

Reproductive status of *Octopus pallidus*, and its relationship to age and size

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Abstract Age-specific information on individual octopus reproductive development and investment from wild populations has until recently been unobtainable. Using daily-formed increments within stylets (internal shells) the individual ages of 503 wild *Octopus pallidus* were determined. In addition, detailed reproductive information was collected for each of the aged octopus, along with reproductive data for an additional 925 octopus. All of the octopus were collected from Bass Strait waters in south-eastern Australia from November 2004 to November 2006. This information was used to investigate seasonal trends in reproductive scheduling and investment, fecundity and egg size. Maturation in *O. pallidus* primarily depends on size with little relationship to age and is highly variable between genders, with females >350 days still maturing in comparison to all males >142 days being mature. Size at 50% maturity for females was approximately 473 g, which is considerably larger than male 100% maturity at <250 g. This indicates that for females at least, maturity does not necessarily come with age. Seasonal scheduling in reproductive investment between genders revealed an optimal spawning period between late summer and early autumn. These results reinforce the view that individual growth and maturity is highly variable in cephalopods.

Introduction

To accurately understand the population dynamics of a species and ensure the ecologically sustainable development of associated fisheries, it is essential to have an understanding of the reproductive biology, age and growth of the species being investigated (King 1995). Size-at-maturity and seasonal patterns in maturation have been determined for several octopus species (i.e. *Octopus bimaculoides*, Forsythe and Hanlon (1988b); *Eledone massyae*, Alvarez Perez and Haimovici (1991); *Octopus mimus*, Cortez et al. (1995); *Octopus vulgaris*, Otero et al. (2007)). Accompanying age information for any octopus species in the wild has not been obtainable, until very recently (Loporati et al. 2008). Octopus populations are known to have variable sizes-at-maturity between and within genders (Boyle and Knobloch 1982, 1983; Voight 1991), high individual growth plasticity (Forsythe and Van Heukelem 1987), generally short life spans (<2 years) (Boyle and Rodhouse 2005), and the majority of their biological processes (i.e. growth, food consumption and egg development) strongly influenced by temperature and diet (DeRusha et al. 1987; Klaich et al. 2006). In this context, age information has been a primary missing factor leading to reproductive scheduling being completely unexplored. Reproductive scheduling plays an intrinsic role in octopus population abundance, where significant declines in recruitment can occur if environmental conditions and resources are unfavourable during optimal spawning periods for these short lived and semelparous organisms (Cortez et al. 1995; Boyle and Rodhouse 2005). The addition of reliable reproductive scheduling information may assist the effective management of octopus fisheries, potentially reducing the likelihood of population crashes due to over-exploitation (Fernández-Rueda and García-Flórez 2007).

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Stylets, also referred to as vestigial shells, are paired structures found in the mantle musculature at the distal end of funnel retractor muscles in octopus (Bizikov 2004; Doubleday et al. 2006). Stylet increment analysis is a newly developed method of octopus age estimation that utilises concentric growth rings found within stylets, fulfilling a similar role to statoliths in squid and otoliths in teleosts (Semmens et al. 2004). The periodicity of ring deposition has been validated as daily in known age captive *Octopus pallidus* up to 245 days (Doubleday et al. 2006), and this method has recently been applied to determine the growth of a wild population of *O. pallidus* (Leporati et al. 2008). With the introduction of stylet increment analysis, hatch-dates can be back calculated and when combined with reproductive information, seasonal patterns in reproductive investment can be determined and both growth and recruitment can be calculated at individual and population levels (Pecl 2004). This has broad ecological relevance due to the important predator/prey roles octopuses play in the majority of the world's marine ecosystems (Hanlon and Messenger 1996).

Octopus pallidus is a benthic species with no pelagic stage in its development. It has a depth range of 7–275 m and is found from the Great Australian Bight around Tasmania to southern New South Wales (Stranks 1988, 1996). Mean size at hatching is ~ 0.25 g (Leporati et al. 2007) and adults have a maximum size of 1.2 kg. As a semelparous species, females stay with their eggs until they hatch, shortly after which they die. *Octopus pallidus* is the target species of a rapidly expanding Bass Strait fishery (Ziegler et al. 2007), with fishery logbook data revealing that catches have increased from 6 t in 1990 to 81 t in 2007. Despite the increase in catch, very little is known about the distribution, abundance, diet, size-at-maturity, fecundity, sex ratios, movement and migration patterns, and stock status of this species.

This study investigated how reproductive status was related to age and size, for a wild population of *Octopus pallidus*. The specific objectives were: (1) determining size and age at maturity, (2) analysing patterns of reproductive investment over different hatch and haul seasons (3) investigating fecundity and egg size on a seasonal basis, (4) examining patterns of seasonal reproductive scheduling between sexes and (5) determining the effects of continual and concentrated fishing pressure on the age and reproductive structure.

Materials and methods

Specimen collection and dissection

Samples were collected during November 2004 to November 2006, over 21 independent sampling trips, in an

area of Bass Strait lying between longitude 145°06.73 and 145°44.03 east; and latitude 40°18.401 and 40°53.22 south, Tasmania, Australia. Bottom set long lines were used to collect the samples. The lines were ~ 3.7 km long with ~ 500 pots attached (pot volume = 3,000 ml) made from moulded plastic and set on sandy substrates at 18 locations at variable depths of 26.0–50.4 m (mean 35.0 m, ± 1.21 SE). To determine the effects of continual fishing pressure on the age and reproductive structure of a localised population, a shorter (1 km) single research line was maintained at the one continuous location using a Global Positioning System (GPS) receiver (40°43.324 south; 145°20.013 east and 40°43.788 south 145°20.49 east). For biological sampling a target sub-sample of at least 70 individuals was set for each trip. Mean seasonal sea surface temperatures from 1985 to 2006 were derived from satellite data downloaded from the National Oceanic and Atmospheric Administration (NOAA) USA web page (www.noaa.gov). Austral seasons were as follows: summer, December–February (mean 16.7°C), autumn March–May (mean 16.6°C), winter June–August (mean 12.7°C), and spring September–November (mean 12.8°C). Sea surface temperatures were used as a proxy as bottom temperature data were unavailable. This was considered a valid approach due to the generally shallow depths (25–50 m), high wind mixing, strong tidal currents and season variability in water circulation observed in this region of Bass Strait (Sandery and Kämpf 2007).

