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Aspects of the reproductive biology and early life history of black bream, *Acanthopagrus butcheri* (Sparidae), in a brackish lagoon system in southeastern Australia

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Abstract

Aspects of the reproductive biology and early life history of black bream *(Acanthopagrus butcheri)* in the Gippsland Lakes, a large brackish lagoon system in southeastern Australia, are described. Trends in mean gonadosomatic indices of males and females between November 1993 and March 1996 indicate that spawning occurred between October and February, with a peak in October-November when water temperatures were 15-22°C. Larvae (4.6-11.2 mm body length (BL)) were caught in shallow brackish ponds in November 1996 and January 1997 and possess the typical sparid characteristics. Notochord flexion in larvae occurs at 4.6-6.0 mm BL, while early juveniles settle from about 13 mm BL. Ageing of black bream showed that the youngest sexually mature male (15.6 cm fork length (FL)) and female (15.9 cm FL) were 3+ year olds. The ability of black bream to complete their life cycle within estuarine environments appears to be unique amongst members of the Sparidae worldwide.

Zusammenfassung

Vermehrungsbiologie und frühes Lebensstadium der Schwarzen Brasse *(Acanthopagrus butcheri)* aus den Gippsland Seen, einem großen Brackwasser-Lagunensystem, werden beschrieben. Durchschnittliche gonadosomatische Indexe bei Männchen und Weibchen zwischen November 1993 und März 1996 zeigen auf, daß sie in der Zeit von Oktober bis Februar ablaichen, mit einem Höhepunkt im Oktober-November, wenn die Wassertemperaturen 15-22°C betragen. Larven (4.6-11.2 mm Körperlänge (KL) wurden im November 1996 und Januar 1997 in seichten Brackwassertümpeln gefangen. Sie trugen die charakteristischen Merkmale der Familie Sparidae. Die Notochord-Krümmng tritt bei Larven bei einer KL von 4.6-6.0 mm auf und pendelt sich bei jungen Fischen bei einer KL von etwa 13 mm ein. Bei ausgewachsenen Schwarzen Brassen zeigt sich, daß die jüngsten geschlechtsreifen Männchen (15.6 cm Schwanzgabel- Länge) und die jüngsten geschlechtsreifen Weibchen 15.9 cm Schwanzgabel-Länge) 3+ Jahre alt sind. Die Fähigkeit der Schwarzen Brassen, ihren Lebenszyklus innerhalb von Brackwasser-Meeresbuchten zu vollenden, ist weltweit einmalig unter den Sparidae.

Résumé

Certains aspects de la biologie de reproduction et de l'histoire naturelle précoce de la Dorade noire *Acanthopagrus butcheri* dans un vaste système lagunaire saumâtre de l'Australie du sud-est, les Gippsland Lakes, sont évoqués. Les tendances des moyennes des indices gonadosomatiques des mâles et des femelles entre novembre 1993 et mars 1996 indiquent que la ponte se produit entre octobre et févirier avec un pic en octobre-novembre lorsque la température de l'eau atteint 15-22° centigrades. Les larves (4,6-11,2 mm de longueur corporelle (BL)) ont été capturées dans des mares saumâtres peu profondes en novembre 1996 et janvier 1997 et possèdent les caractéristiques sparidées. La flexion de la notochorde se produit chez les larves de 4,6-6,0 mm BL, cependant que les premiers juvéniles sont déterminés à partir de 13 mm BL. La croissance de la Dorade noire montre que les plus jeunes mâles sexuellement matures, 15,6 mm de longueur jusqu'à l'échancrure caudale (FL), et les femelles (15,9 mm FL), sont alors âgés de plus de 3 ans. La capacité de la Dorade noire à compléter son cycle vital dans un environnement purement d'estuaire semble unique chez les Sparidés.

Sommario

Vengono descritti alcuni aspetti del ciclo riproduttivo e della vita larvale del pagro nero *(Acanthopagrus butcheri)* dei laghi del Gippsland, un ampio sistema di lagune salmastre dell'Australia sudorientale. Gli andamenti degli indici medi gonadosomatici di individui maschi e femmine, raccolti nel periodo novembre 1993 - marzo 1996, indicano che la fecondazione delle uova avviene tra ottobre e febbraio, con un picco in ottobre-

