

# RAPID REPRODUCTIVE ANALYSIS AND LENGTH–WEIGHT RELATION FOR RED-BELLIED FUSILIER, *CAESIO CUNING*, AND LONGFIN EMPEROR, *LETHRINUS ERYTHROPTERUS* (ACTINOPTERYGII: PERCIFORMES: CAESIONIDAE AND LETHRINIDAE) FROM A REMOTE VILLAGE IN PAPUA NEW GUINEA

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**Abstract.** We present length–weight relations (LWR) and use rapid, low-cost histological methods to describe the reproductive biology of the red-bellied fusilier, *Caesio cuning* (Bloch, 1791), and the longfin emperor, *Lethrinus erythropterus* Valenciennes, 1830, based on 137 and 139 specimens, respectively, collected from a remote area in Papua New Guinea. The LWR for *C. cuning* is  $W = 0.0208FL^{3.0322}$ . We estimate male  $L_{50}$  at 12.6 cm FL and female  $L_{50}$  at 15.3 cm FL. Overall sex ratio of mature individuals is not significantly different from 1 : 1; however, sex-ratio does vary with length. Females dominate size-classes from 17 through 20 cm and males are more abundant in smaller and larger size classes. The species is a batch-spawning gonochore. Batch fecundity is an exponential function of length  $BF = 0.1163FL^{4.2796}$ . The LWR for *L. erythropterus* is  $W = 0.0145FL^{3.0976}$  for all specimens, but the length–weight relation differs between sexes. We estimate minimum size-at-maturity for males at 19.2 cm FL, and female  $L_{50}$  at 20.4 cm FL. Overall sex ratio of mature individuals is not significantly different from 1 : 1; however sex-ratio does vary with length. Males dominate size classes > 21 cm. The species is a batch-spawning, protogynous hermaphrodite.

**Keywords:** size-at-maturity, reproductive mode, gonadosomatic index, size-specific sex ratios, batch fecundity, Morobe Province

One of the most easily understood concepts in fishery management and conservation is to harvest individuals only after they have grown large enough to reproduce, thus allowing each generation to “seed” the next (Froese 2004). However the concept is difficult to put into practice because basic reproductive information such as size at maturity is lacking for ~83% of exploited species worldwide (Froese and Binohlan 2000). This problem is especially intractable for coral-reef fishes; their sheer diversity, and the supposed cost associated with the reproductive analysis of each species are often cited as barriers to obtaining this important information (Roberts and Polunin 1993, Johannes 1998). Further, many Pacific island nations, where many of the world’s coral reefs are located, have little or no capacity to conduct the reproductive research needed to support fishery management and

conservation (Dalzell 1998). The reason for the latter problem may be as simple as a lack of basic infrastructure (e.g., electrical service needed to operate laboratory equipment) in many parts of these developing countries.

To address these issues, and as part of a larger marine-conservation effort (see Longenecker et al. 2013c), we initiated a research program to generate reproductive information for Pacific coral-reef fishes. We use recently developed methods for rapid, low-cost, on-site, histology-based reproductive analysis that requires minimal research infrastructure (Longenecker et al. 2013a, 2013b). These methods use standard techniques (e.g., plastic embedding) that have been modified such that work can be conducted in remote field settings without electrical service. With these methods, reproductive information can be generated quickly and at low cost, thus eliminating

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the perceived impediments to broad-scale reproductive analysis of Pacific coral-reef fishes. However, in the interest of rapidly increasing the amount of available reproductive information, we analyze only one gonad subsample from the minimum number of specimens necessary to generate estimates of reproductive parameters. Therefore, results of rapid reproductive analysis should be viewed as preliminary.

Our research program consists of annual, two-week field trips to the subsistence-fishing village of Lababia, Papua New Guinea (PNG), which holds traditional tenure over the waters of the Kamiali Wildlife Management Area (KWMA hereafter; Fig. 1). Each year, village residents choose four study species, using the following criteria:

- All are an important part of village fish catch;
- Residents are interested in learning more about each species;
- Published reproductive information is lacking or incomplete;
- Each species is distinctive enough that the chance of misidentification is low.

Lengths, weights, and gonad samples are obtained through regular village fishing activities, which include hook-and-line, spear, and *Derris* fishing. These collecting activities were approved by the relevant local and national authorities.

Our 2013 field season yielded a suitable number of specimens for analysis of the red-bellied fusilier, *Caesio cuning* (Bloch, 1791), and longfin emperor, *Lethrinus erythropterus* Valenciennes, 1830. Both are widespread food fishes in the Indo-Pacific. *C. cuning* ranges from Sri Lanka to Vanuatu and from southern Japan to northern Australia (Carpenter 1988). *L. erythropterus* ranges from the east coast of Africa to the Caroline Islands and from the Philippines to northwestern Australia (Carpenter 2001).

