in (a) Tamar River (n= 108), (b) Georges Bay (n= 89), and (c) Coles Bay (n= 232) between March 2001 and May 2003.

Chapter 4





Chapter 4

4.3.2. Gonad weight vs. size/age

There were differences in the correlation of gonad weight with age and total length among locations (Table 4.1). Correlations of gonad weight, both ovary and testis, with age and total length were stronger for the Coles Bay population than for the Georges Bay and Tamar River populations (Table 4.1). Unexpectedly, correlations of ovary weight with age or total length were similar for Georges Bay and the Tamar River populations. However, higher correlations of testis weight with age and total length were found in Georges Bay population compared with the Tamar River population.

Table 4.1. Correlations between gonad weight and total length and age for populations in each location.

	Total length	Age
Ovary weight		
Georges Bay	r=0.65, n=77, P<0.001	r=0.46, n=74, P<0.001
Coles Bay	r=0.79, n=139, P<0.001	r=0.67, n=105, P<0.001
Tamar River	r=0.67, n=136, P<0.001	r=0.47, n=131, P<0.001
Testis Weight		
Georges Bay	r=0.63, n=88, P<0.001	r=0.39, n=88, P<0.001
Coles Bay	r=0.79, n=41, P<0.001	r=0.79, n=39, P<0.001
Tamar River	r=0.44, n=105, P<0.001	r=0.31, n=101, P<0.001

4.3.3. Size and age at sexual maturity

 L_{50} was not estimated for the Tamar River population because <3% of the individuals sampled were mature. Size and age at maturity were different between males and females at Coles Bay and Georges Bay (Figs 4.5 & 4.6). In both locations the size at which 50% of males were mature was 21.7 cm TL (Fig 4.5). All males
were mature at size 31 cm TL in Coles Bay. In the Georges Bay population, there was no age or size class for either sex where 100% of individuals were sexually mature. L_{50} 's for female were 24.7 and 26.3 cm in Coles Bay and Georges Bay respectively (Fig 4.5). Females attained \geq 95% sexual maturity at 28 cm in Coles Bay.

The age at which 50% of males were mature was 2.5 and 3.5 years for Coles Bay and Georges Bay, respectively (Fig 4.6). Estimated age of maturity for Georges Bay female (5.2 years) was twice that of Coles Bay (2.6 years). In Coles Bay, all 7 year old males and 8 year old females were sexually mature (Fig 4.6).



Figure 4.5. Percentage of sexually mature male and female sand flathead, *Platycephalus bassensis*, by 1-cm length intervals, with a logistic model fitted to the data collected at the height of the spawning season. r^2 for all cases was 0.99. Symbols represent probability of maturity of fish within 1-cm intervals.



Figure 4.6. Percentage of sexually mature male and female sand flathead, *Platycephalus bassensis*, by 1-year age classes, with a logistic model fitted to the data collected at the height of the spawning season.

4.3.4. Sex ratios

There was no evidence of monthly changes in sex ratio in Georges Bay (χ^2 =9.4, df 6, P=0.15) or the Tamar River (χ^2 =18.2, df 14, P=0.19), with almost the same ratio between sexes across all times. In contrast, the sex ratio in Coles Bay depended upon the month of sampling (χ^2 =55.2, df 10, P<0.001). The percentage of females in the Coles Bay population was significantly greater in October (start of the spawning season) in both 2001/02 (79%) and 2002/03 (83%).

4.4. DISCUSSION

There was evidence of spatial and temporal variability in reproductive investment, duration of spawning activity, and size/age at maturity of *P. bassensis* among the three locations sampled. The Coles Bay population showed consistently better reproductive condition than the other two locations. In contrast, the Tamar River population revealed minimal reproductive effort, while reproductive characteristics of the Georges Bay population were intermediate to these two populations.

Differences in reproductive investment among the locations were evident based on gonad weight, with individuals from Georges Bay and Tamar River having significantly lighter gonads than those from Coles Bay during the spawning season. Gonad weight also showed seasonal changes both in Coles Bay and Georges Bay, whereas the Tamar River population did not exhibit any evidence of seasonal changes in gonad weight. As seasonal changes in gonad weigh is an indicator of reproductive investment (DeVlaming *et al.*, 1982; Tamate & Maekawa, 2000), lack of seasonal changes in gonad weight in the Tamar River suggests an absence of reproductive activity in the population sampled. In contrast, very high gonad weight in Coles Bay during spring and summer suggests high reproductive investment. As

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the Coles Bay population consisted predominantly of larger individuals (Chapter 2), larger body sizes would allow the production of larger gonads as reproductive capacity is strongly influenced by size of individuals (Marteinsdottir & Begg, 2002). Such capability was evident in sand flathead as gonad weight, especially in Coles Bay, which was strongly correlated with total length. In contrast, because of the relatively small size of Georges Bay individuals (Chapter 2), gonad weight was less than Coles Bay due to constrains of body size (Myers & Doyle, 1983; Heino & Kaitala, 1999). Therefore, population that mainly consisted of bigger individuals, because of larger gonads, may have greater reproductive potential, compared to population with smaller individuals.

In many fish species gonad weight together with proportion of different reproductive stages is considered a reliable method to estimate the duration of the reproductive season (Fowler *et al.*, 2000; Brown-Peterson *et al.*, 2001). A single peak in gonad weight during spring and minimal gonad weight in summer in the Georges Bay population suggests a shorter spawning season, compared to the protracted spawning season (~6 months) of Coles Bay. Apart from inter-population differences in the duration of spawning, the length of the spawning season differed between the two years of spawning, particularly in Coles Bay, which was two months longer in the 2002/03 than in 2001/02. For fishes that spawn multiple batches of eggs during a single spawning season the length of the spawning period of individuals increases with fish sizes (Trippel *et al.*, 1997). Hence, the presence of larger fish in the Coles Bay population is the most probable explanation for the longer spawning season. In serial spawners a longer reproductive season ensures a greater number of spawning events in each reproductive season (Hunter *et al.*, 1992; Barbieri *et al.*, 1994; Schaefer, 1996). However, while it is believed that the time

between releasing of egg batches increases with body size (Kjesbu *et al.*, 1990; Kjesbu *et al.*, 1996), spawning frequency does not significantly vary between populations of *P. bassensis* with predominantly large and small individuals. However, due to a longer spawning season the Coles Bay population spawn at least three times more than the Georges Bay population within a single spawning season (Chapter 3). Therefore, given equal batch fecundity, the population with the longer spawning season (e.g. Coles Bay) would have increased chance to spawn more batches of eggs and therefore higher reproductive output is expected, compared to a population with shorter spawning season (e.g. Georges Bay). Moreover, a shorter spawning period may be disadvantageous for larvae, as it may reduce the probability that larvae hatch when environmental conditions favour growth and survival (Trippel *et al.*, 1997).

