

First record of mosquitofish, *Gambusia holbrooki*, in Tasmania, Australia: stock structure and reproductive biology

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Abstract The first population of mosquitofish, *Gambusia holbrooki*, was discovered in a wetland area of the upper Tamar Estuary, northern Tasmania, Australia, in November 2000. We report aspects of the structure and reproductive biology of this population, based on 1567 fish collected between August 2001 and January 2002. Females dominated most catches. Maximum lengths were 48.9 and 23.6 mm standard length (SL) for females and males, respectively. Growth of the over-wintered cohort was evident from October, when temperatures reached $>19^{\circ}\text{C}$; growth rates in the young-of-season cohort from length frequency plots were 0.38 mm/day for females and 0.19 mm/day for males. Estimated SL at 50% maturity for females (25.0 mm) and males (17.4 mm) were attained within 7 weeks of birth. Developing embryos were present from mid October and offspring from mid November; average number of stage III embryos was 55.5 (3–144). Given their rapid reproductive turnover (c. 34-day gestation period) and resilience to broad environmental conditions, it is likely that this exotic pest will spread to other Tasmanian localities, as it has already been discovered in areas near the wetlands since the completion of this study.

Keywords mosquitofish; reproductive biology; *Gambusia holbrooki*; exotic pest; Tamar Estuary; Tasmania

INTRODUCTION

Gambusia holbrooki was first introduced for mosquito control in mainland Australia in 1925 (Wilson 1960), and rapidly became well established in many freshwater systems of every State and Territory except Tasmania. The first report of *Gambusia* in Tasmania dates from 1993, after they were inadvertently introduced into a farm dam in northern Tasmania and subsequently eradicated by the Inland Fisheries Service (Warwick Nash pers. comm.). However, mosquitofish were rediscovered in the nearby Tamar Island Wetlands Reserve in November 2000, and formally identified as *G. holbrooki* in July 2001 by one of us (F. J. Neira). This follows taxonomic verification of *G. holbrooki* as the only mosquitofish species present in Australia (Lloyd & Tomasov 1985), which includes all previous reports of *G. affinis* before 1985.

Mosquitofish are livebearing (ovoviviparous) fishes, capable of releasing broods of well-developed offspring at approximately monthly intervals during the warmer months (Milton & Arthington 1983; Constanz 1989; Haynes & Cashner 1995). Females can store sperm from one breeding season to the next (Howe 1995). Oocytes begin vitellogenesis during the gestation of the preceding brood, and are fertilised within days of the birth of the previous brood (Koya et al. 2000). Warmer water temperatures induce females to reproduce at an earlier age and at a larger size, and result in longer reproductive seasons, shorter interbrood intervals, and larger broods (Vondracek et al. 1988; Meffe 1992; Koya & Kamiya 2000). The average length of the reproductive season of *G. holbrooki* is 5–7 months (Milton & Arthington 1983; Pen & Potter 1991), depending on both environmental conditions and geographic locality (Hubbs & Valdes-Gonzales 1995).

This paper describes for the first time aspects of the structure and reproductive biology of the population of *G. holbrooki* discovered in the Tamar Island Wetland Reserve in northern Tasmania, and compares the findings with data reported for this introduced pest fish from other localities.

MATERIALS AND METHODS

Sampling area and procedures

Samples were obtained weekly between August 2001 and January 2002 from two freshwater ponds within the Tamar Island Wetland Reserve, c. 8 km north of Launceston (Tasmania), on the upper Tamar Estuary (41°23.1'S; 147°4.4'E). On each sampling occasion, mosquitofish were randomly captured using a 30-cm diameter, 2-mm mesh dip net at the time of peak daily water temperatures (mid afternoon), after they were observed actively schooling in shallow vegetated areas. Specimens were killed and fixed in 10% formaldehyde immediately upon capture, and preserved in 70% ethanol after 2 days.

Individuals were classified as "adult male" if they possessed a fully developed gonopodium, as "juvenile male" if there was evidence of a gonopodium but not fully developed, or as "female" if they were larger than the smallest male and possessed no evidence of a gonopodium. Individuals which did not fit into any of these categories were regarded as "juvenile undetermined".

Treatment of samples and data analyses

Standard length (SL) was obtained for all captured mosquitofish to the nearest 0.1 mm. Samples from the two sites were combined for all subsequent analyses, after a preliminary ANOVA showed no significant differences in the SL of males and females ($P > 0.05$) by site. Total body and ovary (females) weights were recorded for all individuals to the nearest 0.0001 g. In the instance of females, ovaries and embryos were staged according to the criteria shown in Table 1; only stage III embryos were counted in mature females. The ovariosomatic index (OSI; in reference to an ovoviviparous rather

than an oviparous fish) of females was calculated using the equation $OSI = (OW/BW) \times 100$, where OW = ovary weight (g); and BW = body weight (g). The mean SL (mm) at which 50% of the male and female mosquitofish were sexually mature ($LM_{50\%}$) were obtained from the logistic relationship between fraction of mature fish by length represented by $P = 1/(1 + \exp[-r(L - LM_{50\%})])$, where P is the proportion of mature fish (embryo stage 0 [gravid] and above for females), L is length, and r the slope of the curve (King 1995).

Water temperatures at the two sampling sites were recorded every 10 min with a temperature data logger. Weekly averages of maximum daily temperatures were used throughout this study. Regression analyses between maximum daily air and water temperatures were used to predict maximum water temperatures when site readings were unavailable.

