

Many immature individuals and largest size classes lacked females for three coral reef fishes (Actinopterygii) in Fiji market surveys: Implications for fishery management

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Abstract

Data-limited fisheries benefit from using life-history traits as biological indicators of targeted stocks. We used histology-based reproductive analyses to estimate size at maturity, per capita egg production, and the number and biomass of immature individuals in the catch for three common coral reef fishes in Fiji market surveys during 2010–2019. We studied *Lutjanus gibbus* (Forsskål, 1775), *Parupeneus indicus* (Shaw, 1803), and *Chlorurus microrhinos* (Bleeker, 1854), which represent three families: Lutjanidae, Mullidae, and Scaridae, respectively. Fork length comprising 50% mature individuals for females of *L. gibbus* was 22.7 cm, that of *P. indicus* was 25.9 cm, attaining 38.0 cm for *C. microrhinos*. Females were rare or absent in the largest size classes of all three species. Immature fish represented up to 50% by number and 41% by biomass of the catch in market surveys, with *P. indicus* having the greatest immature number (8%–50%) and biomass (6%–41%), followed by *C. microrhinos* (20%–30% by count, 11%–18% by biomass) and *L. gibbus* (9%–28% by count, 5%–14% by biomass). Individuals ≤ 30 cm for *L. gibbus* and *P. indicus* and ≤ 45 cm for *C. microrhinos* were responsible for $\geq 90\%$ of egg production per spawning. Skewed size-specific sex ratios suggested that exploitation of the largest size classes had minimal effect on overall egg production. Decreased catches of immature fishes would increase the reproductive population sizes for these species.

Keywords

Chlorurus microrhinos, histology, *Lutjanus gibbus*, *Parupeneus indicus*, per capita egg production, size at maturity, weight–length relation

Introduction

Coral reef fisheries supply protein to more than half of the people living in tropical coastal areas and support jobs, recreational and cultural activities. However, balancing long-term conservation of the coral reef resources with the cultur-

al, food security, and monetary needs of coastal communities is difficult due to increasing fishing efforts, reinforced by access to new technologies and driven by expanding markets. As a result, overall decline and/or overexploitation of coral reef fish stocks has been consistently reported since the 1940s (Fenner 2012; Lachs and Oñate-Casado 2020).

Fiji's subsistence and artisanal marine fisheries generate annual landings of 27 000 t (Gillett 2016), and prior to COVID-19, was the third largest natural resource sector in the country after sugarcane and other crops (Hand et al. 2005). Per capita annual consumption rates are estimated between 20.7 and 36.8 kg, and therefore its fish are crucial to Fiji's food security and nutrition (Bell et al. 2009; Gillett and Tauati 2018). However, decades of poor management means that many fisheries are heavily exploited (Mangubhai et al. 2018), with many species sold in markets below reproductive size, and many species have spawning potential ratio estimates below 20% (Prince et al. 2019).

Two less obvious causes of mismanagement potentially leading to overexploitation are poorly defined size restrictions and the deficiency of fish reproductive biology information. A common size restriction is the minimum size limit, where fishers can only retain the fishes above a certain size—usually, the estimated length at or near maturity. This approach typically relies on the assumption that each fish has reproduced at least once in its life before being caught. This way, each fish has contributed recruitment to at least one cohort of a fished population. However, reproduction can only be achieved when both sexes are present and mature, which does not happen at the same size in sequential hermaphroditic fishes. Eleven of the fourteen families where sex exchange is known in at least one species, inhabit coral reefs (Warner 2011). A size limit based on the sex that matures first has cascading negative effects on protogynous and protandrous fished populations, as only a reduced number of individuals will survive until maturity in the other sex. Knowledge of size at maturity for both sexes is therefore required for many coral reef fishes—this information can be used either to set a minimum and a maximum size limit (i.e., a slot limit), or to push the minimum limit to the bigger of the two sizes.

The identification of basic reproductive biology information (e.g., size at maturity) for each population of a coral reef fishery, where catches may contain up to 200 species whose abundance change seasonally (Dalzell et al. 1996), requires time and economic efforts that are often unattainable (Roberts and Polunin 1993; Johannes 1998). When size at maturity estimates are not available for local populations, researchers may use estimates generated at other locations. However, the practice necessarily assumes that the “borrowed” estimates are representative of the local fish populations. That assumption, if not valid, may lead to mismanagement. Temporal and geographic variability in life history parameters is known for several coral reef fish species (Gust 2004; DeMartini et al. 2014). In addition, estimates of reproductive parameters should be obtained via histological examination, when possible, to minimize biases (Grandcourt et al. 2006, 2011; Vitale et al. 2006; Longenecker et al. 2017). For example, empirical relations (Froese and Binohlan 2000) that underly the Fish-Base life history tool (Froese and Pauly 2019) increasingly overestimate female size at maturity as the maximum size of a species increases (Longenecker and Langston 2016; Longenecker et al. 2017). Also, macroscopic evaluation of gonads results in misclassification of sex and/

or reproductive status of up to half of the inspected specimens (Longenecker et al. 2013a, 2013b, 2020), with the misclassifications tending to overestimate the number of mature females (Longenecker et al. 2013a, 2013b), underestimate female size at maturity (Grandcourt et al. 2006, 2011), and overestimate female spawning biomass (Vitale et al. 2006). Finally, histological analysis is required to diagnose sex change (Sadovy and Shapiro 1987).

In this case study from Fiji, we used rapid, low-cost, on-site, histology-based reproductive analysis (Longenecker et al. 2020), to assess the reproductive parameters including size at maturity and per capita egg production of three coral reef fishes. Each is vital to Fiji's subsistence and/or artisanal fisheries, has been identified by Fiji's Ministry of Fisheries as vulnerable to overexploitation, and is common across Pacific Island countries and territories: the humpback red snapper, *Lutjanus gibbus* (Forsskål, 1775), the Indian goatfish, *Parupeneus indicus* (Shaw, 1803), and the steephead parrotfish, *Chlorurus microrhinos* (Bleeker, 1854). We combine the reproductive analyses with data from fish market surveys to determine the size composition of the three species relative to size at maturity to determine the proportion of immature fish in the catch.

Materials and methods

This research was approved by Fiji's Ministry of Education, Heritage and Arts (research permit RA 19/18) and conducted in accordance with relevant guidelines and regulations. No live animals were used. The methods we used for reproductive analysis followed established, statistical methods (Longenecker et al. 2020), summarized below, to describe weight–length relations (WLR), size at maturity, sexual pattern, and sex ratios.

Specimen acquisition and whole specimen processing.

All specimens for reproductive analysis originated from Labasa in Vanua Levu and were purchased between 9 March and 25 June 2018 from fishers in fish markets (Fig. 1). Length was determined for each specimen by measuring to 0.1 cm the distance from the front of the head, with mouth closed, to the distal end of the middle caudal ray (called fork length, L_F , for consistency although the caudal fin of *C. microrhinos* is not forked), and weight was determined with the smallest-possible capacity hanging spring-scale (100, 1000, 2500, or 10 000 g capacity, with 1, 10, 20, or 100 g increments, respectively). Gonads were excised, then examined macroscopically to evaluate sex and maturity status (for comparison with histological results). From each gonad a small, cuboid subsample (approximately 3 mm in each dimension) was excised and fixed in Dietrich's solution for at least 24 h pending histological analysis. The subsample was a partial cross section that included the most central part of the gonad adjacent to the lumen (if ovarian) where oocytes were most likely to be mature.

