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## CHAPTER 4: FLEXIBLE REPRODUCTIVE STRATEGIES IN TROPICAL AND TEMPERATE SEPIOTEUTHIS SQUIDS

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### 4.1 INTRODUCTION

An individual's "fitness" in the evolutionary sense, is determined by both absolute fecundity and generation interval (Roff 1986). Both of these life history traits are dependent on the reproductive strategy of a species, and indeed are likely to be divergent between those species or individuals that breed once and die, and those that breed over an extended time frame. Optimal age or size at maturity and the associated age- and size-specific schedules of reproductive investment are just some of the life history characteristics that are also intimately related to the reproductive strategy of a species (Stearns 1977). As a consequence of the very short life span typical of most cephalopods, annual recruitment is essential to sustain populations (Boyle 1990), and as such an understanding of the reproductive strategy of a cephalopod fisheries resource is crucial.

Determining how long an individual takes to complete egg maturation and deposition, and assessing what portion of the life span this period represents, is a major difficulty confronting detailed examinations of cephalopod reproductive biology in field populations (Collins *et al.* 1995b). Although coleoid cephalopods have traditionally been viewed as semelparous organisms that reproduce once and die (Arnold & Williams-Arnold 1977; Calow 1987; eg: *Illex illecebrosus* O'Dor 1983; *Todarodes pacificus* Okutani 1983), it is becoming increasingly apparent that many species are not restricted to this strategy. Reproductive strategies that involve spawning within one season only, but where reproductive effort is distributed over space and time over a portion of the life span are

now known to be common among cephalopods (Villanueva 1992b; Hun Baeg *et al.* 1993; Wada & Kobayashi 1995; González & Guerra 1996, Maxwell *et al.* 1998).

In species with non-asymptotic growth patterns, growth and reproduction necessarily proceed together over much of the life cycle, and it is likely that the diversity of spawning modes is related to growth patterns (Mangold *et al.* 1993). In general, the growth and life spans of tropical and temperate species differ. Temperate and sub-tropical loliginids live for approximately one (Natsukari *et al.* 1988, Collins *et al.* 1995a), or two years (Hanlon *et al.* 1989), whereas tropical species have lifespans of less than six months (Jackson 1990b, Jackson & Choat 1992, Jackson & Yeatman 1996). There is, however, little information about how the reproductive biology of closely related species from disparate temperature zones may differ. Within a population the growth characteristics of cephalopod species are highly plastic with small changes in temperature producing large changes in growth rates and final size (Forsythe 1993). Consequently, in cephalopod populations where spawning takes place all year round there may be seasonal influences on age and size-specific schedules of reproductive investment and subsequent patterns in egg maturation and deposition.

The mature eggs of *Sepioteuthis* spp. are very large compared to other squids (Hanlon 1990), in the range of 5-10 mm. Large eggs cannot be matured all at once, and *S. lessoniana* is known to have the capacity, at least in the laboratory, to lay multiple batches of eggs over a significant portion of the life span (Wada & Kobayashi 1995). Back-calculated hatching dates of both *S. lessoniana* (Pecl, unpubl. data) and *S. australis* (Chapter 2) suggest spawning takes place all year round, although there is little information on the temporal patterns of spawning intensity. Extended spawning seasons tend to be

associated with multiple spawning (Lum-Kong *et al.* 1992, Porteiro & Martins 1994), however, it is often unclear if prolonged spawning is due to extended individual spawning or asynchronicity in the population (Boyle *et al.* 1995).

This chapter uses a combination of histological and morphological assessment measures, in conjunction with other biological information, to assess the reproductive strategies of the tropical *Sepioteuthis lessoniana* from two locations in northern Australian waters and the temperate *S. australis* from two locations in southern Australia. An examination of the patterns in egg maturation between squid caught in summer and winter was also conducted for *S. australis* at the most southern location. Recent research has demonstrated that *S. australis* from the two regions examined in this study constitute two distinct genetic stocks (Triantafillos & Adams in press). Differences in the reproductive biology have been put forward as a reason to support the hypothesis of these two genetic types as distinct taxa, so the examination of regional differences in the reproductive biology of *S. australis* is particularly pertinent.

## 4.2 MATERIALS & METHODS

### 4.2.1 Collection and processing

*Sepioteuthis lessoniana* individuals were obtained from waters adjacent to Townsville (Table 4.1) by jigging, and from Brisbane by a combination of tunnel-netting by the commercial sector and jigging. *Sepioteuthis australis* was obtained in Newcastle by jigging, and in Tasmania by a combination of jigging and modified purse-seine. The 196 females from Tasmania include 42 females caught during winter and 154 caught in summer.

**Table 4.1:** Sample sizes, collection locations and dates for *Sepioteuthis lessoniana* and *Sepioteuthis australis*.

| Species & location             | Latitude & longitude | Collection dates  | Total sample size | No. of females |
|--------------------------------|----------------------|-------------------|-------------------|----------------|
| <i>Sepioteuthis lessoniana</i> |                      |                   |                   |                |
| Townsville                     | 19°10'S; 146°55'E    | Feb 1995-Oct 1997 | 116               | 50             |
| Brisbane                       | 27°20'S; 153°3'E     | Aug 1995-Apr 1997 | 173               | 83             |
| <i>Sepioteuthis australis</i>  |                      |                   |                   |                |
| Newcastle                      | 32°45'S; 152°10'E    | Aug 1995-Dec 1995 | 131               | 51             |
| Tasmania                       | 42°15'S; 148°10'E    | Jan 1996-Jul 1997 | 493               | 196            |

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. The mantle muscle, ovary, oviduct, nidamental and oviducal glands were dissected out and weighed separately. A gonadosomatic index (GSI) was derived for each individual as follows:

$$\text{GSI} = \frac{\text{OW} + \text{NW} + \text{ODW} + \text{OV}}{\text{BW} - \text{RW}}$$

where OW = ovary weight, NW = nidamental gland weight, ODW = oviducal gland weight, OV=oviduct weight; BW = total body weight and RW = total reproductive weight (combined weight of ovary, oviduct, nidamental and oviducal glands).

Weights could not be measured for twelve *Sepioteuthis lessoniana* caught in Townsville, however total body weight was estimated for these from the relationship:  $\text{Weight} = 0.00042 \times \text{ML}^{2.6045}$  ( $r^2=0.99$ ,  $n=34$ ).

All squid were assigned to a maturity stage according to the relative size and colour of reproductive organs following the six-stage maturity scale of Lipinski (1979). Under this scheme stages IV and V are mature and are hence part of the spawning stock. Each individual was thoroughly examined for external skin lesions on the head, mantle or fins and any signs of deterioration of the reproductive organs. Feeding in spawning individuals of some semelparous species is reduced or may even stop completely (Mangold *et al.* 1993). The presence or absence of food in the stomach and spermatophores in the buccal pouch was determined for all individuals to assess if females had fed or mated recently.

Age information was determined from increments in the statolith, as previously described in chapters 2 & 3

#### 4.2.2 Analysis of oocyte maturation

For histological inspection of the ovaries, tissue was fixed in a formalin acetic-acid calcium-chloride solution (FAACC), sectioned at 6µm and stained with Young's Haematoxylin and Eosin. Frozen squid were not used for histology. Ovarian oocyte stage frequency distributions were obtained for each female by allocating 50 randomly selected oocytes to one of five oocyte maturation stages as per Moltshaniwskyj (1995). The number of ovulated oocytes in the oviduct of mature individuals was estimated by weighing 20 eggs and scaling this by total oviduct egg weight. Twenty oviduct eggs, or all oviduct eggs if less than 20 were present, from each individual were also measured. Oviduct eggs were oval in shape, so eggs were measured along the long axis using an ocular micrometer and a stereomicroscope. Damaged or deformed eggs were not measured.

Degree of oviduct fullness was estimated for Tasmanian caught *Sepioteuthis australis* following the method described by Harman *et al.* (1989), modified for oviduct weight rather than volume. Briefly, maximum oviduct weight in each 10mm ML size class was noted and plotted against mantle length (linear relationship:  $r^2=0.88$ ,  $n=17$ ,  $P<0.0001$ ). An equation to predict the potential maximum oviduct weight for any maturing female was derived from the linear regression through these maximum values. Percent oviduct fullness was calculated for each female by dividing the actual oviduct weight by the maximum predicted by the equation: Maximum oviduct weight =  $(0.157 \times \text{ML}) - 22.566$ . As this method involves regression analyses, some estimates of oviduct fullness consequently exceeded 100%.

All parameters examined in this study were examined initially at the location level for each species. The trends observed for *Sepioteuthis lessoniana* from Townsville and Brisbane were the same, and so individuals from these two locations were combined to simplify analyses. Pooling individuals from the two locations did not alter the results. There were however substantial differences evident in the reproductive biology of *S. australis* individuals from Newcastle and Tasmania, and between seasons of capture in Tasmania, thus data were graphed and analysed separately.

## 4.3 RESULTS

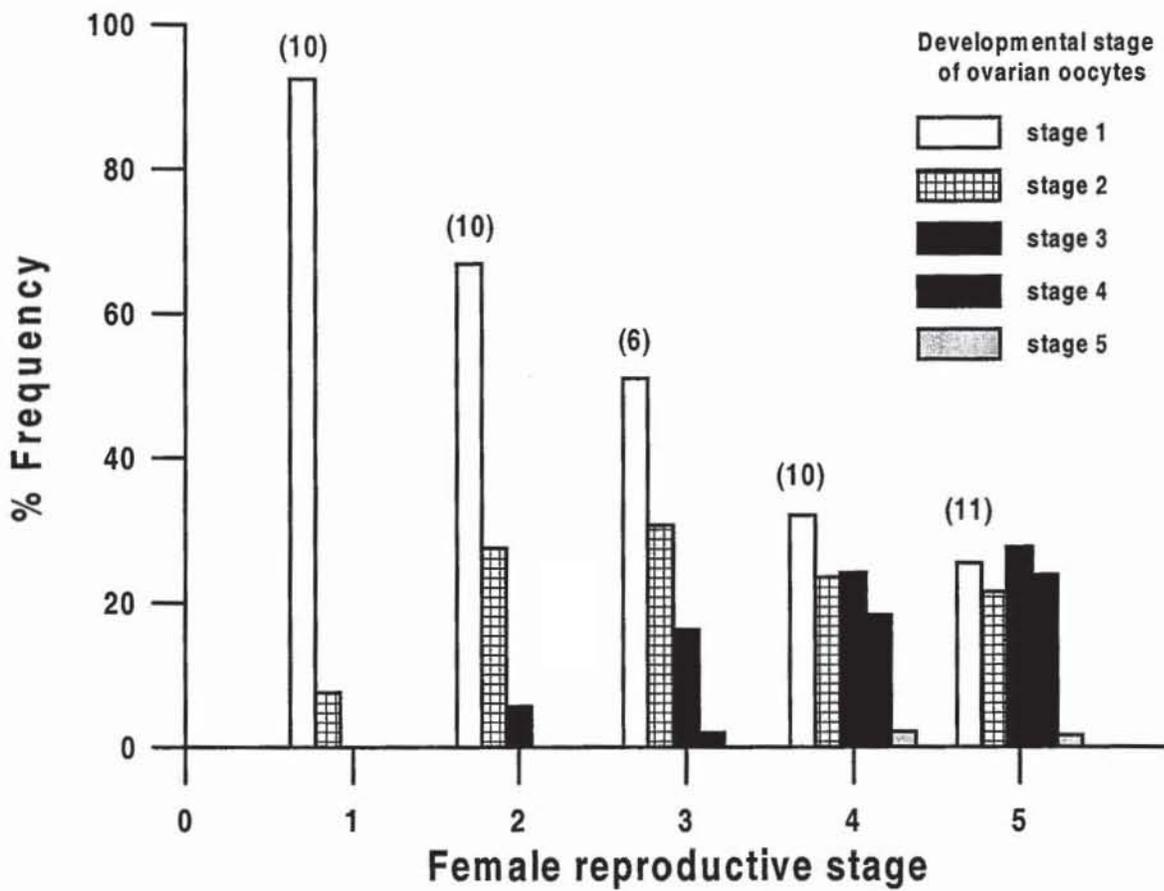
### 4.3.1 *Sepioteuthis lessoniana*

Early stage *Sepioteuthis lessoniana* females with small developing ovaries showed a predominance of primary and secondary oocytes, with the range of oocyte stages present in the ovary increasing with the progression of female maturation stage (Plate 4.1, Figure 4.1). This confirms that the macroscopic features used in the allocation of maturation stage are consistent with microscopic changes occurring within the ovary. Ovarian oocyte stage frequency distribution showed little variability between females of the same maturity stage. In fully mature stage V females all ovaries had a low proportion of hydrated stage 5 oocytes and at least 65% of oocytes were in the first three stages of oocyte development.

Maturation in female *Sepioteuthis lessoniana* individuals was a size related process. Weight of the ovary, nidamental glands and oviducal glands were all highly correlated with total wet weight, more so than with age (Table 4.2). However, total body weight of mature females was not related to oviduct weight ( $r=0.18$ ,  $n=35$ ,  $P=0.30$ ), or the number of eggs present in the oviduct ( $r=0.22$ ,  $n=21$ ,  $P=0.33$ , Figure 4.2). In all but one individual the oviduct was lighter than the ovary and oviduct weight never exceeded 15% of mantle wet weight in all individuals.

**Plate 4.1** Histological section through the ovary of a mature *Sepioteuthis lessoniana* female (556g, 212 mm ML & 152 days of age), showing oocytes at development stages 1-4. Scale bar: 660  $\mu\text{m}$ .



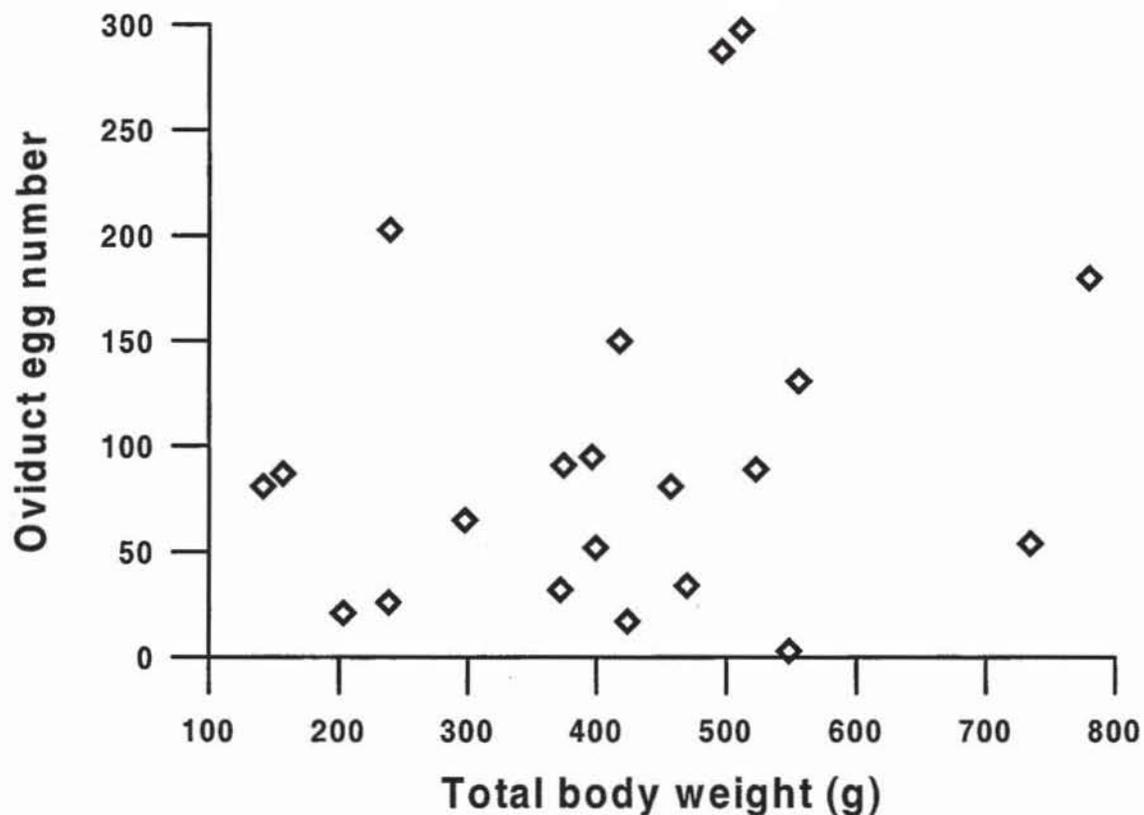


**Figure 4.1:** Ovarian oocyte stage frequency distribution for *Sepioteuthis lessoniana* females in each of the five reproductive stages. Number of females in each reproductive stage in brackets.

**Table 4.2:** Correlations of the weights of the major components of the reproductive system of female *Sepioteuthis lessoniana* with total wet weight (g) and age (days).

|        | Ovary                    | Nidamental glands       | Oviducal gland          |
|--------|--------------------------|-------------------------|-------------------------|
| Weight | $r=0.60, n=114, P<0.001$ | $r=0.63, n=95, P<0.001$ | $r=0.66, n=93, P<0.001$ |
| Age    | $r=0.33, n=50, P=0.018$  | $r=0.34, n=44, P=0.022$ | $r=0.37, n=43, P=0.015$ |

The size of oviduct eggs ranged from 5.33-7.45mm (mean  $6.21 \pm 0.12$ s.e.,  $n=171$ ), and the maximum number of ovulated eggs present in any one oviduct was 298. Although there was variation in oviduct egg size between females, within a female the size of oviduct eggs was very consistent. Average size of ovulated oocytes was not related to weight of the oviduct ( $r=-0.21, n=21, P=0.36$ ) or number of eggs within the oviduct ( $r=-0.40, n=21, P=0.076$ ) suggesting that oocytes were not continuing to grow within the oviduct and were therefore ready to be laid. Average size of the oviduct eggs was also not related to total body weight ( $r=0.30, n=21, P=0.19$ ) or mantle wet weight ( $r=0.38, n=20, P=0.10$ ).



