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COMPARATIVE LIFE HISTORY OF TROPICAL AND TEMPERATE *SEPIOTEUTHIS* SQUIDS IN AUSTRALIAN WATERS.

Thesis submitted by

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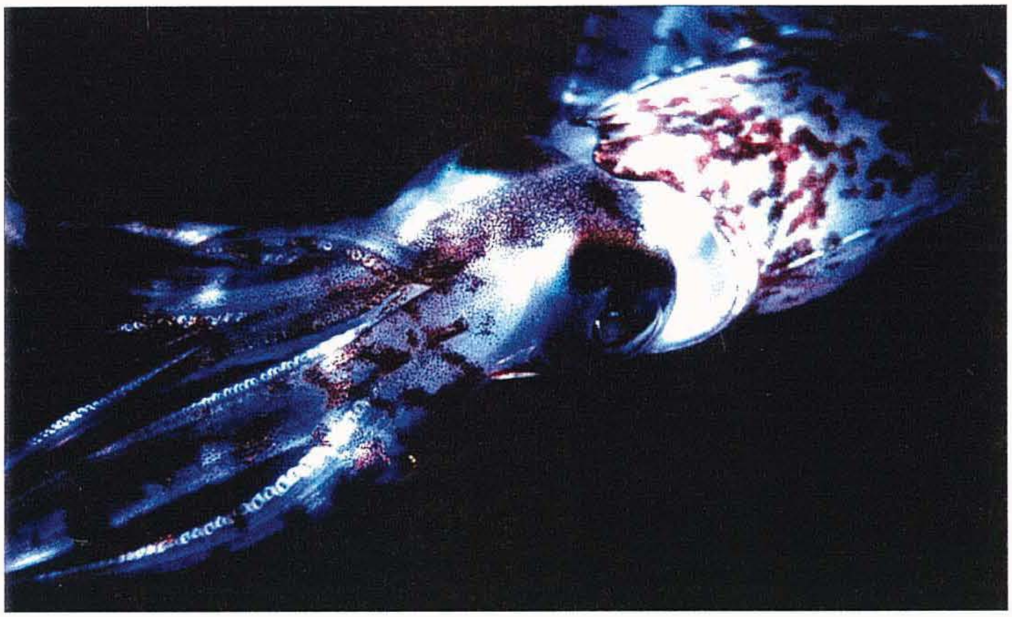

Frontispiece: *Sepioteuthis australis*

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ABSTRACT

The population dynamics of cephalopods are principally influenced by marked phenotypic plasticity in response to environmental factors, yet we have a poor understanding of how the life history characteristics of natural populations may alter over spatial or seasonal scales. The focus of this thesis is an examination of the variation in the life history traits of two closely related cephalopod species, *Sepioteuthis lessoniana* and *S. australis*, each from two divergent latitudinal zones along the east coast of Australia. The study centred on an assessment of the growth, lifespan, patterns of energy allocation between growth and reproduction, and the timing and mode of reproduction of each species as a function of geographical location, and for temperate *S. australis,* season of hatching.

The growth, lifespan, body size and maturation of *Sepioteuthis lessoniana* and *S. australis* from the different latitudinal zones was examined using validated statolith derived age estimations. In tropical waters, *S. lessoniana* grew fast initially, however the growth rate declined rapidly with age and individuals matured at small sizes and young ages. In the sub-tropical waters of Brisbane, *S. lessoniana* grew comparatively slower early in the life span, but growth rate did not decline as rapidly with age and individuals matured at larger sizes and older ages. In *S. australis*, although growth appeared faster in individuals from the sub-temperate waters of Newcastle, maturation occurred at younger ages and smaller sizes in *S. australis* from temperate Tasmania, despite Tasmanian squid having a longer lifespan and achieving a larger maximum size.

Back-calculated dates of hatching derived from statolith age estimations revealed that growth rate of *S. australis* from Tasmania was strongly influenced by hatching season, with individuals hatched in warmer seasons having a final size that could surpass that of earlier hatched (and therefore older) individuals. Faster growing squid hatched under the warming temperature regimes of spring and summer generally had heavier mantles at a given length, suggesting better condition at the whole animal level compared with slow growing squid hatched during the cooling temperatures of autumn and winter. Although males and females showed similar patterns in condition, the relative levels of reproductive investment of individuals in each hatching season differed between the sexes. Males hatched in warmer seasons had a higher level of reproductive investment compared with males from cooler seasons, whereas females hatched in spring and summer had lower levels of reproductive investment relative to their autumn and winter hatched counterparts.

This study assessed the potential of *Sepioteuthis lessoniana* and *S. australis* to spawn multiple batches of eggs at discrete times throughout the adult lifespan. This was achieved by histological examination of the ovarian gametogenic cycle and detailed morphological assessments of the reproductive system, in conjunction with other biological information. *Sepioteuthis australis* caught in Newcastle showed evidence of a high correlation between body size and quantity of mature eggs, suggesting that eggs may be accumulating to be laid in a single batch. Although maturation was also a size related process in *S. lessoniana* and Tasmanian *S. australis,* oviduct size was not correlated with body weight in mature females, which is indicative of multiple spawning. Further supporting evidence included relatively low gonadosomatic indices, the heavier weight of the ovary relative to the oviduct, and the sustained feeding activity of mature animals. In Tasmanian waters, summer caught females showed a negative correlation between egg size and egg number within the oviduct, suggesting that some individuals were producing fewer larger eggs and others many smaller eggs.

Sepioteuthis lessoniana and *S. australis* demonstrate a high degree of plasticity in their life history processes in terms of growth, reproduction and repro-somatic investment, and such flexibility in life history strategies within populations is consistent with an opportunistic lifestyle. Although there were substantial differences in the growth and reproductive biology between *Sepioteuthis lessoniana* and *S. australis*, and across latitudinal zones, seasonally related intra-specific variation in these traits within the *S. australis* population from temperate Tasmania were of similar magnitude. Importantly, this research also highlights the fact that a species may employ substantial variations on a reproductive strategy within different parts of their distribution, or with small genetic differences between populations. This, combined with other findings of this study, demonstrates that caution must be applied when extrapolating life cycle characteristics of cephalopod species across large geographical scales.

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CHAPTER 1:INTRODUCTION

1.1 BACKGROUND

The life history of an organism refers to the schedule of biological events that occur over its life span (Hall & Hughes 1996). This includes an animal's size, allocation of energy between growth, maintenance and reproduction, as well as the timing and mode of reproduction. Cephalopods demonstrate considerable intra-specific plasticity in many life history traits, such as age and size at maturation (Boyle 1990; Rocha & Guerra 1996), as well as both growth rates (Lipinski 1986, Hatfield 1991, Villanueva 1992a) and form of the growth curve (eg: *Loliolus noctiluca* Jackson & Choat 1992, Dimmlich & Hoedt 1998). This plasticity in the life history traits is related to the indeterminate growth patterns of cephalopods where growth is continuous and plastic, with individuals retaining the capacity to respond to biotic and abiotic factors throughout their entire lifetime. It is assumed that an organism cannot simultaneously dedicate energy to growth and reproduction without compromising survivorship, therefore plasticity of life history traits has evolved to favour individuals whose energy allocation maximises survival and fecundity (Stearns 1992). Most traits of ecological interest are continuous in character (eg: fecundity, age at maturity, clutch size), with very few traits that do not vary with environmental conditions and hence phenotypic plasticity is an integral part of life history variation (Roff 1992). It is upon the variation in an individual's traits that selective processes act, determining which individuals reproduce and the quality of their offspring (McCormick 1998).

Levels of genetic variation in cephalopods are relatively low and their population dynamics appear to be influenced principally by phenotypic plasticity in response to environmental variability (Boyle & Boletzky 1996). The role of environmental factors such as temperature, photoperiod and nutrition as origins of plasticity in the life history characteristics of squid (Sakurai *et al.* 1996), cuttlefish (Moltschaniwskyj & Martínez 1998) and octopuses (Forsythe & Hanlon 1988) has been the focus of much experimental work. The results of this research, together with field studies examining cephalopod growth and maturation, have led to the generation of several predictions concerning the life cycles of cephalopods:

1. Tropical species may be faster growing, shorter lived and mature earlier than temperate species (Jackson & Choat 1992).
2. Species that have a broad latitudinal distribution are expected to demonstrate different life cycles from north to south (Hanlon *et al.* 1983).
3. Cohorts within a population will experience different thermal conditions, with growth and maturation dependent upon the season in which individuals hatch (Rodhouse & Hatfield 1990, Forsythe 1993).

This thesis advances our knowledge of the life history characteristics of tropical and temperate squids as a function environmental processes operating over large spatial scales and in different seasons. This will be assessed by quantifying variation in growth, maturation and energy allocation. Ecologists have long been aware of the decisive influence of individual variability on population dynamics (Lowerre-Barbieri *et al.* 1998), and quantifying and contrasting the levels of variability in phenotypes is the first step in evaluating the consequences of varying environments on life history characters (McCormick 1998).

Cephalopods have often been considered functional equivalents of teleost fishes (Packard 1972), however, while coleoid cephalopods and fish may have a similar 'style of life' their 'pace of life' is dramatically different (O'Dor & Webber 1986). Short lifespans, continuous growth, and simultaneous allocation of energy to reproduction and growth sets cephalopods apart from similar sized teleosts. Teleosts usually show a dramatic slowing of growth after reproductive maturation that is not evident in most cephalopods. Cephalopods are universally carnivorous, with a physiology that is almost entirely protein based, using this substrate for fuel, growth and energy storage (Mommsen & Hochachka 1981, Wells 1983, Boucher-Rodoni & Boucher 1993). High gross conversion efficiencies (Mangold 1983, Segawa 1990), exceptional protein retention abilities (Houlihan *et al.* 1990) and a high metabolism (DeMont & O'Dor 1984) all contribute to the attainment of high growth rates, with the overall growth rates of cephalopods exceeding those of fish because they do not cease growing (Alford & Jackson 1993). Our understanding of cephalopod growth and maturation has been derived largely from field surveys of commercially important species and laboratory-based studies, with the two approaches leading to somewhat conflicting results.

Controlled laboratory studies have been invaluable in determining the effect of some environmental variables on the growth, maturation and energetics of cephalopods (Forsythe & Van Heukelem 1987, Segawa 1990, Forsythe 1993, Moltschaniwskyj & Martínez 1998). Cultured benthic octopods and loliginid squids consistently demonstrate two-phase growth, with an initial temperature dependent exponential phase followed by an abrupt transition into a less temperature dependent logarithmic phase (Forsythe 1993). If food is not limiting growth during the exponential phase then warmer temperatures will result in a faster and shorter exponential phase (Forsythe & Van Heukelem 1987). Temperature and nutrition also affect maturation, with slow growth caused by under-nutrition resulting in maturation at a smaller size, but if temperature reduces growth rates then maturation occurs at larger sizes (Van Heukelem 1979).

The benefits of laboratory studies in isolating individual factors, examining responses and generating hypotheses are indisputable, however the application of experimental results to wild populations requires extreme caution. While growth of some squids in wild populations approximates that of cultured individuals (eg: *Alloteuthis subulata*, Lipinski 1986, Arkhipkin & Nekludova 1993), in many cases it does not (*Loligo opalescens,* Jackson, 1994; *Loligo forbesi,* Forsythe & Hanlon 1989, Collins *et al.* 1995a). It is possible that the logarithmic growth phase sometimes observed for cephalopods is due to culture conditions (Alford & Jackson, 1993, Pecl & Moltschaniwskyj 1999).

While aquaria reared animals at fixed temperatures have consistently demonstrated two-phase growth with an initial exponential phase (eg: *Loligo opalescens*, Yang *et al.* 1986; *Octopus digueti*, DeRusha *et al.* 1987; *Loligo forbesi*, Hanlon 1990), the staggering array of growth functions used to describe cephalopod growth in wild populations provide examples of widely divergent patterns of growth. Power equations have been used to describe post-juvenile growth in species such as *Todarodes angolensis* (Villanueva 1992a) and *Loligo forbesi* (Forsythe & Hanlon 1989). However other growth studies have used linear (eg: *Gonatus fabricii,* Kristensen 1980; *Ommastrephes bartrami,* Yatsu *et al.* 1997), exponential (*Idiosepius pygmaeus,* Jackson 1989) or logistic equations (*Ornithoteuthis antillarum,* Arkhipkin *et al.* 1998; *Loliolus noctiluca,* Dimmlich & Hoedt 1998) to describe growth. It is unclear as to what extent the modification of growth patterns by processes operating over seasonal and geographical scales is responsible for the variety of growth patterns evident in field populations.

Field studies have indicated that tropical squid are in general much smaller, shorter lived and faster growing than temperate species suggesting that warmer temperatures may promote faster growth rates, but at the cost of earlier maturation and senescence (Jackson & Choat 1992). However, while the few field studies comparing growth and maturation of individuals from different locations or hatching seasons have identified significant differences, these have not always been as would be predicted from laboratory studies. While *Illex illecebrosus* matures at smaller sizes in warmer regions of its distribution (Coelho & O'Dor 1993), *Loligo forbesi* shows little difference in its reproductive characteristics or timing of maturation over similar geographical scales (Boyle & Ngoile 1993a). Growth of some species appears to be faster in individuals hatched over warmer months (Brodziak & Macy 1996, Hatfield 2000), yet in others growth is faster in individuals hatched over cooler months (Gonzalez *et al.* 1996, O'Dor *et al.* 1996).

The utility of field studies in revealing geographical or seasonal differences in the life history traits of cephalopods is complicated by several factors. Some studies examine growth in terms of weight (Forsythe & Van Heukelem 1987) and others in terms of length (Le Goff & Daguzan 1991, Nakamura & Sakurai 1993). If only length data are analysed the precise nature of growth patterns may be masked (Forsythe & Van Heukelem 1987), and comparisons with studies using only weight data are difficult. Across studies there may also be substantial variation in the definition of sexual maturity, maturity stages and also a variety of indices that may be derived to describe sexual maturation (Voss 1983, Boyle & Ngoile 1993a). Assessments of growth and maturation of a species over geographical or seasonal scales using similar techniques or approaches, and therefore directly comparable, are rare in the literature with some notable exceptions (Boyle & Ngoile 1993b, Coelho & O'Dor 1993).

This research focused on examining and comparing the life history strategies of tropical and temperate inshore loliginid squids. The strength of this research is an examination of growth and maturation patterns between species, and over seasonal and spatial scales, using comparable techniques and analyses. There are two approaches to the examination of life cycle strategies -theoretical studies, which use general evolutionary principles to deduce optimal strategies expected under specified ecological conditions, and observation studies, which arrive inductively at the way natural selection optimises life cycles under natural conditions by correlating strategies with particular ecological circumstances. The observation approach is most powerful when carried out on closely related species (Calow 1979). This study takes the latter approach and focuses on two *Sepioteuthis* species, with each species obtained from populations in two divergent latitudinal zones from the east coast of Australia, and has two major aims:

1) To compare and contrast the growth, lifespan, resource allocation between growth and reproduction, and the timing and mode of reproduction in *Sepioteuthis lessoniana* from tropical and sub-tropical waters, and *S. australis* from sub-temperate and temperate waters.

2) To quantify the influence of season of hatching in driving the life history characteristics of temperate squids, and a comparison of the relative magnitude of

seasonally induced variation in life history vs. that observed across geographical scales and between closely related species.

The thesis is organised into five data chapters (2-6), as well as a general discussion chapter (7). The primary aims and topics addressed in each of the data chapters are as follows:

Chapter 2: Seasonal patterns in growth and maturation of *Sepioteuthis australis*.

As Tasmania has the greatest seasonal variation in water temperature compared to the other sites examined in this thesis, it was chosen to assess the importance of environmental variation in influencing the life history characteristics of *S. australis* within the one location, prior to examining geographical variation in life history characteristics within the *Sepioteuthis* genera. This chapter examined the seasonal patterns in growth, maturation, and condition at the whole animal level, of *Sepioteuthis australis* from the east coast of temperate Tasmania using dates of hatching back-calculated from statolith derived age estimations, and also provided validation of the one ring per day hypothesis for this species.

Chapter 3: Age, growth and maturation in tropical and temperate *Sepioteuthis* species.

The main aim of this chapter was to determine if *Sepioteuthis* squids from warmer regions of their distribution conform to the expected life history pattern of faster growth, earlier maturation and smaller final body size compared to conspecifics and closely related species from cooler regions. This was achieved by comparing the growth, maturation, lifespan and body size of *Sepioteuthis lessoniana* and *S. australis* from different latitudinal zones along the east coast of Australia using statolith derived age estimations. Of particular interest was the magnitude of differences in growth and maturation across latitudinal zones and how they compared to the seasonal differences observed for *S. australis* at the most temperate location in the previous chapter.

Chapter 4: Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids.

This chapter assessed the potential of the tropical *Sepioteuthis lessoniana* and temperate *S. australis*, to spawn multiple batches of eggs at discrete times throughout the adult lifespan. This was achieved by histological examination of the ovarian gametogenic cycle and detailed morphological assessments of the reproductive system, in conjunction with other biological information. Recent research has demonstrated that *S. australis* from two regions examined in this study constitute two distinct genetic stocks (Triantafillos & Adams in press). As differences in the reproductive biology, using size and age at maturation information only, have been used to support the hypothesis of these two genetic types as distinct taxa, the assessment of regional differences in the reproductive biology of *S. australis* is particularly pertinent. This chapter forms the majority of a paper currently in press in *Marine Biology*.

Chapter 5: Patterns of repro-somatic investment in tropical and temperate *Sepioteuthis* species.

The process and patterns of resource allocation between reproduction and other competing needs such as maintenance and growth are essential to understanding the life history strategy adopted by an animal. In this chapter the relative growth of the mantle, gonad and digestive gland was examined to determine the differential allocation of resources during sexual maturation in order to assess the role of the mantle muscle and digestive glands as organs for storage of energy for reproduction in *Sepioteuthis lessoniana* and *S. australis*. This chapter also explored the relationship between the divergent life history patterns exhibited by *Sepioteuthis* species from different latitudinal zones and the process of resource allocation between growth and reproduction with body size and age. Closely related to this aim was an assessment of the existence of trade-offs between the competing processes of growth and reproduction.

Chapter 6: Resource allocation between growth and reproduction in *Sepioteuthis australis* as a function of hatching season.

