Coral Reefs (2018) 37:1197–1208
https://doi.org/10.1007/s00338-018-1723-9

REPORT

The world's largest parrotfish has slow growth and a complex reproductive ecology

Brett M. Taylor[1] · **Richard J. Hamilton**[2,3] · **Glenn R. Almany**[4] · **J. Howard Choat**[5]

Received: 28 May 2018 / Accepted: 23 July 2018 / Published online: 30 July 2018

Abstract The bumphead parrotfish (*Bolbometopon muricatum*) is an iconic coral reef species of commercial, subsistence, and cultural value that has faced severe declines across the Indo-Pacific. In this study, we summarized the age-based biological characteristics of *B. muricatum* based on comprehensive surveys of a small-scale but high-yield fishery in Solomon Islands. We examined the full breadth of the life history, including pelagic larval duration, growth patterns throughout the ontogeny (post-settlement, juvenile, and adult), life span, mortality, age at maturity, and reproductive timing, as well as the size-dependent relative contribution of females to overall reproductive effort. The age-based demographic information supports a sexual pattern of functional gonochorism, whereby sex ratios were consistent throughout the lifespan. After a 25-day pelagic larval duration, the species growth pattern is comparatively slow and differs by sex, where males generally reach larger sizes at a given age than females. This growth pattern is associated with a long life span (at least 30 yrs) and low mortality rates ($< 0.2\ \text{yr}^{-1}$). Annual and lunar tracking of ovary weights confirmed cyclical spawning activity synchronized just prior to new moon throughout the year. Surprisingly, ovary weights declined in the largest and oldest females, implying lower reproductive output. Instead, lower ovary weights may reflect alternative mating strategies among the largest females whereby spawning frequency and strategy differs among females of different body sizes. These results highlight several novel and previously unknown aspects of this species' biology, and our analyses generate information that can strengthen population models, facilitate stock assessments, support regional management, and provide a baseline for comparative work.

Keywords Reproductive timing · Parrotfish · Life history · Age at maturity · Senescence · Alternative mating strategies

Introduction

The population dynamics and vulnerability of commercially important species are dependent on their fundamental life-history traits and strategies (Abesamis et al. 2014). Fisheries associated with coral reefs face multiple threats, including accelerated rates of habitat degradation from sediment and nutrient run-off (Dubinsky and Stambler 1996; Fabricius 2005; Wenger et al. 2015), coral bleaching (Hughes et al. 2018), increasing harvesting pressure (Jackson et al. 2001; Newton et al. 2007), and a rise in the use of unsustainable fishing methods (Rhodes et al. 2018). Reef-associated fisheries in areas of the highest biodiversity, such as the Coral Triangle, often

---

Topic Editor Dr. Andrew Hoey

Glenn R. Almany: Deceased.

✉ Brett M. Taylor
brettmtaylor@gmail.com

[1] Pacific Otolith Services, Honolulu, HI 96701, USA

[2] The Nature Conservancy, Asia Pacific Resource Centre, 48 Montague Road, South Brisbane, QLD 4101, Australia

[3] ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

[4] CRIOBE-USR 3278, CNRS-EPHE-UPVD and Laboratoire d'Excellence "CORAIL", 58 Avenue Paul Alduy, 66860 Perpignan Cedex, France

[5] College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

target over 300 species of fish and invertebrate for commercial and subsistence purposes. Despite the staggering diversity, when fishers target predictable aggregations of fish much of the harvested biomass may be comprised of only a handful of species (e.g., Hamilton et al. 2012).

Fisheries management suffers in the absence of high-quality life-history information, as species-level data provide a powerful path for interpreting patterns of change and predicting the value of management measures for highly valued species. Insights based on life-history information provide an essential complement leading to effective management, even in diverse multi-species fisheries. Parrotfishes (Family Labridae) are among the most targeted groups on coral reefs, and differences in life-history traits among species have been found to predict vulnerability to overexploitation (Taylor et al. 2014, 2018). Typical traits of interest include life span, growth, and size and age at maturity, all of which relate directly to population productivity and recovery potential.

However, further life-history strategies such as reproductive behavior and the relative contribution of females across different life stages also influence vulnerability and the effectiveness of fishery management measures. There has been considerable interest in the relative reproductive importance of large, old females, especially in species of long-lived, harvested fishes (Berkeley et al. 2004a; Birkeland and Dayton 2005; Hixon et al. 2014; Barneche et al. 2018). General principles of hyperallometric scaling between body size and fecundity (reviewed in Hixon et al. 2014; Barneche et al. 2018), as well as examples of increased larval quality from older females (Berkeley et al. 2004b; but see Marshall et al. 2010) have established the benefit to fisheries management of preserving age structures by avoiding widespread age truncation through the common practice of selectively harvesting larger individuals in a population. However, our understanding of this concept in tropical reef-associated fisheries is presently poorly developed.

The bumphead parrotfish *Bolbometopon muricatum* is among the most recognizable species from Indo-Pacific coral reef fish assemblages. The species is the largest of the parrotfishes by a considerable margin (exceeding 1 m in length and 50 kg in mass; Hamilton and Choat 2012), is phylogenetically distinct among the parrotfishes (Choat et al. 2012), can live to approximately 40 or more years (Andrews et al. 2015), and is known to form schools of several individuals to up to 60+ individuals (Donaldson and Dulvy 2004; B. Taylor, pers. obs.). Where abundant, *B. muricatum* plays an important role in reef structural dynamics, with an adult capable of removing an estimated 5.7 t of carbonate material from the reef matrix per year through processes of feeding (Bellwood et al. 2003). Because of these characteristics, the species has been found to disproportionately influence functional and phylogenetic diversity of fish assemblages across broad spatial scales (Bellwood et al. 2012; D'Agata et al. 2014; Taylor et al. 2015).

Many reef fishes have specific habitat affinities throughout their ontogeny, and *B. muricatum* is no exception. Newly settled juveniles recruit to habitats with branching *Acropora* spp. in clear sheltered lagoons (Hamilton et al. 2017) and later migrate to fringing or barrier reefs as adults. Presence and amount of recruitment habitat is a limiting factor for adult abundance, and degradation of nursery habitats through logging and sediment erosion has been found to limit local populations (Hamilton et al. 2017). Further, because of the nature of small-scale night spear fisheries that target *B. muricatum*, coupled with the behavioral tendency of *B. muricatum* social groups to sleep together in shallow water, hyperstability (when catch remains high despite declining fish abundance) is a problematic issue complicating the management of this species, and further compounds their vulnerability to overexploitation (Hamilton et al. 2016).

