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Spawning and nursery habitat partitioning and movement patterns of *Pagrus auratus* (Sparidae) on the lower west coast of Australia

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Abstract

The ages and lengths of *Pagrus auratus* caught by line fishing in three marine embayments (Owen Anchorage, Cockburn Sound and Warnrbo Sound) and inshore (< 80 m depth) and offshore waters (> 80 m depth) on the lower west coast of Australia (31°45’ to 32°45’ S) were used to infer the movement patterns and habitats occupied by this species at different stages in its life cycle on this coast. These data were supplemented by results obtained by tagging individuals in spawning aggregations in the embayments. 0+ *P. auratus* < 200 mm FL were caught exclusively in the three adjacent embayments. The ages and lengths of immature *P. auratus*, ranging from 1+ (*ca* 200 mm FL) to 5+ years (*ca* 400 mm FL), increased progressively with distance from these embayments. During the spawning period (from September to January), the relative abundances of *P. auratus* with either developing, developed or recently-spent gonads were far greater in the three embayments (91 %) than in either inshore (12 %) or offshore waters (30 %). Some tagged *P. auratus* were recaptured among spawning aggregations in the same embayment during subsequent spawning seasons, while others were recaptured in these embayments outside the spawning period. However, some other tagged individuals were recaptured up to 92 km north, 33 km west and 134 km south outside the spawning period and up to five years after tagging. The results of this study emphasise that the above three adjacent marine embayments constitute important spawning and nursery areas for *P. auratus* and are thus potentially critical for sustaining the stocks of this recreationally and commercially important species on the lower west coast of Australia.

Keywords: *Pagrus auratus*, Sparidae, tagging, movement, spawning aggregation, nursery, embayment.

Running heading: Distributions and movement of *P. auratus* in WA

Introduction

The development of sound management policies for sustaining heavily-fished stocks of a species requires reliable data on various aspects of the life cycle of that species, including their habitats. It is important to determine, however, not only the habitats occupied by such species at different stages in their life cycles, but also the ages, lengths and life cycle stages and times of the year at which any movements occur between habitats. Thus, for example, if the stock of a species is shown to congregate predictably in restricted locations at a certain time of the year, it will be identified as potentially prone to particularly heavy exploitation by fishers at that time. A thorough knowledge of habitat use and migrations of the individuals of a heavily-fished stock is thus required to identify which life cycle stages of that stock and their habitats may require special protection. Finally, information on habitat use and movements is important for developing an ecosystem-based approach to fisheries management and thereby to ensure that ecosystem function in the different habitats is maintained.

Habitat partitioning between life stages, e.g. juveniles and adults, has been reported for many sparids (e.g. Bennett, 1993; Gillanders, 2002; Hesp et al., 2004a). Evidence for connectivity between juvenile and adult habitats is most commonly obtained from differences in the abundance of size and/or age classes in these habitats (Gillanders et al., 2003). The movement patterns of juveniles (0+ and 1+) inferred from this approach would otherwise be difficult to obtain from direct methods, due, for example, to the high levels of mortality and low recapture rates that are associated with traditional dart and anchor tagging of small fish. Mature individuals of many fish species also undergo seasonal movements each year to and from specific locations at the commencement and completion of the spawning period, respectively (e.g. Colin, 2010; Domeier and Colin, 1997; Heyman and Kjerfve, 2008). Seasonal accumulations of mature conspecific fish at specific locations and in significantly higher densities than are found outside the spawning period have been termed spawning aggregations (Domeier and Colin, 1997). The locations where spawning aggregations occur may also act as important nursery areas (Fowler et al., 2005; Hamer et al., 2005).

Pagrus auratus (Forster 1801) is distributed throughout the temperate Indo-Pacific coastal waters of Australia and New Zealand between 18º and 38º S (Paulin, 1990). Throughout its distribution, this species forms a few spawning aggregations (as defined by Domeier and Colin, 1997; Society for the Conservation of Reef Fish Aggregations, www.scrfa.org) in sheltered marine embayments (Coutin et al., 2003; Crossland, 1977; Jackson and Cheng, 2001; McGlennon, 2004; Scott et al., 1993). In Western Australia, these spawning aggregations are typically found in embayments where the geomorphology, hydrology and habitat characteristics facilitate the retention of eggs, larvae and, to a certain extent, juveniles (Doak, 2004 unpublished honours thesis; Lenanton, 1974; Nahas et al., 2003; Wakefield, 2006). The areas where spawning aggregations of *P. auratus* form in South Australia and Victoria also constitute important nursery areas (Fowler et al., 2005; Hamer et al., 2005). For example, Fowler et al. (2005) showed that, in South Australia, the progenies of the spawning aggregations of *P. auratus* in the northern areas of Gulf St Vincent and Spencer Gulf in 1991 remained in those areas for up to the first three years. This strong year class derived from spawning in those gulfs dominated the catches taken along more than 2,000 km of the South Australian coast in at least the year 2000 (Fowler et al., 2005), which demonstrated the importance of such discrete spawning/nursery areas for recruitment and sustainability of broader adult stocks.

Tagging studies have shown that the extent to which adult *P. auratus* move varies among populations. For example, individuals of this species can move up to 1,650 km in a northerly direction along the lower east coast of Australia (Sanders, 1974), whereas, those of the three stocks of *P. auratus* in the inner gulfs of Shark Bay in Western Australia (ca 26º S) remain in the same area, with the majority moving < 20 km from their location of release (Moran et al., 2003). The extent of the movements undertaken by the individuals of a given population of *P. auratus* thus presumably represents the degree to which the various life cycle stages are adapted to a given environment (Moran et al., 2003).

Pagrus auratus forms spawning aggregations during the austral spring/summer in three adjacent marine embayments on the lower west of Australia, i.e. Owen Anchorage, Cockburn Sound and Warnbro Sound (Fig. 1), but do not apparently spawn in the waters immediately to the west (Wakefield, 2010). The geomorphology of Cockburn and Warnbro Sounds and the prevailing south-westerly winds during spring/summer result in a counter-clockwise gyre, which coincides with the spawning period of *P. auratus* and facilitates the retention of eggs and larvae in these embayments during this period (Wakefield, 2010). This suggests that these relatively small, discrete embayments are potentially an important source of recruitment for nearby adult stocks along the lower west coast of Australia.

This study compares the length and age compositions of *P. auratus* in the three marine embayments (and particularly Cockburn and Warnbro Sounds, in which the spawning aggregations are by far the largest) with those in the nearshore shallow (< 80 m depth) and offshore deeper (> 80 m) areas. These comparisons were used to determine whether habitat partitioning by *P. auratus* occurs in this region during the year and at different stages of their life cycle. Particular attention was paid to ascertaining the relative abundance of juvenile and mature *P. auratus* in all areas to gain an understanding of the importance of the three embayments as spawning and nursery areas for *P. auratus*. Finally, a mark-recapture tagging program was undertaken at known spawning aggregation locations (Cockburn and Warnbro Sounds) during the spawning period, in an attempt to determine the directions and distances that adult *P. auratus* might move from such locations.

