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Research Article

Reproductive Biology of Black Jewfish (*Protonibea diacanthus*) off the East Coast of Australia

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The black jewfish (*Protonibea diacanthus*) occurs in tropical coastal waters throughout the central Indo-Pacific. It has long been valued as an important recreational and artisanal fishery species but has become increasingly targeted by commercial fisheries due to demand for its large swim bladder. To better understand how changes in fishing pressure may impact the sustainable exploitation of *P. diacanthus* populations throughout Eastern Australia, we evaluated the reproductive biology of the species across two management regions in Central Queensland. Reproductive characteristics studied included the size at maturity, fecundity, spawning mode, and season. Spawning periodicity was evaluated throughout the two major management regions and revealed an increase in the gonadosomatic index during the early austral spring, followed by evidence of spawning occurring from September through March with a peak from September to November. Females were found to produce ~4.5 million ± 1.4 million oocytes (mean ± SE) per batch. Spawning periodicity did not vary latitudinally but was found to differ from other regions in northern Australia. The present study provides reliable maturity and fecundity information to improve future assessment and sustainable management of *P. diacanthus*.

1. Introduction

The family Sciaenidae includes a diverse range of species, which are commonly known as "Croakers" or "Drums" due to their ability to make sounds [1]. Sciaenids are also often characterised as maintaining large seasonal or year-round aggregations, making them susceptible to targeted fishing pressure [2, 3]. Their risk of depletion by fisheries is compounded by the high value and market demand for their large swim bladders, which are considered a premium product when dried and sold as "maw" [4]. As a result, many species are targeted in commercial fisheries. The high fishing pressure has led to concern around the sustainability of Sciaenid fisheries worldwide [5, 6].

The black jewfish (*Protonibea diacanthus*) is one of the largest Sciaenid species and occurs throughout the Indo-West Pacific region. The species has experienced population declines throughout its range, with localised depletion of some populations being associated with large increases in targeted fishing practices [7]. In most cases, intensification of fishing pressure on *P. diacanthus* populations has been driven by increasing prices and demand for their swim bladder [5]. As a result, the global status of the species was recently listed as "near threatened" by the IUCN Red List [8].

Although generally characterised by fast growth and early maturation, *P. diacanthus* are also known to form discrete populations that have been shown to exhibit variation in their reproductive characteristics including length and age at maturity, fecundity, spawning season, spawning frequency, and growth rates [9, 10]. The observed variability in the population biology among regions and the continued increase in demand for the species highlight the need for characterisation of their reproductive biology at a local level.

In Australia, *P. diacanthus* are found in estuaries and coastal waters from approximately the Burnett River in Central Queensland, around northern Australia to Broome in Western Australia. The maximum age and size of *P. diacanthus* have previously been reported from studies in the Northern Territory (13 years old and 126 cm total length) and the Gulf of Carpentaria (12 years old and 154 cm total length) [9, 11]. Within Australian waters, spawning of *P. diacanthus* has been identified to occur from the austral spring in October to the end of autumn in April in the Northern Territory (NT) and is suspected to occur between April and September in Cape York [9]. In north-western India, the spawning season for *P. diacanthus* (or ghol as they are referred to locally) commences at the start of the monsoon period in June and continues until August [12]. Variation in other reproductive characteristics such as length at maturity has also been observed among populations, with estimates of total length at 50% maturity varying from 80 to 84 cm in Cape York [7] and India [12] to 89 cm in the Northern Territory (NT) [9] and 98 cm in the Gulf of Carpentaria (Australia) [11].

No literature on the fecundity of *P. diacanthus* currently exists from Australian waters, and as a result, the most recent assessment of the NT stocks recommended a detailed study into the reproductive biology of *P. diacanthus*, with an emphasis on fecundity (Grubert et al., 2013). Several batch fecundity estimates do exist from Northern Hemisphere populations, with estimates from India ranging from 1,743,010 to 6,868,368 oocytes [12, 13] and 3,883,840 oocytes reported in a fish sampled in Taiwan (based on the assessment of a single ovary) [14]. Rao [12] observed that the ratio of maturing to mature oocytes gradually decreased throughout the spawning season, supporting a batch mode of fecundity for the species. Given the identification of the fine-scale population structure and high variability in current fecundity estimates, there remains a need for greater information on their reproductive biology that is directly applicable to population models of *P. diacanthus* from Australian waters.

In waters off the East Coast of Queensland, a large increase in commercial targeting and landings of *P. diacanthus* (from ~30 to 136 tonnes) occurred within the space of two years between 2016 and 2018. This increase was reportedly driven solely by demand for maw within the Chinese market [15]. The absence of biological information to inform the assessment and management of the stock meant that the status of the fishery has been classified as undefined, and conservative management measures were implemented to safeguard against population decline [15]. This management included a 20-tonne competitive Total Allowable Commercial Catch, which resulted in a full fishery closure (for both recreational and commercial sectors) approximately two months after the season opening each year (resulting in a fishing season spanning January and February). In addition to these, the existing output controls for the fishery including a size limit of 75 cm total length, and recreational in possession limit also remained in place. To address the gaps in knowledge around the reproductive biology of *P. diacanthus* within Australian waters, we aimed to evaluate their reproductive characteristics within the Queensland East Coast fishery.