Spawning in the Georges Bay population occurred in early spring given that the highest gonad weights and greatest proportion of ripe fish were present in September. In contrast, the greatest gonad weight in Coles Bay occurred 3 months later in early summer (December). Temperature and hours of daylight have been proposed as the main environmental factors that can cause differences in the initiation of spawning among populations (Kojima, 1981; Wootton, 1982; Scott & Pankhurst, 1992). Water temperatures increased in Georges Bay one month earlier than in Coles Bay (Chapter 2), possibly explaining the difference in the start of spawning. However, the start of spawning may be affected by other exogenous factors like, plankton productivity (Cushing, 1972; Leggett & Deblois, 1994), and/or endogenous hormones (Stacey, 1984; Bye, 1990), which was not explored in this study. Advancing or delaying spawning may result in larvae missing the peak densities of appropriately sized plankton prey (Leggett & Deblois, 1994; Trippel *et*

al., 1997), however, early spawning may provide a longer growing season for fish and the cumulation of stored energy may prolong survival of larvae when food supply diminish (Shuter *et al.*, 1980). From population dynamics points of view, such variability in birth date, together with plasticity of fish growth can cause large variation in size-at-age and potentially effect growth rate of the population.

Sex ratios of *P. bassensis* varied temporally rather than spatially. During both years of sampling, the sex ratio was in favour of females in Coles Bay during October. The absence of hydrated oocytes in females during October, together with a significantly greater proportion of females in this month, suggests that *P. bassensis* males do not associate with the groups that comprised of non-hydrated females. Alheit *et al.* (1984) similarly showed segregation between groups composed mostly of males with hydrated (ready to spawn) females and other groups with fewer males and non-hydrated females. It is also possible that males join the spawning grounds later than females, as for example in Atlantic croaker males (Barbieri *et al.*, 1994). It can be assumed that temporal variation in sex ratio resulted from differences in *P. bassensis* reproductive behaviour during spawning periods, rather than any other factors like fishing disturbances.

In comparison to the other two populations, the reproductive output in the Tamar River population was minimal or absent. Small changes in gonad weight were evident during the spawning season, very few individuals (< 3%) were sexually mature, and there was a very high (100%) occurrence of atresia. All these factors suggest that the Tamar Estuary is most probably not part of the spawning grounds for *P. bassensis*. This may be a function of the low salinity in the Tamar Estuary, which was consistently lower than the other two locations and lowest (30-31 ‰) in

September and October (Chapter 2). There is a weak vertical stratification in the Tamar Estuary as a function of the freshwater flow of the Tamar River which decreases salinity, particularly in early spring (Lara & Neira, 2003). Such environmental conditions may not be optimal for spawning of a marine species like sand flathead. The reproductive biology of marine species that normally experience very little variation in the salinity is sensitive to variations in salinity (Gunter, 1961; Bye, 1990). To ensure more optimal conditions some marine species use estuaries as nursery grounds and migrate out of estuary as adults (Dando, 1984; Jaureguizar et al., 2004). Other proximate control factors like chemical cues, light, flow rate, and productivity of environment may influence on pattern of movement behavior of adult fish (Bye, 1990). This information is not available for any of the locations in this study, however, their potential influence would warrant future investigation via laboratory experiments and collection of these parameters in the wild. However, it is possible that the Tamar Estuary may be an unsuitable habitat for spawning by P. bassensis.

Estimated males size at maturity in the present study was similar to that found in a previous study (Jordan, 1998). However, our estimates of female size at maturity are slightly larger than previously reported (23.5 cm). This discrepancy may be attributed to: 1) the use of total length in this study compared to fork length for previous study, and 2) estimation of size at maturity for each population separately in this study, rather than pooling data from different populations as done in the previous study. The difference between the smallest and largest *P. bassensis* to reach maturity was large for both males (17.8-29.1 cm) and females (18-33 cm). Extreme variation in size at first sexual maturity is a feature common to serial spawners as a

consequence of a large range of birth dates (Nikolskii, 1969; Cargnelli & Gross, 1996; Lowerre-Barbieri et al., 1998).

With the exception of male size at maturity, for both sexes the size and age at which 50% of individuals' attained maturity, was higher in Georges Bay compared to Coles Bay. Differences in size and age of sexual maturity between these two populations may be attributed to the relatively high growth rate of Coles Bay individuals (Chapter 2), as a decrease in size/age at maturity of fish species can be result of higher growth rates (Trippel, 1995; Poortenaar et al., 2001). Therefore, slower growth rates of Georges Bay individuals, either due to fishing effect and/or environmental conditions, may explain a delay in maturity. Furthermore, the larger size at maturity may reflect the movement of the faster growing and maturing individuals out of Georges Bay to other spawning areas. Maturation at a larger size in this population could be problematic as >60% of the Georges Bay population was smaller and younger than the estimated size and age at maturity (Chapter 2). In many exploited fish stocks a decrease in size/age at maturity is accompanied by lower population mean size/age (Beacham, 1983; Joergensen, 1990; Bowering & Brodie, 1991; Trippel, 1995). However, in this study the smaller size and younger age at maturity (e.g. Coles Bay) were not coincident with a lower population mean size/age. Such a contradiction may result from less-selective recreational fishing effects on the population studied, whereas in almost all previous studies highly selective commercial fishing accounted for changes in size/age at maturity. The effects of recreational fishing on size/age at maturity, and its possible relation to stock structure need to be explored in the future.

Both spatial and temporal variability in reproductive characteristics of *P. bassensis*, seen in this study, indicate that reproductive output and performance of

this species vary from year to year and among populations. This is due to either environmental conditions and/or specific size/age structure of stock because of fishing or movement of fish. Apart from causative parameter(s) of reproductive variability in P. bassensis, such variability can have a marked impact on conservation of the next generation of each population, as reproduction is the main component of stock restoration. Under the current fishing regulations, spawners are still fished during the spawning season. Removal of spawning individuals could potentially be detrimental for the stability of the populations and in particular for less productive populations, e.g. Georges Bay, as the level of egg production may not be sufficient for survival of the next generation. Approximate spawning time of sand flathead at each location can be helpful for managing fishing activity during the spawning period of heavily fished populations. While the risk of fishing in spawning ground is higher during spawning periods, overfishing of immature individuals in nursery grounds, e.g. the Tamar Estuary, is no less detrimental. Productivity and sustainability of a fishery is dependent on the continued availability of juveniles, which originate from nursery ground. Hence, special consideration in management seems to be essential for a nursery ground like the Tamar Estuary. Neither minimum size limits nor daily bag limits would be quite efficient for a sustainable recreational fisheries management, unless temporal and spatial variability in reproductive performance is taken into account.