RESULTS

Population assessment

Over-wintered (OW) *G. holbrooki*, i.e., those individuals born in the previous season and which survived winter, were generally confined to the shallow vegetated areas of the northern shorelines of the ponds, and were rare in open areas and other shorelines. By contrast, young-of-season (YOS) individuals, i.e., offspring from the first reproductive cycle of the season, were generally highly abundant around all shorelines.

The population structure of *G. holbrooki* varied significantly over the sampling period. Females dominated throughout most of the study, although sex ratios (female/male) were highly variable (Fig.

Table 1 Criteria used to distinguish the stages of ovarian and embryonic (embryo stage, ES) development in female *Gambusia holbrooki* (adapted from Trendall 1981).

Stage	Description
Ovarian development	
Immature	Ovaries small and white. No sign of vitellogenesis in oocytes.
Maturing	Oocytes in ovaries undergoing vitellogenesis but not fully developed. Yellow to orange in colour.
Embryonic development	
ES 0 (Gravid)	Mature, unfertilised oocytes, and newly fertilised oocytes where embryonic development is not apparent. Translucent yellow/orange with many marked oil droplets clearly visible.
ES I	From fertilised oocyte showing streak or groove to embryo with eyes apparent, but somatic development indistinct.
ES II	From ES I to stage where embryo completely encircles yolk sac and caudal fin is in contact with head.
ES III	From ES II until birth.

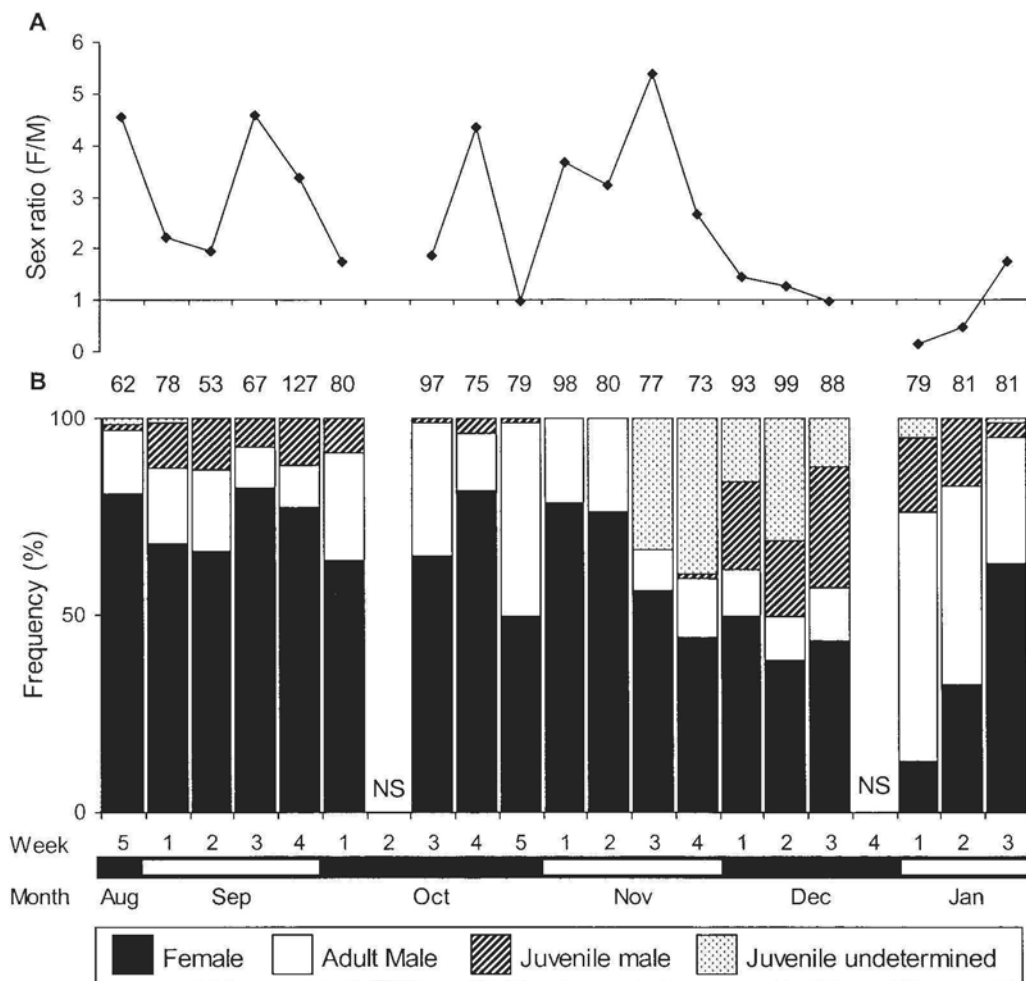


Fig. 1 Temporal changes in **A**, the sex ratio (females (F)/male (M)) and **B**, population structure of *Gambusia holbrooki* from the Tamar Island Wetlands Reserve, Tasmania, Australia between August 2001 and January 2002. Numbers above bars denote total numbers of individuals caught on each sampling occasion. (NS, no sample.)

1). Female occurrences declined quickly after their first observed birth (21 November 2001), before increasing again in January 2002 (Fig. 1). The sex ratio remained <1 between 19 December 2001 and 9 January 2002, as OW females and males disappeared from the ponds and the YOS cohort was initially dominated by males.

The maximum recorded lengths for female and male *G. holbrooki* caught during this study were 48.9 and 23.6 mm SL, respectively. Maximum body weights recorded for both females and males were 2.46 and 0.19 g, respectively.