2. Materials and Methods

2.1. Sample Collection and Study Sites. Between September 2020 and October 2021, biological samples were collected monthly with the assistance of commercial fishers in Central Queensland. Sampling during the *P. diacanthus* fishing season (January and February) occurred through the collection of samples from those caught within the commercial fishery. The fishery operates by targeting fish at known black jewfish aggregation sites using standard hook-and-line methods. Outside of the fishing season (March to December), sampling was undertaken by contracting commercial fishers to collect samples indicative of normal fishing activity. To ensure that the greatest possible length range of *P. diacanthus* was sampled, specimens smaller than the minimum legal length (75 cm TL) were also targeted in each region by means of scientific collection permits (using line fishing methods). Samples were collected from two regions, corresponding to the Queensland Inshore Fishery Management Regions: Region 3 (19°00′ S to 22°00′ S) and Region 4 (22°00′ S to 24°30′ S) (Figure 1). Sampling was designed to collect at least 20 specimens per month per management region for the purpose of biological data collection. The research sampling was carried out under General Fisheries Permits 208082, Great Barrier Reef Marine Parks Permit G20/44421.1, and Animal Ethics Approval CA 2020/04/1368. Biological data recorded for each sampled fish included total length (TL, ±0.5 cm), body weight (±1 g), sex, gonad weight (±0.1 g), and gonad phase. Monthly male-to-female sex ratios were characterised and compared between regions using a one-way ANOVA.

2.2. Gonad Development. Gonads were assigned to a macroscopic gonad phase based on appearance as outlined in Supplementary Table S1 which has been developed in line with the black jewfish staging [16]. The gonadosomatic index (GSI) was calculated based on the following equation:

$$\mathrm{GSI} = \frac{\text{gonad weight (in g)}}{\text{fish total weight (in g)}} \cdot 100. \quad (1)$$

The mean monthly GSI was calculated separately for females and males. Only fish that were phase 2 or greater were included to remove immature fish and reduce any potential bias.

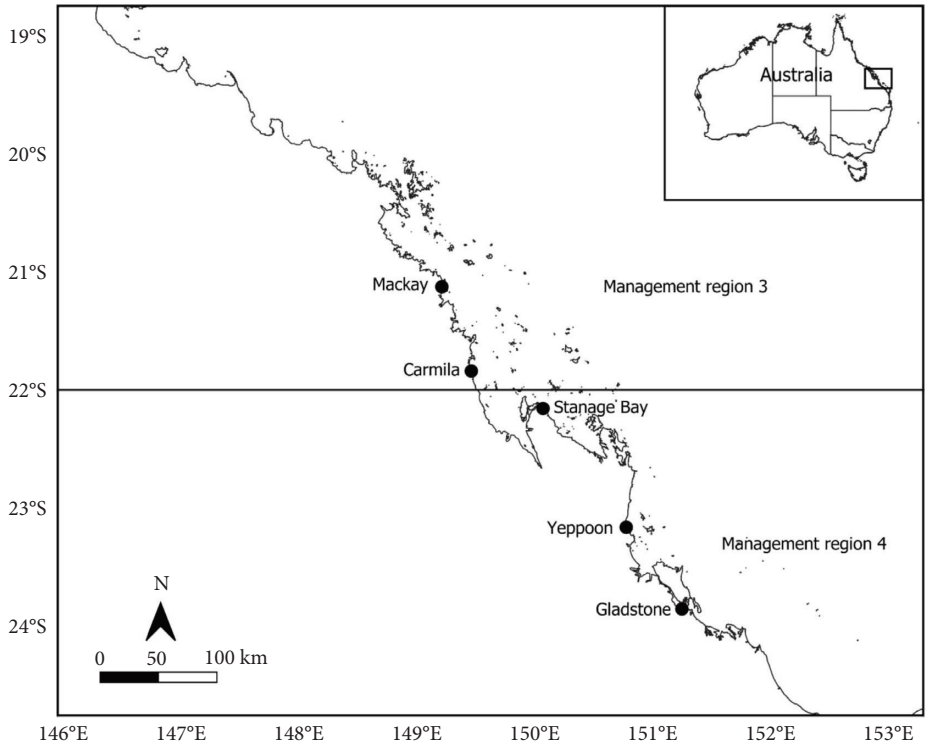

FIGURE 1: Map of the Central Queensland coast showing the locations where *Protonibea diacanthus* were sampled.

