Journal of Applied Ichthyology

J. Appl. Ichthyol. 31 (2015), 442–450

ISSN 0175–8659

Received: July 18, 2014
Accepted: September 19, 2014
doi: 10.1111/jai.12703

Spawning, maturity, growth and movement of *Platycephalus fuscus* (Cuvier, 1829) (Platycephalidae): fishery management considerations

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Summary

The dusky flathead (*Platycephalus fuscus*) is an important teleost harvested by recreational and commercial fishers throughout its endemic distribution along eastern Australia. This study indicates that the species has an extended spawning period throughout the austral summer, with females in spawning condition occurring in lower estuarine and coastal waters. Total length (L_{50}) and age (A_{50}) at which 50% (±1 SE) of the population was mature was 31.72 (±1.08) cm TL and 1.22 (±0.44) years for males and 56.75 (±0.60) cm TL and 4.55 (±0.13) years for females. The von Bertalanffy growth parameters differed significantly between sexes; females grew faster and attained a greater maximum TL and age than males. The largest female was 98.5 cm TL (7.5 kg), and the oldest 16 years, whereas the largest male was 61.5 cm TL (1.58 kg) and 11 years of age. A tag-and-release study identified the exchange of sub-adult and mature-sized individuals among estuaries. Determinations of length-based management regulations for the species are compounded by the large gender-based differences in growth and length-at-maturity. Current minimum legal lengths of 30–40 cm TL protect approximately 3–9% of the female spawning population. Alternative management options, including harvest slot sizes, need to be investigated and tested.

Introduction

The teleost family Platycephalidae, commonly referred to as flatheads, contains approximately 65 species from 18 genera, most of which are distributed in the Indian and Pacific oceans (Keenan, 1991; Imamura, 1996). Platycephalids are dorso-ventrally flattened, benthic carnivores (Fairbridge, 1951; Platell and Potter, 1998; Barnes et al., 2011a) that typically occur on soft substrates across a variety of environments ranging from shallow estuarine to deep continental slope waters (Shao and Chen, 1987; Keenan, 1991). Many platycephalid species are exploited in fisheries, especially those that attain large sizes (Shao and Chen, 1987; Bawazeer, 1989; Kailola et al., 1993), yet there is a dearth of biological and demographic information for many species within the family.

The dusky flathead, *Platycephalus fuscus*, is endemic to estuaries, embayments and nearshore coastal waters of Australia's east coast (Keenan, 1991). It is the largest platycephalid, attaining a maximum total length (TL) over 100 cm (Imamura and Knapp, 1997; Gray et al., 2002) and an iconic recreational fishing species that is also prominent in estuarine commercial fisheries (Gray et al., 2002, 2004; Henry and Lyle, 2003; Roelofs et al., 2012). Whilst data are limited, it is generally assumed that the total recreational retained catch of dusky flathead is an order of magnitude greater than the reported total commercial retained catch of approx. 200 tonnes per annum (Henry and Lyle, 2003; Rowling et al., 2010; Roelofs et al., 2012). Concerns over high rates of mortality and exploitation (Gray et al., 2002) and the long-term sustainability of dusky flathead populations have seen several investigations into the development of more selective fishing gear and practice (Broadhurst et al., 2003, 2009; Gray et al., 2005; Butcher et al., 2008) and changes in management strategies (Gray et al., 2004; Roelofs et al., 2012) for the species over the past decade. However, some fundamental, yet vital, demographic and biological parameters for the species have yet to be resolved.

Dusky flathead display gender-related differences in length-at-age and can live for up to 10 years (Gray et al., 2002), a trait typical among platycephalids (Barnes et al., 2011b). Growth has not been described adequately and data concerning particular aspects of the species' reproductive biology, including the length and age at maturity, spawning mode, season and locations, are either ambiguous or unknown. Debate also surrounds whether dusky flathead undertake a protandrous sex change (Dredge, 1976; SPCC, 1981). No published information is available on the movements and population connectivity of the dusky flathead. Such information is required for developing appropriate management strategies for the species (Chateau and Wantiez, 2009; Jakobsen et al., 2009).

In this study we specifically investigate the time of reproductive activity, length and age at sexual maturity, mode of oocyte development and spawning, and test for differences in growth and longevity between sexes of dusky flathead. We also examine large-scale movements and potential population connectivity among estuaries by using a historical tag-recapture study.

Materials and methods

Sampling

Retained commercial catches of dusky flathead were sampled on a regular (mostly monthly) basis for 2 years between 2001 and 2002 from four estuaries: the Clarence River (29.43°S), Wallis Lake (32.17°S), Tuggerah Lake (33.34°S) and Lake Illawarra (34.54°S). Further sampling using a variety of research sampling gear including gillnets, seine nets and angling techniques, was conducted between 2004 and 2006 in the Clarence River, Lake Macquarie (33.09°S), Tuggerah Lake, St Georges Basin (35.19°S) and the Tuross River (36.07°S) to obtain greater representation of the species' entire length range (i.e. not just legal-sized individuals). Dusky flathead were also collected from coastal waters adjacent to the Clarence River aboard commercial prawn trawl vessels between November 2005 and March 2007.