The major aim of this research was to evaluate the importance of individual hatch date as a factor driving the generation of flexible reproductive strategies, and to assess the relationship of alternative strategies with other aspects of the life cycle. An unexplored area of the literature is the role that season of hatching may play in explaining some of the intra-specific variation in reproductive investment typically evident amongst mature cephalopods. This chapter examined the relationship between the level of reproductive investment, somatic condition at the whole animal level, and growth as a function of hatching season in male and female *Sepioteuthis australis* from temperate Tasmania. It also assessed the role of hatching season and individual somatic condition as factors potentially responsible for some of the variation in batch and egg size present in mature females.

1.2 STUDY SPECIES

The squid family Loliginidae is a rather homogenous grouping of 30-40 species, typically limited worldwide to coastal regions of the shelf <200m deep (Boyle & Boletzky 1996). Fifteen loliginid species from three genera have been recorded in Australian waters (Dunning & Lu 1998). Of these only *Sepioteuthis* species are regularly available to fisheries in any quantity, although small numbers of *Photololigo* and *Loliolus* are also caught (Kailola *et al.* 1993). This study focused on two squid within the genera *Sepioteuthis*. *Sepioteuthis* is a distinctive genus with a more robust and thickset body in contrast to that of the typical streamlined loliginid squid. The three members of this genus have a body form somewhere between that of the other loliginids and cuttlefish (Boycott 1965), with an undulatory marginal fin extending along the length of the mantle.

1.2.1 *Sepioteuthis lessoniana*

Sepioteuthis lessoniana (Lesson 1830) (Plate 1.1) exhibits rapid growth and has a short lifespan (Jackson 1990a) reaching a maximum size of 360 mm and 2200 g in 184 days (Hanlon 1990). It is a relatively large species that lives in inshore waters to depths of at least 110 m (Lu & Tait 1983) and appears to be predominantly reef associated (Jackson 1991). *Sepioteuthis lessoniana* has a wide geographical distribution that covers almost the entire Indo-West Pacific (Roper *et al.* 1984), including much of the Indo-Pacific from the Red Sea and southern Africa to Hokkaido, Japan, Hawaii and Australia (Lu & Tait 1983, Nesis 1987). Its distribution within Australia extends across the tropical northern coast, and down both east and west coasts into the sub-tropical waters of Fraser Island (27°12' S) on the east coast and Geraldton (28°12' S) on the west coast

(Winstanley *et al.* 1983, Jackson 1991). In this study *S. lessoniana* were obtained from the tropical waters of Townsville, and sub-tropical waters of Brisbane from the east coast of Australia (Figure 1.1). Townsville waters have average monthly sea surface temperatures (SST) ranging from 24.6 to 29.1°C throughout the year, with an annual average of 26.5°C. Brisbane waters are much cooler with average monthly SST of 21.5-26.2°C, and an annual average of 23.9°C (Figure 1.2).

1.2.2 *Sepioteuthis australis*

Sepioteuthis australis (Plate 1.2, Quoy & Gaimard 1832) is a relatively large inshore species endemic to southern Australian and northern New Zealand waters (Winstanley *et al.* 1983). It is the most common cephalopod in the coastal waters of southern Australia and is an important component of the coastal ecosystem as a primary consumer of crustaceans and fishes and as a significant food source for numerous marine animals (Gales *et al.* 1993). Based on length-frequency information, *S. australis* is thought to have a lifespan of 18 months (Smith 1983), and very little other biological information is currently available. Directed fisheries exist for *S. australis* in Tasmania and South Australia, with targeted effort and catch increasing four fold in the last five years in Tasmania, raising concerns about sustainability of the fishery and highlighting the need for biological information on this species (Jordan & Lyle 2000). In this study, *S. australis* were obtained from Newcastle, which has a range in average monthly SST of 18.8-24.6°C (annual average 21.6°C), and Great Oyster Bay on the east coast of Tasmania which has average monthly SST of 11.8-16.8°C (annual average 14.4°C, Figures 1.1 & 1.2).

Plate 1.1 *Sepioteuthis lessoniana*

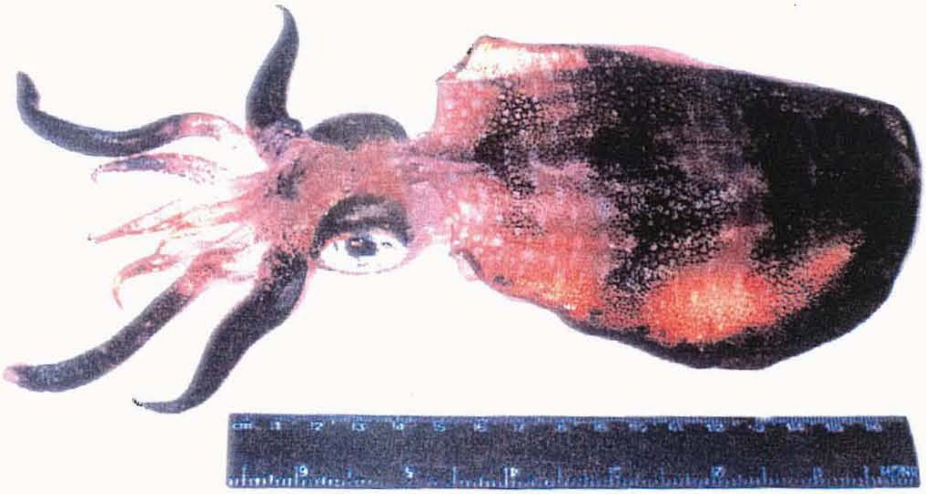


Plate 1.2 *Sepioteuthis australis*

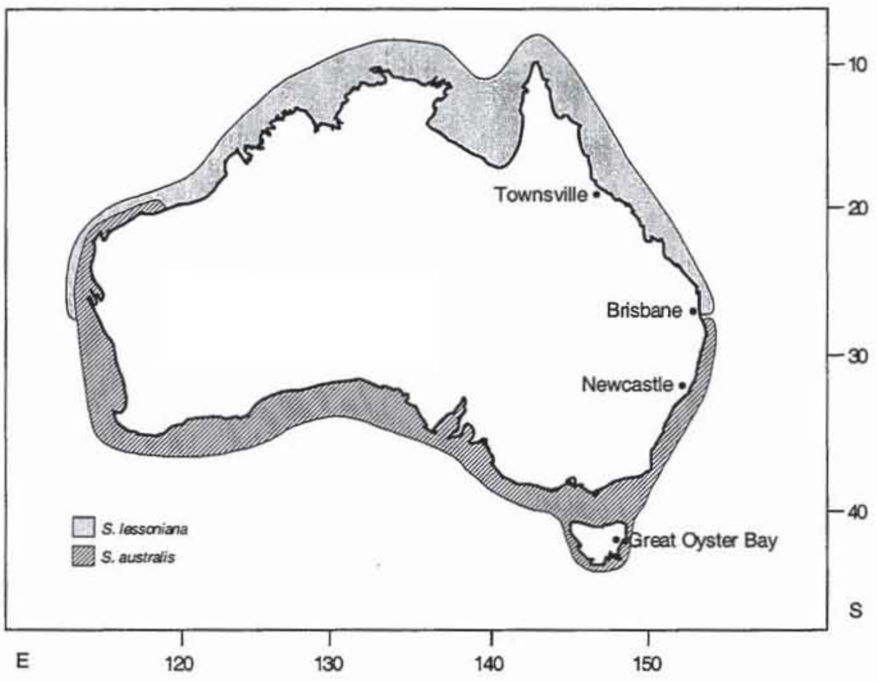


Figure 1.1: Study sites for *Sepioteuthis lessoniana* and *S. australis*. The map also shows the distribution of each species in Australian waters.

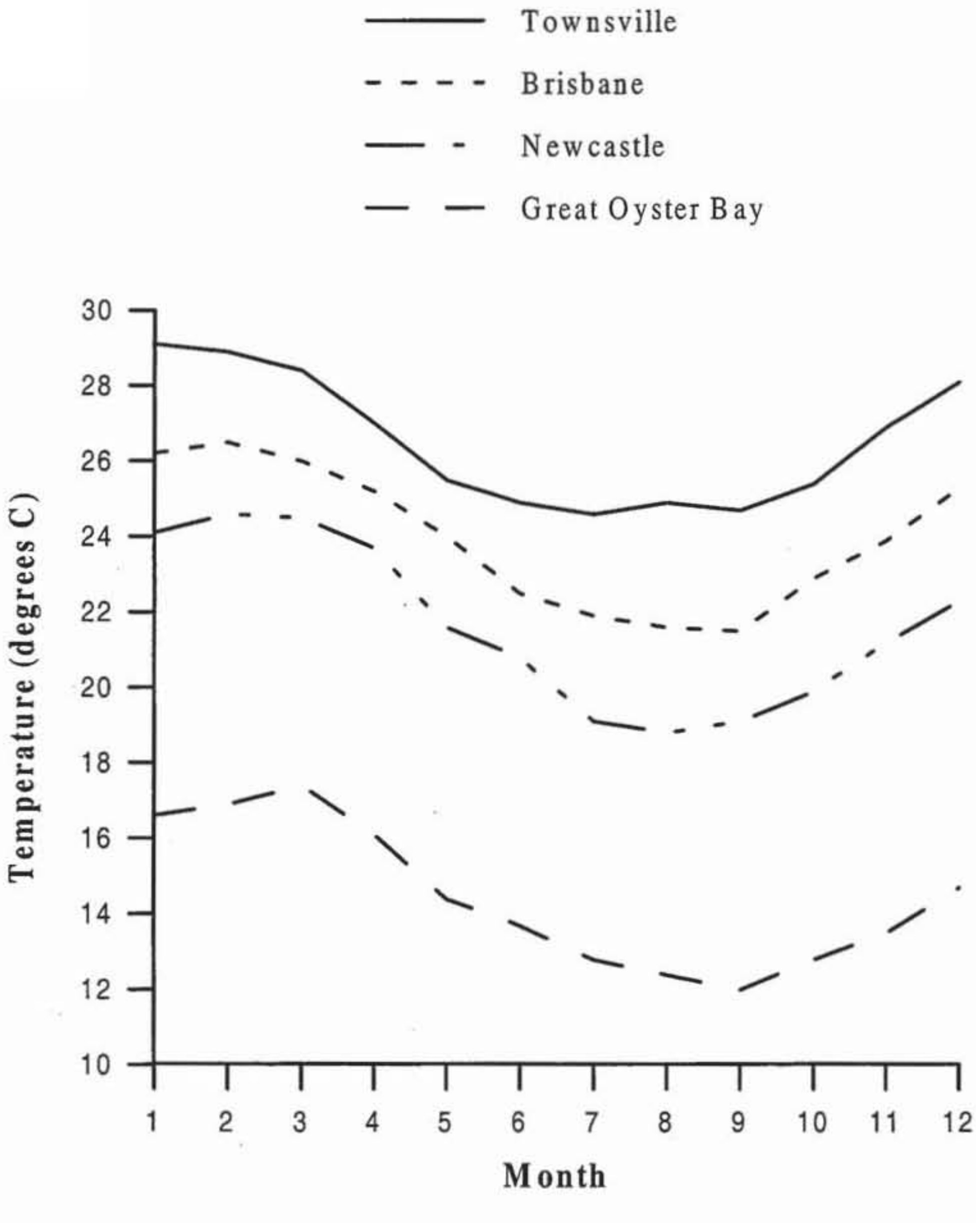


Figure 1.2: Average monthly sea surface temperatures in the coastal waters off Townsville, Brisbane, Newcastle and Great Oyster Bay (Tasmania). Data are a mean of SST within a one-degree radius of each town, and was provided by the Australian Oceanographic Data Centre using data extracted from the NODC-World Ocean Atlas 1998.

CHAPTER 2: SEASONAL PATTERNS IN GROWTH AND MATURATION OF *SEPIOTEUTHIS AUSTRALIS*.

2.1 INTRODUCTION

Cephalopods are generally fast growing animals displaying plastic indeterminate growth patterns with no asymptotic size limits being approached (Alford & Jackson 1993). The critical factor of 'indeterminate' growth is that the growth trajectory responds to environmental conditions throughout the entire lifetime of the individual (Sebens 1987). The plastic growth responses of cephalopods may be influenced by factors as varied as prey availability (O'Dor *et al.* 1980 in Brodziak & Macy 1996), population density (Dawe 1988), sexual maturation (Moltschaniwskyj 1995) and temperature (Forsythe 1993, Jackson *et al.* 1997). Even small differences in growth rates, particularly during the juvenile phase, may lead to substantial variations in final size (Forsythe 1993) and therefore have significant impacts on the size and age structure of wild populations (Grist & des Clers 1999).

The positive effect of temperature on cephalopod growth is clear and consistent in laboratory animals reared at a constant temperature (Forsythe & Van Heukelem 1987, Forsythe & Hanlon 1989), however we do not know precisely how growth of hatchlings responds to changing temperatures. Furthermore, the effect of seasonal environment changes on growth is not consistent between cephalopod species in field populations. In some cases growth is fastest in individuals hatched in warmer months (eg: *Loligo pealei*, Brodziak & Macy 1996; *Lolliguncula brevis,* Jackson *et al.* 1997; *Loligo vulgaris*, Raya *et al.* 1999). In contrast, *Illex coindetti* individuals hatched in winter attained a larger size-at-age than individuals hatched in other seasons, although differences were only evident after

8 months of age (González *et al.* 1996). O'Dor *et al.* (1996) found the growth rate of *Illex illecebrosus* actually decreased as the season progressed, while Dawe & Beck (1997) found the opposite trend. Growth in *Todarodes angolensis* also appears to be faster during cooler years (Villanueva 1992a). All studies, however, agree that temperature plays a crucial role in the dynamics of cephalopod life cycles and that environmental effects on growth in natural populations are quite pronounced in areas which have marked seasonal differences (Villanueva 1992a, Arkhipkin & Laptikhovsky 1994, Dawe & Beck 1997).

In the case of short lived animals, different cohorts experience different thermal and nutritional conditions resulting in variation between and within generations (Jackson & Choat 1992), with growth rates varying according to the season in which they hatched (Natsukari *et al.* 1988, Rodhouse & Hatfield 1990). Age and size at maturation have also been shown to vary substantially between different seasonal hatching groups (Arkhipkin *et al.* 2000). The environment may vary temporally and spatially although it is temporal variation that typically modifies life history characteristics more than spatial variation (Roff 1992).

This chapter examines the seasonal patterns in growth, maturation, and condition at the whole animal level, of *Sepioteuthis australis* from the east coast of Tasmania using dates of hatching back-calculated from statolith derived age estimations. The one ring per day hypothesis is also examined for this species. This description was undertaken with the aim of assessing the importance of environmental variation in influencing the life history characteristics of *S. australis*.

2.2 MATERIALS & METHODS

2.2.1 Squid sampling

Sepioteuthis australis individuals were obtained from January 1996 to July 1997 from the shallow inshore waters of Great Oyster Bay on the east coast of Tasmania, Australia (42°15'S; 148°10'E). Squid were caught by a combination of jigging and modified purse-seine through co-operation with the commercial sector and jigging from small research vessels. A total of 493 squid were captured (196 females, 237 males, 60 juveniles). Most individuals were refrigerated or placed on ice within a few hours of capture and processed within 12 hours. Dorsal mantle length (ML) was measured to the nearest millimetre and total body weight and mantle weight to the nearest 0.01g. All squid were sexed and assigned a maturity stage following the six-stage maturity scale of Lipinski (1979). Squid that could not be sexed were classed as juvenile.

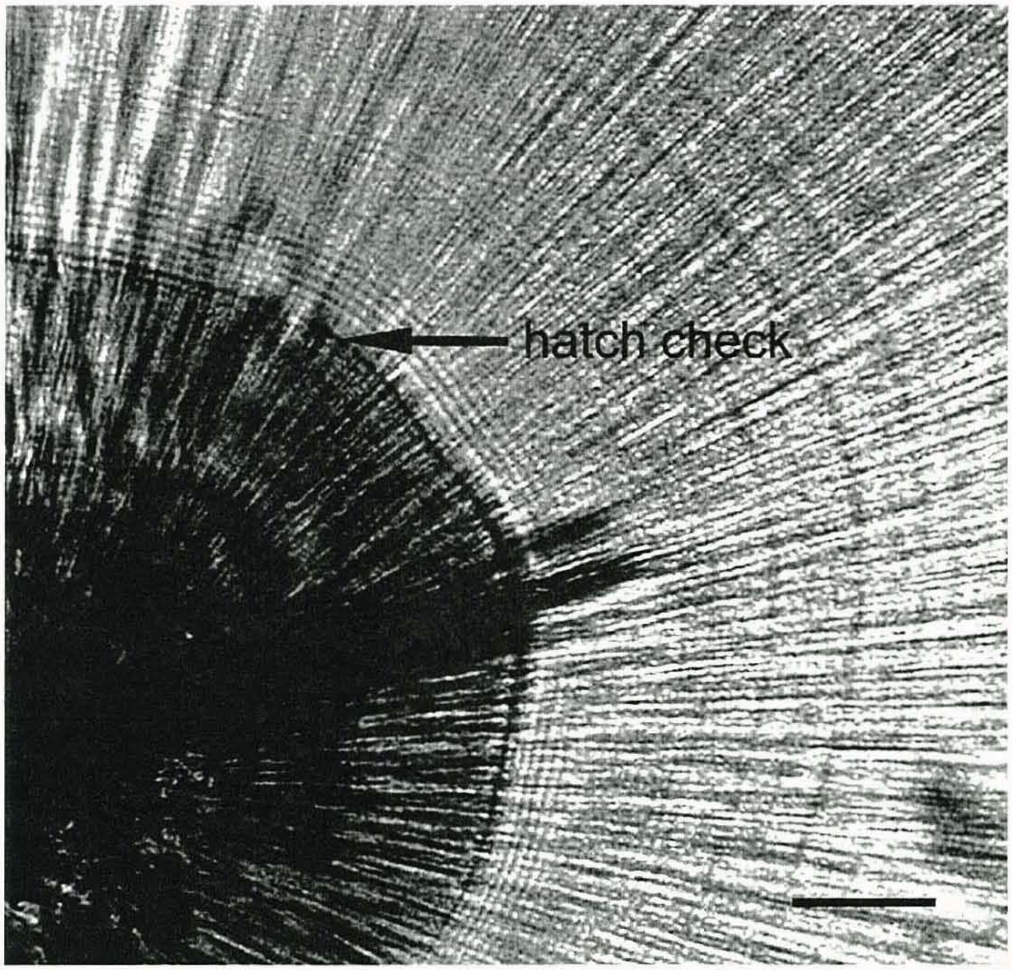
2.2.2 Statolith preparation

Age information was determined from increments in the statolith. Statoliths were stored in 70% ethanol, later rinsed in distilled water, dehydrated with 100% ethanol and then mounted in Crystal Bond. Statoliths were ground on both anterior (concave) and posterior (convex) surfaces with wet 1200 μm carborundum paper and polished with 0.05 μm alumina powder on wet suede polishing cloth. It was necessary to make frequent stops during the grinding process in order to check progress under a microscope and to alter the plane of grinding, much like the method described by Brodziak & Macy (1996) for *Loligo pealei*. Increments in very large *Sepioteuthis australis* statoliths were enhanced by heat treatment where the statolith was placed on a hot plate for 1-2 minutes until light brown in colour. Increments were most discernible in the dorsal dome (Plate 2.1) and were counted from the natal ring to the margin of the dorsal dome under a light microscope at 400x magnification with a polarised light source. Statoliths were discarded as unreadable if the natal ring was unclear or if two consecutive counts differed by more than 10%, or less than 90% of rings were visible. A total of 397 squid were successfully aged (165 females, 185 males, 47 juveniles). Over 93% of the unaged specimens were due to breakage of the statolith during the grinding process or over-grinding of the statolith where the natal ring or increments near the natal ring were no longer visible. Very few statoliths (7%) were discarded as unreadable as a consequence of the statolith microstructure. To confirm adequate precision, increment counts by two independent readers using the same statolith preparations were compared by a Student's paired *t*-test.

