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Development of reproductive potential in protogynous coral reef fishes within Philippine no-take marine reserves

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ABSTRACT

Empirical evidence for increases in the reproductive potential (egg output per unit area) of coral reef fish in no-take marine reserves (NTMRs) is sparse. Here, we inferred the development of reproductive potential in two species of protogynous reef fishes, *Chlorurus bleekeri* (Labridae: Scarinae) and *Cephalopholis argus* (Epinephelidae), inside and outside of Philippine NTMRs. We estimated key reproductive parameters and applied these to species-specific density and length data from 17 NTMRs (durations of protection 0–11 years) and paired fished sites (controls) in a space-for-time substitution approach. For *C. argus*, we also used density and length data collected almost annually over 29 years from a NTMR and an adjacent control at Apo Island. The results suggest that *C. bleekeri* can develop 6.0 times greater reproductive potential in NTMRs than controls after 11 years of protection, equivalent to approximately 582,000 more eggs produced 500 m^{-2} inside NTMRs. Enhancement of reproductive potential in *C. argus* was not evident after 11 years in the space-for-time substitution. At Apo Island NTMR, reproductive potential of *C. argus* increased approximately 6-fold over 29 years but NTMR/control ratios in reproductive potential decreased through time (from 3.2 to 2.4), probably due to spillover of *C. argus* from the NTMR to the control. *C. argus* was estimated to produce approximately 113,000 more eggs 500 m^{-2} inside Apo Island NTMR at the 29th year of protection. Ratios of reproductive potential between NTMR and controls in *C. bleekeri* and *C. argus* were often greater than corresponding ratios in density or biomass. The study underscores the importance of species-specific reproductive life history traits that drive variation in the development of larval fish subsidies that originate from NTMRs.

KEYWORDS

egg production, fecundity, larval production, marine protected areas, recruitment subsidy, sex change

1 | INTRODUCTION

Areas of the sea where fishing has been banned permanently, known as no-take marine reserves (NTMRs), are widely promoted as a fisheries management tool due to substantial evidence demonstrating that targeted species can recover over time within their boundaries (Babcock *et al*., 2010; Lester *et al*., 2009). The build-up and subsequent spillover of adult individuals from NTMRs to adjacent fished areas can improve local fishery yields (Goñi *et al*., 2010; Kerwath *et al*., 2013). However, increased reproductive output of targeted species within NTMR boundaries, which leads to higher larval export and recruitment to fished areas, is more likely to enhance fisheries over larger spatial scales (Aalto *et al*., 2019; Harrison *et al*., 2012; Pelc *et al*., 2010). This recruitment subsidy effect is based on the expectation that sexually mature individuals, such as egg-producing females, will attain greater densities and larger body sizes over time inside NTMRs, resulting in higher reproductive potential (egg production per unit area) than fished areas (Evans *et al*., 2008; Marshall *et al*., 2019).

Theoretical studies suggest that tangible recruitment subsidies will require substantially greater reproductive potential inside NTMRs relative to fished areas (Halpern *et al*., 2004; Pelc *et al*., 2010). However, empirical estimates of differentials in reproductive potential between NTMRs and fished areas (*i.e*., NTMR/fished ratios or absolute differences) are lacking for the many species of coral reef fishes that support food fisheries, due in part to the paucity of detailed reproductive information for reef fishes (Carter *et al*., 2017; Evans *et al*., 2008). Population density and biomass have been used as proxies for reproductive potential when key reproductive data are unavailable (Halpern *et al*., 2004; Pelc *et al*., 2010). However, these proxies cannot fully account for differences in reproductive potential inside and outside of NTMRs for several reasons. First, reproductive output scales hyperallometrically with body mass, and therefore a smaller number of large female fish can generate most of the egg production within a NTMR (Barneche *et al*., 2018; Carter *et al*., 2014a, 2014b, 2017; Marshall *et al*., 2019). Second, density and biomass proxies could overestimate differentials in reproductive potential if nonegg-producing individuals (*e.g*., immature and male fish) dominate local population density or biomass in NTMRs (Adams *et al*., 2000; Carter *et al*., 2017). Third, density and biomass proxies cannot account for spatially labile sexual ontogenies, which can occur at localized scales in reef fishes (Munday *et al*., 2006; Taylor, 2014; Warner & Hoffman, 1980). Rather, age-based reproductive information and detailed data on population sex-structure is required to determine differentials in reproductive potential inside and outside NTMRs.