Bumphead parrotfish have long been considered to be vulnerable to overexploitation based on their behavioral characteristics as well as life-history traits that yield slow population turnover times, and thus low recovery potential (Donaldson and Dulvy 2004). Age-based life-history information from all life stages of targeted species is necessary input for stock assessment or spatial metapopulation models that is often lacking for tropical marine ecosystems. Here, we holistically examine *B. muricatum* by combining life history across all life stages with reproductive ecology. We surveyed fishery catches and sampled specimens of *B. muricatum* from a night spearfishery in Solomon Islands for > 1.5 yrs to provide detailed estimates of spawning cycles, relative reproductive output, and age-based life-history traits of importance to fishery management. Specifically, we characterized pelagic larval duration, juvenile and adult growth, life span, mortality, age at maturity, and annual and lunar spawning cycles. We also compared ovary weight, female gonadosomatic index values, and body size against the hypothesis that the largest females would provide the greatest relative reproductive contribution, based on relationships between length, weight, and ovary size. The results provide an important quantitative baseline that facilitates future assessments of population dynamics and ecological function in response to fishery exploitation and environmental change.

Materials and methods

Study area and environment

This study was conducted in the Kia District at the western end of Isabel Province, Solomon Islands, extending from 7°19′ to 7°39′S over a linear distance of 82 km. This region contains a diversity of complex coral reef habitats, including exposed barrier reef slopes, fringing and patch reefs, subtidal reef flats and back reefs, and an abundance of coastal mangrove forests. Although historically targeted, *B. muricatum* stocks in this region remained lightly exploited until 2001 through the commercialization of night spearfishing when the European Union-funded Bahana Provincial Fisheries Centre (BPFC) began purchasing reef fish species for domestic export to the capital, Honiara. In 2012, a new, private fisheries centre and storage facility in the community of Babahairo also began purchasing harvested *B. muricatum* for commercial fishery purposes.

Survey and sample collection techniques

Between February 2012 and October 2013, all commercially harvested specimens of *B. muricatum* that passed through the BPFC and the Babahairo private fisheries centre were surveyed by fisheries staff trained in standardized sampling protocols. For all specimens surveyed, we measured total length (TL, mm) using a measuring board and total weight (TW, g) using a digital balance or hanging scales, as appropriate, based on the size of the fish. We extracted sagittal otoliths from the brain cavity and stored them dry for subsequent processing. We removed gonad lobes from individuals and weighed them to the nearest 0.5 g using a digital balance. Identification of sex was based on macroscopic examination of gonads, which is highly accurate for *B. muricatum* (Hamilton et al. 2008). Date, geographic zone, reef name, lead fisher name, and lunar stage associated with each specimen were also recorded. Lunar stages were considered new moon, first quarter, full moon, and last quarter, with up to 6 or 7 d separating each of these phases depending on the lunar calendar. Fisheries center catch records were periodically double-checked and transcribed by researchers on eight separate occasions during the sampling period.

Additional fishery-independent sampling was carried out to obtain juvenile specimens (< 200 mm TL) to determine pelagic larval duration, post-settlement growth trajectories, and age at ontogenetic habitat shifts through examination of daily growth increments. These samples were collected in shallow (0.5–2 m) branching coral-algae assemblages on sheltered lagoonal reefs that fringe mangrove forested shorelines. The smallest (recently settled; 12–35 mm TL) specimens are found in *Acropora aspera* and *A. microphthalma* colonies, whereas larger individuals up to 200 mm TL occupied nearby structurally complex reefs intermixed with seagrass (Hamilton et al. 2017). We used data from all specimens for which TL and TW data were obtained to model the length–weight relationship. Raw data were fitted with a standard power curve whereby Total Weight (in g) = a(Total Length [in mm])^{b}.

Derivation of age, growth profiles, and mortality

We derived age information from individual bumphead parrotfish specimens based on both annual and daily increments in transverse sections of sagittal otoliths. From a random subsample of commercially harvested specimens, one sagittal otolith was weighed to the nearest 0.0001 g and mounted on the edge of a glass slide using a thermoplastic glue (Crystalbond 509©) with the primordium situated just inside the slide edge and the sulcul groove approximately perpendicular to the slide edge. The otolith material was sanded away using a 600-grit diamond lap on a GEMMASTA lapping machine with constant water flow. The slide was then heated (200 °C) and remounted with the newly sectioned surface affixed flat against the surface of the glass slide, and the remaining bulk of material was ground away until a thin transverse cross section (~ 250 µm) remained. Finally, the section was covered with thermoplastic glue to improve clarity and annual bands were enumerated using a stereo microscope with transmitted light. To expose daily ring structures in small fish (< 200 mm TL), sectioning protocols were the same as above, except that lapping film of 30 µm grit was used to sand away otolith material, and optimal clarity of the final section was achieved by successively polishing the transverse section with 9, 3, and 0.3 µm lapping film. Both annuli and daily rings were counted on three separate occasions using a stereo microscope for annual increments and a compound microscope for daily growth increments. Final age (in years) of fish with one or more annuli was derived when two or more ages matched (e.g., 12, 12, 13 = 12), or when the three counts differed by no more than two annuli (e.g., 14, 12, 13 = 13). The accuracy of growth zone derived ages using this technique has been validated for this species using bomb radiocarbon dating (Andrews et al. 2015). For fish with no annulus, pelagic larval duration was derived by counting increments up to the settlement mark. Post-settlement ages for these fish were derived as the mean of three counts of daily growth increments (from the settlement ring to the edge), provided that all counts differed by < 10% from the median.

Sex-specific and overall patterns of growth were examined using length-at-age data fitted with the von Bertalanffy growth function (VBGF), represented by:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right]$$

where L_t is the predicted mean TL (mm) at age t (years), L_∞ is the asymptotic TL, k is the coefficient used to describe the curvature of fish growth toward L_∞, and t_0 is the hypothetical age at which TL is equal to zero, as described by k. Immature fish considered sexually undifferentiated were used for both the female and male growth curves, in order to anchor the curve to an approximate size at settlement and to characterize the first years of growth before sexual maturation. Male and female growth patterns were compared by plotting 95% bivariate confidence ellipses surrounding paired estimates of L_∞ and k following Kimura (1980).

Age composition and the instantaneous rate of total mortality were explored through the age frequency distribution based on a random subsample of commercially harvested bumphead parrotfish. We used a multinomial likelihood-based catch curve using logistic selectivity by minimizing the multinomial negative log-likelihood λ associated with O_t and the expected proportion (P_t) of fish at or above the age at peak observed frequency.

$$\lambda = -\sum_{t=1}^{A} O_t \ln(P_t)$$

$$P_t = \frac{C_t}{\sum_{t=1}^{A} C_t}$$

where A refers to the maximum age assumed in the analysis, arbitrarily set much larger than the observed maximum age, thereby avoiding calculation of a “plus group,” and O_t is the observed frequency of harvested individuals. C_t is the expected catch at age t, calculated using the Baranov catch equation:

$$C_t = \frac{F_t}{Z_t} N_t\left(1 - e^{-Z_t}\right)$$

$$Z_t = F_t + M$$

$$F_t = FV_t$$

$$V_t = \frac{1}{1 + e^{\frac{-\ln(19)(t-A_{50})}{(A_{95}-A_{50})}}}$$

where F_t is the fishing mortality at age t, F is the “full” instantaneous fishing mortality, and V_t is the estimated gear selectivity at age t following a logistic function with selectivity parameters A_{50} and A_{95}, the ages at 50 and 95% selectivity, respectively.