After landing, morphological measurements and dissections were performed on fresh specimens. Whole weight (WW) and eviscerated body weight were measured and the visceral mass of each specimen fixed in formaldehyde (10%), acetic acid (5%), calcium chloride (1.3%) and freshwater (83.7%) solution. After a period of 14–28 days the visceral mass was transferred to 70% ethanol for preservation. The reproductive organs of a sub-sample of 50 females in various reproductive stages were freshly weighed prior to preservation, and again after 14 days, in order to determine the effects of preservation on the weight of the reproductive organs.

The reproductive organs were removed from the preserved visceral mass and weighed to 0.001 g for each octopus. The parameters measured for males were: the whole reproductive complex (MRW), which was then dissected so the testis, and Needham's sack could be weighed independently. The presence or absence of spermatophores in the Needham's sack and penis was noted. Parameters weighed for females were: the whole reproductive complex (FRW), which was then dissected so the ovary, left and right distal oviducts, left and right oviducal glands, and left and right proximal oviducts could be weighed independently. Somatic weight was determined by subtracting the weight of the MRW or FRW from the WW.

Maturity stages

Maturity stages were determined by visual identification of characteristics in the preserved reproductive organs and derived from scales used by Alvarez Perez and Haimovici (1991) and Smith et al. (2006). Each scale was expanded and modified for *O. pallidus* accordingly. For males four reproductive stages were determined: (I) immature, the accessory gland systems and testis are indistinct; (II) maturing, testis larger than the accessory gland and visible through the wall of the genital bag; (III) mature, testis and accessory gland of similar size and spermatophores present in the penis and/or Needham's Sack; and (IV) spent, testis small and striated and spermatophores present in the penis and/or Needham's Sack. For females five reproductive stages were determined: (I) immature, small ovary generally weighing <3 g with no follicles present and a thick outer wall, small white oviducal glands located mid-way down very narrow proximal and distal oviducts; (II) maturing, ovary slightly larger and with a thinner wall than stage I with follicles and or very small eggs present, oviducts longer and white oviducal glands larger and positioned further up the proximal oviduct; (III) mature, ovary very large (>20 g) packed tightly with elongated striated eggs without stalks, the oviducal glands are large and dark in colour and positioned high up the proximal oviduct; (IV) spawning, majority of eggs have stalks, are fully formed and less compressed than in stage III, eggs present in the oviducts and dark oviducal glands located further down the proximal oviduct; (V) post-spawning, shrunken ovary with only follicles and a few fully formed eggs still present, oviducts slightly reduced in size unless containing eggs, the oviducal glands smaller but still dark in colour.

Fecundity and egg size

The number of eggs in the ovaries and oviducts of stage III ($n = 173$) and IV ($n = 104$) females were counted as estimates of potential fecundity. To calibrate the technique 20 stage III individuals had all their eggs counted, the remaining 153 individuals had a sub-sample of 20% of the weight of the ovary counted. Due to the smaller number of eggs in stage IV females, these 104 individuals had all their eggs counted. To provide an indication of mature egg size, the total lengths of 20 eggs were measured from 20 stage IV individuals. Due to uniformity of egg lengths the remaining 84 individuals had only 10 eggs measured; all lengths were measured to the nearest 0.001 mm. The number of eggs from brooding females in 12 pots were counted, along with the number of eggs in the ovary and oviducts, and compared to stage III potential fecundity estimates to provide an indication of how many eggs are laid by a female and how many are resorbed in the ovary. A

sub-sample of ten eggs from five of the pots were measured and compared with eggs found in the ovaries of the corresponding females.