Size-selective fishing can reduce reproductive rates in protogynous coral reef fishes, as fishing mortality is indirectly sex-selective. This is particularly true for monandric protogynous hermaphrodites with developmentally constrained timing of maturation or sex change, as all individuals mature and reproduce as females before undergoing sex change to become functional secondary males (Sadovy de Mitcheson & Liu, 2008; Warner, 1988). Because males are only produced through sex change, and fishing targets larger individuals, fishery-induced changes to the operational (*i.e*., mature) sex ratio can potentially result in sperm limitation and reduction in reproductive output, compared with similar rates of harvest in populations with separate sexes (*i.e*., gonochores) (Alonzo & Mangel, 2004; Heppell *et al*., 2006; McGovern *et al*., 1998). On the other hand, sex change in protogynous fishes may limit the accumulation of larger, older and more fecund females in NTMRs, as the largest fish are mostly male and only provide a marginal contribution to reproductive potential (Chan *et al*., 2012). However, the onset of protogynous sex change can be influenced by localized variations in fish density, habitat and fishing pressure (Lowe *et al*., 2021; Taylor, 2014; Warner & Hoffman, 1980). Conversely, empirical evidence shows that many protogynous coral reef fishes, such as parrotfishes (Family Labridae, Subfamily Scarinae) and groupers (Family Epinephelidae), can alter the timing of reproductive life history events (sexual maturation, sex change) and/or their reproductive mode (*e.g*., monandry, diandry) in response to changes in local densities and mortality rates (Munday *et al*., 2006; Taylor, 2014; Warner & Hoffman, 1980). Protogynous fishes with plastic reproductive traits may therefore be less affected by size-selective fisheries, particularly where the mating system allows for near-maximum fertilization with very few males (*e.g*., in haremic or lek-like mating systems; Warner, 1988; Petersen *et al*., 1992). Thus, simply knowing that a species exhibits protogyny and that males are disproportionately removed by fishing is necessary but not sufficient to predict how a population will respond to fishing pressure (Alonzo & Mangel, 2005; Easter *et al*., 2020). Age-based estimates of reproductive potential are among the information needed to understand the complex responses of protogynous reef fishes to fishing both spatially and temporally.

Here, we investigated the development of reproductive potential in two protogynous coral reef fishes within NTMRs in the Philippines: a parrotfish (*Chlorurus bleekeri*) and a grouper (*Cephalopholis argus*) that are targeted by local fisheries. For each species, we first estimated key reproductive parameters from market samples of fish, specifically female size and age at first maturity, size and age at sex change, and the female size-fecundity relationship. These parameters were then used to infer egg output per unit area in NTMRs with different durations of protection and in corresponding control (fished) sites for which data on density and individual body size of the two species were collected at one point in time. From these one-point-in-time data, development of reproductive potential ‘through time’ was inferred using a space-for-time substitution approach. For *C. argus*, we also conducted a separate analysis using data on its density and individual body size collected almost annually for three decades from one NTMR (Apo Island reserve) and an adjacent fished control site. Changes in density and biomass in the two species were examined to understand how these potential proxies for reproductive potential would differ from estimated egg output between NTMRs and control sites. We tested the following predictions:

1. Female reproductive potential (density, biomass and egg output per unit area) and secondary male density and biomass would increase in NTMRs with longer duration of protection, but not increase in fished controls.
2. Greater differentials in reproductive potential (total density, total biomass, mature female density, mature female biomass and egg output per unit area) between NTMRs and fished controls would develop earlier in the fish species that reaches female sexual maturity at a younger age.
3. The differentials in egg output per unit area between NTMRs and fished controls would be greater than the corresponding differentials for total or mature female density and biomass.

2 | MATERIALS AND METHODS

2.1 | Study region

We conducted this study in the central Philippines, where multi-species stocks of coral reef fishes are heavily exploited (Nañola *et al*., 2011) and numerous small (<40 ha) NTMRs that protect coral reefs have been established by coastal communities to help manage fisheries (Alcala & Russ, 2006) (Figure 1). NTMR establishment in this region started in the early 1970s, but very old and well-enforced reserves are rare (Alcala & Russ, 2006; Cabral *et al*., 2014).