novembre, allorché la temperatura dell'acqua si aggira tra 15 e 22°C. Le larve (lunghezza del corpo [BL, *Body Length]* pari a 4,6 - 11,2 mm) sono state catturate in pozze salmastre poco profonde tra novembre 1996 e gennaio 1997 e possedevano le tipiche caratteristiche degli sparidi. Nelle larve il ripiegamento della notocorda avviene allo stadio di 4,6 - 6,0 mm BL, mentre i primi stadi giovanili s'insediano a circa 13 mm BL. Lo studio sull'invecchiamento del pagro nero ha mostrato che gli individui più giovani sessualmente maturi, un maschio (15, 6 cm di lunghezza alla biforcazione della coda, FL, *Fork Length)* e una femmina (15,9 cm FL), avevano oltre tre anni d'età. La capacità del pagro nero di completare il proprio ciclo vitale nell'habitat salmastro degli estuari sembra l'unico caso al mondo tra gli sparidi.

Introduction

The black bream *(Acanthopagrus butcheri)* is endemic to estuarine and coastal waters of temperate Australia between Shark Bay (Western Australia) and Mallacoota (Victoria), including Tasmania (Gomon *et al.,* 1994). The species is fished throughout its distributional range and constitutes one of the most valuable commercial and recreational fish species in southeastern Australia. Most of the black bream catch in the latter region originates from the Gippsland Lakes, a large brackish lagoon system which is connected to the sea in Bass Strait through a narrow entrance channel (Bird, 1978).

Little is known about the reproductive biology and/or early life history of black bream in southeastern Australia. Past studies show that black bream in the Gippsland Lakes spawn mainly in spring and early summer, based on observations of developing and ripe gonads (Butcher, 1945). Available information on the larval stage is limited to a description of artificially-reared early postflexion and early juvenile stages (Miskiewicz & Neira, 1998).

This paper describes aspects of the reproductive biology of black bream in the Gippsland Lakes, based on adults sampled between 1993 and 1996. It also provides for the first time a description of the early life history stages of this species, based on larvae collected within this brackish lagoon system.

Materials and methods

Study area and sampling regime:

The Gippsland Lakes are a series of coastal lagoons located in eastern Victoria, and cover an area of about 400 km^2 (Bird, 1978). The system comprises three mostly shallow (average 3 m), interconnected lakes (Wellington, Victoria and King), which are joined to Bass Strait through a short artificial channel at Lakes Entrance (Fig. 1).

A total of 1173 black bream (10.0-40.0 cm fork length (FL)) were sampled from monthly random catches obtained with commercial beach-seine and gill nets throughout the Gippsland Lakes (except Lake Wellington) from November 1993 to March 1996. An additional 385 female black bream (11.0-37.0 cm FL) were examined from a sample of 680 black bream caught in December 1996 with a research seine net at 32 random sites. Water temperatures at several sites throughout the lakes during the study period were obtained for various