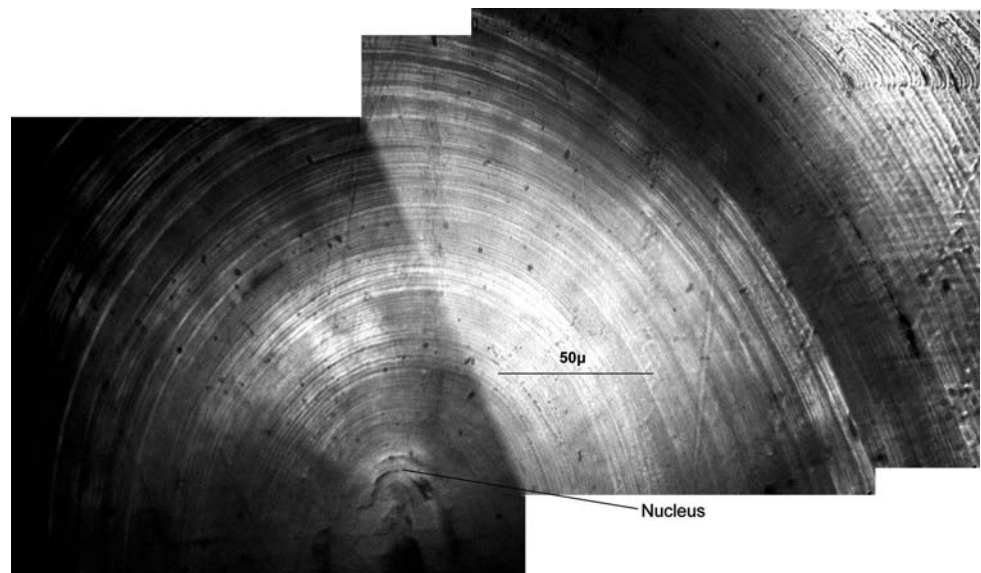
Ageing

Age was determined using stylet increment analysis (Doubleday et al. 2006; Leporati et al. 2008). Stylets were extracted from the mantle musculature and preserved in 70% ethanol. A transverse section was cut from the region immediately after the elbow on the posterior side of the stylet (Doubleday et al. 2006). The section was positioned on a glass microscope slide and embedded in thermoplastic cement (Crystal Bond™ 509). The slide was then placed on a hotplate (approximately 130°C) until the crystal bond was viscous enough to be moulded. The section was then ground on damp 1,200- μm sand paper and progressively polished on 12, 9 and 5- μm damp lapping film to a thickness of approximately 0.5 mm. A final polish on a pellaon PSU PA-K polishing disk impregnated with an alumina powder (0.05- μm) and water slurry was performed to remove surface scratches. The section was then viewed under a compound microscope (Nikon Eclipse E400), connected to a video camera (Leica DC300F) and computer using Leica IM50 (version 1.20) software. At 400 \times magnification, approximately 5–10 images were taken per section depending on the width of the section. Images were taken sequentially from the nucleus to the outer edge following the clearest line of concentric rings. The images were then stitched together Using Adobe Photoshop (elements) to create a composite plane of the section (Fig. 1). The concentric rings were then counted using a hand counter from the nucleus to the outer edge. Ages were only determined for a sub-sample of individuals, all of which were taken from the permanent research line. This was conducted so the effects of continual fishing pressure on age structure could be determined.

Data analysis

Paired *T*-tests were performed to determine if there were any significant differences between the preserved and fresh organs, and the WW of males and females. Chi-square (χ^2) was performed to assess differences in the sex ratios among seasons. Pearson's correlations were performed to determine the strength of the relationship between fecundity and WW, somatic weight, ovary weight and age. Size-at-maturity (WW) was determined by calculating the point where 50% of the females were mature. This was estimated by creating a relative frequency distribution for 20-g weight classes and fitting the results by the least squares method to a logistic curve with the formula (Tafur et al. 2001):

Fig. 1 Composite image of a stylet at $\times 400$ magnification (reduced to 46%), taken from a female *Octopus pallidus*, total weight 377 g, estimated age 202 days



$$P_i = \frac{1}{1 + e^{-(a+bW_i)}}$$

where P_i represents the relative frequency of the mature individuals in weight class W_i , a and b are the regression constants, and 50% maturity weight ($MW_{50\%}$) = a/b .

The mean standardized residuals for the relationship between WW and MRW, and WW and FRW were calculated as an indication of an individual's investment in the development of reproductive organs at time of capture (Pecl and Moltschanivskyj 2006). The residuals, defined as the difference between the actual measured weight and the predicted weight, were calculated using mean non-linear regression (Model II) equations based on log-transformed data. To standardize the residuals they were divided by the standard deviation of the predicted values. The resultant values were either negative or positive values, with the negative representing individuals that had less reproductive investment than expected for their size. ANOVAs were performed to determine if there were differences in reproductive investment among female reproductive stages, and hatch and haul seasons, with post hoc least-significant difference (LSD) tests used to determine the nature of any differences. Only mature stage III males and IV females were used in the haul season analysis to ensure the reproductive investment results were comparable and not influenced by immature and post-spawning individuals. For the hatch season analysis only stage III and IV females aged between 155 and 275 days were used to insure that accurate comparisons could be made between individuals of similar ages and stages of development. A restricted age range was used in these analyses as growth and reproductive development are linked in captive octopus, where younger individuals generally grow faster on average than

older individuals (Forsythe 1993). Using a restricted age range ensured that results demonstrated seasonal influences on reproductive development as opposed to the effects of differing growth rates. The specific range of 155–275 days was chosen because it constituted 35% of the total age range and 70% of the sample. Hatch season analysis was not performed for males due to insufficient numbers. All data were tested for normality prior to analyses and log transformed (log 10), where necessary.

Results

A total of 466 males and 962 females were collected for reproductive analysis. The weights of the preserved and fresh reproductive organs were significantly different ($t = -8.865$, $df 28$, $P = 0.000$), with the preserved organs on average 13% heavier than the fresh. This effect was uniform across all samples, and weights were subsequently corrected accordingly, prior to any analysis. The WW for males ranged from 245 to 1,004 g (mean = 568 g \pm 5.001 SE) and for females 243–981 g (mean = 519.7, \pm 3.554 SE), with no significant difference in WW between the sexes ($t = 0.659$, $df 465$, $P = 0.51$). Sex ratios were significantly different among seasons ($\chi^2 = 420.592$, $df 11$, $P = 0.000$) (Fig. 2). Females dominated at a mean of 69% (± 6.114 SE) of the catch across all seasons. However, during the 2004–2005 and 2005–2006 summers, female sex ratios were at their lowest levels for each of the corresponding years.

All males caught were stage III ($n = 399$) and IV ($n = 66$) individuals, except for a single stage II male. Spermatophores were found in the penis or Needham's sack of all of the males, except for the solitary stage II

male. All female reproductive stages were represented in the catches: stages I ($n = 105$), II ($n = 137$), III ($n = 412$), IV ($n = 169$), V ($n = 139$). MW50% for females was 473 g (Fig. 3).

Ages were determined for 94 males and 409 females, with back-calculated hatch dates revealing that spawning occurred throughout the year. The males ranged in age from 142 to 589 days (mean = 259 days, ± 7.623 SE), whereas the females ranged in age from 110 to 475 days (mean = 243 days, ± 3.182 SE). Reproductive development showed no relationship with age for females with the proportions of immature, mature and post-spawning females consistently represented in most age classes (Fig. 4). The youngest post-spawning (stage V) female was 121 day old in contrast to the oldest immature female (stage I), which was 459 day old.

The mean standardized residuals for the MRW–WW relationship for stage III males were significantly different among seasons ($F = 12.777$, $df 8$, $P = 0.000$) with peaks in reproductive investment occurring during the summer (Fig. 5a). The mean standardized residuals from the FRW–WW relationship for mature females (stages III and IV) also displayed significant differences among seasons ($F = 15.637$, $df 8$, $P = 0.000$) with generally lower reproductive investment during the autumn than spring in each year (Fig. 5b). Significant differences in reproductive investment of mature females (stage III and IV) were also evident among hatch seasons ($F = 2.787$, $df 7$, $P = 0.011$), with females from the early winter and spring 2004 hatch seasons displaying the lowest levels of reproductive

investment followed by progressively higher investment in the subsequent hatch seasons (Fig. 6).