**Figure 4.2:** Estimated number of mature eggs in the oviduct with total body weight of mature *Sepioteuthis lessoniana* females.

Although maturation appeared to be a size dependent process, mature females were still present in the population over very wide age, weight and length ranges, as were maturing individuals (Table 4.3). There was no macroscopic evidence of any female being spent or dying as there was no deterioration of any of the reproductive organs or exterior lesions on the head, mantle or fins. However, three of the 38 mature individuals were found with large, stretched empty oviducts and may have spawned previously as they were quite distinct from stage IV females in which the unused oviduct is visible as a thin tube or strip lying over the ovary. These individuals had lower gonadosomatic ratios (range 3-6%, average  $4.1\% \pm 1.2\%$  s.e.) relative to other mature females (range 5.1-19.6%, average

12.7%  $\pm$  0.7% s.e.). All mature females had mated recently except for one of the individuals with a very large, stretched empty oviduct. Mature females were still feeding, with the percentage of mature females with food in their stomachs similar to that of immature and maturing females (Brisbane  $\chi^2=0.22$ ,  $df=1$ ,  $P=0.64$ ; Townsville  $\chi^2=0.99$ ,  $df=1$ ,  $P=0.32$ ).

**Table 4.3:** Age, weight and mantle length range for mature and immature *Sepioteuthis lessoniana* females.

|                     | <i>n</i> | Age range<br>(days) | Weight range<br>(g) | ML range<br>(mm) |
|---------------------|----------|---------------------|---------------------|------------------|
| Mature              | 38       | 107-187             | 108-960             | 118-252          |
| Immature & maturing | 144      | 71-178              | 46-567              | 84-200           |

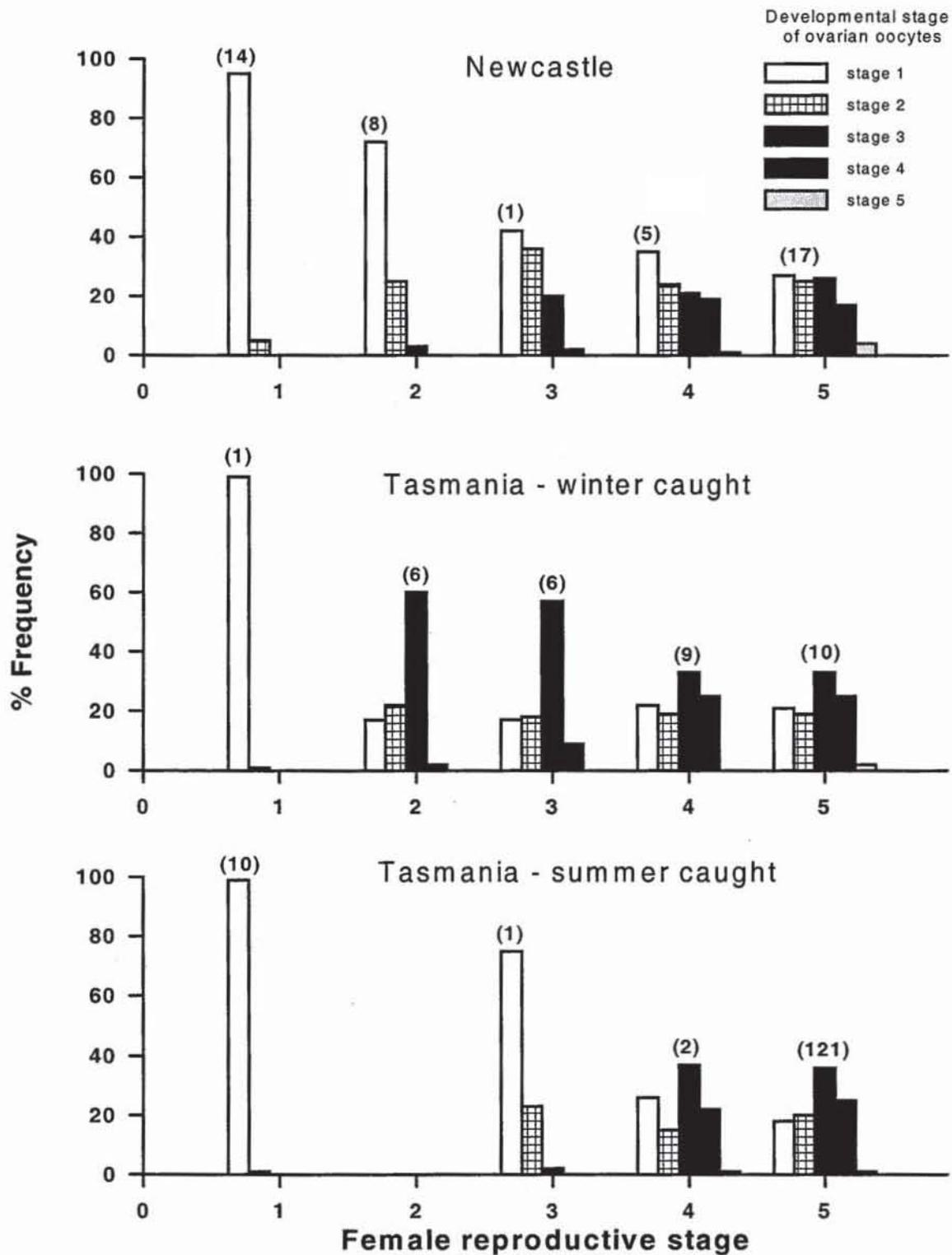
#### 4.3.2 *Sepioteuthis australis*.

In Tasmanian winter caught females the microscopic condition of the ovary was not consistent with the macroscopic features used in the allocation of maturation stage, as immature females had substantial numbers of stage 3 and 4 oocytes in their small ovaries (Figure 4.3). However, at least 50% of oocytes were in the first three stages of development in the ovaries of all mature *Sepioteuthis australis* individuals from both Tasmania and Newcastle (Figure 4.3). Maturation in female *S. australis* from both locations was a size related process (Table 4.4) with the weights of the ovary, nidamental and oviducal glands all highly correlated with female total weight. Weights of the major

components of the reproductive system of individuals from Newcastle and summer caught Tasmanian individuals also showed correlations with age (Table 4.4).

**Table 4.4:** Correlations of the weights of the major components of the reproductive system of female *Sepioteuthis australis* with total wet weight (g) and age (days).

|                         | Ovary                    | Nidamental glands        | Oviducal gland           |
|-------------------------|--------------------------|--------------------------|--------------------------|
| <i>Total wet weight</i> |                          |                          |                          |
| Newcastle               | $r=0.85, n=50, P<0.001$  | $r=0.90, n=50, P<0.001$  | $r=0.90, n=50, P<0.001$  |
| Tasmania–summer         | $r=0.92, n=151, P<0.001$ | $r=0.96, n=154, P<0.001$ | $r=0.95, n=154, P<0.001$ |
| Tasmania-winter         | $r=0.73, n=39, P<0.001$  | $r=0.80, n=41, P<0.001$  | $r=0.83, n=41, P<0.001$  |
| <i>Age</i>              |                          |                          |                          |
| Newcastle               | $r=0.56, n=43, P<0.001$  | $r=0.57, n=43, P<0.001$  | $r=0.58, n=43, P<0.001$  |
| Tasmania –summer        | $r=0.78, n=124, P<0.001$ | $r=0.78, n=127, P<0.001$ | $r=0.77, n=127, P<0.001$ |
| Tasmania-winter         | $r=0.35, n=35, P=0.039$  | $r=0.35, n=37, P=0.033$  | $r=0.39, n=37, P=0.016$  |



**Figure 4.3:** Ovarian oocyte stage frequency distribution for *Sepioteuthis australis* females in each of the five reproductive stages, caught in Newcastle, and summer and winter in Tasmania. Number of females in each reproductive stage in brackets.

Gonadosomatic index was positively correlated with female size in Newcastle caught *Sepioteuthis australis* ( $r=0.70$ ,  $n=22$ ,  $P<0.001$ ) and the maximum GSI values for mature individuals (7.4–22.7%, average  $15.9\% \pm 1\%$  s.e.) were only marginally higher than those of *S. lessoniana*. Gonadosomatic indices for mature summer caught Tasmanian squid spanned a very broad range (8.8–35.4%, average  $18.7\% \pm 0.3\%$  s.e.) and were much higher than the GSI values in winter caught individuals (3.4–13.6%, average  $9\% \pm 0.7\%$  s.e.;  $t$ -test,  $t=12.98$ ,  $df=158$ ,  $P<0.0001$ ). In summer caught squid, smaller individuals tended to have higher GSI values ( $r=-0.20$ ,  $n=134$ ,  $P=0.026$ ).

The oviduct was lighter than the ovary in all *Sepioteuthis australis* individuals. The weight of the oviduct was 16.8% of the mantle weight in the smallest and youngest mature Tasmanian summer caught individual, however it did not exceed 15% of mantle weight in all other *S. australis*. The weight of the oviduct and number of eggs within the oviduct in mature *S. australis* from Newcastle and summer caught Tasmanian squid were both correlated with total body weight (Table 4.5, Figure 4.4). In Tasmanian caught females there was a great deal of variation in oviduct fullness, where mature females ranged from having either very full, heavy oviducts to oviducts that were completely empty (Figure 4.5). There was no correlation between body size and degree of oviduct fullness for summer (Spearman rank,  $r=0.048$ ,  $n=129$ ,  $P=0.42$ ) or winter (Spearman rank,  $r=-0.049$ ,  $n=15$ ,  $P=0.80$ ) caught individuals.

The maximum number of ovulated eggs in the oviduct of Tasmanian summer caught females was double that of females caught in winter or Newcastle caught females (Table 4.6). As with *Sepioteuthis lessoniana*, although average egg size varied between *S. australis* females, within a female egg size was very consistent (Figure 4.6). Average

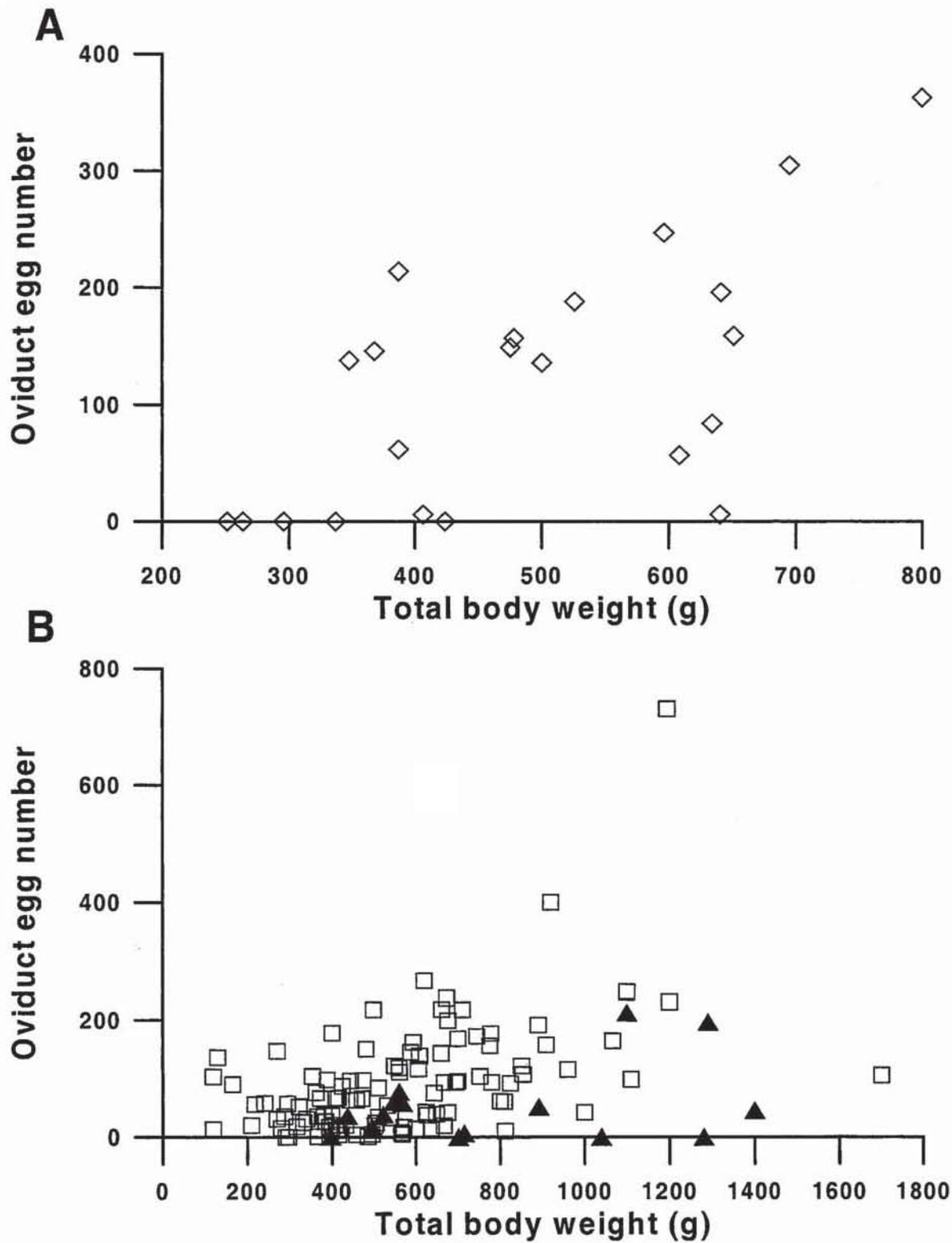
egg size was not related to weight of the oviduct, or female total weight (Table 4.5). However females caught in summer from Tasmania showed a weak negative correlation between egg size and number of eggs within the oviduct (Table 4.5), suggesting that individuals were producing fewer, but larger eggs or many smaller eggs. Newcastle individuals with heavier mantles were producing larger eggs (Table 4.5).

**Table 4.5:** Correlations of reproductive parameters in *Sepioteuthis australis* at each location & season caught.

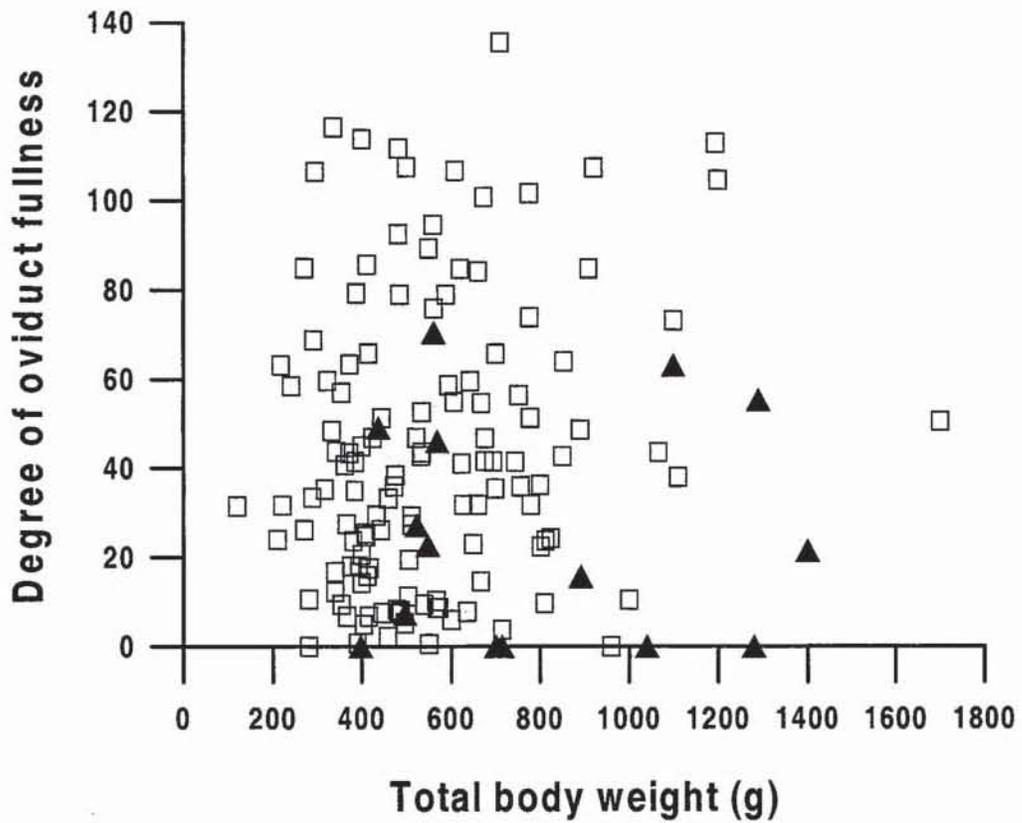
| Correlation            | Newcastle               | Tasmania-summer           | Tasmania-winter        |
|------------------------|-------------------------|---------------------------|------------------------|
| Oviduct & body wt      | $r=0.71, n=22, P<0.001$ | $r=0.58, n=131, P<0.001$  | $r=0.37, n=16, P=0.15$ |
| No. eggs & body wt     | $r=0.64, n=22, P=0.001$ | $r=0.49, n=107, P<0.001$  | $r=0.37, n=15, P=0.17$ |
| Egg size & oviduct wt. | $r=0.05, n=16, P=0.84$  | $r=0.02, n=103, P<0.80$   | $r=-0.01, n=7, P=0.99$ |
| Egg size & egg number  | $r=-0.14, n=16, P=0.61$ | $r=-0.29, n=103, P=0.004$ | $r=-0.30, n=8, P=0.48$ |
| Egg size & body wt.    | $r=0.46, n=16, P=0.07$  | $r=0.08, n=103, P=0.48$   | $r=-0.47, n=8, P=0.24$ |
| Egg size & mantle wt.  | $r=0.56, n=16, P=0.02$  | $r=0.09, n=103, P=0.37$   | $r=-0.48, n=8, P=0.22$ |

**Table 4.6:** Estimated number and size of oviduct eggs in mature *Sepioteuthis australis* at each location & season. Size and age of females with the highest number of oviduct eggs is shown in brackets.