Analysis of reproductive patterns and relative contribution

Designations of sex and stage from macroscopic examination of gonads followed Hamilton et al. (2008). Bumphead parrotfish develop as inactive bisexuals, whereby early spermatogenic tissue co-occurs with previtellogenic oocytes. These structures occur within gonads < 5 g, and length at maturation generally occurs between 450 and 700 mm TL. Mature female and male gonads are easily identifiable macroscopically. A gonadosomatic index (GSI) was calculated as the ratio of gonad-to-gonad-free body weight for each female and male specimen.

$$\mathrm{GSI} = \frac{\text{Gonad weight}}{\text{Total weight} - \text{Gonad weight}} \times 100$$

We then examined temporal trends in GSI across calendar months and lunar days by plotting mean GSI values across these timeframes. To ensure only mature individuals were considered in these analyses, we used individuals larger than 700 mm TL (the size at which 100% of both males and females are reproductively mature). We further plotted raw ovary weight by TL for each of four quarters of the lunar phase (new moon—NM +6/7 d; first quarter—FQ + 6/7 d; full moon—FM + 6/7 d; and last quarter—LQ + 6/7 d).

Finally, we examined the relative reproductive contribution of females across size classes. To do this, we plotted TL by natural-log transformed ovary weight and fitted the relationship with a loess smoothing curve with a span of ½. Because ovary weight scales with body weight, and body weight is a cubic function of body length, we hypothesize that ovary weight will increase drastically upon sexual maturation ($\sim$ 500–700 mm TL) and then continue to increase, albeit at a lesser rate, with increasing TL. We then similarly plotted both TL and TW by natural-log transformed GSI (GSI × 100 to avoid log-transforming values < 1) and fitted a loess smoothing curve to discern patterns across length and weight.

Results

Fishery surveys

We surveyed a total of 2719 commercially harvested *B. muricatum* through the fishery markets during the study period. Harvested individuals ranged from 195 to 1190 mm TL. The frequency distribution of lengths was unimodal, with the largest peak at 865 mm (Fig. 1a). The length distributions of mature, differentiated females and males overlapped considerably, but the modal size range for males was nearly 200 mm larger than that of females

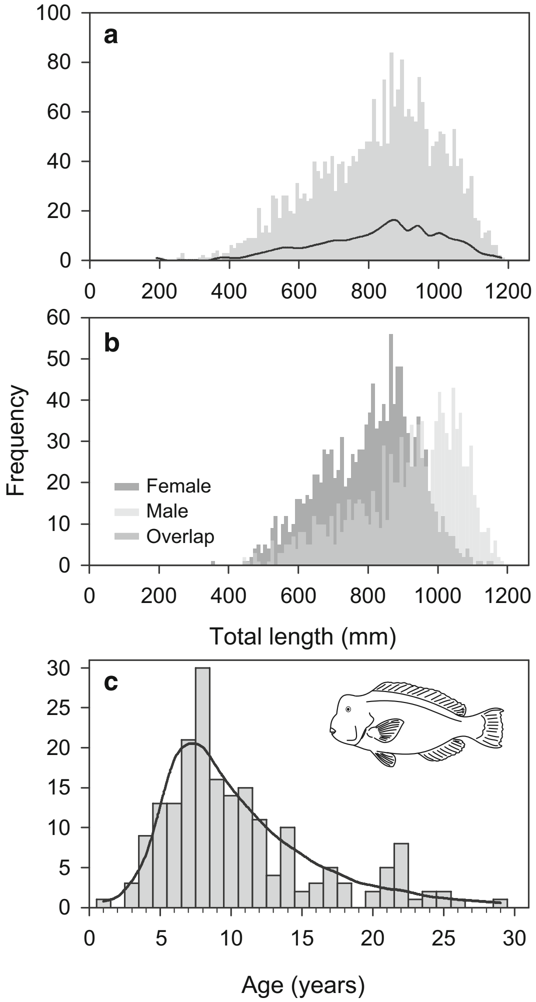

Fig. 1 **a** Length–frequency distribution of 2719 harvested *Bolbometopon muricatum* surveyed from the Isabel Province, Solomon Islands, commercial fishery between February 2012 and October 2013. Solid line represents the distribution of 195 aged specimens taken from the fishery. **b** Length–frequency distributions of mature female ($n = 1310$) and mature male ($n = 1113$) individuals from **a**. **c** distribution of ages based on annuli counts from sagittal otoliths of a random subsample ($n = 195$) of surveyed specimens. The solid line represents the multinomial catch curve fitted to catch-at-age data

(Fig. 1b). The mean TL of mature females was 804 mm (± 4 mm S.E.), the mean TL of mature males was 918 mm (± 5 mm S.E.), and the mean TL of harvested bumphead parrotfish was 835 mm (± 4 mm S.E.).

Age, growth, and mortality

We sectioned and interpreted totals of 216 otoliths for annual increments and 41 otoliths for daily growth increments. Interpretation of both annual and daily growth increments were straightforward using standard techniques. Annuli followed a consistent banding pattern and were interpreted along the ventral margin near the sulcul groove (Fig. 2a). Larger otoliths had a fragile outer otolith structure because of a branching crenulation pattern described in Andrews et al. (2015). This pattern is apparent on the right, ventral side in Fig. 2a where the branched material was lost during the sectioning process. Estimates of pelagic larval duration were derived by counting daily growth increments from the core to the settlement mark in 33 individuals (out of 41 processed for reading daily growth increments). Pelagic larval duration estimates ranged from 21 to 29 d with a mean of 24.8 d (± 0.3 SE). The transition from pre-settlement to post-settlement otolith growth was evident through a substantial increase in the size of increment widths (Figs. 2b, 3), which we presume occurs immediately after transitioning from the pelagic environment to the reef. Post-settlement ages of fish without an annulus ranged from 13 to 310 d old.

