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REPRODUCTIVE BIOLOGY OF THE RED THROAT EMPEROR *LETHRINUS MINIATUS* (PISCES: LETHRINIDAE) FROM THE SOUTHERN GREAT BARRIER REEF, AUSTRALIA

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ABSTRACT

The reproductive biology of the red throat emperor, *Lethrinus miniatus* (Schneider, 1801) was examined in the southern Great Barrier Reef (GBR), Australia. The species was found to display the characteristics of an incomplete metagynous hermaphrodite based on histological evidence and size frequency information. Over 95% of functional males possessed a remnant lumen, but there was no evidence of oocytes in the testes of males. A single transitional fish was sampled which had both ovarian and testicular tissue present in its gonad. Size frequency data showed that females dominated the smaller size classes with the majority of fish < 40 cm being females. *Lethrinus miniatus* had an extended spawning season from July–November, although spawning was more pronounced during the spring. Spawning was initiated earlier at lower latitudes. There was no particular size or age when sex change occurred since females older than 20 and males as young as 2-yrs old were sampled.

Yield models have commonly been used in the assessment of reef fisheries where data are limited (Buxton, 1992). Their application is somewhat confounded when the species under investigation is a hermaphrodite, as is the case for many reef-dwelling species (Punt et al., 1993). Shapiro (1979) has already stated the need for management plans to be based on yield models that consider sex change in the life history of reef fish. To achieve this, information on the size and/or age at which fish change sex is necessary.

The red throat emperor *Lethrinus miniatus* (Schneider, 1801) is a reef-associated lethrinid fish found across northern Australia, the Coral Sea, New Caledonia, and Norfolk Island. The species is also found in the northern hemisphere around the Ryukyu Islands of Japan (Loubens, 1980; Carpenter and Allen, 1989). It is harvested in all locations, with > 500 t taken in 2000 by commercial line fishermen on the Great Barrier Reef (GBR) alone. The main fishing grounds for *L. miniatus* on the GBR are in the central and southern areas, particularly the Capricorn-Bunker group of reefs and the Swains Reef complex.

We previously reported on the age, growth, and mortality of this species (Brown and Sumpton, 1998), although little is known about its reproductive biology. Walker (1975) described the seasonal change in gonosomatic index (GSI) around Townsville in North Queensland and concluded that the species spawned around July and August. However, he provided limited information on potential sex change and size and age of maturity. Young and Martin (1982) described evidence that *L. miniatus* is a protogynous hermaphrodite based on histological analysis (presence of brown bodies, sperm sinuses at the periphery of the gonad, and a remnant lumen in males) of a few specimens sampled in the Gulf of Carpentaria, but provided no information on the size and/or age at which the presumed sex change occurred. Other species of this genus exhibit a range of reproductive strategies such as juvenile hermaphroditism in *Lethrinus nebulosus* (Ebisawa, 1990), and protogynous hermaphroditism in both *Lethrinus rubioperculatus* (Ebisawa, 1997) and *Lethrinus elongatus* (Wassef and Bawazeer, 1992).

In this study we describe the reproductive biology of *L. miniatus* in the southern GBR, comparing populations from the Swains reefs and the Capricorn-Bunker Group. In particular, we provide further evidence of protogynous hermaphroditism and examine the size and age at which sex change occurs.

Materials and Methods

Lethrinus miniatus were obtained from two areas of the Great Barrier Reef (GBR) between 1990 and 1992: the Capricorn-Bunker Group of reefs at the southern extreme of the GBR (23°10′–24°0′ S) and the southern reefs in the Swains Reef Complex (21°30′–22°20′ S). The fork length (FL) of each fish was measured (± 0.5 cm) and on occasion, the standard length (SL) and total length (TL) were noted. Samples from the Swains were predominantly frozen filleted fish frames that were purchased from commercial fishers. Gonads were removed from these fish in the laboratory and fixed in 10% neutral buffered formalin. Fishes from the Capricorn-Bunker Group were collected by members of the research team during regular monthly sampling trips to the area. Gonads from these fish were generally removed within 4 hrs of death and fixed in the same manner as the Swains samples. Where possible, whole wet weights of fish were recorded to the nearest gram and gonads weighed (± 0.1 g). Gonosomatic indices were calculated as the percentage gonad weight to the gonad-free wet body weight for all fish older than 2 yrs. Where the whole body weight was not available, it was estimated from the relationship between fork length and total wet weight.