2.3. Histology. Histological analysis was undertaken to validate macroscopic staging and was completed on a minimum subsample of five female gonads from each gonad phase across the sampling period. Representative gonads from a range of lengths, phases, and sampling sites were kept in a fixative solution of 10% neutral buffered formalin (NBF) for histology and fecundity estimates. After 10 days, the gonad samples were rinsed in water before being transferred into 70% ethanol for storage. The fixed gonad tissue was embedded in paraffin wax, and three 6 μm cross sections were taken through the middle of each gonad and stained with haematoxylin and eosin. Histological sections were examined under a compound microscope, and a microscope-mounted camera was used to collect images of each gonad phase in accordance with Supplementary Table S1.

2.4. Maturity. Maturity was based on the macroscopic staging of gonads (validated by histology) and categorized into either immature (phase 1) or mature (phases 2, 3, 4, and 5). The lengths at maturity were calculated as per Ogle [17] by determining the proportion of mature fish in 1 cm TL classes and fitting a logistic curve for each sex as well as for pooled sex data in *R* (version 4.0.5). The logistic curves for maturity for each sex were compared using a Wald's *F*-test in the *R* package "aod" to test the null hypothesis that male and female lengths at maturity did not differ [18, 19].

2.5. Fecundity and Oocyte Development. Batch fecundity (BF) was estimated for a subset of phase 3 and 4 ovaries that were selected based on them meeting the criteria of containing hydrated oocytes but no early postovulatory follicles being present. Formalin-fixed ovaries were weighed whole and by lobe to the nearest 0.1 g, after which subsamples of 0.4 g of tissue were removed for each lobe. An image of the oocytes collected was taken by placing oocytes in a Petri dish filled with 70% ethanol. The oocytes in each subsection of the ovary were counted by capturing an image of the subsection with a Leica M205A microscope-mounted camera. The image analysis software (ImageJ version 1.381) was employed to automatically count oocytes for a gravimetric estimate of BF (as described in [20]).

To account for possible differences in the number of oocytes in different lobes and different sections of the ovary, a series of subsamples were undertaken. For each ovary, four subsamples were collected from each of the left and right lobes to account for potential nonuniform bias in the oocyte content. The subsamples collected from each gonad were then averaged to produce a representative estimate of the number of oocytes per gram, which could be upscaled to determine the BF per gonad using the gravimetric method, where

$$F = n\frac{G}{g}, \tag{2}$$

where "F" is fecundity, "n" is the number of oocytes in the subsample, "G" is the weight of the ovary, and "g" is the weight of the subsample. Mean estimates were then used to evaluate the relationship of fecundity with total length in *R*.

3. Results

3.1. Length Distribution and Sex Ratios. A total of 574 fish were sampled throughout two management regions of the fishery (females: 225, males: 268, and immature fish with

indeterminate sex: 42). Gonads of juveniles below ~70 cm in TL were visually very similar between male and female fish and therefore prevented the identification of sex for many immature specimens (Figure 2). Samples collected during the open fishing season spanned the entire fishery areas, while samples collected under a scientific permit outside of the fishing season were focused on the main fishing grounds. Fish total length ranged from 43 cm to 140 cm, with most specimens being between 105 and 125 cm. There was no significant difference in monthly sex ratios by the region (one-way ANOVA; $p = 0.378$).

3.2. Spawning Period. The monthly mean GSI and gonad staging identified clear seasonal transitions in the reproductive condition. The monthly mean GSI showed the peak reproductive condition occurring during September and October (females ~3.4%, males ~0.8%, Figure 3), coinciding with a high proportion of phase 4 males and females (Figure 4). The GSI value steadily declined from December to March for both sexes (Figure 3) as the proportion of phase 5 (regressing) and phase 2 (regenerating) fish increased (Figure 4). The mean GSI remained at its lowest point (females ~0.5% and males ~0.2%) between March and June (Figure 3), which was characterised by high proportions of regressing and regenerating gonads (Figure 4). The reproductive condition increased during June, July, and August (Figure 3), with large numbers of developing gonads present in both sexes (phase 3) (Figure 4).

Three fish had degenerate gonads either due to the presence of large urinary bladder stones that appeared to obstruct key reproductive organs or were linked to fish in a noticeably poor condition. In three fish, the presence of large urinary bladder stones was observed to affect gonad development, with stones reaching 8.8 cm in diameter and 88 g weight (Supplementary Figure S1). While the presence of degenerate gonads was rare, these specimens did have the potential to downward bias maturity estimates and so were excluded from subsequent analyses. However, in most cases, small urinary bladder stones (which occurred in ~2% of gonads) did not appear to obstruct the reproductive biology.

3.3. Gonad Histology. Histology was able to validate macroscopic staging, with clear differences in oocyte development among macroscopically examined ovaries. Female immature ovaries were dominated by previtellogenic oocytes (Figure 5(A)), while regenerating phase 2 ovaries were characterised by primary growth oocytes, with early-stage regenerating gonads containing late-stage atresia and postovulatory follicles (Figure 5(B)). Developing ovaries in phase 3 had cortical alveolar oocytes, as well as primary and secondary vitellogenic oocytes (Figure 5(C)). Phase 4 gonads include those spawning-capable that were dominated by tertiary vitellogenic oocytes, as well as those that were actively spawning and had oocytes undergoing late germinal vesicle migration or breakdown (Figures 5(D) and 5(E)). Phase 5 regressing gonads ranged from those which contained many oocytes undergoing atresia (any stage) to those which were similar to early-stage phase 2 gonads (apart from having fewer postovulatory follicles and less densely packed primary growth oocytes) (Figure 5(E)).