2.2 | Study species

C. bleekeri is a relatively large-bodied parrotfish (up to 49 cm total length, TL) that has distinct female (initial phase, IP) and male (terminal phase, TP) coloration patterns (Supporting Information Table S1). Parrotfishes derive their nutrition from microscopic photoautotrophs that mostly live on or within various reef substrata (Clements *et al*., 2017). *C. argus* is a relatively large grouper (up to 50 cm TL) that mainly consumes fish (Schemmel *et al*., 2016). The maximum age, size or age at maturity, and size or age at sex change of the two species are either unknown or have been estimated only for populations at higher latitudes (north-east Australia and Hawaii), which are likely to differ significantly from estimates of these life history parameters at lower latitude regions such as the central Philippines (Supporting Information Table S1). *C. bleekeri* exhibits both pair and group spawning (Claydon *et al*., 2014), indicating that the species may be diandric (some individuals may mature directly as primary males) and less territorial, with a less rigid social organization. *C. argus* is a monandric protogynous hermaphrodite, with males defending territories and exhibiting pair spawning with females within their territory during mating (Schemmel *et al*., 2016). The peak breeding season and annual spawning frequencies of the two species in the Philippines are unknown.

2.3 | Market sampling

Samples of fish purchased from local markets were used to estimate species-specific reproductive parameters to avoid negative social consequences of sampling fish inside NTMRs. Most (94%) of the fish samples were obtained from the Dumaguete City market on Negros Island (Figure 1). Sampling was conducted every 1–3 weeks from September 2013 to July 2014, with the aim of collecting the largest sample size and size range possible per species to ensure collection of immature, female and male fish. Fish specimens were occasionally purchased from a fish market on Siquijor Island (Figure 1). A total of 201 *C. bleekeri* and 53 *C. argus* were collected. It was not possible to pinpoint the sites of capture of each specimen, but information from fish vendors indicated that the samples originated from the reefs of southern Negros and south-western Siquijor, and offshore reefs in the Sulu Sea (Figure 1).

2.4 | Reproductive biology

2.4.1 | Sex, growth, female maturity and sex change

The total length (to the nearest 1 mm) and weight (to the nearest 0.1 g) of each fish specimen were measured. Sagittal otolith pairs were extracted from each fish, cleaned and stored dry for age determination. Age was determined for a subsample of specimens for each species through interpretation of sectioned sagittal otoliths (Age determination methods). The subsamples of specimens were selected without knowledge of sex or gonad stage. Gonads were extracted from each fish and macroscopically staged (Supporting Information Table S2). Stage III and IV ovaries were fixed in 10% formalin for estimation of batch fecundity (see below). Female gonadosomatic indices (GSIs) were also determined and plotted across sampling months to reveal any spawning seasonality. Gonads that were difficult to stage macroscopically were fixed and processed for histology following conventional methods (Longenecker & Langston, 2016). Histological gonad sections were subject to microscopic examination to determine the sex, reproductive stage and maturity of each individual. Out of 44 gonad samples (*C. bleekeri* = 20 and *C. argus* = 24) processed for histology, 43 (98%) were correctly staged by macroscopic identification according to sex and maturity. The type of oocyte development (group-synchronous or asynchronous) evident in the histological slides of female gonads was also determined.

Length at 50% female maturity (L_{m50}) and length at 50% sex change (L_{s50}) from female to male were estimated based on the results of macroscopic and histological examination of gonads. To determine L_{m50}, logistic regression was performed on the proportional frequency of immature individuals and mature females in 20 mm TL size classes. Logistic regression was also performed to estimate L_{s50} using the proportional frequency of males and females in 20 mm TL size classes. To estimate the timing of L_{m50} and L_{s50} from samples of *C. bleekeri* which were aged, we used the age class at which the median size was closest to L_{m50} and L_{s50} estimates based on all samples. For ages <1 year, mid-points were approximated according to von Bertalanffy growth functions (VBGFs) fitted to age data (Age determination methods). For *C. argus*, which had a low sample size, the VBGF was used rather than the median size of each age class.

2.4.2 | Female size-fecundity relationship

Batch fecundity (*i.e*., the number of eggs released per spawning event) was estimated from the fixed stage III and IV ovaries, using the gravimetric method (Hunter *et al*., 1985). This involved taking subsamples of known weights (~0.01 g) from each ovary and then counting hydrated (mature) oocytes under a compound microscope at 40× magnification. Batch fecundity was estimated by extrapolating averaged counts of hydrated oocytes from subsamples to the entire weight of the ovary. For consistency, subsamples were taken from the anterior, median and posterior regions of the left gonad lobe ($n = 3$ subsamples per ovary). Estimates of batch fecundity per species were plotted against corresponding female size and fit with linear