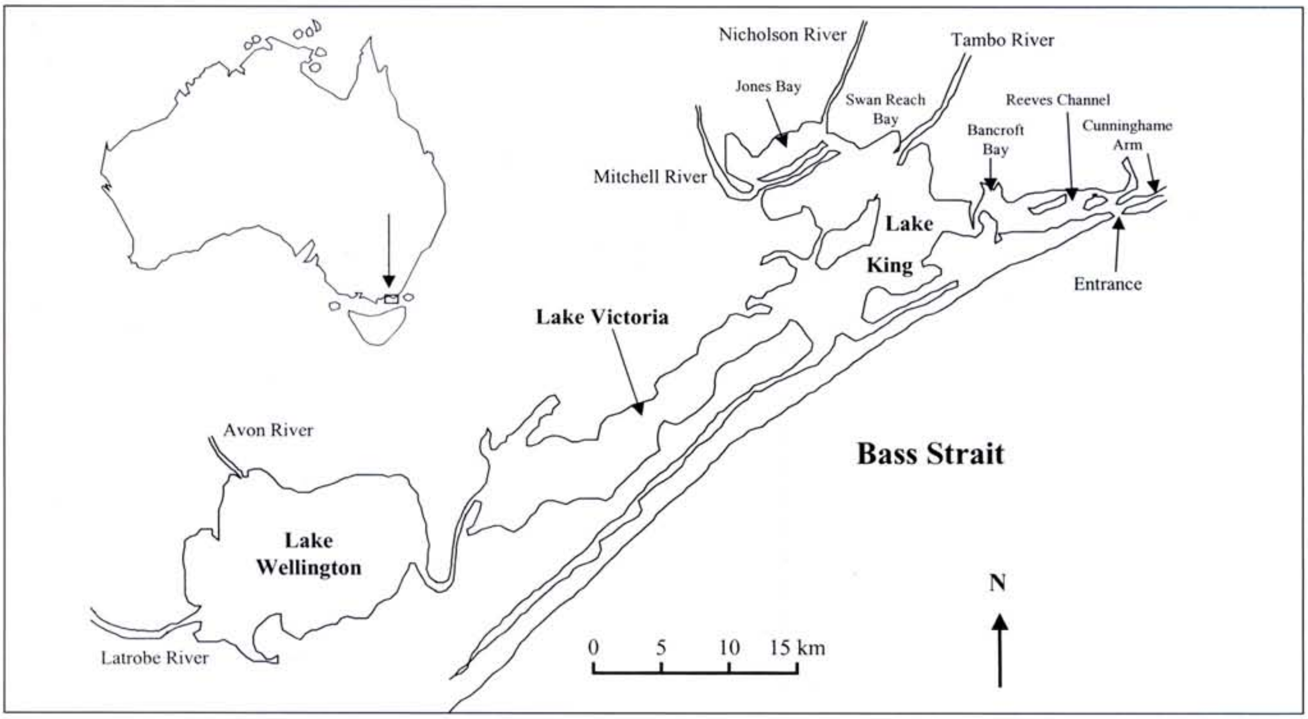

Fig. 1. Map of the Gippsland Lakes in Victoria, south-eastern Australia, showing the localities mentioned throughout the text.

months from the Environmental Protection Authority (Victoria) and averaged by month across all sites.

Larvae and early juveniles of black bream were sampled on six occasions in shallow ponds (<1 m) and connecting creeks along the eastern end of Cunninghame Arm (Fig. 1). Samples were collected fortnightly during the daytime between November 1996 and January 1997, with a 1.5 m long, 0.6 m diameter, 300 mm mesh, plankton net. On each sampling occasion the net was held at or just below the surface and towed by hand for five minutes. Samples were fixed in 5% formalin and later preserved in 70% ethanol.

Laboratory procedures:

Each adult black bream was measured to the nearest 0.1 cm FL and weighed to the nearest 1.0 g. Gonadal stages (I-V) were macroscopically determined following Laevastu (1965), where I is immature, II is maturing or recovering spent, III is ripening, IV is running ripe, and V is spent. Gonads were weighed to the nearest 0.1 g (wet), and the gonadosomatic indices (GSIs) calculated for both sexes and expressed as a percentage of gutted weight. Otoliths from 100 black bream, randomly selected from the December 1996 sample (9.0-27.0 cm FL), were removed and sectioned for ageing, to determine the age at first maturity (see Morison *et al.,* 1998 for details).

Examination of larvae:

A total of 27 field-collected larvae and early juveniles (4.64-18.57 mm body length (BL)) of black bream were used to describe meristics, morphometrics, and pigmentation. An additional nine laboratory-reared postflexion larvae and early juveniles (7.10-11.70 mm BL) were examined to complete the description. Representatives of the larvae examined were lodged in The Australian Museum (AMS, Sydney).

Terminology used to describe head spines and morphometric measurements follows Neira *et al.* (1998). All measurements were made to the nearest

Table I. Number of individuals by age (years) and gonadal stage (I-V) of black bream sampled from the Gippsland Lakes in December 1996. The length range (FL, cm) is provided under each age. Fish of 4+ to 6+ years of age were absent from the sample.

	Age (years)						
	0+	1+	2+	3+	7+	9+	Total (n)
Fork length (cm)	11	9-13	9-15	15-18	15-27	19-22	
Stage I	1	29	18	1	0	0	49
Stage II	0	2	0	0	1	1	4
Stage III	0	0	0	3	30	2	35
Stage IV	0	0	0	1	6	1	8
Stage V	0	0	0	0	4	0	4
Total (n)	1	31	18	5	41	4	100

Table II. Body length and body proportions of larval and juvenile stages of black bream caught in the Gippsland Lakes. *n* = no. of larvae; BL = body length; HL = head length; BD = body depth; PAL = pre-anal length; VAFL = length of gap between anus and anal fin origin. Values for HL, BD, PAL and VAFL are given as percentages of body length (%BL), and shown as range and mean ± 2 s.e. (in parentheses) for each stage.