3.4. Maturity. The lengths at which 50% (L50) of females and males reached sexual maturity were not significantly different (Wald's test, $p = 0.11$), so maturity data for both sexes were combined (Figure 6). The combined L50 was 87 cm· TL, and the length at full maturity (L100) was estimated at 105 cm· TL.

3.5. Fecundity. A total of nineteen ovaries met the conditions for supporting an evaluation of batch fecundity. Mean gravimetric fecundity (GF) was estimated at 4,495,172 ± 1,415,862 oocytes (mean ± SE), with a range from 489,738 oocytes to 27,893,709 oocytes. The relationship between GF and TL was best described by the exponential relationship ($n = 19$, $R^2 = 0.78$; Figure 7):

$$\text{gravimetric fecundity} = 32.3 \cdot e^{0.09 \cdot \text{TL}}. \quad (3)$$

Relative fecundity (RF) ranged from 31 to 910 oocytes g^{-1} body mass. The relationship was observed to be strongly influenced by the largest individual within the dataset (140 cm TL, ~28 million oocytes). After the removal of data related to this specimen, the fit of the data reflected a flat, nonsignificant linear relationship ($R^2 = 0.003$) (supplementary material Supplementary Figures S2 and S4).

4. Discussion

The results of this study yielded new insights into the reproductive biology of *P. diacanthus* from the Queensland East Coast. The GSI values for *P. diacanthus* and histological staging of ovaries indicated a single spawning period from September until March, which coincided with the peak of the wet season. Based on counts of hydrated oocytes, mature females preparing to spawn were capable of releasing 489,738 to 27,893,709 oocytes during each season, with very large females (≥140 cm) capable of producing exponentially greater numbers of oocytes. Histological and macroscopic staging data indicated that the size at 50% maturity was 83 cm and L100 was 105 cm, with no significant differences between sexes.

Macroscopic and microscopic examination of *P. diacanthus* gonads also showed clear seasonality in spawning periodicity. The presence of both phases 4 and 5 gonads from September until March indicates that spawning activity was occurring throughout this period. This information was supported by GSI values which peaked in September, before reducing throughout the subsequent months as the reproductive condition of fish deteriorated following the release of oocytes. The timing of the spawning season coincided with the wet season in Central Queensland. The occurrence of spawning in periods of monsoonal activity is consistent with the timing of peak reproductive activity in NT (October and April) and Indian (June and August) populations [7, 9, 12]. Improving the understanding

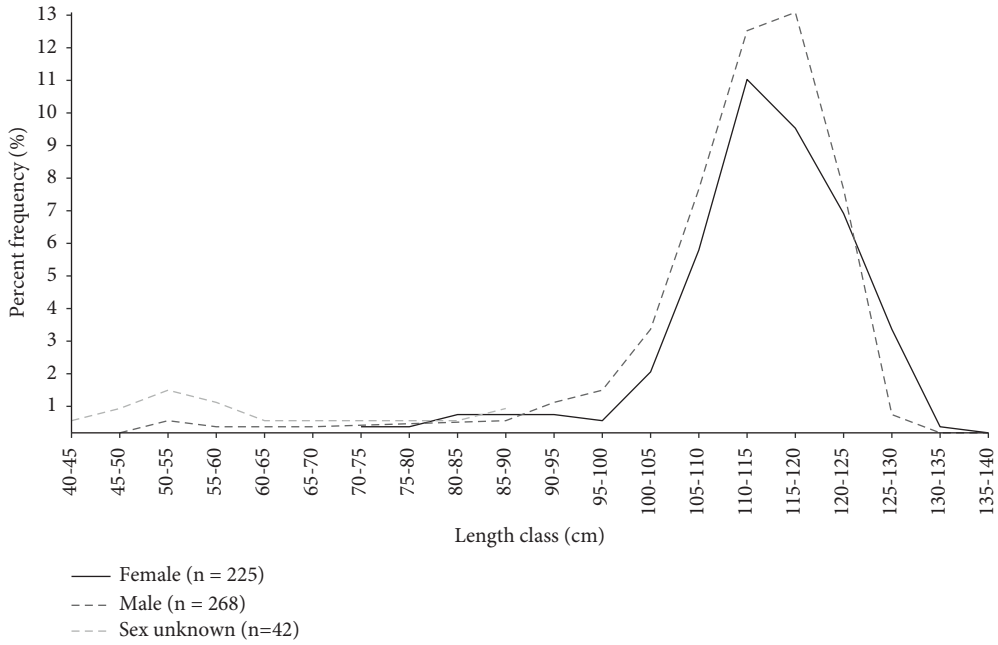

FIGURE 2: Length-frequency distributions of male, female, and indeterminate-sex *Protonibea diacanthus* samples collected.