Size-at-maturity and sexual pattern. The Dietrich's-fixed gonad subsamples were trimmed to approximately 2 mm

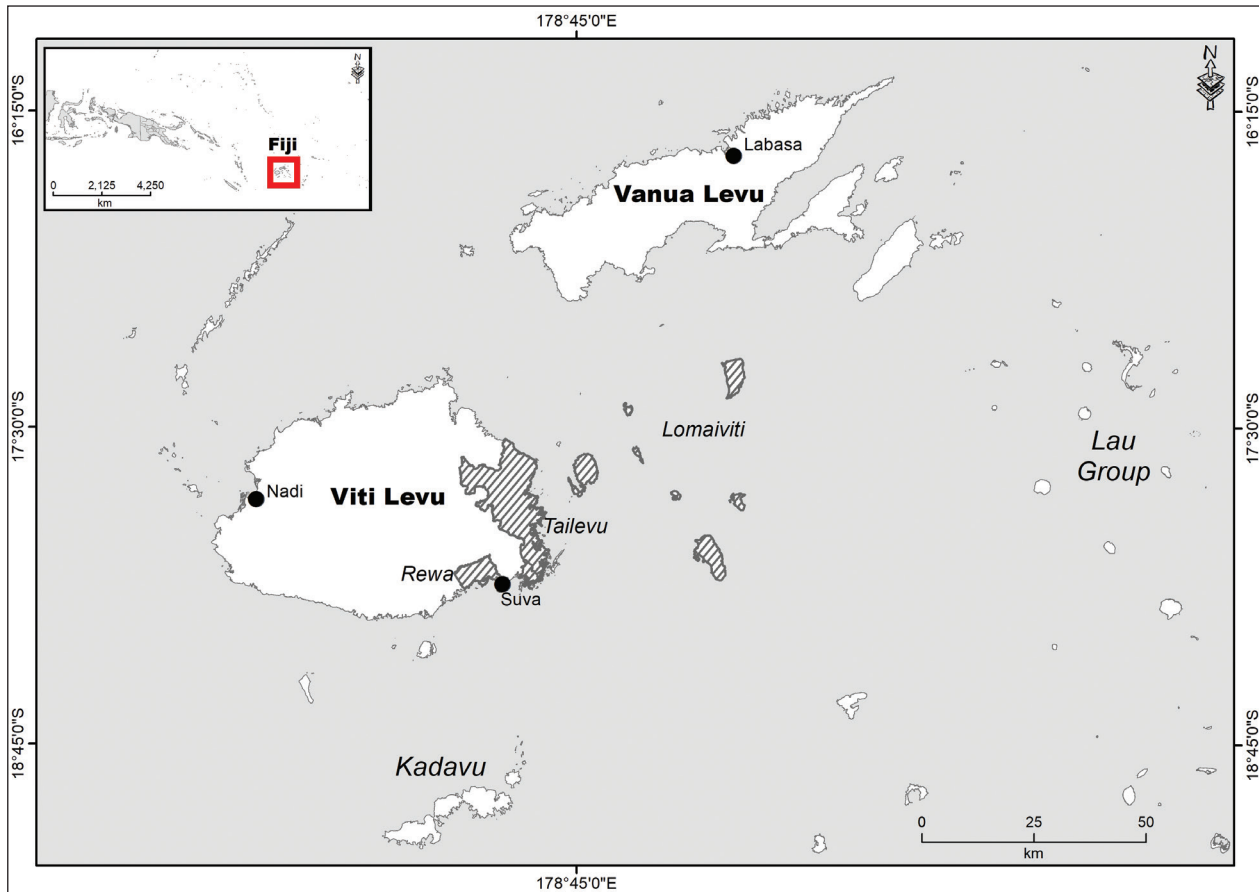


Figure 1. Map of the Republic of Fiji. Specimens were obtained in Labasa from fish-market vendors and from individual fishers. Additional specimens, also originating from the northern island of Vanua Levu, were purchased from vendors at Bailey Bridge market in Suva. Shaded areas represent locations referenced in the description of market survey data.

in each dimension, then dehydrated in alcohol (60 min in each of 50%, and two changes of 95% ethanol). Using glycol methacrylate embedding kits (HistoResin, Leica Biosystems; or JB-4, Electron Microscopy Sciences) and following manufacturer instructions, gonad subsamples were infiltrated with two changes of infiltration solution (1 h and > 8 h, respectively), transferred to embedding capsules (BEEM®, size 00), then embedded in catalyzed resin. Tissue blocks were then dehydrated for 12 h in a watertight case containing silica gel packets. Ten tissue sections (approximately 7 µm thick), distributed evenly throughout each tissue subsample, were obtained from each tissue block by serial sectioning with an MT1 Porter–Blum ultramicrotome fitted with a glass knife. Tissue sections were affixed to glass microscope slides, then stained with Toluidine Blue. Ovary sections were examined at 100× and testis sections at 400× for evidence of reproductive maturity. Guides to gamete development were used to classify ovaries (Wallace and Selman 1981) and testes (Nagahama 1983); females were considered mature when vitellogenic oocytes or post-ovulatory follicles were observed in ovary sections, and males were considered mature when spermatozoa were observed in testis sections.

Data analysis. We constructed WLR using log-transformed data and following established statistical protocols (Froese et al. 2011). We considered all data points

with a residual >0.1 to be outliers. We used analysis of covariance (ANCOVA) to analyze data from histologically sexed individuals to evaluate whether WLRs varied between sexes, and for regional comparisons of grouped-sex WLRs for *L. gibbus* and *P. indicus*. We report size-at-maturity as L_{50} , the length predicted to comprise 50% mature individuals (L_{50}) of a given sex. We also report L_{95} , the length comprising 95% mature individuals. Here, we used logistic regression analysis of the dependent variable, proportion of mature individuals, and the independent variable, the midpoint of each 2-cm size class, to produce a maturation curve. Our regression model was:

$$p_M = (1 + e^{((-\ln(19))(L - L_{50})/(L_{95} - L_{50}))})^{-1}$$

where p_M is the predicted proportion of mature individuals at a given length (L), L_{50} is the length comprising 50% mature individuals, and L_{95} is the length comprising 95% mature individuals. We report size of transition for protogynous species as the length predicted to comprise 50% males (X_{50}). We used logistic regression analysis of the dependent variable, proportion of males, and the independent variable, the midpoint of each 2-cm size class, to produce a sexual transition curve for protogynous species. Our regression model was:

$$p_\sigma = (1 + e^{((-\ln(19))(X - X_{50})/(X_{95} - X_{50}))})^{-1}$$

where $p_{\frac{3}{3}}$ is the predicted proportion of males at a given length (X), X_{50} is the length comprising 50% males, and X_{95} is the length comprising 95% males. We used chi-square (χ^2) analysis to test whether overall or operational sex ratios differed from 1:1. We described size-specific sex ratios of mature-sized individuals, by plotting the percent of mature females within a size class as a function of mean length within each size class. We then used exploratory regression analysis to evaluate whether sex ratios of mature individuals varied predictably with length.

Market survey data collection. Fish market surveys were conducted between 2010–2013 at Laqere, Bailey Bridge and Suva fish markets and within 2016–2018 at Bailey Bridge. All markets are located in Suva on the island of Viti Levu. In general, the majority of the fishes sold at Bailey Bridge were most likely from Labasa, with a much smaller amount from Lomaiviti, those sold at Laqere were most likely from the Rewa and Tailevu areas on Viti Levu, and those sold in Suva were most likely from a diversity of locations, ranging from Labasa in the North to Kadavu in the South, with no one area being the dominant supplier (Gillett and Musadroka 2020) (Fig. 1). Data were collected on fish species abundance and size (fork length, to the nearest centimeter) and pooled to determine the size class distribution patterns for the three study species. Within 2010–2013, we surveyed 180 specimens of *C. microrhinos*, 443 specimens of *L. gibbus*, and 215 specimens of *P. indicus*. In 2016–2018, we surveyed 65 specimens of *C. microrhinos*, 169 specimens of *L. gibbus*, and 12 specimens of *P. indicus*.

Per capita egg production. We used size at maturity and size-specific sex ratios to estimate per capita egg production: the number of eggs produced per spawning event by an individual fish, regardless of sex. Fecundity should, in theory, be proportional to the cube of female body length (Leary et al. 1975; Healey and Heard 1984). We therefore assumed that batch fecundity (F_B) is a cubic function of fork length (i.e., $F_B = L_F^3$) and used the midpoint of each size class to estimate batch fecundity for a female in that size class. We multiplied that estimate by the proportion of females in that size class (from size-specific sex ratio formulae), then multiplied the product by the proportion of females in that size class that were mature (from female size-at-maturity relations). We compared the result with what per capita egg production would be estimated to be under the common assumption of an equal, invariant sex ratio (i.e., the proportion of females in all size classes is 0.5).