Methods

Sample collection and measurements

Samples of *Pagrus auratus* were collected from 2002 to 2006 from three areas between *ca* 31°45’ and 32°45’ S on the lower west coast of Western Australia (Fig. 1). The offshore and inshore areas were located at depths > and < 80 m, respectively, and were situated immediately west of the marine embayments area which comprised Owen Anchorage, Cockburn Sound and Warnbro Sound (Fig. 1). These marine embayments have been identified previously as locations where spawning aggregations of *P. auratus* (Wakefield, 2006) and assemblages of 0+ juveniles (Lenanton, 1974) occur each year.

Pagrus auratus was caught by line fishing from either research vessels or recreational charter vessels with research staff onboard who were permitted to keep fish less than the minimum legal length (410 mm total length at that time). This sampling, which was undertaken at least monthly from April 2003 to March 2005, was not accompanied by the tagging of fish (described later). Although fishing effort was not quantified, the sample sizes of *P. auratus* were sufficient to determine the proportions of the different life history stages in each area in all months. The same range of hook sizes and variety of rig types, which were known collectively to catch a large size range of *P. auratus* (Otway and Craig, 1993), were used on each sampling occasion. *Pagrus auratus* caught from research vessels were later processed in the laboratory, while those caught from recreational charter vessels were processed onboard during each trip. The fork length (FL) of each *P. auratus* was measured to the nearest 1 mm. The two sagittal otoliths were removed from each fish, cleaned and stored in paper envelopes, and the macroscopic appearance of the gonads were used to sex each fish and to determine its stage of development (Table 1).

Treatment of otoliths

The right otolith of each fish was embedded in epoxy resin and, using a slow speed saw (Buehler Ltd.) with a diamond tipped saw blade, sectioned transversely through its primordium, perpendicular to the sulcus acusticus. The sections were mounted on a glass microscope slide with a cover slip using casting resin.

The opaque zones in each otolith section were counted under reflected light at 20 to 40 times magnification, without any knowledge of the length of the fish or its date of capture. The first opaque zone was easily distinguished, as its formation resulted in the development of an inflection point in the Subcupular Meshwork Fibre zone (Francis et al., 1992).

A single opaque zone has previously been shown to form annually in the otoliths of *P. auratus* from the lower west coast of Australia (Wakefield, 2006). Thus, the age of each

P. auratus on its date of capture was estimated using a combination of an average birth date and the number of opaque zones in its otolith. An average birth date of 1 November was chosen because it represented the approximate peak time of spawning derived previously from the trends exhibited throughout the year by mean monthly values for gonadosomatic indices and the proportions of mature fish in samples collected from the lower west coast of Australia (Wakefield, 2006). These trends in gonadal variables demonstrated that *P. auratus* spawn from spring to mid-summer, *i.e.* from September to January each year (Wakefield, 2006).

Juvenile habitat partitioning

The differences between the abundances of juvenile *P. auratus* in the marine embayments and the inshore and offshore areas were described using length and age distributions up to the minimum length and age at which a fish was recorded with mature gonads (stages II-V, Table 1), i.e. 320 mm FL and 3.74 yr. The proportions of juveniles at a given fork length in the marine embayments, i.e. $P_{L,embayments}$, compared with those in areas outside were calculated using a reparameterised form of the logistic equation (Hesp et al., 2004b; Punt and Kennedy, 1997),

$$P_{L,embayments} = 1 - \left\{ 1 + \exp\left[-\ln(19) \frac{(L - L_{50})}{(L_{95} - L_{50})} \right] \right\}^{-1},$$

where the parameters L_{50} and L_{95} represent the estimated lengths at which 50 and 95 % of *P. auratus* were present in the marine embayments, respectively. The L_{50} and L_{95} values and their 95 % confidence intervals were determined by bootstrapping, where estimates were obtained from the analysis of data sets produced by random resampling, with replacement, of each data assemblage to generate 1000 estimates of the parameters of the logistic equation. The parameters for the reparameterised logistic equation were calculated as the median of the 1000 bootstrap estimates of each length class. Estimates of the proportions of juvenile *P. auratus* at a given age in the marine embayments, i.e. $P_{A,embayments}$, compared to outside areas were calculated using the same equation, but with A_{50} and A_{95} substituted for L_{50} and L_{95}, respectively.

Tagging study

Pagrus auratus caught in spawning aggregations in Cockburn Sound and, to a lesser extent, Warnbro Sound were tagged in each year between 2003 and 2008. This study is restricted to recapture data recorded up to September 2009. Each tag had a unique identification number, the name of the responsible governing organisation, ‘FISHERIES WA’, and a free-call phone number to report recaptures. A reward was offered for reporting recaptures and was stated on the tag as ‘REWARD – MEASURE’. The tagging program was advertised through multi-media sources. Tags were 9 cm in length and constructed of yellow plastic with a large dart tip (type PDA, Hallprint Australia Pty Ltd). Tags were inserted with a hollow needle through the dorsal musculature and locked behind the pterygiophore bones approximately 1 to 2 cm below the base of the dorsal fin. Two tags were inserted in the majority of *P. auratus* to increase the likelihood of being able to identify recaptured individuals in case of tag loss, and to estimate rates of such losses. Previous studies using dart tags and identical tag insertion methods have demonstrated that tagging did not have a detrimental influence on the survival and growth of *P. auratus* elsewhere (McGlennon and Partington, 1997; Quartararo and Kearney, 1996).

Results

Length and age compositions

A total of 837 *P. auratus* were collected (not including tagged fish) ranging from 68 to 980 mm FL (Table 2). The majority of *P. auratus* caught in the offshore area were between 300 and 450 mm FL, with a prominent modal length class at 375-399 mm FL (Fig. 2). In contrast, the samples caught in the inshore area contained a substantial number of fish with FL < 300 mm, with no conspicuous mode in the length-frequency composition. The marine embayments essentially contained fish encompassing the entire length range of *P. auratus* (Fig. 2) and was the only area where fish < 200 mm FL were caught. However, in contrast to the situation in offshore and inshore waters, the fish between 300 and 400 mm FL, which represented fish approaching maturity, were poorly represented in this area (Fig. 2). Further, the length-frequency distribution in the marine embayments contained a prominent mode at *ca* 600 to 800 mm FL, representing the majority of mature individuals caught during this study (Fig. 2).

The majority of *P. auratus* in the marine embayments belonged to the 0-1+ or 5-12+ age classes (Fig. 3). In contrast, the majority of fish in both inshore and offshore areas belonged to the 2-6+ age classes, producing modal age classes of 3+ and 4+ years, respectively (Fig. 3).