Potential fecundity estimates for stage III females ranged from 270 to 910 eggs (mean = 634, ± 8.235 SE), 58% of which were within the range of 550–700 (Fig. 7). Fecundity was significantly correlated with WW (Pearson correlation = 0.647, $n = 172$, $P = 0.000$, $r^2 = 0.419$), and with somatic weight (Pearson correlation = 0.568, $n = 172$, $P = 0.000$, $r^2 = 0.329$), and ovary weight (Pearson correlation = 0.544, $n = 172$, $P = 0.000$, $r^2 = 0.328$), but not age (Pearson correlation = -0.032 , $n = 55$, $P = 0.815$, $r^2 = 0.004$). However, there were significant differences among haul seasons ($F = 4.257$, $df 8$, $P = 0.000$), with peak fecundity occurring during the summer of 2004–2005 followed by a progressive decline until the spring of 2005 (Fig. 8). The number of individuals with both hatch date and fecundity data was limited to $n = 55$ distributed over eight seasons (mean = 6.1 ± 1.585 SE) with no significant differences detected among females from all hatch seasons ($F = 0.624$, $df 8$, $P = 0.753$). Octopus with stage IV ovaries had a fecundity range of 18–590 eggs (mean = 197.38 eggs, ± 14.740 SE) with egg sizes ranging from 9.07 to 13.45 mm (mean = 11.57 mm, ± 0.067 SE). Egg size showed no relationship with age ($n = 36$, $r^2 = 0.0061$), WW ($n = 101$, $r^2 = 0.0205$), somatic weight ($n = 101$, $r^2 = 0.0169$) or ovary weight ($n = 101$, $r^2 = 0.0392$). The number of eggs female⁻¹ counted in the 12 pots that contained brooding females ranged from 466 to 778 (mean = 424, ± 43.774 SE). Lengths of the eggs in the pots

Fig. 2 Proportion of female to male *Octopus pallidus* caught per haul season with n values. The octopus were sourced from all lines

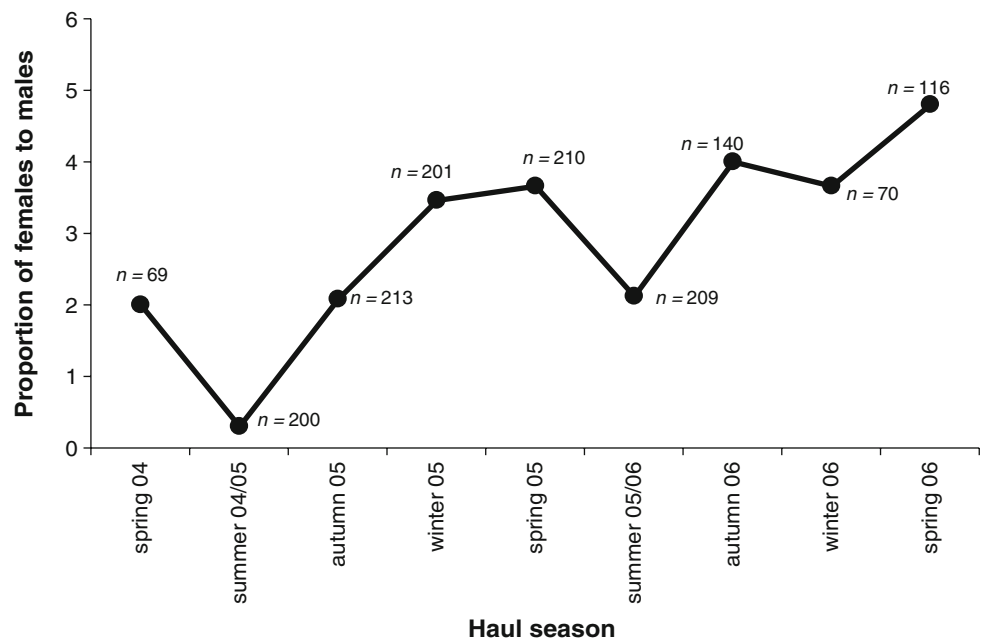


Fig. 3 Size (whole weight) at 50% maturity (MW50%) for *O. pallidus* females from all lines in 20-g weight classes, $n = 657$