Immature individuals in fisheries catch. We used size at maturity and weight–length relations with the length composition data for the three species from market surveys to estimate the number and biomass of immature fish in the catch. We calculated the proportion of immature fish in each 1-cm size class from the specimens collected during the 2019 market survey and used them for reproductive analysis for each market survey data set (i.e., 2010–2013, 2016–2018, 2019). The product of the proportion of immature fish by length and the weight at that length from the

WLR provided an estimate of the immature biomass in the catch for each size class, which were summed to give a total immature biomass. We calculated percentages of the number and biomass of immature fish relative to the total market catch of both immature and mature fish for each species.

Results

We estimated reproductive parameters for *Lutjanus gibbus*, *Parupeneus indicus*, and *Chlorurus microrhinos* using histology-based methods (Table 1). For all three species, total body weight (W) in g was an approximately cubic function of fork length (L_F) in cm. The ovaries of mature females of all three species contained several discrete stages of oocytes, indicating group-synchronous oocyte development (Wallace and Selman 1981). We therefore classify all of them as batch spawners. Species-specific information is presented in separate sections, below.

Lutjanus gibbus. The weight–length relation (WLR) regression parameters a and b had 95% confidence intervals of $4.90 \cdot 10^{-6}$ – $1.16 \cdot 10^{-5}$ and 3.10 – 3.26 , respectively ($r^2 = 0.977$, $n = 155$, L_F range: 17.2–35.4 cm, W range: 100–960 g). Per ANCOVA results, there was no significant sex-based difference in WLRs ($F = 0.60$, $df = 1$, $P = 0.441$).

We examined the gonads of 49 male and 61 female *L. gibbus*. Photomicrographs of immature and mature gonads of both sexes are presented as supplementary information (Fig. 2). Vitellogenic oocytes were seen in females as small as 21.7 cm L_F and all females ≥ 26.3 cm L_F were mature. We estimated female L_{50} at 22.7 cm L_F (Fig. 3A) and L_{95} at 27.2 cm L_F .

Table 1. Summary of weight–length relations and reproductive information for four exploited reef fishes from Fiji. L_m is the length of the smallest mature individual. L_{50} and L_{95} are the lengths comprising 50% and 95% mature individuals, respectively. Lengths are in cm.

	<i>Lutjanus gibbus</i>	<i>Parupeneus indicus</i>	<i>Chlorurus microrhinos</i>
Weight–length (overall)	$W = 7.55 \cdot 10^{-6} (L_F)^{3.18}$	$W = 1.04 \cdot 10^{-5} (L_F)^{2.71}$	$W = 1.01 \cdot 10^{-5} (L_F)^{3.13}$
Male weight–length	—	$W = 1.09 \cdot 10^{-5} (L_F)^{2.70}$	—
Female weight–length	—	$W = 3.35 \cdot 10^{-5} (L_F)^{2.48}$	—
Male L_m	22.5	21.0	33.7
Female L_m	21.7	20.5	36.2
Male L_{50}	23.1	24.2	—
Female L_{50}	22.7	25.9	38.0
Male L_{95}	25.3	30.0	—
Female L_{95}	27.2	32.5	47.8
Oocyte development	Batch synchronous	Batch synchronous	Batch synchronous
Sexual pattern	Gonochore	Gonochore	Protogynous (presumed)
Size of transition (X_{50})	n/a	n/a	40.0
Overall sex ratio (M:F)	1:1.25	1:0.51	1:0.87
Functional sex ratio (M:F)	1:0.95	1:0.27	1:0.49
Size specific sex ratios	See Fig. 3B	See Fig. 5B	See Fig. 7C

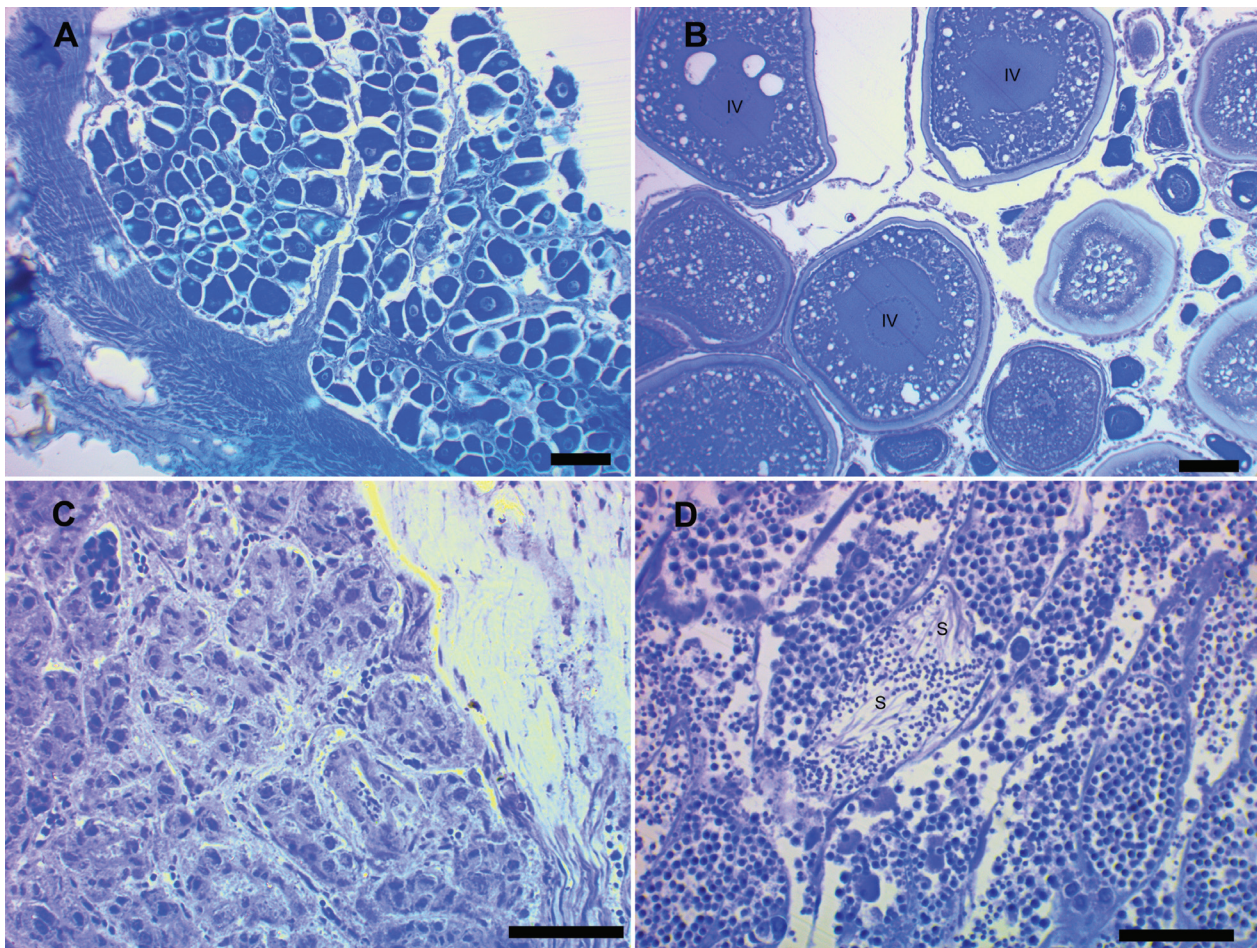


Figure 2. Histological sections of gonads of *Lutjanus gibbus* from Fiji. (A) Ovary of immature female (21.6 cm L_F) containing only primary-growth oocytes; (B) ovary of mature female (27.3 cm L_F) containing a mixture of oocyte stages including final maturation (IV); (C) testis from an immature male (22.6 cm L_F) containing no tailed spermatozoa; (D) testis of a mature male (29.8 cm L_F ;) with tailed spermatozoa (S); scale bars = 100 μm (A and B) or 50 μm (C and D).