CHAPTER FIVE

SPATIAL VARIATION IN CONDITION AND PATTERNS OF REPRO-SOMATIC INVESTMENT IN SAND FLATHEAD, *PLATYCEPHALUS BASSENSIS*.

Spatial variation in condition and patterns of repro-somatic investment in sand flathead, *Platycephalus bassensis*.

5.1. INTRODUCTION

Animals with indeterminate growth (like fishes) experience trade-offs in resource allocation between growth and reproduction throughout their lives (Roff, 1983; Stearns, 1992), and individuals select when and how to channel energy between these two components. Energy partitioning in fish is often closely linked to the size/age of animal which in turn is related to status of maturity (Schultz & Conover, 1997). While immature or younger individuals allocate almost all of their available energy to somatic growth, fully mature individuals channel most of their available energy to reproduction and less to growth (Roff, 1992). In the intermediate situation, individual fish that are in the transitional stage from immaturity to maturity, or who are close to or just become mature, reproduction and growth are closely linked to each other (Roff, 1984).

In mature individuals of many fish species, the pattern of resource allocation between growth and reproduction changes seasonally (Griffiths & Kirkwood, 1995; Fox & Crivelli, 1998). In the females of the most species, the majority of available energy is allocated to reproduction during the spawning period, resulting in minimal somatic growth (Fox & Crivelli, 1998). In contrast, during non-spawning periods energy either is kept as reserve or is channelled toward somatic growth (MacKinnon, 1972). Although the pattern of energy allocation does not differ between sexes for many fish species, the energy costs for reproduction in males are not as great as females (Wootton, 1984). Resource allocation is also affected by environmental factors, such as availability of resources for individuals (Heino & Kaitala, 1999). These processes can drive life history strategies of a species and are therefore fundamental for understanding differences in life history traits among local populations of a species.

Maturing individuals or individuals in the first years of reproductive activity sensibly allocate part of the available energy to the reproduction, while still maintaining investment for growth (Diana, 1983). These individuals may postpone reproduction or change the duration and timing of reproduction within the season to maximize reproductive success (Schultz *et al.*, 1991), and to balance trade-offs between reproduction and growth, and between reproduction and survival. In contrast, older and/or larger fully-matured individuals, tend to have relatively higher weight-specific levels of energy storage (Henderson *et al.*, 1984; Larson, 1991). The scaling of storage may be one of the possible reasons that larger mature individuals have a higher potential for spawning than their smaller counterparts (DeMartini & Fountain, 1981; Parrish *et al.*, 1986). Hence, depletion rates of energy storages should decrease in larger individuals, due to the allometric scaling of metabolic rates (Paloheimo & Dickie, 1966).

Seasonal accumulation and depletion of reserves occurs in many aquatic animals; e.g. bivalve molluscs (Barber & Blake, 1991), amphibians (Wells *et al.*, 1995), and fishes (Larson, 1991; Encina & Granado-Lorencio, 1997). Fishes commonly store energy reserves as lipid and protein in various organs, mainly the liver and muscle tissue (Pekkarinen, 1980; Adams & Huntingford, 1997). Body musculature in many fish species is the main protein depot, while lipid is primarily stored in the liver (Jobling, 2001) and these reserves are generally delivered to the gonads during the spawning season (Lambert & Dutil, 2000). Variations in proximal composition, particularly in the liver and muscle, are believed to be related to changes in the extent of reproductive investment (Love, 1962). Several studies have demonstrated

relationships between proximal compositions, growth and reproductive parameters (Eliassen & Vahl, 1982; Holdway & Beamish, 1984). Proximal constituents of some fish species appear to be correlated with general condition (Lambert & Dutil, 1997). In this study, we examine the condition of *P. bassensis* at the level of the whole animal and at the level of proximal composition to quantify changes in energy allocation associated with reproductive life history characteristics.

Furthermore, because of the vitellogenesis process, which mobilises lipid and other energetic components from different tissues (mainly from liver) toward the ovaries (Henderson *et al.*, 1984), females may show different pattern in proximal composition changes, compared to males (Shulman & Love, 1999). Despite a wealth of information about energetic expenditure of reproduction especially in females (Wootton, 1998), little is known about the pattern of proximal composition changes in relation to reproduction for both sexes. This study, therefore, investigates variations in the main proximal composition as a function of reproductive states for each sex separately.

Life history characteristics of *P. bassensis* display considerable variability among locations in Tasmania (see Chapters 2, 3 & 4). The Georges Bay population grew slower than Coles Bay and the Tamar River populations after the second year of growth. *Platycephalus bassensis* also matured at larger sizes and older ages in Georges Bay, compared with Coles Bay. They also showed different reproductive strategy in different locations, with a shorter spawning period and less frequency spawning in Georges Bay compared with Coles Bay, and no evidence of spawning activity in the Tamar River. The broad aim of this chapter is to assess the relationship between these differences in life history patterns and the spatial variation in reproductive and somatic condition of *P. bassensis*. Central to this aim is the

concept of trade-offs evident between the processes of growth and reproduction. This allows us to elucidate the mechanism(s) that underlie the life history variability of *P. bassensis* populations and highlight the effect of each causative factor (i.e. environmental conditions, movement patterns, and fishing pressure) for such variability.

The life history strategy adopted by an animal and its lifetime reproductive allocation can only be understood in terms of resource allocation between reproduction and other competing needs, like growth (Heino & Kaitala, 1999). Our specific objectives were to: 1) assess the process of resource allocation between reproduction and growth in mature and immature individuals to improve our understanding of size/age dependent of resource allocation between reproduction and growth; 2) quantify gender specific seasonal changes in condition and resource allocation to distinguish effects of reproduction in resource allocation within years; and 3) examine the somatic, reproductive, and liver conditions of *P. bassensis* to quantify spatial variation in the differential allocation of energy. By having this knowledge, we would be able to compare the condition of *P. bassensis* populations, which improves our understanding of variations in life history characteristics of this species.

5.2. MATERIALS AND METHODS

5.2.1. Study sites and sampling

Fish were sampled from three locations (Tamar River, Georges Bay, and Coles Bay) around the north, north-eastern, and east coasts of Tasmania, Australia (see Chapter 2 for details). Sampling was undertaken seasonally from inshore sites in the three locations between March 2001 and March 2003, using hook and line (Table 5.1). Hook and line method is a less size-selective collection method compared to demersal trawls and gill nets, which typically under-represent smaller fish (King, 1995). This ensures that the animals collected are in a size range that encompassed immature, maturing, and mature individuals. All fish were caught in 5-25 m water depth. To obtain a representative sample of the *P. bassensis* population, fishing was carried out at 4-6 haphazardly selected sites at each location. Upon capture, animals were stored on ice until dissection later in the day of collection.