	STAGE		
	Flexion	Postflexion	Early juvenile
BL (mm)	(*n*, 11) 4.64 - 5.90	(*n*, 13) 7.60 - 11.25	(*n*, 3) 13.97 -18.57
HL (% BL)	21.5 - 28.5 (24.2 ± 1.2)	25.1 - 33.8 (27.9 ± 1.3)	33.9 - 35.0 (34.4 ± 0.7)
BD (% BL)	19.8 - 26.2 (22.2 ± 1.0)	23.2 - 30.2 (26.4 ± 1.3)	31.1 - 37.6 (35.1 ± 4.0)
PAL (% BL)	39.2 - 48.5 (43.3 ± 1.8)	46.6 - 57.8 (52.0 ± 1.4)	57.9 - 59.8 (59.1 ± 1.2)
VAFL (% BL)	—	0.0 - 5.6 (3.6 ± 1.0)	2.3 - 5.4 (4.1 ± 1.8)

0.01 mm using a dissecting microscope fitted with an eyepiece micrometer. Body length (BL) corresponds to the notochord length (snout tip to notochord tip) in preflexion and flexion larvae, and to standard length (snout tip to posterior hypural margin) in postflexion larvae and early juveniles; size of larvae given throughout the text corresponds to BL (mm). Measurements of head length (HL), body depth (BD), pre-anal length (PAL) and length of gap between the anus (= vent) and the anal fin origin (VAFL) were converted to percentages (%) of BL, and the ranges and means (± 2 s.e.) given for each of the flexion, postflexion, and early juvenile stages (Table II); values given throughout the text correspond to the means (% BL). The pigment described refers solely to melanin. Larvae were illustrated with the aid of a camera lucida.

Results

Seasonal trends in GSIs and gonadal stages:

The mean GSIs of both male and female black bream in the Gippsland Lakes between November 1993 and March 1996 followed a similar trend (Fig. 2). Mean GSIs were <2.0% in February-August 1994 and reached 6.9% (males) and 4.6% (females) in November 1994. No fish were collected in either December 1994 or January 1995, and the GSIs of all fish examined in February-August 1995 were <2.0%. In 1995, male and female GSIs peaked at 7.2 and 6.8% in October, respectively, and reached 10.1% in December 1995 in males only. Peaks in both male and female GSIs during 1994-95 occurred two months before the highest mean water temperatures in the Gippsland Lakes (20.8-22.5°C), which were recorded in January of both years (Fig 2). A linear regression, fitted to mean monthly GSIs and temperatures using the least squares method, showed that GSIs were significantly associated with water temperature lagged by 2 months, both for males (R^2, 0.83; $F_{1,10}$ = 56.62, P <0.0001) and females (R^2, 0.65; $F_{1,10}$ = 21.36, P <0.001).

All female black bream examined in February-August 1995 had resting or maturing ovaries (stage II), except for a few in February that had running ripe ovaries (stage IV) (Fig. 3). About 20% of females had ripening ovaries (stage III) in September 1995, while almost 75% had running ripe ovaries by October 1995. The percentage of females with running ripe ovaries decreased to <10% by December 1995, but increased again slightly by February 1996. By March 1996, nearly 86% of the females examined had spent ovaries (stage V) (Fig. 3).

Of the 100 black bream that were aged, immature fish (n = 50) were <3 year olds of 9.0-15.0 cm FL, whereas the smallest black bream with stage III-V gonads were 3+ year olds of ≥15 cm FL (Table I). The smallest 3+ year-old male and female black bream with stage III gonads measured 15.6 and 15.9 cm FL, respectively

Larval identification and occurrence:

Larvae and early juveniles collected in the Gippsland Lakes were identified as those of *Acanthopagrus butcheri* (Munro, 1949) using the description of Miskiewicz and Neira (1998), and their identification confirmed by comparing the fin meristics obtained from