The date and location of capture, TL (nearest 0.1 cm) and total weight (nearest 0.1 g), of each retained dusky flathead was recorded. Fish were dissected for reproductive investigation and sagittal otoliths were removed for age determination.

Reproductive biology

Each retained fish was dissected and its sex determined by macroscopic examination of the gonads (ovaries and testes). When gonads lacked development (i.e. not able to distinguish sex), the fish was classified as juvenile. Macroscopically examined gonads were assigned a reproductive developmental stage based on size, colour and visibility of oocytes (adapted from Scott and Pankhurst, 1992). Female and male stages I and II were considered immature, female stages III–V and male stages III and IV were considered mature, whereas female stage VI and male stage V were spent. The macroscopic staging of females was validated by microscopic examination of a small subset of individuals (see below).

Gonads of each fish were removed and weighed (0.1 g) to calculate a Gonadosomatic Index (GSI): GSI = (gonad weight/total fish weight) $\times$ 100. The timing of reproductive activity was assessed by examining temporal trends in the: (i) peaks and troughs in the mean male and female GSI, and (ii) proportions of each macroscopic gonad stage present in samples. Elevated GSI values were interpreted as indicating reproductive activity.

During periods of observed reproductive activity, fish with gonads staged III–VI were considered mature and capable of spawning during the current reproductive period, whereas individuals staged I and II were considered immature and not capable of spawning during the current reproductive period. The estimated TL and age at which 50% (L_{50} and A_{50}, respectively) of males and females attained reproductive maturity was determined by fitting a logistic regression model using the binomial GLM function in *R* to the proportions of mature (stage III and above) and immature (stage I and II) fish in each 1 cm length category and in each age category. Maturity calculations were determined using samples pooled across all locations and sampling periods.

Histological examination of a selection of preserved stage II, III and IV ovaries was used to determine the development pattern of oocytes and to verify the macroscopic gonad staging of females. Gonad samples were dissected from fixed specimens and treated in an automated tissue processor, with the resulting tissues embedded in paraffin wax and sectioned at 5 μm thickness on a rotary microtome. Sections were deparaffinised, differentiated in acidified alcohol and stained in alcoholic eosin. Histological staging was based on the most advanced oocytes in each ovary section (West, 1990).

Length-at-age and growth

Sectioned sagittal otoliths were used to estimate the age of dusky flathead as they are easier to interpret and also produce more accurate estimates of age than whole otoliths (Gray et al., 2002). One sagittae of each fish was embedded in clear resin and sectioned at approx. 250–300 μm thickness in a transverse plane through the focus using a low speed saw fitted with two diamond blades. Both sides of the resulting thin section were polished on 9 μm lapping film, after which the section was mounted on a standard glass slide and viewed under a binocular microscope (6–25 $\times$ magnification) with reflected light against a black background. Assignment of age of each fish was based on independent counts of completed opaque bands (i.e. number of opaque bands from the sulcus to the outer edge, usually along the line of the sulcus) by at least two readers. Previous analyses of marginal increments demonstrated that the alternate translucent and opaque bands are formed in the otolith structure annually and can be used to accurately estimate age (Gray et al., 2002). The length of fish used for ageing ranged from 5.7 (juvenile) to 61.5 cm TL (male) and 98.5 cm TL (female).

Growth was modelled separately for each sex by fitting the length-at-age data for all locations across all years to the von Bertalanffy growth function (VBGF). Juvenile fish (not assigned a sex) were assigned to both sexes for each analysis. The best-fit VBGF for each sex was determined using non-linear least squares procedures and differences in growth curves between sexes were tested using likelihood ratio (LR) tests (Kimura, 1980; Cerrato, 1990).

The length-weight relationships for both sexes of dusky flathead were calculated using the function: fish weight (g) = $a \times$ fish total length (cm)^b, where a and b are constants. The model parameters a and b were calculated by minimising the sums of squares between the observed and expected values using a solver routine in Excel. Juvenile fish (>10 cm) were assigned to both sexes for each analysis.

Movement

Between 1988 and 1995, a total of 1683 dusky flathead across eleven estuaries were captured (either using a beach-seine net or rod and reel), measured (TL to the nearest 0.5 cm), tagged with a unique numbered plastic T-bar (Hallprint) between the dorsal fin rays and released *in situ*. The TL of tagged fish ranged between 19 and 76.5 cm. Tagging took place year-round in association with commercial fishers (except Botany Bay and Port Hacking), so the time of tagging in a particular estuary was often dependent on the fisher's activity. The tag-release program was highly publicised, with commercial and recreational fishers offered a reward upon the return of tagged fish and he supply of information including where and when the fish was recaptured and, where applicable, re-released. The extent of movements between the points of release and subsequent capture were plotted on a map.

