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Reproductive biologies of *Psammogobius knysnaensis* and *Caffrogobius gilchristi* in a warm-temperate South African estuary

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Abstract

Reproductive biologies (spawning period, length at maturity and fecundity) of Knysna sand goby *Psammogobius knysnaensis* and Prison goby *Caffrogobius gilchristi* were investigated between September 2018 and August 2019 in the warm-temperate Sundays Estuary, South Africa. The two species reproduced during the same period (spring and summer), with peak reproduction occurring in January. *Psammogobius knysnaensis* egg production was higher than *C. gilchristi* and was not affected by fish size. Although *C. gilchristi* egg production increased with fish size, this was not significant. *Psammogobius knysnaensis* reached L_{M50} at smaller sizes than *C. gilchristi.* Reproductive periods were likely coupled with prey availability, as phytoplankton and zooplankton abundances are highest in warm-temperate estuaries during this period. The ability of these gobies to reproduce at small sizes (< 40 mm TL), which is an adaptive trait of many r-selected species, underpins their high abundance in South African estuaries as they are well adapted to stochastic environments.

Keywords: fecundity, goby, length at maturity, spawning

Introduction

Reproductive strategies determine species persistence and vary across the r/K continuum (Pianka 1970). Many small fish species are r-selected, demonstrating adaptive traits for stochastic and resource limited environments such as estuaries (Teichert et al. 2017). These traits include multiple spawning periods (Torricelli et al. 1985; Mofu et al. 2020), fast growth rates and short life spans, promoting early maturation resulting in high brood and lifetime fecundity (Miller 1961; Arruda et al. 1993; Azevedo and Simas 2000). Quantitative assessment of reproductive traits, i.e. fecundity, length at maturity, and spawning period can be used to estimate species-specific relative abundance and reproductive success (Sarker et al. 2002).

Gobies are small benthic fishes with generalist habitat associations, ranging from marine, brackish to freshwater environments, although the majority of species are marine (Tutman et al. 2020). The family Gobiidae is the largest teleost family globally, with more than 2000 species worldwide (Thacker and Roje 2011), occupying a broad range of biogeographic locations (Tutman et al. 2020). Gobiidae are abundant in the subtropical and temperate regions of southern Africa (Whitfield 1999). In South African estuaries gobies dominate the benthic fish assemblage in terms of richness and abundance, and are present in estuaries across the country (Harrison and Whitfield 2006; James et al. 2007). In South African estuaries, the family is represented by 24 species, with the number of species decreasing from the subtropical to the warm-temperate and cool- temperate regions, respectively (Whitfield 2019).

Within temperate estuaries, two of the most abundant gobies are the Knysna sand goby *Psammogobius knysnaensis* (Smith, 1935) and Prison goby *Caffrogobius gilchristi* (Boulenger, 1898) (James et al. 2007). *Psammogobius knysnaensis* is endemic to southern Africa, ranging from Port Nolloth to KwaZulu-Natal (Whitfield 2019) and is abundant in the sandy lower reaches of estuaries (Richardson et al. 2006; Bailey and James 2013; Nodo et al. 2018). *Caffrogobius gilchristi* is also endemic to South Africa, occurring from the Olifants Estuary on the west coast to Durban Bay on the east coast (Whitfield 2019). The species is associated with muddy habitats located in the middle and lower reaches of estuaries (e.g. Nodo et al. 2018). Limited information on the reproductive biology of *P. knysnaensis* and *C. gilchristi* is available from the permanently open Palmiet Estuary and the temporarily open/closed Kleinmond and Bot estuaries on the southwestern Cape coastline (transition zone between the cool and warm-temperate regions) as part of a larger study on the fish communities of these estuaries (Bennett 1989). There is, however, no detailed data on the reproductive biology of these species and no comparative data from the southeastern Cape, which is in the middle of the warm-temperate region.