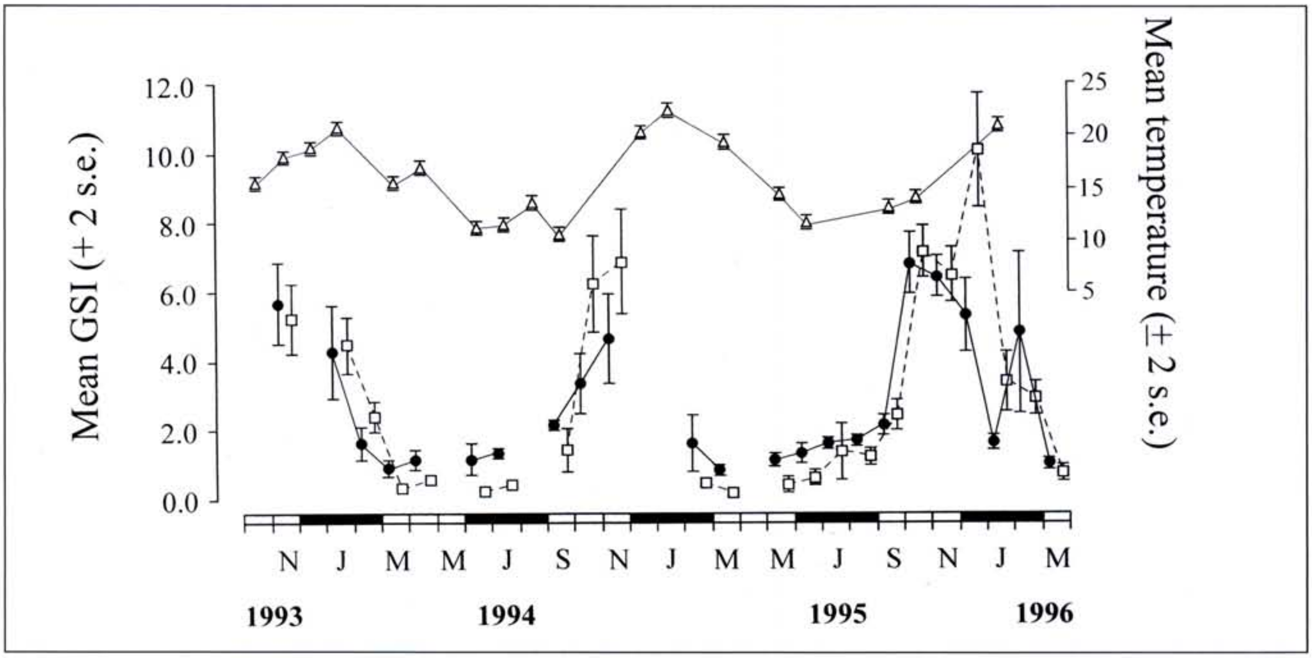

Fig. 2. Monthly trends in mean water temperatures (—Δ—) (± 2 s.e.), and mean GSIs (± 2 s.e.) for male (---□---) and female (—●—) black bream from the Gippsland Lakes between October 1993 and March 1996. Lines join data of months for which samples were obtained.

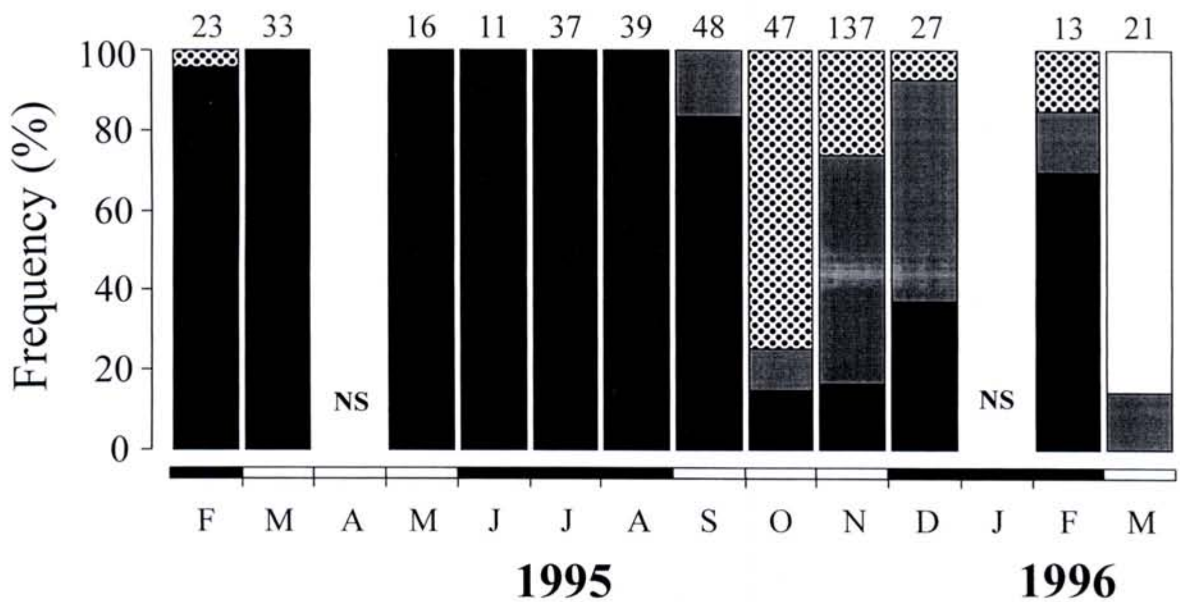

Fig. 3. Monthly variation in the proportion (%) of different gonadal stages (II to V) in female black bream from the Gippsland Lakes between February 1995 and March 1996 (n = 452). Data are missing for April 1995 and January 1996. The values above bars correspond to sample size (see text for developmental stages).