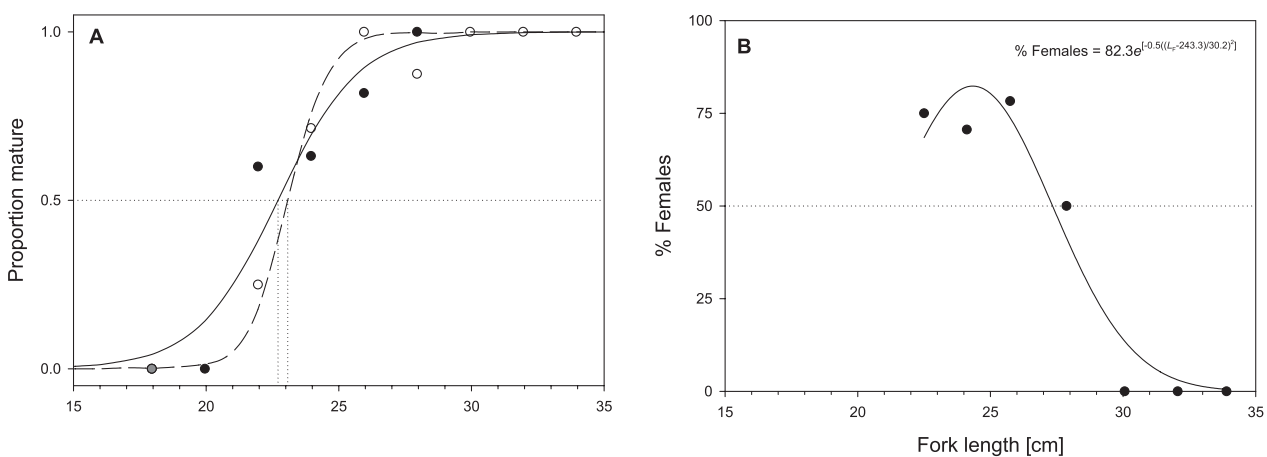


Figure 3. Reproductive information for *Lutjanus gibbus* from Fiji. (A) size at maturity (L_{50}); (B) percentage of mature females, relative to all mature individuals, versus length. Females are represented by closed circles and the solid curves, males are represented by open circles and the dashed curve.

Spermiated testes were seen in males as small as 22.5 cm L_F and all males ≥ 27.5 cm L_F were mature. We estimated male L_{50} at 23.1 cm L_F (Fig. 3A) and L_{95} at 25.3 cm L_F .

A t -test detected a sex-based bimodal size distribution in *L. gibbus*. The mean length of males was significantly

greater than that of females ($t = -6.218$, $df = 83$, $P < 0.001$). However, there was no histological evidence of hermaphroditism in *L. gibbus*; testes did not contain a central membrane-lined lumen, and we did not detect a mixture of ovarian and spermatogenic tissue in any gonad. We classified *L. gibbus* as a gonochore.

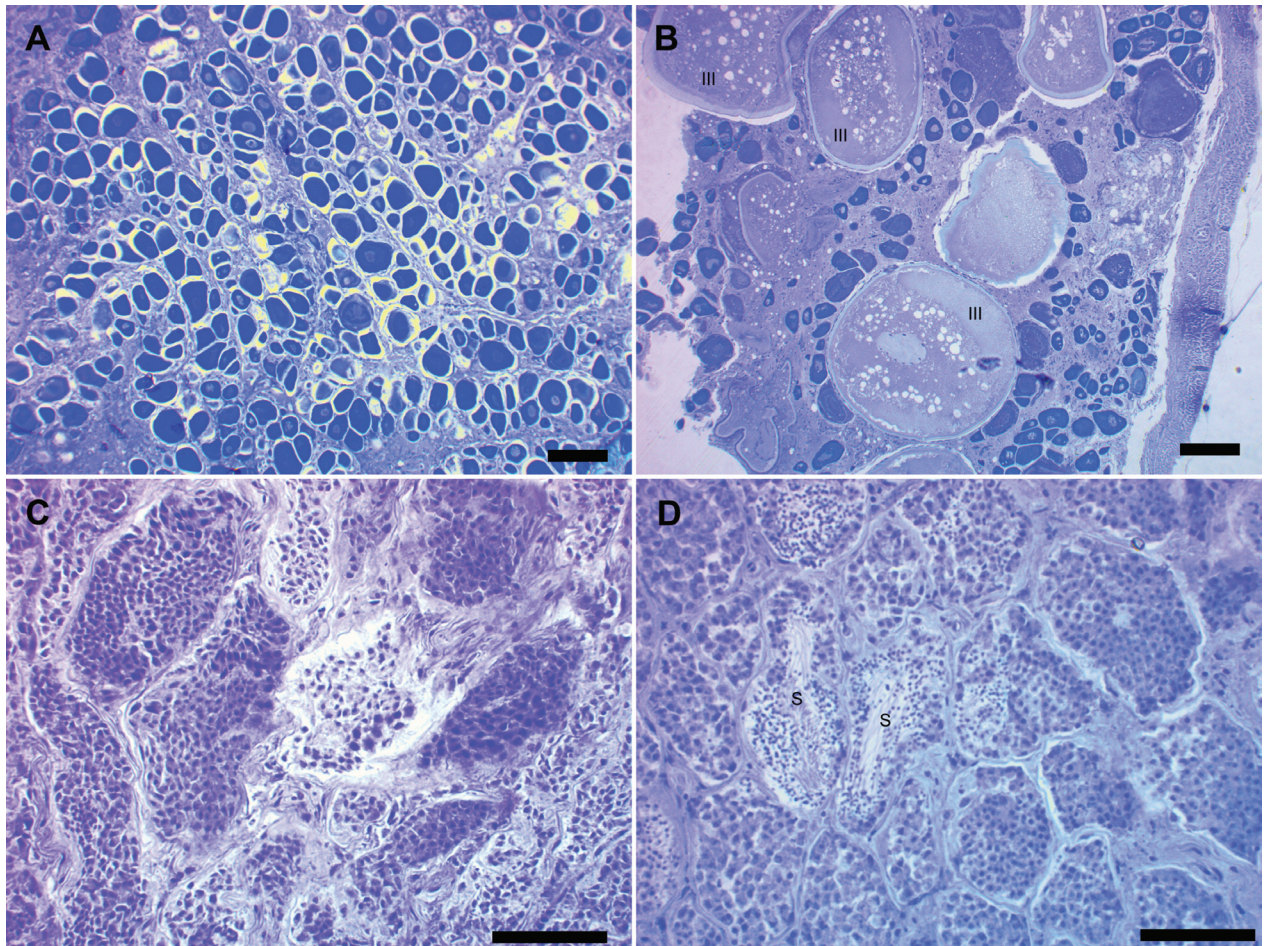


Figure 4. Histological sections of gonads of *Parupeneus indicus* from Fiji. (A) ovary of immature female (22.2 cm L_F) containing only primary-growth oocytes; (B) ovary of mature female (23.6 cm L_F) containing a mixture of oocyte stages including vitellogenesis (III); (C) testis from an immature male (31.5 cm L_F) containing no tailed spermatozoa; (D) testis of a mature male (26.3 cm L_F) with tailed spermatozoa (S); scale bars = 100 μm (A and B) or 50 μm (C and D).

Overall sex ratio in this *L. gibbus* population was female-biased, but not statistically different from 1:1 (Table 1, $\chi^2 = 1.309$, $df = 1$, $P = 0.253$). Operational sex ratio (considering only mature individuals) was essentially 1:1 ($\chi^2 = 0.049$, $df = 1$, $P = 0.825$). However, sex ratios varied predictably throughout the size range of mature individuals (Fig. 3B). Curvilinear regression analysis of the percent of mature females (% $_c$) versus L_F (Table 1, $r^2 = 0.946$) indicates that the smallest mature individuals were female biased. The percentage of females reached a maximum at 24.3 cm L_F , then decreased as length increased; sexes were present in approximately equal numbers at 27.4 cm L_F but males dominated at larger sizes (Fig. 3B). All mature individuals ≥ 28.4 cm L_F were male.