Gonads from 1979 fish were examined microscopically after sectioning the middle portion of one lobe at a thickness of 6 μm and staining with haematoxylin and eosin. Classification of male and female gonads followed the scheme of Moe (1969), as did the classification of female oocytes. The presence or absence of brown bodies, oocyte atresia, and a remnant lumen was also noted (Sadovy and Shapiro, 1987).

Fishes were aged from sectioned (300 μm) sagittal otoliths, removed at the same time as the gonads (see Brown and Sumpton, 1998 for detailed methods of ageing). Only 92% of the fish could be aged due to difficulties in otolith interpretation.

Results

Females dominated the regional (Fig. 1) and site-specific catch (Fig. 2). Overall, 1612 females and 367 males were sampled. Significantly more ($t = 7.81$, $df = 16$, $P < 0.001$) females were sampled from both the Capricorn-Bunker reefs and Swains Reefs ($t = 4.39$, $df = 18$, $P < 0.001$). July was the only month where males outnumbered females. All fish < 30 cm (FL) were females, although there were females captured throughout the entire size range sampled. By contrast, males often dominated the larger size classes (Fig. 3). It was not until fish reached around 45 cm (FL) that males comprised 50% of the samples. Similarly, males did not appear in samples until about age three (Fig. 4). Only four, 2-yr old fish were classified as males. These ranged in length between 31–33.5 cm (FL) and were all captured in the period July–October. Males and females were equally represented in 6-yr old fish, and females became progressively outnumbered by males in older year-classes. However, the oldest fish sampled was a 25-yr old female.

Over 95% of all males (including both 2-yr old males) that were examined histologically had a remnant lumen, although none had any residual oocytes. In the majority of the other 5% male sections, these features were not visible because of inadequate sample preparation and sectioning. There was only one fish whose gonad contained both ovarian

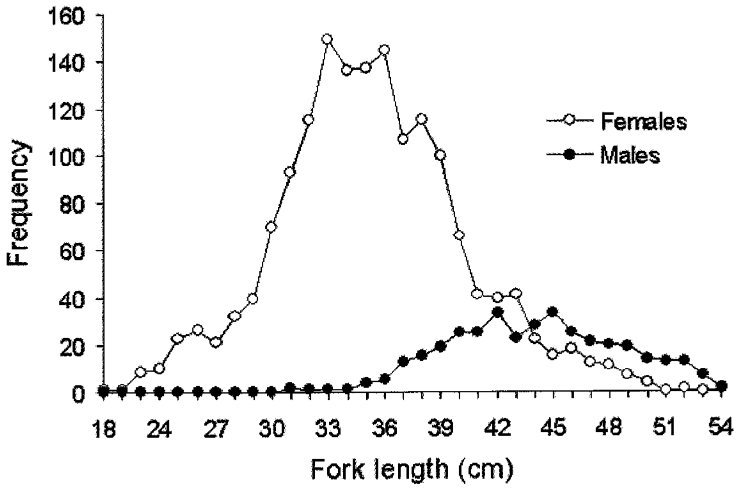

Figure 1. Length frequency of male and female *Lethrinus miniatus* taken from the southern GBR (all samples pooled).

and testicular tissue. That fish was a 41-cm (FL), 5-yr old fish captured during September (Fig. 5).

GSIs calculated for males aged ≥ 2 yrs (Fig. 6) suggested that reproductive activity was taking place in spring, although there was evidence of earlier development of male gonads in the Swains during 1992. Unfortunately, lack of samples during some months hindered any statistical comparisons of the two regions, but there were no obvious dissimilarities. Female GSIs (Fig. 7) similarly showed most reproductive activity during September–November and there was an indication of some gonad development

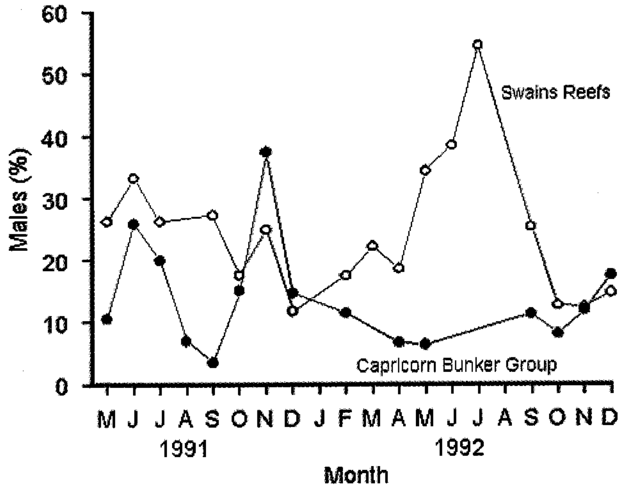

Figure 2. Seasonal change in sex composition of *Lethrinus miniatus* from the Swains Reefs and the Capricorn-Bunker Group, GBR.