the largest postflexion larva in our series with that provided for the adults of this species in the literature (D X-XIII, 10-13; A III, 8-10; P_1 14-16; P_2 I, 5; Gomon *et al.*, 1994). A developmental series through to the smallest flexion larva was then assembled using body shape, head spines and pattern of pigmentation. Larvae and early juveniles were caught in November 1996 (n = 17) and January 1997 (n = 10), when temperatures and salinities in the ponds were 18.1-22.7°C and 15.5-17.8, respectively.

Description of larvae:

Development and morphology: Larvae are moderately elongate (BD 22.2-35.1%). The head is moderate in flexion and postflexion larvae (HL 24.2-27.9%), becoming large in early juveniles (HL 34.4%) (Table II; Fig. 4). Tiny teeth are present along both jaws in the smallest flexion larva examined (4.64 mm; Fig. 4a). One small spine on the anterior (= inner) and up to four on the posterior (= outer) margin of the preopercle are present in early flexion larvae. Anterior preopercular spines increase to three by the early postflexion stage and disappear by the early juvenile stage; posterior preopercular spines increase to six and become very small by the early juvenile stage. An opercular spine forms by 9.0 mm and remains thereafter. A smooth supraocular ridge forms during the flexion stage while a low supracleithral ridge appears during the early postflexion stage. The gut is coiled and compact in the smallest flexion larva examined and it is moderate in flexion larvae (PAL 43.3%) becoming long in postflexion larvae and early juveniles (PAL 52.0-59.1%). A conspicuous, inflated gas bladder is visible above the foregut until the early postflexion stage. There is a small gap between the anus and the anal fin origin from the flexion stage, which disappears once the fin is fully formed (Fig. 4e). There are 24-25 (7-10 +14-17) myomeres. Scales start to develop from about 13 mm.

Pigmentation: Larvae remain lightly pigmented until the early juvenile stage. Head pigment is absent in early flexion larvae. One to six melanophores appear over the midbrain from the midflexion stage and a few along the isthmus by the early postflexion stage; scattered melanophores develop on the premaxilla and dentary, and many more over the head, by the late postflexion stage. Internal head pigment forms at the nape during flexion, and both ventrally under the brain and at the junction of the mid- and hind-brain from the postflexion stage; the nape melanophore is no longer visible from the postflexion stage due to the musculature. A large ventral melanophore is present anterior to the anus in all larvae examined; additional melanophores appear ventrally along the gut from the late postflexion stage. Internal trunk pigment is present dorsally along the gas bladder and along the hindgut, with often a large, expanded, melanophore above the anus. A single series of up to 17 closely-spaced melanophores is present along the tail in preflexion larvae, most of which are confined to the posteriormost 13-14 caudal myomeres; these decrease in number with growth and remain along the anal fin base and ventral midline of the caudal peduncle from the postflexion stage. Dorsal body pigment develops from the postflexion stage, with one to three melanophore