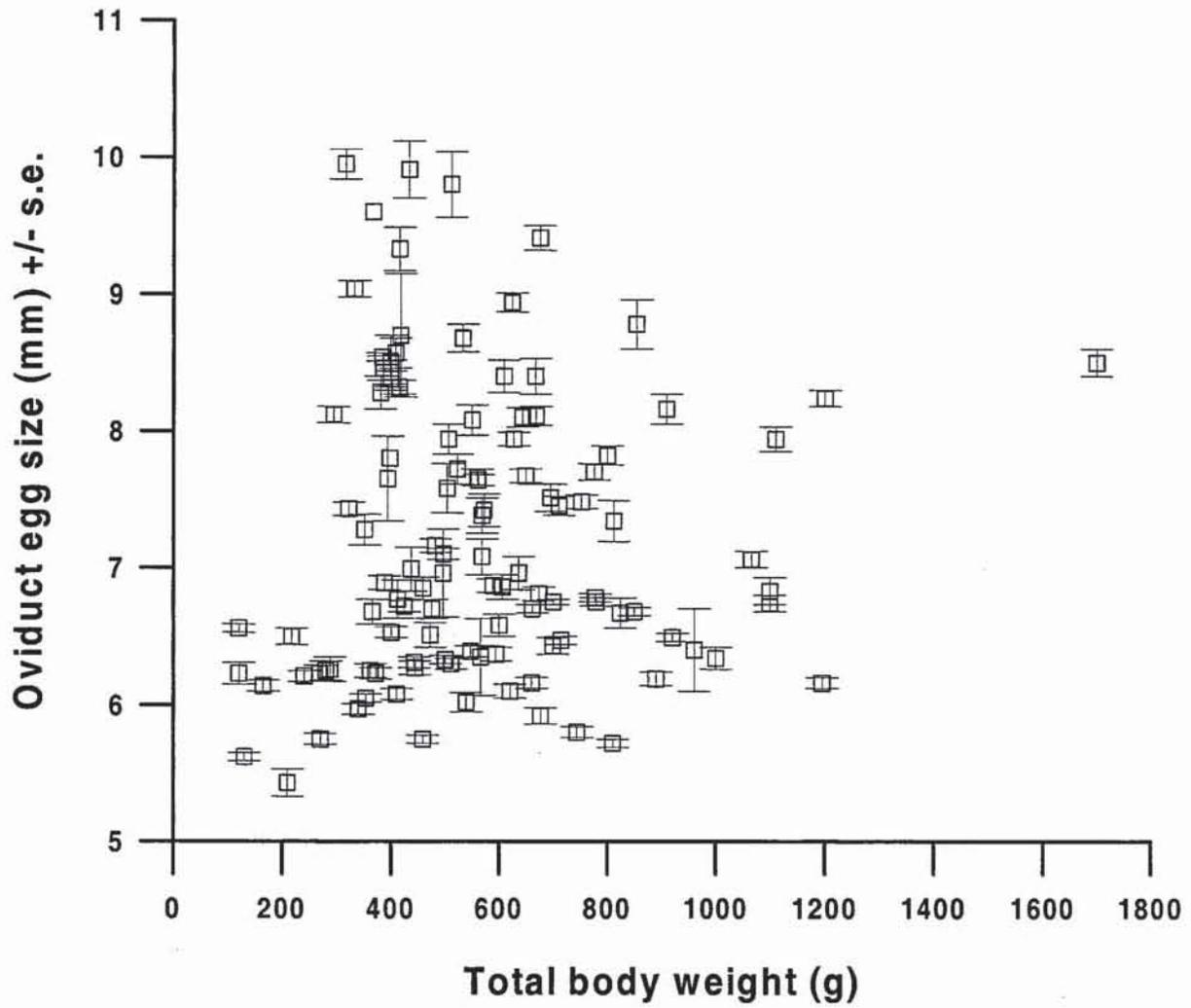
| Parameter            | Newcastle                               | Tasmania-summer                         | Tasmania-winter                          |
|----------------------|---|---|--|
| Max. no. of eggs     | 363 (800g)                              | 731 (1195g & 203d)                      | 212 (1100g & 175 d)                      |
| Size of oviduct eggs | 6.34 – 7.67mm<br>(mean 6.79 ± 0.09 s.e) | 5.43 - 9.95mm<br>(mean 7.2 ± 0.10 s.e.) | 6.39 - 7.80mm<br>(mean 7.07 ± 0.19 s.e.) |



**Figure 4.4:** Estimated number of mature eggs in the oviduct with total body weight of mature *Sepioteuthis australis* caught in a) Newcastle and b) summer (squares) and winter (triangles) in Tasmania.



**Figure 4.5:** Estimated degree of oviduct fullness with total body weight in Tasmanian caught *Sepioteuthis australis*. Method of estimation involved regression analyses, hence some values exceed 100% (see methods section). Squares are summer caught females, triangles winter caught.



**Figure 4.6:** Average oviduct egg size with total body weight, of each mature *Sepioteuthis australis* female caught in Tasmania. Standard errors shown.

*Sepioteuthis australis* females were mature over very wide age and size ranges at all locations sampled, with the ranges particularly wide in summer caught females from Tasmania (Table 4.7). Immature and maturing females were only found up to half the maximum weight attained in mature females. Only one mature individual caught in Newcastle had a stretched but empty oviduct. In Tasmanian caught *S. australis*, three individuals from the winter sample and 12 from the summer sample had stretched empty oviducts. Three Tasmanian females caught in summer also had small mantle lesions occupying less than 10% of mantle area and two individuals had stretched oviducts and small mantle lesions. Despite the small lesions there was no macroscopic evidence of deterioration of the reproductive organs or any other tissues. In Tasmanian summer caught females, those with stretched oviducts or lesions had no difference in the proportion found with food in the stomach ( $\chi^2=0.21$ ,  $df=1$ ,  $P=0.65$ ) or average GSI values ( $t$ -test,  $t=2.738$ ,  $df=132$ ,  $P=0.007$ ) compared to other mature individuals. At least 30% of mature individuals at each location had ingested prey in the stomach, and all mature females had mated.

**Table 4.7:** Age, weight and mantle length range for mature *Sepioteuthis australis* females.  $n$ = number of mature females, value in brackets is the total number of females examined. Values in brackets after age, weight and ML ranges are the maximums recorded for immature and maturing females.

| Location/season   | $n$          | Age range<br>(days) | Weight range<br>(g) | ML range<br>(mm) |
|-------------------|--------------|---------------------|---------------------|------------------|
| Newcastle         | 22<br>(51)   | 129-183<br>(162)    | 251-799<br>(404)    | 160-272<br>(197) |
| Tasmania – summer | 134<br>(154) | 117-263<br>(176)    | 120-1700<br>(550)   | 147-358<br>(255) |
| Tasmania – winter | 26<br>(42)   | 129-212<br>(196)    | 277-1400<br>(636)   | 178-314<br>(240) |

#### 4.4 DISCUSSION

The primary evidence for multiple spawning in *Sepioteuthis lessoniana* and Tasmanian *S. australis* is the lack of a strong correlation in mature females between body size and oviduct fullness or quantity of eggs, together with evidence of continuous egg production throughout adult life. Supplementary evidence for this conclusion includes a lighter oviduct compared to the ovary since it would be reasonable to expect the oviduct to become heavier if oocytes were accumulating (Moltschaniwskyj 1995). Individuals of both *S. lessoniana* and *S. australis* were found with large stretched but empty oviducts thought to indicate previous spawning, however they did not appear to be spent or in the process of dying. A multiple spawning strategy is further supported by the relatively low gonadosomatic index of both *S. lessoniana* and *S. australis* compared to known semelparous squid (eg: up to 50% in *Loligo opalescens*, Fields 1965; 23% for the oviducal eggs alone in *Illex illecebrosus*, O'Dor 1983). The proportion of body mass committed to reproductive structures assists in the interpretation of a species spawning biology as life history theory predicts that reproductive effort of a semelparous animal should be high (Calow 1987). Alternatively, low gonadosomatic indices suggest that relatively less energy is channelled into egg development at any one time during reproduction and are an indication of a non-semelparous reproductive strategy.

Ovarian oocyte stage frequency distribution revealed continuous egg production in individuals at all maturity stages. Although this appears to be a necessary characteristic of cephalopods that spawn multiple times (eg: *Idiosepius pygmaeus* Lewis & Choat 1993, *Photololigo* sp. Moltschaniwskyj 1995), this evidence alone cannot be used to support a multiple spawning mode (Mangold *et al.* 1993). Many known semelparous squid eg: *Illex illecebrosus* (O'Dor 1983) and *Teuthowenia megalops* (Nixon 1983)

show a single size mode in the ovarian oocyte size frequency distributions. The critical measure appears to be the numerical importance of the largest oocyte size mode (Mangold *et al.* 1993). The proportion of mature or nearly mature oocytes was always much less than the total number of developing eggs in the ovaries of all mature *Sepioteuthis lessoniana* and *S. australis* individuals, as has been found in *Loligo vulgaris reynaudii* (Sauer & Lipinski 1990).

Mature eggs are stored in the oviducts and unless spawning intervenes eggs must accumulate in the oviduct (Harman *et al.* 1989, Moltshaniwskyj 1995). In a simultaneous terminal spawning species the majority of egg production must be available for egg laying within a very brief period of time (Jackson & Mladenov 1994) and consequently the oviducts become very full and heavy. However, in *Sepioteuthis lessoniana* there was no relationship between oviduct weight and body size suggesting that mature oocytes were not resident in the oviduct for long and do not accumulate to be laid in a single batch. While oviduct weight was moderately correlated with body size in summer caught Tasmanian *S. australis*, oviduct fullness was not, again indicating that mature oocytes were not accumulating. In a large sample size, a certain degree of correlation between body size and oviduct weight would still be expected under this scenario, as larger animals have the capacity for a higher number of eggs even if they are not resident within the oviduct for a long time period.

Growth and reproduction appear to occur simultaneously in mature animals, with the large size range of mature females indicating that considerable growth takes place after the onset of sexual maturity. Immature *Sepioteuthis australis* were only found up to half the maximum weight of mature individuals. A high but variable growth rate combined

with variation in the timing of sexual maturity may account for the very wide size range at maturity noted for many cephalopod species (Boyle 1990). It has also been suggested that the wide variation in the total number of oocytes in the oviduct and ovary of females at the same stage of maturity and body size may also be explained by variable growth rates between individuals (Rocha & Guerra 1996). However, a high correlation between body size and weights of all the major reproductive organs, except for oviduct weight or fullness, cannot be explained solely by variability in growth between individuals. A more likely explanation for *S. lessoniana* and Tasmanian *S. australis* is a multiple spawning reproductive strategy.

*Sepioteuthis lessoniana* is known to spawn multiple times in captivity (Wada & Kobayashi 1995) supporting the association of these morphological and histological features to a multiple spawning capacity in wild populations. In addition, spent or dead females have not been recorded in *S. lessoniana* or *S. australis* on known spawning grounds and mortality may be sporadic over a prolonged period or occur at low levels continuously. Cannibalism of weak or dying squid may account for the absence of any moribund or dead squid on spawning grounds as has been suggested for *Loligo vulgaris reynaudii* (Sauer & Smale 1993). The stomach contents of Tasmanian summer caught *S. australis* suggest cannibalism (unpubl data, Jackson GD & Pecl GT) and top level predators are common in the spawning area (eg: seals, dolphins and sharks).

*Sepioteuthis australis* females from South Australian waters are known to copulate more than once per season, as tagged females initially caught with spermatophores were subsequently recaptured a month later with fresh spermatophores (Triantafillos, 1998). Tagged females remain on spawning grounds for up to two months in South Australia,

and in Tasmania females tagged towards the end of the spawning season were still present on the spawning grounds for at least two weeks (unpubl data, Jackson GD & Pecl GT). Examination of stomach fullness suggested that mature females were still feeding whilst in spawning condition at all locations examined for both species.

There were several distinct differences between populations of female *Sepioteuthis australis* caught in summer and winter in Tasmania suggesting that the reproductive strategy may have a seasonal component in temperate waters. Reproductive and accessory reproductive tissues accounted for a much higher percentage of the total body mass in summer caught females, with gonadosomatic indices twice that of winter caught animals. Summer caught females appeared to be laying larger egg batches and winter caught females smaller batches, suggesting quite large seasonal differences in age and size specific schedules of reproductive investment. These observed differences between summer and winter caught females may be generated by varied growth patterns due to differences in season of hatching between the groups (explored in Chapter 6), or a function of the temporal synchronisation of spawning activities. Many temperate species synchronise their life cycle to that of conspecifics (Scott & Kenny 1998), to produce offspring at a time to maximise the chance of survival to maturity (Grist & Gurney 1995).

Life history theory predicts a trade-off between egg size and fecundity. Although egg size was consistent within an individual, between females there was substantial variation in oviduct egg size, with some females laying fewer larger eggs and other females more smaller eggs. Larger eggs are usually associated with a longer development time and egg size determines the size of hatchlings and their subsequent

growth and survivorship properties (Calow 1983). The relationship between egg size, hatchling size and hatchling survivorship warrants further investigation in squids (Maxwell & Hanlon 2000).

The spawning strategy of *Sepioteuthis australis* females caught in Newcastle is unclear. Females showed a high correlation between body size and oviduct weight despite a small sample size, suggesting that perhaps this genetic form of *S. australis* may tend more towards the terminal end of the spawning continuum, although the relatively low gonadosomatic index values do not support this conclusion. However, the largest female examined was only 800g and the oldest 183 days and it is unlikely that this represents the maximums achieved by this species in the temperate waters off Newcastle. Gonadosomatic index was positively correlated with size suggesting that perhaps if larger animals were caught, higher gonadosomatic indices may have been found. Further confusing the situation is that 75% of the mature Newcastle females were caught in winter. If the relationship between oviduct weight and body size is examined for these individuals only, an even higher correlation is found ( $r=0.89$ ,  $n=19$ ,  $p<0.0001$ ). Tasmanian winter caught *S. australis*, for a similar sample size, did not show a significant correlation for the same relationship and the gonadosomatic indices were also lower compared with Newcastle females. Differences in the reproductive biology, although not previously described, have been suggested as evidence for the two genetic types of *S. australis* examined in this study as constituting distinct taxa (Triantafillos & Adams in press) and the preliminary results presented here support this hypothesis. Many of the individuals used in the present study are the same individuals analysed in the genetic study of Triantafillos & Adams (in press). Further investigation of the

spawning biology of the genetic type of *S. australis* found in Newcastle is warranted with larger, seasonal samples and a wider size range of individuals.

Ultimately it is the links between environment, individual energy reserves and the degree to which population synchronicity occurs that will determine the nature of the reproductive strategy and its inherent flexibility. Spawning strategies may not be limited simply to early maturation and the laying of many small batches or late maturation and fewer but larger batches. It seems possible that individuals may also mature early and lay a few large batches or mature later if growing during colder seasons, but lay smaller batches more frequently. Considerable flexibility occurs in the reproduction of captive *Loligo pealei*, where reproductive output is not tightly constrained by length or age (Maxwell & Hanlon 2000). Small young females were as fecund as large older ones and substantial variation was evident between females with some laying small clutches frequently and others large clutches several weeks apart. Considerable flexibility is inherent in the reproductive strategy of *Sepioteuthis australis* and *S. lessoniana*, which like *Loligo forbesi* (Boyle *et al.* 1995) and *Loligo pealei* (Maxwell & Hanlon 2000) would allow potential to cope with fluctuations in abiotic and biotic conditions.

## CHAPTER 5: PATTERNS OF REPRO-SOMATIC INVESTMENT IN TROPICAL AND TEMPERATE *SEPIOTEUTHIS* SPECIES

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### 5.1 INTRODUCTION

Animals with indeterminate growth experience a life history trade off in resource allocation between reproduction and growth throughout their lives (Stearns 1992), and individuals must decide how to allocate energy between growth and reproduction over all ages and sizes. Cephalopod species typically display non-asymptotic growth patterns, with growth and reproduction necessarily proceeding together over much of the life cycle (eg: *Illex argentinus*, Rodhouse & Hatfield 1990; *Idiosepius pygmaeus*, Jackson 1993; *Photololigo* sp., Moltschaniwskyj 1995). As a function of this, the reproductive biology of a species is closely linked to growth patterns (Mangold *et al.* 1993), and the processes of reproductive and somatic energy allocation are probably related to some degree to the semelparity or iteroparity of a species (Guerra & Castro, 1994).

In Chapter 3, the life history characteristics of *Sepioteuthis lessoniana* and *S. australis* varied considerably as a function of geographical location. In tropical waters *Sepioteuthis 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 was maintained for longer 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. Additionally, female *S. australis* from Newcastle showed equivocal evidence of adopting a different reproductive strategy to both *S. australis* from Tasmania and *S. lessoniana*. The broad aim of this chapter is to assess the relationship between these divergent life history patterns and the process of resource allocation between growth and reproduction throughout the lifetime of *S. australis* and *S. lessoniana*. Central to this aim is the concept of trade-offs evident between the processes of growth and reproduction.