Length-frequency distributions show OW females gradually increasing in size range from 11.3–30.4 mm SL on 29 August to 33.3–43.3 mm

SL on 12 December 2001, with very few large OW females (40.5–48.9 mm SL) caught in January 2002 (Fig. 2). By contrast, the change in size range of OW males during the same period was minimal, ranging from 17.2–23.2 to 18.2–21.2 mm SL (Fig. 3). YOS were first recorded on 21 November 2001, as clearly shown by the bimodal length-frequency distributions (Fig. 2, 3). The resultant YOS cohort became dominant by December 2001 as the OW cohort declined (Fig. 2, 3).

Growth was observed in the OW and YOS female cohorts throughout the study, which closely followed an increasing trend in mean water temperatures in the sampling area (Fig. 4A,B). The mean length of the OW cohort increased from 18.9 to 38.0 mm SL

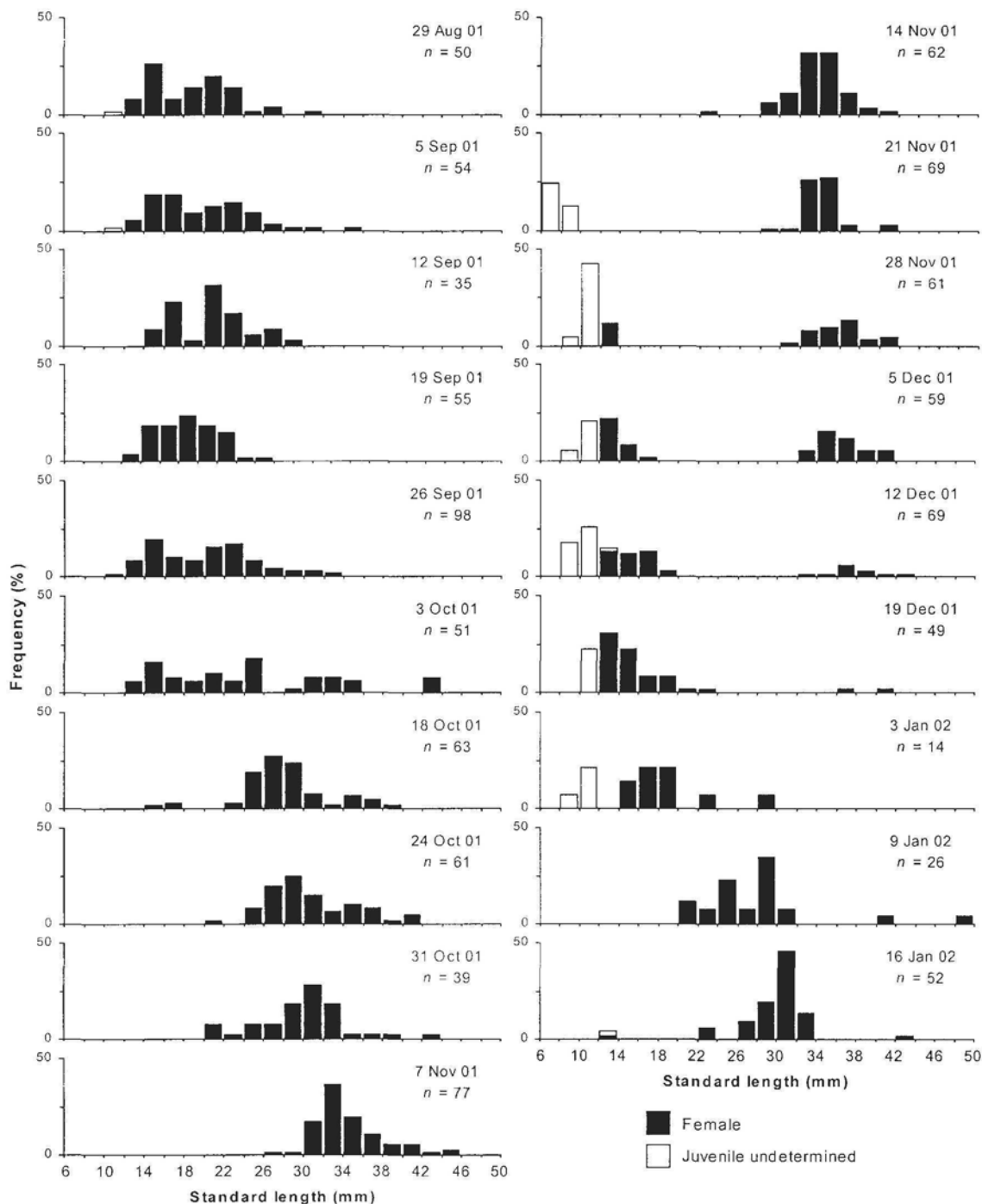
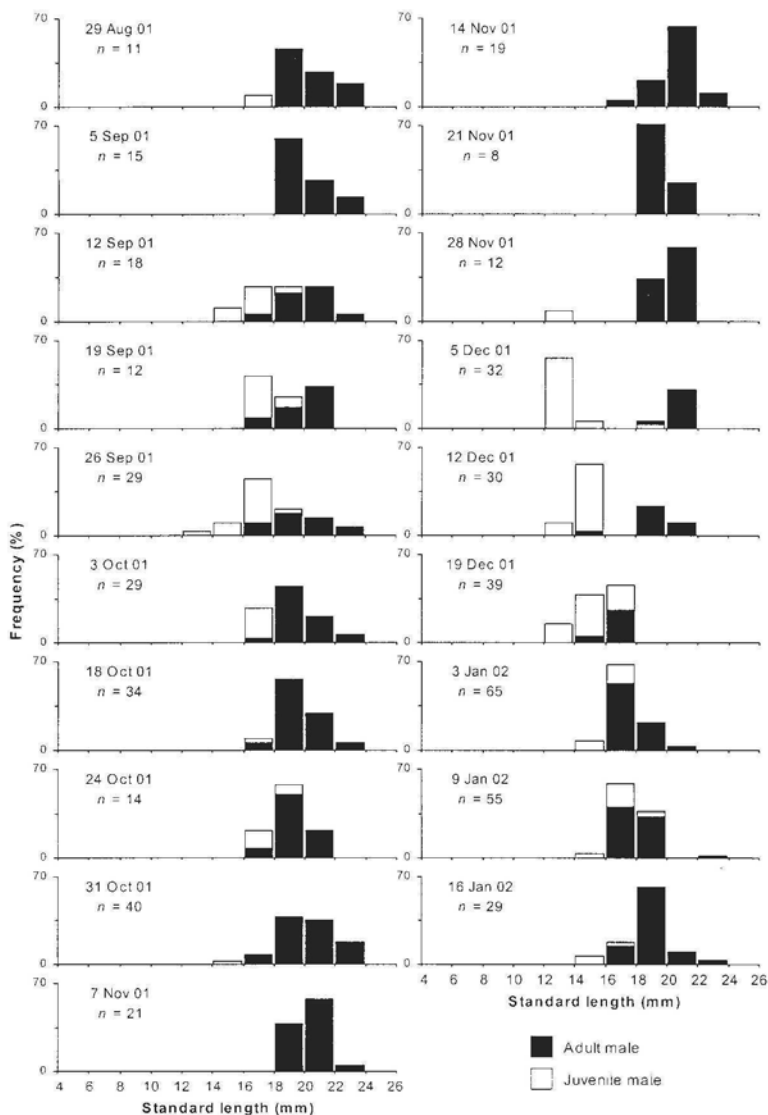