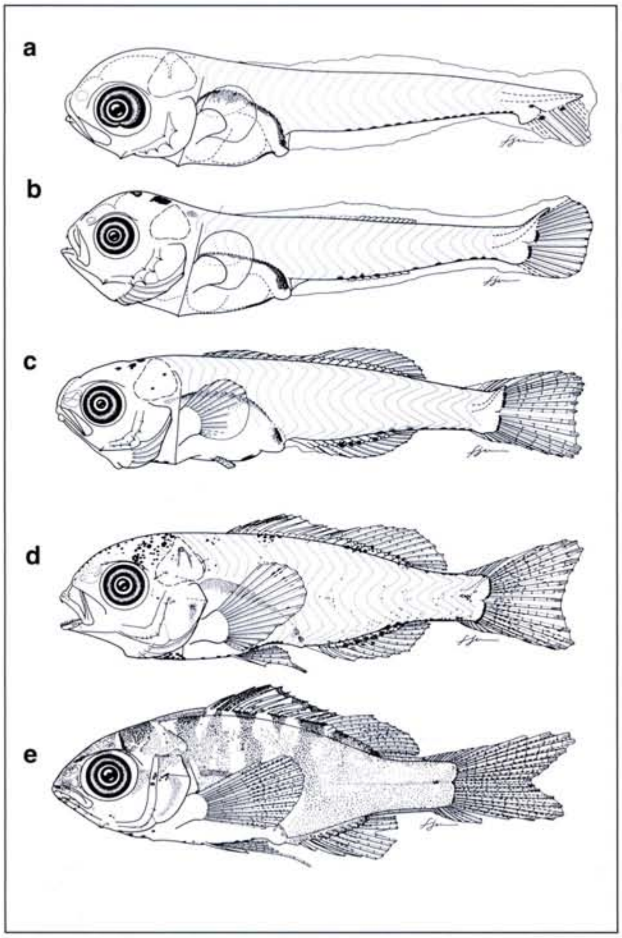

Fig. 4. Larvae and early juvenile of *Acanthopagrus butcheri* from the Gippsland Lakes, south-eastern Australia. (**a**) 4.64 mm BL early flexion larva. (**b**) 5.90 mm BL flexion larva. (**c**) 8.84 mm BL early postflexion larva. (**d**) 11.35 mm BL postflexion larva; note forming third anal fin spine. (**e**) 13.68 mm BL early juvenile; myomeres and forming scales omitted. Illustrated by F. J. Neira.

patches along the dorsal fin base being present by the late postflexion stage; these increase in number and intensity to form 6-8 distinct, pigmented, vertical bands that spread dorso-laterally along the trunk and tail in early juveniles, and all of which expand downwards to about the lateral midline of the body. Two melanophores are present along each developing hypural plate in early flexion larvae; these increase in number with growth and remain along the hypural margin from the early postflexion stage. Pigment appears along the anteriormost four dorsal fin spines and interconnecting membranes from the late postflexion stage; melanophores are also present along the rays of all but the pelvic fins in early juveniles (Fig. 4e).

Notochord flexion and fin formation: Notochord flexion commences by about 4.6 mm and is complete by 6.0 mm; the smallest and largest flexion larvae examined measured 4.64 and 5.90 mm, respectively, whereas the smallest postflexion larva was 7.60 mm (Table II). Principal caudal fin rays start developing prior to notochord flexion and all 9+8 rays are formed by the early postflexion stage (Fig. 4c). Dorsal and anal fin pterygiophores form during the midflexion stage and the full complement in both fins is present in the late postflexion stage (Fig. 4d); the last spine of the dorsal (XI) and anal (III) fin are still soft rays in late postflexion larvae but are fully ossified in early juveniles from 13 mm (Fig. 4e). Pectoral and pelvic fin rays start to develop shortly after notochord flexion is complete, and both fins are formed by 12 mm; the first pelvic fin ray is noticeably longer than the other four rays from the postflexion stage (Fig. 4d,e).

Discussion

Spawning season:

The trend in GSIs found during this study indicates that black bream in the Gippsland Lakes spawn between October and February, with a peak between October and November. This is further supported by the occurrence of the early larval stages of black bream caught in November and January. These results are consistent with earlier findings by Butcher (1945), who reported spawning of black bream in the lakes between October and March. Spawning of black bream elsewhere in temperate Australia has been reported in November-December in the Hopkins River estuary in western Victoria (Newton, 1996), October to January in Western Australia (Sarre & Potter, 1999), September to November in South Australia (Harbison, 1974), and November in Tasmania (Haddy & Pankhurst, 1998). Although timing and duration of spawning differ across temperate Australia, all black bream populations appear to have protracted spawning periods with an October-November spawning peak. An extended spawning season is a common feature of many temperate and tropical sparids (eg. Pulfrich & Griffiths, 1988; Horvath *et al.,* 1990; Buxton & Clarke, 1991; Garratt, 1993; Mann & Buxton, 1998).

Spawning of black bream in the Gippsland Lakes occurs in water temperatures >15°C, which is also the case with populations in Tasmania (15.5-26.2°C; Haddy & Pankhurst, 1998) and Western Australia (19.7-23.4°C; Sarre & Potter, 1999). In addition, spawning females (stage IV) sampled in December 1996 in the Gippsland Lakes were caught in salinities of 5-23, which lie within the full salinity range (3.5-45.0) recorded for spawning black bream across temperate Australia (Newton, 1996; Haddy & Pankhurst, 1998; Sarre & Potter, 1999).