Most evolutionary life history theory has developed within the context of optimal allocation of limited resources to the competing ends of growth, reproduction and survivorship (Charnov & Berrigan 1991). The total dedication of energy to reproduction results in a terminal spawning event, whereas a partial cost both before and during reproduction will allow individuals to spawn a number of times (Calow 1979). As the reproductive effort of a semelparous animal should be high (Calow 1987), more energy is channelled into gonad development at any one time during reproduction when compared with an animal partitioning reproductive effort over a longer portion of the lifespan. Survival after the reproductive event is less important in a terminal spawning animal (Stearns 1992), and so the balance of energy expenditure between the somatic and reproductive components may be directed away from the soma, with this consequently reflected in the somatic condition of individuals.

Although many animals store energy reserves to support reproduction later in the life cycle (Barber & Blake 1991), for cephalopods the storage substrate and organs used for this purpose are unclear. Lipid in the digestive gland and protein in the muscle tissue have

both been suggested as possible substrates and sites for energy storage in cephalopods (O'Dor & Webber 1986, Castro *et al.* 1992), although to date there is no evidence to suggest that changes in lipid concentrations within the digestive gland are associated with egg production (Clarke *et al.* 1994, Semmens 1998). There is however evidence of somatic tissue supporting gonad development in some terminal spawning cephalopods (O'Dor *et al.* 1984; Jackson & Mladenov 1994), while others appear to derive energy for reproductive processes directly from food (Mangold *et al.* 1993; Hatfield *et al.* 1992, Molschaniwskyj & Semmens 2000).

Lifetime reproductive allocation, and therefore the life history strategy adopted by an animal, can only be understood in terms of resource allocation between reproduction and other competing needs such as maintenance and growth (Heino & Kaitala 1999). This chapter has three specific aims, with the broad goal of enhancing the understanding of the life history strategies of *Sepioteuthis lessoniana* and *S. australis* generated in the previous chapters. Firstly, the relative growth of the mantle, gonad and digestive gland is examined to determine the differential allocation of resources during sexual maturation to assess the role of the mantle muscle and digestive gland as organs for storage of energy for reproduction in *S. lessoniana* and *S. australis*. Secondly, the processes of resource allocation between growth and reproduction with age, body size and maturity stage, are compared between *S. lessoniana* from Townsville and Brisbane and *S. australis* from Newcastle and Tasmania to improve our understanding of the relationship between growth and reproduction in cephalopods. An examination of resource allocation across individual maturity stages may reveal trade-offs between growth and maturation within a population, whilst a comparison of resource allocation patterns between closely related species from a number of divergent environments may

elucidate trade-offs on broader evolutionary scales. Lastly, an assessment of the somatic condition and the rate of gonad growth in *S. australis* from Newcastle, in comparison to that of multiple spawning *Sepioteuthis*, is undertaken to assist in clarifying the reproductive strategy of this genetic type of *S. australis*.

## 5.2 MATERIALS AND METHODS

*Sepioteuthis lessoniana* from Townsville and Brisbane, and *S. australis* from Newcastle and Tasmania were collected, processed and aged as detailed in Chapter 3. The digestive gland was also dissected out of each individual and weighed to the nearest gram.

Mantle weight-length geometric mean regression (Model II) equations were calculated separately for males and females at each of the locations, using log transformed data to linearise the relationship. From these equations residuals were calculated for each individual and standardised by dividing each residual by the standard deviation of the predicted values. An individual that is lighter for its length than predicted from the regression equation (negative residual) is suggested to be in poorer condition than an individual who is heavier for its length than predicted from the regression equation (with a positive residual). To determine if the magnitude of residuals were a function of reproductive maturation, the average residuals among the maturity stages were analysed separately for each sex using one-way ANOVA's. Hochberg's GT2-method post-hoc test for unequal sample sizes was then used to determine where differences among means occurred (Day & Quinn 1989). Residuals from the size-at-age relationship were analysed in the same way to determine if rate of growth was similar among the maturation stages.

As both the mantle and digestive gland have been proposed as sites for energy storage in cephalopods (O'Dor & Webber 1986), it was of interest to determine if individuals with lighter mantles than predicted by the regression equation also had lighter digestive glands than predicted. To achieve this, residuals from the digestive weight-length and

mantle weight-length relationships were correlated against each other. To evaluate any association between growth and condition residuals from the mantle weight-length and size-at-age relationships were also correlated against each other. In order to determine if condition of *Sepioteuthis lessoniana* and *S. australis* individuals from the different populations were equivalent, an analysis of covariance was used to compare mantle weight, with ML as a covariate.

## 5.3 RESULTS

### 5.3.1 Repro-somatic investment of *Sepioteuthis lessoniana*.

The increase in gonad weight with ML was almost three times faster in females than males in Townsville caught *Sepioteuthis lessoniana*, however, Brisbane caught males and females had equivalent rates of increase of the gonad (Table 5.1). Mantle length explained 71% of the variation in gonad weight of Townsville and Brisbane caught males. However, ML accounted for 64% of the variability in ovary weight of Townsville caught females as opposed to only 37% for Brisbane caught females. The increase in ovary weight with ML was also twice as fast in Townsville caught females compared to Brisbane caught females. Using the confidence limits as a guide, the weights of the digestive gland and mantle increased with ML at similar rates in males and females at both locations (Table 5.1).

Although Townsville caught females had a faster rate of gonad increase compared to Townsville caught males and Brisbane caught females, this did not appear to be at the expense of somatic condition as Townsville females had a similar mantle weight at length to both groups (Table 5.2). Neither males nor females at either location had any relationship between the residuals from the size-at-age and mantle weight-length relationships suggesting that individual condition at the whole animal level was not related to growth (Table 5.3). There was, however, a significant positive relationship for all groups of squid between the mantle weight-length residuals and the digestive gland-length residuals, indicating that squid with heavier mantles for their length also had heavier digestive glands (Table 5.3).

**Table 5.1:** Geometric mean regression descriptions between dorsal mantle length and weights of the gonad, digestive gland and mantle for *Sepioteuthis lessoniana* caught in Townsville and Brisbane.

|                                       | Slope | 95% Confidence intervals | Intercept | $r^2$ | $n$ |
|---------------------------------------|-------|--------------------------|-----------|-------|-----|
| <b><u>Sepioteuthis lessoniana</u></b> |       |                          |           |       |     |
| <b><u>Townsville</u></b>              |       |                          |           |       |     |
| Females                               |       |                          |           |       |     |
| Ovary weight                          | 8.92  | 7.02-10.83               | -45.42    | 0.64  | 35  |
| Digestive gland weight                | 2.47  | 1.94-2.99                | -11.33    | 0.82  | 24  |
| Mantle weight                         | 2.76  | 2.63-2.89                | -9.54     | 0.98  | 33  |
| Males                                 |       |                          |           |       |     |
| Testis weight                         | 2.66  | 2.16-3.15                | -13.03    | 0.71  | 37  |
| Digestive gland weight                | 2.98  | 2.49-3.46                | -13.98    | 0.84  | 28  |
| Mantle weight                         | 2.80  | 2.62-2.98                | -9.86     | 0.97  | 28  |
| <b><u>Brisbane</u></b>                |       |                          |           |       |     |
| Females                               |       |                          |           |       |     |
| Ovary weight                          | 3.86  | 2.02-5.69                | -20.06    | 0.37  | 80  |
| Digestive gland weight                | 2.26  | 1.76-2.76                | -9.85     | 0.76  | 37  |
| Mantle weight                         | 2.62  | 2.42-2.82                | -8.68     | 0.89  | 77  |
| Males                                 |       |                          |           |       |     |
| Testis weight                         | 3.58  | 3.05-4.17                | -17.80    | 0.71  | 51  |
| Digestive gland weight                | 2.24  | 1.96-2.52                | -9.84     | 0.81  | 49  |
| Mantle weight                         | 2.53  | 2.32-2.74                | -8.20     | 0.92  | 50  |

**Table 5.2:** Analysis of covariance table, comparing log mantle weight of Townsville caught males and females, and females from Townsville and Brisbane, using log ML as a covariate.

| Source                                   | df  | Type-III<br>SS | MS     | F-value | P>F     |
|--|-----|----------------|--------|---------|---------|
| <u>Townsville males &amp; females</u>    |     |                |        |         |         |
| Log ML                                   | 1   | 24.223         | 24.223 | 2353    | <0.0001 |
| Sex                                      | 1   | 0.016          | 0.016  | 1.562   | 0.216   |
| Log ML x Sex                             | 1   | 0.017          | 0.017  | 1.693   | 0.198   |
| Residual                                 | 58  | 0.597          | 0.010  |         |         |
| <u>Townsville &amp; Brisbane females</u> |     |                |        |         |         |
| Log ML                                   | 1   | 31.908         | 31.908 | 1273    | <0.0001 |
| Location                                 | 1   | 0.060          | 0.060  | 2.422   | 0.123   |
| Log ML x Location                        | 1   | 0.046          | 0.046  | 1.844   | 0.177   |
| Residual                                 | 106 | 2.656          | 0.025  |         |         |

**Table 5.3:** Correlations between residual values from the mantle weight-length relationship with that of size-at-age and digestive gland weight-length relationships for *Sepioteuthis lessoniana*.

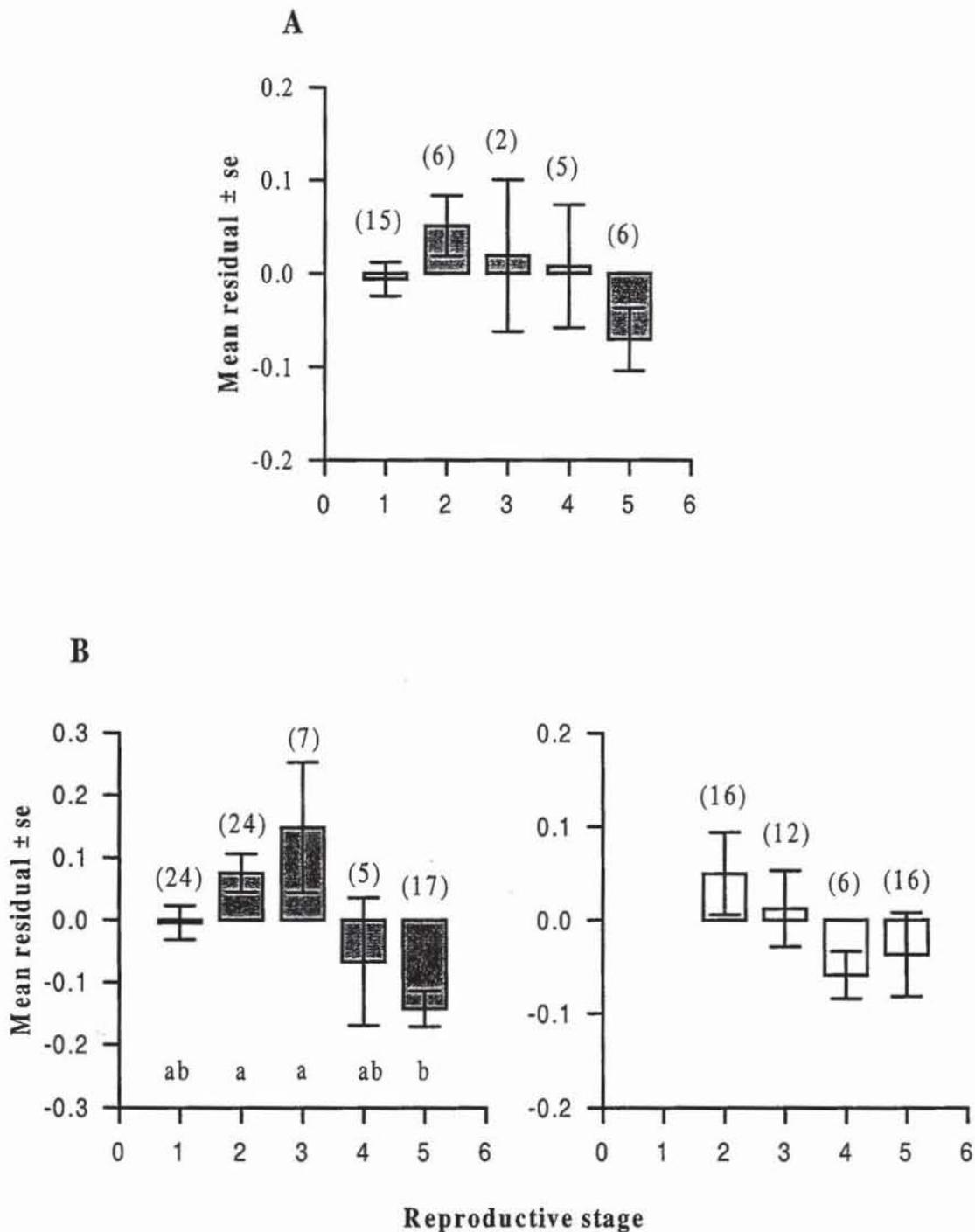
|                   | Size-at-age vs mantle weight-length residuals | Mantle weight-length vs digestive gland weight-length residuals |
|-------------------|---|---|
| <b>Townsville</b> |   |   |
| Females           | $r=-0.09, n=28, P=0.660$                      | $r=0.79, n=12, P=0.002$   |
| Males             | $r=-0.40, n=22, P=0.067$                      | $r=0.72, n=9, P=0.030$  |
| <b>Brisbane</b>   |   |   |
| Females           | $r=-0.25, n=21, P=0.278$                      | $r=0.40, n=37, P=0.015$   |
| Males             | $r=-0.15, n=32, P=0.423$                      | $r=0.42, n=48, P=0.003$   |

Squid at different maturity stages had mantle weights that were neither heavy nor light for their length in all groups, except Brisbane caught females where stage V individuals had lighter mantles than predicted when compared to stage II and III individuals (Table 5.4, Figure 5.1). Size-at-age also appeared to be similar amongst the maturation stages for Townsville and Brisbane caught squid, with residuals from the size-at-age relationship not differing significantly among the stages (Table 5.4).

The transfer of energy from storage organs may be detected as a loss of mass in one organ and gain in another. In Brisbane caught individuals changes in the digestive gland mass were in the same direction as the mantle ( $r_{\text{females}}=0.49$ ,  $n=34$ ,  $P=0.003$ ;  $r_{\text{males}}=0.57$ ,  $n=45$ ,  $P<0.001$ ) and there was no correlation with mass of the gonad ( $r_{\text{females}}=0.09$ ,  $n=34$ ,  $P=0.61$ ;  $r_{\text{males}}=-0.23$ ,  $n=46$ ,  $P=0.12$ ). In Townsville caught individuals there was no significant correlation between mass of the digestive gland and mass of the mantle ( $r_{\text{females}}=0.52$ ,  $n=11$ ,  $P=0.121$ ;  $r_{\text{males}}=0.56$ ,  $n=9$ ,  $P=0.149$ ). Townsville caught males also did not show a correlation between digestive gland mass and mass of the gonad ( $r=0.05$ ,  $n=15$ ,  $P=0.85$ ), however digestive gland mass of Townsville caught females had a negative correlation with gonad mass ( $r=-0.52$ ,  $n=12$ ,  $P=0.05$ ).

**Table 5.4:** Summary of one-way ANOVA's, examining average residual values between maturation stages for mantle weight-length and size-at-age relationships for female *Sepioteuthis lessoniana* from Townsville and Brisbane, and males from Brisbane.

|                   | Size-at-age residuals & maturation stage | Mantle weight-length residuals & maturation stage |
|-------------------|--|---|
| <u>Townsville</u> |  |   |
| Females           | $F=1.174$ , df 4,41, $P=0.338$           | $F=1.417$ , df 4,33, $P=0.253$                    |
| <u>Brisbane</u>   |  |   |
| Females           | $F=0.294$ , df 3,22, $P=0.829$           | $F=6.499$ , df 4,76, $P<0.0001$                   |
| Males             | $F=1.138$ , df 3,39, $P=0.347$           | $F=1.080$ , df 3,49, $P=0.367$                    |



**Figure 5.1:** Average residuals from the mantle weight-length relationship in each of the reproductive maturation stages for *Sepioteuthis lessoniana* from (a) Townsville and (b) Brisbane. Shaded bars are females, white bars are males. The values above each bar are the number of individuals in each stage. The letters for the Brisbane caught females indicate means that are similar as determined using Hochberg's GT2-method post-hoc test.

### 5.3.2 Repro-somatic investment of *Sepioteuthis australis*.

Mantle length explained more of the variability in gonad weight of both males (68%) and females (81%) caught in Newcastle, compared with Tasmanian caught individuals (37% and 61% for males and females respectively, Table 5.5). The increase in gonad weight with ML was faster in females compared with males at both locations. Both males and females caught in Newcastle had twice the rate of gonad increase compared with squid from Tasmania (Table 5.5). However, the mantle weight-length relationships were similar among males and females, and between locations (Table 5.6).