2.2.3 Determination of natal ring

To estimate age in days after hatching, the natal ring, a structure formed within the statolith upon hatching, should be identified as a starting point for counting increments. In the statoliths of *Sepioteuthis australis* the natal ring was a prominent structure bordering the edge of a distinctly opaque zone within the centre of the statolith (Plate 2.1). The natal ring was determined by comparing statolith size in ten hatchlings from a field egg mass (discovered in the process of hatching), with the size of the "first check" in the ground statolith of older squid. In addition, the smallest squid from this study (0.06g & 6.8mm ML) was probably newly hatched and the presence of only four growth increments after the first check indicates that this feature probably represents the natal ring. The diameter of the natal ring was of similar size in all specimens examined.

Plate 2.1 Natal ring (hatch check) and daily growth rings in a ground and polished statolith of a field captured *Sepioteuthis australis*. Scale bar: 100 μm.


hatch check

2.2.4 Known age individuals

An egg mass was found washed up on Taroona Beach, Tasmania (42°55'S; 147°20'E) on January 17 1998. Some individuals were already hatching, and the rest hatched immediately when the egg mass was placed in sea water. Hatchlings were maintained for a period of up to 102 days in mesh covered 500 litre tanks with a flow through system using unfiltered water from the Derwent River estuary. Live food was introduced into the tanks at least once a day. At two days of age hatchlings were actively feeding on *Artemia*, after one week squid were fed mysids, then Galaxiid juveniles and progressively larger fish. Towards the end of the maintenance period squid were weaned onto dead fish.

2.2.5 Growth rate estimation and statistical analyses

The following curves were used to fit size-at-age data: exponential, linear, power, logistic and von Bertalanffy. The best fitting curve was determined by examination of residuals for any systematic pattern and the highest r^2. Date of hatching was estimated by back-calculation from the time of capture using statolith estimated age. To examine the effect of hatching season on growth, individuals were grouped by sex according to season of hatching. Differences in growth between sexes and between animals hatched in different seasons were compared with analysis of covariance using size-at-age data and length-mantle weight regressions. Instantaneous growth rate, G, was calculated for each individual averaged over its lifetime using the equation given in Forsythe & Van Heukelem (1987):

$$G=(\ln W_2-\ln W_1/T_2-T_1)*100, \text{ where } W=\text{total wet weight and } T=\text{time.}$$

Individual growth calculations assume a hatch weight and length of 0.06g and 4.75mm ML respectively, based on unpublished data of 20 hatchlings.

To examine the association between growth and condition, residuals from the age-weight and mantle weight-length relationships were correlated against each other. Only mature individuals were used in assessing this relationship as maturation stage has an effect on the mantle weight-length relationship (see Chapter 5). Residuals from the age-weight relationship are a measure of the difference in an individual's lifetime growth from the population average, and residuals from the mantle weight-length relationship are a size independent measure of an individual's condition at the whole animal level (Moltschaniwskyj & Semmens 2000). An individual that is lighter for its length than predicted from the regression is in poorer condition than an individual who is heavier for its length than predicted by the regression. Residuals were standardised by dividing each residual by the standard deviation of the predicted values.

Seasonal temperature information for the region of squid capture was estimated from interpolated sea surface temperature data produced weekly on a one degree grid by the National Centres for Environmental Modelling (U.S.). Great Oyster Bay is a known to be a major spawning area for *Sepioteuthis australis*, and evidence to date suggests that large scale migrations do not take place in this species (unpubl. data Jackson GD & Pecl GT). Thus the temperatures approximated to the growth conditions are likely to have been experienced by the squid sampled.

2.3 RESULTS

2.3.1 Validation of statolith increment periodicity and accuracy of counts

Sepioteuthis australis were reared in captivity for up to 102 days, approximately a third of the estimated maximum life span for this species. There was a close agreement between the number of post-natal increments counted and the number of days post-hatching for the 15 *S. australis* reared in captivity (Table 2.1; paired *t*-test, t=-0.829, df=14, P=0.421). The average difference between statolith estimated age and known age was 0.74 days ± 0.21 s.e, supporting the one ring: one day hypothesis. Although growth increments were faint compared to many other squid species (Jackson, pers. comm.), there was no significant difference between counts by independent readers using the same statolith preparations (paired *t*-test, t=1.613, df=21, P=0.301) confirming appropriate ring identification and counting. Subsequent analyses and discussions in this study are therefore based on the premise of daily statolith increment formation.

Table 2.1: Weight, length, actual age and statolith increment counts for cultured *Sepioteuthis australis*, hatched 17 January 1998. Statolith increment number is an average of two counts (s.d.= standard deviation).

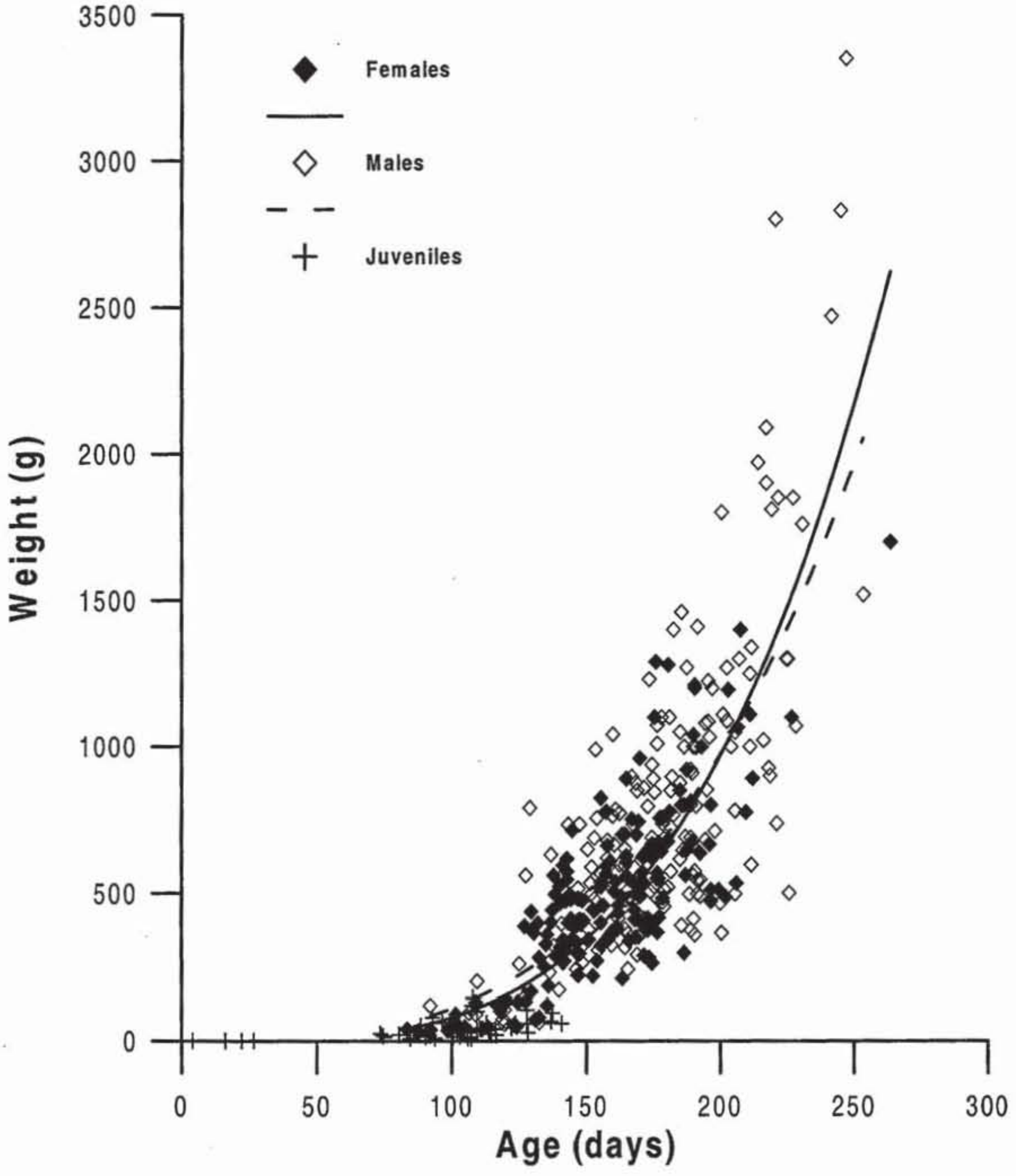
Weight (g)	ML (mm)	Date died	Actual age (days)	Statolith increments counted (± s.d.)	Difference (days)
2.13	29.0	30 March	72	74.3 (± 1.15)	2.3
1.06	22.6	30 March	72	70.7 (± 2.08)	1.3
2.33	3.02	29 April	102	100 (± 1.41)	2
4.00	36.0	29 April	102	102.5 (± 2.12)	0.5
2.60	33.5	29 April	102	102 (± 1.41)	0
3.01	34.0	29 April	102	102 (± 1.41)	0
3.64	36.7	29 April	102	100 (± 1.41)	2
4.06	37.7	29 April	102	102 (± 2.83)	0
2.54	32.6	29 April	102	101 (± 1.41)	1
2.47	32.9	29 April	102	101.5 (± 2.12)	0.5
3.19	34.0	29 April	102	101.5 (± 2.12)	0.5
4.61	39.7	29 April	102	102.5 (± 0.71)	0.5
2.49	32.2	29 April	102	102 (± 2.83)	0
2.19	31.3	29 April	102	102.5 (± 0.71)	0.5
1.83	30.0	29 April	102	102 (± 1.41)	0
					Average ± s.d. 0.74 (±0.21)

2.3.2 Age & growth of females, males and juveniles

The relationship between age in days and total wet weight was best described by power functions (often referred to as logarithmic in the literature) for adults and juveniles (Figure 2.1, Table 2.2). For males, females and juveniles the difference between exponential and power weight-at-age fits in the coefficient of determination was marginal, however examination of the residuals revealed that the exponential equation did not adequately describe growth in older individuals, particularly for females. Growth in length was also power in nature for adults of both sexes and juveniles (Figure 2.2). Considerable variation in individual growth rates was evident. At 200 days males differed by as much as 1500g and 180mm ML and females by as much as 900g and 140mm ML. Less variation was evident for growth in both weight and length of juveniles compared to adults (Table 2.2).

Table 2.2: Summary of curve parameters and associated statistics for weight-at-age and length-at-age power growth curves for all female, male and juvenile *Sepioteuthis australis* sampled in the study.

Sex	n	Slope	95% Confidence intervals of slope	Intercept (lna)	r^2	P
Growth in weight						
Females	165	3.610	3.239-3.980	-12.250	0.69	<0.0001
Males	185	3.149	2.785-3.514	-9.805	0.61	<0.0001
Juveniles	47	2.523	2.135-2.910	-8.267	0.79	<0.0001
Growth in length						
Females	165	1.380	1.240-1.520	-1.605	0.70	<0.0001
Males	185	1.230	1.094-1.366	-0.726	0.64	<0.0001
Juveniles	47	1.066	0.902-1.230	-0.543	0.79	<0.0001



Figre 2.1: Growth in total wet weight for all male, female and juvenile *Sepioteuthis australis* individuals collected in the study. Power curves fitted.

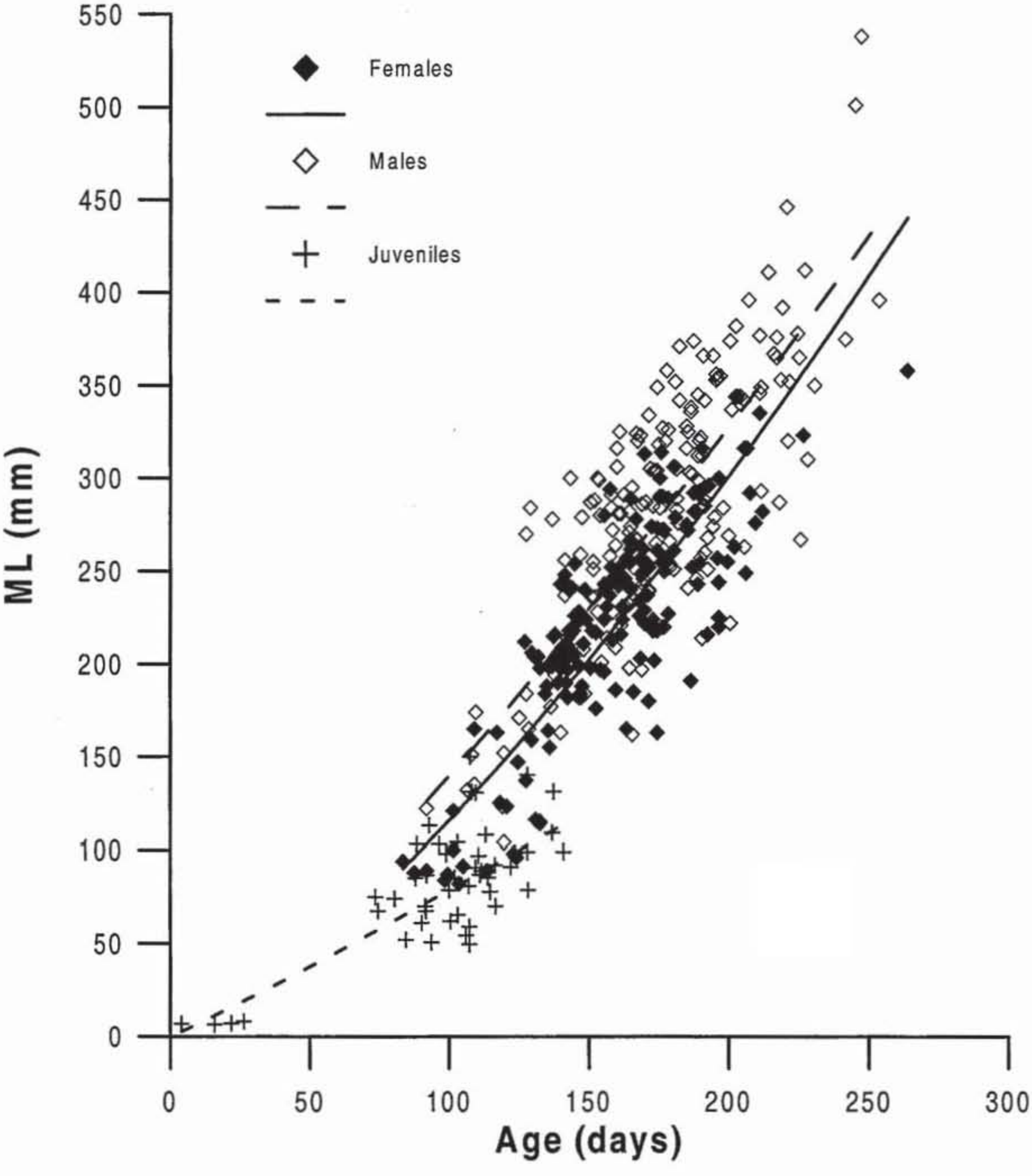


Figure 2.2: Growth in dorsal mantle length (ML) for all male, female and juvenile *Sepioteuthis australis* individuals collected in the study. Power curves fitted.

The instantaneous growth rate (%BW day^{-1}) averaged over the life time and calculated on an individual basis, declined with age as expected for power growth (Figure 2.3). In young individuals (<100 days) growth in weight was as high as 8.5% BW day^{-1}, with a mean rate to adulthood of 4-5% in the oldest individuals (>200 days). Although male *Sepioteuthis australis* were larger in length at a given age compared with females, there was no significant difference between the sexes in the rate of growth in length (Table 2.3). There was also no significant gender difference in the rate of growth in weight, or average weight adjusted for age (Table 2.4). Males were, however, on average larger than females (740g ± 31g s.e., *n*=237 and 498g ± 20g s.e., *n*=196 respectively) as a function of living slightly longer (176 days ± 2 days s.e., *n*=185 and 158 days ± 2 days s.e., *n*=165 respectively). Examination of the 95% confidence limits around the weight-at-age and length-at-age slopes show that juveniles were growing at rates similar to males, but slower than females, in both weight and length.