Harvested bumphead parrotfish ranged from 1 to 29 yrs of age, with a modal age in the fishery of 8 yrs (Fig. 1c). The multinomial logistic catch curve estimated the instantaneous rate of total mortality to be 0.169 yr^{-1} (95% CI 0.132–0.207; Fig. 1c, Table 1). Overall, bumphead parrotfish reached an asymptotic length (L_{∞}) of 1070 mm TL, with a growth coefficient (k) of 0.150 yr^{-1} (Fig. 4a). Growth parameters differed significantly between females and males, with males reaching considerably larger asymptotic lengths on average. In the first year of life, growth is approximately linear with a rate of nearly 0.5 mm d^{-1} until ~ 250 d post-settlement, when growth rate appears to shift slightly (Fig. 4b, Table 1). Estimates of sex-specific and combined growth parameters with associated confidence intervals are presented in Table 1. By combining the overall growth curve with the logistic maturation curve from Hamilton et al. (2008), we determined that median age at maturity is approximately 5–7 yrs for both females and males.

Spawning periodicity and relative female output

We found no annual patterns of change in female or male GSI across calendar months, suggesting that reproductive activity is consistent throughout the year (Fig. 5). However, clear patterns emerge for female GSI across the lunar calendar, whereby GSI slowly increases from full moon to last quarter moon, and then peaks in the days prior to new moon (Fig. 6). This pattern was not evident for males, which showed little change in GSI across lunar days. One large outlier occurred for males (full moon +3 d), which we interpreted as an artifact of sampling given that all of the high-GSI samples that positively influenced the mean were collected on the same fishing trip.

The length–weight relationships for females, males, and all sexes and stages combined are displayed in Fig. 7a and summarized in Table 1. On average, males increased in

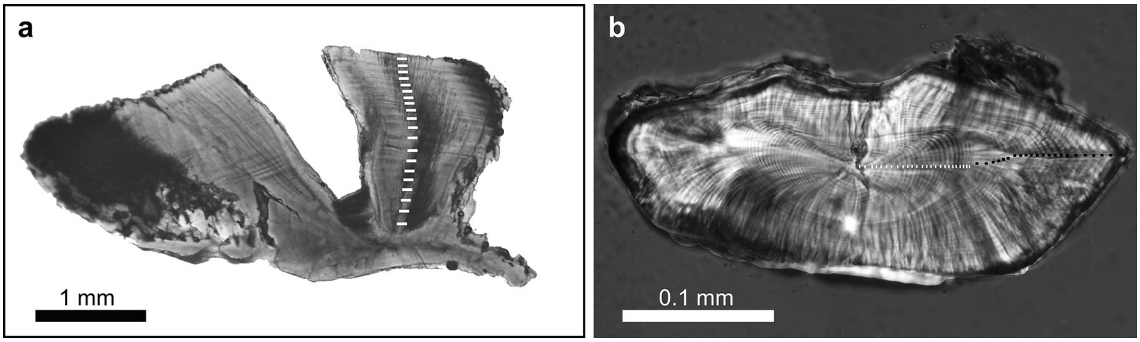

Fig. 2 Photomicrographs of transverse sections of sagittal otoliths from **a** an adult female (850 mm TL) bumphead parrotfish showing annual growth increments (denoted by white rectangles) and **b** a juvenile (16 mm TL) bumphead parrotfish showing daily growth increments. In **b**, white rectangles represent daily growth increments prior to settlement from the pelagic to the back-reef environment, whereas black rectangles denote post-settlement growth increments

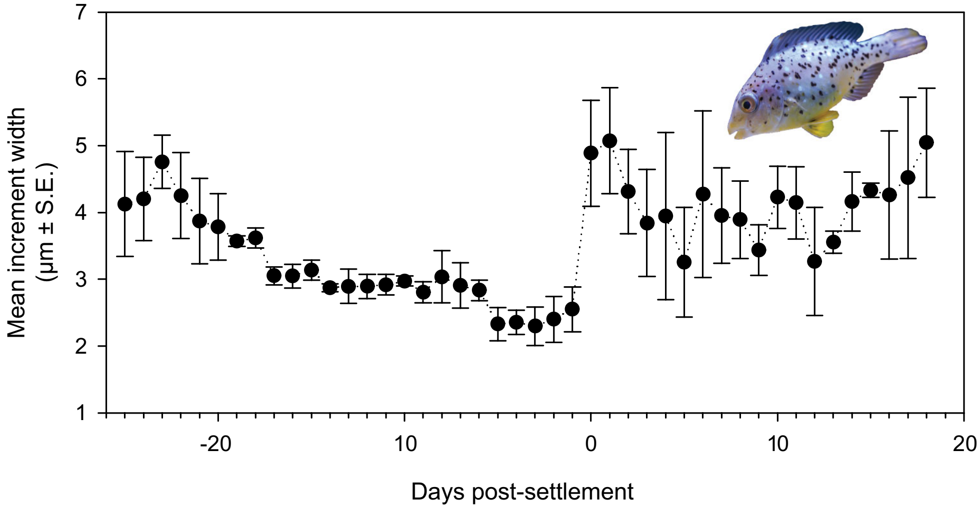

Fig. 3 Mean increment width profiles across pre- and post-settlement life stages of *Bolbometopon muricatum*. Inset photograph is of a recently settled *B. muricatum* from Palau. Photo credit: T. Sinclair-Taylor

Table 1 Summary of life-history trait estimates for *Bolbometopon muricatum* from Isabel Province, Solomon Islands

Trait	Females	Males	Combined
L_∞ (mm TL)	1047 (1010–1087)	1145 (1084–1213)	1070 (1035–1109)
k (yr^{-1})	0.150 (0.137–0.164)	0.135 (0.120–0.152)	0.150 (0.137–0.164)
t_0 (yr)	− 0.102	− 0.085	− 0.074
n (growth)	177*	138*	243
Pelagic larval duration (d)	–	–	24.8 (24.2–25.4)
Maximum age (yrs)	26	29	29
Maximum TL (mm)	1160	1190	1190
Mortality (yr^{-1})	–	–	0.169 (0.132–0.207)
Growth rate (mm d^{-1}) [first 250 d]	–	–	0.48 (0.46–0.51)
Length weight: *a*	3.469×10^{-6}*	1.639×10^{-6}*	1.168×10^{-6}
Length weight: *b*	3.246*	3.362*	3.409

Associated 95% confidence intervals are presented in parentheses where appropriate

*Includes sexually immature and undifferentiated fish in growth or length–weight model

weight at a slightly greater rate than females, but sex-specific differences were largely negligible. As we predicted, ovary weight increased dramatically with body length through the sizes of maturation onset, and then increased gradually from approximately 750 to 1000 mm TL (Fig. 7b). Beyond 1000 mm TL, the pattern began to