All *P. auratus* < 200 mm FL were caught in the marine embayments (Figs 2 & 4). The percentage contribution of individuals caught in the marine embayments to the total catch from all areas declined progressively from 100 % in the 150-199 mm FL class to 5.4 % in the 300-349 mm FL class (Fig. 4). This marked decline in the proportions of juveniles in the marine embayments was reflected in the logistic parameter L_{50} and L_{95} values of 251 and 322 mm FL, respectively (Fig. 4). The proportions of *P. auratus* in the marine embayments then increased progressively to > 90 % in all length classes from 600 to 849 mm FL (Fig. 4).

The above trends exhibited by the prevalence of successive length classes of *P. auratus* in the marine embayments were paralleled by those of the age classes. Thus, the proportion of juveniles caught in the marine embayments declined from 100 % in the 0+ age class to ca 50 % at two years of age and 5 % by three years of age, i.e. A_{50} and A_{95} of 1.9 and 2.9 yr, respectively (Fig. 4). All 1+ *P. auratus* were either caught in the marine embayments or inshore areas (Fig. 4), with the youngest *P. auratus* caught in the offshore area being 2.2 yr. The lowest percentage contribution to the catches of *P. auratus* in the embayments was 5.4 % in the 4+ age class, with ca 70 % of this age class being recorded in the offshore area (Fig. 4). The percentage contribution to the catches in the embayments increased progressively after the 4+ age class, with fish from this area representing ≥ 80 % in the majority of age classes above 7+ (Fig. 4).

The trends exhibited by monthly length-frequency distributions emphasised that very few *P. auratus* > 200 mm FL were caught in the marine embayments between March and July, but that the numbers of such fish increased markedly after August when spawning commenced, and declined in January when spawning ceased (Fig. 5). Juveniles < 250 mm FL were caught in the marine embayments in several months. Substantial numbers of *P. auratus* between 250 and 500 mm FL were caught outside the embayments in all months (Fig. 5).

The proportions of *P. auratus* in spawning condition (*i.e.* with gonads at stages II to V, Table 1) between September and January, when spawning occurs, was greatest in the three adjacent embayments (91 %) than in offshore waters immediately west at depths > 80 m, i.e. 12 %, and in inshore waters < 80 m depth (, i.e. 30 %,Fig. 6). Thus, although *P. auratus* in spawning condition were caught outside the embayments, catches in that location were dominated by smaller, immature individuals (Fig. 6). In contrast, essentially all *P. auratus* > 325 mm FL in catches from the embayments during the spawning months of September to January possessed gonads that were developing (stage II), developed (stages III), spawning (stage IV) or had recently spawned (stage V, Fig. 6). The lengths of the majority of fish caught in the embayments during the spawning period in each year from 2003 to 2008 were between 550 and 800 mm FL (Fig. 6), a length range that was poorly represented in the samples from the other two areas at this time of year (Fig. 6).

Fish recaptures

The lengths of the 777 *P. auratus* that were tagged and released in Cockburn and Warnbro Sounds between September and December of 2003 to 2009, *i.e.* during seven successive spawning seasons, ranged from 355 to 920 mm FL. Forty-nine of these tagged fish were reported to have been recaptured (6.3 %, Table 3), with their times at liberty ranging from 4 to 1,827 days (*ca* 5 yr). All but 11 of these fish were recaptured in Cockburn Sound. The longest distances moved by these 11 exceptions were 92 km to the north, *ca* 35 km to the west and 125 and 134 km to the south and southwest, respectively (Fig. 1). All but one of these eleven *P. auratus* were re-caught during non-spawning months, with the single exception originally tagged in October 2006 and re-caught 51 days later, *i.e.* in December, south-east of Rottnest Island. The greatest movement northwards (92 km) was that exhibited by a mature fish of 832 mm FL, when tagged in October 2003 in Cockburn Sound and recaptured 454 days later in January

2005. The greatest movement southwards (134 km) was that exhibited by a mature fish of 783 mm FL, which was tagged in October 2008 in Cockburn Sound and recaptured 231 days later in June 2009.

The 38 *P. auratus*, which were recaptured in Cockburn Sound, comprised 12 that were caught in the spawning season in which they were tagged and 12 that were caught in spawning periods subsequent to that of their tagging and release. The remaining 14 were caught in Cockburn Sound during non-spawning months. A total of 530 of the 777 tagged *P. auratus* had two tags inserted. A total of 31 of these fish were recaptured, 11 of which had lost one tag. Due to the low number of recaptures of double-tagged *P. auratus*, the tag shedding rates with respect to time at liberty and a taggers ability to insert tags was uncertain.

Discussion

The data collected during this study showed that the distribution of *P. auratus* between *ca* 31°45’ and 32°45’ S on the lower west coast of Western Australia varied with life cycle stage. Within these latitudes, the coastal marine embayments of Cockburn Sound, Warnbro Sound and Owen Anchorage were found clearly to constitute nursery and spawning areas for this species. The monthly length- and age-frequency distributions demonstrated that *P. auratus* use these embayments as a nursery area during the first two years of life. This finding is consistent with the results of Lenanton (1974), who collected small (< 150 mm FL) and young (< ca 15 months old) *P. auratus* by trawling over soft substrates in Cockburn Sound. Studies of *P. auratus* in New Zealand and south-eastern Australia also found that the abundance of juveniles was relatively high in sheltered inshore areas (e.g. Francis, 1995; Hamer and Jenkins, 2004; Paul and Tarring, 1980). In addition, two recent studies on the age-related elemental profiles of otoliths showed that *P. auratus* collected over a large stretch of coast, i.e. 700 km in Victoria and > 2000 km in South Australia, could be linked to one or two points of origin (nursery areas) in coastal marine embayments (Fowler et al., 2005; Hamer et al., 2005). This highlights the importance of discrete nursery areas for *P. auratus*, and in Western Australia could apply to these three adjacent marine embayments (between 32°15' and 32°40'S). In contrast, two tagging studies of *P. auratus* that targeted stocks in large sub-tropical marine embayments on the east and west coasts of Australia found that there was limited or no exchange of juveniles and adults between these bays and outside waters (Moran et al., 2003; Sumpton et al., 2003). This suggests that these two subtropical embayments provide the necessary resources (e.g. habitat and prey) to support the full life cycle of *P. auratus* (see Ross, 1986).

In the case of immature *P. auratus* on the lower west coast of Australia, i.e. those with lengths < L_{50} of 488-505 mm FL and A_{50} of 5.6-5.7 years at maturity (Wakefield, 2006), their lengths and ages increased progressively from within to immediately outside the embayments (< 80 m) and then to the area further offshore (> 80 m). This increase in length and age with distance west of the embayments and prior to maturation indicates dispersal from a nursery habitat. It is thus concluded that the three adjacent marine embayments constitute important nursery areas, at least between 32°15' and 32°40'S on the lower west coast of Australia. The increase in size and age from shallow, inshore to deeper, offshore waters parallels the trends exhibited by other sparids, including *P. auratus* in the East Cape region of New Zealand (Paul and Tarring, 1980), *Rhabdosargus sarba* in Western Australia (Hesp et al., 2004a) and *Argyrozona argyrozona* in South Africa (Griffiths and Wilke, 2002).