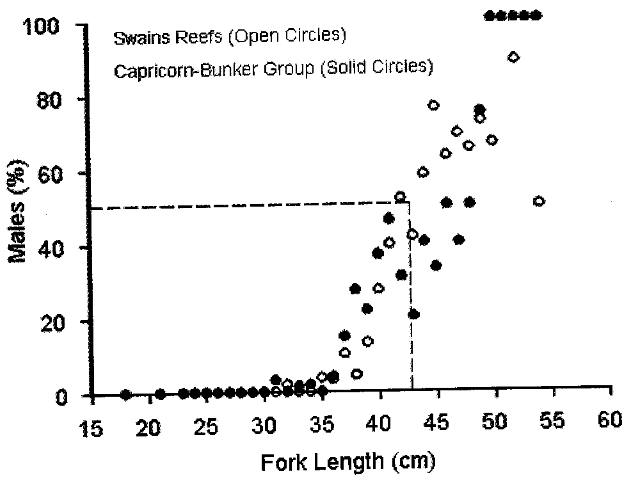

Figure 3. Change in *Lethrinus miniatus* sex composition for samples grouped by fork length.

for Swains fish during the winter of 1992. Histological staging of gonads (Figs. 8,9) was in broad agreement with conclusions drawn from the GSIs and provided more evidence suggesting an earlier spawning of the Swains population. Female fish with active gonads (stage 4) were caught during June/July 1991 at the Swains when they were absent in samples collected in the Capricorn-Bunker Group. There was some evidence of spawning activity at both areas in all months apart from February–May 1992 and December 1992.

Histological examination of gonads failed to adequately provide features that could be used to consistently distinguish resting females from virgins. This made it difficult to determine the size or age at sexual maturity. However, by examining the size and age of fish of various gonad stages during the presumed spawning season (July–November), it was possible to determine the size and age at which *L. miniatus* are capable of spawning (Tables 1,2). There were no 1-yr old fish or fish < 30 cm (FL) which showed any sign of

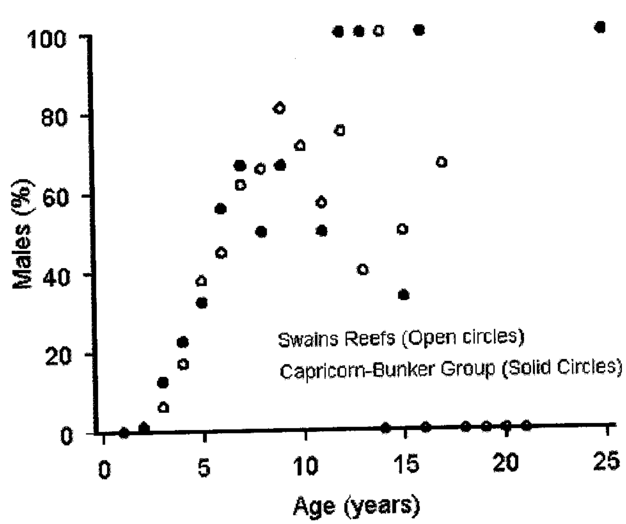

Figure 4. Change in *Lethrinus miniatus* sex composition for samples grouped by age.