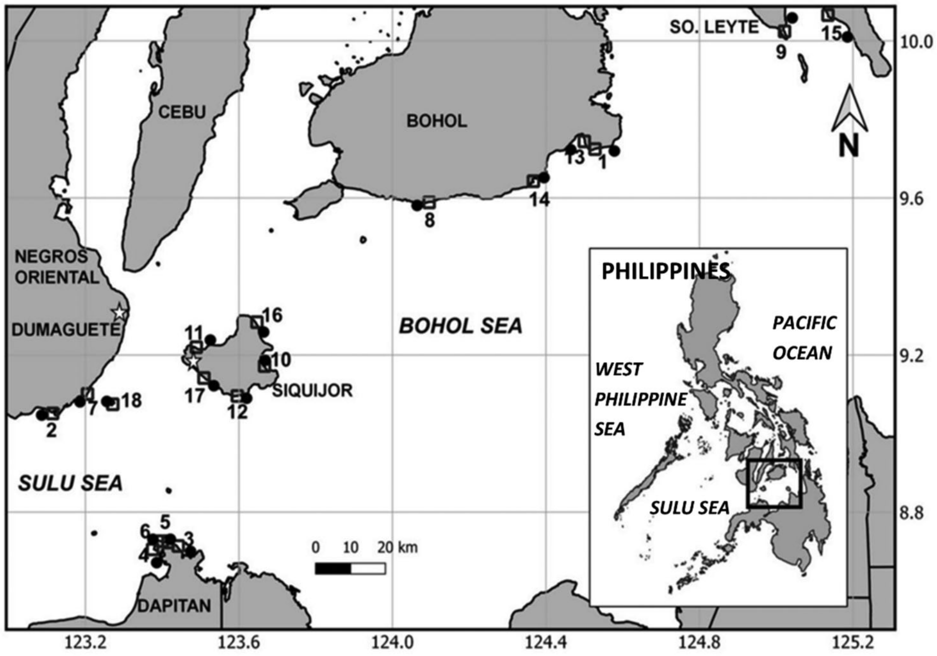

FIGURE 1 Map of the study region (boxed in inset map) in the central Philippines. Fish markets in Dumaguete and Siquijor Island are indicated by stars. Sampling sites are indicated by open squares (NTMRs) and black dots (fished controls). Pairs of sites used in the space-for-time substitution approach are numbered 1 to 17 (see Supporting Information Table S3). Apo Island is indicated by number 18

($y = a + bx$) and exponential ($y = e^{a + bx}$) models, where y is fecundity (eggs × 1000), x is fish size (mm TL), a is the intercept and b is the slope. Regression analysis was performed in R v.4.0.2 (R Core Team, 2020). The model with the smaller Akaike Information Criterion (AIC) value was selected to best describe the female size-fecundity relationship for each species.

2.5 | Reproductive potential

Field data on the density and individual body size of *C. bleekeri* and *C. argus* in selected NTMR and fished sites across the study region were converted to density and biomass of total individuals, immature individuals, mature females, secondary males and batch fecundity per unit area (BFUA). Conversions used estimates of L_{m50} and L_{s50} (*i.e.*, the lower and upper thresholds for mature female size, respectively) and the top-performing female size-fecundity models. BFUA assumes that all mature female fish of the species in question within a given area would spawn simultaneously at one time (Carter *et al*., 2014a,b, 2017; Evans *et al*., 2008).

Two types of field data were used to investigate how density, biomass and BFUA would develop in NTMRs after cessation of fishing. The first provided inputs for a space-for-time substitution approach (*e.g.*, McClanahan & Graham, 2005; Stockwell *et al*., 2009). Data were obtained from fish and benthic surveys performed in 2012 and 2015 inside 17 pairs of coastal NTMRs with different ages and nearby fished sites that served as controls (Figure 1 and Supporting Information Table S3). Sites were surveyed using 50 m long × 10 m wide transects with a width of 10 m (2012) or 5 m (2015) [$n = 6$ replicate transects on the reef crest (2–3 m) and reef slope (10–12 m) per NTMR and control; fish size was estimated to the nearest 1 cm TL (see Stockwell *et al.* (2009) for similar methods)]. The 17 NTMRs and corresponding controls were selected from a pool of 33 NTMRs and 37 fished sites distributed across the study region, with the aim of representing the widest range of reserve age possible while keeping general habitat quality as similar as possible (*i.e.*, excluding sites at small offshore islands and avoiding poorly developed reef slopes). The NTMRs were of different sizes (Supporting Information Table S3) and coral cover was variable across sites, despite the effort to control for habitat quality (see statistical analysis below to account for potential effects of NTMR size and habitat). The 17 NTMRs had durations of protection ranging from 0 ('proposed' status) to 11 years at the time of survey (Supporting Information Table S3). Duration of protection is the number of years the NTMR had been continuously and strictly protected from fishing at the time of survey, which was based on the best available information from local managers. In about one-third of the cases, duration of protection was much lower than the official age of the NTMR because protection from fishing was not necessarily strict following its formal establishment (Supporting Information Table S3).