Fig. 2 Length-frequency distributions of female and juvenile undetermined *Gambusia holbrooki* from the Tamar Island Wetlands Reserve, Tasmania, Australia for each sampling occasion between August 2001 and January 2002.

Fig. 3 Length-frequency distributions of adult and juvenile male *Gambusia holbrooki* from the Tamar Island Wetlands Reserve, Tasmania, Australia for each sampling occasion between August 2001 and January 2002.



between 29 August and 12 December 2001, which equates to an average growth rate of 0.18 mm/day over that period. The mean length of the female YOS cohort increased from 8.0 to 29.4 mm SL between 21 November 2001 and 16 January 2002, corresponding to an average of 0.38 mm/day (Fig. 4B).

The increase in the mean SL of OW males between 29 August and 12 December 2001, i.e., 19.5 to 19.9 mm SL, was not significant ($P > 0.05$). By contrast, the mean length of the male YOS cohort increased from 8.0 to 18.8 mm SL between 21 November 2001 and 16 January 2002, corresponding to an average of 0.19 mm/day (Fig. 4C).

The first significant increase ($P > 0.05$) in weekly mean standard length of OW females (20.4 to 24.6 mm SL) was observed between 26 September and 3 October 2001, which coincided with a sharp increase in mean water temperatures from 15.8 to 21.9°C over that period (Fig. 4A,B). The OW females continued to grow gradually after 3 October, with the steady increase in mean SL following a similar trend to that of mean water temperatures (Fig. 4A,B).

Estimated lengths at 50% maturity ($LM_{50\%}$) for male and female *G. holbrooki* derived from the logistic curves were 17.4 and 25.0 mm SL,