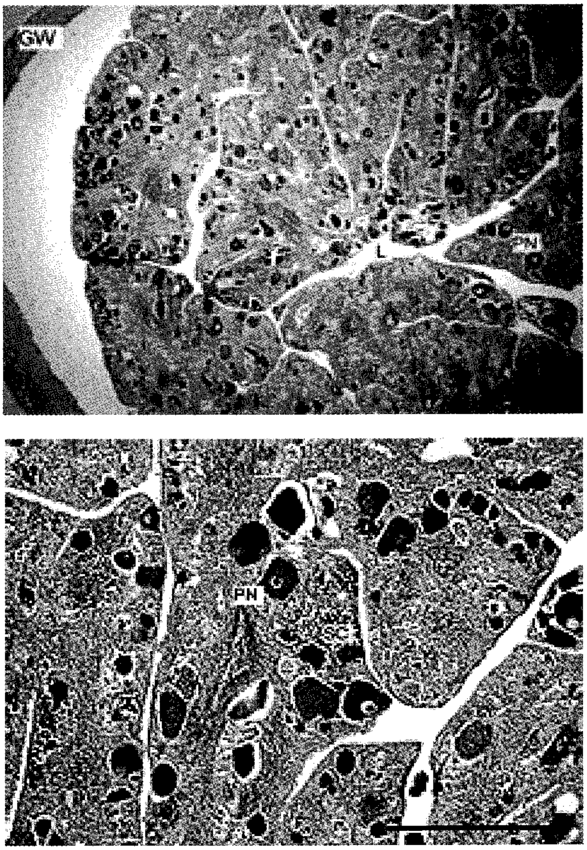

Figure 5. Late transitional gonad showing oocytes and sperm proliferation. (GW = gonad wall, PN = perinucleolus oocytes, SC = spermatocytes, L = ovarian lumen, Scale bar = 200 μ).

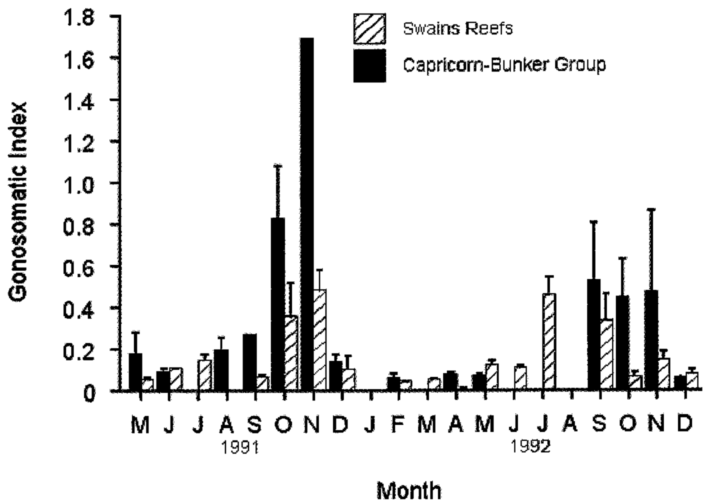

Figure 6. Seasonal change in gonosomatic indices of male *Lethrinus miniatus* greater than 2-yrs old. Bars are means +1 SE.

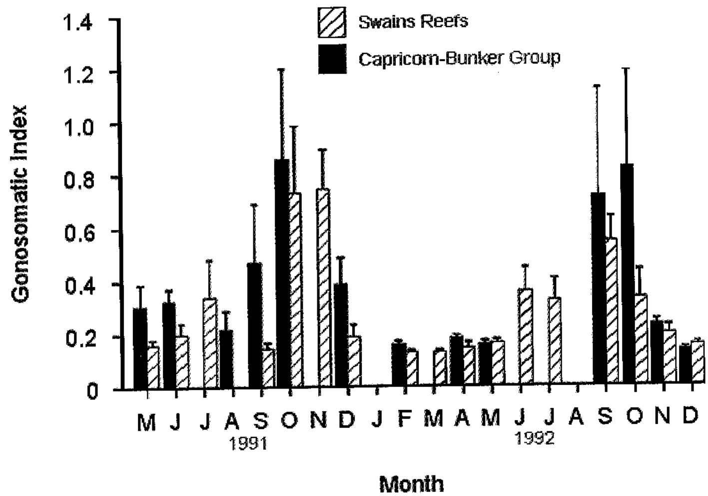

Figure 7. Seasonal change in gonosomatic indices of female *Lethrinus miniatus* greater than 2-yrs old. Bars are means +1 SE.

vitellogenesis (stage 3 oocytes) during the spawning season. Likewise, there were few 2-yr old fish or fish between 30 and 34 cm (FL) with vitellogenic oocytes (stage 3). It was not until age six (40 cm FL) that the majority of fish caught during the spawning season had active gonads and even then most of them were males. No immature male fish were sampled during the spawning season.