The second type of field data allowed a more direct examination of how reproductive potential in *C. argus* would develop inside a NTMR over a much longer period of full protection. These data were obtained from fish and benthic surveys inside Apo Island NTMR (established in 1982), and an adjacent fished control site. Sites at Apo Island were surveyed using 50 m long × 20 m wide census areas ($n = 6$ replicate areas each in the NTMR and control situated on the reef slope from 6–17 m in the NTMR and 9–17 m in the control site). Twenty-two fish surveys were carried out almost annually between 1983 and 2011 by a single observer (GRR, *i.e.*, year 1 to 29 of NTMR protection). Fish size was estimated to within ±2 cm TL (see Russ & Alcala (1996) for full methods). These surveys are part of a long-term ecological monitoring program but data from 2012 onwards were not included in this study because typhoons impacted the NTMR, resulting in a significant shift in the structure of fish and benthic assemblages (Russ *et al*., 2015, 2021). Development of reproductive potential in *C. bleekeri* at Apo Island could not be investigated because the survey protocol did not include estimating the individual body sizes of this species. However, Russ *et al*. (2015) showed that parrotfish density at Apo Island did not differ significantly between the NTMR and the control over the period covered by the present study, suggesting that reserve protection may have had little to no effect on the local abundance of *C. bleekeri* at Apo Island.

2.6 | Data analysis

Trends in density, biomass and BFUA in NTMRs and controls were described by computing mean values (standardized to an area of 500 m^2) for specific time blocks of duration of protection: 0–3, 4–7 and 8–11 years for the space-for-time substitution approach ($n = 3$, 6 and 8 replicate NTMRs or controls per time block). For the real-time monitoring at Apo Island, the time blocks of duration of protection used were 1–3, 4–7, 8–11, 12–15, 16–19, 20–23, 24–27 and 28–29 years ($n = 2$, 1, 3, 3, 4, 2, 4 and 2 replicate surveys, respectively, in the NTMR and the control). Time blocks were used to better visualize changes in the relative contribution of immature individuals, females and secondary males to density and biomass. Statistical testing of the effects of protection status (NTMR *vs*. control) and duration of protection (in time blocks) on density, biomass and BFUA was performed on the space-for-time data using two-way ANOVA (duration of protection in time blocks) and on the Apo Island data using two-way repeated measures ANOVA (duration of protection in 22 levels, the years when surveys were conducted). The potential effect of NTMR size on density, biomass and BFUA across the 17 reserves in the space-for-time substitution approach was examined using linear regression. The potential effect of benthic habitat on density, biomass and BFUA was tested using two-way ANCOVA. Two habitat variables were treated separately as the covariate in the analysis: percentage cover of live hard coral and dead substrate (*i.e*., the cover of bare rock, rubble and sand combined). Both have been shown to strongly influence reef fish density and biomass in the study region (McClure *et al*., 2020; Russ *et al*., 2015, 2021). Almost all (97%) of the benthic data in the NTMR and control at Apo Island were collected during 16 surveys done between 1993 and 2011 (years 11 to 29 of protection). The ANCOVA at Apo Island only considered this period (16 levels of the factor 'duration of protection') to provide a more robust estimate of the effect of benthic habitat on *C. argus* density, biomass and BFUA. Data were log ($x + 1$) transformed to meet the assumptions of statistical tests.

Differentials in density, biomass and BFUA between NTMRs and controls were first estimated by modelling how each variable would change with duration of protection using the space-for-time substitution and using the real-time Apo Island data. Linear, exponential and logistic models were fitted to the data using R (Fox & Weisberg, 2011). Models with the smallest AIC values were selected to best describe trends. Differentials were then derived from modelled trends for specific time points (duration of NTMR protection): 3, 7 and 11 years for the space-for-time substitution approach, and 3, 7, 11, 15, 19, 23, 27 and 29 years for the real-time monitoring at Apo Island. Zeros in the data were eliminated before modelling by adding one individual fish with a length equal to L_{m50} (and the equivalent biomass and egg output for the appropriate variable) to all replicate samples at all sites. This ensured that all values predicted by models were greater than zero, avoiding problematic calculations of differentials between NTMR and control sites. For density and biomass, differentials were expressed as NTMR/control ratios (density or biomass in NTMRs divided by density or biomass in controls). For BFUA, differentials were expressed both as ratios and in terms of the absolute difference in egg output per unit area between NTMRs and controls.