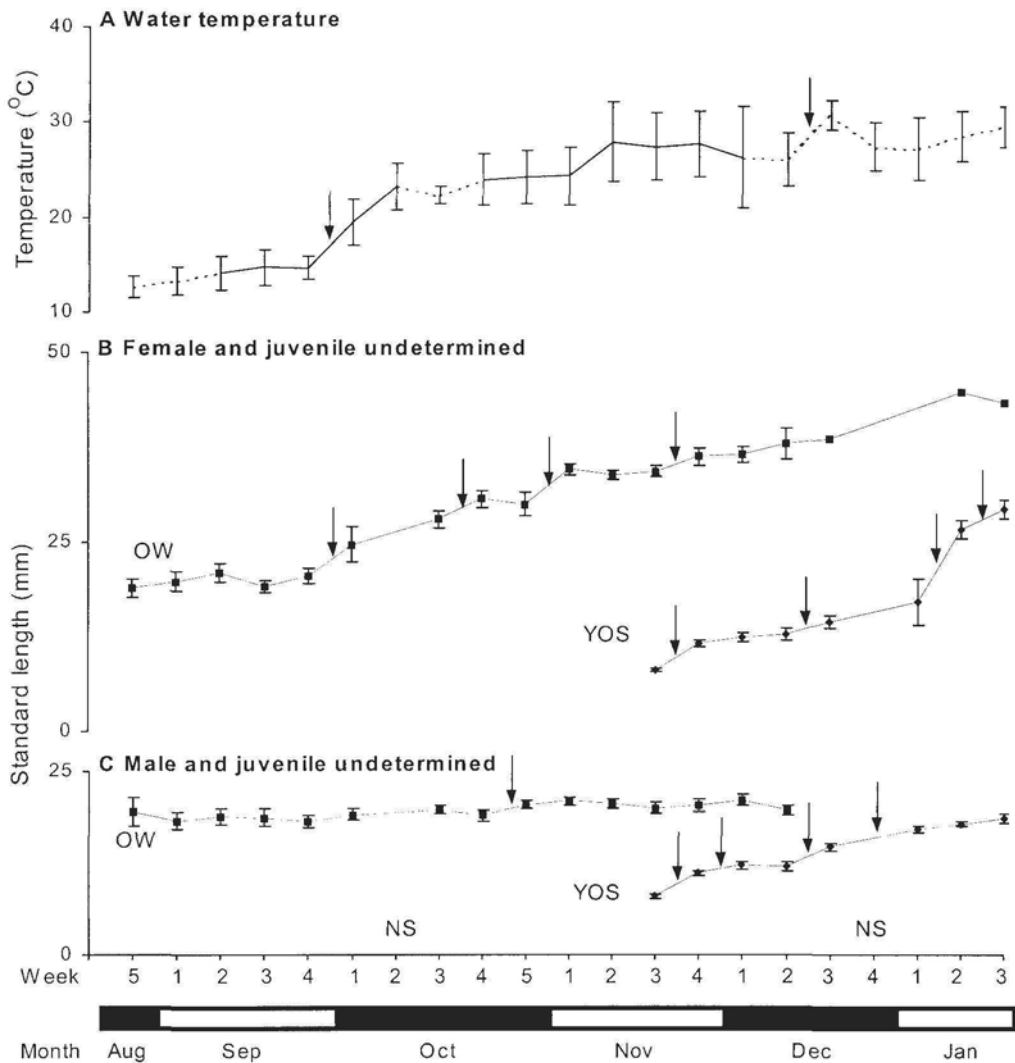


Fig. 4 Weekly mean ($\pm 95\%$ CI) of **A**, daily maximum water temperatures ($^{\circ}\text{C}$), and mean length (SL, mm) ($\pm 95\%$ CI) of identifiable cohorts (over-wintered (OW) and young-of-season (YOS)) of **B**, female and juvenile undetermined, and **C**, male and juvenile undetermined *Gambusia holbrooki* from the Tamar Island Wetlands Reserve, Tasmania, Australia between August 2001 and January 2002. Solid and dotted lines in **A** show actual and predicted temperature respectively (see text for details). No error bars are shown for the last three data points in the female OW cohort because of the small sample sizes (2, 2, and 1, respectively). Arrows indicate statistically significant difference between points. (NS, no sample.)

respectively (Fig. 5). Both YOS females and males reached their respective $\text{LM}_{50\%}$ within 7 weeks of birth.

Reproductive biology

Female *G. holbrooki* began maturing by late September 2001, with the percentage of mature females ($\text{ES} \geq 0$) increasing from 8.2 to 66.7%

between 26 September and 18 October 2001 (Fig. 6B). This sharp increment in maturity coincided with a marked rise in mean water temperatures from 14.6 to 22.3 $^{\circ}\text{C}$ over that period (Fig. 4A). Developing embryos were first recorded on 18 October 2001, and offspring first present from 21 November 2001 (Fig. 6A), corresponding to a gestation period of c. 34 days. Female maturity had declined to 7.9% by 19

Fig. 5 Maturity curves of male (open boxes) and female (closed circles) *Gambusia holbrooki*. Length at 50% maturity ($LM_{50\%}$) values for males and females are 17.4 and 25.0 mm standard length, respectively. Logistic curve parameters, males: $a = 28.42$; $b = -1.63$ ($r^2 = 0.99$; $n = 521$); females: $a = 26.62$; $b = -1.06$ ($r^2 = 0.96$; $n = 927$).

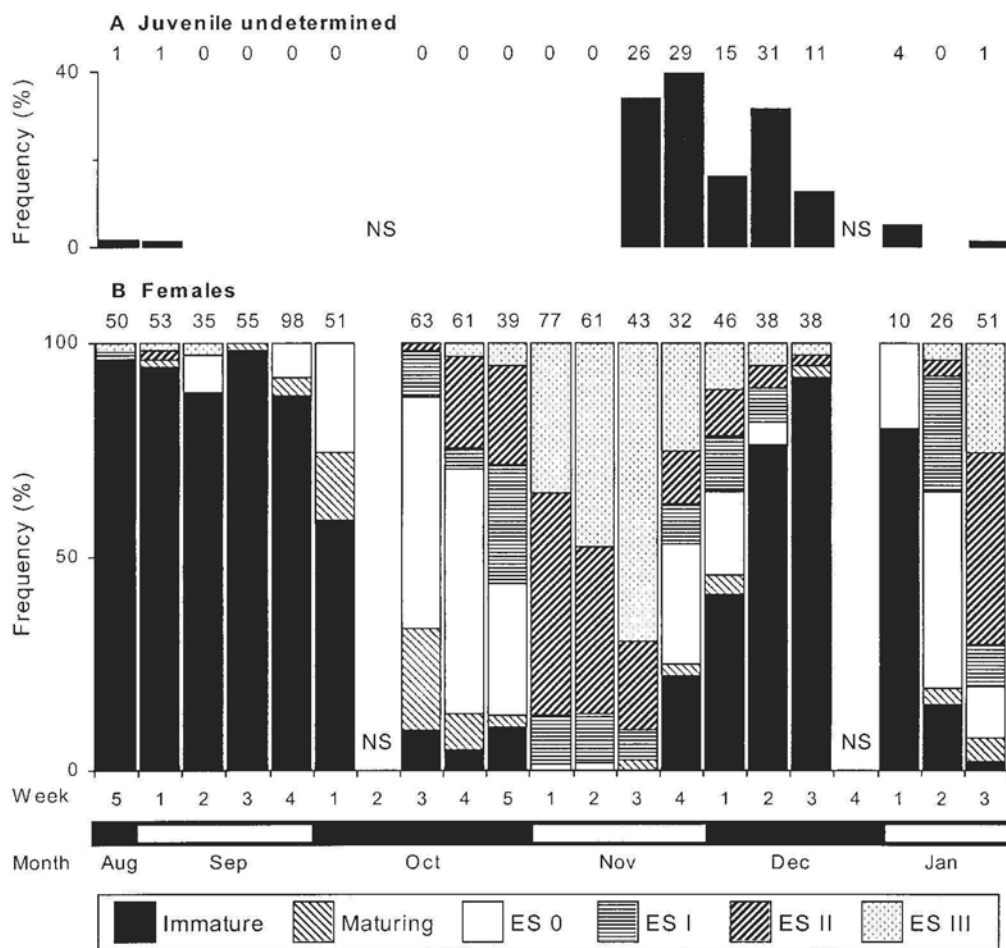
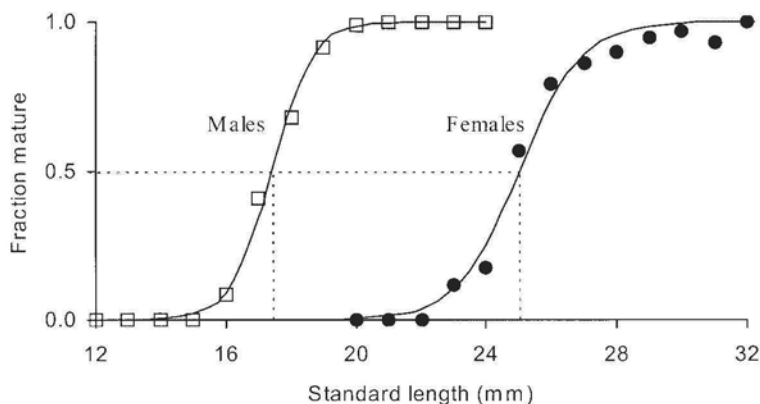