Table 5.1. Months of *Platycephalus bassensis* collection. Values in parenthesis are total number of sampling at each season and location. n = sample size.

_	Spring	Summer	Autumn	Winter
Georges Bay	Sep & Nov (3)	Jan & Feb (2)	May (1)	Jul (1)
n	166	74	45	40
Tamar River	Sep, Oct, Nov (5)	Dec & Jan (2)	Mar (1)	Jun (1)
n	182	77	61	52
Coles Bay	Oct & Nov (4)	Jan & Feb (3)	Mar & May (3)	Jun (1)
	127	156	155	62

5.2.2. Laboratory processing

All fish were sexed, measured to the nearest millimetre total length, and weighed to the nearest gram. Visceral (viscera plus gonads) weight for each fish was recorded and somatic weight was calculated as total body weight minus visceral weight. To assess the water content of muscle tissue a piece of muscle tissue (5-10 gr) was taken from the left side of each fish above the lateral line and between the dorsal fin and the head, and weighed to the nearest 0.1 mg. To obtain liver water and lipid content the whole liver was removed and weighed to the nearest 0.1 mg. Water content was determined as the difference in tissue weight before and after 3-4 days of freeze-drying. Liver lipid content was estimated using a chloroform-methanol extraction method (Bligh & Dyer, 1959). Duplicates were run on a random sample of five males and five females from each location and season.

5.2.3. Analysis

To explore changes in the condition of fish as a function of the allocation of energy to reproduction, reproductively mature individuals were classified into one of three reproductive states depending on the season of capture; pre-spawning (winter), spawning (spring & summer), and post-spawning (autumn). As Georges Bay individuals did not show any evidence of reproductive activity in summer (Chapter 3), individuals caught in this season were classified as post-spawning. Reproductively mature fish (Chapter 3) were defined by the size-at-maturity for each location. Size at 50% maturity for female is 24.7 and 26.3 cm in Coles Bay and Georges Bay, respectively (Chapter 4). Females larger than this were therefore selected as mature at each specified location. Males > 21.7 cm were categorised as mature for both Coles Bay and Georges Bay. Insufficient mature individuals were caught in the Tamar River, therefore, this location was not included in the analysis of mature individuals. However, the Tamar River males ≤ 22 cm and females ≤ 25 cm were conservatively selected as immature individuals based on the smallest mature size records, and therefore only immature samples from the Tamar River included in the analysis of condition.

For mature and immature individuals, separately geometric mean regression (Model II) analyses were used to describe the relationship between total length (TL) and somatic weight (SW), using log-transformed data to linearise the relationship. A residual (actual weight minus predicted weight) for each individual was obtained

from these equations and standardised by dividing each residual by the standard deviation of the predicted values. These residual values provided a size-independence measure of somatic condition (Jakob *et al.*, 1996; Hayes & Shonkwiler, 2001). An individual with a large positive residual is heavier for its length and is suggested to be in better somatic condition than an individual with a negative residual. Variation in somatic weight of immature individuals was explored as a function of location and season using a 2-way analysis of covariance (ANCOVA), with total length as the covariate. A 3-way ANCOVA, with location, sex, and reproductive state as the factors of interest and total length as the covariate, was used to explore variation in somatic weight of mature individuals.

A 3-way ANCOVA, with location, sex, and reproductive state as the factors of interest and somatic weight as the covariate, was used to explore variation in gonad weight of mature individuals. As an indicator of the level of reproductive investment, residuals were also generated from gonad weight-somatic weight regression relationships in the same way as for somatic condition. To assess the degree of association between somatic condition and level of reproductive investment, residuals from somatic weight-at-length and gonad weight-at-somatic weight regressions were correlated against each other.

Geometric mean regression was used for mature and immature individuals separately to generate liver weight-somatic weight relationships, using logtransformed data. Standardised residual values from these equations were used as measures of liver condition. The effects of location, sex, and reproductive state on the variation of liver weight in mature individuals was analysed using a 3-way ANCOVA, with somatic weight as the covariate. For immature individuals, sex was

not a factor of interest in looking at variation in liver weight. Therefore, the effects of location and season were analysed by a 2-way ANCOVA.

The concentrations of lipid and water in liver and water in muscle were analysed, using a 3-way and 2-way ANOVA, for mature and immature individuals, respectively. The factors of interest were season, location, and reproductive state, for mature individuals and location and season for immature individuals. Following the above univariate analysis, when a significant difference was obtained, a Tukey's HSD post-hoc test was used to determine where significant differences were occurred, using ANOVA.

Significant levels were adjusted (Bonferroni procedure) in multiple correlations of proximal composition to control Type I error (Quinn & Keough, 2002).

5.3. RESULTS

5.3.1. Condition

The length-weight (TL-SW) relationship of immature individuals did not change as a function of the interaction of location*season (F=0.44, df 4, 441, P=0.777), season (F=1.32, df 2, 441, P=0.266), or location (F=1.76, df 2, 441, P=0.173). In contrast, in mature individuals, reproductive state was the only factor that showed a significant impact on the TL-SW relationships (Table 5.2). The slope of TL-SW relationships for mature individuals differed between the reproductive states (Fig 5.1). During and after the spawning period, increases in weight with length were 7% slower than in the pre-spawning period.

Table 5.2.	ANCOVA exploring the effect of gender, location, and reproductive
state on the so	matic weight of Platycephalus bassensis using total length (TL) as a
covariate.	

Source of variation	df	Type III SS	MS	F	P>F
Location*Log TL	1	0.00007	0.00007	0.10	0.746
Sex*Log TL	1	0.00146	0.00146	2.36	0.125
Reproductive state*Log TL	2	0.00533	0.00267	4.31	0.014
Location*Sex*Log TL	1	0.00106	0.00106	1.71	0.190
Location*Reproductive state*Log TL	2	0.00015	0.00008	0.12	0.884
Sex*Reproductive state*Log TL	2	0.00001	0.00001	0.01	0.989
Location*Sex*Reproductive state*Log TL	2	0.00116	0.00058	0.93	0.393
Residual	564	0.33452	0.00062		



Figure 5.1. The slope (\pm 95% confidence limit) of the total length-somatic weight relationships of mature individuals for each reproductive state. Value above each point is the sample size. r^2 was 0.98 for each state.

Variation in gonad weight with somatic weight in mature individuals was only a function of reproductive state (Table 5.3). Gonad weight relative to somatic weight

for mature individuals increased 36% faster during the spawning season than during the pre-spawning period (Table 5.4). The slopes of this relationship were similar between the spawning and post-spawning periods. However, somatic weight explained around 55 and 62% of the variability in gonad weight during and after the spawning period, respectively. Furthermore, individuals during spawning had a higher intercept than individuals after spawning (Table 5.4), suggesting a larger gonad for somatic weight during spawning than post-spawning.