**Table 5.5:** Geometric mean regression descriptions between dorsal mantle length and weights of the gonad, digestive gland and mantle for *Sepioteuthis australis* caught in Newcastle and Tasmania.

|                                      | Slope | 95% Confidence intervals | Intercept | $r^2$ | $n$ |
|--------------------------------------|-------|--------------------------|-----------|-------|-----|
| <b><u>Sepioteuthis australis</u></b> |       |                          |           |       |     |
| <b><u>Newcastle</u></b>              |       |                          |           |       |     |
| Females                              |       |                          |           |       |     |
| Ovary weight                         | 10.34 | 9.05-11.62               | -53.28    | 0.81  | 51  |
| Digestive gland weight               | 2.53  | 2.21-2.85                | -10.96    | 0.94  | 20  |
| Mantle weight                        | 2.44  | 2.23-2.65                | -8.01     | 0.91  | 49  |
| Males                                |       |                          |           |       |     |
| Testis weight                        | 7.56  | 6.14-8.98                | -38.56    | 0.68  | 39  |
| Digestive gland weight               | 1.87  | 1.13-2.61                | -5.10     | 0.85  | 11  |
| Mantle weight                        | 2.67  | 2.50-2.84                | -9.27     | 0.96  | 39  |
| <b><u>Tasmania</u></b>               |       |                          |           |       |     |
| Females                              |       |                          |           |       |     |
| Ovary weight                         | 5.17  | 4.59-5.75                | -25.11    | 0.61  | 180 |
| Digestive gland weight               | 3.45  | 2.96-3.94                | -16.35    | 0.89  | 20  |
| Mantle weight                        | 2.46  | 2.37-2.56                | -8.42     | 0.92  | 196 |
| Males                                |       |                          |           |       |     |
| Testis weight                        | 3.21  | 2.90-3.51                | -15.41    | 0.37  | 237 |
| Digestive gland weight               | 2.72  | 2.24-3.21                | -12.55    | 0.81  | 35  |
| Mantle weight                        | 2.54  | 2.44-2.63                | -8.84     | 0.92  | 235 |

**Table 5.6:** Analysis of covariance table, comparing log mantle weight between sexes and locations, for *Sepioteuthis australis*, using log ML as a covariate.

| Source                  | df  | Type-III<br>SS | MS     | F-value | P>F     |
|-------------------------|-----|----------------|--------|---------|---------|
| Log ML                  | 1   | 141.16         | 141.16 | 3895    | <0.0001 |
| Sex                     | 1   | 0.164          | 0.164  | 4.525   | 0.034   |
| Location                | 1   | 0.014          | 0.014  | 0.377   | 0.539   |
| Log ML x Sex            | 1   | 0.150          | 0.150  | 4.135   | 0.053   |
| Log ML x Location       | 1   | 0.053          | 0.053  | 1.478   | 0.225   |
| Location x Sex          | 1   | 0.018          | 0.018  | 0.489   | 0.485   |
| Location x Log ML x Sex | 1   | 0.019          | 0.019  | 0.519   | 0.472   |
| Residual                | 510 | 18.48          | 0.036  |         |         |

*Sepioteuthis australis* from Newcastle did not have significant correlations between the residuals from the mantle weight-length and size-at-age or digestive gland weight-length relationships (Table 5.7). Individuals from Tasmania, however, had a weak positive correlation between residuals from the mantle weight-length and size-at-age relationships (Table 5.7), suggesting that faster growing individuals were in better condition. Males from Tasmania also had a positive correlation between the mantle weight-length residuals and those from the digestive gland weight-length relationship suggesting that males with heavier digestive glands than predicted were in good somatic condition. Residuals from the size-at-age relationship differed across maturation stages for females from both locations, and males from Newcastle, with mature individuals achieving a greater size-at-age than predicted from the regression equation compared to

stage I individuals (Table 5.8, Figure 5.2). There were also differences in the average residuals from the mantle weight-length relationship across maturation stages for Tasmanian caught females, with stage V squid having lighter mantles than predicted, and stage III squid heavier mantles (Table 5.8, Figure 5.3). Neither males nor females from Newcastle showed significant differences in the average mantle weight-length residuals between maturation stages (Table 5.8).

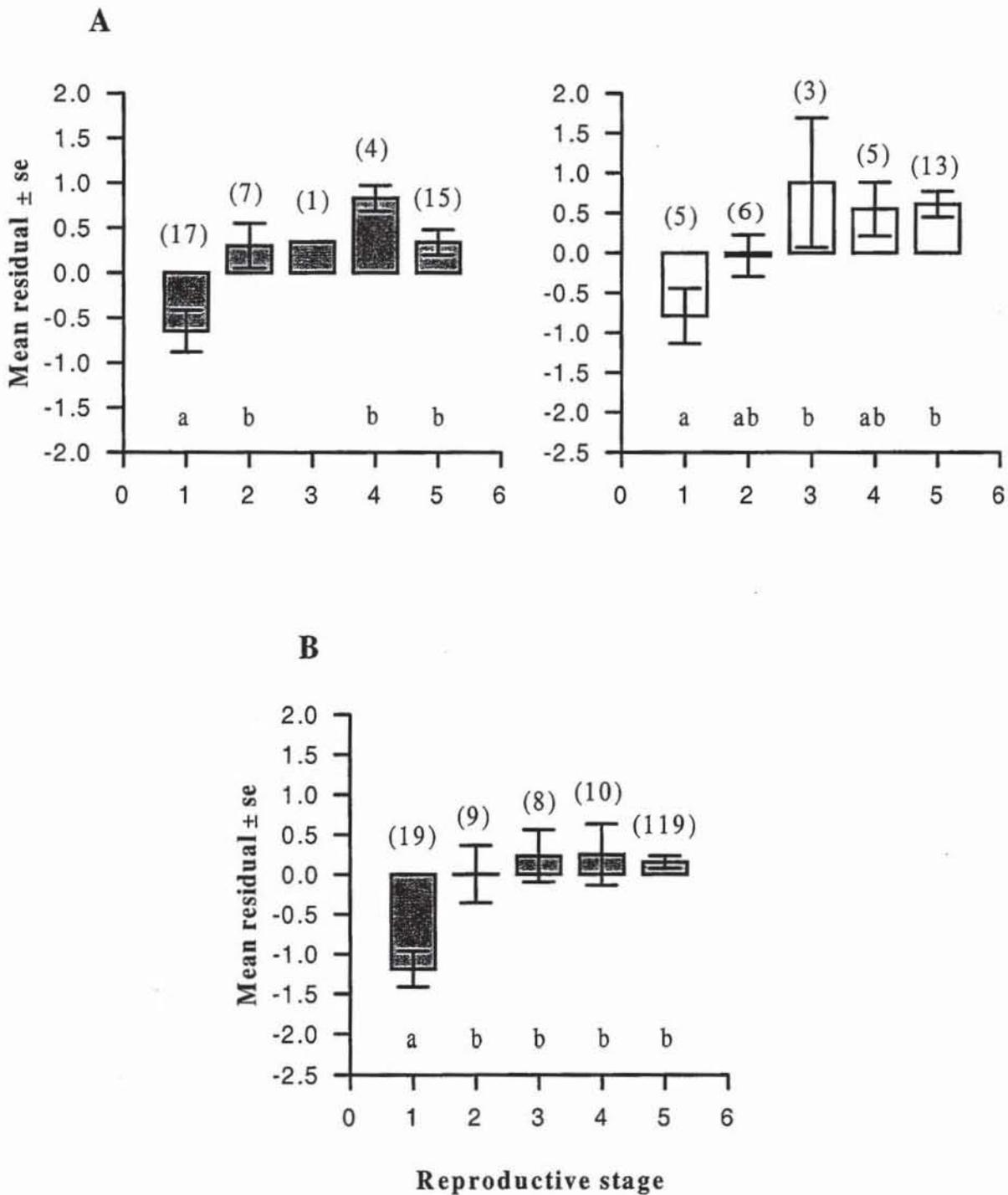
Changes in digestive gland mass were in the same direction as both the mantle ( $r_{\text{males}}=0.88$ ,  $n=31$ ,  $P<0.0001$ ;  $r_{\text{females}}=0.72$ ,  $n=17$ ,  $P=0.001$ ) and gonad ( $r_{\text{male}}=0.62$ ,  $n=32$ ,  $P<0.0001$ ;  $r_{\text{female}}=0.65$ ,  $n=17$ ,  $P=0.003$ ) for male and female *Sepioteuthis australis* caught in Tasmania. In Newcastle caught squid, changes in the digestive gland mass were in the same direction as the mantle for both sexes ( $r_{\text{male}}=0.64$ ,  $n=11$ ,  $P=0.47$ ;  $r_{\text{female}}=0.54$ ,  $n=17$ ,  $P=0.018$ ). Although changes in the digestive gland mass were in the same direction as the gonad for females caught in Newcastle ( $r=0.46$ ,  $n=17$ ,  $P=0.048$ ), there was no relationship evident for males ( $r=-0.003$ ,  $n=11$ ,  $P=0.992$ ).

**Table 5.7:** Correlations between residual values from the mantle weight-length relationship with that of size-at-age and digestive gland weight-length relationships for *Sepioteuthis australis*.

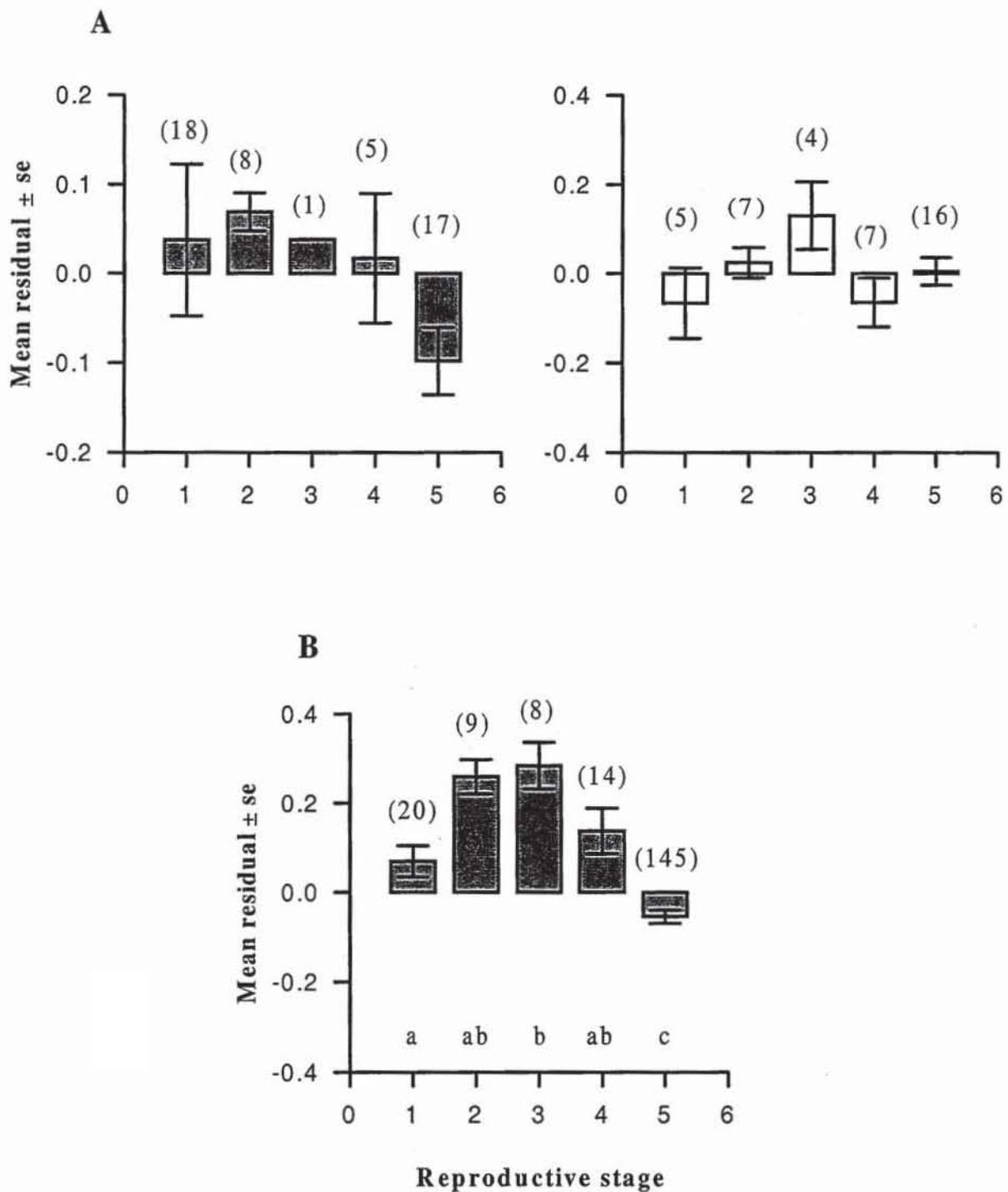
|                  | Size-at-age & mantle weight-length residuals | Mantle weight-length & digestive gland weight-length residuals |
|------------------|--|--|
| <b>Newcastle</b> |  |  |
| Females          | $r=0.14, n=42, P=0.386$                      | $r=0.19, n=20, P=0.430$  |
| Males            | $r=0.20, n=32, P=0.281$                      | $r=0.03, n=11, P=0.928$  |
| <b>Tasmania</b>  |  |  |
| Females          | $r=0.17, n=165, P=0.031$                     | $r=0.29, n=20, P=0.209$  |
| Males            | $r=0.34, n=183, P<0.0001$                    | $r=0.61, n=34, P<0.0001$                                       |

**Table 5.8:** Summary of one-way ANOVA's, examining average residual values between maturation stages for mantle weight-length and size-at-age relationships for female and male *Sepioteuthis australis* from Newcastle, and females from Tasmania.

|                  | Size-at-age residuals vs maturation stage | Mantle weight-length residuals vs maturation stage |
|------------------|---|--|
| <b>Newcastle</b> |   |  |
| Females          | $F=7.381, df 3,42, P<0.0001$              | $F=1.212, df 3,47, P=0.317$                        |
| Males            | $F=4.091, df 4, 31, P=0.010$              | $F=1.751, df 4, 38, P=0.162$                       |
| <b>Tasmania</b>  |   |  |
| Females          | $F=9.479, df 4,164, P<0.0001$             | $F=16.513, df 4,195, P<0.0001$                     |



**Figure 5.2:** Average residuals from the size-at-age relationship in each of the reproductive maturation stages for *Sepioteuthis australis* from (a) Newcastle and (b) Tasmania. Shaded bars are females, white bars are males. The values above each bar are the number of individuals in each stage. The letters indicate means that are similar as determined using Hochberg's GT2-method post-hoc test.



**Figure 5.3:** Average residuals from the mantle weight-length relationship in each of the reproductive maturation stages for *Sepioteuthis australis* from (a) Newcastle and (b) Tasmania. Shaded bars are females, white bars are males. The values above each bar are the number of individuals in each stage. The letters for the Tasmanian caught females indicate means that are similar as determined using Hochberg's GT2-method post-hoc test.

## 5.4 DISCUSSION

The allocation of energy between somatic growth and reproduction was clearly different between *Sepioteuthis lessoniana* and *S. australis*, and between geographical locations within each species. These patterns of energy allocation are probably linked to the contrasting life history characteristics exhibited by each species at the different locations, a function of the divergent environmental conditions experienced by individuals at each location and perhaps genetic differences.

At the most northern location for each species rate of ovary growth with body size was double that of individuals from the southern location. For *Sepioteuthis lessoniana*, the rapid growth of the ovary of Townsville females coincides with a dramatic decline in growth rate, compared with *S. lessoniana* from Brisbane which maintains a more moderate growth rate for longer. This is consistent with the current idea that increased allocation of energy to reproduction is at the expense of somatic growth (Charnov & Berrigan 1991), and contributes to the smaller final size of tropical squids. However, body growth of male *S. lessoniana* from Townsville declined more rapidly with age than in *S. lessoniana* from Brisbane and yet the rate of testis growth was comparable between individuals from the two locations. Clearly increased allocation of energy to reproduction is not solely responsible for the shorter average lifespan and smaller average size of *S. lessoniana* in warmer portions of its range. Additionally, rate of ovary growth of female *S. australis* from Newcastle was the fastest of both species at either location, and yet growth rate of the body is maintained for longer than in *S. lessoniana* from Townsville, and growth is faster overall compared with *S. australis* from Tasmania.

Gonad growth of females of *Sepioteuthis lessoniana* from Townsville and *S. australis* from Tasmania was twice that of males, as was also found in *Photololigo* sp. (Moltschaniwskyj & Semmens 2000). Given this difference in reproductive investment between the sexes, the lack of sex-specific growth rates is perplexing. Males do mature earlier than females (Chapter 3), and so males may invest energy in reproduction for a longer portion of the lifespan but allocate less energy than females at any one point in time. Allocation of energy to reproduction with body size was very similar between *S. lessoniana* males from Townsville and Brisbane and *S. australis* males from Tasmania. However, *S. australis* males from Newcastle had a rate of testis growth double that of any other group, including male *S. australis* from Tasmania, despite Tasmanian *S. australis* males maturing at smaller sizes and younger ages. *Sepioteuthis australis* females from Newcastle also had the fastest rate of ovary growth of both species, and maturation of females was more size dependent than in either species at other locations. A shift in the allocation of energy to growth early in life and gonad growth later is expected in semelparous animals and is reflected as a strong positive allometry of the reproductive organs (Rodhouse & Hatfield 1990). The reproductive strategy of the genetic type of *S. australis* found in Newcastle is still unclear, however, the results of this study suggest that these individuals are tending more towards the terminal spawning end of what is surely a continuum of reproductive strategies, than either *S. australis* in Tasmania or *S. lessoniana*.

*Sepioteuthis lessoniana* and *S. australis* appear to derive energy for reproduction principally from food and not stored energy reserves. At the most southern location for each species mature females had lighter mantles than predicted for their length, suggesting that energy may be diverted to reproductive maturation at the expense of somatic tissue. There was, however, no evidence to suggest that the mantle muscle tissue was being

mobilised to support gametic development, as was also found in *Photololigo* sp. (Moltschaniwskyj & Semmens 2000). Despite the faster growth of the ovary at the most northern location for each species the mantle weight-length relationships were similar across geographical locations within each species, suggesting that faster gonad growth was not generally at the expense of somatic condition. Likewise, *Sepia pharaonis*, which also appears to lay multiple batches of eggs does not use protein from muscle tissue for developing and growing its reproductive tissues (Gabr *et al.* 1998b). This is in contrast to most terminal spawning species which exhibit muscle deterioration in mature animals as energy for reproduction is stored in the mantle muscle (eg: *Moroteuthis ingens*, Jackson & Mladenov 1994; *Todarodes pacificus*, Shikata & Shirata 1999). However, not all terminal spawners use protein from muscle tissue to support reproduction (eg: *Loligo gahi*, Guerra & Castro 1994), and in others males remain muscular until death and it is only females that become gelatinous (eg: *Gonatus fabricii*, Arkhipkin & Bjørke 1999).