Table 2.3: Analysis of covariance table, comparing growth in log ML between male and female *Sepioteuthis australis*, using log age as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Test for equal slopes					
Sex	1	0.083	0.083	3.048	0.082
Log age (covariate)	1	19.083	19.083	699.010	0.000
Sex x Log age (equal slopes)	1	0.063	0.063	2.313	0.129
Residual	346	9.446	0.027		
Test for differences in Log ML					
Sex	1	1.041	1.041	37.988	<0.0001
Log age	1	19.129	19.129	698.044	<0.0001
Residual	347	9.509	0.027		

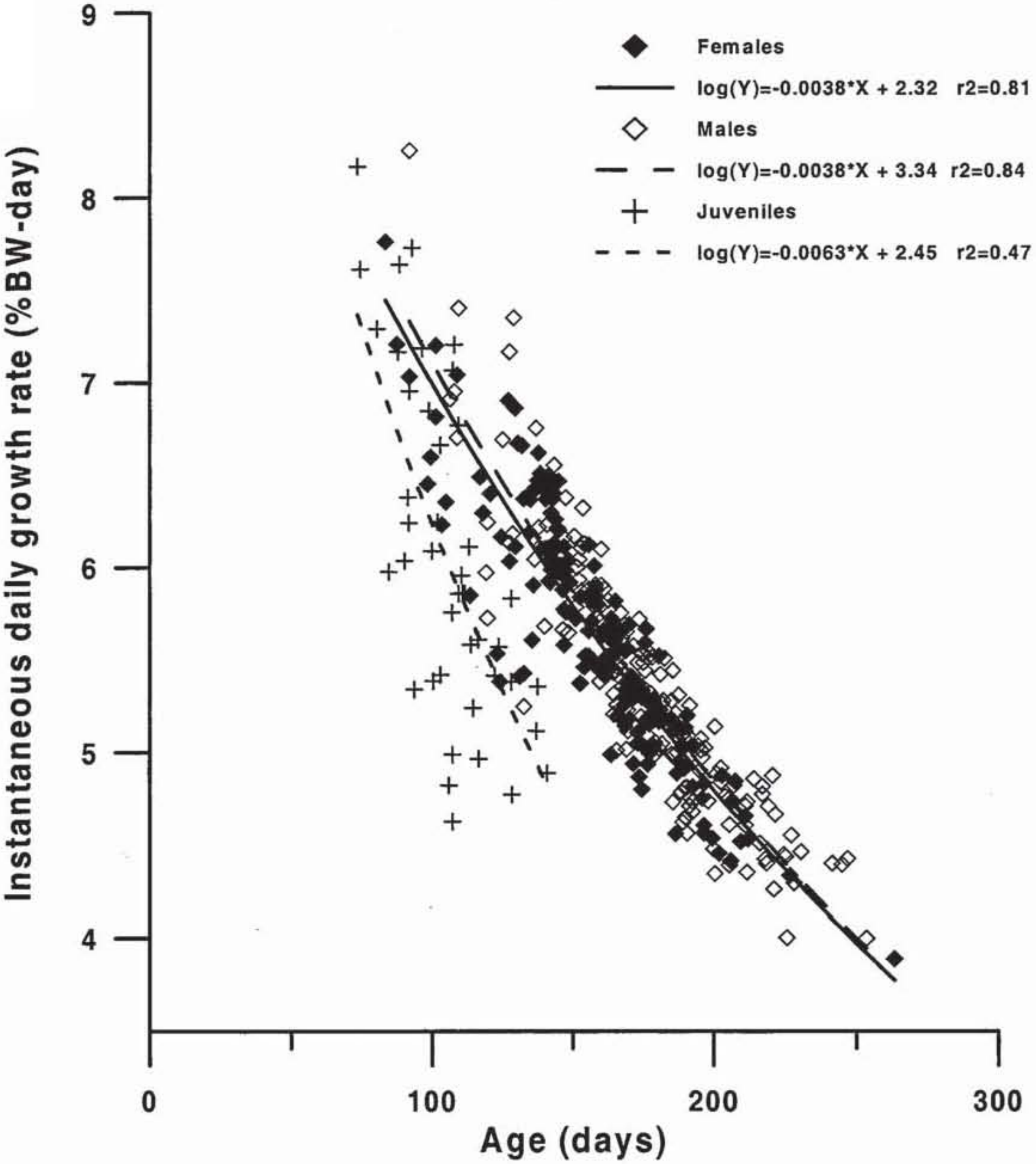


Figure 2.3: Instantaneous growth rate (G) (averaged over life time) in weight, with age of female, male and juvenile *Sepioteuthis australis*. Exponential curves fitted.

Table 2.4: Analysis of covariance table, comparing growth in log weight between male and female *Sepioteuthis australis*, using log age as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Test for equal slopes					
Sex	1	0.643	0.643	3.314	0.070
Log age (covariate)	1	127.967	127.967	659.936	0.000
Sex x Log age (equal slopes)	1	0.594	0.594	3.065	0.081
Residual	346	67.092	0.194		
Test for differences in Log weight					
Sex	1	0.725	0.725	3.715	0.055
Log age	1	128.323	128.323	657.855	<0.0001
Residual	347	67.687	0.195		

2.3.3 Seasonal patterns in growth

Back calculated dates of hatching were used to determine the season of hatching for all individuals to allow examination of differences in size-at-age and growth rates for each seasonal hatching group. Squid hatched in all months of the year, between June 1995 and February 1997. Seasonal averages of sea surface temperatures for the region of squid capture are shown in Table 2.5.

Table 2.5: Maximum, minimum and seasonal averages (± s.e.) of weekly sea surface temperatures (°C) for the region of squid capture.

	1995		1996		1997	
	Range	Mean	Range	Mean	Range	Mean
Summer	15.0-18.3	16.6 (±0.3)	14.1-16.8	15.4 (±0.3)	12.2-18.2	15.6 (±0.4)
Autumn	13.8-18.3	15.2 (±0.4)	13.8-16.6	15.3 (±0.2)	14.7-17.2	15.7 (±0.2)
Winter	11.8-14.1	12.7 (±0.5)	12.4-14.2	12.9 (±0.1)	12.2-14.4	13.1 (±0.2)
Spring	11.8-14.2	12.6 (±0.2)	12.0-13.4	12.6 (±0.1)	12.2-15.0	13.4 (±0.2)

Within each seasonal hatching group, growth of adult squid was still highly variable, with poor to moderate fits obtained for most groups (Table 2.6). Despite containing the fewest individuals of any seasonal hatching group, growth was least variable in spring hatched individuals. Analysis of covariance revealed that growth in weight was dependent upon season of hatching, but not sex (Table 2.7). Individuals hatched in autumn (and growing through winter) had the slowest growth rates, while squid hatched in spring (and growing through summer) had the fastest (Figure 2.4). These seasonal differences in growth rates translate into substantial variations in size-at-age. For example, the mean total weight of summer hatched squid at 170-190 days of age was 1002g (± 98g s.e., *n*=12), compared to 632g (± 27g s.e., *n*=50) in winter hatched squid.

The slope from the log G-at-age relationship describes the rate of deceleration in growth with age. The slope from this relationship did not differ among the seasonal hatching groups, although the intercepts differed significantly (Table 2.8) indicating that summer and spring hatched squid achieved their larger size-at-age, relative to autumn and winter hatched squid, by faster growth throughout the entire lifespan and not simply faster growth early in the life cycle.

Table 2.6: Summary of curve parameters and associated statistics for log transformed weight-at-age power growth curves for adult *Sepioteuthis australis* hatched in different seasons.

Hatching season	*n*	Slope	95% Confidence interval of slope	Intercept (*ln*a)	r^2	*P*
Summer	59	3.299	2.671-3.921	-10.32	0.66	<0.0001
Autumn	88	2.447	1.879-3.016	-6.37	0.46	<0.0001
Winter	163	3.385	2.864-3.905	-11.039	0.50	<0.0001
Spring	40	4.061	3.487-4.636	-14.616	0.84	<0.0001

Table 2.7: Analysis of covariance table, comparing log total weight of male and female *Sepioteuthis australis* within each season of hatching, using log age as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Log age	1	62.888	62.888	403.29	<0.0001
Sex	1	0.164	0.164	1.053	0.306
Hatch season	3	2.013	0.671	4.302	0.005
Sex x log age	1	0.198	0.198	1.271	0.260
Hatch season x sex	3	0.541	0.180	1.156	0.327
Hatch season x log age	3	1.901	0.634	4.064	*0.007*
Hatch season x sex x log age	3	0.464	0.155	0.991	0.397
Residual	334	52.082	0.156		

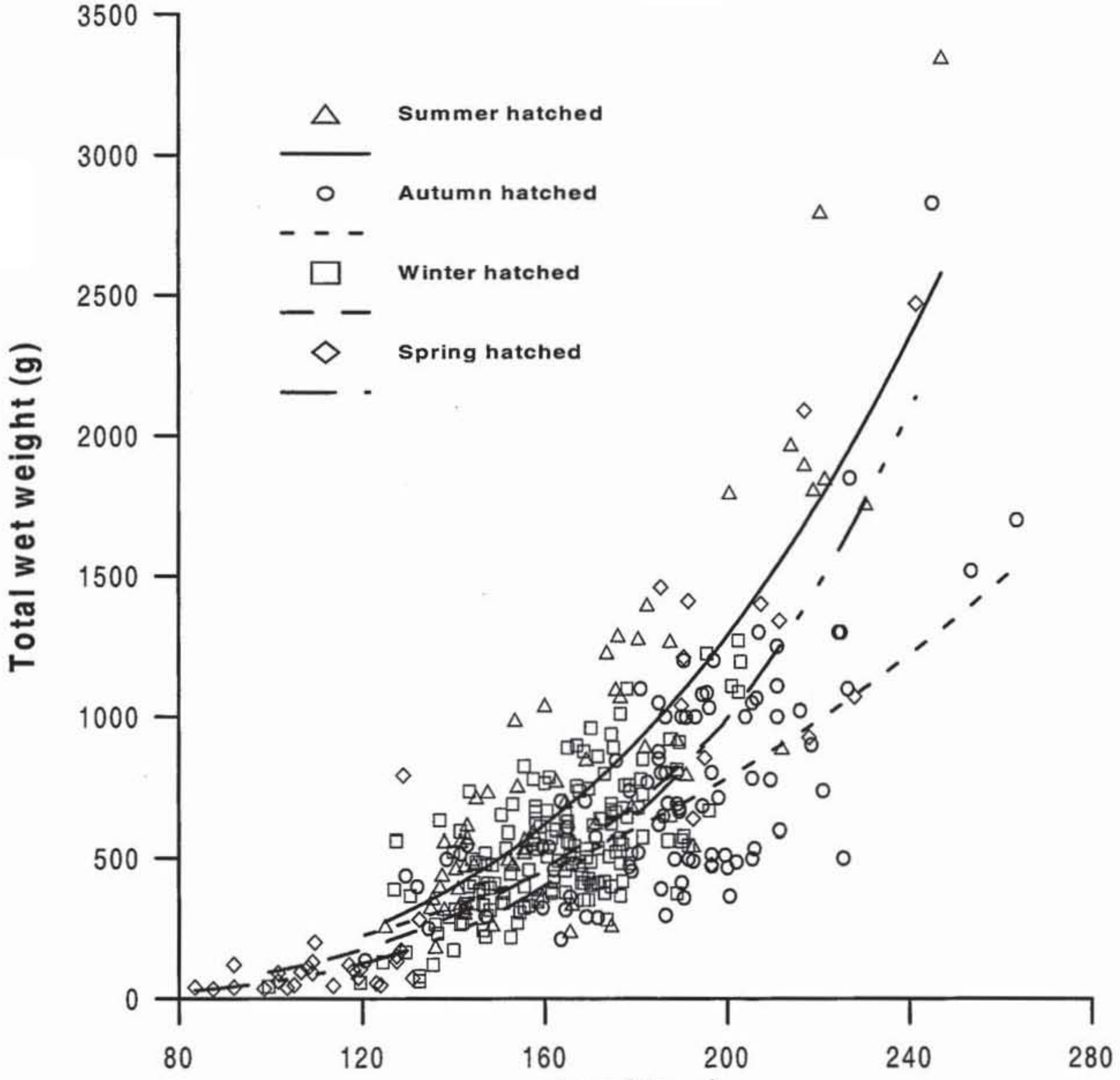


Figure 2.4: Growth in weight for adult *Sepioteuthis australis* hatched in different seasons.

Power curves fitted.

Table 2.8: Analysis of covariance table, comparing log G (bw day^{-1}) of adult *Sepioteuthis australis* hatched in different seasons, using age as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Test for equal slopes					
Hatch season	3	0.0175	0.0059	2.593	0.053
Age (covariate)	1	3.215	3.215	1422	0.000
Hatch season x Age	3	0.0147	0.0049	2.169	0.091
Residual	342	0.773	0.0023		
Test for differences in Log G					
Hatch season	3	0.0874	0.0291	12.76	0.000
Age	1	3.315	3.315	1451	0.000
Residual	345	0.788	0.0023		

Although individuals were hatched over all months of the year, most juveniles captured hatched within a four month period of gradually increasing temperatures (July-October) in 1995 and 1996. In both years instantaneous growth rate (bw day^{-1}) was positively correlated with hatch date (r=0.75, n=41, P<0.0001; r=0.77, n=28, P<0.0001 for 1995 and 1996 respectively). An individual growth trajectory for each juvenile was constructed from back calculated date of hatching to collection date (Figure 2.5). Juveniles hatched in the lowest temperatures (~12°C July and August) had the shallowest individual growth slopes indicating a slower rate of growth (4.7-5.5% bw day^{-1}). Individuals hatched in warming temperatures (end of October) had progressively faster growth (6.7-8.5% bw day^{-1}) such that their final size at the time of capture actually surpassed that of earlier hatched, and therefore older, individuals.

2.3.4 Length-total weight and length-mantle weight relationships with sex and season

The relationship between length and total wet weight was best described by power functions for female, male and juvenile *Sepioteuthis australis* (Table 2.9). The length-weight relationship was similar for females and males (Table 2.10), with males showing greater variation in total weight at a given length than females. Juveniles could not be directly compared to adults due to unequal variances, however, examination of 95% confidence limits around the slopes show that juveniles were lighter at a given length than females of equivalent size. In contrast, the mantle weight-length relationships show that juveniles had heavier mantles than males or females of the same length, however there was no gender difference in mantle weight (Table 2.10). The mantle weight-length relationship was dependent upon season of hatching (Table 2.11), with summer and spring hatched squid having heavier mantles at a given length compared with squid hatched in winter or autumn.

2.3.5 Relationship between growth and condition.

As both condition and growth of *Sepioteuthis australis* varied as a function of hatching season, a factor of interest was the nature and degree of any association between these two characteristics. Both male and female *Sepioteuthis australis* showed a positive, but relatively weak correlation between the residuals from the mantle weight-length relationship and the size-at-age relationship ($r_{\text{females}}=0.396$, $n=129$, $P<0.0001$; $r_{\text{males}}=0.361$, $n=180$, $P<0.0001$). Individuals that were small for their age, predominantly those individuals hatched in autumn and winter, were also in poorer condition at the whole animal level (Figure 2.6). Conversely, squid that were large for their age, primarily summer and spring hatched squid, appeared to be in better condition than the population average.

2.3.6 Seasonal patterns in maturation.

The maturation patterns of females hatched in spring and summer were different to that of females hatched in autumn and winter (Figure 2.7). Although mature females (stage IV & V) were present in low proportions from 100 days of age in the spring/summer hatched group, high proportions of maturing females (stage II & III) were present up to 200 days of age. In the autumn/winter hatched group at least 75% of females were mature from 120 days onwards, and the proportion of maturing females did not exceed 8% in any of the age classes (Figure 2.7). Only four immature and maturing males were caught (aged 100-160 days) and these were hatched in autumn/winter. All other males from both hatching groups were mature over 92 days of age.

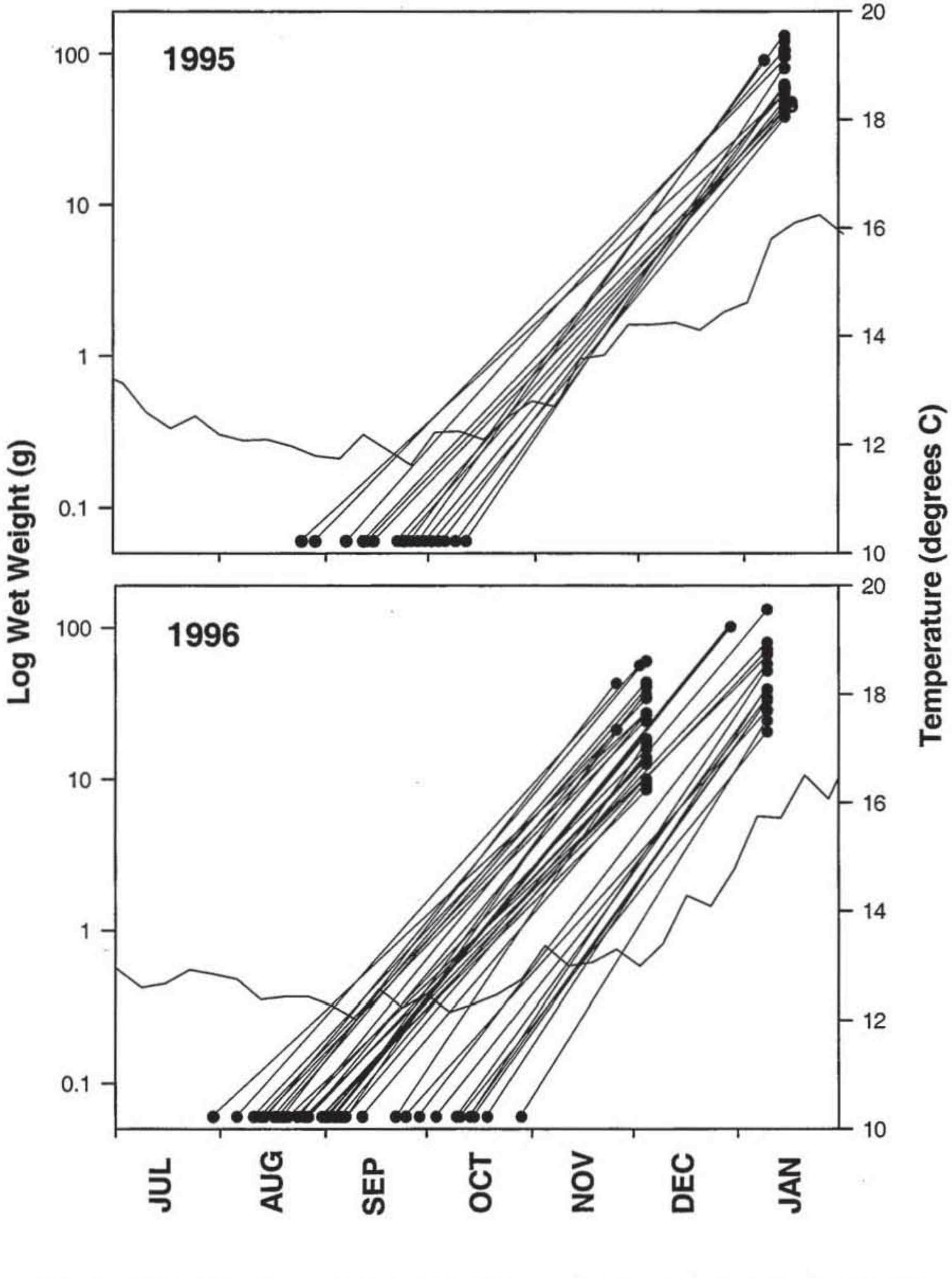


Figure 2.5: Individual growth trajectories (in weight) for each juvenile *Sepioteuthis australis*, drawn from back-calculated hatching date to date of capture. Weekly sea surface temperature for region of collection also plotted. Note the log scale for weight.