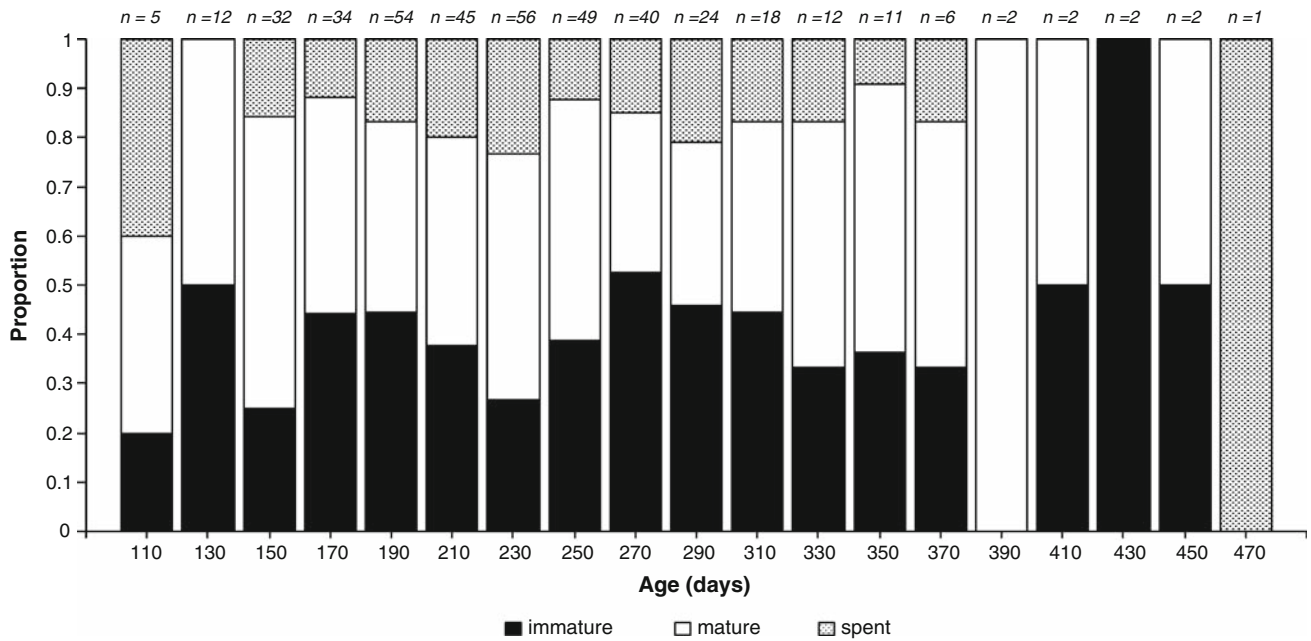
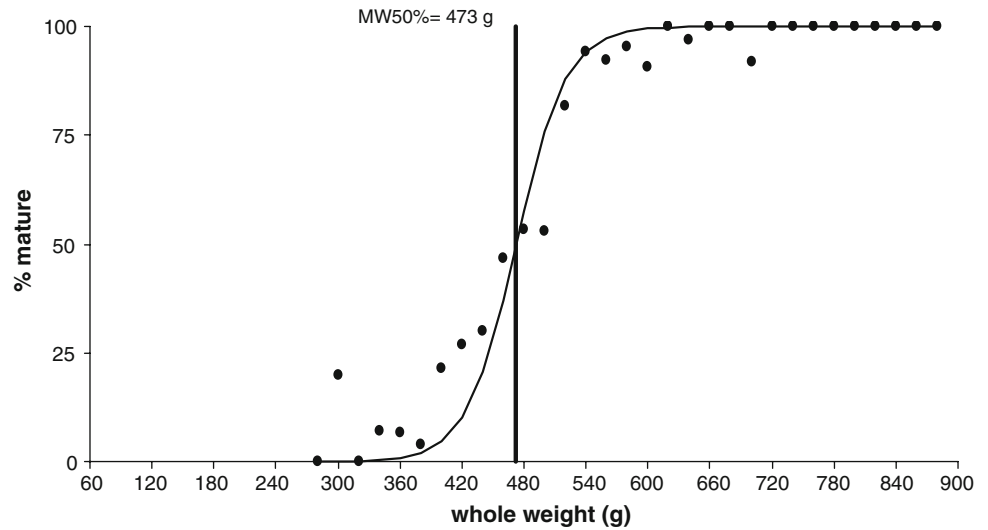


Fig. 4 Proportion of immature (stages I, II), mature (III, IV) and spent (V) *Octopus pallidus* females from the research line in each 20-days age class

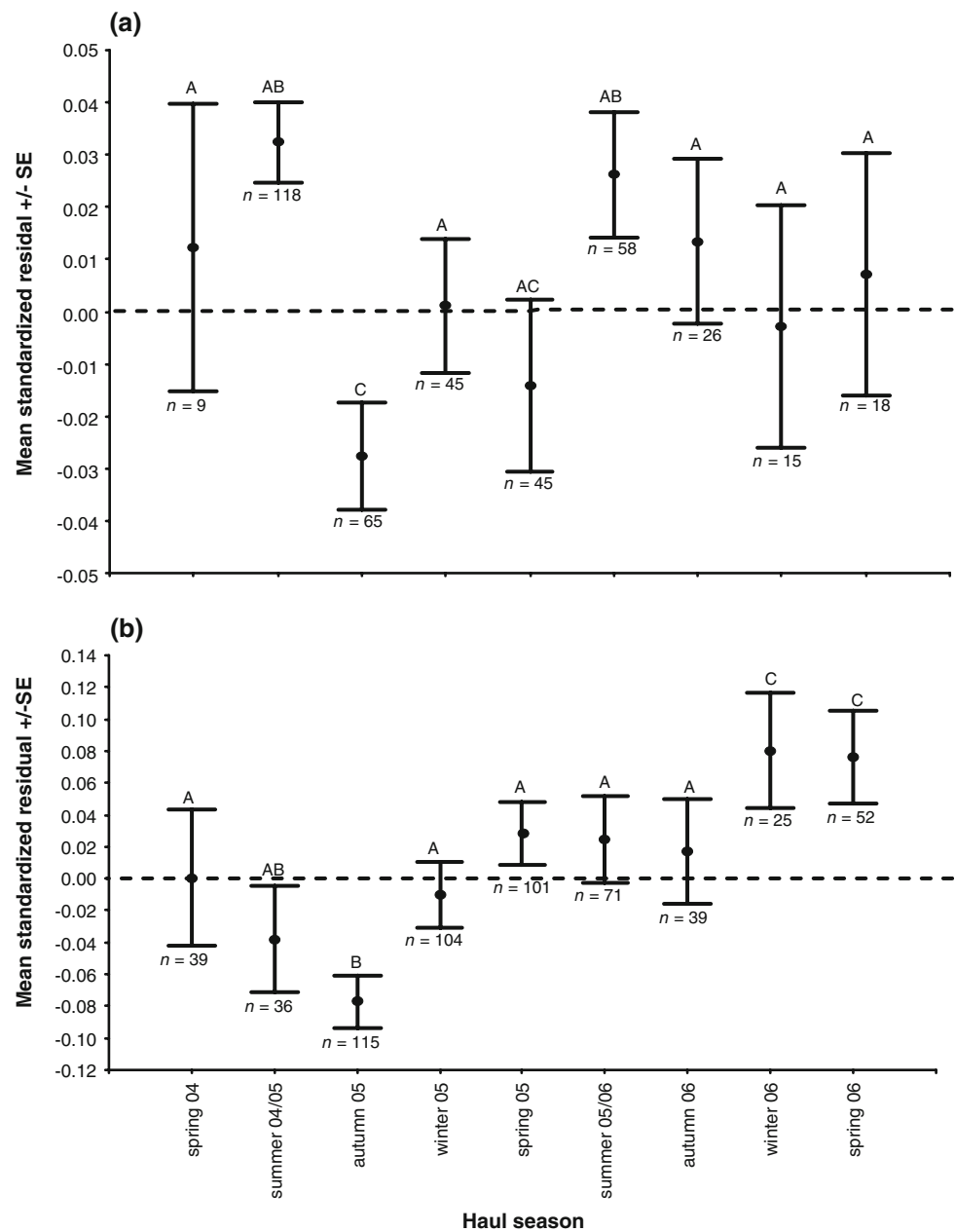
(mean = 12.02 mm ± 0.102 SE) were equivalent to those in the ovary and oviducts of each female examined (mean = 11.83 mm ± 0.101 SE).