As the water circulation in Cockburn and Warnbro Sounds during the spawning period of *P. auratus* facilitates the retention of eggs and larvae in those embayments (Wakefield, 2010) and 0+ fish < 200 mm FL were found exclusively in these embayments, the period and mode of dispersal for this species on the lower west coast of Australia appears to be that derived from movement of individuals from these embayments at ca 2-4 years of age and thus prior to reaching sexual maturity (Wakefield, 2006). Fowler et al. (2005) found that, in South Australia, *P. auratus* moved considerable distances between the ages of 2-5 years, which also represents its sub-adult stage in that region and is consistent with the movements inferred from length and age compositions in this study.

During the spawning season, the relative abundances of *P. auratus* $\geq L_{50}$ at maturity of 505 mm FL females and 488 mm FL for males (Wakefield, 2006), were far greater in the marine embayments than in surrounding oceanic waters. As large numbers of large fish were not present, however, in these embayments after spawning had been completed, the majority of *P. auratus* that had aggregated and spawned in marine embayments had apparently moved back into inshore and offshore waters. This conclusion is consistent with tag-recapture data, which demonstrated that, at least some but not all *P. auratus*, underwent such a movement. The relatively low numbers of large fish (> 600 mm FL) in all areas during non-spawning months (February to August), suggest that fish belonging to the spawning aggregations in the marine embayments undergo a wide dispersal to surrounding waters and become less vulnerable to capture throughout these locations and months. Such movement patterns associated with spawning and non-spawning periods parallel those of *P. auratus* off the mid-west coast of Australia (near Koks, Bernier and Dorre Islands in the waters outside of Shark Bay), approximately 620 km to the north. At those latitudes, adults move from surrounding waters of the continental shelf to form a few spawning aggregations on the inshore reefs during the spawning season (Moran et al., 2003). Tag-recapture results from the current study demonstrated that the home range of *P. auratus* during non-spawning months extended ca 100 km north to 31º25’ S (south of Lancelin, Fig. 1), ca 135 km south to 33º20’ S (west of Bunbury) and ca 35 km west from Cockburn and Warnbro Sounds.

Fowler et al. (2005) found that, after ca five years of age, the individuals of *P. auratus* in South Australia remained in the regions to which they had moved. However, *P. auratus* from that study were collected over more than 2000 km of coast, whereas, in the present study, the distance from the coastal marine embayments to the western border of the study area was only ca 65 km and the latitudinal range sampled was only ca 110 km. Thus, the proportion of young *P. auratus* that move beyond the study area, after leaving the coastal marine embayments where they were spawned, and the distance along the Western Australian coast they travel is not well understood.

The movements inferred by the length and age distributions and tagging results would benefit from further investigation using the elemental profiles of otoliths of *P. auratus* collected over a larger range of coast, similar to the approaches used by Fowler et al. (2005) and Hamer et al. (2005). This would help identify the extent to which *P. auratus* from the three adjacent marine embayments recruit to adult stocks along the west coast of Australia. Nonetheless, the present study has demonstrated that the three adjacent marine embayments of Owen Anchorage, Cockburn Sound and Warnbro Sound constitute important spawning and nursery areas for *P. auratus*. Based on available data, the importance of these embayments as a recruitment source for *P. auratus* stocks should not be underestimated, considering there is a paucity of similar nearshore marine embayments and hence potential recruitment sources along the essentially linear lower west coast of Australia. It is thus important for the sustainability of at least nearby adult stocks to maintain adequate biomass levels associated with spawning aggregations in those embayments. Furthermore, knowledge of the current status of those stocks would benefit from annual monitoring of both spawning aggregation biomass and subsequent juvenile recruitment strength. This should be undertaken in conjunction with existing monitoring of age structures and rates of fishing mortality at the broader scale, which are currently the main method used to assess stock status (see Wise et al., 2007). However, the present study has revealed that such monitoring would need to consider both temporal and spatial effects of the movement of individuals of this species on sampled age structures, to ensure that they are representative of the populations along the lower west coast of Australia. It is also vital that habitats within these nursery embayments are protected in order to maintain adequate recruitment success to nearby exploited adult fisheries for this species. This is particularly the case with Cockburn Sound, as this embayment has a history of ecosystem changes resulting from intense human use (e.g. Kendrick et al., 2002), with further large-scale development and dredging proposed, given that larvae of *P. auratus* are susceptible to gill-fouling caused by increased sedimentation in the water column (Partridge and Michael, 2010).

In summary, this study has demonstrated that three embayments on the lower west coast of Australia constitute very important spawning grounds and nursery areas for *P. auratus* in this region. From a fisheries perspective, this makes the stock of this species particularly susceptible to the effects of recreational and commercial fishing and habitat degradation in the embayments. This point was recognised by the Department of Fisheries Western Australia and led to the closure of the embayments to fishing for *P. auratus* from October to January, which encompasses the majority of its spawning period. Furthermore, the data produced during the study has led to the development of a more sophisticated and ongoing approach to determining the status of the stock within and outside the embayments. Our results have also highlighted the need to guard against deleterious anthropogenic changes to the three embayments as these habitats are so important to *P. auratus* and thus apparently required to sustain the stocks of this species at a level that will maintain the structure of the ecosystem of which this species is a part.

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Table and Figure captions

Table 1. Macroscopic characteristics in the appearance of ovaries and testes of *Pagrus auratus*.

Table 2. Sample sizes and fork lengths (FL, mm) of *Pagrus auratus* caught by hook and line in each of the three areas.

Table 3. Numbers of *Pagrus auratus* tagged and recaptured in each year.

Figure 1. Map showing the three sampling areas, *i.e.* (1) offshore (depth > 80 m), (2) inshore (depth < 80 m) and (3) marine embayments (black areas, *i.e.* Owen Anchorage, Cockburn Sound & Warnbro Sound) and the recapture locations of snapper that had been tagged in Cockburn Sound (dashed lines with circles).

Figure 2. Length-frequency distributions of *Pagrus auratus* that were retained (grey bars) or tagged and released (white bars, embayments only) in sequential 25 mm length classes from the three areas (sample sizes given).

Figure 3. Age-frequency distributions for *Pagrus auratus* in successive age classes up to 15+ years caught in each of the three areas. The solid line represents the age at 50 % maturity (A_{50}) ± 95 % CI (dashed lines) for females and males (Wakefield, 2006).

Figure 4. Cumulative frequency (%) contributions made by the numbers of *Pagrus auratus* in successive length (excludes tagged fish) and age classes in samples obtained from the embayments (dark grey bars), inshore (light grey bars) and offshore (white bars) areas. Sample sizes are given for each length and age class (above). Lines represent the expected percentage (± 95 % CI) of juvenile *P. auratus* in the marine embayments (solid) as determined from logistic regression analysis.