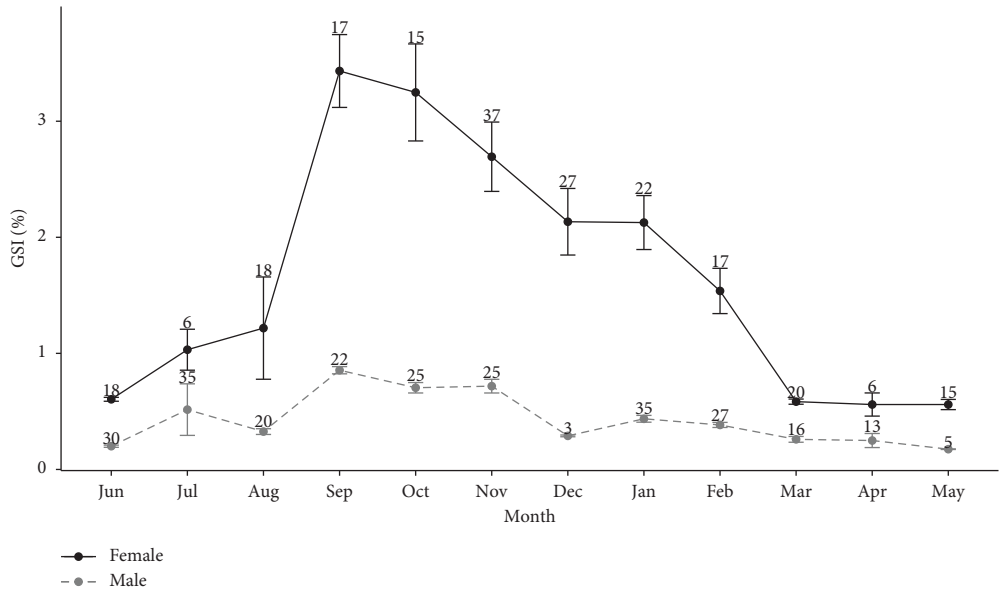

FIGURE 3: Mean GSI (±SE) by month of male and female *Protonibea diacanthus*. Numbers represent sample sizes.

of whether environmental cues are linked to spawning behaviour would be valuable for informing any regulatory measures associated with spawning behaviour (e.g., seasonal closures) and understanding whether variability in recruitment such as that observed in the NT may be linked to egg production [15].

As with many other Sciaenids, *P. diacanthus* is known to form large aggregations around oceanographic features with high current differentials [21, 22]. The purpose of these aggregations has long been speculated to be linked to spawning behaviours, as seen in many other commercially important species [23]. Given that all sampling was undertaken at known black jewfish aggregation sites and that fish were found year-round at most sites (including outside of spawning periods), we were able to surmise that the purpose of fish aggregating at these sites did not appear to be solely driven by spawning behaviour. Furthermore, the trend in the GSI did not appear to vary among sampling fishery management regions (Supplementary Figure S3). This observation may indicate that the presence of aggregations could simply be a result of schooling behaviour at favourable habitats, with spawning occurring at specific times of the year, rather than aggregations forming for the sole purposes of spawning [21]. Additional information