Results

Sample composition

A total of 7790 dusky flathead comprising 394 juveniles, 1752 males and 5644 females ranging from 5.7 to 98.5 cm TL were examined throughout the study. The length composition of samples varied according to sex. Individuals classified as juvenile and not sexed were generally <20 cm TL, whereas males were mostly between 20 and 50 cm TL and females between 20 and 70 cm TL (Fig. 1).

Spawning

Mean male and female GSI values were elevated between September and May and peaked between December and March (Fig. 2a). Maximum GSI value for a male and female was 4.7 and 16.6%, respectively. Based on the macroscopic staging of gonads, the greatest proportion of mature female fish (stage III–stage VI) also occurred between December and March (Fig. 2b). No females and only three males were observed in reproductive condition for the 3 months between June and August. Females with hydrated oocytes and ovulating individuals (Stage V) were collected between November and April from sites in the lower reaches and close to the entrance of the Clarence River, Wallis Lake, Tuggerah Lake, Lake Illawarra and Tuross River. Stage V females were also observed in samples collected in summer in ocean waters offshore from the Clarence River.

The microscopic examination of gonads validated the macroscopic staging of gonads and identified that oocyte development was asynchronous: stage II immature ovaries contained primary growth unyolked oocytes of a variety of sizes; stage III ovaries contained a mixture of unyolked, partially yolked and advanced yolk stage oocytes (Fig. 3); stage IV ovaries contained hydrated oocytes and oocytes in each of the previous stages of development.

Maturity

The length at which 50% ($L_{50} \pm 1$ SE) of individuals sampled in estuaries attained sexual maturity during periods of

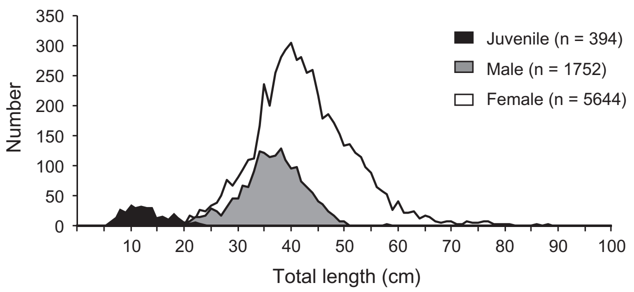

Fig. 1. Length frequency composition of sampled juvenile (n = 394), male (n = 1752) and female (n = 5644) *Platycephalus fuscus*, eastern Australia, 2001–2007

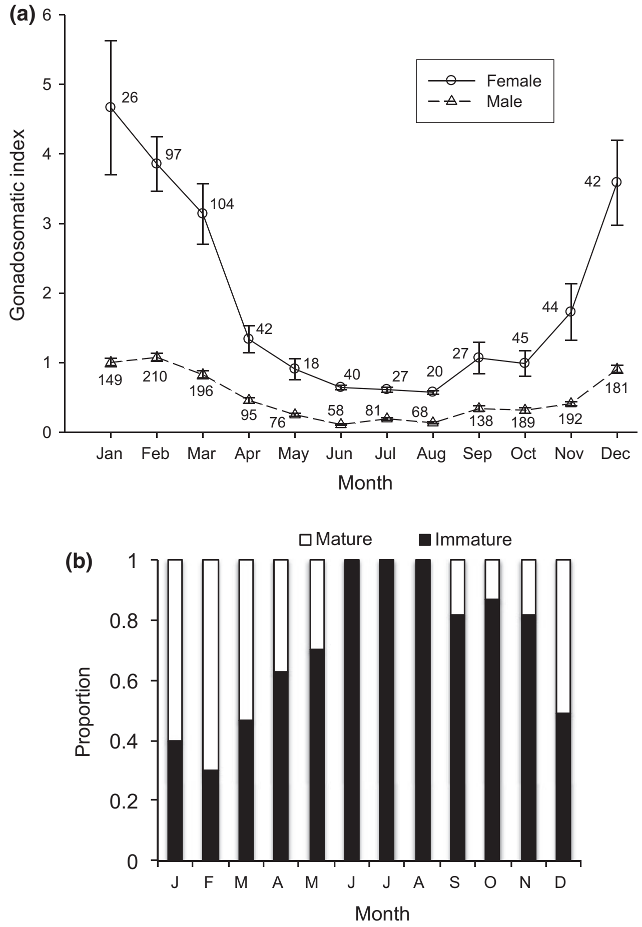

Fig. 2. (a) Mean (±1SE) monthly gonadosomatic indices of male and female *Platycephalus fuscus* equal to or larger than the estimated L_{50}. (b). Proportion of immature and mature female *Platycephalus fuscus* equal to or larger than estimated L_{50}. Data pooled from samples collected in east Australian estuaries, 2001–2007

peak reproductive activity was estimated to be 56.75 ± 0.6 cm TL for female and 31.72 ± 1.08 cm TL for male dusky flathead (Fig. 4). There was considerably more variation among samples for length at maturity for males than for females. The corresponding estimated age at which 50% ($A_{50} \pm 1$ SE) of individuals attained sexual maturity was 4.55 ± 0.13 years for females and 1.22 ± 0.44 years for males (Fig. 5). The smallest observed mature female and male was 22.3 and 18.8 cm TL, respectively.