Here we describe the reproductive biology of *P. knysnaensis* and *C. gilchristi* in the permanently open Sundays Estuary on the southeast coast of South Africa. The purpose of the study is to fill the current data paucity and further our understanding of how these two closely related species coexist in high numbers in warm-temperate estuaries and determine a baseline in reproductive traits for future monitoring purposes. In particular, we determine and contrast (1) the spawning period, (2) length at maturity and (3) fecundity for both gobiid species.

Methods and study area

Sampling was conducted over a 12-month period between September 2018 and August 2019 in the Sundays Estuary. This is a predominantly open estuary flowing into Algoa Bay in the Indian Ocean at 33°43'14.5"S 25°51'10.4"E, 35 km north-east of Gqeberha, South Africa. During the sampling period, both mean surface temperature (19.55°C – 16.83°C) and salinity (27.58‰ – 5.40‰) decreased from the mouth to the head of the estuary.

Sampling was conducted once a month using a small mesh (5 mm) seine net (30 m long x 2 m deep). Seine netting was conducted until a minimum of 30 individuals per species were caught each month, with sampling mainly focused in the lower reaches. After capture, fish were placed in a bucket containing water with 40 mg l^{-1} clove oil for humane euthanasia (Neiffer and Stamper 2009) and then stored on ice until preservation in 70% ethanol in the laboratory.

In the laboratory, all fish were measured for total length (mm TL), weighed (g) (wet weight), dissected and sexed. Monthly sex ratio, together with sex ratio per size class, was determined. A chi-square goodness of fit test was used to compare the monthly and sex ratio per size class with the expected sex ratio of 1:1. Gonadal developmental stages were classified following the procedure developed by Booth and Weyl (2000) for *Glossogobius callidus* in the Sundays River. Spawning season was determined using assessment of monthly gonad maturity stage and the gonado-somatic index (GSI) (wet gonad mass as a percentage of the eviscerated wet body mass). To determine the length of the spawning season, monthly GSI was calculated in Microsoft Excel only from individuals that were larger than mean length-at-maturity (L_m) using the equation:

$$GSI = \frac{gonad\ mass\ (g)}{Eviscerated\ body\ mass\ (g)} * 100 \qquad (1)$$

A chi-square contingency table (12 X 2) was used to detect for significant differences in size class sex ratio and monthly (male and female) GSI among species.

Length at 50% maturity (L_{M50}) was calculated by fitting a logistic equation to the proportion of reproductively capable fish (developed, ripe or spent gonads) collected during the spawning season. The logistic function (fitted in Microsoft Excel) was expressed as:

$$P(L) = \frac{1}{1+\ e^{-(TL-Lm50)/\delta}} \qquad (2)$$

where *P(L)* is the percentage of fish that were found mature at the length TL, L_{M50} is the length at which 50% of the fish in the length class are mature, and δ is the steepness of the ogive (Weyl and Booth 1999).

Curve fitting was performed using the Solver routine in Microsoft Excel by employing the least-squares method. Length at first maturity was taken as the length of the smallest mature male and female. Length at 100% maturity was the length at which all individuals in the sample were mature. The maximum likelihood estimates of the parameters were obtained by minimizing the binomial negative log-likelihood of the form as illustrate in the equation below:

$$-LL = \sum_i \quad [miln\ (\hat{P}) + (ni -\ mi)in(1 -\ \hat{P}i)] \qquad (3)$$

Where $\hat{P}i$ is the proportion predicted of mature fish in length class *i*, *ni* is the number of individuals sampled and *mi* is the number of these individuals that are mature. Likelihood ratio tests were used to test the null hypothesis that male and female L_{M50} values were equal between species. Individuals staged as developing, ripe and spent were used to calculate length at maturity.

Individuals (47 *P. knysnaensis* and 50 *C. gilchristi*) caught during the reproductive period (December to February) were further analysed to calculate relative fecundity for *P. knysnaensis* and *C. gilchristi*. A Zeiss Stemi 508 dissecting microscope was used for manual counting of eggs to determine fecundity (relative fecundity), which is the number of mature, yolked and un-ovulated eggs of fish before spawning (Indira et al. 2013). Relative fecundity was assessed by dividing the number of all vitellogenic oocytes by wet body mass.