With the following modifications, we used methods described in Longenecker et al. (2013a) to describe length–weight relations, size-at-maturity, reproductive mode, sex-ratios, and length-batch fecundity relations. For batch fecundity analysis, we analyzed ovarian samples that had reached at least maturation ( $\geq$  stage IVa, see Longenecker et al. 2013b for a description of oocyte classification) rather than late vitellogenesis ( $\geq$  IIIb), and we liberated oocytes from the stroma by vigorous shaking rather than with an ultrasonic cleaner. Additionally, we used a gonadosomatic index (GSI) to explore patterns of reproductive periodicity in females:

$$GSI = 100GS^{-1}$$

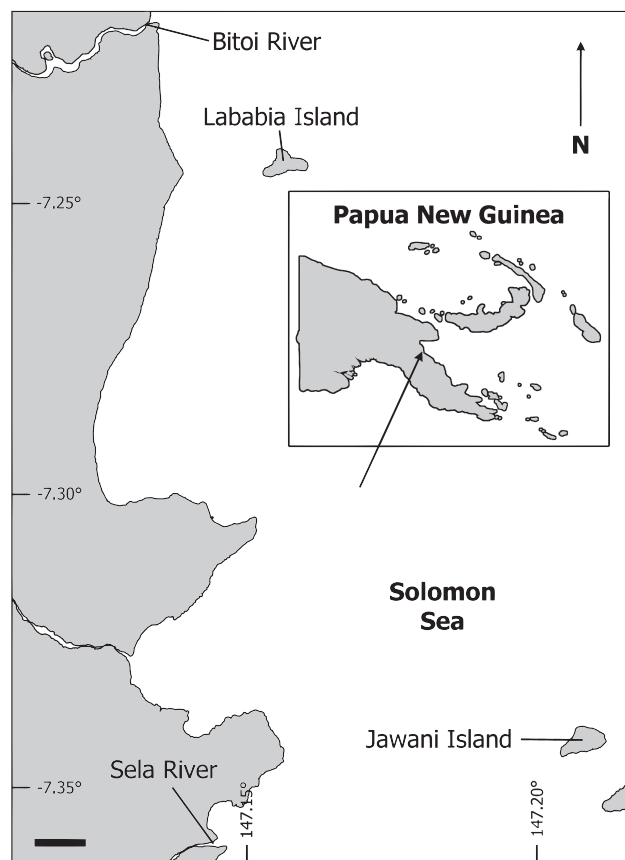
where:  $G$  is total gonad weight and  $S$  is somatic body weight. Results are summarized in Table 1 and presented more fully in separate sections for each species, below.

***Caesio cuning*.** Total body weight ( $W$ ) in g is an approximately cubic function of fork length (FL) in cm (Table 1, Fig. 2). 95% CI of regression parameters  $a$  and  $b$  are  $0.0208 \pm 0.1201$  and  $3.0322 \pm 0.1139$ , respectively ( $r^2 = 0.954$ ,  $n = 137$ , FL range: 8.0–22.7,  $W$  range: 10–250). ANCOVA did not detect a significant sex-based difference in the length–weight relation for this population ( $F = 3.56$ ,  $DF = 1$ ,  $P = 0.061$ ).

The length–weight relation presented here may not be applicable throughout the range of the species. *Caesio cuning* populations in the Coral Triangle represent three stocks, with significant limits to genetic exchange between individuals from New Guinea and those in Pacific and Indian Ocean clades (Ackiss et al. 2013). Further, the maximum length of individuals at KWMA appears to be smaller than the maximum reported length of approximately 42 cm FL, derived by applying the TL–FL relation of Froese and Pauly (2013) to the maximum total length of 50 cm (Carpenter 1988, Allen and Swainston 1993). The largest specimen in the presently reported study was 22.7 cm FL, whereas the largest published length for *C. cuning* at KWMA is 31 cm FL (Longenecker et al. 2013c). The latter value is based on laser-videogrammetry-based length estimates for 1262 free-swimming individuals observed over five field seasons between depths of 0–94 m.

We calculated GSI values for 78 female *Caesio cuning*. The time period represented by our collection was limited (21 February to 8 April, 2013), during this period GSI values appear elevated around the new moon in March (Fig. 3).

We histologically examined gonads of 3 undifferentiated, 49 male, and 80 female *Caesio cuning*. Figure 4 shows examples of immature and mature testes and



**Fig. 1.** Map of the sampling area; Kamiali Wildlife Management Area, Papua New Guinea, is bounded by the Bitoi and Sela Rivers and includes Lababia and Jawani Islands; Scale bar = 1 km

ovaries. Ovaries of mature females contained several discrete stages of oocytes (Fig. 4B), indicating group-synchronous oocyte development (Wallace and Selman 1981). We therefore classify *C. cuning* as a batch spawner. Sexual differentiation occurs around 12 cm FL. The smallest male with spermiated testes was 12.6 cm FL. For males, the size at which 50% of individuals are mature ( $L_{50}$ ) is 12.6 cm FL (Fig. 5). This estimate assumes one-half of undifferentiated specimens were male. All males  $\geq 18$  cm were mature. Ovaries contained vitellogenic oocytes in females as small as 15.1 cm FL. On the basis of specimens collected in March (including one-half of undifferentiated specimens), we estimate female  $L_{50}$  at 15.3 cm FL (Fig. 5). Plotting all female specimens or only

those collected in March and April changed the  $L_{50}$  estimate by a maximum 2 mm.

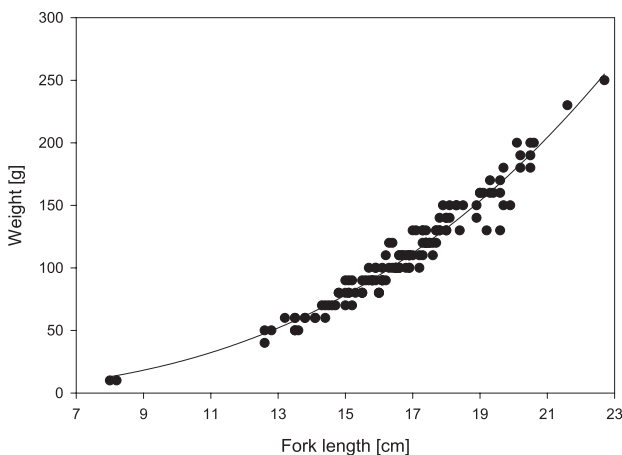
Our minimum-size-at-maturity ( $L_m$ ) and  $L_{50}$  values for both sexes are substantially smaller than  $L_m$  estimates (26.7 cm for males, 32.3 cm for females) derived from the empirical equations of Froese and Binohlan (2000). For instance, considering the more conservative of the size-at-maturity values we present,  $L_{50}$  for either sex is only 47% of the empirically derived  $L_m$  value. Because the estimate derived from Froese and Binohlan (2000) is based on maximum length, this discrepancy appears to be driven by the maximum published length for *C. cuning* being greater than the maximum length observed for the population at KWMA. When maximum length at KMWA is