Ovarian and testicular tissue was never observed together in the same gonad throughout extensive macroscopic (and microscopic) examination, even though 3755 gonad samples were examined from dusky flathead with varying lengths and ages, taken from multiple locations and over several years of sampling.

Length-at-age and growth

The length-weight relationship for male and female dusky flathead (>10 cm TL) was:

Male: Weight (g) = $2.76 \times 10^{-3} \times$ Total Length$^{(3.223)}$; (n = 2087), $r^2 = 0.975$

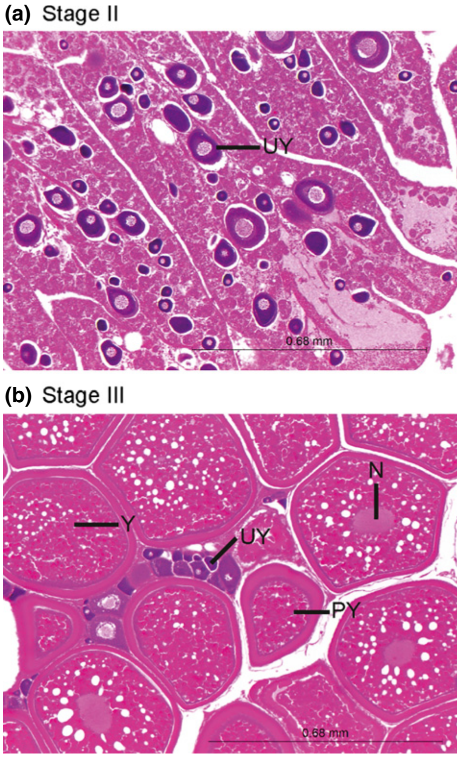

Fig. 3. Photo image of microscopic characteristics, ovary stages II and III, *Platycephalus fuscus*. (a) Stage II: immature ovary containing developing primary growth unyolked (UY) ooctyes; (b) Stage III: mature ovary containing unyolked oocytes, partially yolked (PY) oocytes and advanced yolk (Y) stage oocytes. Nucleoli (N) visible within some oocytes

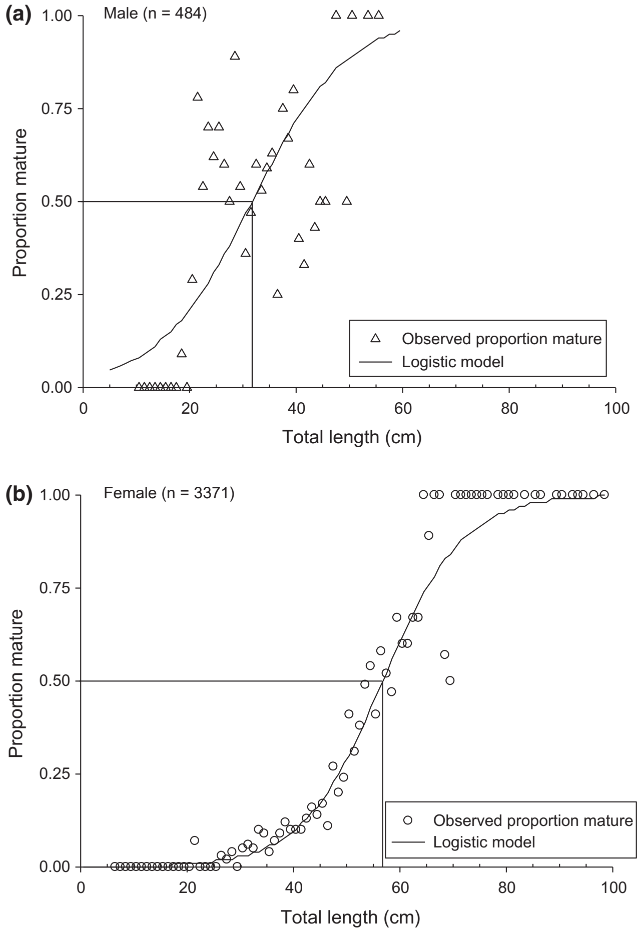

Fig. 4. *Platycephalus fuscus* estimated length at maturity (L_{50}) ($\pm$1SE), sampled from east Australian estuaries, 2001–2007: (a) Male 31.72 $\pm$ 1.08 cm (n = 484), (b) Female 56.75 $\pm$ 0.6 cm (n = 3371)

Female: Weight (g) = 2.09 $\times$ 10^{-3} $\times$ Total Length$^{(3.282)}$; (n = 5906), r^2 = 0.976

There was considerable variation among individuals in length-at-age for both sexes (Fig. 6). The parameter estimates of the von Bertalanffy growth curves differed significantly between sexes ($P < 0.01$). For fish >2 years old, the estimated mean length at age was consistently greater for females than for males. Female *Platycephalus fuscus* grew faster and attained a greater maximum length and age compared to males (Fig. 6). The largest female sampled was 98.5 cm TL, weighing 7.5 kg and an estimated age of 12 years. The oldest female was estimated at 16 years (88.5 cm TL). The largest male sampled was 61.5 cm TL, weighing 1.58 kg and with an estimated age of 11 years.