Age at first maturity:

Our sample of sectioned otoliths showed that the onset of maturity in female black bream in the Gippsland Lakes starts at 3+ years of age. This age differs from that of 2+ reported by Butcher (1945) for females in this system, which was based on unvalidated age estimates derived from length-frequency modes (Morison *et al.,* 1998). A much wider range in the age at both first (1+ - 3+) and 50% maturity (~2 - 4+ years) was reported by Sarre and Potter (1999) for black bream from four different locations in Western Australia and was attributed to growth variability. Thus black bream < 2+ years of age from south-eastern and south-western Australia are unlikely to have matured or spawned, whereas a proportion of 3+ year old fish have probably spawned at least once. At the current legal minimum for black bream in Victoria, fish presently recruit to the fishery between 5+ and 7+ years of age and thus are likely to have spawned for up to four years prior to capture.

Development and distribution of larvae:

This study provides the first description of the early life stages of *Acanthopagrus butcheri* based on field-collected material. An earlier description of black bream larvae by Miskiewicz and Neira (1998) was based on artificially-reared material and dealt only with postflexion larvae and early juveniles (7.1-11.7 mm). The only difference between the larvae described by Miskiewicz and Neira (1998) and those described here is the relatively heavier pigmentation in the former, which is usually the case with reared larvae (Hunter, 1984).

The morphology and development of black bream larvae is typical of that described for most sparids (Miskiewicz & Neira, 1998). This includes: a round, gently sloping head; a moderate to long, coiled and compact gut; a small to moderate gap between the anus and the anal fin origin, which closes by the postflexion stage; head spination that includes spines along the anterior (inner) and posterior (outer) preopercular margins; the formation of the caudal, dorsal and anal fin anlagen shortly before the start of notochord flexion; a size at flexion between 4.6 and 6.0 mm; and an initially lightly pigmented body, with the characteristic single melanophore series along the ventral midline of the tail.

Black bream larvae can be confused with those of resident gobiids in the Gippsland Lakes. However, the latter can be distinguished by their two separate dorsal fins, 26-27 myomeres, and lack of head spines (Miskiewicz & Neira, 1998). Moreover, early juveniles of the few marine stragglers that are frequently found within the Gippsland Lakes could be separated from those of black bream using dorsal and anal fin counts (Neira *et al.,* 1998).

Larval and early juvenile black bream examined in this study were caught in shallow brackish ponds in a region of Gippsland Lakes that was once the natural opening to Bass Strait (Bird, 1978). Whether these habitats are important spawning areas for black bream is unknown, as no attempt was made to sample larvae elsewhere in this system during this study. Newly-hatched black bream larvae have been reported in deep pools (11 m) some 7 km upstream from the Hopkins River mouth in Victoria (Newton, 1996), whereas none have been caught during extensive larval fish surveys in other temperate Australian estuaries where black bream are known to reside (eg. Neira *et al.,* 1992; Neira & Potter, 1994).

Concluding remarks:

Acanthopagrus butcheri is the only sparid in Australia that can be considered as true estuarine, ie capable of spawning and completing its entire life cycle within estuarine systems. The other four sparid species recorded in Australia, including *A. australis* and *A. berda,* are marine spawners that enter estuaries at various stages of their life cycles (Blaber & Blaber, 1980; Pollock *et al.,* 1983; Miskiewicz, 1986; Sheaves *et al.,* 1999). Except for black bream, there is no evidence in the literature of any other true estuarine sparid worldwide, not even in southern Africa, where the sparid species diversity is highest (eg. Whitfield, 1999). Although *A. berda* have been observed spawning at the mouth of the Kosi Estuary, a marine-dominated system in South Africa (Garratt, 1993), they are not known to spawn in estuaries which are either temporarily closed or that have a high freshwater input (A. K. Whitifield, pers. com.). It is possible that the adaptation of black bream to inhabit estuarine environments throughout southern Australia is related to the fact that many estuaries in this region frequently become closed to the sea owing to the formation of sandbars across their entrances. In addition, a combination of characteristics in black bream, such as high fecundity, and multiple spawnings (Haddy & Pankhurst, 1998; Sarre & Potter, 1999) over a protracted season in waters of a wide salinity range, may be beneficial to their survival in predominantly brackish systems such as the Gippsland Lakes. However, the fact that recruitment of black bream in the Gippsland Lakes is episodic (Morison *et al.* 1998) clearly suggests that spawning success is highly variable, and whether this is related to the influence of environmental conditions on egg production, spawning frequency, and/or egg and larval survival, remains to be examined.

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