Discussion

Results of the present study support earlier suggestions of protogynous hermaphroditism in *L. miniatus*. Protogynous hermaphroditism was first suggested by Young and Martin (1982), who examined eight *L. miniatus* collected from the Gulf of Carpentaria and observed crypts of spermatogonia in gonads with degenerating oocytes, and Church (1985) who found the length frequency distribution of male *L. miniatus* at Norfolk Island to be displaced to the right. However, Sadovy and Shapiro (1987) reviewed the criteria

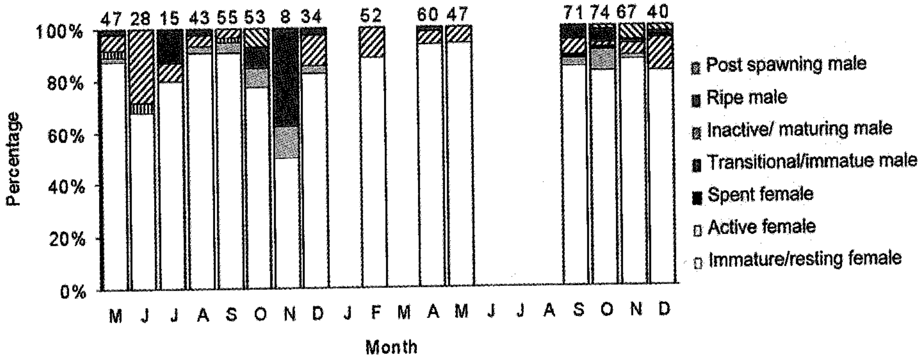

Figure 8. Seasonal changes in the percentage of *Lethrinus miniatus* of various gonad stages sampled from the Capricorn-Bunker Group. Sample sizes are shown above each bar.

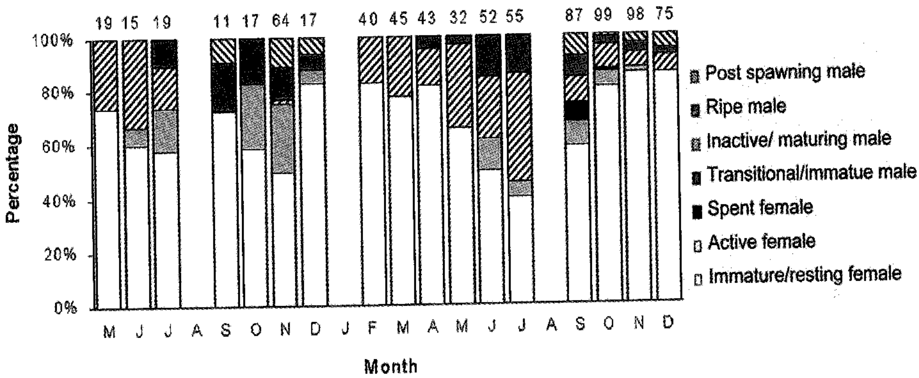

Figure 9. Seasonal changes in the percentage of *Lethrinus miniatus* of various gonad stages sampled from the Swains Reef. Sample sizes are shown above each bar.

for diagnosing hermaphroditism in fishes and noted that bimodality in size-frequency distributions on its own was not a reliable indicator of sex reversal. They suggested that a number of indicative features such as brown bodies, sperm sinuses at the gonad periphery, a remnant lumen, and transitional individuals are necessary for diagnosis. Here we recorded a remnant lumen in the histological sections of the majority of male gonads, as well as a single specimen with both male and female gonadal tissues. Sexual bimodality in both age and length frequency distributions was further evidence of protogynous hermaphroditism. It was not until approximately age six (40–45 cm FL) that the number of males in samples equaled the number of females. It was interesting to note the sampling of a few 2-yr-old males. These fish were all close to 3-yrs old because they were sampled after June when there was a large marginal increment between the last opaque band and the edge of the otolith (Brown and Sumpton, 1998). It is possible that these fish were primary males that developed directly from immature fish.

The mechanism that triggers sex reversal in these fish is unknown, although it is clear that there is no set size or age at which sex change occurs since primary females > 20 yrs of age, and secondary males < 3-yrs old were caught. The fact that many older females were found (indeed the oldest fish was female) may suggest that not all fish undergo sex change. According to Smith (1967), the features observed in the present study would classify *L. minatus* as an incomplete metagynous hermaphrodite, that is, where the sex change is a continuous process that takes place over a wide range of sizes and ages.