3 | RESULTS

3.1 | Growth, maturity and fecundity

3.1.1 | *Chlorurus bleekeri*

Specimens of *C. bleekeri* ranged from 144 to 328 mm TL. Eighteen (9.0%), 136 (67.7%), 42 (20.9%) and 5 (2.5%) individuals were classified as immature, mature females, secondary males and primary males, respectively. The presence of primary males confirmed that the species is diandric. L_{m50} was estimated to be approximately 170 mm TL and L_{s50} approximately 272 mm TL (Supporting Information Figure S1a,b and Table S4). Size-at-age data for a subsample of specimens ($n = 100$, 156–328 mm TL) suggested that L_{m50} occurs at an age of approximately 0.51 years ($\sim$6 months) and L_{s50} at 3 years (Supporting Information Figure S2a). The minimum age of males (primary and secondary) in the subsample was 1 year. The largest female was 280 mm TL, which indicates a narrow size overlap between females and males larger than L_{s50} (Supporting Information Figure S1a,b). Estimated batch fecundity ranged from 9993 to 157,863 eggs per spawn ($n = 24$ females) (Supporting Information Figure S1c). The female size-fecundity relationship was best described by an exponential model (Supporting Information Figure S1c and Table S5), which predicted an 8.5-fold difference in batch fecundity between the lower (L_{m50}) and upper (L_{s50}) thresholds of mature female size. Although only 13 of the 24 females with mature or running ripe ovaries were included in the subsample for age determination, the age data for this subset suggested that older females (up to 5 years) had higher batch fecundity than younger females (Supporting Information Figure S3a). Female GSIs showed minimal monthly variation from September 2014 to March 2015, indicating a protracted breeding period, although it was not possible to know if GSI peaks during warmer months (April–August) due to the lack of female samples in these months (Supporting Information Figure S4a). Histological slides of ovaries showed asynchronous oocyte development, which suggests frequent spawning (Supporting Information Figure S5a).

3.1.2 | *Cephalopholis argus*

Specimens of *C. argus* ranged from 177 to 355 mm TL. Eight (15.1%), 25 (47.2%) and 20 (37.7%) of these fish were found to be immature, mature females and secondary males, respectively. L_{m50} was estimated to be approximately 216 mm TL and L_{s50} at 312 mm TL

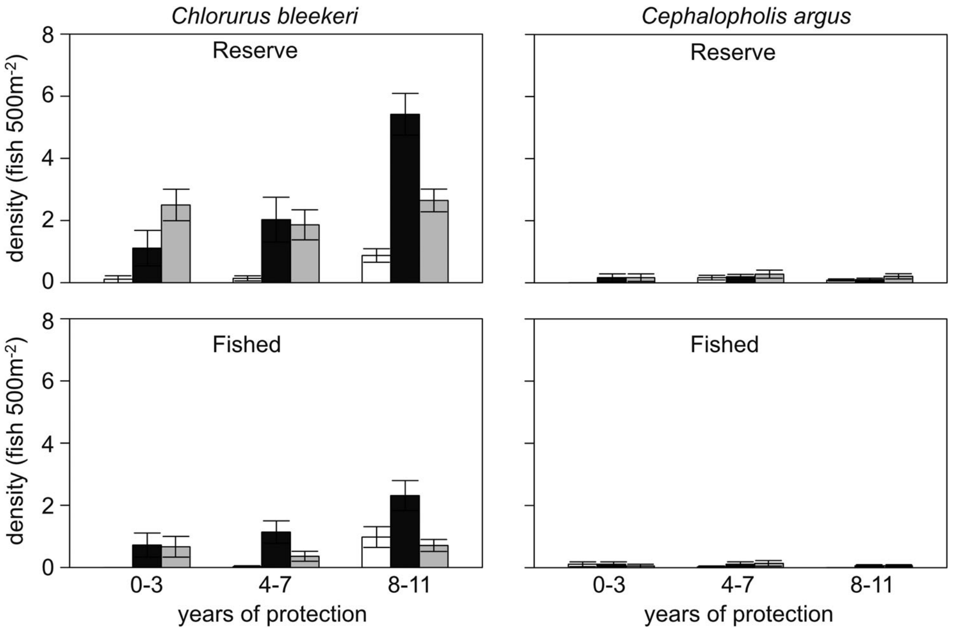

FIGURE 2 Density of immature, mature female and secondary male *Chlorurus bleekeri* and *Cephalopholis argus* inside NTMRs relative to fished sites (upper and lower rows, respectively) with increasing duration of NTMR protection, inferred from surveys of different NTMRs and paired fished sites (controls) done at one time in the central Philippines. Error bars are standard errors (s.e.) (□) Immature; (■) mature female; (▨) secondary male