Parupeneus indicus. The WLR regression parameters a and b had 95% confidence intervals of $4.63 \cdot 10^{-5}$ – $2.36 \cdot 10^{-4}$ and 2.56–2.85, respectively ($r^2 = 0.908$, $n = 134$, L_F range: 18.9–34.1 cm, W range: 150–730 g). Per ANCOVA results, there was a significant sex-based difference in WLRs ($F = 14.50$, $df = 1$, $P < 0.001$). Sex-specific WLRs are presented in Table 1. For males, the WLR regression parameters a and b had 95% confidence intervals

of $3.86 \cdot 10^{-5}$ – $3.06 \cdot 10^{-4}$ and 2.51–2.89, respectively ($r^2 = 0.938$, $n = 57$, L_F range: 18.9–31.5 cm, W range: 150–670 g). For females, the WLR regression parameters a and b had 95% confidence intervals of $6.92 \cdot 10^{-5}$ – $1.62 \cdot 10^{-3}$ and 2.19–2.77, respectively ($r^2 = 0.917$, $n = 30$, L_F range: 19.4–27.9 cm, W range: 160–420 g).

We examined the gonads of 61 male and 32 female *P. indicus*. Photomicrographs of immature and mature gonads of both sexes are presented as supplementary information (Fig. 4). Vitellogenic oocytes were seen in females as small as 20.5 cm L_F . Inactive/immature females (range 19.4–27.0 cm) were scattered throughout the size range of mature females (range 20.5–27.9 cm). We estimated female L_{50} at 25.9 cm L_F (Fig. 5A) and L_{95} at 32.5 cm L_F . Spermiated testes were seen in males as small as 21.0 cm L_F . Inactive/immature males (range 18.9–33.3) were scattered throughout the size range of mature males (range 21.0–30.6 cm). Ignoring the two largest individuals, which were immature, we estimated male L_{50} at 24.2 cm L_F (Fig. 5A) and L_{95} at 30.0 cm L_F .

A t -test detected a sex-based bimodal size distribution in *P. indicus*. The mean length of males was significantly greater than that of females ($t = -3.536$, $df = 80$,

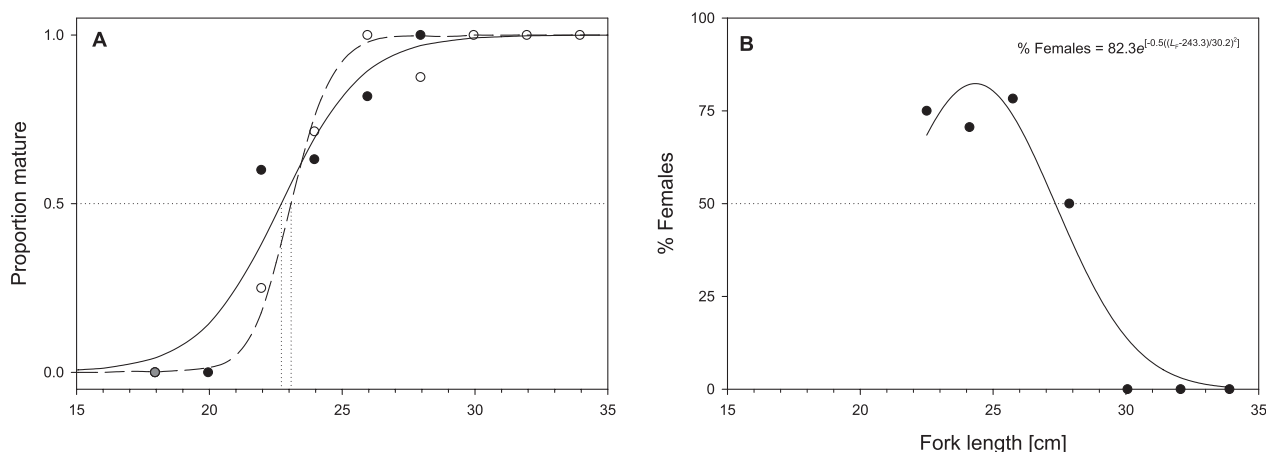


Figure 5. Reproductive information for *Parupeneus indicus* from Fiji. (A) size at maturity (L_{50}); (B) percentage of mature females, relative to all mature individuals, versus length. Females are represented by closed circles and the solid curves, males are represented by open circles and the dashed curve.

$P < 0.001$). However, there was no histological evidence of hermaphroditism in *P. indicus*; testes did not contain a central membrane-lined lumen, and we did not detect a mixture of ovarian and spermatogenic tissue in any gonad. We classified *P. indicus* as a gonochore.

Overall sex ratio in this *P. indicus* population was significantly male-biased (Table 1, $\chi^2 = 9.783$, $df = 1$, $P = 0.002$). Operational sex ratio was also significantly male-biased ($\chi^2 = 15.511$, $df = 1$, $P < 0.001$). Sex ratios varied predictably throughout the size range of mature individuals (Fig. 5B). Curvilinear regression analysis of the percent of mature females ($\%_Q$) versus L_F (Table 1, $r^2 = 0.814$) indicates that males were more abundant than females at all sizes. However, smaller size classes had a higher percent of females than larger size classes. The percentage of females reached a maximum at 23.2 cm L_F , then decreased as length increased (Fig. 5B). All mature individuals ≥ 28.0 cm L_F were male.

***Chlorurus microrhinos*.** The WLR regression parameters a and b had 95% confidence intervals of $4.98 \cdot 10^{-6}$ – $2.05 \cdot 10^{-5}$ and 3.01–3.24, respectively ($r^2 = 0.966$, $n = 100$, L_F range: 29.6–52.2 cm, W range: 660–3300 g). Per ANCOVA results, there was no significant sex-based difference in WLRs ($F = 0.00$, $df = 1$, $P = 0.982$).

We examined the gonads of 47 male and 41 female *C. microrhinos*. Photomicrographs of immature and mature gonads of both sexes are presented as supplementary information (Fig. 6). Vitellogenic oocytes were seen in females as small as 36.2 cm L_F . We estimated female L_{50} at 38.0 cm L_F (Fig. 7A) and L_{95} at 47.8 cm L_F . Spermiated testes were seen in males as small as 33.7 cm L_F . We could not reliably estimate male L_{50} because of the low number of immature males (Fig. 7A).

A t -test detected a sex-based bimodal size distribution in *C. microrhinos*. The mean length of males was significantly greater than that of females ($t = -5.471$, $df = 81$, $P < 0.001$). There was some histological evidence of sex change in *C. microrhinos*; 17 testes contained a central membrane-lined lumen. However, we did not

detect a mixture of ovarian and spermatogenic tissue in any gonad. We provisionally classify *C. microrhinos* as a protogynous hermaphrodite. Assuming we correctly evaluated its sexual pattern, the size of transition (X_{50}) for *C. microrhinos* in Fiji was 40.0 cm L_F (Fig. 7B). All individuals ≥ 44.3 cm L_F were male.

Overall sex ratio in this *C. microrhinos* population was not statistically different from 1:1 (Table 1, $\chi^2 = 0.409$, $df = 1$, $P = 0.522$). However, operational sex ratio was significantly male-biased ($\chi^2 = 8.471$, $df = 1$, $P = 0.004$). Sex ratios varied predictably throughout the size range of mature individuals (Fig. 7C). Curvilinear regression analysis of the percent of mature females ($\%_Q$) versus L_F (Table 1, $r^2 = 0.750$) indicates that the population was female biased from 38.7–41.4 cm L_F . The percentage of females reached a maximum at 40.1 cm L_F , with males dominating ≥ 41.5 cm L_F (Fig. 7C). All mature individuals > 43.0 cm L_F were male.