Table 2.9: Summary of power curve parameters and associated statistics for total weight-at-length and mantle weight-at-length relationships for all female, male and juvenile *Sepioteuthis australis* sampled in the study.

Sex	*n*	Slope	95% C.I. of slope	Intercept (*ln*a)	r^2	*P*
Total wet weight						
Females	196	2.564	2.490-2.637	-7.776	0.98	<0.0001
Males	237	2.502	2.414-2.589	-7.629	0.93	<0.0001
Juveniles	60	2.359	2.297-2.420	-6.952	0.99	<0.0001
Mantle weight						
Females	196	2.366	2.269-2.463	-7.895	0.92	<0.0001
Males	235	2.470	2.375-2.565	-8.481	0.92	<0.0001
Juveniles	56	2.750	2.606-2.895	-9.746	0.96	<0.0001

Table 2.10: Analysis of covariance table, comparing log weight of female and male *Sepioteuthis australis*, using log ML as a covariate, and log mantle weight using log ML as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Log total weight					
Test for equal slopes					
Sex	1	0.0058	0.0058	0.210	0.647
Log ML (covariate)	1	211.14	211.14	7547.71	<0.0001
Sex x log ML (equal slopes)	1	0.0319	0.0319	1.140	0.286
Residual	429	12.001	0.0279		
Log mantle weight					
Test for equal slopes					
Sex	1	0.0913	0.0913	2.396	0.122
Log ML (covariate)	1	188.44	188.44	4943.42	<0.0001
Sex x log ML (equal slopes)	1	0.0868	0.0868	2.276	0.132
Residual	427	16.277	0.0381		

Table 2.11: Analysis of covariance table, comparing log mantle weight of male and female *Sepioteuthis australis* within each season of hatching, using log ML as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Log ML	1	97.792	97.792	4645.09	<0.0001
Sex	1	0.0789	0.0789	3.751	0.054
Hatch season	3	1.551	0.517	24.557	<0.0001
Sex x log ML	1	0.0708	0.0708	3.364	0.068
Hatch season x sex	3	0.153	0.0509	2.422	0.066
Hatch season x log ML	3	1.614	0.538	25.562	*<0.0001*
Hatch season x sex x log ML	3	0.129	0.0431	2.047	0.107
Residual	332	6.990	0.0211		

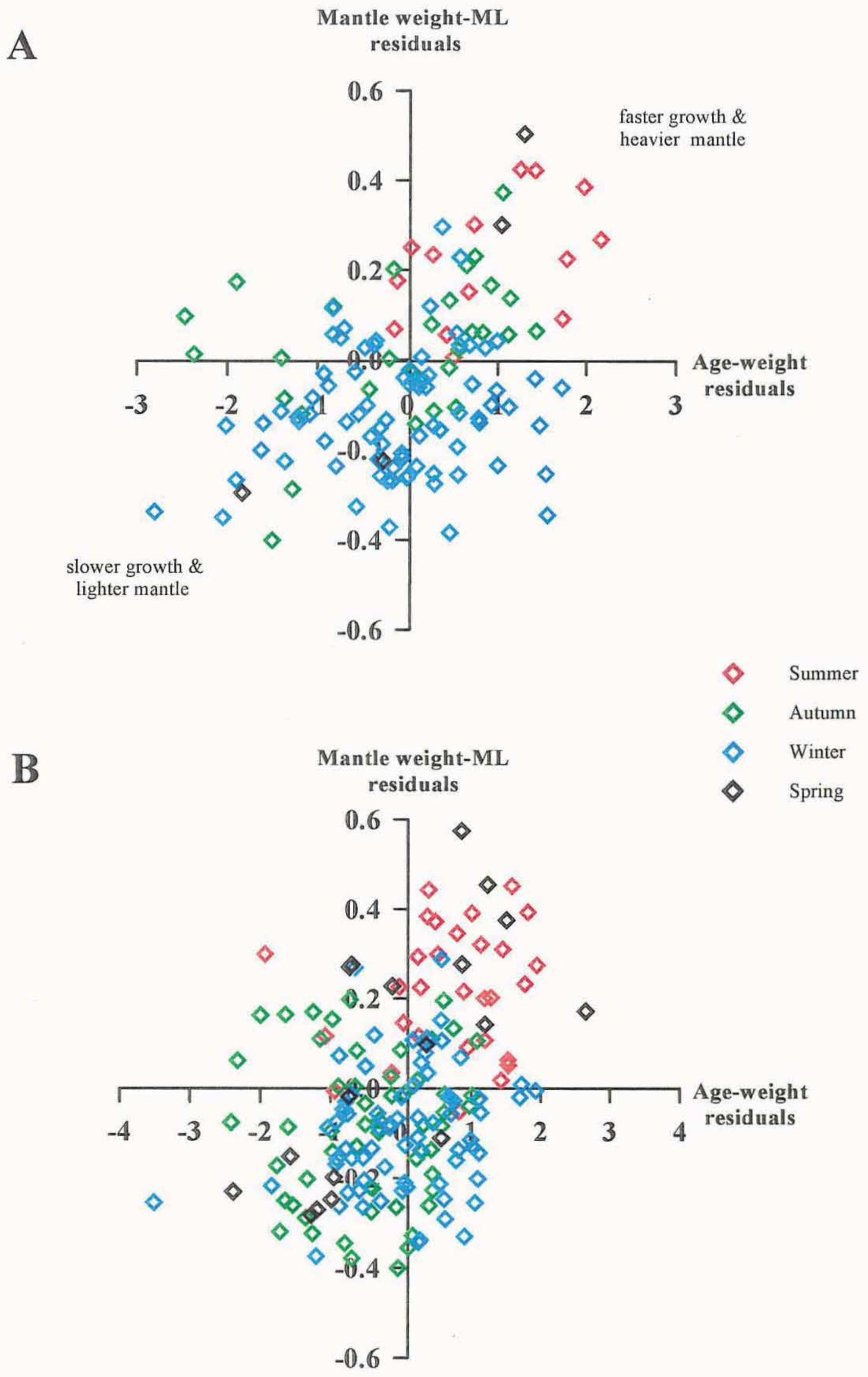


Figure 2.6: Residual values for each individual from the mantle weight-length and size-at-age relationships for (a) females and (b) males.

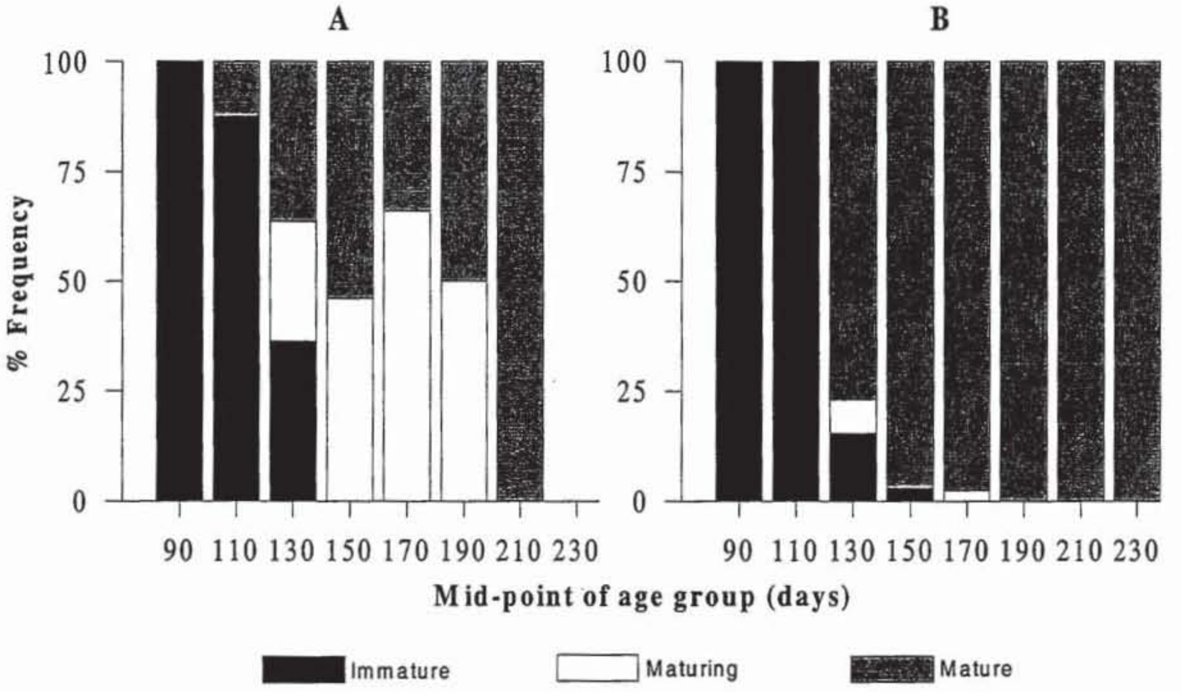


Figure 2.7: Proportion of immature (stage I), maturing (stage II & III), and mature (stage IV & V) females in each 20 day age class for a) spring and summer and b) winter and autumn hatched individuals.

2.4 DISCUSSION

Date of hatching clearly affected growth rates in juvenile *Sepioteuthis australis,* with individuals hatched in warmer temperatures having a final size that could surpass that of earlier hatched (and therefore older) individuals. In adult squid, growth averaged over the lifetime of spring-hatched squid was the fastest of all seasonal hatching groups, and autumn the slowest. This is potentially a function of spring individuals hatching, and consequently growing through, progressively warming temperatures, and autumn hatched squid hatching and growing during seasonally decreasing temperatures. Arkhipkin & Laptikhovsky (1994) also suggest that faster growth of winter hatched *Illex argentinus* was due to these individuals foraging in the more favourable conditions of spring and summer.

The coastal shelf waters of eastern Tasmania follow a seasonal cycle of warming and cooling, which is primarily driven by the changing influence of cool nutrient-rich water of subantarctic origin and warm nutrient-poor subtropical water. There is however, considerable inter-annual variability in the broad patterns of oceanic circulation (Harris *et al.* 1987). In addition, the northerly and southerly movement of water masses off the east coast are very episodic with rapid advances and retreats occurring resulting in strong intra-annual variability (up to 4°C difference) in sea-surface temperature, particularly in summer and autumn (Harris *et al.* 1987). The growth rates of individuals, and therefore the structure of *Sepioteuthis australis* populations on the east coast of Tasmania are likely to alter in response to these environmental variations. In aquaria reared *Loligo forbesi*, a 1°C temperature increase enhanced growth rate by 2% BW day^{-1} (Forsythe & Hanlon 1989) and Grist & des Clers (1999) have demonstrated how physiological responses to relatively small temperature fluctuations may substantially affect the population structure of wild cephalopod populations.

Despite the obvious merits of examining correlations between temperature and growth in field populations, any analysis of the role of seasonal temperature variations is constrained by a limited knowledge of both lateral and vertical migrations which may take place during the life cycle (Grist & des Clers 1999), information which is not available for *Sepioteuthis australis*. Additionally, in wild populations the seasonal cycle of growth is not always, perhaps never, solely under temperature control (Ricker 1979), as there are concomitant changes in food type and availability, day length and oxygen saturation. Growth and reproductive characteristics of some cephalopods are more effected by food availability than temperature (eg: *Idiosepius pygmaeus*, van Camp 1997). Although both ration and temperature increases have a positive effect on growth, the mechanism at the cellular level by which these factors manifest their effects on growth are different (eg: *Sepia elliptica*, Moltschaniwskyj & Martínez 1998). O'Dor *et al.* (1996) suggests that resolving the relative influence of ocean dynamics vs quality and quantity of food is complex. For example, although growth of juvenile *Illex illecebrosus* increases in response to increased temperatures, juveniles may be food limited once peak of the spring bloom has passed (O'Dor *et al.* 1996). The main prey of juvenile *S. australis*, *Nyctiphanes australis* (unpubl. data Jackson GD & Pecl GT) peaks in abundance on the east coast of Tasmania in autumn and spring, although annual abundance varies by two orders of magnitude (Young *et al.* 1993). Food availability is an unquantified factor that may potentially effect growth of *S. australis* as much as variations in temperature, and any seasonal effect on growth probably involves an interaction between ambient temperature, individual size and food related factors (González *et al.* 2000).

In this study the length-mantle weight relationship of adults was dependent on season of hatching, with individuals hatched in summer and spring having heavier mantles at a given length than those hatched in autumn or winter. Differential rates of growth or varying levels of condition, or perhaps both, may affect survivorship of individuals (Calow 1987), and therefore, persistence of micro-cohorts within the population of *Sepioteuthis australis*. The exponential or logarithmic growth curve reported for cephalopod species by its very nature ensures that a large portion of the life span is spent at small sizes relative to the size at sexual maturity. Survivorship of juvenile cephalopods is estimated to be very low (Saville 1987), suggesting a typical type III survivorship curve where small changes in juvenile mortality rates have a large effect on adult recruitment. Faster growing juveniles may survive better than slower growing ones because they remain vulnerable to predation for a shorter period of time - relative survival is often proportional to growth (ie: the growth-predation hypothesis) (Fortier & Quiñonez-Velazquez 1998). Robin & Dennis (1999) showed a link between mild winter conditions and cohort success of *Loligo forbesi* and *Loligo vulgaris*, suggesting that differential juvenile survival or growth was involved. Alternatively size may not be disadvantageous to the survivorship of cephalopods as condition may play a more important role in the population dynamics (Moltschaniwskyj & Martínez 1998).

Growth was logarithmic in nature in both length and weight for adult and later-stage juvenile *Sepioteuthis australis*, with a rate of up to 8.5% BW day^{-1} in the youngest individuals (<100 days), and an average rate over the life time of 4-5% BW day $^{-1}$ in the oldest individuals. It seems that *S. australis* has an efficient metabolism that produces fast overall growth even in the cool waters of Tasmania, as this is 1-3% BW day $^{-1}$

higher than growth rates reported for other temperate squid (eg: 1.2-1.5% BW day $^{-1}$ *Illex argentinus,* Rodhouse & Hatfield 1990; 1.8-3.1% *Loligo pealei*, Brodziak & Macy 1996; 1.4-1.9% *Onychoteuthis borealijaponica*, Bigelow 1994). Although larger squid were more likely to be male, this study did not detect a gender difference in the rate of growth. Instead males may be larger as they appear to live slightly longer on average than females. Males are usually larger than females in loliginid species where agonistic competition for females takes place (Hanlon & Messenger 1996), behaviours that have been observed on the spawning grounds of *S. australis* (pers. obs.).

The lifespan of *Sepioteuthis australis* is likely to be less than one year, probably around 6-10 months not including the egg stage. Faster growth rates are associated with shorter life spans (Forsythe & Hanlon 1988), and so squid hatched in warmer seasons may have shorter lifespans, adding to the complex effect of environment on the population structure. However, a large proportion of spring and summer hatched females were still maturing at 180-200 days of age, and a shorter life span relative to autumn and winter hatched females therefore implies a much shorter duration of reproductive output for spring and summer hatched females. Temperature, photoperiod and food availability affect maturation rates (Van Heukelem 1979, Mangold 1987), however, little is known about the maturation rates of squids hatching in different seasons in field populations. Culture experiments have shown that low temperature and long day length lead to late spawning at a larger size, while high temperature and short day length results in individuals spawning at a younger age and smaller size (Van Heukelem 1979). *Sepioteuthis australis* hatched in spring and summer would be beginning maturation in autumn during decreasing temperatures and photoperiod, resulting in late maturation, whilst autumn and winter hatched squid would be experiencing increasing temperatures and photoperiod during their maturation period and consequently maturation would occur at a younger age. However *Illex coindetii* in the Strait of Sicily show the opposite trend, with late maturation of autumn and winter hatched squids and early maturation of spring and summer hatched individuals (Arkhipkin *et al.* 2000). The critical life cycle stage at which the temperatures and photoperiod experienced by individuals determine the timing and size at maturation may be species specific.

Back-calculated dates of hatching suggest that hatching, and therefore spawning, occurs all year round in *Sepioteuthis australis*. The short life span clearly necessitates the need for year round spawning, a feature that appears to be common in other loliginids (eg: *Loligo vulgaris*, Guerra & Rocha 1994, *Loligo forbesi*, Boyle *et al.* 1995; *Lolliguncula brevis*, Jackson *et al.* 1997) and is the mechanism by which exposure of hatchlings within the population to seasonal extremes occurs. Given that growth, condition, maturation, and potentially also life-span of *S. australis* are dependent on environmental factors, the dynamic nature of oceanographic conditions on the east coast of Tasmania are likely to result in a highly variable and fluctuating population structure which has important implications for population modelling and fishery management. In this study, seasonal hatching groups were pooled across years, obviously incorporating a degree of inter-annual variability and it is likely that if sample sizes were large enough to allow examination of growth across years and seasons, an even greater seasonal effect may be found. Intensive multi-year collections are necessary to ascertain the importance of inter-annual effects on the growth rate, maturation, and population structure of *S. australis*, relative to seasonal influences.