Discussion and conclusions

Maturation in *Octopus pallidus* is primarily size-dependent, with little relationship to age. Even at the latter stages of the life span (i.e. 300 days) an older but smaller female can still be maturing, when much younger larger females have already matured. This supports the increasing view that cephalopods are highly dynamic organisms that grow

and mature with great degrees of individual variability, often influenced by external factors such as temperature and diet (Moltschaniwskyj 2004), and biological factors such as genetic differences (Triantafillos 2004). By including age information, this study has provided insights into the seasonal reproductive scheduling of *O. pallidus*, revealing that even though spawning occurs year round, there are distinct seasonal trends in reproductive investment for males and females. Peak female reproductive investment occurred during spring (ovary maturation) in conjunction with increases in male reproductive investment (spermatophore production) during summer, leading to a potential optimal spawning period during late summer,

Fig. 5 Mean standardized residuals for the relationship between whole weight (WW) and the whole reproductive complex weight for stage III and IV *Octopus pallidus* from all lines, with significant differences in mean standardized residuals between haulseasons denoted by letters (A, B, C) derived from LSD post hoc tests. **a** Males and **b** females. Values above the line indicate higher levels of reproductive investment for their size, whereas values below the line indicate lower levels of reproductive investment



indicated by reductions in both male (spent) and female (egg laying) reproductive investment during the autumn.

Female size at 50% maturity was ~473 g indicating that females larger than this are most likely to be mature and increasingly so as their weight increases. However, this pattern was not mirrored for WW < 473 g. Given that *O. pallidus* is a semelparous species, like the vast majority of benthic octopus species (Norman 2000), females that were either in reproductive stages IV or V generally weighed less than stage III females, because sub-473 g females included immature, spawning and post-spawning individuals. As observed in other octopus species, i.e. *Octopus mimus* (Cortez et al. 1995) and *Octopus bimaculatus* (Ambrose 1988), this was not just a product of weight

reduction from the laying of eggs, but also the decrease in somatic weight for stages IV and V octopus as the females lost muscle mass after laying their eggs.

All males sampled in this study were >250 g, mature and older than 142 days, indicating that males mature at a size <250 g. Octopuses <250 g are generally not caught in the *O. pallidus* commercial fishery, suggesting that immature males are generally not vulnerable to fishing pressure. In contrast, all five female reproductive stages were represented in the sampling, even though all females sampled were in the same age and size range as the males, caught with the same fishing gear, and during the same times and locations. Male and female *O. pallidus* are known to reach similar maximum sizes and ages, and have

Fig. 6 Mean standardized residuals for the relationship between whole weight (*WW*) and the whole female reproductive complex weight (*FRW*) for stage III and IV *Octopus pallidus* from each hatch-season, with significant differences in mean standardized residuals denoted by letters (A, B) derived from a LSD post hoc test. Dashed line represents expected levels of reproductive investment. Values above the line indicate higher levels of reproductive investment for their size, whereas values below the line indicate lower levels of reproductive investment. All octopus were sourced from the research line