(Supporting Information Figure S6a,b and Table S4). Size-at-age data for a subsample of specimens ($n = 38$, size range $= 135$–355 TL) suggested that L_{m50} and L_{s50} correspond to an age of sexual maturity of approximately 4.3 years and an age of sex change at approximately 12.6 years (Supporting Information Figure S2b). The minimum age of secondary males in the subsample was 7 years. The largest female was 353 mm TL, which indicates a narrow size overlap between females and males at sizes greater than L_{s50} (Supporting Information Figure S6a,b). Estimated batch fecundity ranged from 2446 to 254,782 eggs per spawn ($n = 14$ females) (Supporting Information Figure S6c). The relationship between female size and fecundity was best described by an exponential model (Supporting Information Figure S6c and Table S5), which predicted a 4.5-fold difference in fecundity between L_{m50} and L_{s50}. Only seven out of the 14 females with ovaries that were mature or running ripe ovaries were included in the subsample for age determination but the age data for this subset suggested that older females (up to 13 years) had much higher batch fecundity than younger females (Supporting Information Figure S3b). Female GSIs peaked in October and April, suggesting restricted breeding periods that coincide with the intermonsoon months (Supporting Information Figure S4b). Histological slides of ovaries showed group-synchronous oocyte development, which indicates less frequent spawning during breeding periods (Supporting Information Figure S5b,c).

3.2 | Development of reproductive potential

3.2.1 | Space-for-time substitution approach

The density and biomass of mature female *C. bleekeri* was consistently higher in NTMRs than fished controls, and higher in NTMRs with greater duration of protection (Figures 2 and 3). Density and biomass of mature female *C. bleekeri* also tended to be higher in controls associated with older NTMRs (Figures 2 and 3). Mature females of *C. bleekeri* dominated local population density in older NTMRs, with a mean of approximately five fish 500 m^{-2} in reserves aged 8–11 years (Figure 2). Secondary males of *C. bleekeri* tended to be more abundant in NTMRs than controls (Figure 2), dominating local population biomass regardless of duration of protection (Figure 3). Immature individuals of *C. bleekeri* were commonly recorded in NTMRs and controls, although at relatively low mean densities (0–1.6 fish 500 m^{-2}; Figure 2), suggesting that recruitment in these species is relatively frequent. In contrast to the parrotfish, *C. argus* showed no tendency for higher density or biomass in NTMRs with higher duration of protection (Figures 2 and 3). Immature, female and male *C. argus* had low mean density (<0.3 fish 500 m^{-2}) and biomass (<0.3 kg 500 m^{-2}) in NTMRs regardless of duration of protection, a pattern also seen in controls.

Two-way ANOVA detected significant effects of protection status and duration of protection on the density and biomass of mature female and secondary male *C. bleekeri* (Table 1). The interaction term was always significant for tests that involved the density and biomass of mature female *C. bleekeri*, suggesting that the higher values in NTMRs were due to higher duration of protection. However, two-way ANCOVA suggested that live hard coral cover was a significant covariate for densities of secondary male *C. bleekeri*, while dead substratum was a significant covariate for both biomass and density of secondary males in *C. argus* (Supporting Information Figure S7 and Table S6). Two-way ANOVA did not detect a significant effect of protection status and duration of protection on the density and biomass of *C. argus* (Table 1). There was no significant relationship between NTMR size and the density and biomass of mature females in any of the two species (Supporting Information Table S7).