Results

Overall, 1090 individuals of *P. knysnaensis*, (492 male, 598 female) and 948 individuals of *C. gilchristi*, (497 male, 452 female) were caught (Table 1). Monthly sex ratio significantly changed in both species (*P. knysnaensis* $X^2 = 31.13$, $p < 0.05$; *C. gilchristi* $X^2 = 24.61$, $p < 0.05$) (Table 2). There was a significant difference in sex ratio per size class for both species (*P. knysnaensis* $X^2 = 49.03$, $P < 0.05$; *C. gilchristi* $X^2 = 80.76$, $p < 0.05$) (Table 2). In both species, males were observed to be larger than females. Male and female *P. knysnaensis* ranged in size from 17.06–69.40 mm and 18–62.19 mm respectively. Male and female *C. gilchristi* ranged in size from 17.26–94.00 mm and 22.58–69.28 mm respectively. Distinguishing between sexes in individuals below 37.00 mm TL in *C. gilchristi* was difficult, as all appeared to have male characteristics.

In male and female *P. knysnaensis* mean GSI did not exceed 2% and 8%, respectively, indicating low gonadal investment (Figure 1a). The mean GSI of males and females was highest in summer, reaching its peak in January (Figure 1a). For both sexes of *P. knysnaensis*, a sharp decrease in GSI was observed in autumn (March, April, May) (Figure 1a). Male and female GSI of *C. gilchristi* did not exceed 2% and 14% respectively (Figure 1b). In both sexes of *C. gilchristi* GSI was highest from late winter to summer (August to February), with peak spawning occurring in October, January and August (Figure 1b). There were significant monthly differences between the GSI of males and females of both species. However, GSI of male *P. knysnaensis* and male *C. gilchristi* ($p > 0.05$, $X^2 = 0.25$, df = 11) did not differ, and similarly GSI of female *P. knysnaensis* and female *C. gilchristi* ($p > 0.05$, $X^2 = 4.82$, df = 11) did not differ (Table 2).

The smallest mature male and female *P. knysnaensis* were 29.82 and 26.68 mm TL, respectively (Figure 2a, b). Male *P. knysnaensis* reached L_{M50} at 39.00 mm TL, while in females L_{M50} occurred at 45.00 mm TL (Figure 2a, b). The smallest mature male and female *C. gilchristi* were 31.62 and 38 mm TL respectively (Figure 2c, d). Male and female *C. gilchristi* reached L_{M50} at 45.00 and 40 mm TL respectively (Figure 2c, d). All individuals over 60.00 mm TL were mature. There was no significant difference in L_{M50} between sexes among the species ($p > 0.05$, $X^2 = 0.14$, df = 1) (Table 2). Female and male *C. gilchristi* and female *P. knysnaensis* reached 100% maturity at 60 mm TL. Male *P. knysnaensis* reached L_{M100} at 50.00 mm TL.

Fecundity in *P. knysnaensis* had no relationship with fish length ($R^2 = 0.0037$). *Caffrogobius gilchristi* fecundity was weakly positively correlated to length ($R^2 = 0.2475$). *Psammogobius knysnaensis* had higher absolute fecundity (2321.6), regardless of *C. gilchristi* (1650.17) having a stronger fecundity/length relationship.

Discussion

Determining differences in functionally similar, sympatric species reproductive strategies may further our understanding of their mechanisms of coexistence (Gómez-Llano et al. 2021). Both species exhibited similar temporal variations in sex ratios and had overlapping spawning seasons. As the reproductive period of the two species overlaps, this suggests that they need to partition resources (e.g. food and space), particularly during peak spawning periods unless resources are not limited. We determine both species share life history strategies (fast paced, r-selected) common across the gobiid family where reproductive periods are linked to resource peaks (Bennett 1989; Froneman 2001).