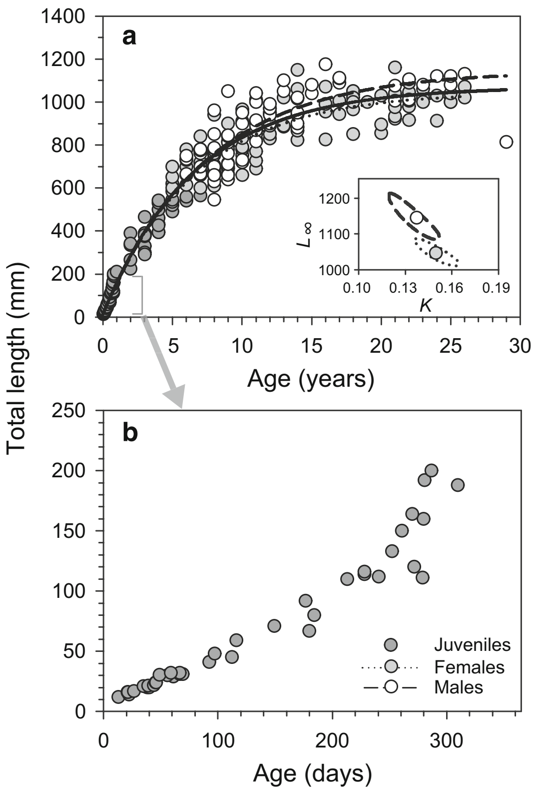

Fig. 4 **a** Growth profile of *Bolbometopon muricatum* from Solomon Islands ($n = 243$). Sex-specific von Bertalanffy growth models are delineated by dotted (female) and dashed (male) lines, total (sexes combined) growth profile is represented by a solid line. In set of **a** displays bivariate 95% confidence ellipses surrounding sex-specific estimates of growth parameters K and L_∞. **b** High-resolution growth plot of the first year of life post-settlement based on counts of daily rings in 41 specimens ranging from 12 to 200 mm TL and 13 to 310 d post-settlement

decrease because of a considerable number of large females with ovary weights smaller than all other mature females of any length. This pattern of decrease in large females was also evident for GSI data (i.e., relative reproductive output scaled by body weight) across body length (Fig. 7c) and body weight classes (Fig. 7d), whereby relative potential reproductive output decreased in females above ~ 1000 mm TL and ~ 20,000 g TW.

Discussion

The bumphead parrotfish is the largest parrotfish in the world and has proven easy to capture in large quantities at night due to its behavior of sleeping in groups in relatively shallow water. These reasons, coupled with perceived or documented declines in regional *B. muricatum* populations (Aswani and Hamilton 2004; Dulvy and Polunin 2004; Bellwood et al. 2012), have led to widespread concern for this species' vulnerability to overexploitation. Of note, the IUCN lists the species as *Vulnerable*, whereas the US government determined the species not warranted for listing under the Endangered Species Act (Kobayashi et al. 2011). Our results greatly improve our understanding of *B. muricatum* biology by confirming long life span, low mortality, late maturation, spawning periodicity highly synchronized with the lunar cycle, and a pelagic larval duration of approximately 25 d for *B. muricatum* based on comprehensive collections from a small-scale but high-yield fishery in Solomon Islands. Our results also (1) support a sexual pattern of functional gonochorism following Hamilton et al. (2008) based on sex-specific body size and age distributions, and (2) provide evidence for either reproductive senescence or a more complex reproductive ecology of the largest and oldest *B. muricatum* females. The information provided facilitates assessments of stock status, provides a benchmark for *B. muricatum* populations at low latitudes, and generates discussion on the importance of large females in the context of reproductive contribution and life-history strategies.

Age information presented here confirms the species has slow growth to its maximum size as well as a long life span and low instantaneous mortality rate relative to other parrotfish species. Unlike most parrotfish species examined to date, sex-specific differences in growth were not pronounced, although males do tend to reach slightly larger body sizes in the oldest age classes. The appearance of both mature males and mature females in the ontogeny suggests an age of maturation between 5 and 7 yrs, and corresponds with a shift in habitat preference from sheltered lagoonal reefs to offshore reef slopes (Hamilton et al. 2017, 2008). The age-based data further support the designation of *B. muricatum* as a functional gonochore (i.e., no post-maturational sex change), following Hamilton et al. (2008), because sex ratios upon maturation remain highly stable around 60–70% females throughout the life span. The slight and consistent female bias likely reflects a ratio socially controlled through pre-maturational sex determination.

Bumphead parrotfish are known to spawn in aggregations, with detailed descriptions of spawning behavior at the Great Barrier Reef (Gladstone 1986), Wake Island (Muñoz et al. 2014), and Palau (Roff et al. 2017). At these locations, approximately ~ 100–1000 s of individuals were observed displaying lek-like defense of territories by males, and pairs or small clusters of individuals performed casual to rapid spawning rushes toward the surface. All three descriptions pinpoint aggregative spawning behavior to occur up to or at 3 d prior to new moon. Our profiles of female gonadosomatic index across the lunar calendar unequivocally corroborate the same pattern in the present study, with a clear lunar GSI pattern and peak GSI occurring 3 d prior to new moon. The ubiquity of this

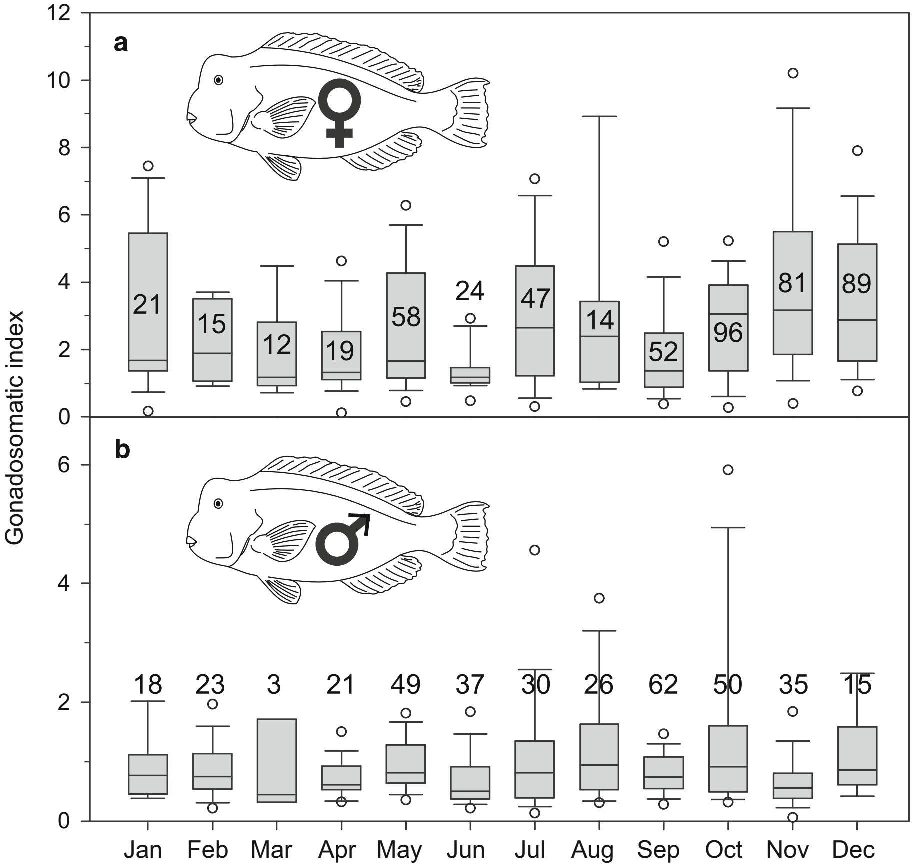

Fig. 5 Cumulative monthly gonadosomatic index distributions for **a** female ($n = 528$) and **b** male ($n = 369$) *Bolbometopon muricatum* individuals larger than 700 mm TL surveyed from April 2012 to July 2013. Values in or above boxes represent sample sizes