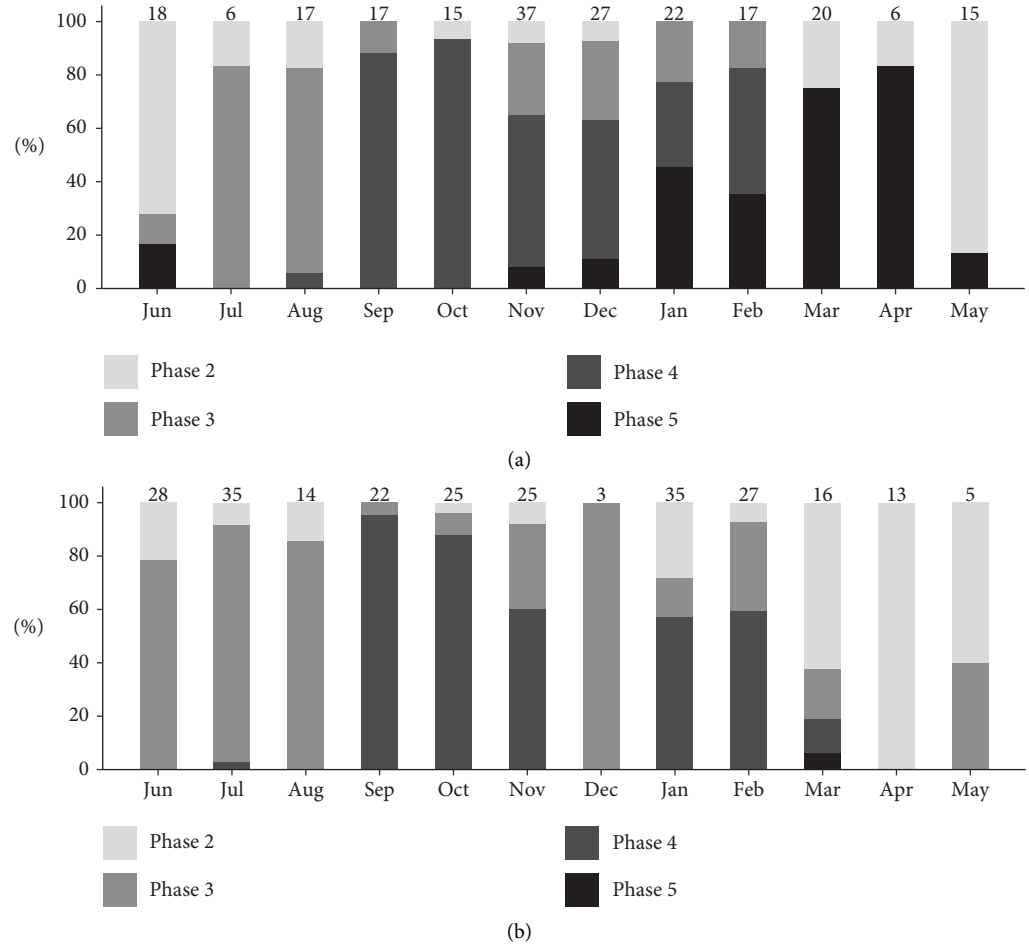

FIGURE 4: Change in the relative occurrence of phase 2–5 gonads in female (a) and male (b) *Protonibea diacanthus* from Central Queensland waters. Numbers indicate sample sizes.

around the residency of fish at, and movement of fish between, prominent aggregation sites would help to further resolve the importance of this behaviour [22].

The gravimetric fecundity estimates identified herein represent the first quantitative evaluation of batch fecundity from *P. diacanthus* populations within the southern hemisphere. The mean fecundity estimate of 4,495,172 ± 1,415,862 oocytes (mean ± SE) was within the range of previous work from populations in the Northern Hemisphere. However, the range of estimates observed in the current study (489,738 to 27,893,709 oocytes) greatly expands on known information regarding intraspecific variability and maximum spawning potential of the species. The maximum estimated fecundity for the species from previous studies was ~7 million, which is around four times smaller than the maximum estimate identified here [12]. Overall, we found a very weak relationship between fecundity and fish length when examining fish ranging from ~105 to ~130 cm (Figure 7). The inclusion of a single very large specimen (142 cm) that was estimated to have ~28 million oocytes was the main driver of the observed exponential relationship between fish size and fecundity. Interestingly, recent reproductive evaluations of another large-bodied Sciaenid, the totoaba (*Totoaba macdonaldi)*, found any relationship between fecundity and TL to be driven by a single, large, and highly fecund specimen (25,132,320 oocytes) [24]. Furthermore, Rodríguez-Jaramillo et al. [24] also found the *T. macdonaldi* to average 2,662,626 oocytes, with fecundity not related to TL when the outlier specimen was removed, which is consistent with what we observed herein. We recommend examination of more specimens with a TL greater than 130 cm to help verify the strength of this relationship and whether there is an inflection point in the fecundity-to-length relationship.

The length at maturity indicates an early maturation based on the age-length relationship described by Mcpherson [11] for *P. diacanthus* landed in the Gulf of Carpentaria fishery (Queensland, Australia). Our estimate of 50% maturity at ~83 cm TL was found to be within the length range (80–84 cm) observed in Cape York [23] and India [12], but less estimates in both the Northern Territory (89 cm) [9] and the Gulf of Carpentaria (98 cm) [11]. This estimate is also higher than the current minimum legal size (MLS) for *P. diacanthus* within the Queensland East Coast fishery, which is set at 75 cm. However, as fish smaller than