Per capita egg production. When considering size-specific sex ratios, peak per capita egg production per spawning event was, for all species, estimated to be within a few centimeters of female L_{50} and less than 2/3 of the maximum length observed during market surveys (Fig. 8). For the gonochores *L. gibbus* and *P. indicus*, peak per capita egg production was in the 26 cm size class (Fig. 8A, B). For the likely protogynous *C. microrhinos*, the peak was in the 41 cm size class (Fig. 8C), one cm larger than the size at sexual transition (X_{50}). Greater than 90% of cumulative per capita egg production per spawning event was represented by individuals < 30 cm L_F for *L. gibbus* and *P. indicus*, and by individuals < 45 cm L_F for *C. microrhinos*. For all three species, larger individuals were exclusively male (Figs. 3B, 5B, 7C). These estimates of egg production are vastly different from those obtained when sex ratios are assumed to be 1:1 and invariant across size classes. Assuming equal sex ratios, the size at which 90% of cumulative per capita egg production per spawning event is predicted to occur is at greater lengths, from an additional 10.7 cm L_F for *P. indicus* to 22.8 cm L_F

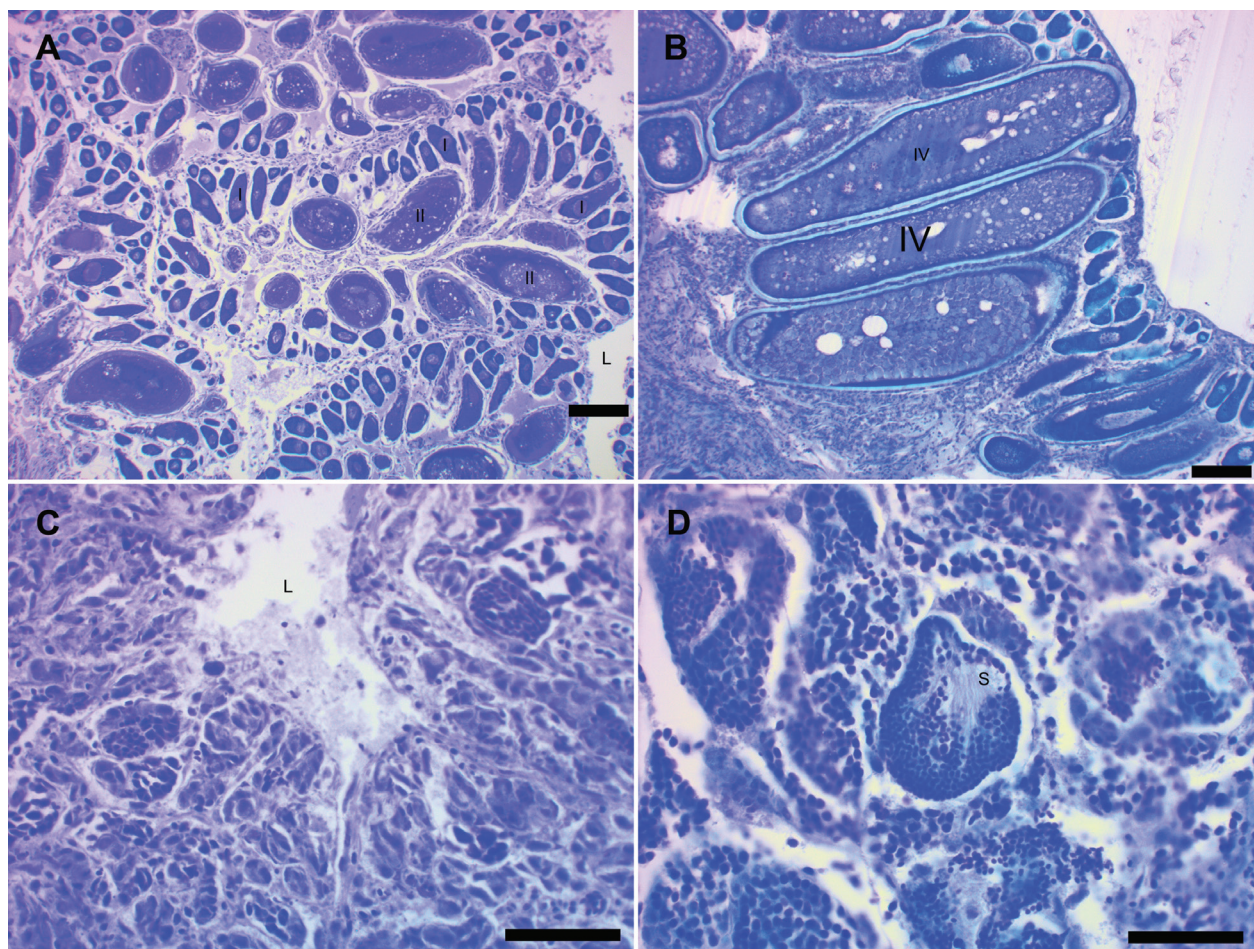


Figure 6. Histological sections of gonads of *Chlorurus microrhinos* from Fiji. (A) ovary of immature female (36.3 cm L_F) containing primary-growth (I) and cortical vesicle (II) oocytes, plus a conspicuous lumen (L); (B) ovary of mature female (37.1 cm L_F) containing a mixture of oocyte stages including final maturation (IV); (C) testis from an immature male (38.0 cm L_F) containing no tailed spermatozoa, but with a conspicuous lumen (L); (D) testis of a mature male (38.7 cm L_F) with tailed spermatozoa (S); scale bars = 100 μm (A and B) or 50 μm (C and D).

for *L. gibbus* (Fig. 8). Further, assuming equal sex ratios overestimates peak per capita egg production from 365% (*C. microrhinos*) to 1745% (*P. indicus*) per spawning event (Fig. 8).

Immature individuals in fisheries catch. Immature fish of the three species represented between 8%–50% by

number and 5%–41% by biomass of the catch in market surveys (Table 2). Of the three species, *P. indicus* had the greatest immature number of fish (28% in 2010–2013 and 8% in 2016–2018 from market surveys, 50% in 2019 from fish sampled for histology) and biomass (17%, 6%, 41%, respectively). For *C. microrhinos*, 30%, 20%, and

Table 2. The number and estimated weights of immature and mature fishes for three reef fish species from Fijian fish market surveys (years 2010–2013 and 2016–2018). The fish number and weights of the reproductive samples (year 2019) were measured.

Parameter	<i>Lutjanus gibbus</i>			<i>Parupeneus indicus</i>			<i>Chlorurus microrhinos</i>		
	2010	2016	2019	2010	2016	2019	2010	2016	2019
Total fish No.	443	169	163	215	12	141	180	65	101
Female No.	314	79	104	44	1	50	97	27	48
Males No.	129	90	59	171	11	91	83	38	53
Total immature No.	123	16	44	60	1	71	54	13	22
Immature Female No.	113	13	38	29	1	35	54	13	22
Immature Male No.	10	3	6	31	0	36	0	0	0
Total W [kg]	119.4	56.8	41.4	203.6	11.4	92.8	214.8	84.7	121.9
Female W [kg]	62.8	19.7	20.0	25.4	0.6	27.8	84.0	24.9	45.5
Male W [kg]	56.6	37.1	21.3	178.2	10.8	65.0	130.8	59.8	76.4
Total immature W [kg]	17.1	2.8	6.0	33.7	0.6	38.0	38.4	9.0	18.0
Immature Female W [kg]	15.4	2.3	5.0	14.8	0.6	18.0	38.4	9.0	18.0
Immature Male W [kg]	1.7	0.5	1.0	18.9	0.0	20.0	0.0	0.0	0.0