Fig. 6 Percentage of **A**, juvenile undetermined and **B**, frequency of gonadal and embryonic developmental stages (ES 0 – ES III) in female *Gambusia holbrooki* on each sampling occasion from August 2001 to January 2002 from the Tamar Island Wetland Reserve, Tasmania, Australia. Numbers above bars denote total numbers of individuals caught on each sampling occasion. (ES, embryo stage; NS, no sample.)

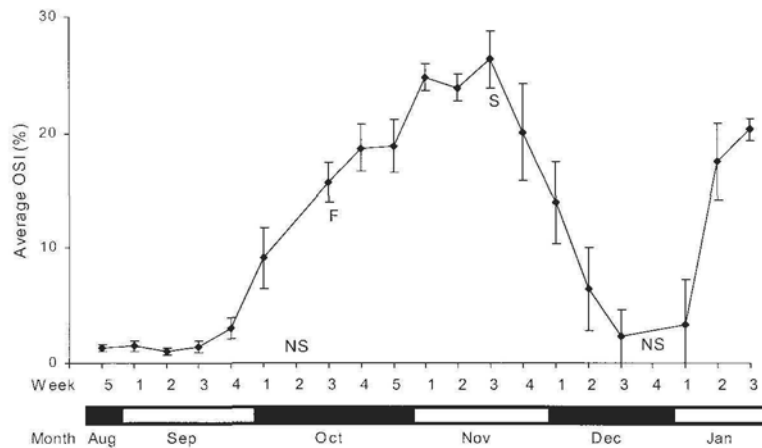


Fig. 7 Average Ovariosomatic Index (OSI, %) (\pm 95% CI) of female *Gambusia holbrooki* from the Tamar Island Wetlands Reserve, Tasmania, Australia for each sampling occasion between August 2001 and January 2002. (F, fertilisation; NS, no sample; S, spawning.)

December 2001, as the YOS recruits dominated the sample. These new recruits began to mature in early January 2002, and by 16 January 92.2% of females were mature (Fig. 6B).

The average ovariosomatic index (OSI) of female *G. holbrooki* increased from <3 in September 2001 to a maximum of 26.3 by 21 November 2001, which corresponded to the first spawning (Fig. 7). The average OSI then decreased to 2.3 by 19 December 2001 before increasing again in January 2002. The maximum individual female OSI recorded (69.8%) was obtained from a 33.6 mm SL female carrying 76 stage III embryos, captured on 21 November 2001.

DISCUSSION

Growth pattern

This study found that the modal length of female *G. holbrooki* increased over time, whereas little variation was observed in males. This is because females continue growing throughout their life to maximise reproductive output, whereas males stop growing shortly after reaching sexual maturity (Vondracek et al. 1988). It is also disadvantageous for males to keep growing, as smaller males have greater efficiency in achieving matings, which explains why small males are genetically maintained in most populations of poeciliid fishes (Bisazza & Pilastro 1997).

The minimum critical temperature for growth of *G. holbrooki* found during this study was 15–19°C. No significant increases in female length were recorded at temperatures <15°C (August to September 2001), whereas significant growth of the

OW cohort was observed at >19°C (October 2001). Similarly, growth in *G. affinis* was found to be nil at 10°C and maximum at 30°C (Wurtsbaugh & Chec 1983), with the transition from slow to relatively rapid growth occurring at 20–25°C (Vondracek et al. 1988).