**Table 1**

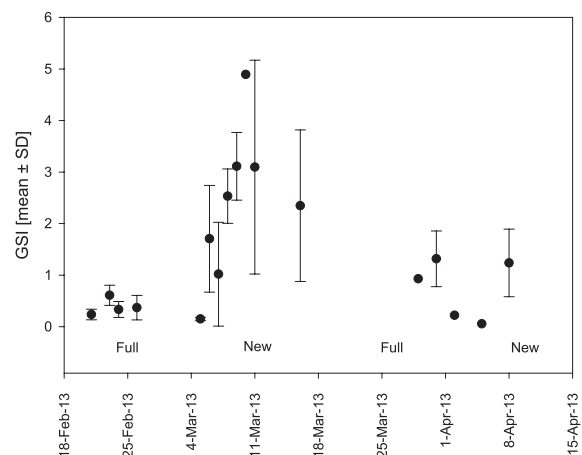
Summary of length–weight relations and reproductive information for red-bellied fusilier, *Caesio cuning*, and longfin emperor, *Lethrinus erythropterus*, from the Kamiali Wildlife Management Area, Papua New Guinea

	<i>Caesio cuning</i>	<i>Lethrinus erythropterus</i>
Length–Weight ♂ + ♀	$W = 0.0208FL^{3.0322}$	$W = 0.0145FL^{3.0976}$
Length–Weight ♂	—	$W = 0.1673FL^{2.3023}$
Length–Weight ♀	—	$W = 0.0077FL^{3.2264}$
♂ $L_m$	12.6	19.2
♀ $L_m$	15.1	18.0
♂ $L_{50}$	12.6	—
♀ $L_{50}$	15.3	20.4
Reproductive mode	gonochore	protogynous
Oocyte development	group synchronous	group synchronous
Sex ratio (overall) ♂ : ♀	1 : 1.63	1 : 5.21
Sex ratio (mature) ♂ : ♀	1 : 0.90	1 : 0.92
Size-specific sex ratio	$\% \text{ ♀} = 85.81e^{(-0.5(\frac{FL-18.62}{1.65})^2)}$	$\% \text{ ♀} = 456.71 - 19.13FL$
Batch fecundity	$BF = 0.1163FL^{4.2796}$	—

$L_m$  = minimum mature length (the smallest mature individual observed during the presently reported study),  $L_{50}$  = length at 50% maturity.



**Fig. 2.** Length–weight relation for red-bellied fusilier, *Caesio cuning*, from the Kamiali Wildlife Management Area, Papua New Guinea



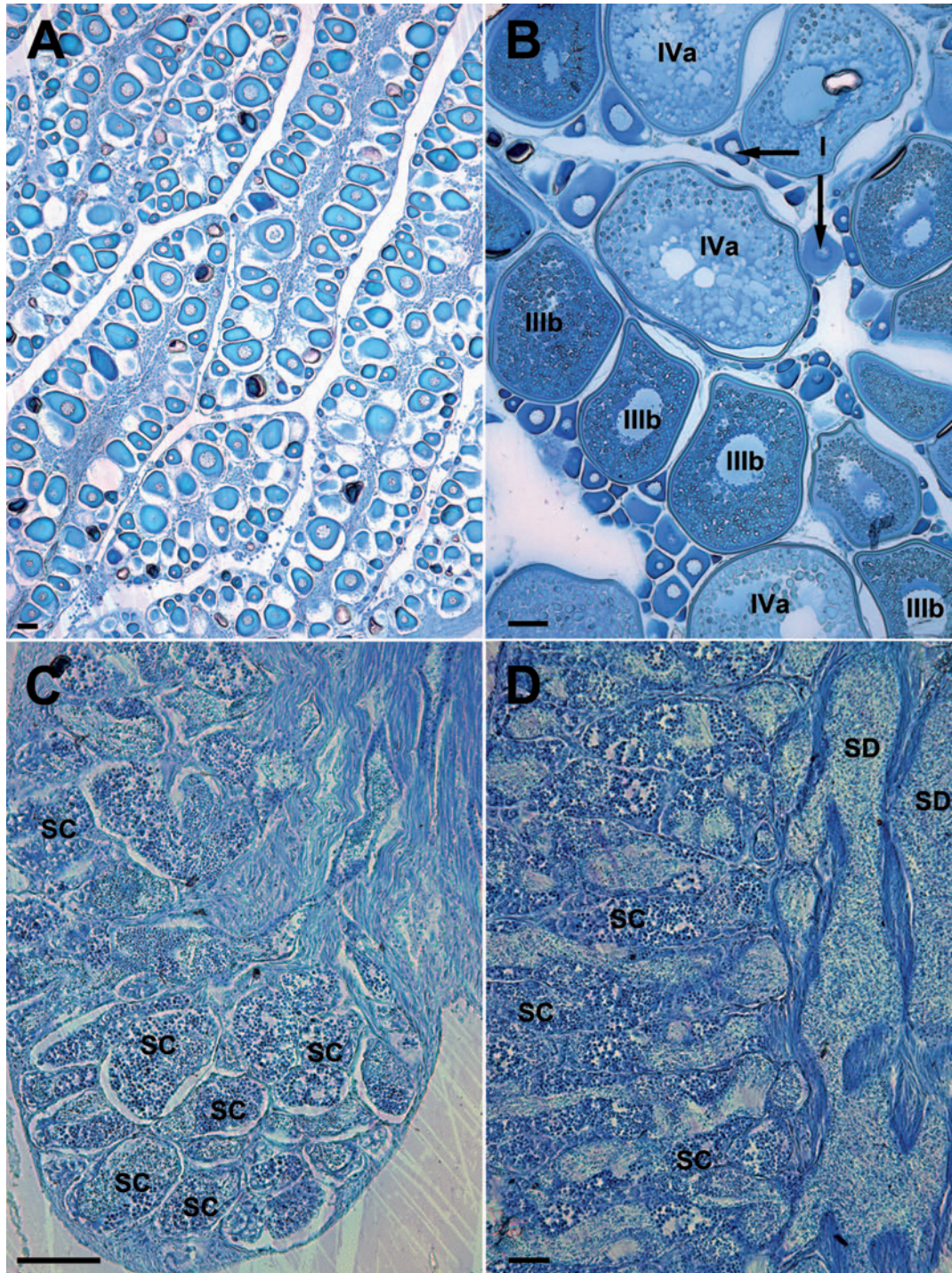
**Fig. 3.** GSI values for red-bellied fusilier, *Caesio cuning*, from Papua New Guinea; “Full” and “New” indicate moon phases