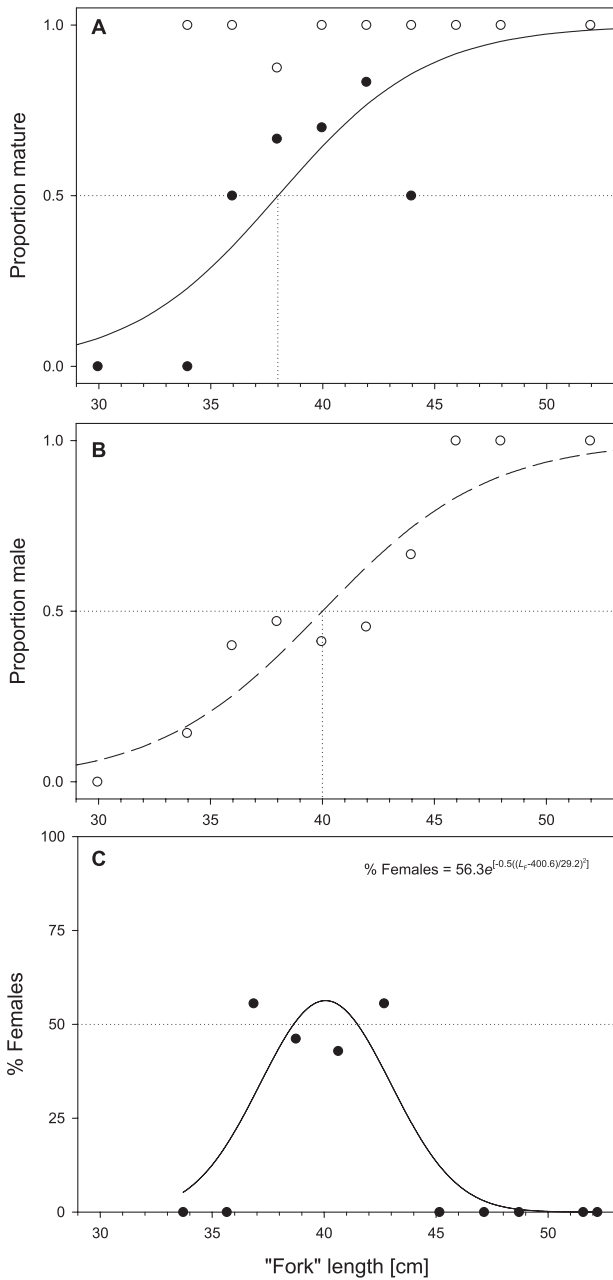


Figure 7. Reproductive information for *Chlorurus microrhinos* from Fiji. (A) size at maturity (L_{50}); (B) size of transition (X_{50}); (C) percentage of mature females, relative to all mature individuals, versus length. Females are represented by closed circles and the solid curves, males are represented by open circles and the dashed curve.

22% of fish were immature and 18%, 11%, and 15% of biomass was immature, respectively. Immature *L. gibbus* contributed 28%, 9%, or 27% by number, and 14%, 5%, or 14% of the biomass.

Discussion

We used rapid, histological methods to estimate a suite of reproductive parameters for three coral reef fishes. We acknowledge that estimates of life history parameters for

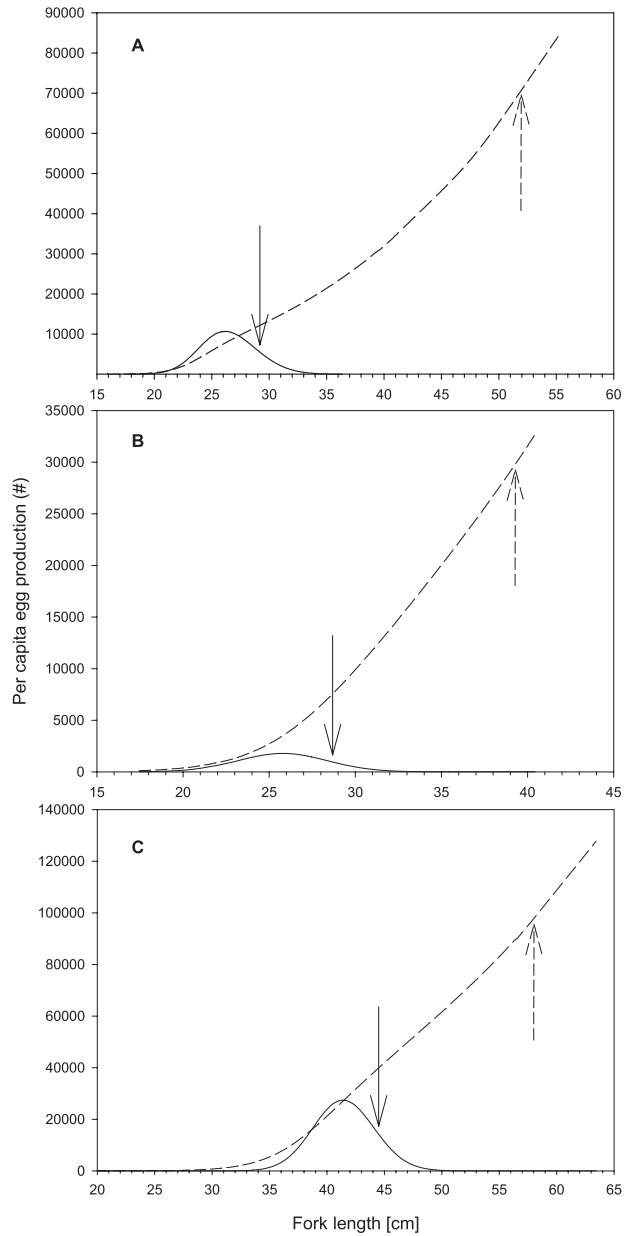


Figure 8. Estimated per capita egg production per spawning event. The solid curve represents estimates when size-specific sex ratios are considered, the dashed curve represents estimates when sex ratios are assumed to be equal and invariant. (A) *Lutjanus gibbus*; (B) *Parupeneus indicus*; (C) *Chlorurus microrhinos*. Arrows indicate 90% cumulative egg production. Note that x- and y-axis scales vary.

high value fishery species are typically based on hundreds to thousands of specimens, often collected and compared annually or spatially. For small-scale tropical fisheries, a similar production-scale effort for life history studies is rarely feasible. The approach that we present follows a scientifically valid methodology working with relatively smaller sample sizes that provides important life history information for conservation and management guidance on coral reef species in data limited fisheries.

Our results allow comparisons of method (different methods used in the same location) and location effects

Table 3. A comparison of macroscopic (from Prince et al. 2019) and histology-based (present report) estimates of L_{50} (cm) for three reef fishes from Fiji.

	<i>Lutjanus gibbus</i>	<i>Parupeneus indicus</i>	<i>Chlorurus microrhinos</i>
Macroscopic L_{50}	29.8	32.5	37.5
Histological L_{50} male	23.1	24.2	—
Histological L_{50} female	22.7	25.9	38.0

(the same methods used in different regions). Table 3 presents the species-level (i.e., grouped sexes) L_{50} estimates produced during a three-year-long macroscopic analysis of Fijian reef fishes (Prince et al. 2019) and the histology-based, sex-specific L_{50} estimates we produced. Our histology-based results indicate that males mature from >1 cm (*P. indicus*) to nearly 7 cm (*L. gibbus*) shorter than suggested by macroscopic methods. For females, the different methods produced similar results for two species; histology-based results suggest that *C. microrhinos* matures about 0.5 cm larger than was reported for macroscopic analysis. Conversely, our histology-based results suggest that *Lutjanus gibbus* and *Parupeneus indicus* mature ~ 7 cm shorter than was indicated by macroscopic analysis. These differences likely result from inaccuracy in macroscopic evaluation. For instance, in the presently reported study, we misclassified sex and/or maturity status in 20.0%–60.2% of specimens (*L. gibbus* and *P. indicus*, respectively). Similar differences between histological and macroscopic results have been reported elsewhere (Vitale et al. 2006; Grandcourt et al. 2011; Longenecker et al. 2013a, 2013b, 2020; Longenecker and Langston 2016). Although the accuracy of macroscopic staging improves as personnel gain experience, the misclassification rate exceeds 40% for many gonad stages, even when workers are experienced (Mackie and Lewis 2001).