CHAPTER 3: AGE, GROWTH AND MATURATION OF TROPICAL AND TEMPERATE *SEPIOTEUTHIS* SPECIES

3.1 INTRODUCTION

This chapter examines and compares growth, body size and maturation in the tropical *Sepioteuthis lessoniana* and temperate *S. australis* from populations along the east coast of Australia. Body size and age at maturity are key features in life histories, largely influencing an individual's fitness by determining the timing and amount of energy allocated to reproduction. Delaying reproduction may result in a larger size at maturity and therefore higher fecundity (Stearns 1992). However, organisms that mature earlier have an increased probability of surviving to maturity due to a shorter time period between birth and reproduction. Additionally, offspring that are produced earlier also have a higher reproductive value (Yampolsky & Scheiner 1996), as these will in turn also start reproducing earlier.

For animals with indeterminate growth (eg: snakes, fish, crustaceans and cephalopods) timing of maturation is a critical life history trait (Heino & Kaitala 1997) because individuals will experience life history trade-offs between survival and reproduction, and between reproduction and growth. Since reproduction requires energy which is then not available for maintenance or growth, age at maturity partly determines the life time growth pattern of an individual. Consequently, the optimal age at maturity may be affected by environmentally determined overall growth potential and the age- or size-specific mortality or fertility patterns (Heino & Kaitala 1997). Growth and mortality rates vary with environment and so organisms in spatially or temporally changing environments should develop phenotypic plasticity for age and size at maturity (Perrin & Rubin 1990).

Cephalopod life history characteristics show plasticity in response to environmental variation. Laboratory studies have clearly demonstrated the effect of both temperature and feeding levels on the growth, reproductive biology and life span of cuttlefishes (Moltschaniwskyj & Martínez 1998, Koueta & Boucaud-Camou 1999), squids (Forsythe & Hanlon 1989, Sakurai *et al.* 1993, Villanueva 2000) and octopuses (Joll 1977, Forsythe & Hanlon 1988). Small changes in temperature produce large changes in growth rates and final size (Forsythe 1993), although higher temperatures usually result in shorter lifespans (eg: *Octopus bimaculoides*, Forsythe & Hanlon 1988). Other than temperature, only food has as dramatic effect on growth of cephalopods (Forsythe 1993), often producing a linear relationship between daily growth rate and daily food consumption (eg: *Sepioteuthis lessoniana*, Segawa 1990; *Eledone cirrhosa,* Houlihan *et al.* 1998).

In general, cephalopods exhibit a negative correlation between growth rate and size at maturity (Wood & O'Dor 2000). If low temperatures reduce growth rates maturation occurs at larger sizes, but if under-nutrition results in slow growth then individuals mature at smaller sizes (Van Heukelem 1979). As juvenile cephalopods generally grow exponentially, small changes in growth rate as a function of either feeding levels or temperature may have large subsequent effects on final size and age and size at maturity. Consequently, growth rates, age and size at maturity, and final body size may vary substantially between and within species, particularly among those species which inhabit a wide geographical range.

Many studies have suggested that the life histories of tropical and temperate species differ considerably. In tropical waters there is relatively little seasonal variation and sub-annual life cycles generally occur (Jackson 1990b, Jackson & Choat 1992). In temperate waters, annual (Natsukari *et al.* 1988) and, in some cases longer cycles seem to predominate (Hanlon *et al.* 1989), presumably because food production is largely driven by annual variation in temperate climates (O'Dor & Coelho 1993). Squid, even of the same species grow larger, reproduce later and are individually more fecund in cooler waters (O'Dor & Coelho 1993). Tropical forms of *Loliolus noctiluca* exhibit a linear growth pattern, live for less than four months and have a year round breeding cycle (Jackson & Choat 1992). In contrast, although the maximum body sizes were comparable, growth in a temperate population of *L. noctiluca* was better described by a logistic function within a nine month life span and a distinct seasonal breeding cycle (Dimmlich & Hoedt 1998). Maximum body size and age and size at maturity of the ommastrephid *Ornithoteuthis antillarum* also varies across latitudinal zones, with individuals from the tropical Atlantic not exceeding 140 mm ML whereas in the south-west Atlantic squids attain 190-210 mm ML and are still immature at 140 mm ML (Arkhipkin *et al.* 1998).

This chapter examines the maturation, growth, lifespan, and body size of *Sepioteuthis lessoniana* and *S. australis* from different latitudinal zones along the east coast of Australia using statolith derived age estimations. Of particular interest is the magnitude of differences in growth and maturation and how they may compare to the seasonal differences observed for *S. australis* at the most temperate location (Chapter 2).

3.2 MATERIALS AND METHODS

3.2.1 Collection and processing

Sepioteuthis lessoniana individuals were obtained from waters off Townsville (Table 3.1) by jigging, and off Brisbane by a combination of tunnel-netting by the commercial sector and jigging. *Sepioteuthis australis* were obtained off Newcastle by jigging and Tasmania by a combination of jigging and modified purse-seine. Juvenile *S. lessoniana* individuals were collected from the Breakwater Marina in Cleveland Bay, Townsville and Brisbane marinas using dip-nets. Juvenile *S. australis* from Tasmania were also collected using dip-nets from shallow waters above inshore *Amphibolis* seagrass beds. Most individuals were refrigerated or placed on ice within a few hours of capture and processed within 12 hours. Some individuals obtained from the commercial sector had been frozen; 37 from Brisbane, 24 from Townsville, and 10 from Tasmania. Dorsal mantle length (ML) was measured to the nearest millimetre and total body weight to the nearest 0.01g. Body weight could not be measured for twelve *S. lessoniana* caught in Townsville, however, total body weight was estimated for these individuals from the relationship: Weight=0.00042 x $ML^{2.6045}$ (r^2=0.99, n=34). Adults were sexed and assigned a reproductive maturity category; I (immature) to V (mature) using Lipinski's Universal scale (Lipinski 1979). Individuals with no sexual development were classed as juveniles.

3.2.2 Age estimation

The age of each individual was determined from increments in the statolith, validated as daily for both *Sepioteuthis lessoniana* (Jackson 1990a) and *S. australis* (Chapter 2). *Sepioteuthis australis* statoliths were stored, treated and processed as detailed in Chapter

2. Smaller *S. lessoniana* statoliths were ground on the anterior (concave) surface only, larger *S. lessoniana* and all *S. australis* statoliths were ground on both surfaces.

Table 3.1: Sample sizes, collection locations and dates for *Sepioteuthis lessoniana* and *Sepioteuthis australis.*

Species & location	Latitude & longitude	Collection dates	Total sample size
Sepioteuthis lessoniana			
Townsville	19°10'S; 146°55'E	Feb 1995-Oct 1997	116
Brisbane	27°20'S; 153°3'E	Aug 1995-Apr 1997	173
Sepioteuthis australis			
Newcastle	32°45'S; 152°10'E	Aug 1995-Dec 1995	131
Tasmania	42°15'S; 148°10'E	Jan 1996-Jul 1997	493

3.2.3 Growth rate estimation and statistical analyses

The following curves were used to fit size-at-age data: exponential, linear, power, logistic and von Bertalanffy. The best fitting curve was determined by examination of residuals for any systematic pattern and the highest r^2. Differences in growth rates between sexes at each location were compared with analysis of covariance using size-at-age data. Differences in the age or weight frequencies were examined by χ^2 frequency analysis using 20 day age classes and 100g weight classes. Across the geographical locations, differences in growth rates were compared with analysis of covariance on size-at-age data. Of interest were the comparative differences in size-at-age, and so only animals within an age range common to all groups were considered (80-190 days). Differences in average body size and age between the populations were analysed using a 1-way ANOVA followed by Tukey's honestly significant post-hoc test to determine where differences among the means occurred. Individual growth calculations assume a hatch weight and length of 0.06 g and 4.75 mm, based on unpublished data of 20 *Sepioteuthis australis* hatchlings, and within the range reported for *Sepioteuthis lessoniana* hatchlings (Ikeda *et al.* 1999). Instantaneous growth rate, G, was calculated for each individual as described previously in Chapter 2. All ± values in the text refer to standard errors.

3.3 RESULTS

3.3.1 Size and age structure

There were no significant gender differences in the age or weight frequencies between male and female *Sepioteuthis lessoniana* caught in Townsville and Brisbane or *S. australis* caught in Newcastle (Table 3.2). In contrast, there were differences in the age and weight frequencies between the sexes of *S. australis* from Tasmania, with larger and older individuals more likely to be males (Table 3.2).

The maximum ages and body sizes of *Sepioteuthis lessoniana* in Townsville and Brisbane and *S. australis* in Newcastle were all within similar ranges (183-202 days and 801-1055g respectively, Figures 3.1 & 3.2). However, *S. lessoniana* from Townsville were 26-70% smaller on average compared to individuals from the other locations (F=60.26, df=3,760, P<0.0001) and also 14-32% younger (F=84.23, df=3,570, P<0.0001). *Sepioteuthis australis* from Tasmania were larger on average compared to individuals from all other groups, and older compared to individuals from Townsville and Newcastle (Figures 3.1 & 3.2). Squid from Tasmania achieved the largest maximum body size (1700g for females and 3350g for males) and attained the greatest maximum age (264 days for females and 254 days for males).

Table 3.2: Comparison of age and weight frequencies of male and female adults caught at each geographical location.

Location	Age frequency			Weight Frequency		
	χ^2	df	P	χ^2	df	P
Sepioteuthis lessoniana						
Townsville	5.36	6	0.50	4.79	7	0.69
Brisbane	7.13	4	0.13	13.39	9	0.15
Sepioteuthis australis						
Newcastle	5.45	4	0.24	9.88	10	0.45
Tasmania	65.18	9	<0.0001	53.12	21	0.0001

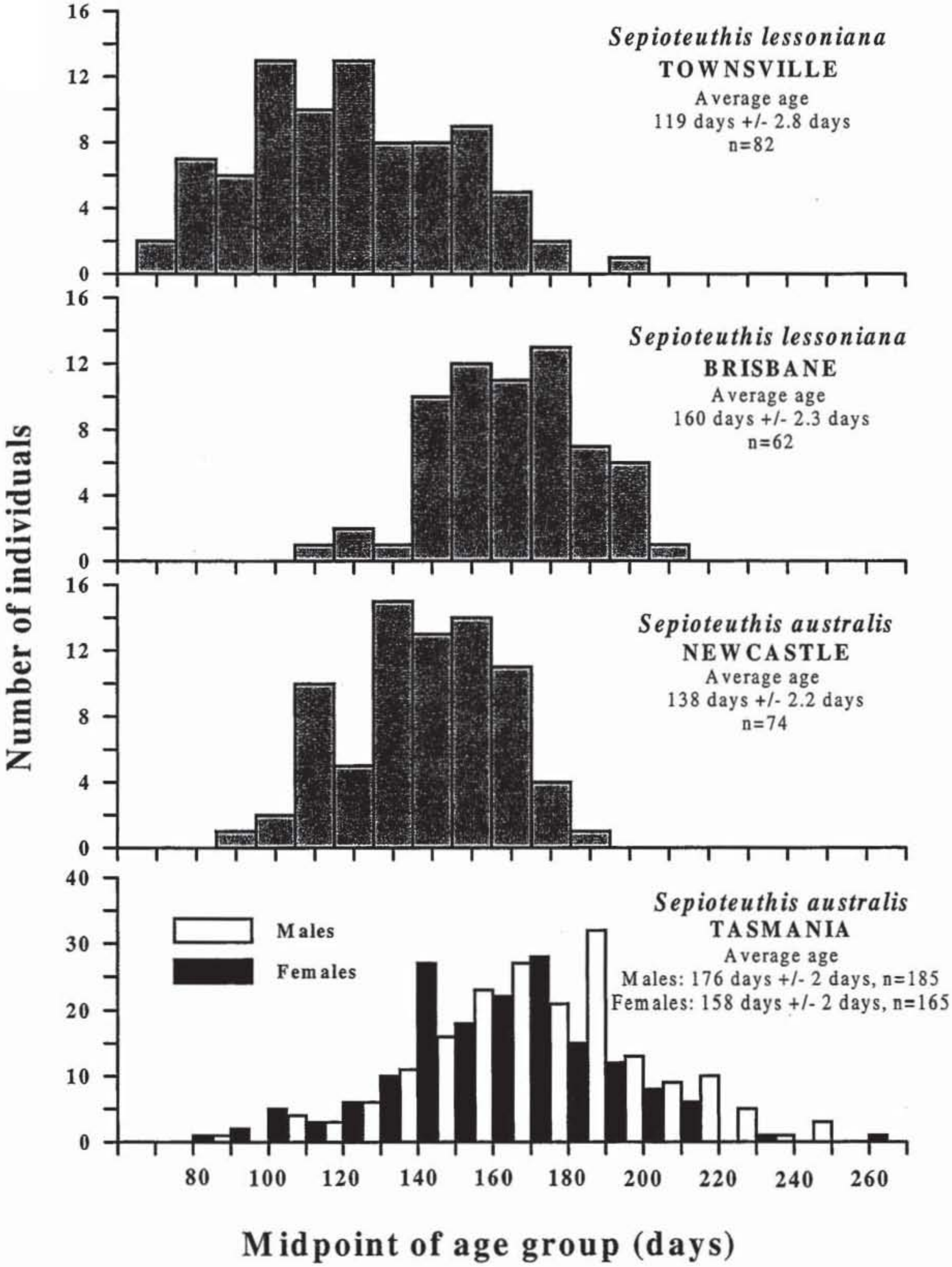


Figure 3.1: Age frequency of adult *Sepioteuthis lessoniana* from Townsville and Brisbane, and *Sepioteuthis australis* from Newcastle and Tasmania. Mean ages of adults ± se also shown.

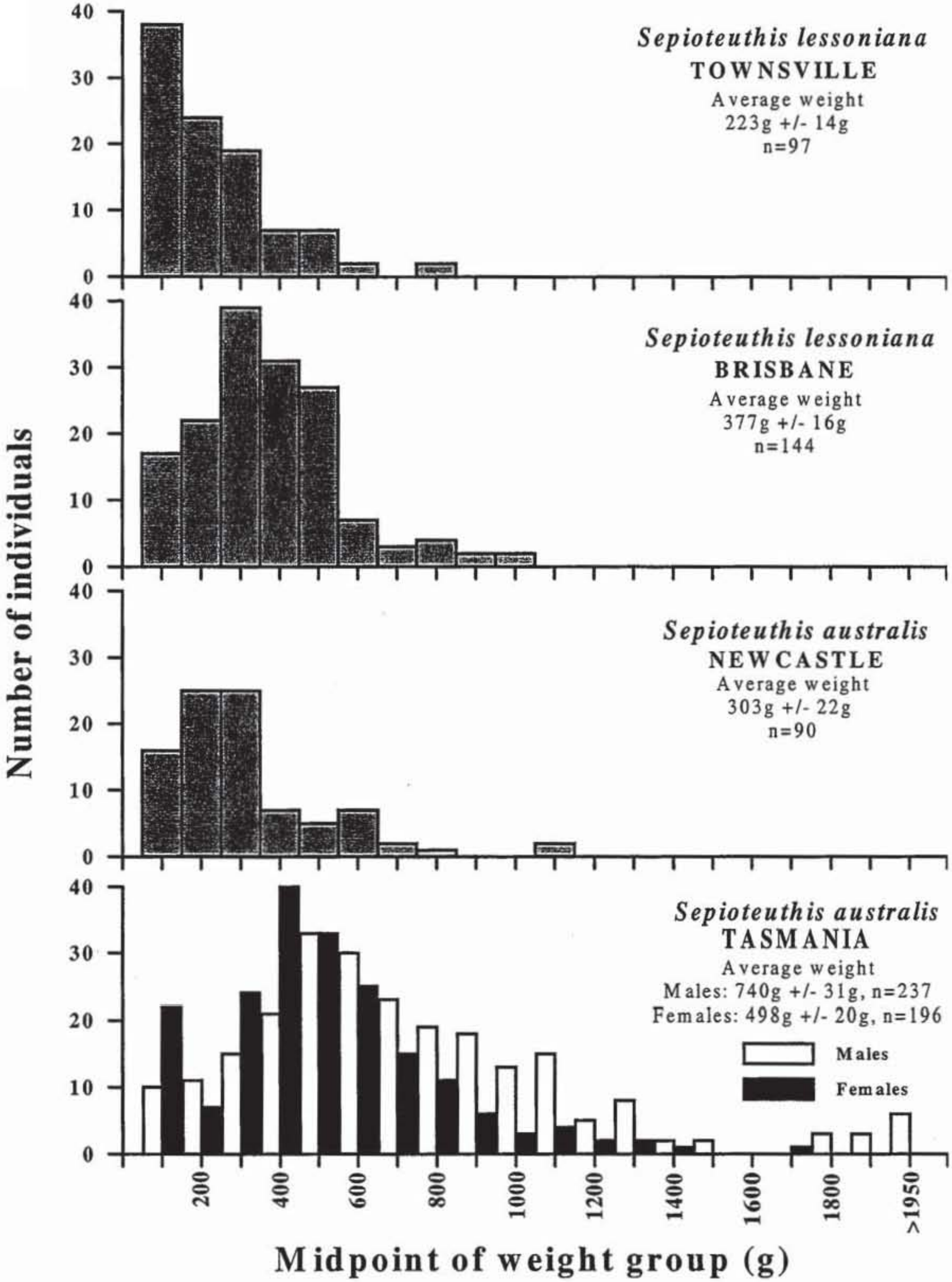


Figure 3.2: Weight frequency of *Sepioteuthis lessoniana* from Townsville and Brisbane, and *Sepioteuthis australis* from Newcastle and Tasmania. Mean adult weight ± se also shown for each location.

3.3.2 Growth

For both species at each location the age-total wet weight relationship was best described by power functions for adults and juveniles (Table 3.3). Considerable variation in growth rates were evident in both species at each location (Figures 3.3-3.5). There were no significant gender differences in the rate of growth in weight, or average weight adjusted for age in any of the groups (Table 3.4, see also Chapter 2).

An examination of the confidence limits around the growth curves for adults revealed that overall, *Sepioteuthis lessoniana* from Townsville were growing slower than squid from Brisbane, and *S. australis* from Tasmania were growing slower than squid from Newcastle. Over a common age range (80-190 days) analysis of covariance on size-at-age data also revealed significant differences in growth in weight between the geographical locations (Table 3.5). At young ages, *S. lessoniana* from Townsville were heavier for their age compared with individuals from the other groups, with squid at 100-120 days of age from Newcastle and Tasmania only 57% and 46% the size of squid from Townsville (Table 3.6). This trend was reversed at older ages with individuals from Townsville the smallest for a given age and *S. australis* from Tasmania the largest. At 160-180 days of age squid from Townsville and Brisbane were 65% and 86% the size of individuals from Tasmania (Table 3.6).