Table 5.3. ANCOVA examining the effect of gender, location, and reproductive state on the gonad weight of *Platycephalus bassensis* using somatic weight (SW) as a covariate.

Source of variation	df	Туре III SS	MS	F	P>F
Location*Log SW	1	0.008	0.008	0.06	0.805
Sex*Log SW	1	0.316	0:316	2.37	0.124
Reproductive state*Log SW	2	0.926	0.463	3.46	0.032
Location*Sex*Log SW	1	0.004	0.004	0.36	0.850
Location*Reproductive state*Log SW	2	0.311	0.155	1.16	0.313
Sex*Reproductive state*Log SW	2	0.508	0.254	1.90	0.150
Location*Sex*Reproductive state*Log SW	2	0.067	0.033	0.25	0.775
Residual	564	72.296	0.134		

Table 5.4. Geometric mean regression relationships of somatic weight vs gonad weight for mature *Platycephalus bassensis* at different reproductive states with the locations and genders pooled.

	n	Slope	95% C.I. of slope	Intercept (SE)	r ²	p>t
Pre-spawning	70	2.03	1.74-2.32	-4.32 (0.32)	0.64	< 0.001
Spawning	306	3.21	2.98-3.44	-6.26 (0.25)	0.55	< 0.001
Post-spawning	189	2.95	2.69-3.21	-6.45 (0.29)	0.62	<0.001

The correlation between the somatic weight-length residuals and gonad weightsomatic weight residuals for each reproductive state was not significant in the Georges Bay individuals (Table 5.5). However, in Coles Bay, pre and post-spawning mature individuals had a significant negative correlation between the somatic weight-length residuals and gonad weight-somatic weight residuals (Table 5.5). This was mostly due to relative light gonads during pre-spawning and regressed gonads in post-spawning periods in mature individuals, which had high somatic weight (Fig 5.2). During the spawning season no significant correlation was found between somatic condition and reproductive investment for individuals at either location.

Table 5.5. Pearson's correlation coefficients between somatic condition and gonad condition in mature *Platycephalus bassensis* at different reproductive states at each location. See text for details of calculations of somatic and reproductive condition.

Location &	· · · ·	, <u></u> ,	
reproductive state	r	n	p>r
Coles Bay			<u></u>
Pre-spawning	-0.41	54	0.002
Spawning	-0.11	224	0.118
Post-spawning	-0.42	126	0.001
Georges Bay			·
Pre-spawning	0.13	16	0.630
Spawning	0.16	82	0.139
Post-spawning	-0.12	63	0.345



Figure 5.2. Residual values for mature *Platycephalus bassensis* derived from the total length-somatic weight and somatic weight-gonad weight relationships for Coles Bay (triangles) and Georges Bay (squares) at different reproductive states.

There was no evidence for mature individuals that variation in liver weight, adjusted for somatic weight, was explained by location, reproductive state, or sex (Table 5.6). There was also no significant difference observed in liver weight-somatic weight relationships for immature individuals in combination with season and location (F=2.01, df 4, 441, P=0.092), location (F=2.51, df 2, 441, P=0.082) or season (F=0.28, df 2, 441, P=0.755).

Table 5.6. ANCOVA exploring the effect of gender, location, and reproductive state on the liver weight of mature *Platycephalus bassensis* using somatic weight (SW) as a covariate.

Source of variation	df	Type III SS	MS	F	P>F
Season*Log SW	-2	0.008	0.008	0.35	0.703
Sex*Log SW	1	0.020	0.020	1.67	0.196
Location*Log SW	1	0.032	0.032	2.73	0.099
Location*Sex*Log SW	1	0.026	0.026	2.20	0.138
Location*Season*Log SW	2	0.028	0.014	1.18	0.309
Sex*Season*Log SW	2	0.003	0.002	0.13	0.876
Location*Sex*Season*Log SW	2	0.016	0.008	0.67	0.514
Residual	564	6.327	0.012		

5.3.2. Proximal analysis

In mature individuals, the concentration of liver lipid was dependent on an interaction between location, reproductive state, and sex (F=16.58, df 2, 56, P<0.001). Differences in lipid concentration were not consistent among the genders and location or reproductive states (Fig 5.3). Males and females from Georges Bay and females from Coles Bay showed changes in liver lipid concentration with reproductive state, while Coles Bay males showed no changes (Fig 5.3). A significant decrease was seen in the liver lipid concentration of Coles Bay females from the pre-spawning period to the spawning period, as expected if stored lipid is used from the liver (Fig 5.3a). In contrast, Georges Bay females showed a dramatic doubling in lipid content between pre-spawning and spawning period, followed by a halving in the post-spawning period. As a result, Georges Bay females during the spawning period had a higher proportion of liver lipid storage, compared with their

counterparts in Coles Bay. Prior to spawning, Georges Bay females had lower lipid content than Coles Bay females.

Georges Bay males, however, revealed different pattern from females in variation of liver lipid across the seasons. Prior to spawning, Georges Bay males had a higher liver lipid content than during and after spawning, causing differentiation between sexes in Georges Bay during the spawning season (Figs 5.3a & 3b). The decrease of liver lipid content between the pre-spawning period and the spawning period however, did not occur for Coles Bay males. Moreover, in Coles Bay, the concentration of liver lipid was the same between the sexes in all three reproductive states. In the liver of immature individuals, there was no evidence of location*season impact on concentrations of either lipid concentration (F=0.74, df 6, 44, P=0.618), or water (F=1.54, df 6, 44, P=0.196).

The pattern of changes in liver water content was also a function of reproductive state, sex, and location (F=17.48, df 2, 57, P<0.001). Except in two cases, the pattern of change was the inverse to changes seen in liver lipid concentration (Fig 5.4). During the pre-spawning period, liver water content differed between sexes in Coles Bay. Differences in liver lipid content between Coles Bay males and females were not detected. For females, liver water content did not differ between the two locations, although there were differences in liver lipid concentration between theses locations.



Figure 5.3. Average liver lipid concentration of mature (a) females and (b) males *Platycephalus bassensis* in each reproductive state. Superscripts were generated from a Tukey's HSD post-hoc comparison of means for every combination of sex, season and reproductive state.



Figure 5.4. Average liver water concentration of mature (a) females and (b) males *Platycephalus bassensis* in each reproductive state. Superscripts were generated from a Tukey's HSD post-hoc comparison of means for every combination of sex, season and reproductive state.

Differences in water content in muscle tissue of mature individuals were not attributed to location, sex, or reproductive state (Table 5.7). In contrast, muscle water content in immature individuals differed significantly among seasons, but this difference depended upon the location (Table 5.8). In Georges Bay and Tamar River populations, there was no difference among seasons, while in individuals from Coles Bay, water content in autumn was 4-5% lower than during summer and winter (Fig 5.5).