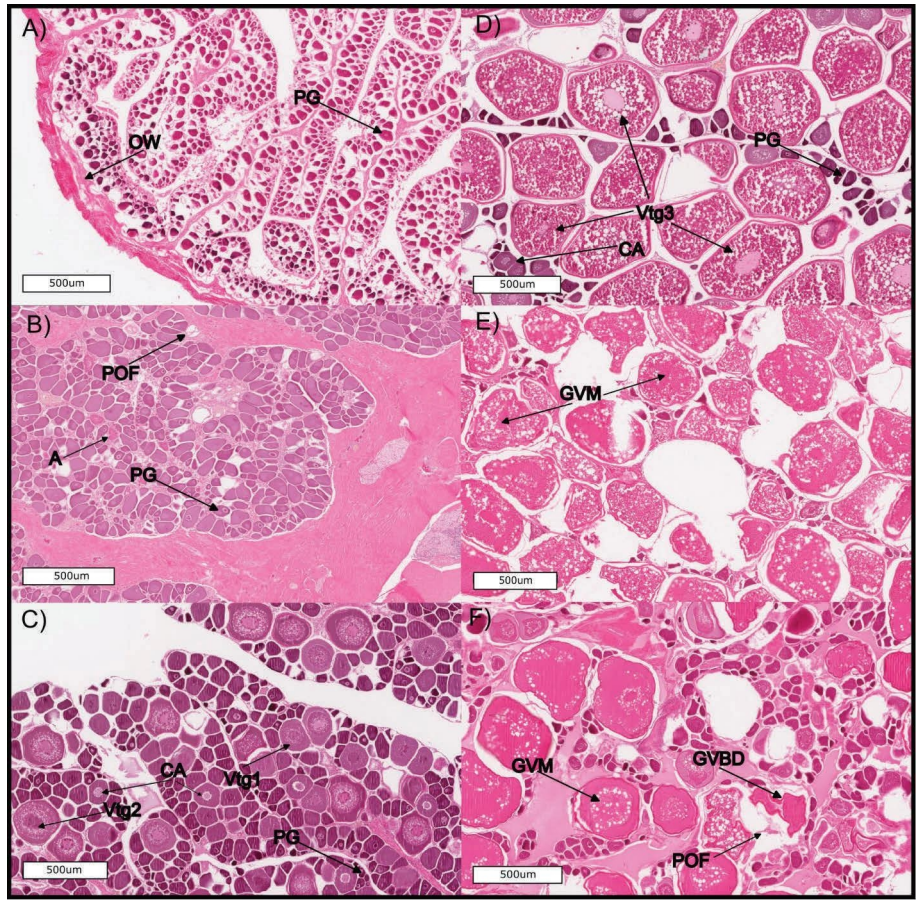

FIGURE 5: Histological sections of *Protonibea diacanthus* ovarian tissue illustrating (A) phase 1 (immature); (B) phase 2 (regenerating); (C) phase 3 (developing); (D) phase 4 (spawning capable); (E) phase 4 (actively spawning); (F) phase 5 (regressing). A, atretic oocyte; CA, cortical alveolar oocyte; GVM, germinal vesicle migration; GVBD, germinal vesicle breakdown; PG, primary growth oocyte; POF, postovulatory follicles; Vtg, vitellogenic oocyte (1 = primary, 2 = secondary, and 3 = tertiary).

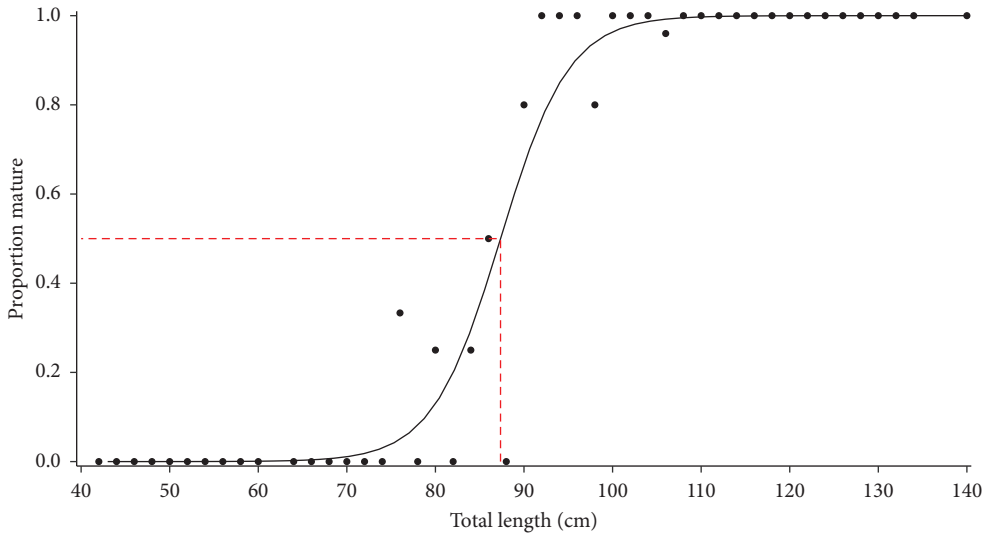

FIGURE 6: Length at maturity with a fitted logistic curve for *Protonibea diacanthus* from Queensland East Coast waters for combined males and females. Displayed points are the proportion of mature fish in 2 cm·TL classes. The red dashed line indicates L50.