Movements

A total of 203 (12.1%) of the 1683 dusky flathead tagged was recaptured, but the majority (92.1%) of these reported recaptures were within the estuary of original tagging (Table 1; Fig. 7). Only 16 individuals were recaptured outside the estuary of original release and all but one of these was recaptured north of its release location. The distances relocated by emigrating fish ranged from 10 to 280 km, the largest being between the Clarence River and southern Moreton Bay (Fig. 7). Duration at large of tagged *P. fuscus* ranged from 1 to 1285 days, the longest duration being a fish tagged and recaptured in the Bellinger and Kalang River system.

Discussion

Spawning

The predominant spawning period for dusky flathead was over the austral summer (December through March), although some were in spawning condition as early as September and as late as May. The larvae of *P. fuscus* have also been collected between September and May in estuaries and coastal waters of eastern Australia (Miskiewicz, 1987; Gray and Miskiewicz, 2000). This prolonged (non-winter) timing of spawning is concordant with other platycephalids that typically spawn throughout the months of warmest water temperatures (Bawazeer, 1989; Hyndes et al., 1992).

Ovaries of mature *P. fuscus* contained oocytes at varying stages of development, indicating that individuals likely spawn multiple times throughout each spawning period (West, 1990; Pavlov et al., 2009). This mode of spawning has been observed in other platycephalids (L.M. Barnes, C.A.

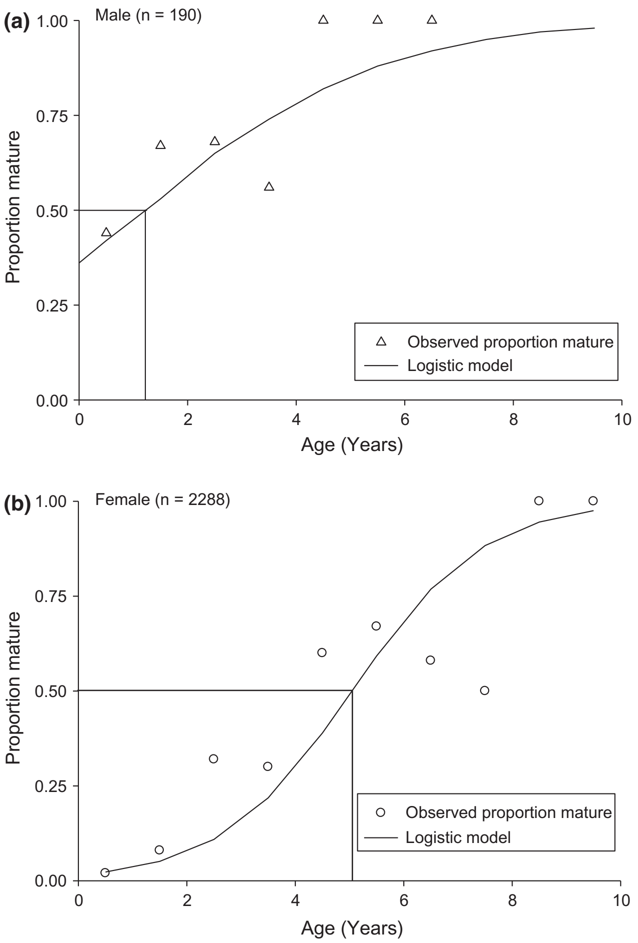

Fig. 5. *Platycephalus fuscus* estimated age at maturity (A_{50}) ($\pm$1SE), sampled from east Australian estuaries, 2001–2007: (a) Male 1.22 $\pm$ 0.44 years (n = 190), (b) Female 4.55 $\pm$ 0.13 years (n = 2288)