In *Sepioteuthis australis*, and *S. lessoniana* from Brisbane and males from Townsville, changes in digestive gland mass was in the same direction as the gonad and mantle, or no relationship was found, providing no evidence of storage and transfer of energy within the body for the purpose of reproduction. This is also the case with *Photololigo* sp. (Moltschaniwskyj & Semmens 2000). *Sepioteuthis lessoniana* females from Townsville however showed equivocal evidence of a decline in digestive gland weight associated with an increase in the size of the ovary. The current proposed roles of the lipid within the digestive gland of cephalopods are a conflict between storage (Castro *et al.* 1992) and excretion (Semmens 1998), although there is no evidence to suggest that changes in lipid concentrations in this organ are associated with egg production (Clarke *et al.* 1994, Semmens 1998). The role of the digestive gland for reproductive energy storage may be

species specific and Semmens (1998) has shown that lipid in the digestive gland of *S. lessoniana* is dietary excess that is probably excreted rather than used as an energy store. The weight of the digestive gland may also be correlated with short and long term feeding levels as it is in *Eledone cirrhosa* (Houlihan *et al.* 1998). *Sepioteuthis lessoniana* and *S. australis* individuals from Tasmania with heavier mantles than predicted also had heavier digestive glands, suggesting a link between these two organs that warrants further investigation.

*Sepioteuthis lessoniana* from both locations showed no difference in size-at-age with maturation stage, suggesting that maturity stage is not a source of intra-specific plasticity in the growth rates of *S. lessoniana*. Unexpectedly, and in contrast with *Sepioteuthis lessoniana*, immature *Sepioteuthis australis* individuals of both sexes, at both locations, achieved a smaller size-at-age than predicted. Life history theory predicts that somatic growth will slow once reproductive maturity begins as organisms would be allocating energy to gametic growth at the expense of somatic growth (MacDonald & Bayne 1993, Sato 1994). Slower growth may occur as energy resources are mobilised directly from the somatic tissue, or merely diverted away from somatic growth. Slower growth rates do occur in reproductively mature *Illex argentinus* (Arkhipkin 1993) and *Photololigo* sp. (Moltschaniwskyj 1995), as well as many fish species (Whalen & Parrish 1999), although some fish species (eg: capelin) can accelerate growth during sexual maturation (Huse 1998).

While slower growth in reproductively mature cephalopods is undoubtedly a real biological occurrence in some species, growth rate may also appear to decrease in mature animals if faster growing individuals spawn and die ahead of slower growing

individuals (ie: Lee's phenomenon) (Villanueva 1992a). This occurs because fast growing individuals are usually underestimated in the population as they leave the population more quickly than slow growers (Alford & Jackson 1993). For many cephalopods displaying continuous growth, growth does not slow down with the onset of maturity and, as found in this study for *Sepioteuthis lessoniana* and *S. australis*, a co-ordination of somatic and gametic growth is implied (Jackson & Choat, 1992). *Idiosepius pygmaeus* are also serial spawners that continue to grow throughout most of their life with no apparent decrease in growth rate during maturation (Lewis & Choat, 1993).

The reproductive investment of individuals was in this study estimated by the relative mass of the dissected reproductive organs of males and females. With individuals of both sexes and species likely to spawn over an extended time frame, an important factor that could not be assessed is the reproductive and nutritional history of each individual. Females hold no record of when they started to produce eggs, or how many batches they have produced, with both these factors affecting growth and the use of energy reserves (Moltschaniwskyj & Semmens 2000). As such, when an assessment of reproductive investment is made at time of sampling only, it must represent a variable proportion of the lifetime investment, whereas the growth assessment is an average over the entire lifetime of an animal. This is likely to be more of a concern where comparisons between mature individuals are involved, than comparisons across maturation stages.

This study revealed little evidence of trade-offs between reproduction and growth or condition of individuals. The costs of reproduction and associated trade-offs may be difficult to identify despite their importance to a complete understanding of life history processes (Wheelwright *et al.* 1991), and may only be apparent when environmental

conditions are poor (Weeks 1996). However, no organism can be simultaneously good at growth, survival and reproduction (Stearns 1989). Jones (1990), neatly summed up life history theory as 'nobody gets a free lunch', and for cephalopods this means their life cycles must be necessarily short (Guerra 1993). Although trade-offs were not detected in this study between growth and reproduction, there was some evidence of a trade-off between reproduction and longevity in *Sepioteuthis lessoniana* and *S. australis*. Each species was smaller and younger on average in the most northern part of its range (Chapter 3), coinciding with a faster rate of gonad growth. The results of this chapter suggest that the drain of energy utilisation for reproduction is not driving the growth patterns observed in *S. lessoniana* and *S. australis*. However, as temperature affects not only rates of growth and maturation, but also the rate at which food can be assimilated and metabolised (Krohn *et al.* 1997), ambient temperatures will have a major effect on the energy budget of squids. As such, it would be necessary to compare metabolism and energy efficiency in tropical and temperate squids to develop a full understanding of the interaction between growth and reproduction. Allocation of energy to reproduction at the expense of continued somatic growth is a complex process (Sebens 1987).

**CHAPTER 6: RESOURCE ALLOCATION BETWEEN GROWTH  
AND REPRODUCTION IN *SEPIOTEUTHIS AUSTRALIS* AS A  
FUNCTION OF HATCHING SEASON.**

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**6.1 INTRODUCTION**

Recently, the approach to analysing cephalopod growth data has shifted in emphasis from examining individuals in groups based on when they are caught, to looking at individuals that are likely to have experienced similar environmental conditions. This approach has revealed that the growth patterns and rates exhibited by many cephalopods are influenced by the season in which individuals have hatched (*Illex argentinus*, Rodhouse & Hatfield 1990, Arkhipkin & Laptikhovsky 1994; *Illex coindetti*, González *et al.* 1996; *Loligo pealei*, Brodziak & Macy 1996; *Illex illecebrosus*, O'Dor *et al.* 1996, Dawe & Beck 1997; *Lolliguncula brevis*, Jackson *et al.* 1997; *Loligo vulgaris*, Raya *et al.* 1999; *Sepioteuthis australis*, Chapter 2). Likewise, size and age at maturation is also largely influenced by season of hatching (*Illex argentinus*, Arkhipkin & Laptikhovsky 1994; *Loligo pealei*, Brodziak & Macy 1996). However, there is little field-based information currently available that relates to how life-history characteristics other than growth and age and size at maturation may also vary according to environmental conditions experienced by individuals.

Energy is viewed by most biologists as being the closest thing there is to a common currency of life (Calow 1985), with lifetime patterns of energy allocation central to life-history theory. Both population dynamics and individual fitness are partially determined by the dynamics of reproductive allocation of energy from different sources. The

amount of energy allocated affects the number and success of offspring, which in turn may affect population size and stability over time (Boggs 1997). For an individual that continues to grow while laying multiple batches of eggs over a significant portion of the lifespan, repro-somatic allocation decisions must continue beyond the attainment of reproductive maturity. This chapter examines the process of resource allocation between growth and reproduction in *Sepioteuthis australis* individuals as a function of hatching season.

Once reproductive maturation has been achieved many cephalopod species show a high degree of individual variation in the degree of anatomical investment in reproductive structures (usually reported as a percentage of body mass), particularly for females (eg: *Loligo chinensis*, *Idiosepius pygmaeus*, Jackson 1993; *Sepioteuthis lessoniana* and *S. australis*, Chapter 4). 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 evident amongst mature individuals. Hatching season could potentially effect reproductive investment either directly through resource quality and quantity or indirectly through seasonal growth patterns. In animals living within one year and displaying indeterminate growth, expected reproductive output could also oscillate as a function of changing mortality. High mortality makes small final size optimal as it is better to start reproduction early in life as resources put to growth are at a greater risk of being wasted (Kozłowski 1996). Consequently, the high growth rate and decrease in age at maturity observed in many ectotherms at high temperatures (Atkinson 1994) can be explained by increased mortality (Kozłowski 1996). Squid populations with protracted spawning seasons may be composed of numerous broods or micro-cohorts that may

experience different growth and survival rates (Caddy 1991), with both these factors potentially affecting resource allocation decisions.

Considerable flexibility is evident in the reproductive strategies adopted by individuals within some cephalopod populations in terms of age and size at maturation (Boyle *et al.* 1995, Arkhipkin *et al.* 2000). The size of egg batches and frequency of batch deposition may also vary substantially among females of a species (Moltschaniwskyj 1995), with neither factor necessarily tightly constrained by size or age (Maxwell & Hanlon 2000). *Sepioteuthis australis* also exhibits considerable variation in mature egg size among females (5-10 mm), with evidence of an energetic trade-off between egg size and number (Chapter 4). Multiple spawning species have a greater potential for inter-individual variability in resource allocation compared with terminal spawning species as reproductive output is a function not only of size at first maturity, but additionally batch fecundity, spawning frequency and duration of individual maturity (Lowerre-Barbieri *et al.* 1998). As such, a simple assessment of age and size at maturity may not provide the resolution necessary to understand the impact of hatching season on the reproductive strategy adopted by an individual.

This chapter examines the relationship between the level of anatomical investment in reproduction, somatic condition at the whole animal level and growth as a function of hatching season in *Sepioteuthis australis* from the east coast of Tasmania. It also assesses 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 *S. australis* females. The major aim of this research is to evaluate the importance of individual hatch date as a factor driving the generation of flexible reproductive

strategies evident among individuals within cephalopod populations and to assess the relationship of alternative reproductive strategies with other aspects of the life cycle.

## 6.2 MATERIALS AND METHODS

Squid were collected from Great Oyster Bay, Tasmania, and processed as detailed in Chapter 2. All squid were assigned to a maturity stage according to the relative size and colour of reproductive organs, following the six-stage maturity scale of Lipinski (1979). Under this scheme stages IV and V are mature and are hence part of the spawning stock. All analyses were calculated using only mature squid to avoid any confounding effects of maturation stage. Dorsal mantle length (ML) was measured to the nearest millimetre and total body weight to the nearest 0.01g. The mantle muscle and each of the reproductive organs were dissected out and weighed separately. Squid were assigned to seasonal hatching groups (austral summer, autumn, winter, spring) based on estimated back-calculated hatching dates (Chapter 2).

Mantle weight-length geometric mean regression (Model II) equations were calculated for males and females separately using log-transformed data, and from these equations residuals were calculated for each individual. A residual is the difference between an individual's actual measured weight and the weight predicted by the regression equation. Residuals were standardised by dividing each residual by the standard deviation of the predicted values. Residuals of the mantle weight-length relationship provide a size independent measure of the condition of an individual at the whole animal level (Moltschaniwskyj & Semmens 2000). An individual that is lighter for its length than predicted from the regression equation (negative residual), is suggested to be in poorer condition than an individual who is heavier for its length than predicted from the regression equation (with a positive residual). As an indicator of the level of reproductive investment, residuals were also generated from reproductive weight-at-length regressions for each sex. Reproductive weight was calculated as the combined mass of the testis,

spermatophoric complex, needhams sac and penis for males, and the ovary, oviduct, oviducal and nidamental glands for females. To determine if the magnitude of residuals were a function of hatching season, the average residuals were compared among seasonal hatching groups, separately for each sex, using one-way ANOVA's. Hochberg's GT2-method post-hoc test for unequal sample sizes was then used to determine where differences among means occurred. To test for an association between somatic condition and level of reproductive investment, residuals from mantle weight-at-length and reproductive weight-at-length regressions were correlated against each other for each sex separately. Residuals were also generated from the weight-at-age relationship (Chapter 2) as a measure of the difference in an individuals lifetime growth from the population average, and correlated against residuals from the reproductive weight-length relationship to assess the degree of association between growth rate and level of reproductive investment. Residuals were correlated across all individuals for each sex, and also for each season of hatching separately. Spring hatched females were however not analysed separately due to insufficient sample size of this group for correlation purposes.

*Sepioteuthis australis* females are multiple spawners (Chapter 4), and so another factor of interest was how individual females from each seasonal hatching group were allocating their respective reproductive investment into discrete egg batches. The number of ovulated oocytes in the oviduct of mature individuals and the sizes of mature oocytes were estimated as per Chapter 4. Analysis of covariance, using body weight as a covariate was used to assess the number of eggs within the oviduct of females as a function of hatching season. A correlation between the residuals from the mantle weight-length relationship and egg size was used to evaluate the relationship between an individual's condition and egg size. As larger females have the capacity to hold a larger

number of eggs, a partial correlation using body weight as a controlling variable was employed to examine the relationship between female condition and number of eggs within the oviduct.

### 6.3 RESULTS

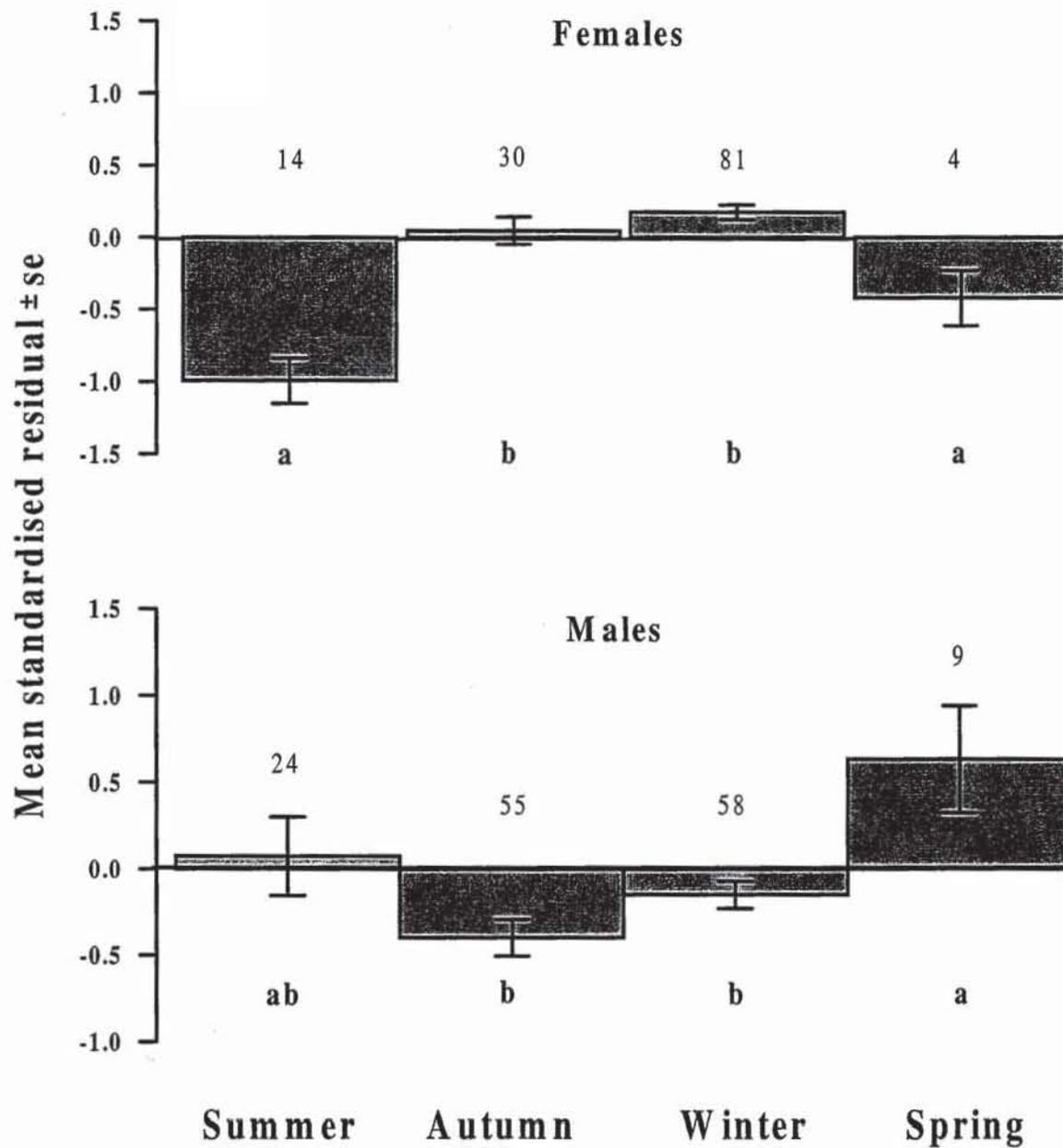
The increase in total reproductive weight with ML was twice as fast in female *Sepioteuthis australis* caught in Tasmania compared to males, however only 64% and 60% of the variability in reproductive weight was explained by ML for females and males respectively (Table 6.1). This suggests that factors other than body size determine the nature of repro-somatic investment in mature squid. The average residuals from the reproductive weight-length regression equations differed as a function of hatching season for both sexes (Figure 6.1), and are a measure of the divergence in an individual's investment in reproductive structures from the population average. Spring hatched males had a greater commitment to reproductive structures compared to autumn and winter hatched males ( $F=5.329$ ,  $df\ 3,142$ ,  $P=0.002$ ), although summer hatched males had reproductive weights that were neither heavy nor light for their length. In stark contrast to male squid, autumn and winter hatched females had more energy invested in reproductive structures compared to summer and spring hatched females ( $F=20.827$ ,  $df\ 3,125$ ,  $P<0.0001$ ).