used in the Froese and Binohlan (2000) equation, theoretical and observed size-at-maturity values are closer, but the former still overestimates  $L_{50}$  for males and females (5.0 and 5.4 cm, respectively).

Testes of one immature male contained a lumen, and testes of one mature male contained yellow bodies. Testicular lumina and yellow bodies are frequently found

in secondary males of protogynous species (Sadovy and Shapiro 1987), however we do not think they indicate sex change in *Caesio cuning*. They were rare in *C. cuning*, but tend to be common in protogynous species (Sadovy and Shapiro 1987). Further, testicular lumina and yellow bodies have been observed in gonochoristic species (Takahashi 1977), where they may be an artifact of phylogeny or result



**Fig. 4.** Histological sections of gonads of red-bellied fusilier, *Caesio cuning*, from Papua New Guinea; **A** ovary of immature female (15.3 cm) containing only primary-growth oocytes, **B** ovary of mature female (19.2 cm) consisting of a mixture of oocyte stages including primary-growth (I), late vitellogenesis (IIIb) and final maturation (IVa), **C** testis from an immature male (12.6 cm) containing spermatogenic cysts (SC), **D** testis of a mature male (16.4 cm) with spermatogenic cysts (SC) and sperm ducts (SD) containing tailed spermatozoa; Scale bars = 100  $\mu$ m



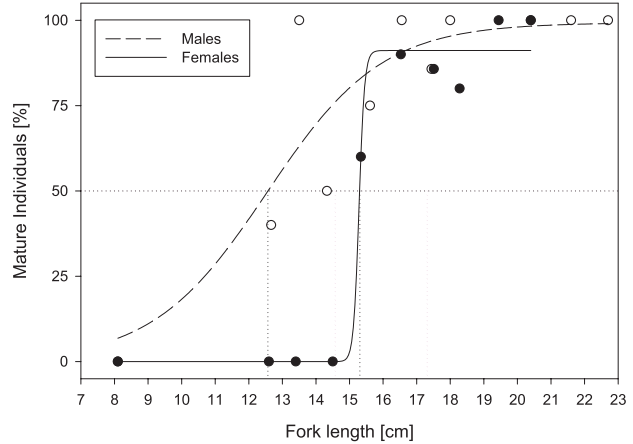
from environmental influences. There was no other evidence of sex change in *C. cuning*. A *t*-test for a sex-based bimodal size distribution was not significant ( $t = 1.8597$ ,  $DF = 73$ ,  $P = 0.067$ ), nor did ovaries contain spermatogenic tissue. In agreement with general expectations for caesionids (Carpenter 1988), we classify *C. cuning* as a gonochore.

Overall sex ratio in this *Caesio cuning* population is female-biased (Table 1,  $\chi^2 = 7.450$ ,  $DF = 1$ ,  $P = 0.0063$ ). Considering only mature individuals, the observed sex ratio is not significantly different from 1 : 1 ( $\chi^2 = 0.200$ ,  $DF = 1$ ,  $P = 0.6547$ ). However, the sex ratio of mature individuals varied predictably with length; size classes are initially male biased, switch to a female-biased state, then again become male biased (Fig. 6). An equation describing the percent of mature females (% ♀), from male  $L_{50}$  through maximum specimen length (Table 1,  $r^2 = 0.82$ ), predicts that the population is female biased between 16.9 and 20.3 cm FL, but male biased at smaller and larger sizes, and nearly exclusively male at male  $L_{50}$  and maximum specimen length.