In the absence of a robust understanding of geographic patterns of size at maturity, it would be prudent to use site-specific estimates of reproductive parameters when developing management strategies. Two of the species we analyzed in this study were the subject of histology-based reproductive analysis at other locations. Similar histology-based methods were used to study *P. indicus* in Papua New Guinea (Longenecker et al. 2016) and *L. gibbus* in the Federated States of Micronesia (Longenecker and Langston 2016). For the majority of parameters that we could statistically compare, there were significant regional differences. WLRs, and overall and operational sex ratios differed for both species. When we used the data from Papua New Guinea (Longenecker et al. 2016) and Federated States of Micronesia (Longenecker and Langston 2016) to estimate L_{50} with the regression model employed in the presently reported study, we found that *P. indicus* females mature at a much larger size in Fiji than in Papua New Guinea (25.9 vs. 18.4 cm L_F , respectively). Additionally, *L. gibbus* females mature at a slightly larger size in Fiji than in the Federated States of Micronesia (22.7 vs. 21.0 cm L_F , respectively). Although of biological and management importance, neither of these differences could be demonstrated to be statistically significant.

The use of rapid histology-based methods allows the identification of emergent patterns in reproduction during processing for each set of specimens. For instance, for the three species analyzed in the presently reported study, mature females are more abundant in the lower range of size classes containing mature individuals and become increasingly rare, then absent, as length increases (Figs. 3B, 5B, 7C). This pattern has been reported elsewhere; however, its impact on the size classes overwhelmingly responsible for population-level egg production is under-recognized (but see Longenecker et al. 2014, 2016, 2017, 2020). The common pattern of large females producing exponentially more eggs than small females has led to a long-standing assumption that large fish are disproportionately responsible for population-level egg production (Roberts and Polunin 1993; Allison et al. 1998; Halpern 2003; Froese 2004; Sale et al. 2005; Birkeland and Dayton 2005). However, the assumption may not be valid if females are rare in the largest size classes and is invalid if females are absent. Considering the size-specific sex ratios reported here, the decreasing proportion of females in the largest size classes overwhelms length-related increases in batch fecundity, resulting in peak per capita egg production well below maximum observed length (Fig. 8). That we report this pattern for the likely protogynous hermaphrodite, *C. microrhinos*, may not be surprising. However, the impact of detecting the same pattern for the gonochores, *L. gibbus* and *P. indicus*, cannot be overstated.

Size-specific sex ratios such as those we report here have two major implications for fishery conservation and management. First, with females absent from the largest size classes, fishing at or near the maximum size will have little impact on population-level egg production. Second, imposing slot limits to protect the largest individuals would direct fishing pressure toward smaller size classes which, because they comprise the highest proportions of females, are the major source of population-level egg production.

Our results suggest that protection of the individuals overwhelmingly responsible for the majority of per capita egg production per spawning event could be achieved by establishing minimum size limits of 30 cm L_F for *L. gibbus* and *P. indicus*, and 45 cm L_F for *C. microrhinos*. These minimum limits would also protect all immature individuals of *L. gibbus* and *C. microrhinos* (Fig. 9A, C), and all immature females of *P. indicus* (Fig. 9B). However, implementation of minimum size limits should also consider other factors, such as monitoring compliance and subsistence fishing needs, to achieve effective management of coastal reef fishes.

Our analyses of per capita egg production do not consider potential maternal effects, such as the possibility that larger females may spawn more often or produce higher quality eggs. Nor do they consider the typical population size structure of fishes, comprising many more small individuals than large individuals. The impact of the latter has been demonstrated by genetic parentage analysis showing that highly abundant mature fish contribute disproportionately to population replenishment

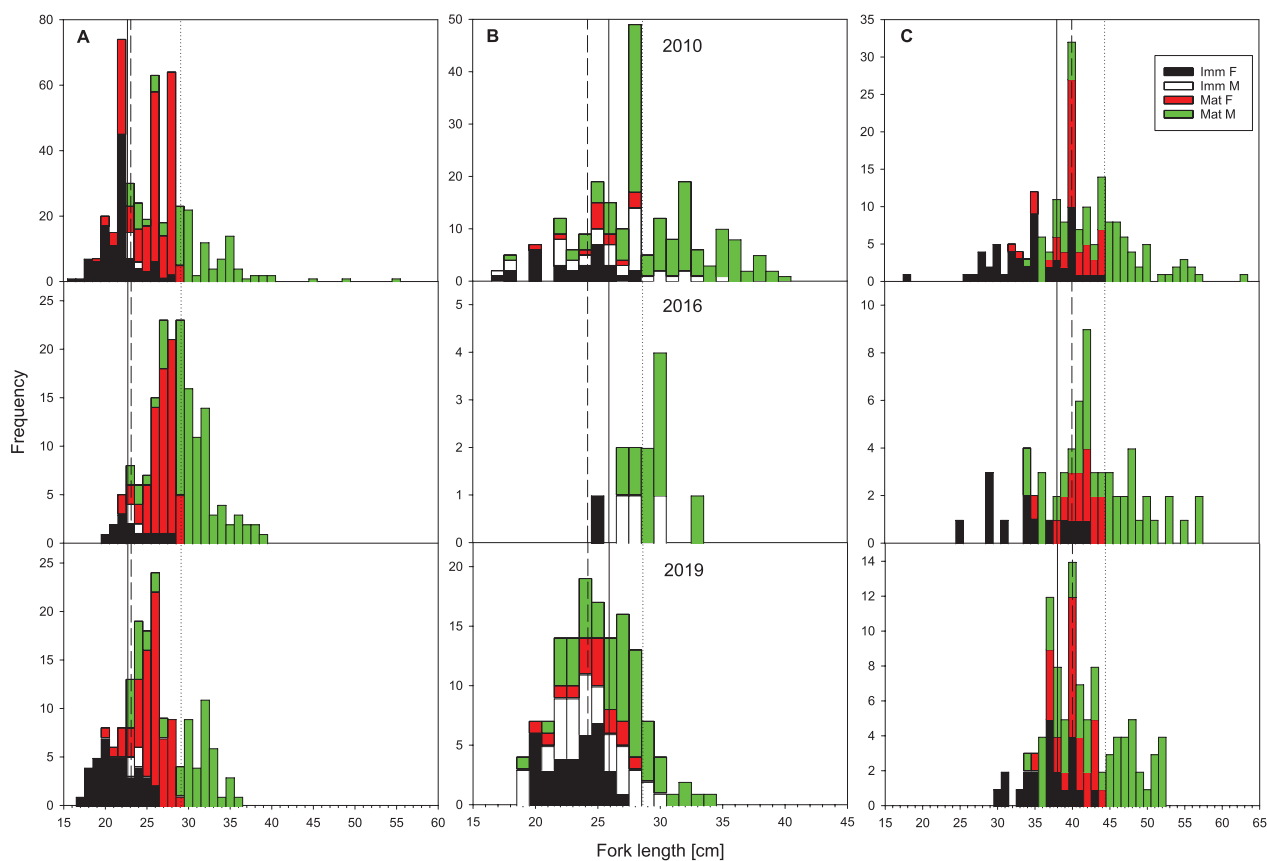


Figure 9. Size class distribution of three exploited reef fishes from three market surveys in Fiji. **A** *Lutjanus gibbus*; **B** *Parupeneus indicus*; **C** *Chlorurus microrhinos*. Solid line = female L_{50} ; dashed line = male L_{50} ; dotted line = 90% cumulative per capita egg production. Note that x - and y -axis scales vary.

(Lavin et al. 2021). At the population level, the typical size structure would magnify the per capita egg production patterns described above.

Conclusions

We used rapid, histology-based methods to estimate Fiji-specific reproductive parameters for three reef fishes. We then used the parameter estimates to describe the reproductive characteristics of fish observed in Suva fish markets. The absence of females in the largest size classes of all three species suggests that, at the population level, individuals well below maximum size are responsible for the majority of egg production. Minimum size limits of 30 cm L_F for *Lutjanus gibbus* and *Parupeneus indicus*, and 45 cm L_F for *Chlorurus microrhinos* may enhance population-level egg production while also protecting almost all immature individuals of all three species.

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