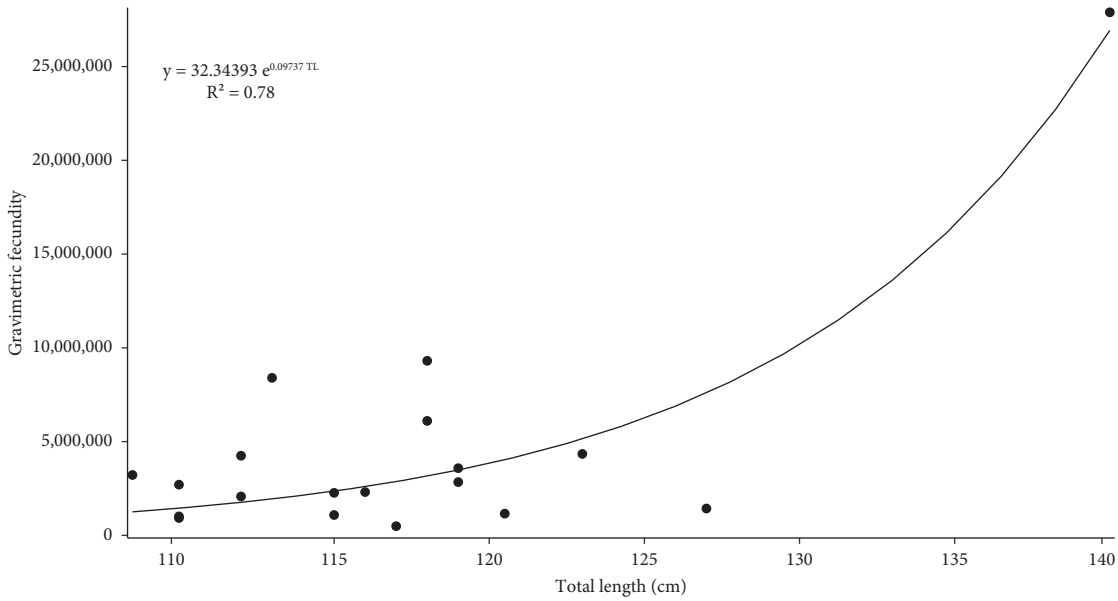

FIGURE 7: Exponential relationship between total length (cm) and batch fecundity for *Protonibea diacanthus* from Queensland East Coast waters.

83 cm are uncommon within the commercial fishery, it is not likely that increases to the MLS would result in a significant reduction in fishing mortality.

The presence of large urinary bladder stones and degenerate ovaries has not previously been reported in *P. diacanthus*. The documentation of urinary stones (urolithiasis) in marine fish remains rare and has been identified to form due to the excretion of an excessive amount of oxalate into the urine, which gets incorporated into a stone [25, 26]. It has been hypothesised that these stones may be linked to rapid acclimation to low salinity environments; however, this remains largely unvalidated [26]. Although most urinary bladder stones observed in *P. diacanthus* were small and did not appear to have negative effects on the reproductive biology, urinary bladder stones in several fish were significant in size and had visually impacted the fish's gonads. The presence of large objects within the peritoneal cavity has been shown to contribute additional stress and have negative effects on the spawning of fish [25]. The stones identified in this study were located at the beginning of the oviduct and appeared to obstruct the development of oocytes. Despite the noted effects on gonadal development, the fish were large, and the stones did not appear to impact their body condition. Further reporting of urinary bladder stones in wild marine populations along with targeted work to determine how urinary bladder stones may link to fish condition factors such as diet or infection would be of benefit.

5. Management Implications

With increasing sustainability concerns around Sciaenids globally, additional biological information around high-demand species such as *P. diacanthus* is useful to ensure that populations are managed at sustainable levels. Our work uncovered multiple insights that interact directly with the assessment and management of the stock. First, the end of the spawning period aligns with the peak period of commercial fishing effort, with the season opening under a competitive Total Allowable Commercial Catch on 1 January. A delay to the commencement of the fishing season or a short spawning closure would help to shift this peak in effort outside of the spawning window for the stock, providing additional protections to the stock both now and in the future. Second, the fecundity estimates identified herein will be available to inform the specifications of suitable stock assessment parameters.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

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Supplementary Materials

Description Supplementary Figure S1: images of large urinary bladder stones that were found in the peritoneal cavity of two black jewfish. The fish in image (A) contained one large stone, while the fish in image (B) contained two stones. This figure shows the size of large urinary bladder stones observed within *P. diacanthus* specimens. Supplementary Figure S2: linear relationship between total length (cm) and batch fecundity for *Protonibea diacanthus* from Queensland East Coast waters. Supplementary Figure S2 demonstrates that when the single large outlier individual is removed from the fecundity dataset, there is a lack of relationship with total length. Supplementary Figure S3: mean GSI (±SE) by month and region for male and female *Protonibea diacanthus*. This figure highlights the variation in the GSI between both sex and region to the provider and shows that there is overall consistency between both regions 2 and 3. Supplementary Figure S4: linear relationship between gonad weight and batch fecundity for *Protonibea diacanthus* from Queensland East Coast waters. Supplementary Figure S4 shows that there is a positive linear relationship between fecundity and gonad weight, which is overall consistent with the trend between fecundity and length observed in Figure 7. Supplementary Table S1: macroscopic and microscopic features of male and female gonads of *P. diacanthus*. Supplementary Table S1 supports detailed descriptions of both the macroscopic and microscopic criteria that were used to stage *P. diacanthus*. (*Supplementary Materials*)

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