Table 5.7. ANOVA examining the effect of gender, location, and reproductive state on the muscle water content of mature *Platycephalus bassensis*.

Source of variation	df	Type III SS	MS	F	P>F
Location	1	0.185	0.185	0.17	0.685
Sex	1	1.524	1.524	1.38	0.247
Reproductive state	2	4.413	2.207	2.00	0.149
Location*Sex	1	0.561	0.561	0.51	0.480
Location*Reproductive state	. 2	4.020	2.010	1.82	0.175
Sex*Reproductive state	2	1.961	0.981	0.89	0.420
Location*Sex*Reproductive state	2	3.163	1.582	1.43	0.251
Residual	52	45.340	1.106		

 Table 5.8. ANOVA examining the effect of location and season on the muscle

 water content of immature Platycephalus bassensis.

Source of variation	df	Type III SS	MS	F	P>F
Location	2	0.516	0.258	0.28	0.758
Season	3	7.616	2.539	2.76	0.059
Location*Season	6	23.902	3.984	4.34	0.003
Residual	54	27.532	0.918		



Figure 5.5. The average muscle water content of immature *Platycephalus* bassensis for every combination of location and season.

Somatic condition did not correlate with liver lipid content in either mature (r=0.18, n=57, P=0.173) or immature (r=0.21, n=45, P=0.162) individuals. Similarly, correlation between liver condition and liver lipid content was not significant either in mature (r=0.13, n=72, P=0.332) or immature (r=0.1, n=54, P=0.546) individuals.

There was, however, a significant negative correlation (r=-0.44, n=52, P=0.014) between muscle water content and liver lipid content of mature individuals (Fig 5.6), while such association was not evident in immature individuals (r=-0.20, n=30, P=0.288). In general, mature *P. bassensis* with 74-78 % muscle water content had a wide range of liver lipid content (3-29 %). At higher values of muscle water content (>78 %), consistently small (~ 4%) amounts of lipid were in the liver.



Figure 5.6. Liver lipid content vs muscle water content for mature *Platycephalus* bassensis caught in Coles Bay and Georges Bay.

5.4. DISCUSSION

The process of energy allocation and condition of P. bassensis populations partially explained the observed spatial and temporal variability in the life history characteristics. Differences in somatic condition among populations were not large relative to the differences in life history parameters of growth and reproduction (Chapters 2, 3 & 4) among the same P. bassensis populations. Most of the observed differences in both somatic and reproductive condition were related to reproductive states, rather than location. Furthermore, this study showed that proximal composition of liver of mature individuals changes with reproductive state, though the pattern of such changes was different between sexes and locations.

Somatic condition of both mature and immature *P. bassensis* was similar between sexes and among the locations. In many fish species, somatic, reproductive, and

liver condition are related to nutritional history, growth, maturation state, and other biological process (Holdway & Beamish, 1984). Similarity in somatic and liver condition among locations may provide a crude indicator of current nutritional status and previous nutritional history of *P. bassensis* populations, as fish in poor feeding conditions typically display poor overall condition (Pedersen & Jobling, 1989; Ratz & Lloret, 2003). Therefore, results obtained from body condition of *P. bassensis* populations suggest similarity in prevailing conditions such as food availability and temperature for populations.

Differences in somatic condition of mature *P. bassensis* were due to the reproductive status of individuals. Decrease in body mass during and after spawning may be due to either depletion of somatic energy stores because of reproductive activity or combination of reproduction effect and seasonal food availability (Lloret & Planes, 2003). As immature individuals did not show any evidence of seasonal changes in somatic condition, seasonal food availability is less likely to be reason for variations in somatic condition of mature individuals throughout seasons. In many fish species, spawning is accompanied by poor somatic condition and the recovery of condition may be slow and is evident until well into the post-spawning period (Whalen & Parrish, 1999; Lambert & Dutil, 2000). This study also showed that increase in body weight relative to length was slower during the post-spawning period than in the pre-spawning period. This is consistent with the hypothesis that no organisms can be simultaneously good at growth, survival, and reproduction (Stearns, 1989), and allocating energy to gonad growth normally occurs at the expense of somatic growth (Macdonald & Bayne, 1993; Sato, 1994).

This study found that the association between somatic condition and reproductive condition of *P. bassensis* varied spatially and temporally. Reproductive condition of

mature individuals at Coles Bay was negatively correlated with somatic condition both before and after spawning, however, this was not the case for the Georges Bay population. This should be treated with caution, because of low association between somatic condition and reproductive condition, especially in Georges Bay. The Coles Bay population had proportionally greater numbers of older and larger individuals, which had greater somatic weight compared with that at Georges Bay. Because of high weight-specific levels of energy storage in larger individuals, compared to their smaller counterparts (Schultz & Conover, 1997), it is expected that larger/older fish would have relatively high energy reserve for reproductive investment. Therefore, the greater somatic mass of most Coles Bay individuals support prolonged and more frequent spawning activities along with high gonad weight (Chapters 3 & 4). The consequence of such extreme reproductive investment during the spawning season in Coles Bay can be seen in the form of the negative correlation between somatic and reproductive condition before and after spawning. In comparison to Coles Bay, lower somatic weight of mature individuals in Georges Bay correspond with a moderate increase in gonad weight and short spawning activity.

Despite similarity in somatic and liver condition of mature individuals from Georges Bay and Coles Bay, the pattern of variation in liver lipid and muscle water contents was different between the two locations. The change in liver lipid content with reproductive state suggests that *P. bassensis* uses this lipid for reproductive activity. This is consistent with the role of liver in processing mobilised fatty acids from muscle prior to their transfer to gonads in different fish species (Henderson *et al.*, 1984; Adams & Huntingford, 1997; Lloret & Planes, 2003). A dramatic decline in the liver lipid content of Coles Bay females from the pre-spawning period to the spawning period suggests usage of liver lipid reserve for reproduction, whereas such

a large investment for reproduction was not evident in Georges Bay females. One possible explanation for such difference is the prolonged spawning season (~ 6 months) in Coles Bay, compared with 1-2 months spawning period in Georges Bay. Apart from this, an early start of spawning activity and short duration of spawning in Georges Bay may have resulted in some mature individuals close to the end of spawning period not being reproductively active, and therefore instead of using liver lipid storage they start reserving it. This is in agreement with increased level of lipid reserve in the spawning period, compared to utilised reserve of lipid in the prespawning period. Thus, variation in proximal condition is directly related to reproductive state.