In the southern GBR, *L. miniatus* are about 3-yrs old and 35–40 cm (FL) at the time of first reproduction, although some fish as small as 30 cm (FL) were sexually mature. Walker (1975) suggested that sexual maturity in *L. miniatus* from the central GBR was attained by fish as small as 35 cm (FL), a size that is considerably larger than the smallest mature female sampled by the present study. However, estimates of average age and size of first reproduction were in broad agreement between the two studies. It was also clear that there was considerable variation in the size and age at which sexual maturity was reached.

Spawning activity of *L. miniatus* from the southern GBR takes place over an extended period between July and November with the bulk of spawning occurring during the latter 3 mo of this period. Fishes also appear to spawn earlier at the Swains Reefs than at the Capricorn-Bunker Group. In the central GBR, *L. miniatus* spawns predominantly during July and August (Walker, 1975). This earlier spawning at lower latitudes is consis-

Table 1. Percentage gonad stages of *Lethrinus miniatus* of various size classes sampled at the Swains and Capricorn-Bunker Group in the GBR from 1990–1992 during July–November.

	Gonad stage (after Moe, 1969)									
Size class (cm)	1 and 2 Immature/ Resting female	3 Mature active female	4 Spent female	5 Transition stage	6 Immature male	7 Mature inactive male	8 Ripening/ Mature male	9 Ripe male	10 Post-spawning male	Sample size
15–19.5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
20–24.5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15
25–29.5	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	97
30–34.5	94.3	3.4	1.0	0.0	0.0	0.0	1.0	0.3	0.0	298
35–39.5	84.5	5.7	1.6	0.0	0.0	0.9	3.2	1.6	2.5	316
40–44.5	49.7	11.5	2.5	0.6	0.0	3.2	10.8	13.4	8.3	157
45–49.5	10.5	22.9	1.9	0.0	0.0	0.0	22.9	30.5	11.4	105
50–54.5	6.9	3.4	0.0	0.0	0.0	0.0	13.8	55.2	20.7	29

Table 2. Percentage gonad stages of *Lethrinus miniatus* of various age classes sampled at the Swains and Capricorn-Bunker Group in the GBR from 1990–1992 during July–November.

	Gonad Stage (after Moe, 1969)									
Age (yrs)	1 and 2 Immature/ Resting female	3 Mature active female	4 Spent female	5 Transition stage	6 Immature male	7 Mature inactive male	8 Ripening/ Mature male	9 Ripe male	10 Post-spawning Male	Sample size
0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	60
2	97.5	0.6	0.3	0.0	0.0	0.3	0.9	0.3	0.0	324
3	84.1	4.5	2.4	0.0	0.0	0.8	2.4	2.0	3.7	245
4	72.8	7.6	2.2	0.0	0.0	1.1	8.7	3.3	4.3	92
5	53.0	15.0	1.0	1.0	0.0	0.0	12.0	11.0	7.0	100
6	45.2	8.1	1.6	0.0	0.0	3.2	19.4	11.3	11.3	62
7	12.5	30.0	0.0	0.0	0.0	2.5	17.5	32.5	5.0	40
8	23.8	4.8	0.0	0.0	0.0	4.8	23.8	42.9	0.0	21
9	0.0	18.8	0.0	0.0	0.0	0.0	18.8	37.5	25.0	16
10	10.0	20.0	0.0	0.0	0.0	0.0	0.0	60.0	10.0	10
11	10.0	30.0	0.0	0.0	0.0	0.0	10.0	40.0	10.0	10
12	0.0	12.5	0.0	0.0	0.0	0.0	12.5	50.0	25.0	8
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	2
14	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
15	0.0	33.3	0.0	0.0	0.0	0.0	0.0	66.7	0.0	3
16	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
17	0.0	33.3	0.0	0.0	0.0	0.0	0.0	33.3	33.3	3
19	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1
20	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	1
25	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	1

tent with the well-documented latitudinal gradient in reproductive timing that has been linked to temperature effects (Roni and Quinn, 1995; Wang and Chen, 1995).

The precise seasonal timing of the sex change process, or indeed if there is a seasonal timing, remains unknown given that only one fish was sampled with both testicular and non-degenerative ovarian material. Given our relatively high sampling intensity, it appears that the sex change process takes place over a relatively short space of time, or alternatively, the catchability of fish undergoing sex change is low.

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