There was considerable variation between individuals of both sexes in the relationship between the mantle weight-length residuals and the reproductive weight-length residuals (Figure 6.2). Across all the males, there was a significant positive correlation between the residuals from the mantle weight-length and reproductive weight-length relationships ( $r=0.522$ ,  $n=190$ ,  $P<0.0001$ ). Males hatched in spring and summer generally had both heavier mantles and more investment committed to reproductive structures than males hatched in autumn and winter. Females, however, did not show an association between the mantle weight-length residuals and the reproductive weight-length residuals ( $r=-0.078$ ,  $n=129$ ,  $P=0.378$ ). However, with each seasonal hatching

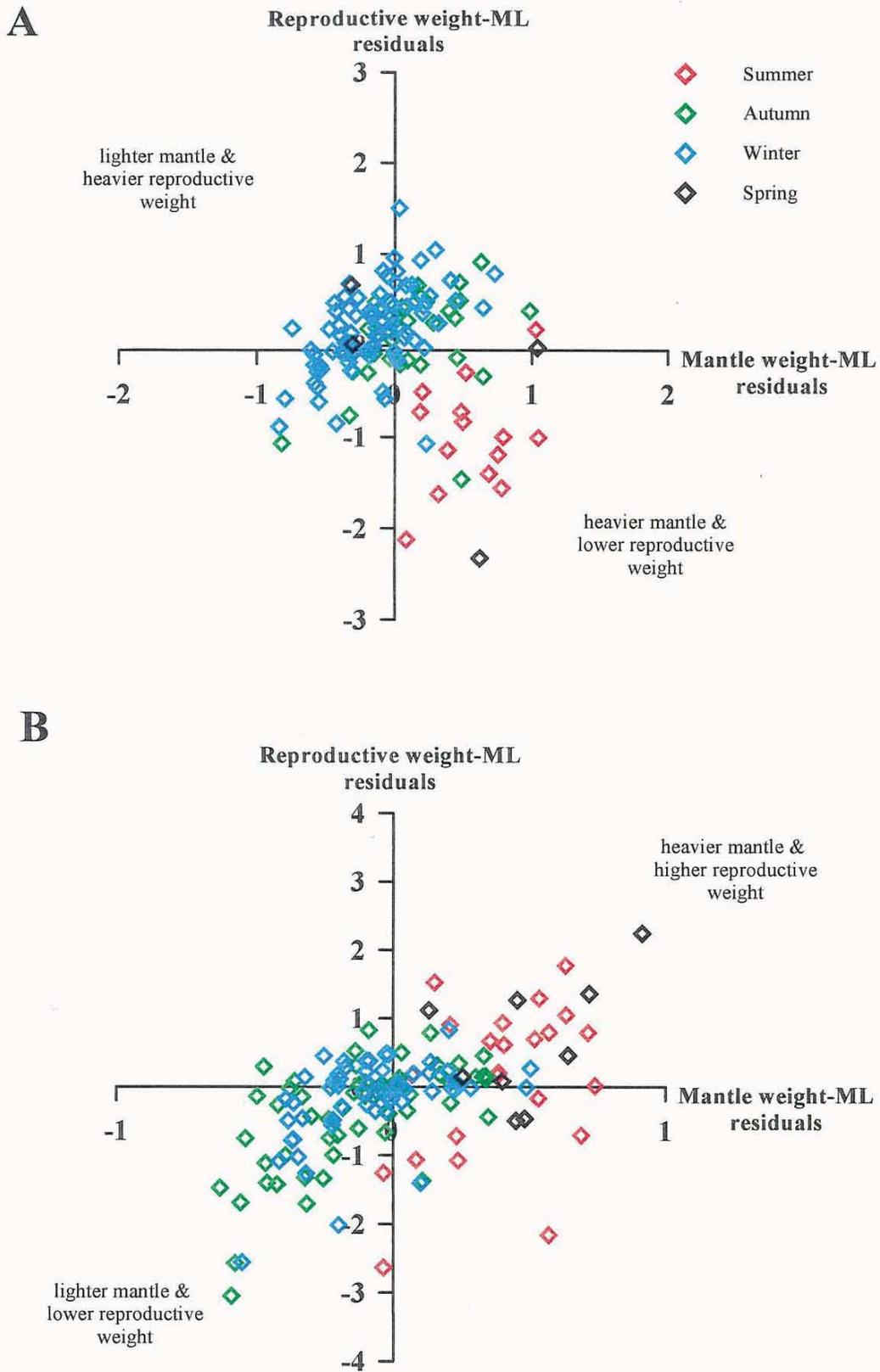
group considered separately, female squid did have a significant positive correlation between the mantle weight-length and the reproductive weight-length residuals for autumn ( $r=0.410$ ,  $n=30$ ,  $P=0.025$ ) and winter ( $r=0.502$ ,  $n=81$ ,  $P<0.0001$ ), but not summer hatched females ( $r=0.303$ ,  $n=14$ ,  $P=0.292$ ). Nevertheless, summer hatched females did quite clearly have heavier mantles and lower reproductive weights compared to the population average (Figure 6.2).

**Table 6.1:** Summary of Model II linear regression statistics for Log mantle and Log reproductive weight vs Log DML relationships for mature male and female *Sepioteuthis australis*.

| Relationship            | $n$ | Slope  | 95% C.I. of slope | Intercept ( $\ln a$ ) | $r^2$ | $P>F$   |
|-------------------------|-----|--------|-------------------|-----------------------|-------|---------|
| <u>Females</u>          |     |        |                   |                       |       |         |
| Log mantle weight       | 159 | 2.7146 | 2.532-2.897       | -9.8313               | 0.82  | <0.0001 |
| Log reproductive weight | 159 | 3.1265 | 2.824-3.429       | -12.8750              | 0.64  | <0.0001 |
| <u>Males</u>            |     |        |                   |                       |       |         |
| Log mantle weight       | 228 | 2.5408 | 2.438-2.644       | -8.8728               | 0.91  | <0.0001 |
| Log reproductive weight | 190 | 1.6956 | 1.504-1.888       | -6.3749               | 0.60  | <0.0001 |



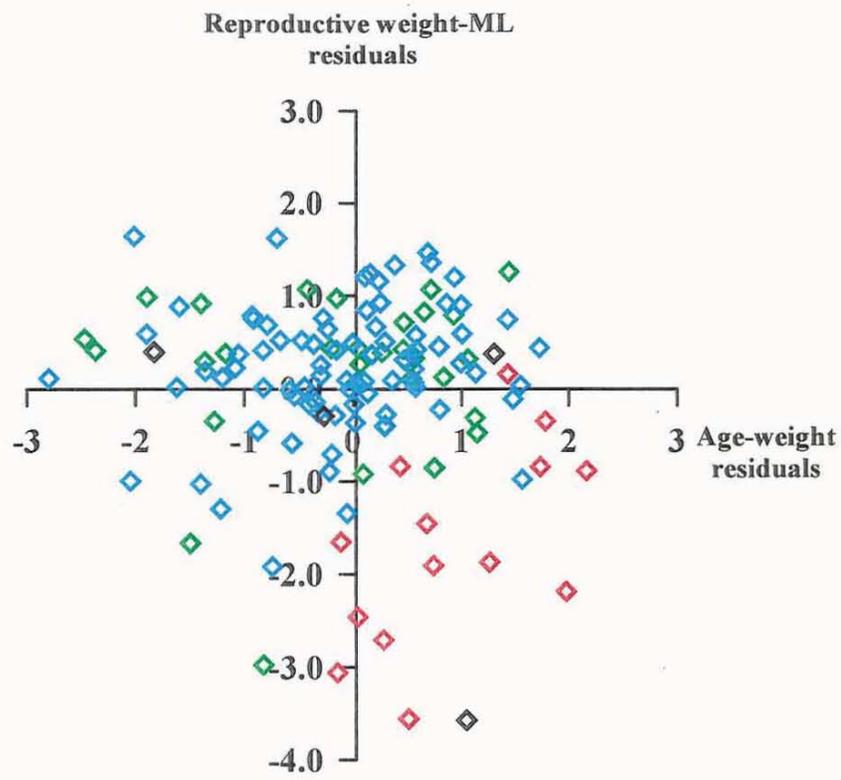
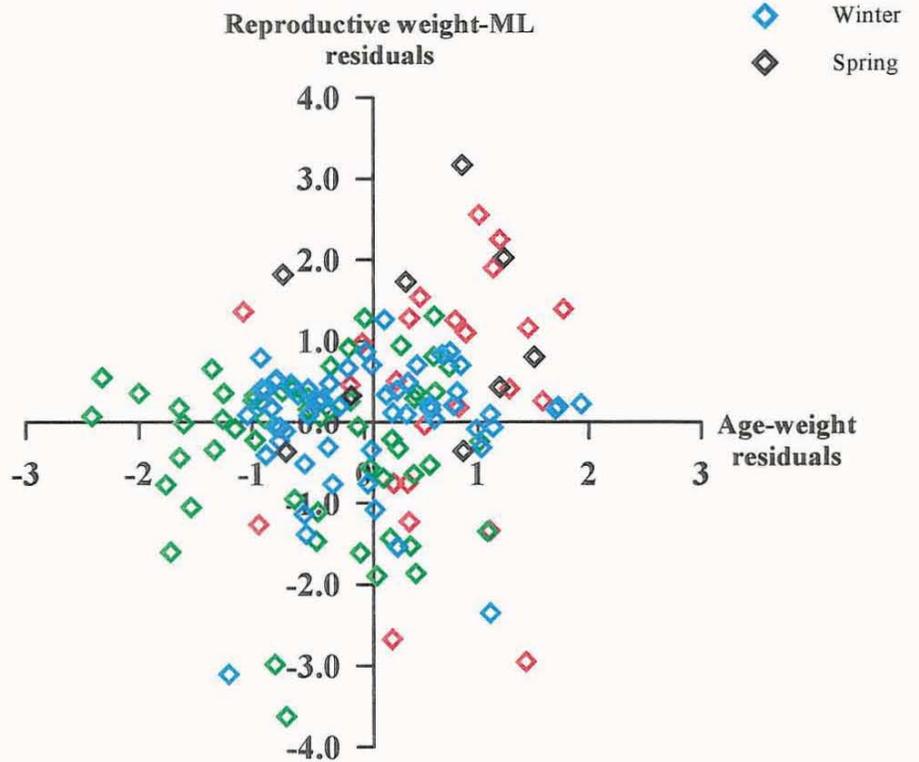
**Figure 6.1:** The average residuals from the reproductive weight-length relationships for *Sepioteuthis australis* females and males hatched in different seasons. The values above each bar are the number of individuals in each hatching season. The letters below each bar indicates means that are similar as determined using Hochberg's GT2-method post-hoc test.



**Figure 6.2:** Residual values for each individual from the mantle weight-length and reproductive weight-length relationships for (a) females and (b) males.

The disparity in somatic condition and reproductive investment observed between squid hatched in different seasons are quite substantial in real terms. A male hatched in spring has a reproductive system that weighs on average 24% more than an autumn or winter hatched male. The divergence in mantle weight-at-length is even larger; a 300 mm ML male hatched in spring or summer may have a mantle that weighs 400 g as opposed to 200 g in an autumn or winter hatched male. Reproductive investment of an autumn or winter hatched female is on average double that of spring and summer hatched females, although at 300 mm ML the mantle weight would be 100 g lighter in an autumn or winter hatched individual of the same length.

Residuals from the size-at-age relationship are a measure of the difference in an individual's lifetime growth from the population average. As both growth (Chapter 2) and reproductive investment vary as a function of hatching season, a factor of interest was the nature and degree of any association between these two characteristics. Across all the males there was a weak but significant positive correlation between the reproductive weight-length and age-weight residuals ( $r=0.176$ ,  $n=146$ ,  $P=0.034$ ) indicating that males that had grown faster also had a higher anatomical investment in reproductive structures compared to slower growing males. This relationship was not evident among all the females combined ( $r=-0.096$ ,  $n=129$ ,  $P=0.277$ ), however, summer hatched females did have a positive correlation ( $r=0.567$ ,  $n=14$ ,  $P=0.034$ ) between the two residuals. This suggests that although level of reproductive investment is related to season of hatching, as is growth and condition, reproductive investment is not necessarily directly associated with growth rate.

**A****B**

**Figure 6.3:** Residual values for each individual from the reproductive weight-length and age-weight relationships for (a) females and (b) males.

As there was a seasonal component influencing the degree to which females invested in reproductive structures, it was relevant to quantify the role of hatching season in explaining any of the variation evident between females in batch sizes of mature eggs within the oviduct, and egg size (Chapter 4). Winter hatched female squid appeared to be laying larger batches of eggs compared to spring and summer hatched females (Table 6.2, Figure 6.4). However, the variability in the size of mature eggs in the oviduct was not a function of hatching season ( $F=0.716$ ,  $df$  3,91,  $P=0.545$ ). Egg size also did not appear to be related to female condition at the whole animal level, as there was no correlation between the residuals from the mantle weight-length relationship and egg size ( $r=-0.011$ ,  $n=111$ ,  $P=0.996$ ). There was however a weak negative correlation between egg number and residuals from the mantle weight-length relationship when controlling for body weight ( $r=-0.23$ ,  $n=119$ ,  $P=0.01$ ), suggesting that females in poorer condition may have been laying larger batches of eggs.

**Table 6.2:** Analysis of covariance table, comparing number of eggs within the oviduct of mature females hatched in each season, using body weight as a covariate.

| Source                | df | Type III SS | MS     | F-value | P>F     |
|-----------------------|----|-------------|--------|---------|---------|
| Hatch season          | 3  | 32906       | 10968  | 1.686   | 0.175   |
| Weight (covariate)    | 1  | 100286      | 100286 | 15.412  | <0.0001 |
| Hatch season x weight | 3  | 119423      | 39807  | 6.118   | 0.001   |
| Residual              | 94 | 611658      | 6507   |         |         |

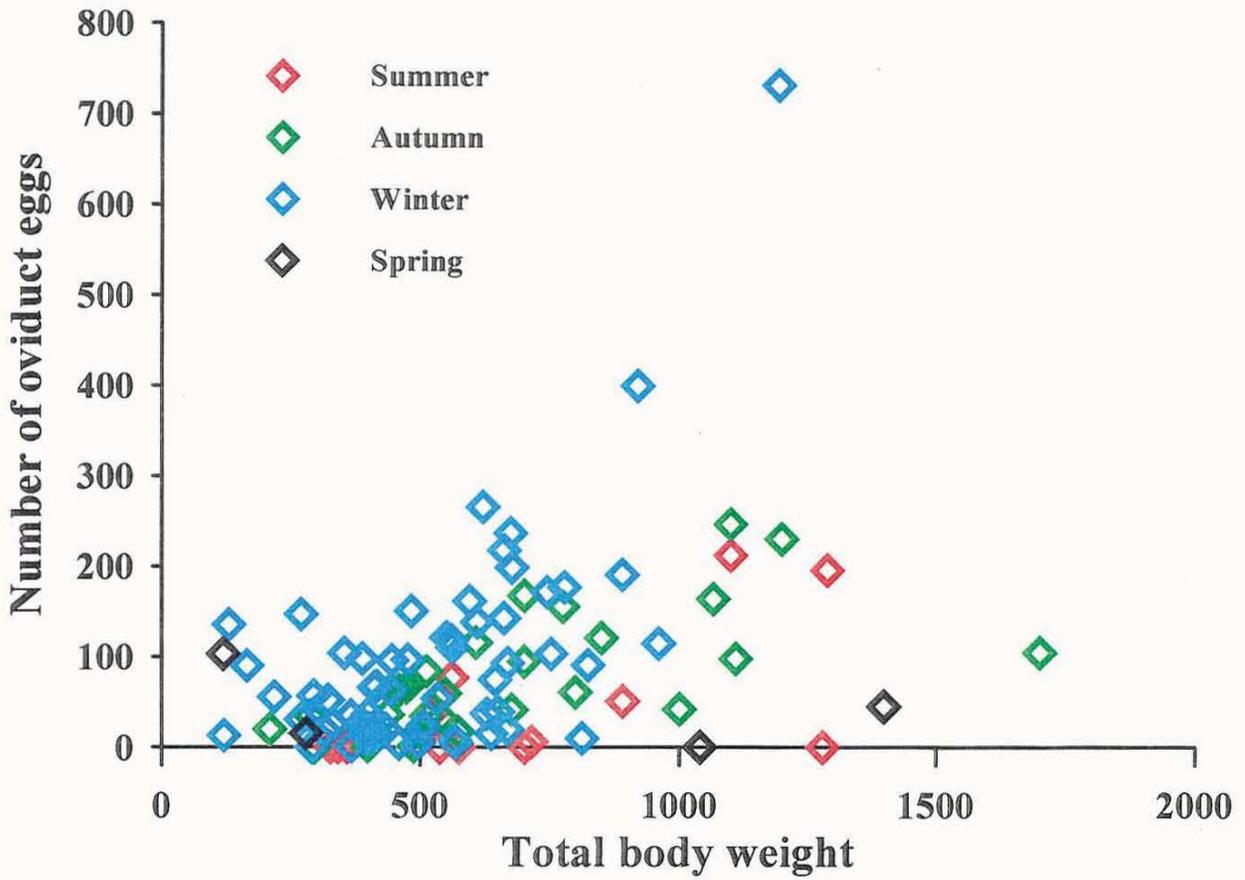


Figure 6.4: Estimated number of eggs in the oviduct of mature *Sepioteuthis australis* females hatched in each season.