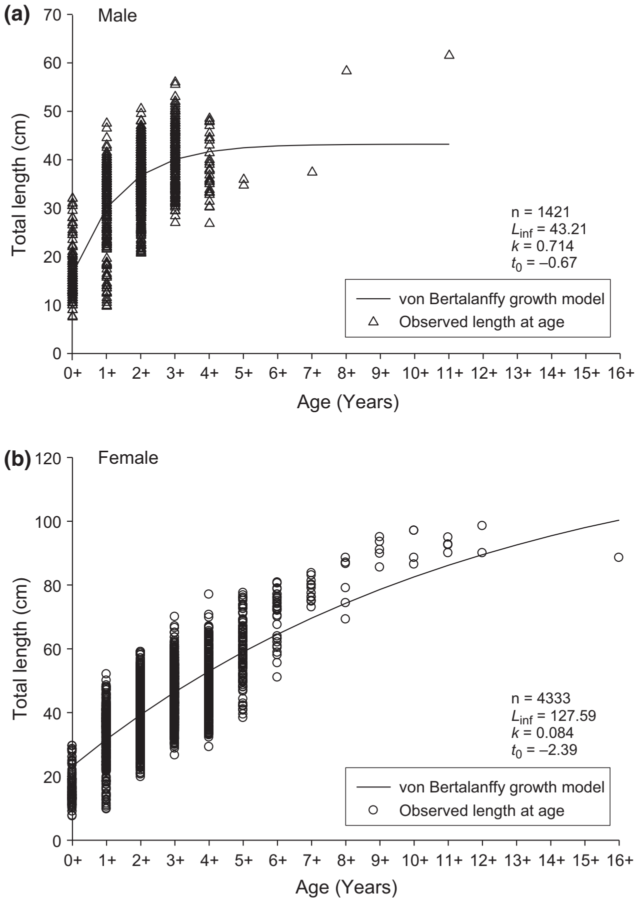

Fig. 6. *Platycephalus fuscus* estimated growth (a) male (n = 1421) and (b) female (n = 4333), sampled from east Australian estuaries, 2001–2007. Growth modelled by fitting length-at-age data to von Bertalanffy growth function $L_t = L_{\inf}[l - e^{-k(t-t_0)}]$; where L_t is the length-at-age t; $L_{\inf}$ is the asymptotic length; k is the rate at which the curve approaches the $L_{\inf}$ and t_0 is the hypothetical age at zero length

Gray and J.E. Williamson, unpubl. data) and is a strategy widespread among teleosts (Burt et al., 1988; Sarre and Potter, 1999; Kendall and Gray, 2009). This strategy, combined with the prolonged and apparent flexible spawning period of dusky flathead, is potentially a risk-adverse evolutionary adaptation to enhance the probability that some reproduction occurs during favourable biotic and abiotic environmental conditions for enhanced survival and dispersal of eggs and larvae (Lambert and Ware, 1984; Roff, 1984).

Dusky flathead were observed to be in spawning condition in the marine dominated lower reaches of estuaries; ovulating females were sampled at sites close to the mouth of five estuaries and also in nearshore ocean waters adjacent to the Clarence River. In contrast, in estuaries where samples were collected at sites upstream (>5 km) of the mouth, only females with vitellogenic oocytes were collected, observations suggesting that *P. fuscus* spawn in the lower reaches of estuaries and in nearshore coastal waters. Although no direct observations of spawning were made, it is generally reported that throughout the summer dusky flathead form small spawning aggregations in the entrance channels of estuaries (Roberts et al., 2014). Nevertheless, we acknowledge that dusky flathead may not actually spawn within the estuary, but move into coastal waters within a short time frame (e.g. diel or tidal cycle) immediately prior to spawning (Walsh et al., 2011). Closer investigation of the spawning activity is required to determine if *P. fuscus* actually spawn within estuaries and if so, whether they exhibit a spawning strategy that promotes eggs being dispersed into coastal waters or retained within an estuary, as observed in other estuarine teleosts (Bilton et al., 2002; van der Meulen et al., 2014).

Maturity

Female dusky flathead reached sexual maturity later and at a larger length than males. On average, males take 1.2 years whereas females take more than 4 years to reach the estimated $L_{50,}$ although we note that some females were mature at approx. 2 years of age. This gender-based divergence in length and age at maturity is typical of many playcephalid species (Fairbridge, 1951; Jordan, 2001; Bani and Moltschaniwskyj, 2008) and may be related to an increase in female

Table 1
Location, time period and numbers of *Platycephalus fuscus* tagged and released in each estuary and a summary of subsequent numbers of reported recaptures in estuarine and coastal waters in eastern Australia

Estuary	Latitude, longitude	Month & year of tagging (mm/yy)	No. tagged	No. recaptures in same estuary	No. recaptures in estuary north	No. recaptures in estuary south	No. recaptures in ocean north	No. recaptures in ocean south	Total recaptures	Percent recaptured
Richmond River	28.874S, 153.591E	02/88–01/90	289	39	1	0	2	0	42	14.5
Clarence River	29.427S, 153.372E	02/88–01/90	177	15	2	0	2	0	19	10.7
Bellinger/ Kalang River	30.502S, 153.032E	11/90–09/91	24	9	0	0	2	0	11	45.8
Nambucca River	30.650S, 153.014E	10/90–08/91	19	5	0	0	0	0	5	26.3
Macleay River	30.874S, 153.025E	10/90–08/91	24	3	0	0	0	0	3	12.5
Botany Bay	34.000S, 151.235E	01/93–01/95	716	72	1	0	4	1	78	10.9
Port Hacking	34.075S, 151.166E	01/93–01/95	10	2	0	0	0	0	2	20.0
Shoalhaven River	34.901S, 150.765E	09/92–01/95	53	11	1	0	0	0	12	22.6
St Georges Basin	35.185S, 150.594E	05/93–06/94	146	22	0	0	0	0	22	15.1
Lake Conjola	35.268S, 150.508E	10/92–12/94	209	5	0	0	0	0	5	2.4
Burrill Lake	35.395S, 150.447E	06/93–12/94	16	4	0	0	0	0	4	25.0
Total			1683	187	5	0	10	1	203	12.1

reproductive potential at larger lengths as reported for other teleost species (Parker, 1992; Hughes and Stewart, 2006; McDermott et al., 2007).