pattern throughout the calendar year suggests that spawning occurs throughout the year, synchronized with lunar cycles. Further, we identified ripe females with large GSI values from across the geographic breadth of the study area, implying that multiple smaller aggregations (10–100 s) of individuals occur rather than one or two large (1000 s of individuals) aggregations, as appears to be the case in Palau (Roff et al. 2017).

Despite being well known for its massive size as an adult, recent research has revealed the early life history of *B. muricatum* to be a critical and dynamic stage with respect to population dynamics, management, and conservation. Our examination of daily growth increments in a wide range of newly recruited and juvenile *B. muricatum* informs the temporal component of ontogenetic processes in the species. We determined that pelagic larval duration was, on average, 25 d from hatching to settlement on the reef. This larval duration is on the low-end compared with other parrotfishes (Ishihara and Tachihara 2011), and based on the periodicity of spawning activity, suggests that subsequent recruitment events would occur slightly before spawning commences each lunar cycle. The observation of various length classes present during juvenile surveys across multiple months and years, rather than obvious cohorts based on starkly modal size classes, corroborates the monthly periodicity of spawning activity throughout the calendar year. Post-settlement growth rates inform of the timeframe for ontogenetic habitat shifts documented in Hamilton et al. (2017). Newly recruited *B. muricatum* settle in colonies of branching *Acropora spp.* occupied by damselfish and remain highly site attached until ~ 50 mm TL (~ 100 d). They are then chased out of territories by damselfishes and expand their ranges across lagoonal fringing reefs intermixed with seagrass, reaching 100 and 200 mm TL at approximately 200 and 300 d, respectively. Individuals > 200 mm TL become more mobile across habitats and will retain home ranges across the lagoonal reef complex for up to 5 yrs before expanding their habitat usage to the channels and fore reef slope. This age-based information on early life histories can inform spatially complex population models, given the emergent understanding of ontogenetic processes in this species.

Given the inherent rarity of large, old females in natural systems and the additional fact that we generally cannot accurately assess age of individuals until after their death, it has been logistically difficult to examine the relative value and influence of these individuals within populations. Although *B. muricatum* reaches a very large size compared with the vast majority of coral reef-associated fishes, we actually found strong evidence of the largest and oldest

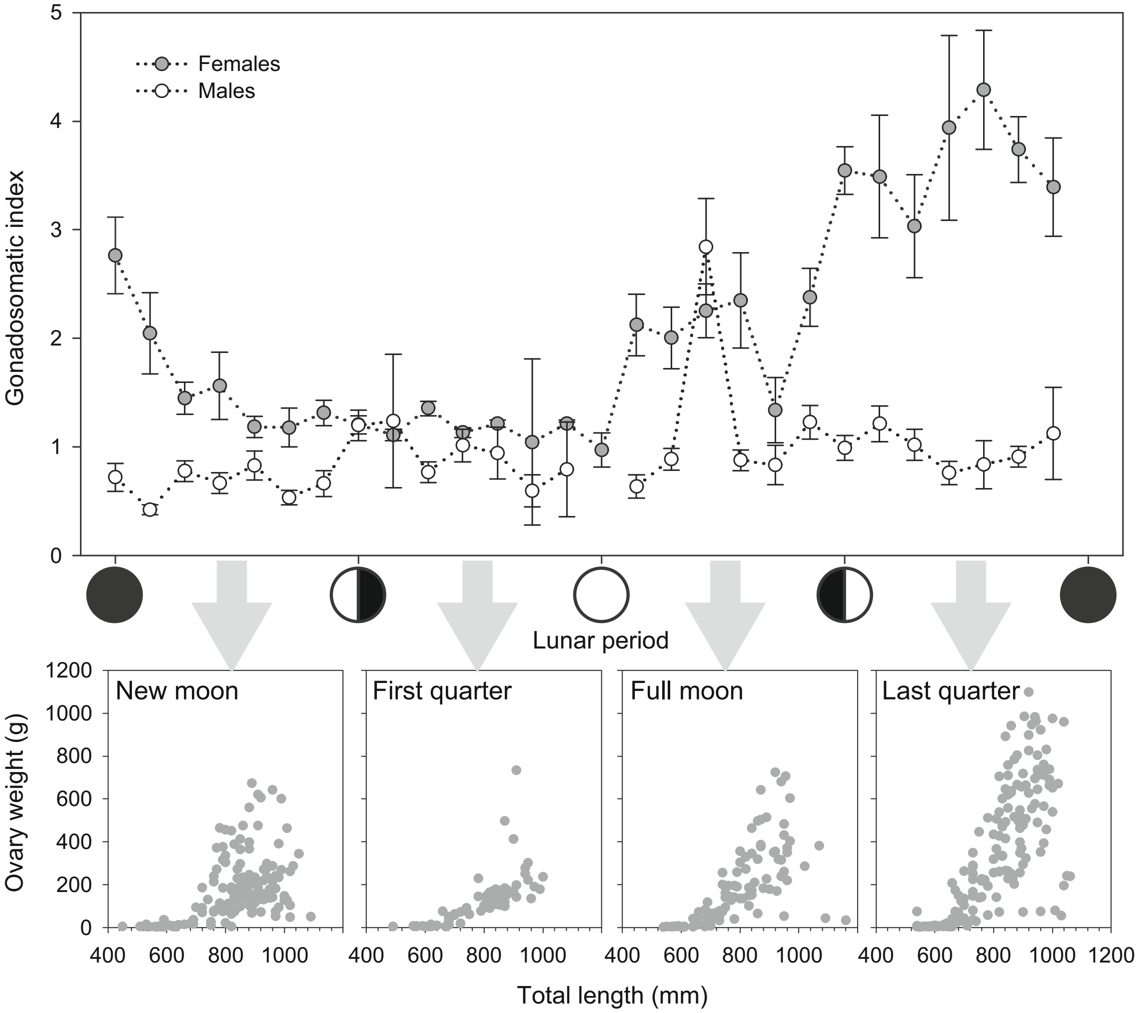

Fig. 6 Mean (± SE) gonadosomatic index values by lunar day for male (n = 370) and female (n = 392) *Bolbometopon muricatum* (> 700 mm TL) surveyed from April 2012 to July 2013. Subplots on bottom display the relationship between body length and ovary weight by lunar quarter (e.g., New moon = ovary weights sampled from new moon up to, but not including, first quarter moon). Black circles represent new moon and white circle represents full moon