Reproductive cycle

Female *G. holbrooki* were dominant in most samples collected during this study. This parallels the fact that wild populations of poeciliids often contain a disproportionately large number of females (Snelson 1989), even though equal numbers of both sexes are known to occur at birth (Krumholz 1948; Haynes & Cashner 1995). It is also well known that sex ratios are biased toward females, as males suffer comparatively higher mortalities resulting from factors such as predation, accelerated physiological aging, and stressors such as temperature, overcrowding, and starvation (Snelson 1989). Female dominance is unlikely to affect reproduction at a population level, as a single dominant male can fertilise many females (Snelson 1989), and females are capable of storing sperm for up to eight broods or eight months (Constanz 1989).

The sex ratio in the present study peaked at the time of first reproduction, possibly because of females congregating in shallow areas to breed. These breeding aggregations could help maximise the chances of survival of the offspring, as *Gambusia* are known to frequent shallow waters with elevated temperatures to assist embryonic development (Huff 1994).

The onset of reproduction of *G. holbrooki* recorded between 19 September and 3 October 2001 coincided with a sharp increase in the mean air and

water temperatures. However, temperatures were on average 2°C warmer than normally observed during this period, suggesting that the onset of reproduction could have begun up to 3 weeks earlier than usual. Between 10 October 2001 and 16 January 2002, mean weekly maximum temperatures were on average 2.6°C cooler than normal. This, in turn, would have slowed down the embryonic development and growth of *G. holbrooki*, thereby resulting in slightly greater estimates of age at maturity and gestation time, as well as lower growth rates than those expected in a “normal” season.

The start of the reproductive cycle for female *G. holbrooki* in late September 2001 was signalled by oocytes undergoing vitellogenesis, when maximum average daily temperatures had increased from 14.6 to 19.5°C. This finding matches several studies on *Gambusia* that have attributed temperature as the key factor in the onset of its reproductive cycle (Vondracek et al. 1988; Pen & Potter 1991; Koya & Kamiya 2000). The temperature range for the onset of reproduction of *G. holbrooki* observed during this study is comparable to the >15–16°C range reported for *G. holbrooki* from Collie River in Western Australia (Pen & Potter 1991), and the >14–>18°C range reported for the closely-related *G. affinis* (Medlen 1951; Koya & Kamiya 2000). Juveniles from the first breeding period during this study appeared in November, which coincided with the timing reported for this species from Collie River (Pen & Potter 1991). However, juveniles in southern Queensland were first observed in August (Milton & Arthington 1983), i.e., 3 months earlier than in Tasmania and Western Australia. The mean estimated fecundity of 55.5 obtained for *G. holbrooki* during this study (range 3–144) was also similar to the 47.4 reported for *G. holbrooki* from Collie River (range 8–237), but was considerably higher than the 22.8 reported from southern Queensland (range 3–108) (Milton & Arthington 1983; Pen & Potter 1991).

The c. 34-day gestation period estimated here for *G. holbrooki* is comparable to the 21–30 days range reported for *Gambusia* spp. (Krumholz 1948; Cadwallader & Backhouse 1983; Hubbs & Valdes-Gonzales 1995; Koya et al. 2000). A possible reason for the slightly longer gestation period estimated for *G. holbrooki* during this study is that it was derived from the first reproductive cycle of the season, at the time when water temperatures had not yet reached the breeding optimum, i.e., 25–30°C (Wurtsbaugh & Chec 1983; Vondracek et al. 1988; Huff 1994).

The reason(s) why OW *G. holbrooki* disappeared from the study site after breeding is unclear.

Resource competition from the large numbers of juveniles from the YOS cohort may have driven OWs to other areas of the wetland. However, no OWs were observed in other areas following intensive visual surveys, nor were there signs of post-breeding mortalities. It is also unclear why the YOS cohort was dominated by males between December 2001 and early January 2002, yet females dominated the YOS cohort by mid January 2002. It is possible that females, being larger and having a better swimming capacity, left the spawning area because of overcrowding and resource competition, before returning in mid January 2002 when sexually mature (Congdon 1994).

Distribution and possible impact to Tasmanian native fauna

Since the completion of this study, *G. holbrooki* has been discovered in areas adjacent to the Tamar Island Wetland Reserve (Kerri Lynch pers. comm.). Given their fast reproductive turnover and high survival rates, it is highly likely that they will spread to and colonise other State waterways in the future, either naturally via the Tamar Estuary and/or accidentally through human dispersal. Although there are no data to support the view of a natural dispersal via estuarine waters, the relatively strong tidal currents of the Tamar Estuary may help reduce the likelihood of dispersal of *G. holbrooki* to rivers, as shown for this species in high flow rate conditions (Congdon 1994).

The potential ecological impact of *G. holbrooki* in Tasmania is unknown. One of the major threats could be to native galaxiids, as suggested from the fact that mosquitofish are known to attack and kill adult *Galaxias gracilis* in New Zealand (Rowe 2003). In Tasmania, for example, native species could include the endangered *Galaxias fontanus*, the vulnerable *Galaxias cleaveri*, and the potentially threatened *Galaxiella pusilla*, all of which inhabit lower lying areas of the State (Allen et al. 2002). *G. holbrooki* may also pose a threat to frog populations, including that of the green and gold frog (*Litoria raniformis*) which is listed as vulnerable on Tasmania's Threatened Species Protection Act 1995. As *G. holbrooki* is a known predator of tadpoles of two other closely-related frog species, namely *L. aurea* and *L. dentata* (Morgan & Buttemer 1996), it is possible that *G. holbrooki* could also feed on tadpoles of the threatened frog.