The reproductive period of both species coincides with a period of high food availability, as phytoplankton and zooplankton abundance are highest in warm-temperate estuaries during spring and summer (e.g., Froneman 2001). Reproduction period in the present study (spring and summer) concurs with those previously reported by Bennett (1989) in the Palmiet, Kleinmond and Bot estuaries on the southwestern Cape coastline. However, in the Sundays Estuary *C. gilchristi* reached 50% maturity at smaller sizes than those reported in Bennett (1989). The majority of gobies sampled by Bennett (1989) were from the Bot Estuary, which had been closed for three years at the time of sampling. Although competition for food can suppress the reproductive success of fish, as they depend on energy investment for reproduction (Fraser and Gilliam 1992; Santos et al. 2010) this is unlikely the case in the current study as reproduction occurred during periods of high prey availability (Froneman 2001).

Psammogobius knysnaensis had higher fecundity with no relation to length, while *C. gilchristi* had lower fecundity, which increased with fish size. This is a type of niche separation, whereby one strategy (*C. gilchristi*) is to reproduce at larger sizes while the other (*P. knysnaensis*) is to reproduce at smaller sizes. In the lower Rhine River (Germany), three co-existing Gobiidae species partitioned their resources by reproducing at different lengths and different seasons (Gertzen et al. 2016). Reproduction can be suppressed when occurring at the same size in each species (Thresher 1983; Persson 1990).

Goby lifespan can range from under a year to over seven years (Arruda et al. 1993; Ilkyaz et al. 2011; Huo et al. 2014). Fish species with short life spans invest highly in reproduction with characteristically early maturity, extended spawning seasons and multiple spawning (Grabowska and Przybylski 2015). Although multiple spawning was not investigated specifically in this study, gobies commonly exhibit a multiple spawning strategy to enhance reproductive fitness and success in dynamic and unpredictable estuary environments (Mazzoldi and Rasotto 2001; Nicholson et al. 2008; Koutrakis and Tsikliras 2009; Dinh 2018). This has been documented in other species such as the Padanian goby *Padogobius martensi* (Bonaparte 1846) and burrowing goby *Trypauchen vagina* (Bloch and Schneider 1801), which can also spawn more than once in the same spawning period (Cinquetti and Rinaldi 1987; Dinh 2018). We suspect both *P. knysnaensis* and *C. gilchristi* may have multiple spawning events due to low GSI and extended reproductive period (spring and summer) (Rizzo and Bazzoli 2020).

Fast growth rate in gobies enables them to reproduce within the first year (i.e. age-0) (Bouchereau and Guelorget 1998; Azevedo and Simas 2000). Both study species matured early and start to reproduce at less than 40.00 mm TL at age-0, a trait linked to r-selected species with fast paced life history (Pianka 1970; Arruda et al. 1993). This is a trait which is common in other goby species, e.g. the Mediterranean striped goby, *Gobius vittatus* (Vinciguerra 1883), marbled goby *Pomatoschistus marmoratus* and rock goby *Gobius paganellus* (Linnaeus 1758), which are also able to reproduce in the age-0 cohort at small sizes (Azevedo and Simas 2000; Kovačić 2007; Koutrakis and Tsikliras 2009). Their high fecundity, rapid reproduction and fast growth rate, promotes their typically high abundance throughout estuaries (MacInnis and Corkum 2000).

Psammogobius knysnaensis and *C. gilchristi* have the same reproduction period in the Sundays Estuary, with peak reproduction occurring in January. Traits typical of the gobiid family are exhibited in both species, which supports their persistence in South African estuaries. We suggest that due to goby species being so well presented in estuarine environments across the country and life histories that are tightly linked to environmental pulses of resources, they are ideal species for biomonitoring and hypothesis testing. Examples could include: early detection of phenological shifts, the effects of climate change on community abundances and composition and predicting the winners and losers of climate change in functionally similar species.

Author Contributions

Conceptualisation: PN, NJ, OLWF; Data Acquisition and Curation: PN, NJ; Formal Analysis: PN, NJ; Supervision: NJ, JS, OLWF; Writing – Original draft, review and editing: PN, NJ, JS.

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