The instantaneous growth rate (%BW day^{-1}) averaged over the lifetime and calculated on an individual basis declined with age in each population as expected for power growth. However, the rate of deceleration in growth with age differed substantially among the populations (Table 3.7). Although squid from Townsville had the highest instantaneous growth rates at young ages (up to 9.34% bw day^{-1}, <100 days), the slope from the log G-age relationship was twice the value compared to the slope for individuals from Newcastle and Tasmania, indicating that the growth rate declined with age more rapidly in squid from Townsville (Figure 3.6).

Table 3.3: Summary of curve parameters and associated statistics for weight-at-age power growth curves for female, male and juvenile *Sepioteuthis* at each location.

Sex	Age range (days)	*n*	Weight range (g)	*n*	Slope	95% C.I. of slope	Intercept (*ln*a)	r^2	*P*
Sepioteuthis lessoniana									
Townsville									
Females	71-186	41	45-556	49	2.219	1.750-2.690	-5.326	0.69	<0.0001
Males	71-174	41	42-801	48	2.222	1.673-2.772	-5.295	0.63	<0.0001
Juveniles	17-63	19	0.57-6.34	19	1.690	1.077-2.302	-5.244	0.63	<0.0001
All adults		82			2.221	1.868-2.522	-5.308	0.66	<0.0001
Brisbane									
Females	111-187	23	87-961	83	2.886	1.806-3.967	-8.696	0.58	<0.0001
Males	124-202	39	138-980	61	3.358	2.535-4.181	-11.020	0.64	<0.0001
Juveniles	7-111	16	0.1-46.1	29	1.284	0.822-1.745	-4.358	0.70	<0.0001
All adults		62			3.158	2.573-3.794	-10.033	0.61	<0.0001
Sepioteuthis australis									
Newcastle									
Females	91-183	43	18-640	51	5.216	4.192-6.240	-20.336	0.72	<0.0001
Males	98-171	31	41-1055	39	3.728	2.298-5.157	-12.847	0.49	<0.0001
Juveniles	58-148	30	5.29-154	41	1.204	0.066-2.342	-2.051	0.14	0.039
All adults		74			4.513	3.700-5.326	-16.780	0.62	<0.0001
Tasmania									
Females	84-264	165	33-1700	196	3.610	3.239-3.980	-12.250	0.69	<0.0001
Males	92-254	185	56-3350	237	3.149	2.785-3.514	-9.805	0.61	<0.0001
Juveniles	4-141	47	0.06-144	60	2.523	2.135-2.910	-8.267	0.79	<0.0001
All adults		350			3.456	3.206-3.700	-10.150	0.68	<0.0001

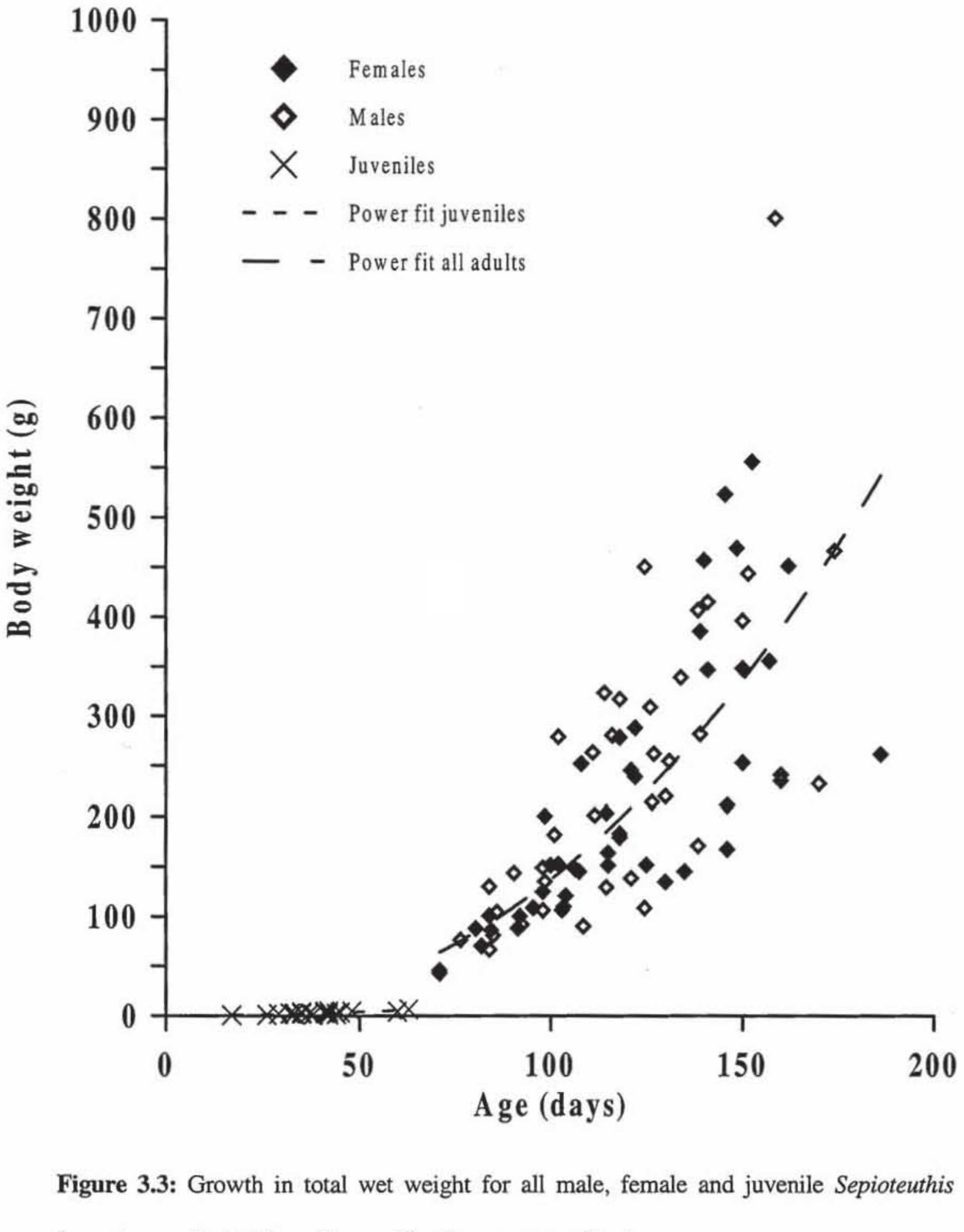


Figure 3.3: Growth in total wet weight for all male, female and juvenile *Sepioteuthis lessoniana* collected from Townsville. Power curves fitted.

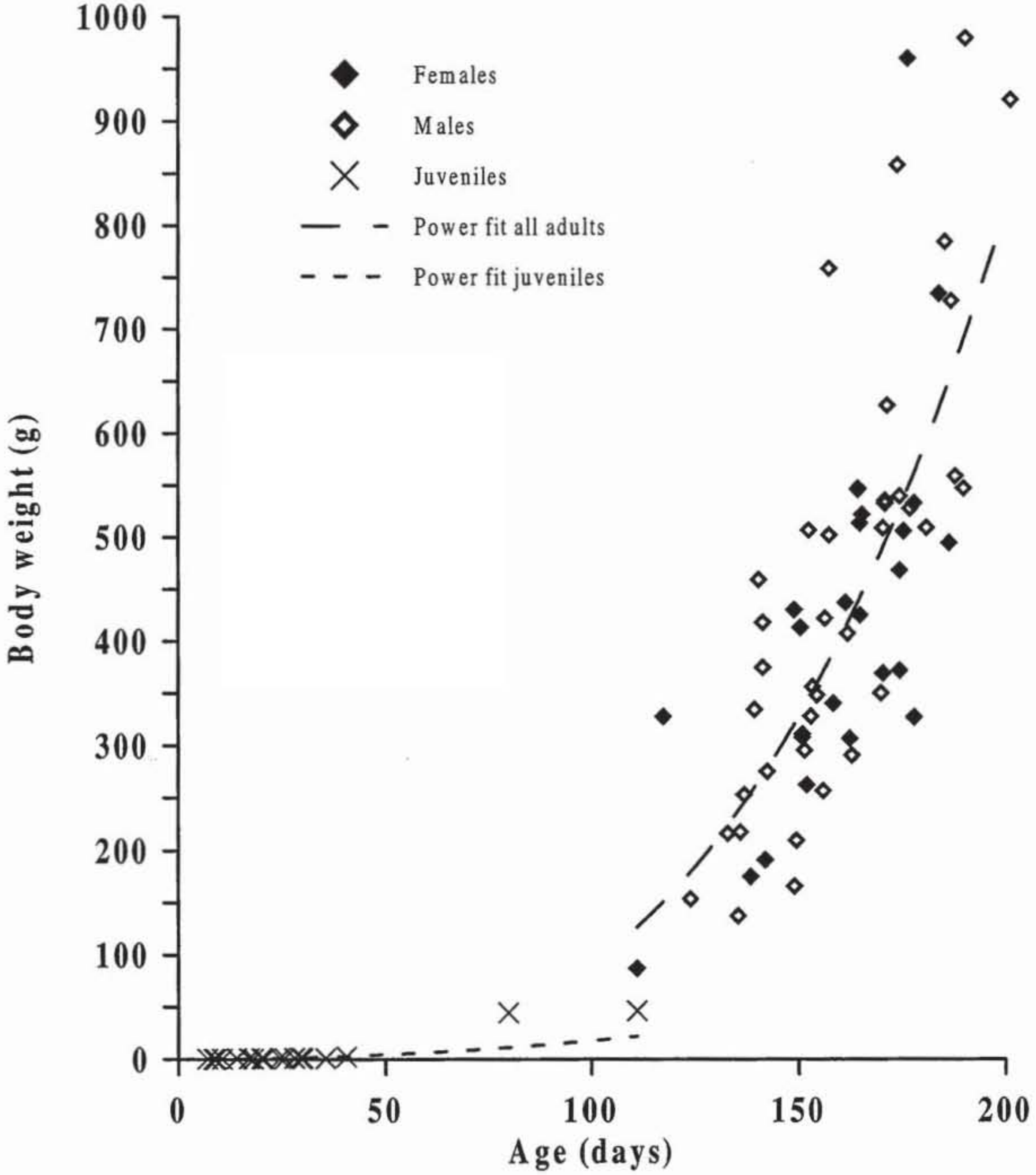


Figure 3.4: Growth in total wet weight for all male, female and juvenile *Sepioteuthis lessoniana* collected from Brisbane. Power curves fitted.

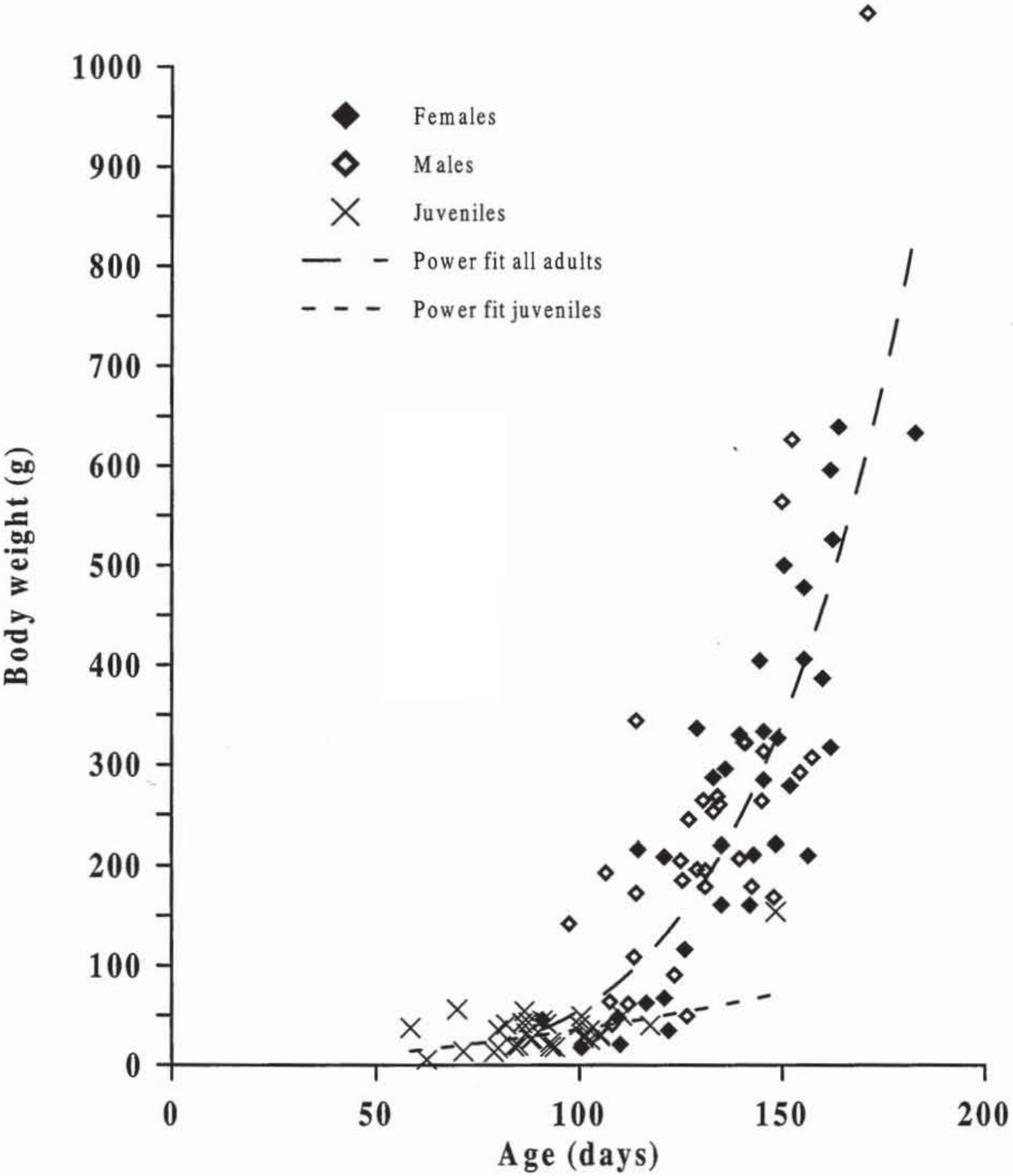


Figure 3.5: Growth in total wet weight for all male, female and juvenile *Sepioteuthis australis* collected from Newcastle. Power curves fitted.

Table 3.4: Analysis of covariance table, comparing growth in log weight between male and female *Sepioteuthis,* using log age as a covariate.

Source	MS	*F*-value	*P>F*
Sepioteuthis lessoniana			
Townsville			
Test for equal slopes			
Sex	4.25×10^{-5}	0.000	0.986
Log age (covariate)	19.864	153.922	0.000
Sex x Log age (equal slopes)	8.06×10^{-6}	0.000	0.994
Test for differences in Log weight			
Sex	0.041	0.325	0.570
Log age	19.866	155.86	0.000
Brisbane			
Test for equal slopes			
Sex	0.047	0.499	0.483
Log age (covariate)	8.715	92.655	0.000
Sex x Log age (equal slopes)	0.05	0.529	0.470
Test for differences in Log weight			
Sex	0.07	0.753	0.389
Log age	9.158	98.157	0.000
Sepioteuthis australis			
Newcastle			
Test for equal slopes			
Sex	0.799	3.164	0.080
Log age (covariate)	27.381	108.354	0.000
Sex x Log age (equal slopes)	0.758	3.001	0.087
Test for differences in Log weight			
Sex	0.675	2.601	0.111
Log weight	32.727	126.05	0.000

Table 3.5: Analysis of covariance table, comparing log total weight of all adult *Sepioteuthis* aged 80-190 days within each geographical location, using log age as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Log age	1	78.412	78.412	429.9	<0.0001
Location	3	9.269	3.090	16.940	<0.0001
Location x log age	3	8.823	2.941	16.125	<0.0001
Residual	484	88.273	0.182		

Table 3.6: Average weight, ML & growth rate in body weight per day (averaged over lifetime) (± s.e.) of adult squid in each of two age categories, at each location.

		Sepioteuthis lessoniana		*Sepioteuthis australis*	
Age group		Townsville	Brisbane	Newcastle	Tasmania
100-120 days	Weight	196g ± 15	207g ± 120	112g ± 29	91g ± 11
	ML	150mm ± 5	139mm ± 26	118mm ± 11	127mm ± 8
	G	7.29 ± 0.08	6.94 ± 0.38	6.47 ± 0.2	6.55 ± 0.13
	n	23	2	12	11
160-180 days	Weight	384g ± 76	507g ± 32	577g ± 76	592g ± 22
	ML	199mm ± 18	191mm ± 5	234mm ± 16	260mm ± 4
	G	5.17 ± 0.19	5.29 ± 0.04	5.50 ± 0.08	5.37 ± 0.02
	n	3	24	9	101

Table 3.7: Analysis of covariance table, comparing log G (bw day^{-1}) of adult *Sepioteuthis,* aged 80-190 days among geographical locations, using age as a covariate.