## 6.4 DISCUSSION

Season of hatching had a major influence on the life cycle of both male and female *Sepioteuthis australis* individuals, however, the effects of hatching season were sex-specific. Although males and females showed similar seasonal patterns in condition and growth, the relative levels of reproductive investment responded differently with hatching season between the sexes. Males hatched in warmer months had a higher level of reproductive investment, whereas females hatched in spring and summer had lower levels of reproductive investment relative to their autumn and winter hatched counterparts. The faster growth, better somatic condition and higher level of energy invested in reproductive structures of males hatched in warmer temperatures suggests that when environmental conditions are favourable for growth processes males are able to achieve faster growth of both the somatic and reproductive components. A positive relationship between gamete production and increased growth rate has also been attributed to favourable environmental conditions in other invertebrates (O'Dea & Okamura 1999).

Although it appears that males did not experience energetic trade-offs between the processes of growth and reproduction, it is critical to note that behavioural investment in reproduction has not been quantified. Behavioural investment is likely to be substantial for males that are competing with other males to acquire mates and subsequently defend their mates from other males (Hanlon & Messenger 1996). Additionally, although life history trade-offs should be detectable as negative correlations between the relevant traits (eg: reproductive output vs energy storage, Roff 1986), trade-offs may be masked by variation in accrual of resources (Doughty & Shine 1997). Van Noordwijk & de Jong (1986) utilise the analogy of the positive correlation commonly evident in the value of a

person's house and car – a higher income may provide for both an expensive house and an expensive car, rather than a more expensive house equating to a cheaper car. This explanation implies that male *Sepioteuthis australis* may be better at acquiring resources than females, however this is unlikely given that females are caught more frequently with ingested food than are males (Pecl, unpub data). Instead it may be a reflection of the greater total energetic commitment of females to reproduction compared with males.

Female *Sepioteuthis australis* individuals hatched during decreasing temperatures of autumn and winter were slower growing and in poorer somatic condition, however, they had a higher level of reproductive investment and may have been laying larger egg batches compared with spring and summer hatched females. Batch fecundity-at-size also has a seasonal component in some fish species (Kjesbu *et al.* 1996), while others may adjust both egg size and egg number according to energetic resources and environmental conditions (eg: Pacific herring, Hay & Brett 1988). In cephalopods, batch size may have a corresponding relationship with frequency of batch deposition. The spring and summer hatched *S. australis* females that appear to have allocated a lower level of investment into reproduction at any one point in time, may have partitioned their allocation to reproduction into smaller and possibly more frequent egg batches. Conversely, autumn and winter hatched females may have laid larger, possibly less frequent egg batches. Captive *Loligo pealei* (Maxwell & Hanlon 2000) and *Idiosepius pygmaeus* (van Camp 1997) females may also lay small frequent batches of eggs or larger less frequent batches. This dichotomy in the reproductive strategies adopted by individuals within a population appears common for cephalopods (Boyle *et al.* 1995, Moltschaniwskyj 1995) and has been suggested to be a function of when energy reserves are available for gametogenesis (Moltschaniwskyj & Semmens 2000). The results of this chapter suggest that the environmental conditions

experienced by individuals will play a large role in determining when energy is made available for reproduction. Interestingly, the extreme variation evident in mature egg size among females was not attributable to hatching season or female condition. While reproductive output is apparently determined at least in part by factors associated with season of hatching, the way in which it is partitioned between size and number of offspring varies independently of season.

The influence of hatching season on the life history characteristics of *Sepioteuthis australis* results in a very interesting population cycle. Females that were hatched over the spring/summer period appear to have deposited eggs over the next winter, 4-8 months later, and individuals hatched in autumn and winter reproduced during the next summer. This results in an alternation of generations where squid that are slow growing and in poor condition but with a high level of reproductive investment, are producing another generation with a completely different set of life history characteristics. However, it must be emphasised that squid from this study were caught over two discrete time periods of summer and winter only, and the reality is going to be a progression between these two extremes.

*Sepioteuthis australis* has a high degree of plasticity in its 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 (Moltschaniwskyj & Semmens 2000). Female *S. australis* hatched in warmer seasons not only matured later than cooler hatched counter-parts, but once they were mature reproductive investment-at-size was lower. How the relative total reproductive output of females from different seasonal groups compares will depend upon their respective lifespans, as well as the

number and size of batches laid and the frequency of batch deposition. Lifetime fecundity, and fecundity-at-size, are important determinants of both an individual fitness and population size in the subsequent generation (Boggs 1997). The results of this chapter raise some interesting questions about the stability of relationships between individual body size and expected lifetime fecundity, and at the population level, parental biomass and subsequent recruitment. Both these relationships are likely to be driven by seasonal influences in *S. australis*.

## CHAPTER 7: GENERAL SUMMARY & FUTURE STUDIES

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### 7.1 SUMMARY

The central thesis of my research was the comparison of life history characteristics of tropical and temperate loliginid squids from the genus *Sepioteuthis*. The findings of this study can be summarised in four major parts:

- 1) A comprehensive description and comparison of the growth, lifespan, body size, age and size at maturation, and patterns of energy allocation for tropical and temperate *Sepioteuthis* species, and an assessment of the variation in these life history characteristics over large geographical scales.
- 2) Quantification of the influence of hatching season on the life history characteristics of temperate *Sepioteuthis australis*.
- 3) Evidence to support a multiple spawning capacity in field populations of *Sepioteuthis lessoniana* and Tasmanian *S. australis*. Suggestions that *S. australis* from Newcastle may be adopting a reproductive strategy different to that of other *Sepioteuthis* populations.
- 4) An assessment of evidence to indicate trade-offs between growth, reproduction and longevity between individuals, and between populations from different seasons and latitudinal zones.

The first and second components of this study examined variation in the life history characteristics of *Sepioteuthis lessoniana* and *S. australis* along latitudinal zones of the east coast of Australia, and for *S. australis*, with season of hatching. In both cases substantial variation in growth and maturation was evident, with temperature suggested to be a major factor responsible. Water temperature has a major influence on the energy budget of a

squid, affecting both food consumption rate (Mangold 1983) and metabolism (Segawa 1995). However, temperature is not the only factor affecting growth and maturation of squids, rather it is the only quantifiable factor in this type of field study and laboratory studies suggest that temperature is a dominant factor in eliciting the observed responses. Surprisingly, the effects of hatching season on size-at-age of *S. australis* were similar in magnitude to differences in size-at-age observed across latitudinal zones. This supports the previous suggestion of Wells & Clarke (1996) that genetic differences between populations or species underlie compensation for the effects of temperature, despite growth rates of individuals changing directly with temperature.

In all loliginids examined so far growth has been faster in the warmer regions of a species distribution (eg: *Loliolus noctiluca*, Jackson & Choat 1992, Dimmlich & Hoedt 1998), or in individuals hatched in warmer seasons (eg: *Loligo pealei*, Brodziak & Macy 1996; *Loligo vulgaris*, Jackson *et al.* 1997), as was the case in the present study. Where this has been examined in oceanic squid, the opposite has been found with only a few exceptions. *Illex coindetti* hatched in warmer months grow slower (Gonzalez *et al.* 1996) and growth in *Todarodes angolensis* is slower in warmer years (Villanueva 1992a). *Illex coindetti* from the warmer Sierra Leone waters off the west African shelf also grow slower than individuals from the cooler Western Sahara area (Arkhipkin 1996). *Illex illecebrosus* (O'Dor *et al.* 1996) and *Illex argentinus* (Arkhipkin & Laptikhovsky 1994) have been shown to grow slower when hatched in warmer months although other studies have reported the opposite trend (Rodhouse & Hatfield 1990, Dawe & Beck 1997).

Hatfield (2000) suggested that faster growth under cooler conditions is indicative that other abiotic factors may also play a role in determining growth potential of individuals.

Although this is most certainly true, with food availability affecting growth as much if not more than temperature in some species (eg: *Idiosepius pygmaeus*, van Camp 1997), there does seem to be a general distinction between the response to temperature of loliginid squids to that of oceanic species. If this is a real phenomenon it may be a function of physiological differences between the two groups, or simply a reflection of the higher maintenance metabolism of oceanic squids (Wells & Clarke 1996). Increased metabolism at increased temperature will reduce growth if energy intake is constant (Atkinson & Sibly 1996). If food consumption rate remains the same, oceanic species may fare better in cooler waters as metabolic costs associated with transport would be lower, potentially leaving more energy to be allocated towards growth. Metabolism also increases with temperature in loliginids (Segawa 1995), although the relatively lower maintenance metabolism and costs of transport (Wells & Clarke 1996) may still allow for increased growth capacity under higher temperature regimes.

The third component of this study is dealt with in chapter 4 and to a lesser extent chapter 5, and will not be greatly expanded on here. This study used morphological and histological techniques, combined with other biological information, to assess the reproductive strategy of *Sepioteuthis lessoniana* and *S. australis* in wild populations. This builds on previous studies that suggest 'big-bang' terminal spawning is not a ubiquitous reproductive strategy among coleoid cephalopods (Coelho *et al.* 1994, Gabr *et al.* 1998a). Several field studies have suggested non-semelparous strategies (eg: *Stenoteuthis oualaniensis*, Harman *et al.* 1989; *Loligo vulgaris reynaudii*, Sauer & Lipinski 1990), as have a few captive studies (eg: *Idiosepius pygmaeus*, Lewis & Choat 1993; *Loligo pealei*, Maxwell & Hanlon 2000). *Sepioteuthis lessoniana* are known to have the capacity in captivity to spawn over periods of at least 6 weeks, at intervals of

1-9 days (Wada & Kobayashi 1995). The present study is the first quantitative field examination of a species confirmed to have the ability to spawn multiple times in captivity, and therefore provides information on morphological and histological features appropriate in assessing cephalopod reproductive strategies in nature. Importantly, the results of this research also highlight the fact that a species may employ substantial variations on a reproductive strategy within different parts of their distribution, or when small genetic differences are evident between populations. Although the exact nature of the reproductive strategy of the genetic type of *S. australis* found in Newcastle was unclear, it was obviously different to that of other *Sepioteuthis* populations. This may be a direct function of the genetic differences between the two *S. australis* populations examined in this study (Triantafillos & Adams in press), or simply a result of the extreme plasticity in life cycle traits that characterises cephalopods - in response to the divergent environmental conditions of Newcastle and Tasmania. This demonstrates that caution must be applied when extrapolating life cycle characteristics of cephalopod species across large geographical scales.

The last component of this study assessed the allocation of energy between growth and reproduction, examined evidence of trade-offs between growth and reproduction, and assessed the use of energy stores to support reproduction. There was little evidence to suggest a trade-off between growth and reproduction among individuals, or among populations from which individuals exhibited differing growth rates. Instead, it appears that the trade-off is between reproduction and longevity. The continuous allocation of resources to both growth and reproduction would not necessarily result in a low lifetime reproductive output, given that the small tropical sepioid *Idiosepius pygmaeus* produces

multiple egg batches over 80% of the observable adult weight range, laying on average five times its final body weight in eggs (Lewis 1991).

The lack of evidence to support the use of energy stores as sources of energy for reproduction in *Sepioteuthis lessoniana* and *S. australis* is not surprising. Stearns (1992) states that animals may be “income-breeders” where current energy is used for reproduction, or “capital-breeders”, where energy is stored and mobilised to support reproduction at a later date, or a combination of these two. Serial spawners are not likely to be at the capital-breeder end of the continuum for two reasons. Storage of resources for use at a later date involves bio-molecular transfer and/or conversion mechanisms that have significant associated costs compared with the direct use of resources (Barber & Blake 1985). This would reduce the total amount of energy available for growth or reproduction, thereby reducing future reproductive potential. Terminal spawners would not have this limitation as they have no future reproductive potential. Substantial allocation of current income to reproduction at the expense of other functions like growth would not be probable as this would also limit future reproductive potential (Jennings & Phillip 1992). Energy stores may play little role in the reproductive output of “income” breeders, instead feeding rate during reproduction is more important (Doughty & Shine 1997).

Given the widely varying physical and biological environments that cephalopods live in, the success of a population depends on having a diversity of life history characteristics (Boyle *et al.* 1995). This ‘bet hedging’ strategy is also seen in some fish species (Perrin & Rubin 1990) where animals in spatially and temporally changing environments develop phenotypic plasticity for size and age at maturity. At the population level, overlap between generations, extended breeding seasons and variable growth rates reduce the probability of

large interannual changes in population size (Boyle & Boletzky 1996). Phenotypic plasticity allows local adaptation to diverse physical environments, particularly for organisms that are widely dispersed but have little control of their present location (Warner 1991), or season they are hatched into. All components of this study suggest considerable plasticity in the life cycle of *S. lessoniana* and *S. australis*. Growth, age and size at maturation, levels of reproductive investment, batch fecundity and egg size were all shown to be highly variable between individuals.

## 7.2 FUTURE STUDIES

A number of questions arise from this study along with a range of avenues of further research.

Studies on the growth performance of animals at the individual and population levels are naturally inhibited by the difficulty of making sequential measurements on the same animals (Houlihan *et al.* 1998). Additionally, the short life span of cephalopods coupled with high growth rate and early reproduction, exaggerate the difficulties of establishing useful generalisations about populations – individuals are highly mobile, able to avoid many types of sampling gear and may move actively on geographical-scale migrations (Boyle & Boletzky 1996). Thus, although captive experiments and field studies have highlighted the importance of environmental variables in influencing cephalopod life history, it is difficult to estimate the environmental conditions encountered by individuals. Statoliths may serve as archives of an individual's thermal history. Otoliths have long been regarded as a potential store of information about the life history of individual fish, with information encoded in the deposition pattern of trace elements in the otolith (Markwitz *et al.* 2000). Ikeda *et al.* (1998) examined the possibility of using

particular trace elements in *Todarodes pacificus* statoliths as thermoindicators, noting that strontium concentration could be the key to reconstructing an individual's vertical temperature profile. Strontium:calcium ratios in the statoliths of *Martialia hyadesi* from antarctic showed great individual variation, however, the ratio altered with age and the Sr:Ca thermometer hypothesis could not be confirmed nor rejected (Rodhouse *et al.* 1994), as was also the case with *Ommastrephes bartrami* (Yatsu *et al.* 1998).

Temperature significantly affects strontium incorporation into the otoliths of some teleost species (Bath *et al.* 2000), although this relationship is not evident in all species (Chesney *et al.* 1998), and in others the effect of temperature on otolith elemental composition is small relative to the effects of ontogeny (Hoff & Fuiman 1993). Likewise, the utility of using trace elements in the statolith to unravel the environmental history of individuals may be species specific for squid, however the benefits of a high resolution reconstruction of individuals temperature history are many and easily justify the laboratory experiments necessary to resolve ontogenetic and environmental effects. Other avenues to explore include the stable oxygen isotope ratios of statoliths, as examination of this in otoliths has shown to be a potentially valuable tool where the range of distribution of a species covers water with different temperature regimes (Newman *et al.* 2000). Width of statolith increments may also contain information about an individual's thermal history, as statolith growth also shows a strong relationship with temperature (Durholtz & Lipinski 2000, Villanueva 2000).

Laboratory studies have been very useful in isolating biotic and abiotic variables and elucidating their effects on various life history characteristics, however to date these

studies have only used fixed temperatures. All studies, both laboratory based and field, have shown that temperature is a crucial factor influencing growth and maturation, however, we still have a very poor understanding of the impact of this variable on juvenile growth in nature. Do loliginids follow a two-phase growth pattern in nature under conditions of seasonally oscillating temperatures? What happens to the length and rate of the respective growth phases under increasing or decreasing temperatures? These questions are critical to our understanding of life history processes in natural environments and may be resolved by laboratory experiments where temperatures are increased or decreased to mirror the natural environment.

The pressing requirement for detailed laboratory experiments is joined by the need for field experiments that complement and extend laboratory results. It is well known both theoretically and empirically that many species can adjust their life histories in response to temperature, food and mortality factors by allocating resources differently to somatic growth and reproduction. This and other sources of phenotypic plasticity have held a prominent role in evolutionary ecology but explicit connections between such phenotypic plasticity and the broader context of ecological interactions and species abundance have rarely been bridged (Chase 1999). Date of hatching influenced the growth and condition of *S. australis*, potentially resulting in differential susceptibility of individuals to predation or other factors that may affect cohort size. Additionally, the batch fecundity of individuals caught in summer and winter also differed. Future research should be directed at examining the duration of maturity, and the spawning intervals of individual females. In squid with flexible strategies we know little about the temporal and spatial influence on spawning biology, the relationships between parental

biomass and subsequent recruitment, and how the sensitivity of individuals and populations to environmental factors effects the overall population structure.

Traditionally, studies of growth and maturation have adopted an approach in which the mean performance of a group of individuals is considered 'real' and variation around the mean 'statistical noise' (Kolok 1999). In the fish and cephalopod literature, an alternative approach has appeared recently that incorporates rather than surpresses individual variation, revealing biologically relevant relationships that can be masked by the traditional use of groups means (Alford & Jackson 1993, Rice *et al.* 1993). Future studies of the consequences and causes of phenotypic variability in life history traits will support the incorporation of squid attributes into individual based models of population dynamics. Using such models, measures of individual performance and condition can be incorporated to predict population responses to simulated changes in environmental conditions.

The phenotype of an organism is a product of its genetic makeup and the effect of the environment in which it has developed and lived (O'Dea & Okamura 1999). The exceptional physiological and metabolic attributes of cephalopods results in a unique and highly variable life history, which in comparison to their molluscan relatives and teleost 'competitors' is still poorly understood. Investigations of the nature outlined above will make advances towards resolving the many unanswered questions in relation to the variation and inherent flexibility in the life history of cephalopods.

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