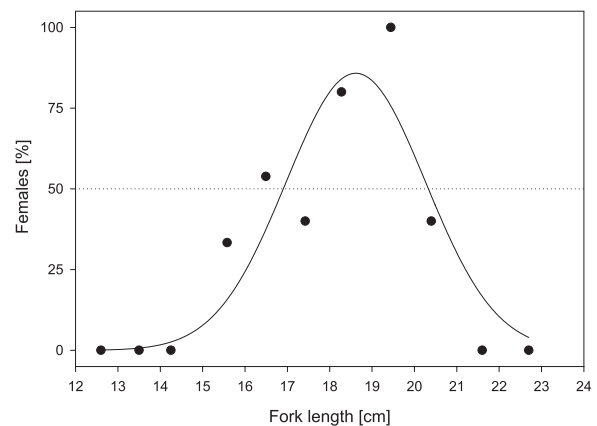
These size-specific sex ratios can have profound impacts on estimates of individual and population-level egg production. For instance, batch fecundity (BF) is an exponential function of fish length for *Caesio cuning* (Table 1, Fig. 7,  $r^2 = 0.557$ ). This length–fecundity relation suggests that, if sex ratio is constant across size classes, larger individuals will produce many more eggs per spawning event than small individuals. However when sex ratios vary with length, the proportion of females in a given size class can greatly alter estimates of egg production for an individual of that size. The curves in Fig. 8 show the relation between length and expected individual batch fecundity with a hypothetically constant sex ratio of 1 : 1 and with observed size-specific sex ratios. We emphasize that the curves represent the expected batch fecundity of any individual in the population (not just females). Estimates of expected batch fecundity per individual equal  $BF \cdot 2^{-1}$  for the hypothetical 1 : 1 sex ratio curve (half of all individuals would be expected to be females) and the product of BF and the proportion of females at a given size for the size-specific sex ratio curve. For the latter example, the small chance of an individual being a female eventually overwhelms increases in batch fecundity such that expected egg production per individual peaks at 19.2 cm. More importantly, there is a more than ten-fold difference in expected individual batch fecundity at the largest observed specimen size; a 22.7 cm individual would be predicted to produce 36 966 eggs at a 1 : 1 sex ratio, but only 2966 eggs given observed size-specific sex ratios. The discrepancy would be even more extreme with extrapolation to the largest observed size of 31 cm. With a 1 : 1 sex ratio, an individual would produce a predicted 140 275 eggs. However, when size-specific sex ratios are considered, expected egg production would be zero because effectively no individuals (< 0.001%) are expected to be female at sizes larger than 26.5 cm.

This peak and rapid decline due to the size-specific sex ratios of *Caesio cuning* is more pronounced at the popula-

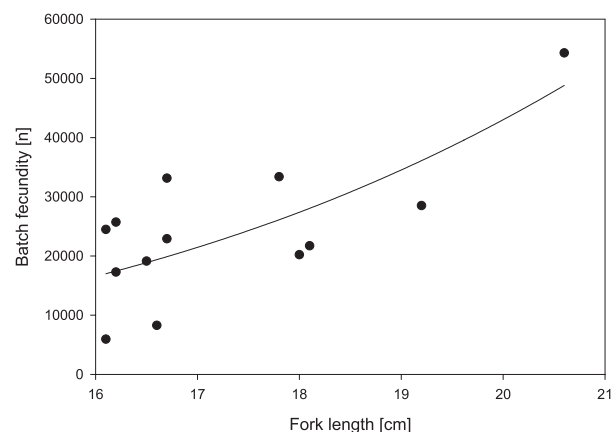
tion level (Fig. 8, bars). Here we used fishery-independent size-structure data from KWMA (Longenecker et al. 2013c) to calculate the relative frequency of individuals in each 1-cm size class, and multiplied the result by expected individual batch fecundity (given size-specific



**Fig. 5.**  $L_{50}$  for red-bellied fusilier, *Caesio cuning*, from Papua New Guinea; 50% of males (open circles, dashed line) are mature at 12.6 cm FL, 50% of females (closed circles, solid line) are mature at approximately 15.3 cm



**Fig. 6.** Size-specific sex ratios for mature red-bellied fusilier, *Caesio cuning*, from Papua New Guinea



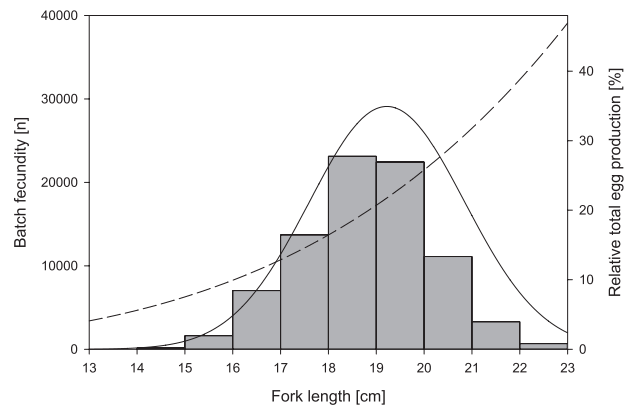
**Fig. 7.** Length–batch fecundity relation for red-bellied fusilier, *Caesio cuning*, from Papua New Guinea

sex ratios) at the mid-point of each 1-cm size class. The size-structure data were from the laser-videogrammetry surveys described above, and comprised 1071 individuals larger than male  $L_{50}$ . Of these data, the 16 cm size class had the greatest frequency and, presumably due to mortality, frequencies declined relatively consistently throughout larger size classes. We therefore assume the relative frequencies for size classes  $\geq 16$  cm are representative for the KWMA population. Assuming all size classes spawn at the same frequency, expected egg production per spawning event peaks in the 18-cm size class, then rapidly declines due to the combined influence of size-specific sex ratios and mortality. Remarkably, these results suggest individuals shorter than 19 cm FL account for slightly more than half (54.8%) of population-level egg production per spawning event.