Figure 5. Monthly length-frequency distributions for *Pagrus auratus* in marine embayments (black bars, excludes tagged fish) and the other areas combined (grey bars).

Figure 6. Length-frequency distributions of immature (gonad stage I, grey bars) and mature (gonad stages II-V, black bars) *Pagrus auratus* in sequential 25 mm length classes caught during the spawning period, *i.e.* September to January, in each of the three areas. Lines represent the length at 50 % maturity (L_{50}) for females (dashed) and males (solid) of 505 and 488 mm FL, respectively (Wakefield, 2006).

Table 1.

Stage	Ovaries	Testes
I. Immature / Resting	Occupy up to one half of length of ventral cavity. Cylindrical, blood capillaries visible and pink to orange.	Occupy up to one half of ventral cavity. Flat and white.
II. Developing	Occupy up to two thirds of ventral cavity. Blood capillaries and oocytes visible.	Occupy up to two thirds of ventral cavity and white colour more apparent.
III. Developed	Occupy full length of ventral cavity. Oocytes clearly visible but not hydrated. Blood capillaries more conspicuous.	Testis much larger occupying up to full length of ventral cavity. No milt discharged when slight pressure is applied to lobes or abdomen.
IV. Ripe / Spawning	Similar in size to stage III. Hydrated oocytes (translucent) visible throughout ovarian lobes or concentrated in oviduct.	Similar in size to stage III. Milt discharged when slight pressure is applied to lobes or abdomen.
V. Spent	Ovaries reduced in size, flaccid and red in areas.	Testes reduced in size, flaccid and red in areas.

Table 2.

Area	***n***	**Fork length (mm)**			***n***	**Age (years)**		
		Range	**Mean**	**SD**		**Range**	**Mean**	**SD**
Offshore								
Retained	337	245 - 869	402	89	274	2.2 - 28.8	5.18	2.98
Inshore								
Retained	227	202 - 980	414	124	193	1.5 - 11.5	4.43	1.81
Marine embayments								
Retained	273	68 - 901	444	245	273	0.3 - 24.0	6.13	4.31
Tagged	777	355 - 920	664	104				

n = Sample size, SD = Standard deviation

Table 3.

			Tagged in						
		Year	*2003* *(from Oct)*	*2004*	*2005*	*2006*	*2007*	*2008*	*Total*
	Year	**Total**	**54**	**277**	**143**	**120**	**22**	**161**	**777**
Recaptured in	*2003* *(from Oct)*	**2**	2						
	2004	**8**	4	4					
	2005	**9**	3	5	1				
	2006	**17**	1	9	4	3			
	2007	**5**	0	1	2	2	0		
	2008	**5**	0	2	1	0	0	2	
	2009 *(to Sep)*	**3**	0	1	0	0	0	2	
	Total	**49**							
	Recapture rate (%)		18.52	7.94	5.59	4.17	0	2.48	