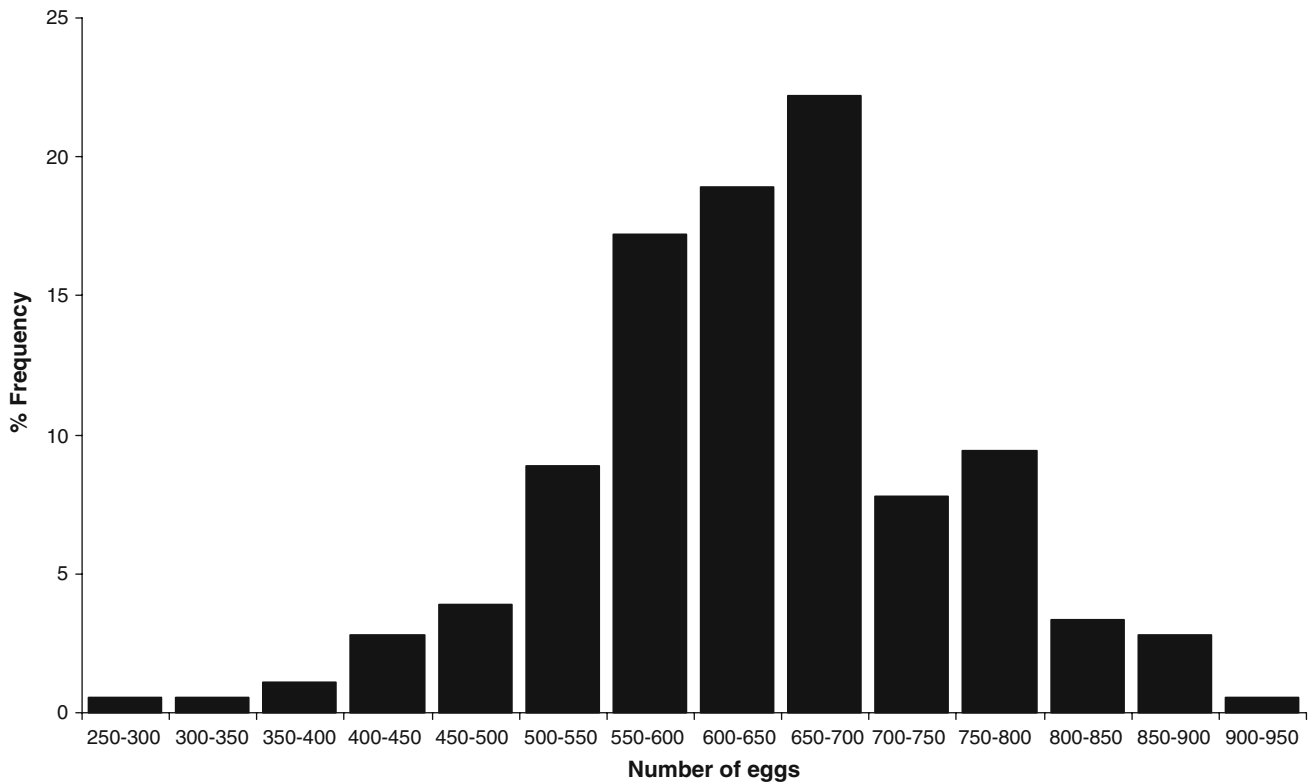
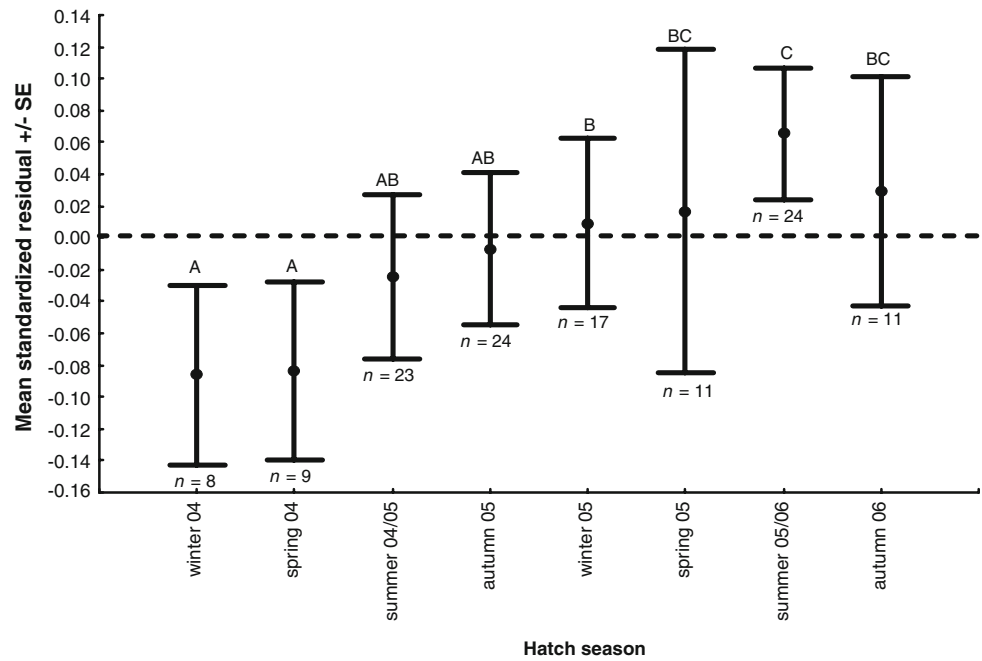
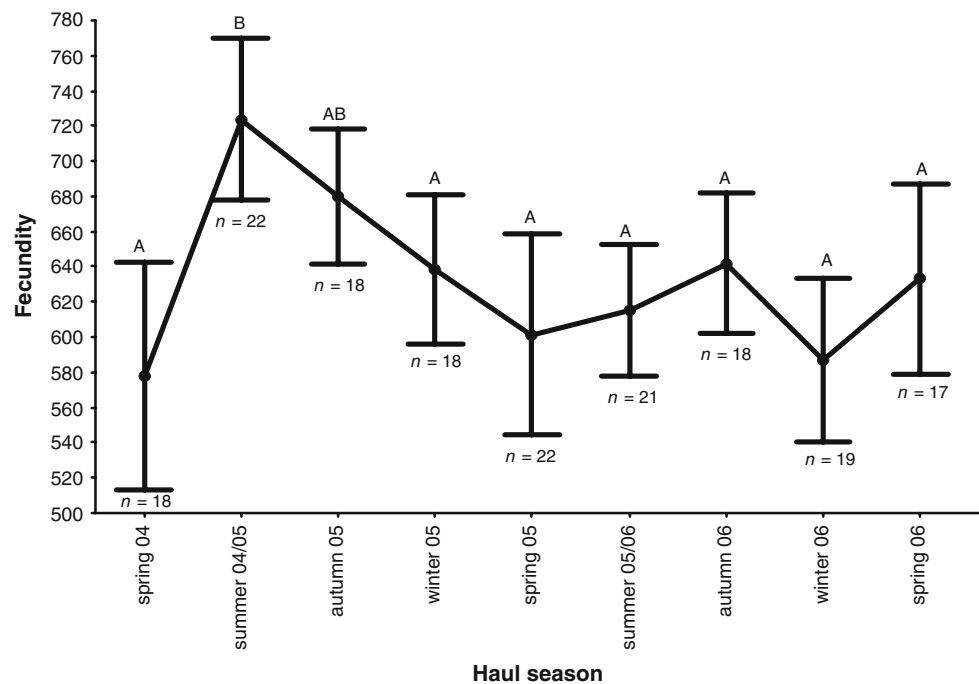


Fig. 7 Percent frequency for number of ovarian eggs for stage III female *Octopus pallidus* from all lines, *n* = 180

similar growth rates calculated over the life span of the individual (Leporati et al. 2007), indicating that males mature at a considerably smaller size and generally younger age (<250 g, <110 days) than females (>460 g, ?–350 days).

Gender-specific size-at-maturation patterns have been observed in *Octopus vulgaris* (Alvarez Perez and Haimovici 1991; Hernández-García et al. 2002; Rodríguez-Rua et al. 2005; Otero et al. 2007), *Eledone massyae* (Alvarez Perez and Haimovici 1991) and *Octopus bimaculoides*

Fig. 8 Mean potential fecundity per haul-season for female *Octopus pallidus* from all lines, with significant differences in mean fecundity denoted by letters (A, B) derived from an LSD post hoc test



(Forsythe and Hanlon 1988a). The later reproductive development and larger size-at-maturity of females compared to males is necessary to build a strong somatic base to withstand the required energy shift associated with committing a larger proportion of body mass to reproductive development (Otero et al. 2007). This was observed in the present study where 12% of the WW of females was in the reproductive organs in comparison to only 2% of WW in males. In addition, earlier maturation of males allows for opportunistic mating between mature males and immature females, for female octopus, i.e. *Octopus tetricus* (Joll 1976) and *O. vulgaris* (Rodríguez-Rua et al. 2005), have the ability to store sperm over lengthy periods and to use them at the onset of maturity. Size-at-maturity and age information is integral for the future management of commercial octopus fisheries and can be used in potential management initiatives such as gender-specific size restrictions on catch, or combined with gender composition, catch, size and growth data, to help determine the potential impacts of commercial fishing on a population.