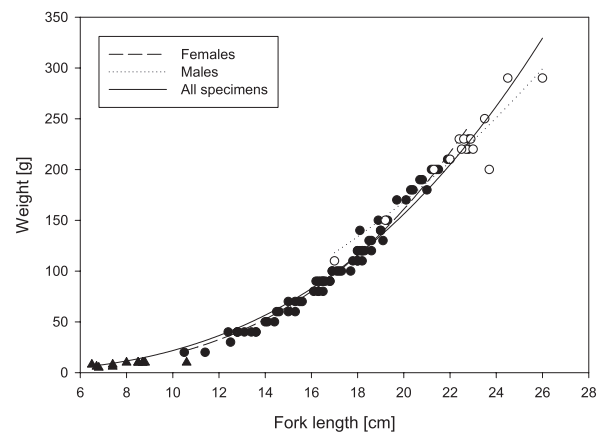
***Lethrinus erythropterus*.** Overall, total body weight ( $W$ ) in g is an approximately cubic function of FL in cm (Table 1, Fig. 9). 95% CI of regression parameters  $a$  and  $b$  are  $0.0145 \pm 0.0619$  and  $3.0976 \pm 0.0538$ , respectively ( $r^2 = 0.990$ ,  $n = 139$ , FL range: 6.4–26.0,  $W$  range: 5–290). However, ANCOVA indicates a significant difference in the length–weight relation for females and males ( $F = 7.39$ ,  $DF = 1$ ,  $P = 0.008$ ). For females, total body weight remained an approximately cubic function of fork length (95% CI of regression parameters  $a$  and  $b$  are  $0.0077 \pm 0.1248$  and  $3.3264 \pm 0.0632$ , respectively;  $r^2 = 0.984$ ;  $n = 73$ ; FL range: 10.5–22.8;  $W$  range: 20–230). For males, total body weight is an approximately square function of fork length (95% CI of regression parameters  $a$  and  $b$  are  $0.1673 \pm 0.5802$  and  $2.3023 \pm 0.0697$ , respectively;  $r^2 = 0.919$ ;  $n = 14$ ; FL range: 17.0–26.0;  $W$  range: 110–290).

We calculated GSI values for 72 female *Lethrinus erythropterus*. Again, the time period represented by our collection was limited (25 February through 6 April 2013). However, it roughly corresponds with spawning months (March, April, and May) reported elsewhere in Papua New Guinea (Hamilton et al. 2004). GSI values at KWMA are elevated a few days before the new and full moons (Fig. 10). Spawning aggregations form only around the new moon in Roviana Lagoon, Western Solomon Islands (Hamilton 2005), but around the third-quarter moon in Manus Province, PNG (Hamilton et al. 2004). Thus, timing of spawning activity appears to be variable in *L. erythropterus*.

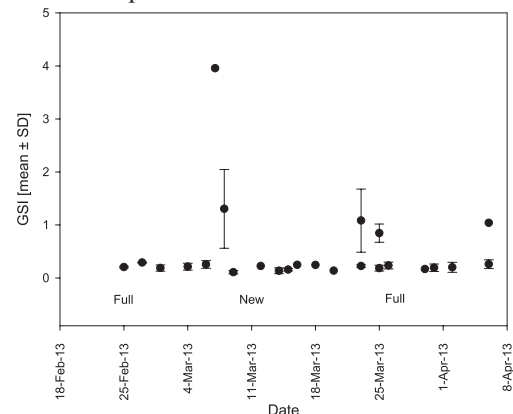
We histologically examined gonads of 13 undifferentiated, 73 female, one (1) transitional, and 14 male *Lethrinus erythropterus*. Figure 11 shows examples of immature and mature testes and ovaries. We found that wetting tissue sections with water induced a temporary counter-stain, allowing us to better distinguish gametes from surrounding stromal tissues. This improved our ability to score gamete stages and increased the quality of photographs (e.g., Fig. 11A and D). Ovaries of mature females contained several discrete stages of oocytes (Fig. 11B), indicating group-synchronous oocyte development (Wallace and Selman 1981). We therefore classify *L. erythropterus* as



**Fig. 8.** The influence of size-specific sex ratios on estimates of egg production for red-bellied fusilier, *Caesio cuning*, from Papua New Guinea; The dashed line represents expected batch fecundity per individual assuming a constant 1 : 1 sex ratio; the solid line indicates how expected batch fecundity per individual is influenced by the proportion of females at a given size (left scale); Bars represent the expected relative contribution of each 1-cm size class to population-level egg production per spawning event (right scale)



**Fig. 9.** Overall and sex-based length–weight relations for longfin emperor, *Lethrinus erythropterus*, from Papua New Guinea; Closed triangles represent undifferentiated individuals, closed circles represent females, and open circles represent males