Georges Bay females had higher lipid storage than males during the spawning period. This is in contrast to many other species, where males had higher lipid level than females because lipid stores are consumed more rapidly during ovulation in females as gonad investment is higher (Shulman & Love, 1999; Okuda, 2001). Although, in some species, female spawners had better liver condition than male spawners (Lloret & Planes, 2003), the reasons for this response are not evident. It is very unlikely that the cost of gamete production in males is higher than females, as basic energy demand for spermatogenesis is not as large as vitellogenesis (Tyler & Sumpter, 1996). Thus, one possible explanation for use of lipid reserve during the spawning period can be the high cost of reproductive behaviour for male spawners. This is hard to reveal as almost no information is available on reproductive behaviour of either *P. bassensis* or other platycephalids. It is also probable that male spawners of *P. bassensis* consume less food during the spawning period. In some fish species, males stop feeding, while females continue to feed throughout the

spawning period (Shulman & Love, 1999). This causes decline in body reserve of males.

An increase in muscle water content is often considered an indication of protein depletion (Stirling, 1976), which is mostly seen during the spawning period or starvation (Johnston, 1981; Maddock & Burton, 1994). However, such changes were not seen in mature *P. bassensis*. This suggests that liver lipid content was not below the critical value, such as in cod, for example, in which it has been shown that increased water content (84%) and protein depletion only occurs once liver lipid stores decreases to $\leq 2\%$ (Black & Love, 1986). This is consistent with our results, as muscle water content in *P. bassensis* increased when liver lipid was around 3%. The variation in muscle water content of immature individuals was minor and only evident in Coles Bay. Such variation might be related to quality and quantity of food consumed during different seasons, as the importance of food in proximal composition of fish muscle has been well documented (Cowey & Sargent, 1979; Walton & Cowey, 1982).

This study did not detect a correlation between liver lipid concentration and liver condition, despite it being confirmed that liver size is mostly related to lipid content (Lloret & Planes, 2003). As there is a converse relationship between water and lipid content of liver (Iles & Wood, 1965; Vijayakumar, 1987), lipid replaced with water kept the size/weight of liver the same as before the mobilization of the lipid from liver to the ovaries (Pekkarinen, 1980). Therefore, a lack of correlation between liver condition and liver lipid content in *P. bassensis* might occur as a result of converse relationship between lipid and water content of liver. The nature of substitution of water and lipid in the liver was mainly related to reproductive status, while the effects of gender and location were minor.

Variation in body condition is potentially one of the contributing factors in variability of the life history characterises (Stearns, 1992). This study did not detect significant differences in the condition of *P. bassensis* populations. However, a significant variation was found in the life history characteristics of *P. bassensis* populations, suggesting that exogenous factors, such as fishing mortality and/or fish movement, most probably drive such variations. Though one cannot draw conclusions on how and to what extent the observed variation in the life history traits result from fishing activity or other exogenous factors, such different life history variations may respond differently to changing fishing pressure. A comprehensive investigation on fishing pressure is required to elucidate such a response. However, the present results should be taken into consideration when reviewing recreational fishing regulations. Spatially structured management would allow populations that need more protection, taking into account differences in life history characteristics despite little evidence at the sub-organismal level i.e. condition of differences.

CHAPTER SIX

Synthesis and future directions

6.1. SUMMARY

This study quantified spatial and temporal variability in life history characteristics of sand flathead *Platycephalus bassensis*, and sought to understand this variability in the context of energy tradeoffs between growth and reproduction. Chapters 2-4 described the extent of the variability in demographic parameters and reproductive characteristics, while Chapter 5 investigated this variability of life history characteristics as a function of the somatic condition of individuals. Variability in demographic parameters (Chapter 2), along with plasticity in reproductive life history characteristics (Chapter 3) suggests that potentially the capacity for population growth varies spatially. A comparison of the pattern of energy allocation and condition of different populations (Chapter 5) indicated that variability in the life history traits cannot be explained in the context of energy allocation (Fig 6.1).

6.2. SYNTHESIS

This study revealed considerable spatial variability in the demographic parameters of exploited sand flathead populations, demonstrating that the populations may not be uniform even in a small latitudinal scale. Smaller maximum and mean size/age in the Georges Bay population reflected the slower growth rates of individuals in the population, movement of larger, mature individuals out of the bay, and possibly higher mortality rates, especially when compared to Coles Bay. Although slow growth rates and high natural mortality rates can be a result of sub-optimal environmental conditions (Donald *et al.*, 1980; Craig, 1985; Wydoski & Wydoski, 2002), there was little evidence in this study of significant environmental differences among locations which could explain this variability. For example, throughout the

course of this study water temperature, as a major component of environmental conditions for changes in growth rate (Atkinson, 1994), was the same in all locations. Furthermore, somatic condition as an indicator for nutritional history (Pedersen & Jobling, 1989; Ratz & Lloret, 2003) did not vary among populations, indicating that food availability is not a strong candidate as a factor responsible for differences in growth rates. Therefore, it is more likely that the Georges Bay population structure resulted from higher migration rates of larger individuals and/or greater mortality rates of fast-growing individuals, compared with Coles Bay population.



Figure 6.1. Further clarification of contributing parameters in population structure in *Platycephalus bassensis* incorporating major finding. [×] signifies little to no contribution, $[\sqrt{}]$ signifies contribution, [?] signifies possible contribution.

However, this study showed that small maximum and mean size/age is not always accompanied by slow growth rates and in some cases may be attributed to the movement of older individuals out of the population. Movement of different size/age classes of a fish species between nursery/feeding ground and spawning ground is not unusual (Northcote, 1978; Gibson, 1997). This may occur where the habitat does not provide the biological and ecological requirements for all age/size classes. For example, variable and low salinity may not be optimal for reproductive biology of marine species that normally experience very little variation in the salinity (Gunter, 1961; Bye, 1990). Results from the components of this study (Chapters 2, 3 & 4) suggest that water salinity below the level of the open ocean may not be optimal for sand flathead spawning activity. This was the case in the Tamar River, where the lower salinity may cause the movement of older, mature individuals away from the estuary. Therefore, movement of older reproductively mature individuals out of estuarine habitats, with low and variable salinity, would result in the population consisting primarily of smaller and younger individuals.

The reproductive strategy of a fish species is recognized as a complex of reproductive traits that will assure the survival of the next generation (Wootton, 1984; Murawski *et al.*, 2001). This study showed that such strategies are tightly correlated to the population structure. Although, as a serial spawner, the length of the spawning season for sand flathead is potentially as long as six months (Jordan, 2001), smaller individuals had a shorter spawning season compared to their larger counterparts. Shorter spawning periods reduce the chance to spawn more batches of eggs during spawning period (Trippel *et al.*, 1997; Brown-Peterson *et al.*, 2001). Furthermore, the spawning frequency of populations with a lower proportion of larger individuals was slightly lower than that of populations predominantly formed

of larger individuals. For serial spawners, lower spawning frequency decreases reproductive effort, providing batch fecundity remains the same (Schaefer, 1996; Lowerre-Barbieri *et al.*, 1998). Additionally, a smaller body size reduces the capacity of having a larger gonad and thereby reduces reproductive investment (Jennings & Philipp, 1992; Marteinsdottir & Begg, 2002). Based on the results of this study, it is predicated that sand flathead populations predominantly consisting of smaller individuals have relatively low reproductive output, mostly due to shorter spawning season, less reproductive investment, and less frequent spawning events of smaller individuals. Such limited reproductive output, if other contributing factors in population size remain unvarying, potentially reduces the capacity of the population to increase in size in the long-term.