Reproductive investment increased progressively with each subsequent hatch season in octopus caught on the research line. A potentially related trend was observed in the size and growth information derived from the same data set (see Loporati et al. (2008)), where octopus from progressive subsequent hatch seasons displayed reductions in size and increased growth rate. These trends may be attributed to the intentional fishing down of the population around the research line, where larger females were being removed and replaced by smaller, younger, faster growing females that invested proportionally more energy in

reproduction. A possible explanation for this is that larger individuals commonly win competitions for brood sites (shelters such as pots) (Aronson 1986), thus leading to larger females being the first to be removed when an area is fished down. Following this trend, the next group to occupy the pots would be the faster growing individuals that reach a large size quickly and hence reach size-at-maturity earlier, equating to higher levels of reproductive investment. This is an important consideration for the management of octopus fisheries and indicates that repeated pressure on the one area may lead to size-selective fishing mortality. The extent to which repeated fishing pressure could affect a local octopus population will vary with reproductive strategy. A holobenthic species, like *O. pallidus* that has 100s of eggs and benthic dispersal of hatchlings, could be more prone to localised impacts than merobenthic species, which have 100,000s of eggs and more broadly distributed planktonic dispersal of hatchlings (Narvarte et al. 2006). These effects could also be seasonally and spatially variable depending on bottom temperature, with optimal spawning periods identified for some octopus species, i.e. *O. vulgaris* (Otero et al. 2007), and maturation and egg development generally slower at lower temperatures within a species natural range (Caveriviere et al. 1999). Prolonged brooding at lower temperatures could also result in greater competition for remaining brood sites, and the likelihood of brooding females being caught in the fishery. These impacts on the composition of the *O. pallidus* population have direct ecological consequences (Coleman and Mobley 1984; Arrenguín-Sánchez 2000). However, to determine the full extent of these effects, further investigations into

O. pallidus' role in the trophic structure of the Bass Strait ecosystem are required. Such studies should include prey profiles, habitat usage at different life stages, and seasonal patterns in predator and prey abundances.

Male catch rates and reproductive investment peaked during the summer. With octopus growth rates generally greater at higher temperatures (Semmens et al. 2004), this suggests that a pulse in fast growing mature males may have occurred during the summer months. Female reproductive investment was generally highest during the spring and lowest during the autumn, with no evident relationship to seasonal catch-rates. However, when placed in context with male reproductive schedules, a potential optimal-breeding season was apparent, i.e.: peak female reproductive investment (late stage III egg vitellogenesis) occurred during spring, which was followed by the summer pulse in the number of mature males, which was then followed by the autumn decrease in female reproductive investment (late stage IV spawning). This suggests that the peak-spawning season for *O. pallidus* is around late summer and early autumn. This is supported by laboratory findings on *O. pallidus* hatchling growth, where octopus hatched at higher temperatures (summer) grew faster and ultimately larger than those hatched at lower temperatures (spring), even if hatchlings experienced equivalent degree days (Leporati et al. 2007). A similar example of seasonal reproductive scheduling was found in wild *Octopus bimaculatus* (Ambrose 1988), where eggs laid during the coldest months were generally non-viable and took 60–100 days to hatch, whereas eggs laid during the warmer months had high viability and took only 30–40 days to hatch. The delay in hatching due to cold temperatures resulted in most of the octopus hatching during summer/autumn, regardless of when they were laid. Even relatively small temperature changes can have a significant influence on cephalopods' physiological responses, which in turn can affect the structure of a population (Grist and des Clers 1999). However, it must be considered that *O. pallidus* is a year round spawner and has a maximum life span of ~18 months (Leporati et al. 2008), hence this should be regarded as an optimum spawning period, as opposed to a discrete spawning season.

The maximum potential fecundity of *O. pallidus* was 910 eggs, however, a more typical fecundity range of 550–700 eggs was identified. The number of eggs actually laid for many octopus species is dictated by available substrate, quality (structure, material and shape) of the shelter used (Iribarne 1990) and resorption rates in the ovary (Melo and Sauer 1998). When considering the mean egg count of 422 eggs female⁻¹ from the 12 pots containing mothers with egg batches, it seems that *O. pallidus* lay a large proportion of the available eggs.

Fecundity was positively correlated with somatic weight, and was also influenced by seasonal temperature changes, with fecundity ~10% higher during summer/autumn than during winter/spring. This coincides with the optimal spawning period identified in this study and the general observation of increased growth at warmer temperatures (within the natural range of a species) for many octopus species (Forsythe 1993; Cortez et al. 1995; Leporati et al. 2007), which results in size-at-maturity being reached at an earlier age. These trends indicate that *O. pallidus* hatched during summer/autumn may grow faster, mature earlier and have potentially higher fecundity than those hatched during winter/spring.

Continual local fishing pressure appeared to have altered the age and reproductive structure of the female *O. pallidus* population, reflecting size selective fishing mortality, which could lead to smaller sizes at maturity, fecundity, and ultimately recruitment. The magnitude of such effects on a localised holobenthic octopus population is unknown and requires further investigation. However, by avoiding heavy localised fishing pressure, particularly during the optimal spawning periods, and monitoring sex ratios and the size of mature females, the potential for localised population depletion could be minimized.

This is the first study to investigate the relationship between reproductive development and age in a wild population of octopus, demonstrating that reproductive development in females is primarily a size-dependent process and that maturation is reached at a broad range of ages. Maturation is more closely linked to size and the parameters that govern growth, such as temperature and probably also diet. Even though age was not related to maturation, age information still plays an essential and interconnected role by enabling the reliable and accurate determination of growth (Semmens et al. 2004). Hence, this study has supplied the missing factor (age) in our understanding of the population dynamics of *O. pallidus*, and will contribute to the ecological sustainability of the *O. pallidus* fishery.

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