Our estimated L_{50} of 56.75 cm TL for females was similar to one previous estimate of 56 cm TL for a northern population (Russell, 1988) but larger than another of 38 cm TL (SPCC, 1981). In contrast, our estimated L_{50} of 31.72 cm TL for males was less than the 46 cm TL estimated for the northern population, but similar to the 32 cm TL reported by SPCC (1981). A plethora of biotic (e.g. social and behavioural cues) and abiotic (e.g. environmental and anthropogenic perturbations) factors can impact length and age at maturity as evidenced in other teleosts (Morgan and Bowering, 1997; Lassalle et al., 2008). Further investigation is required to determine the roles of such factors in driving maturation schedules of male and female *P. fuscus*.

Several platycephalid species have been hypothesised to exhibit protandrous hermaphroditism (Fujii, 1970, 1971; Shinomiya et al., 2003), and it has been argued that dusky flathead change sex, where an individual initially functions as a male before changing to a female (Dredge, 1976). This argument has been based on the observed skewed sex ratios in *Platycephalus fuscus* populations, with the smaller length classes being dominated by males and the larger length classes by females. No hermaphroditic fish were observed in this study or in previous studies (Gray et al., 2002), indicating that dusky flathead do not change sex, but rather as our data demonstrate, males simply do not grow as large as females. Similarly, other Platycephalidae, including *P. Indicus* (Masuda et al., 2000), *P. longispinis* and *P. richardsoni* (Barnes et al., 2011b), display dimorphic growth between sexes with no evidence of sex change.

Growth

Female dusky flathead grew relatively quickly throughout their entire life, whereas male growth slowed after 2 years. Both sexes reached a mean length of approx. 30 cm TL at age 1, whereas females reached 59 cm TL and males 42 cm TL at age 5. Although our estimated rates of growth are consistent with previous estimates (Dredge, 1976; Gray et al., 2002), it is evident that the growth rate is highly variable among individuals, which may be the result of phenotypic flexibility or environmental conditions. Our estimate of longevity of 16 years is comparable to other Platycephalidae, including *P. longispinis* (16 years) and *Ratabulus diversidens* (13 years), but more than double that of other species, such as *P. richardsoni* (6 years) and *P. caeruleopunctutatus* (8 years) (Barnes et al., 2011b).

The female von Bertalanffy growth model maximum length of 128 cm was similar to the largest dusky flathead reported of 120 cm (Kailola et al., 1993); the largest female sampled within the current study was 98.5 cm, which is less than the maximum observed or modelled length. The modelled maximum male length of 43 cm was smaller than the 61.5 cm largest male observed. The poorer fit of the von Bertalanffy growth model to the male growth may be due to the rarity of larger and older male fishes within our sample and the population in general. The paucity of large (and old) males and females in samples could be an effect of fishing on the population structure of *P. fuscus*; length and age