females having reduced reproductive output relative to body size, whereby most females larger than approximately 1 m and 20 kg had gonadosomatic index values lower than all other mature females. There are two possible explanations for this pattern. The first is that the largest females are undergoing senescence and are therefore contributing less than expected to the population-level reproductive output. However, this scenario does not make sense evolutionarily as senescence should occur at ages well after natural mortality has reduced the age-specific population to zero. Indeed, histological examination suggests ovaries from the largest and oldest females with low gonad weights do not appear non-functional or pathological (JH Choat, unpublished data). An alternative explanation is that the largest females have behavioral traits that allow them to secure fertilization by the fittest males.

There is anecdotal evidence for a behavioral trade-off scenario. In Palau, smaller fish (600–850 mm TL) have been observed spawning in mass aggregations of 1000 s of fish at a predictable lunar schedule for several days before the new moon, year round, whereas larger fish (> 1000 mm TL) have been observed pair spawning at other times and locations in smaller groups (S. Lindfield, pers. comm.). Although there are only limited observations of spawning modes in Solomon Islands, GSI values and lunar periodicity in gonad weights of fish > 1000 mm TL may imply a more frequent schedule of spawning. More frequent spawning might explain lower ovary weights in the largest females, as ovary weight is a flawed predictor of reproductive output if alternative reproductive strategies are used. If the largest females can secure priority of egg fertilization with the fittest males through alternative mating strategies, then energetic trade-offs related to egg

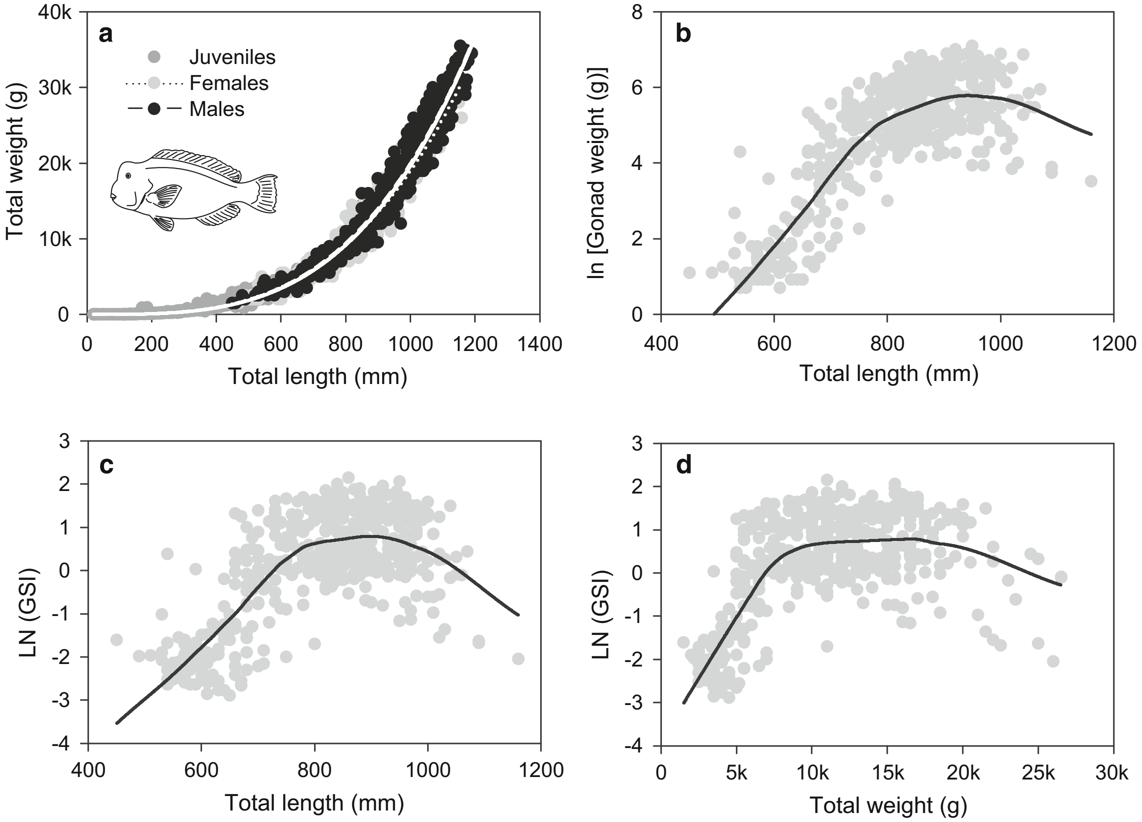

Fig. 7 **a** Length–weight relationship of *Bolbometopon muricatum* based on 3283 harvested or independently-sampled individuals ranging from 20 to 1190 mm TL and 0.07 to 26,500 g; Total Weight (in g) = 1.168×10^{-6} (Total Length [in mm])$^{3.409}$. Relationships between **b** total length and gonad weight (log-scaled), **c** total length and gonadosomatic index (GSI; log-scaled), and **d** total weight and GSI (log-scaled) for female *B. muricatum* to examine relative reproductive output. Solid lines represent loess curves fit to data with a span of ½

production and behavior may be worthwhile. The specific advantages of size-related alternative mating systems within *B. muricatum* can only be speculated on at present. Based on the biological data presented here, we merely suggest that the reproductive ecology of *B. muricatum* is more complex than we yet fully realize.

Hyperstability of fishery catches and coastal erosion have both been identified as acute issues in the Kia District fishery for *B. muricatum* (Hamilton et al. 2016, 2017). This study also highlights that a considerable portion of the fishery catch (over 20% by number harvested) is comprised of potentially juvenile fish. The importance of protecting juvenile life stages of *B. muricatum* is being taken into consideration by Solomon Islands Ministry of Fisheries and Marine Resources, who are considering recommendations to place a national ban on the harvest and sale of *B. muricatum* < 650 mm. Such a management measure would likely not ensure sustainability of this species, but given the life-history characteristics and selective capacity of the fishery, it would complement other management measures by directly increasing the proportion of fish reaching reproductive maturity.