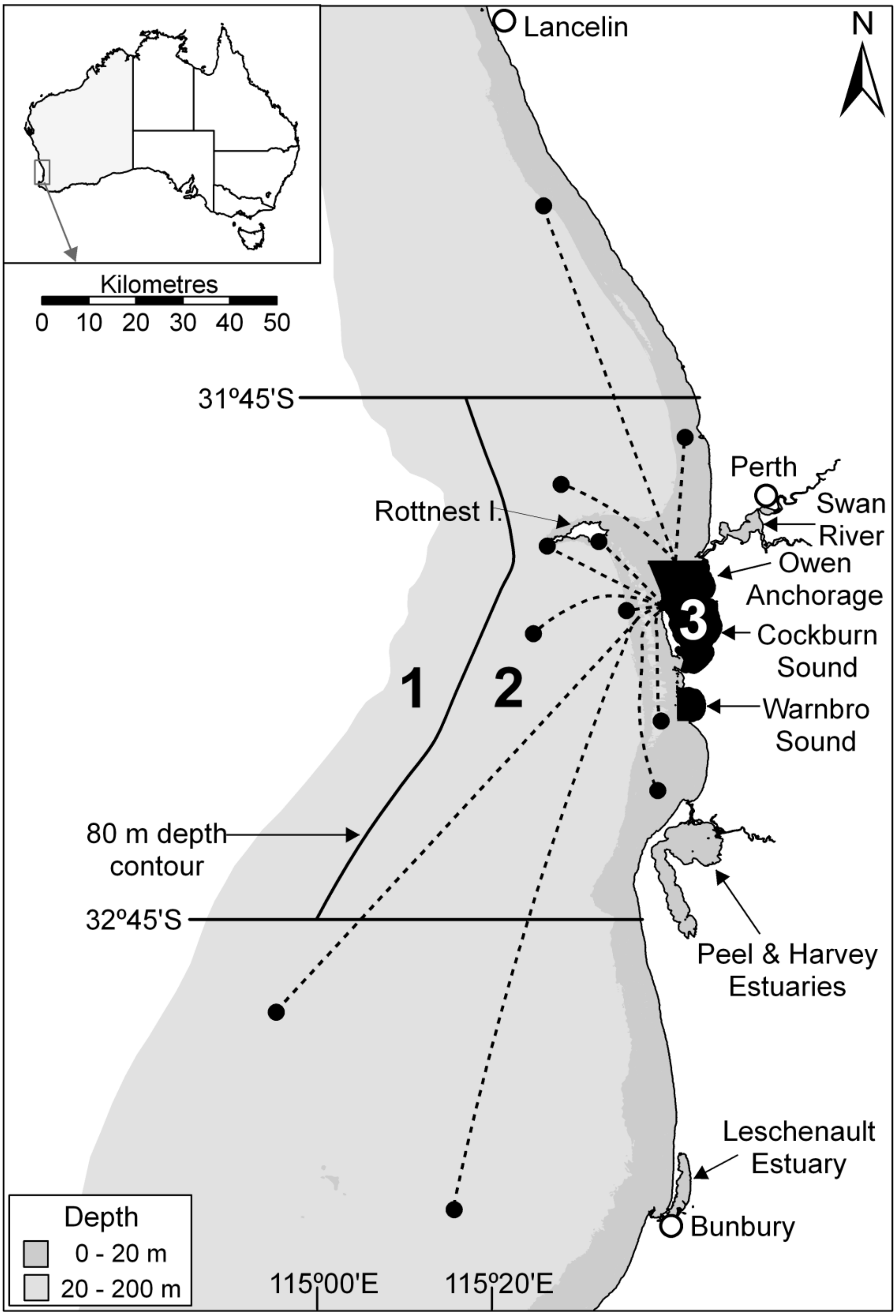
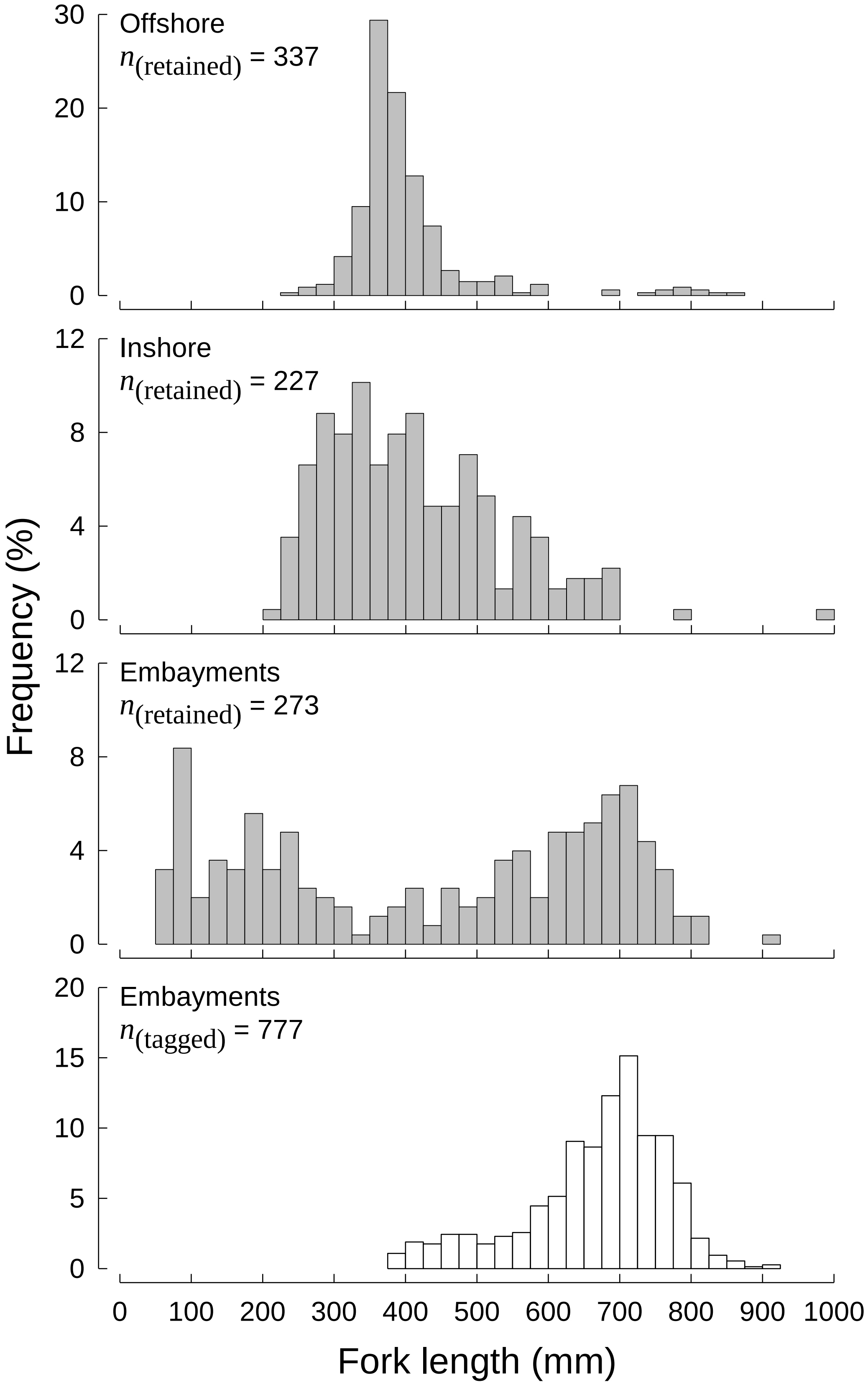
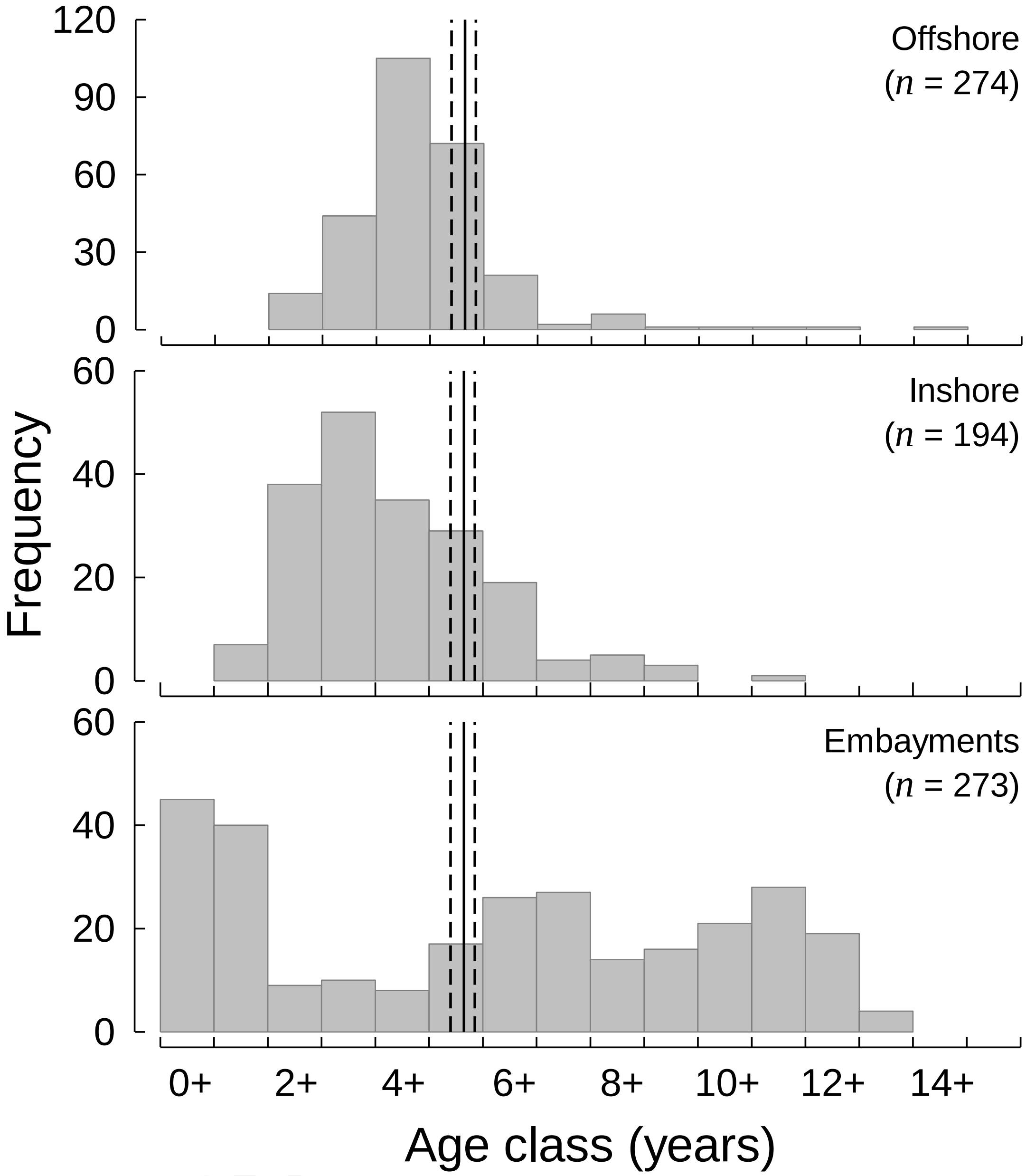

Lancelin
N
Kilometres
0 10 20 30 40 50
31º45'S
Perth
Swan River
Rottnest I.
Owen Anchorage
3
Cockburn Sound
1
2
Warnbro Sound
80 m depth contour
32º45'S
Peel & Harvey Estuaries
Leschenault Estuary
Bunbury
Depth
0 - 20 m
20 - 200 m
115º00'E
115º20'E

Figure 1.