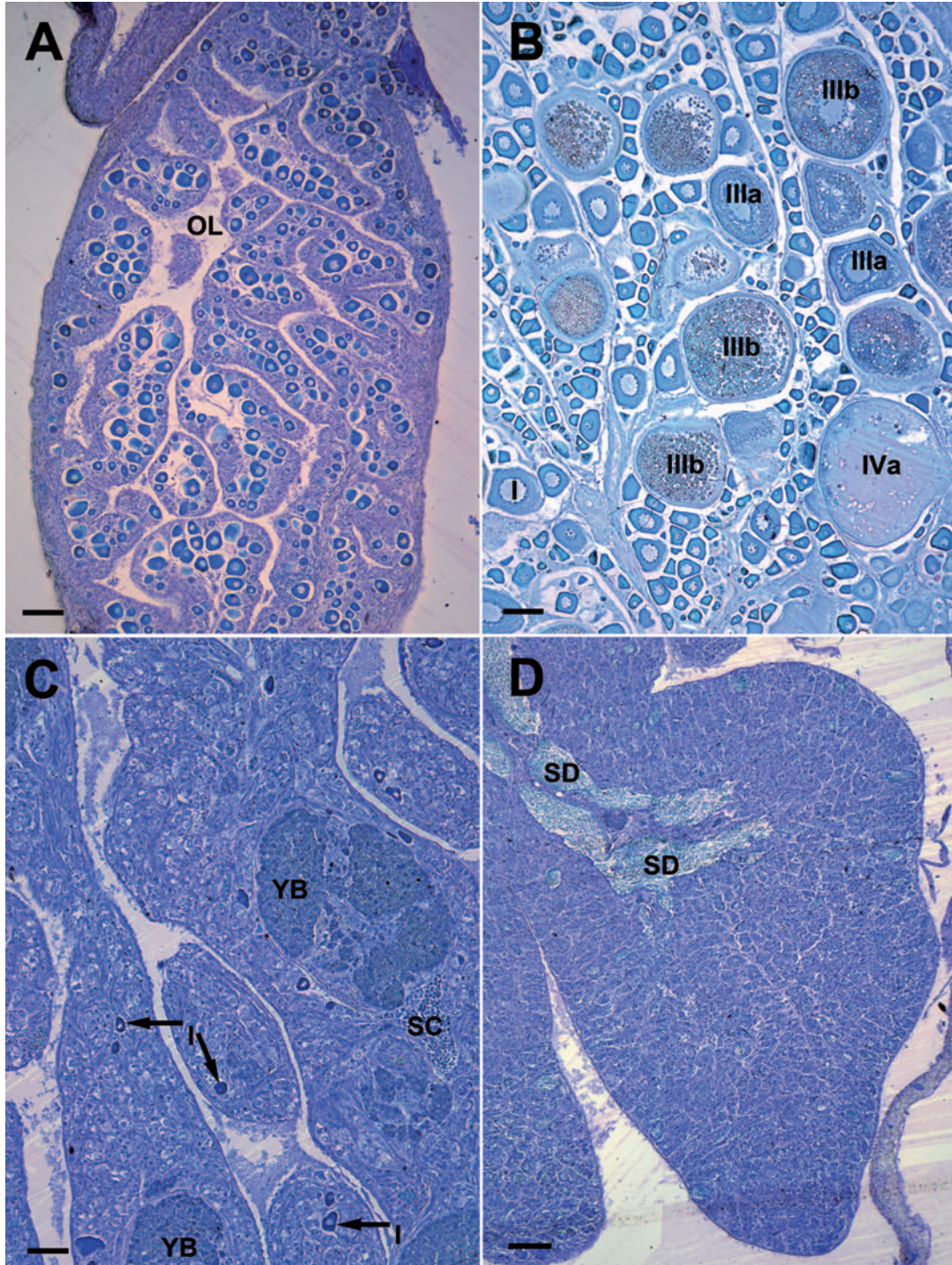


**Fig. 10.** GSI values for longfin emperor, *Lethrinus erythropterus*, from Papua New Guinea; “Full” and “New” indicate moon phases



a batch spawner. Sexual differentiation occurs around 11 cm FL. Ovaries contained vitellogenic oocytes in females as small as 18.0 cm FL. We estimate female  $L_{50}$  at 20.4 cm FL (Fig. 12, this estimate ignores a single immature female at 22.8 cm FL). One transitional individual, not reproductively active as either sex, was 23.2 cm FL. All

males from 19.2 to 24.5 cm FL were mature. However, the smallest and largest males (17.0 and 26.0 cm FL, respectively) were immature. Because of the low number of immature males, we could not reliably estimate male  $L_{50}$ . Figure 13 shows the relative frequency of reproductive states in each 1-cm size class.



**Fig. 11.** Histological sections of gonads of longfin emperor, *Lethrinus erythropterus*, from Papua New Guinea; **A** ovary of immature female (11.4 cm) containing only primary-growth oocytes and a conspicuous ovarian lumen (OL), **B** ovary of mature female (18.6 cm) consisting of a mixture of oocyte stages including primary-growth (I), early vitellogenesis (IIIa), late vitellogenesis (IIIb) and final maturation (IVa), **C** ovo-testis from a transitional individual (23.2 cm) containing spermatogenic cysts (SC), yellow bodies (YB), and primary growth (I) oocytes, **D** testis lobe of a mature male (19.2 cm) with sperm ducts (SD) containing tailed spermatozoa; Scale bars = 100  $\mu$ m

Our minimum-size-at-maturity ( $L_m$ ) and  $\varnothing L_{50}$  values are substantially smaller than  $L_m$  estimates (25.7 cm for males, 31.0 cm for females) derived from the empirical equations of Froese and Binohlan (2000), given a maximum size of 48 cm FL based on a maximum 50 cm TL (Allen and Swainston 1993) converted to FL using the TL–FL relation of Froese and Pauly (2013). For instance, the  $L_m$  values we present are only 75% (for males) or 58% (for females) of the empirically derived  $L_m$  values. Further, the relative sizes-at-maturity for each sex are switched. The Froese and Binohlan (2000) estimate suggests males mature at a smaller length than females. However, our observations indicate that females mature at the smaller length.

We saw evidence of sex change in *Lethrinus erythropterus*. A  $t$ -test indicated mean length of mature males is significantly greater than that of mature females ( $t = -4.1567$ ,  $DF = 21$ ,  $P = 0.0004$ ). Further, the gonad of one 23.2 cm FL individual contained a mixture of ovarian and spermatogenic tissue. In agreement with general expectations for lethrins (Bean et al. 2003, Ebisawa 2006, Marriott et al. 2010, Motlagh et al. 2010, Currey et al. 2013), we classify *L. erythropterus* as a protogynous hermaphrodite.