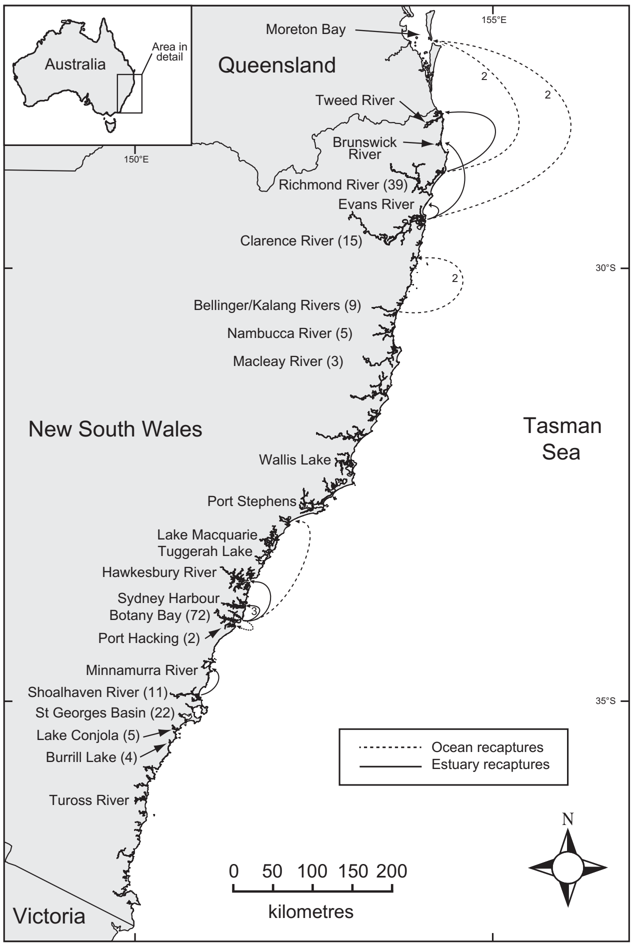

Fig. 7. Locations of tagged released and recaptured *Platycephalus fuscus*, eastern Australia, 1988–1995. Total number of *P. fuscus* recaptured in same estuary as tagged identified in parentheses associated with each estuary name. Solid and dotted lines = movements of *P. fuscus* external to the release estuary recaptured in estuarine and coastal waters, respectively. Each line = one fish unless otherwise denoted by a number against the line

truncation has been reported for several other exploited fish species in eastern Australia (Stewart, 2011).

Movement

The tag-recapture data identified that dusky flathead are capable of moving (up to 280 km detected in this study) between distant estuaries and coastal areas. Although most individuals were recaptured in the original estuary of tagging, the majority of these recaptures were within a short time period and may not indicate permanent residency. The rate of expatriation from estuaries of recaptured tagged dusky flathead (7.9%) was greater than that reported for another estuarine/coastal teleost, *Girella tricuspidata* (3.7%), tagged in east Australian estuaries (Gray et al., 2012). We do not know, however, if the few *P. fuscus* that expatriated from estuaries did so actively or passively (e.g. flood event) or what biotic/abiotic factors triggered such movements. Acoustic telemetry studies are required to better determine the rates of exchanges of dusky flathead between estuaries and coastal waters and relationships with key ecological processes (Walsh et al., 2012; Payne et al., 2013; Taylor et al., 2014). Nevertheless, as most of these distant recaptures occurred during the summer spawning period, we suggest that the predominant northerly directed movement displayed by these expatriated *P. fuscus* is potentially a life-history tactic associated with reproduction to facilitate the dispersal of eggs and larvae to nursery areas by the southward-flowing East Australian Current, as proposed for other species (Gray et al., 2012). The strategy of fish moving upstream into the prevailing current to spawn, and for eggs and larvae to be dispersed by longshore currents, is exhibited by fishes inhabiting other coastal boundary current systems (Hare and Cowen, 1993).

The coastal and inter-estuary movements of adult dusky flathead together with the potential relocation and mixing of eggs and larvae along the coast, suggest there is substantial population mixing along eastern Australia. Although genetic studies on dusky flathead are limited, they do suggest a potentially panmictic population (Roberts et al., 2014) as evidenced for other east Australian teleosts (Roberts and Ayre, 2010). Further widespread genetic sampling is required, however, to test this hypothesis.

Fishery management implications

Length-based fisheries regulations for dusky flathead differ among management jurisdictions with minimum legal lengths (MLLs) of between 30 and 40 cm TL applying to recreational, commercial and indigenous fishers (Roelofs et al., 2012). These MLLs provide little protection for mature female *P. fuscus*, with only 3–9% (but >70% of males) being mature at 30 and 40 cm TL, respectively, during the spawning period. Increasing the MLL for dusky flathead to the female L_{50} (57 cm TL) would virtually eliminate males from being harvested (yet there may still be collateral mortality due to discarding and catch and release; Gray, 2002; Butcher et al., 2008), which could ultimately exert greater fishing pressure on large (and older) females. A harvest slot size may be a more appropriate length-based tool to manage the sustainable exploitation of dusky flathead given the significant gender-based differences in growth and length-at-maturity. Harvest slot sizes may provide greater protection to mature females and allow for greater overall reproductive success (Gwinn et al., 2013), whilst still permitting the harvest of males. The success of recent implementations in two management jurisdictions of harvest slot sizes (30–55 cm TL and 40–75 cm TL) on the population demographic characteristics and reproductive output of dusky flathead need to be investigated as a further step to determining the most appropriate mix of fishery management regulations for the species.

Acknowledgements

The authors were employed by the NSW Government at the (now closed) *Cronulla Fisheries Research Centre of Excellence* when this work was done. The NSW Government and the NSW Recreational Fishing Saltwater Trust funded this study and sampling of wild populations was done under a NSW

Animal Ethics Permit (2000/20). Numerous colleagues at the centre provided assistance with sampling and processing of samples, notably Damian Young, Darren Reynolds, Dylan van der Meulen and Ben Brewer; Caitlin Young helped with microscopic photography. Drs Bob Kearney, Bruce Pease, Ron West and Aldo Steffe managed aspects of the historical tagging program. Drs Kevin Rowling, John Stewart, Aldo Steffe, Doug Rotherham and Mr Ben Kendall provided discussions and constructive comments on the manuscript. We thank the numerous commercial and recreational fishers who assisted with sampling and provided samples of dusky flathead.

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