16
17 **Figure 2.**



120
90
60
30
0
Offshore
(*n* = 274)
60
40
20
0
Inshore
(*n* = 194)
Frequency
60
40
20
0
Embayments
(*n* = 273)
0+
2+
4+
6+
8+
10+
12+
14+
Age class (years)

Figure 3.

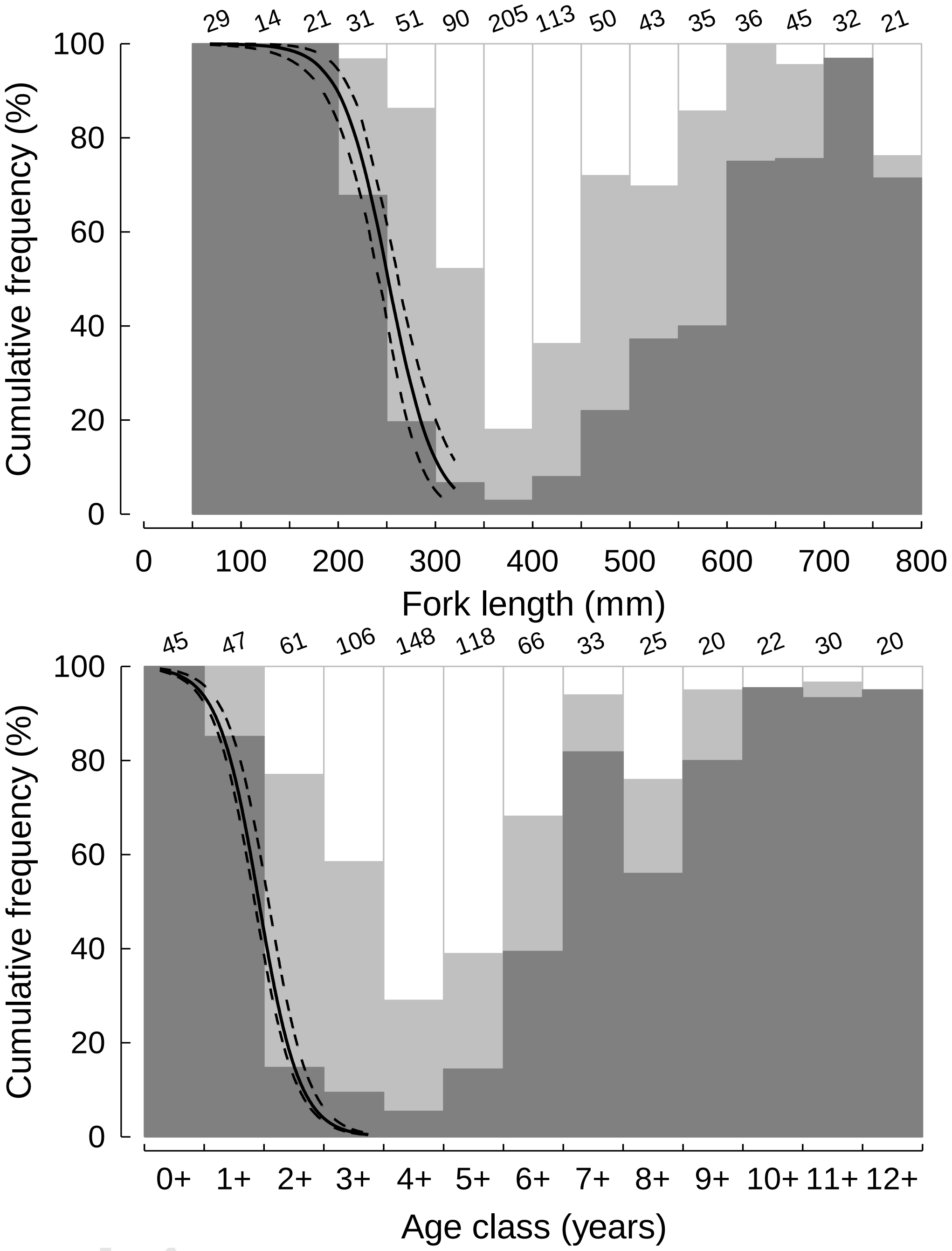
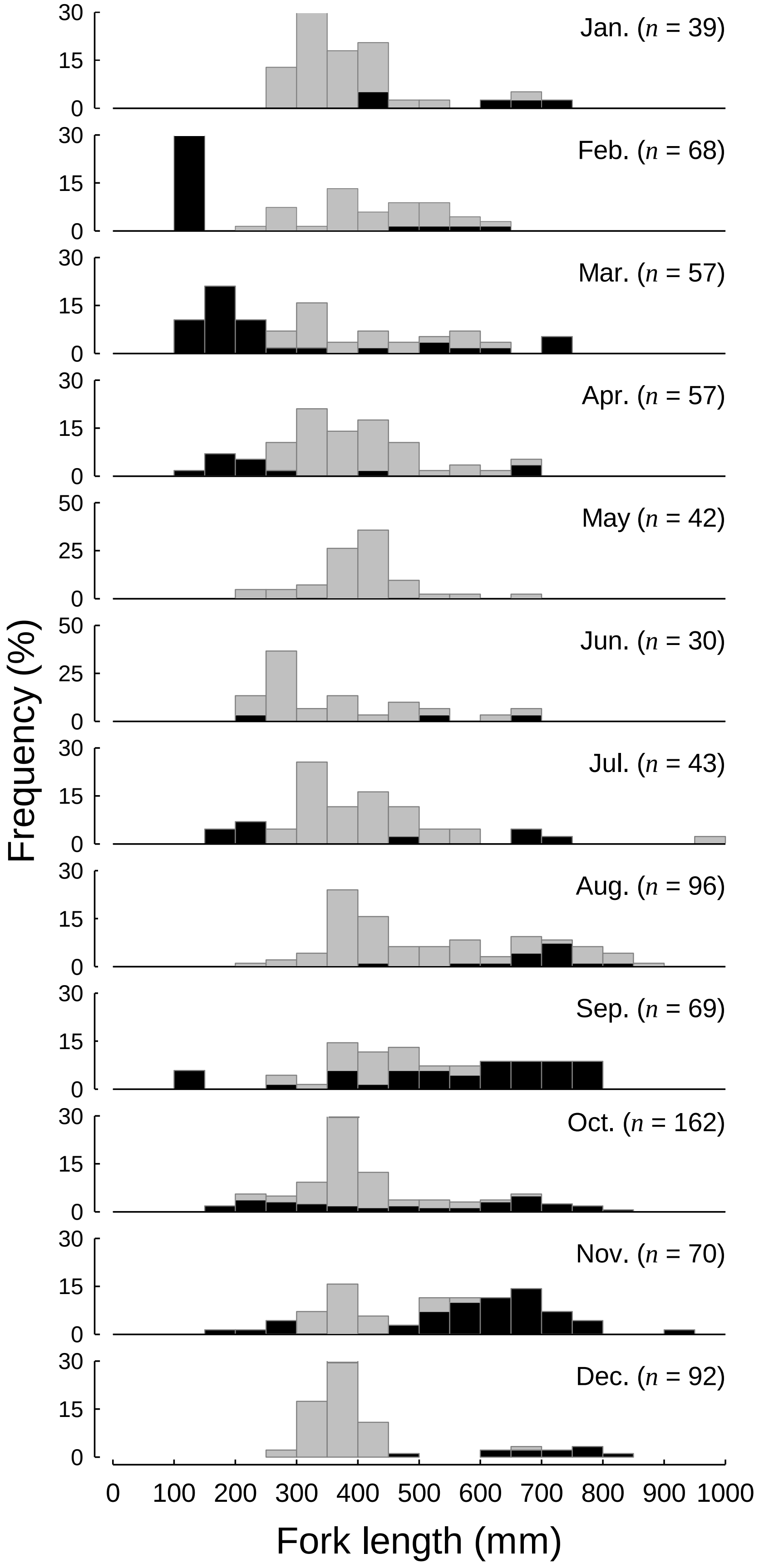
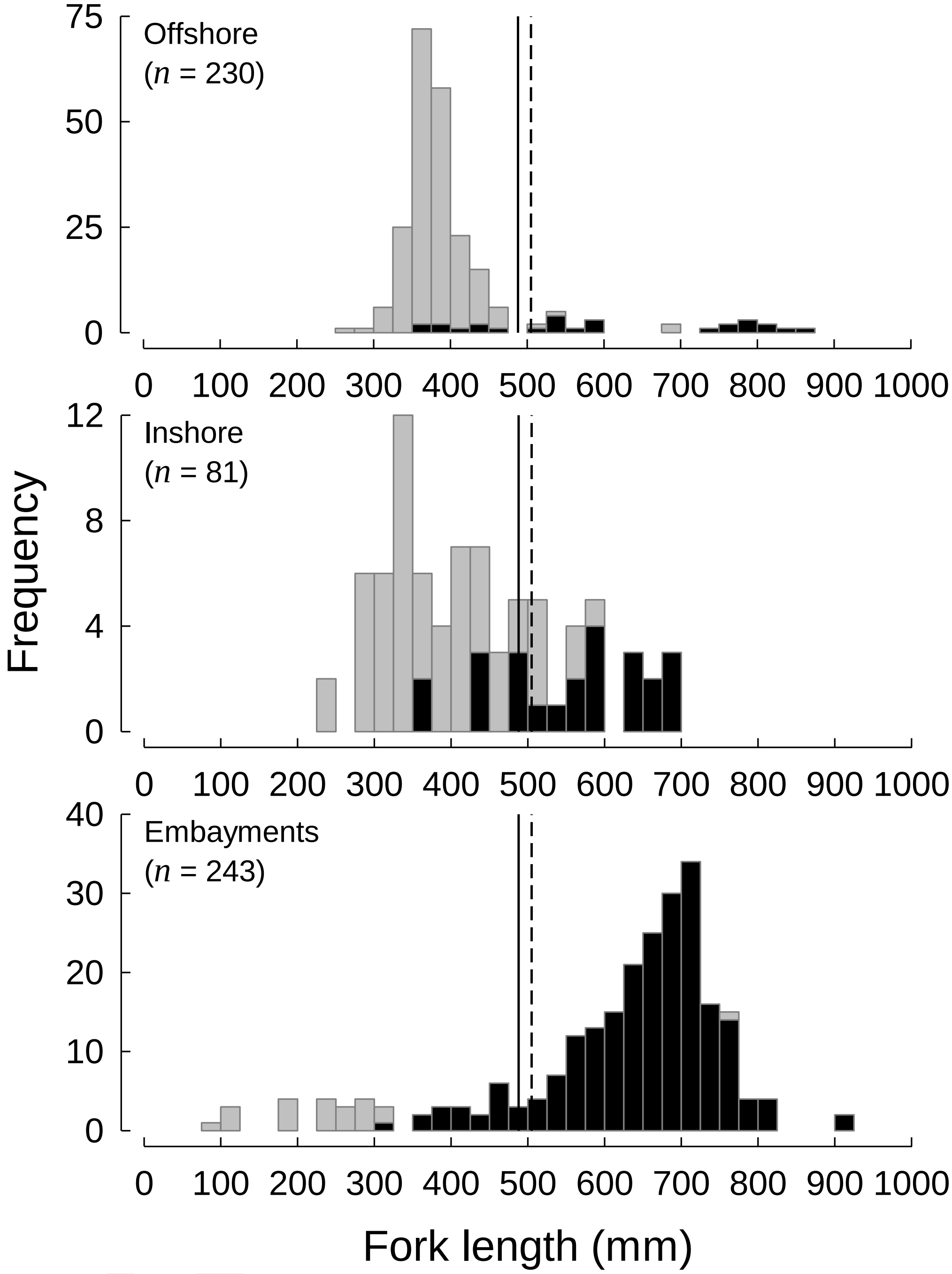

29
14
21
31
51
90
205
113
50
43
35
36
45
32
21
Cumulative frequency (%)
0
20
40
60
80
100
0
100
200
300
400
500
600
700
800
Fork length (mm)
45
47
61
106
148
118
66
33
25
20
22
30
20
Cumulative frequency (%)
0
20
40
60
80
100
0+
1+
2+
3+
4+
5+
6+
7+
8+
9+
10+
11+
12+
Age class (years)

Figure 4.



24

25 **Figure 5**.



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27

28 **Figure 6**.

Highlights

- Habitat partitioning is reported among major life cycle stages of *Pagrus auratus*
- Three metropolitan embayments are crucial for spawning aggregations and juveniles
- Sub-adults occupy deeper offshore waters adjacent to the embayments
- A closure to fishing has been implemented to protect spawning aggregations
- Industrial development in the embayments may influence spawning and recruitment success