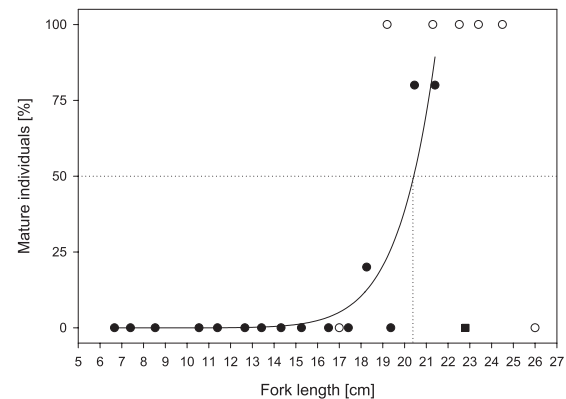
Overall sex ratio in this *Lethrinus erythropterus* population is female biased (Table 1,  $\chi^2 = 40.011$ ,  $DF = 1$ ,  $P = 0.0001$ ). Considering only mature individuals, the observed sex ratio is not significantly different from 1 : 1 ( $\chi^2 = 0.043$ ,  $DF = 1$ ,  $P = 0.8348$ ). However, the sex ratio of mature individuals varied predictably with length; size classes are initially female biased then become male biased (Fig. 14). An equation describing the percent of mature females (%  $\varnothing$ ), from female  $L_{50}$  through maximum specimen length (Table 1,  $r^2 = 0.97$ ), predicts that the transition from a female- to a male-biased state occurs at 21.2 cm FL and that the population is exclusively male  $\geq 23.9$  cm FL.

Because none of the ovarian sections we retained for batch fecundity analysis had oocytes in stages  $\geq 4a$ , we could not construct a length–batch fecundity relationship. However, as for *Caesio cuning*, the effects of size-specific sex ratios would profoundly impact individual batch fecundity estimates. Because *Lethrinus erythropterus* females are not expected to attain 23.9 cm FL, egg production would stop at this size.

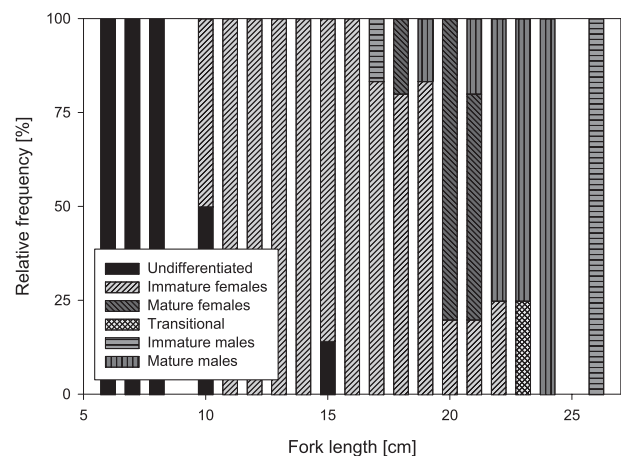
We reiterate that the results of rapid reproductive analysis should be considered preliminary. However, we think our results are a useful contribution to the currently insufficient body of knowledge about reproduction in Pacific coral-reef fishes. In particular, these results will help subsistence-fishing communities, such as Lababia, balance the conflicting desires of conserving marine resources for future generations against the immediate need for and cultural value of exploiting reef fishes.

The potential impact of size-specific sex ratios on reef-fish management and conservation efforts is currently under-recognized. It is commonly assumed that that large fish play a disproportionately important role in the repro-

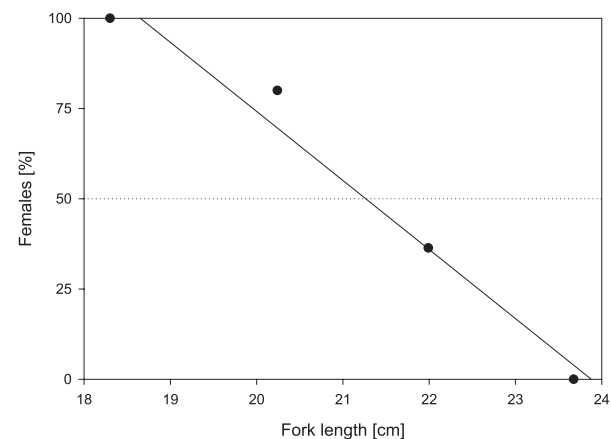
ductive output of a population because large females produce many more eggs than small females (see Roberts and Polunin 1993, Allison et al. 1998, Halpern 2003,



**Fig. 12.**  $L_{50}$  for longfin emperor, *Lethrinus erythropterus*, from Papua New Guinea; 50% of females (closed circles, solid line) are mature at 20.4 cm; this estimate ignores two, immature 22.8 cm females (closed square) in the largest size class; We could not reliably determine  $L_{50}$  for males (open circles)



**Fig. 13.** Relative frequency of reproductive states of longfin emperor, *Lethrinus erythropterus*, from Papua New Guinea in each 1-cm size class



**Fig. 14.** Size-specific sex ratios for mature longfin emperor, *Lethrinus erythropterus*, from Papua New Guinea



Froese 2004, Birkeland and Dayton 2005, Sale et al. 2005). Our results challenge this assumption. Females are absent from the largest size classes of both study species, suggesting that smaller size classes are responsible for the majority of population-level egg production. These results should not be surprising for protogynous species such as *Lethrinus erythropterus*. However, the consequence of a similar pattern in a gonochoristic species such as *Caesio cuning*, particularly with its overall 1 : 1 sex ratio for mature individuals, cannot be overstated.

Despite the value of our results, life-history-based management and conservation requires more than reproductive analysis. As such, aging studies would be a valuable complement to the above results.

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