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

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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

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 life-history 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.

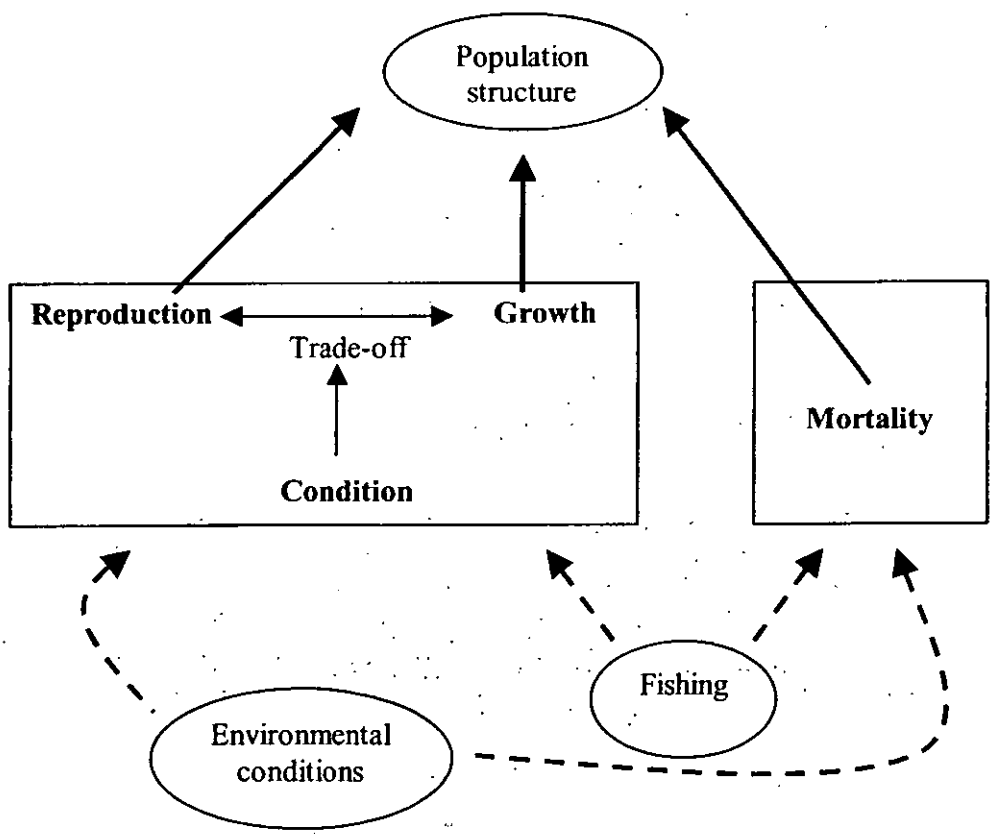

Figure 1.1. Schematic of population formation and contributing parameters in this process.

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 production. The trade-off between current and future reproduction (Roff, 1992; 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

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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.