Source	df	Type-III SS	MS	*F*-value	*P>F*
Age	1	2.528	2.528	952.679	<0.0001
Location	3	0.2869	0.0951	35.87	<0.0001
Location x Age	3	0.233	0.077	29.245	<0.0001
Residual	484	1.284	0.0026		

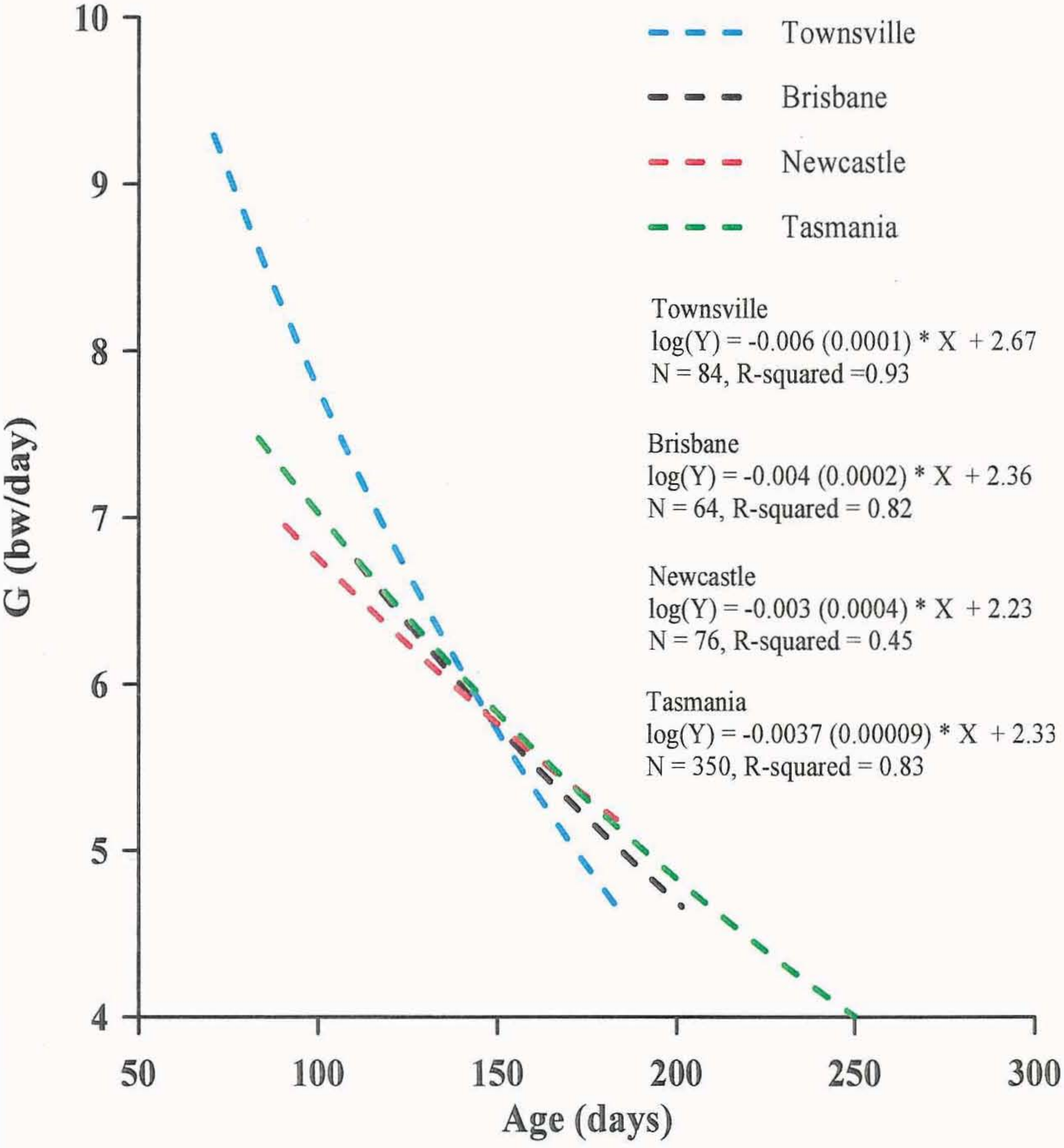


Figure 3.6: Instantaneous growth rate (G) (averaged over lifetime) in weight, with age of adult *Sepioteuthis lessoniana* from Townsville and Brisbane, and *Sepioteuthis australis* from Newcastle and Tasmania. Values in brackets are standard errors of the slopes.

3.3.3 Age and size at maturity

At each location males were mature at much younger ages (25-45 days younger), and except for *Sepioteuthis lessoniana* in Brisbane, also at smaller sizes compared with females. Although both male and female *S. lessoniana* from Townsville were mature at the youngest ages, *S. australis* from Tasmania were maturing at the smallest body sizes. At each location immature and maturing adults were present in the population over considerable age and size ranges (Figure 3.7). *Sepioteuthis lessoniana* from Townsville were mature as young as 77 days for males and 107 days for females, however immature and maturing (stage I-III) squid were found up to 126 and 150 days of age for males and females, respectively. Male and female *S. lessoniana* from Brisbane were mature as young as 141 and 174 days respectively. Female *S. australis* from Tasmania were mature as young as 117 days and as small as 120g, compared to 142 days and 347g for females caught in Newcastle. Male *S. australis* from Tasmania were mature at 92 days and 73g, compared to 97 days and 142g for Newcastle caught individuals. Very few immature and maturing males were present in the Tasmanian population sampled.

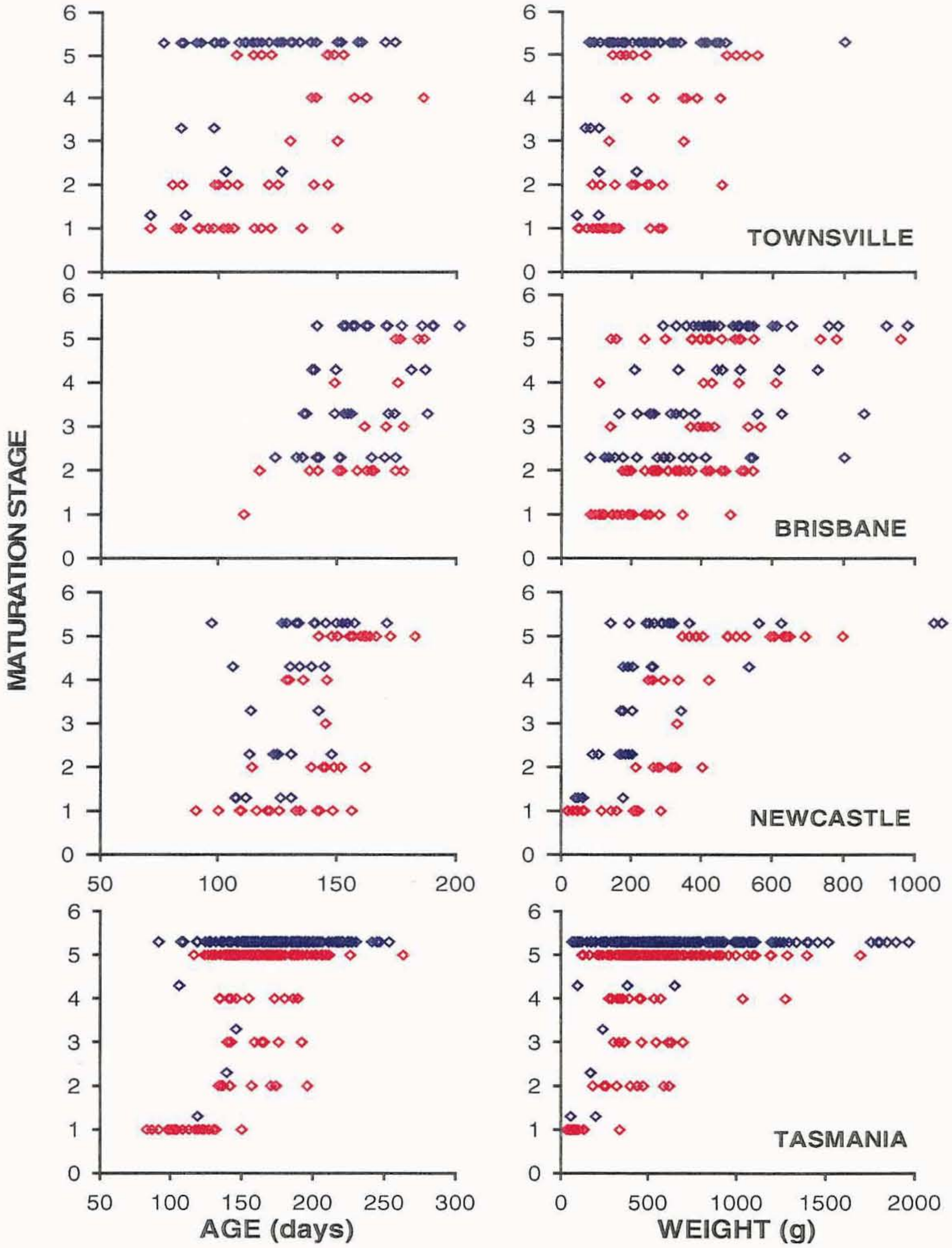


Figure 3.7: Age and size at each maturation stage for male and female *Sepioteuthis lessoniana* and *Sepioteuthis australis.* Males are the darker symbols above females. Note the different x-axis scales for Tasmania, four males (2200-3350g) not shown for Tasmania on weight graph.

3.4 DISCUSSION

Substantial differences in the comparative age-specific growth patterns of tropical and temperate *Sepioteuthis* species were evident in this study, resulting in large differences in size-at-age throughout the lifespan of the groups examined. In the tropics, *Sepioteuthis lessoniana* were younger and smaller and matured at younger ages (and generally smaller sizes) than their counterparts in the sub-tropical waters of Brisbane. The patterns were more complicated in *S. australis*, with squid from Newcastle growing faster overall than Tasmanian squid. However, Tasmanian individuals matured at younger ages and at smaller sizes. *Sepioteuthis australis* from Tasmania also exhibited gender differences in the age and weight frequencies of adults, with males becoming larger than females by living for slightly longer. This pattern was not observed in *S. australis* from Newcastle.

The differences in growth between *Sepioteuthis lessoniana* from the tropics and *S. australis* from temperate Tasmania were substantial and depended critically on the age range considered. Tasmanian squid were only 46% the size of Townsville squid at 100-120 days of age, however, at older ages this pattern was reversed with Townsville squid only 65% the size of squid from Tasmania at 160-180 days of age. Within *S. australis* from Tasmania, individuals hatched in different seasons show comparable differences in size at age, with squid hatched in winter only 63% the size of squid hatched in summer at 170-190 days of age (Chapter 2). However, the growth patterns that ultimately result in these seasonal disparities in size-at-age appear to develop differently to the size-at-age patterns observed across latitudes. Winter hatched *S. australis* grew at slower rates (relative to summer hatched squid) throughout the entire lifespan. In comparison, tropical squid achieved a smaller final size at age by faster growth initially which declined with age very rapidly and therefore resulted in a smaller size at age overall, relative to temperate squid.

Cephalopods reared in aquaria consistently exhibit a two-phase growth pattern of exponential followed by logarithmic growth (Yang *et al.* 1986, Forsythe & Hanlon 1988, Forsythe 1993), where the length and rate of the initial exponential phase varies with rearing temperature. The exponential growth phase of *Octopus maya* lasted 75 days at 30°C (7.5% bw day^{-1}), whereas in individuals reared at 20°C it continued for 165 days at the lower rate of 3.8% bw day^{-1}, with the body sizes of individuals from both groups very similar at the end of their respective exponential phases (Van Heukelem 1976 in Summers *et al.* 1993). *Octopus bimaculoides* also has a shorter exponential growth phase at 23°C compared to 18°C (Forsythe & Hanlon 1988). *Sepioteuthis lessoniana* reared in the laboratory grow exponentially for the first 60 days, although exponential growth models did not provide the best description of growth in the present study for juvenile *S. lessoniana* or *S. australis.* However, a two-phase growth pattern would be extremely difficult to detect in nature, particularly if individuals hatched in different seasons experience different temperatures and thus, not only exhibit different rates of growth in each phase but also differing durations of each phase. If *Sepioteuthis* in the wild also follow a two-phase growth pattern with an initial exponential growth phase then the length of this phase is likely to be longer but at a lower percent increase in body weight per day in cooler climates, and shorter but at a higher percent increase in body weight per day in warmer climates. Such a process would explain the growth patterns observed in this study between tropical and temperate squids.

The age-specific growth rates of tropical and temperate *Sepioteuthis* squids are probably a function of the complex, and in cephalopods poorly understood, relationship between temperature, metabolism, food and body size. Metabolically cephalopods are poikilotherms that display Type 4 adaption where metabolic rate rises or drops directly with temperature with little or no tendency for compensation (O'Dor & Wells 1987, Segawa 1995). Temperature induced changes in metabolic rate are coupled with proportional increases and decreases in feeding rate and growth rate (Forsythe 1993). Growth rate however, may increase or decrease depending on the nature of the *food x metabolism x temperature* relationship (Brett 1979). Furthermore, the act of growing necessarily alters size so that another important biotic factor changes with time. In many ectotherms, metabolic demand for resources generally increases with both increased size and temperature (Atkinson & Sibly 1996), and metabolic requirements increase faster with body size than does foraging capacity (Claessen *et al.* 2000). Additionally, in aquatic environments oxygen availability decreases with increasing water temperature (O'Dea & Okamura 1999). Therefore, although growth is assumed to be faster initially at higher temperatures, growth would slow down sooner and at a smaller body size (Atkinson & Sibly 1997). O'Dor & Wells (1987) have also described such relationships for cephalopods, noting that for each size animal there is an optimum temperature at which growth potential is maximal, with smaller animals faring better at higher temperatures. Thus, it is not surprising that at smaller sizes and younger ages *S. lessoniana* can apparently acquire sufficient resources (oxygen and food) to achieve high growth rates, whereas temperate *S. australis* achieve comparatively faster growth at larger sizes and older ages.

The maximum body sizes and ages of *Sepioteuthis lessoniana* from Townsville and Brisbane and *S. australis* from Newcastle were all within very similar ranges, while squid from Tasmania attained a larger maximum size and greater maximum age. It is interesting to note that the average monthly sea surface temperatures of Townsville, Brisbane and Newcastle are all within approximately 4°C of each other, while the sea surface temperatures of eastern Tasmania are at least 7°C cooler than Newcastle and more than 10°C cooler than Townsville (Figure 1.2). Despite the similar maximum in age and size across squid from Townsville, Brisbane and Newcastle, each species was smaller and younger on average in the warmer part of their range. In some species, such as *Sepia officinalis*, final adult size is inversely proportional to growth rate (Richards 1971 in Boyle & Boletzky 1996). The smaller average size of *S. lessoniana* and *S. australis* in warmer parts of their distributions may therefore be explained by a faster initial growth rate. The size of an individual is a key feature influencing, and determined by, a species' life history and ecology (Chase 1999). Many animals, not just cephalopods, tend to be larger in colder habitats or in the colder portions of their geographic ranges (Sebens 1987; Chapelle & Peck 1999). Temperature-size adaptation is a well-documented response to environmental change, with examples from 109 studies including nine phyla, and both ectothermic and endothermic species, showing that in 84% of cases body size was larger at lower temperatures (Atkinson 1994). Size differences can be caused by some amount of genetic differentiation between populations and by plastic ontogenetic responses to local conditions (Sebens 1987).

Sepioteuthis lessoniana from Townsville matured at younger ages and smaller sizes compared to squid from Brisbane, perhaps as a function of faster initial growth rate. However, *S. australis* from Tasmania matured at smaller sizes compared to squid from

Townsville. One of the difficulties of inter-specific comparisons is the large variation in age and size at maturity within a species (Wood & O'Dor 2000). Size at maturity is typically extremely variable in both males and female loliginid squids. For example *Loligo gahi* males mature over a 300mm range (80-380mm, mode 200mm), and females 180mm (80-260mm mode 210mm) (Hatfield & Rodhouse 1991). Raya *et al.* (1999) commented that given the wide range of size at maturity in *Loligo vulgaris* estimating the size at which 50% of animals are mature is not very meaningful. Across a large number of taxa, cephalopods that mature at smaller sizes grow faster (Wood & O'Dor 2000). To date there is no evidence however that this occurs within each species. Boyle *et al.* (1995) examined size-at-age in large and small mature males of *Loligo forbesi* and found no difference in mean ages of the two groups. However, several fish species show a dome-shaped norm of reaction for size-to-age at maturity, with size at maturity smaller in both fast and slow growing fish, than it is in fish with a medium growth rate (Perrin & Rubin 1990). Such a relationship between growth rate and size-to-age at maturity in cephalopods may be masked by looking only at average size-at-age of small and large maturing squids.

In this study, males of both species matured at younger ages than females by 25-45 days. This appears to be common in loliginids with males of *Alloteuthis subulata* (Rodhouse *et al.* 1988), *Loligo vulgaris* (Boyle & Pierce 1994), and *Loligo gahi* (Guerra & Castro 1994) all maturing younger and smaller than females. Small size at maturity in *Sepioteuthis* males may be due to the presence of small 'sneaker' males, a behaviour that has been observed on the spawning grounds in Tasmania (pers. obs.) and South Australia (Jantzen & Havenhand 2000). Sneaker males have also been observed in *Loligo plei* (DiMarco & Hanlon unpub data in Hanlon & Messenger 1996), *Loligo* *vulgaris reynaudii* (Hanlon *et al.* 1994) and *Loligo pealei* (Hanlon 1996). *Illex argentinus* males also mature one to two months earlier than females (Arkhipkin 2000), as do many cuttlefish (eg: *Sepia officinalis,* Guerra & Castro 1988; *Sepia pharaonis* Gabr *et al.* 1998a). In the Tasmanian *S. australis* population very few immature and maturing males were sampled. It is unclear if this a function of only part of the population being represented in the sample, with immature animals utilising a different habitat, or a result of temporal synchronicity in male sexual development.

Sexual dimorphism in terms of growth was not detected in either *Sepioteuthis lessoniana* or *S. australis,* which was unexpected given the differences in age at maturation between the sexes. Male *S. australis* from Tasmania were achieving larger sizes than females, but this was a function of living slightly longer. Sexual dimorphism in both growth and body size seem common in loliginids, with males of many species growing faster and larger than females (eg: *Loligo pealei*, Brodziak & Macy 1996; *Loligo forbesi*, Guerra & Rocha 1994; *Loligo vulgaris*, Boyle & Pierce 1994). However, this dimorphism is not as extreme as that of oceanic species, such as *Moroteuthis ingens* where females grow twice as fast as males and reach five times their size in weight (Jackson 1997), and females of the mesopelagic *Ancistrocheirus lesueurii* in the central east Atlantic which reach 10 times the size of males (Arkhipkin 1997).

The growth, maturation, body size and life span of both *Sepioteuthis lessoniana* and *S. australis* differed substantially across the latitudinal zones examined in this study. In this respect, the results of this chapter are consistent with other studies that have demonstrated considerable differences in the life history characteristics of tropical and temperate cephalopods, or within a species across geographical locations. However, this study highlights that comparisons of growth patterns should be life cycle stage-specific, as the nature of such differences may depend critically on the age range considered. It also demonstrates that while some species may mature earlier and smaller in warmer parts of their range (eg: *S. lessoniana*), other species are capable of maturation at smaller sizes and younger ages in cooler regions (eg: *S. australis*). Thus, generalisations about expected life history characteristics of a species inhabiting a wide geographical range may not be appropriate.