Habitat conditions in Tasmania are more than adequate for the survival and success of *G. holbrooki*, probably favouring large populations to

thrive in water systems located in the low lying areas of the State. Eradicating *G. holbrooki* from Tasmania, on the other hand, may be difficult (if not impossible) because of their rapid, highly successful reproductive turnover and broad physiological tolerances. Given the highly competitive and destructive nature of fishes of this genus worldwide, *G. holbrooki* undoubtedly poses a great risk to Tasmania's endemic freshwater fauna. Consequently, management should focus on containing this introduced pest fish to areas they have already colonised, and minimising pathways of dispersal to others.

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REFERENCES

- Allen, G. R.; Midgley, S. H.; Allen, M. 2002: Field guide to the freshwater fishes of Australia. Perth, Western Australian Museum. 394 p.
- Bisazza, A.; Pilastro, A. 1997: Small male mating advantage and reversed size dimorphism in poeciliid fishes. *Journal of Fish Biology* 50: 397–406.
- Cadwallader, P. L.; Backhouse, G. N. 1983: A guide to the freshwater fish of Victoria. Melbourne, Victorian Government Printing Office. 249 p.
- Congdon, B. C. 1994: Characteristics of dispersal in the eastern mosquitofish *Gambusia holbrooki*. *Journal of Fish Biology* 45: 943–952.
- Constanz, G. D. 1989: Reproductive biology of poeciliid fishes. In: Meffe, G. K.; Snelson, F. F. Jr. ed. Ecology and evolution of livebearing fishes. New Jersey, Prentice Hall. Pp. 33–49.
- Haynes, J. L.; Cashner, R. C. 1995: Life history and population dynamics of the western mosquitofish: a comparison of natural and introduced populations. *Journal of Fish Biology* 46: 1026–1041.
- Howe, E. H. I. 1995: Studies in the biology and reproductive characteristics of *Pseudonugil signifer*. Sydney, University of Technology. 287 p.
- Hubbs, C.; Valdes-Gonzales, A. 1995: Interbrood intervals of *Gambusia* species. Proceedings of the Desert Fishes Council, 1994 Symposium. Pp. 35–36.
- Huff, E. A. 1994: Temperature and its effects on embryonic development in the western mosquitofish (*Gambusia affinis*). *Proceedings of Nebraska Academy of Science* 114: 17–18.
- King, M. 1995: Fisheries biology, assessment and management. Oxford, Fishing News Books. 352 p.
- Koya, Y.; Inoue, M.; Naruse, T.; Sawaguchi, S. 2000: Dynamics of oocyte and embryonic development during ovarian cycle of the viviparous mosquitofish *Gambusia affinis*. *Fisheries Science* 66: 63–70.
- Koya, Y.; Kamiya, E. 2000: Environmental regulation of annual reproductive cycle in the mosquitofish, *Gambusia affinis*. *Journal of Experimental Zoology* 286: 204–211.
- Krumholz, L. A. 1948: Reproduction in the western mosquitofish, *Gambusia affinis*, and its use in mosquito control. *Ecological Monographs* 18: 1–43.
- Lloyd, L. N.; Tomasov, J. F. 1985: Taxonomic status of the mosquitofish, *Gambusia affinis* (Poeciliidae) in Australia. *Australian Journal of Marine and Freshwater Research* 36: 447–451.
- Medlen, A. B. 1951: Preliminary observations of the effects of temperature and light upon reproduction in *Gambusia affinis*. *Copeia* 1951: 148–152.
- Meffe, G. K. 1992: Plasticity of life-history characters in eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae) in response to thermal stress. *Copeia* 1992: 94–102.
- Milton, D. A.; Arthington, A. H. 1983: Reproductive biology of *Gambusia affinis holbrooki* Baird and Girard, *Xiphophorus helleri* (Gunther) and *X. maculatus* (Heckel) (Pisces; Poeciliidae) in Queensland, Australia. *Journal of Fish Biology* 23: 23–41.
- Morgan, L. A.; Buttemer, W. A. 1996: Predation by the non-native fish *Gambusia holbrooki* on small *Litoria aurea* and *L. dentata* tadpoles. *Australian Zoologist* 30(2): 143–149.
- Pen, L. J.; Potter, I. C. 1991: Reproduction, growth and diet of *Gambusia holbrooki* (Girard) in a temperate Australian river. *Aquatic Conservation: Marine and Freshwater Ecosystems* 1: 159–127.
- Rowe, D. 2003: Balancing native fish diversity, exotic fish impacts, and recreational fishing in New Zealand north island dune lakes. In: Beumer, J. P.; Grant, A.; Smith, D. C. ed. Aquatic protected areas—what works best and how do we know? World Congress on Aquatic Protected Areas proceedings. Cairns, Australia, August 2002. Pp. 96–102.

- Snelson, F. F. 1989: Social and environmental control of life history traits in poeciliid fishes. *In*: Meffe, G. K.; Snelson, F. F. Jr. *ed.*, Ecology and evolution of livebearing fishes. New Jersey, Prentice Hall. Pp. 149–161.
- Trendall, J. T. 1981: Covariation of life history traits in the mosquito-fish, *Gambusia affinis*. Unpublished PhD thesis, University of Western Australia, Perth. 179 p.
- Vondracek, B.; Wurtsbaugh, W. A.; Cech, J. J. Jr. 1988: Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. *Environmental Biology of Fishes* 21: 45–57.
- Wilson, F. 1960: A review of the biological control of insects and weeds in Australia and Australian New Guinea. Bucks, England, Commonwealth Agricultural Bureaux. 102 p.
- Wurtsbaugh, W. A.; Cech, J. J. Jr. 1983: Growth and activity of juvenile mosquitofish: temperature and ration effects. *Transactions of the American Fisheries Society* 112: 653–660.