It is assumed that reproduction channels energy away from growth, thereby reducing somatic condition and probability of survival (Stearns, 1983; Roff, 1984). In this study, there was no evidence to suggest a trade-off between growth and reproduction. If reproduction redirects energy away from growth, possibly appearing as slower growth, there should be an accompanied reduction in somatic condition. However, the somatic condition of both reproductively active populations (Georges Bay & Coles Bay) was the same. Despite similarity in condition, the population that invested more energy to reproductive activity, did not display lower growth rate (i.e. In contrast, a slower growth rate was unexpectedly seen in the Coles Bay). population with lower reproductive investment (i.e. Georges Bay). One hypothesis is that mature individuals of different size classes may partition available energy between these two parts in a different way, while keeping their somatic condition stable. As smaller mature individuals allocate part of the available energy to reproduction whilst still maintaining investment for growth (Roff, 1992), evidence of

partitioning of energy may appear in the form of less reproductive investment, or in delayed maturation. In contrast, larger mature individuals allocate more energy to reproduction, while almost no more energy is required for growth. Thus, the hypothesis that variation in energy allocation is responsible for spatial variability in the life history traits and therefore population dynamics was not supported in the present study. Absence of spatial variability in somatic condition and energy allocation suggests that significant spatial variability in sand flathead life history traits can be the result of population response to exogenous factors, like fishing. Another possible explanation is the movement of faster growing, fully matured individuals out of an area, while slower growing and maturing fish remain in that area until mature and ready to move. Thus, population responses to exogenous factors and/or behavioural process (e.g. movement patterns of fish) can mask other contributing factors in the life history variability and subsequently drive population structure.

Life history theory also predicts that at greater adult mortality rates, selection will occur for individuals that mature at smaller sizes and younger ages (Schaffer, 1979; Stearns, 1983; Charlesworth, 1994). However, there was little evidence of this occurring in the populations studied, with the population with greater mortality rates having individuals bigger and older at maturity than the population with smaller mortality rates. Although such paradoxes in life history theory occur (Schaffer, 1979; Stearns, 1983; Charlesworth, 1994), in none of these populations was recreational fishing as a source of fishing mortality addressed. A delay in maturity in populations with greater mortality rates may be attributed to high mortality of all age classes due to 'growth overfishing' (Sutherland, 1990), resulting in few individuals reaching maturity before they are removed from the population.

In this study we selected different populations of a fish species targeted by recreational fishers, while they have previously been considered, and still is being considered, as a single stock. This selection had two major advantages. First, it provides, demographic and life history information about populations under recreational exploitation. Comparison of these fished populations with those protected within a reserve area in the future can reveal influence of recreational fishing on population dynamics. Secondly, it shows the extent of differences in the demographic and life history parameters of recreationally fished populations distributed over a relatively small regional scale. Results from this study revealed considerable variability in the demographic parameters of exploited sand flathead populations, indicating that the populations may not be uniform even in a small regional scale. Such results reject the assumption that the demography of a target species does not vary significantly in a small scale. This rationalizes the necessity of temporal and spatial fisheries management.

6.3. DIRECTIONS FOR FURTHER RESEARCH

The results in this study offer preliminary insights into aspects of the life history of this species, which have not previously been addressed. A more comprehensive recognition of factors that influence population dynamics is an important first step in understanding spatial and temporal variability in population structure. Further studies such as this can be the first step in a more extensive process.

In this study, significant variability in demographic parameters was found among locations, especially in size and age structure. One of the assumptions for the occurrence of such spatial variability is the movement of fish between locations, and most probably between spawning and feeding/nursery grounds. There are almost no direct data available on the movement of *P. bassensis* on a large scale. Jordan (1998) suggested that sand flathead move seasonally onto the continental shelf, based on seasonal variations in abundance between shelf and inshore waters. Hence, a mark and recapture investigation would quantify the movement and migration patterns of sand flathead. Such investigation may aid in understanding the mechanisms which underlie the variability of population structure.

The two-fold higher total mortality rate in Georges Bay is likely to result from a number of interacting factors that warrant further investigation. Higher total mortality for a population may be due to higher fishing mortality or/and higher natural mortality. The extent of fishing pressure can be assessed through a comprehensive fishing survey and/or a comparative study of demography of fished and unfished areas. Nevertheless, to estimate fishing mortality, abundance estimates in each location are first required (Quinn & Deriso, 1999). Due to the complexity in estimating natural mortality, even in the most intensively studied fisheries, fishery scientists are not often confident about the estimates of natural mortality (Jennings *et al.*, 2001). However, estimates of total and fishing mortality will allow spatial variability in natural mortality to be subsequently assessed.

Egg production estimation provides fishery-independent estimates of biomass and can be used for precise assessment of reproductive output (Lasker, 1985). This study quantified many reproductive parameters required for egg production estimation, including; spawning frequency, occurrence of atresia, and timing and duration of spawning. However, batch fecundity could not be estimated for *P. bassensis*. To estimate batch fecundity, mature females of different size classes with hydrated oocytes needed to be caught prior to the onset of spawning (Hunter *et al.*, 1985). Given the low proportion of females with hydrated oocytes in sand flathead populations (Chapter 4), very intensive sampling at midday and around the time of the new moon (time of spawning peak) may allow estimates of sand flathead batch fecundity to be obtained.

This study did not support the hypothesis that variability in the life history traits and population dynamics resulted from variation in energy allocation. However, this is a preliminary step in understanding tradeoffs between reproductive activity and somatic growth in teleost fish. For fish our understanding of trade-offs between reproduction and growth is incomplete and limited to a few studies (Roff, 1982; Reznick, 1983). Therefore, further controlled experiments are required to investigate the role of energy tradeoffs in variability of the life history traits. Due to the possible implication of other contributing factors in driving variability of the life history traits, a controlled experiment with a short-lived fish, during which time the transition from immaturity to maturity can be followed in a short period would allow the hypothesis to be tested more accurately.

There are still many unanswered questions relating to the life history of sand flathead. The remarkable potential of the species to exhibit variability of life history traits makes it an ideal species for the investigation of the effects of recreational fishing on population dynamics. Studies such as those outlined above, may shed further light on understanding the mechanisms contributing to spatial variability in life history characteristics of fish populations.

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