The bumphead parrotfish is a species of considerable ecological and economic importance to the Isabel Province and elsewhere where it remains abundant. This and other recent studies from the region (Hamilton et al. 2016, 2017) have highlighted and facilitated a better understanding of the challenges this species faces in maintaining ecological and economic viability from habitat destruction and increased fishing pressure. Pace of life for *B. muricatum* is comparatively slow, yet the metabolic demands are undoubtedly high in order to achieve and maintain such large body size with year-round spawning in tropical regions. The associated trade-offs appear to yield a complex sexual ontogeny and reproductive strategy that differs from other parrotfishes and most other reef-associated species in general.

Acknowledgements We thank the Kia House of Chiefs, Isabel Provincial Government, Solomon Islands Ministry of Fisheries and Marine Resources and Solomon Islands Ministry of Environment, Climate Change, Disaster Management and Meteorology for supporting this work. Special acknowledgments go to all of the Kia district spearfishers who partook in this research; this study would have been impossible without your interest and support. We thank W.

Dolava, M. Giningele, P. Kame, A. Kokoe, H. Kokoe, and M. Vaka, for assisting with data collection; S. Lindfield for helpful discussions; and Tane Sinclair-Taylor for providing the image of the recently recruited bumphead parrotfish in Fig. 3.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Abesamis RA, Green AL, Russ GR, Jadloc CRL (2014) The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. Rev Fish Biol Fisheries 24:1033–1063

Andrews AH, Choat JH, Hamilton RJ, DeMartini EE (2015) Refined bomb radiocarbon dating of two iconic fishes of the Great Barrier Reef. Mar Freshw Res 66:305–316

Aswani S, Hamilton RJ (2004) Integrating indigenous ecological knowledge and customary sea tenure with marine and social science for conservation of bumphead parrotfish (*Bolbometopon muricatum*) in the Roviana Lagoon, Solomon Islands. Environ Conserv 31:69–83

Barneche DR, Robertson DR, White CR, Marshall DJ (2018) Fish reproductive-energy output increases disproportionately with body size. Science 360:642–645

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc R Soc B 279:1621–1629

Berkeley SA, Hixon MA, Larson RJ, Love MS (2004a) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32

Berkeley SA, Chapman C, Sogard SM (2004b) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85:1258–1264

Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the big ones. Trends Ecol Evol 20:356–358

Choat JH, Klanten OS, Van Herwerden L, Robertson DR, Clements KD (2012) Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). Biol J Linn Soc 107:529–557

D'Agata S, Mouillot D, Kulbicki M, Andréfouët S, Bellwood DR, Cinner JE, Cowman PF, Kronen M, Pinca S, Vigliola L (2014) Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. Curr Biol 24:555–560

Donaldson TJ, Dulvy NK (2004) Threatened fishes of the world: *Bolbometopon muricatum* (Valenciennes 1840) (Scaridae). Env Biol Fish 70:373

Dubinsky Z, Stambler N (1996) Marine pollution and coral reefs. Glob Change Biol 2:511–526

Dulvy NK, Polunin NVC (2004) Using informal knowledge to infer human-induced rarity of a conspicuous reef fish. Anim Conserv 7:365–374

Fabricius K (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar Pollut Bull 50:125–146

Gladstone W (1986) Spawning behavior of the bumphead parrotfish *Bolbometopon muricatum* at Yonge Reef, Great Barrier Reef. Jpn J Ichthyol 33:326–328

Hamilton RJ, Choat JH (2012) Bumphead parrotfish: *Bolbometopon muricatum*. In: de Mitcheson YS, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, vol 35. Springer Fish and Fisheries Series, Springer Science + Business Media, pp 490–496

Hamilton RJ, Adams S, Choat JH (2008) Sexual development and reproductive demography of the green humphead parrotfish (*Bolbometopon muricatum*) in the Solomon Islands. Coral Reefs 27:153–163

Hamilton RJ, Giningele M, Aswani S, Ecochard JL (2012) Fishing in the dark—local knowledge, nighttime spearfishing and spawning aggregations in the Western Solomon Islands. Biol Conserv 145:246–257

Hamilton RJ, Almany GR, Stevens D, Bode M, Pita J, Peterson NA, Choat JH (2016) Hyperstability masks declines in bumphead parrotfish (*Bolbometopon muricatum*) populations. Coral Reefs 35:751–763

Hamilton RJ, Almany GR, Brown CJ, Pita J, Peterson NA, Choat JH (2017) Logging degrades nursery habitat for an iconic coral reef fish. Biol Conserv 210:273–280

Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J Mar Sci 71:2171–2185

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Ishihara T, Tachihara K (2011) Pelagic larval duration and settlement size of Apogonidae, Labridae, Scaridae, and Tripterygiidae species in a coral lagoon of Okinawa Island, Southern Japan. Fisheries Sci 65:87–93

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. Fish Bull 77:765–776

Kobayashi D, Friedlander A, Grimes C, Nichols R, Zgliczynski B (2011) Bumphead parrotfish (*Bolbometopon muricatum*) status review. NOAA Technical Memorandum NMFS-PIFSC-26, Pacific Islands Fisheries Science Center, Hawaii, p 102

Marshall DJ, Heppell SS, Munch SB, Warner RR (2010) The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? Ecology 91:2862–2873

Muñoz RC, Zgliczynski BJ, Teer BZ, Laughlin JL (2014) Spawning aggregation behavior and reproductive ecology of the giant bumphead parrotfish, *Bolbometopon muricatum*, in a remote marine reserve. PeerJ 2:e681

Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK (2007) Current and future sustainability of island coral reef fisheries. Curr Biol 17:655–658

Rhodes KL, Hernandez-Ortiz DX, Cuetos-Bueno J, Ioanisc M, Washington W, Ladore R (2018) A 10-year comparison of the Pohnpei, Micronesia, commercial inshore fishery reveals an increasingly unsustainable fishery. Fish Res 204:156–164

Roff G, Doropoulos C, Mereb G, Mumby PJ (2017) Mass spawning aggregation of the giant bumphead parrotfish *Bolbometopon muricatum*. J Fish Biol 91:354–361

Taylor BM, Houk P, Russ GR, Choat JH (2014) Life histories predict vulnerability to overexploitation. Coral Reefs 33:869–878

Taylor BM, Lindfield SJ, Choat JH (2015) Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. Ecography 38:520–530

Taylor BM, Trip EDL, Choat JH (2018) Dynamic Demography: Investigations of Life-History Variation in the Parrotfishes. In: Hoey AS, Bonaldo RM (eds) Biology of Parrotfishes. CRC Press, pp 69-98

Wenger AS, Fabricius KE, Jones GP, Brodie JE (2015) Effects of sedimentation, eutrophication and chemical pollution on coral reef fishes. In: Mora C (ed) Ecology of Fishes on Coral Reefs. Cambridge University Press, pp 145-153