BFUA of *C. bleekeri* was much higher in older NTMRs, from a mean of 57,720 ± 27,870 (s.e.) eggs 500 m^{-2} in reserves aged

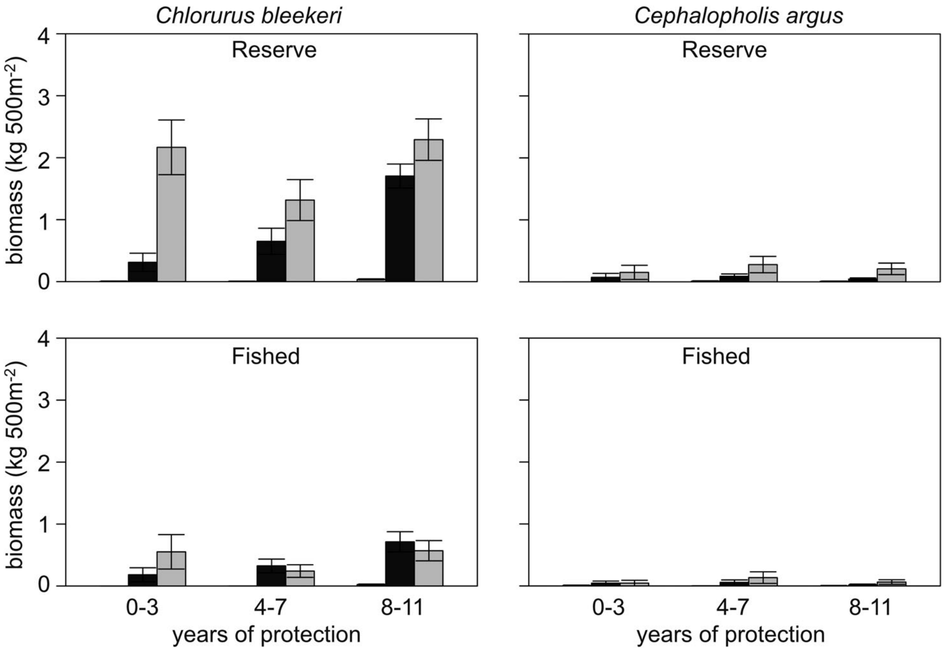

FIGURE 3 Biomass of immature, mature female and secondary male *Chlorurus bleekeri* and *Cephalopholis argus* inside NTMRs relative to fished sites (upper and lower rows, respectively) with increasing duration of NTMR protection, inferred from surveys of different NTMRs and paired fished sites (controls) done at one time in the central Philippines. Error bars are s.e. (□) Immature; (■) mature female; (▨) secondary male

TABLE 1 Results of two-way ANOVA testing the effect of protection status (NTMR or control) and duration of protection (DOP) on the density and biomass of immature individuals, mature females and secondary males of the two study species in the central Philippines

		Density			**Biomass**		
Species	**Source**	***F***	**d.f.**	***P***	***F***	**d.f.**	***P***
Chlorurus bleekeri							
Immature	Status	0.49	1, 198	0.49	2.21	1, 198	0.14
	DOP	13.41	2, 198	**<0.001**	10.73	2, 198	**<0.001**
	Status × DOP	0.02	2, 198	0.98	0.22	2, 198	0.80
Mature female	Status	15.22	1, 198	**<0.001**	20.83	1, 198	**<0.001**
	DOP	15.67	2, 198	**<0.001**	21.33	2, 198	**<0.001**
	Status × DOP	7.31	2, 198	**<0.001**	4.29	2, 198	**0.02**
Secondary male	Status	47.38	1, 198	**<0.001**	48.40	1, 198	**<0.001**
	DOP	4.19	2, 198	**0.02**	4.64	2, 198	**0.01**
	Status × DOP	1.24	2, 198	0.29	0.91	2, 198	0.41
Cephalopholis argus							
Immature	Status	3.49	1, 198	0.06	0.05	1, 198	0.05
	DOP	0.86	2, 198	0.43	0.80	2, 198	0.80
	Status × DOP	2.93	2, 198	0.06	0.08	2, 198	0.08
Mature female	Status	1.49	1, 198	0.22	1.52	1, 198	0.23
	DOP	0.54	2, 198	0.58	0.89	2, 198	0.41
	Status × DOP	0.15	2, 198	0.86	0.06	2, 198	0.94
Secondary male	Status	3.67	1, 198	0.06	3.65	1, 198	0.06
	DOP	0.40	2, 198	0.67	0.44	2, 198	0.65
	Status × DOP	0.02	2, 198	0.98	0.02	2, 198	0.99

Note: Bold values indicate these are significant (<0.05 alpha level).

0–3 years to 592,880 ± 78,770 eggs 500 m^{-2} in reserves aged 8–11 years (Figure 4). This pattern did not occur in controls (Figure 4). Two-way ANOVA detected a significant effect of protection status and duration of protection on the BFUA of *C. bleekeri*, with the interaction term being significant in both cases (Table 2). Two-way ANCOVA suggested that live hard coral cover, but not dead substratum cover, was a significant covariate of BFUA in *C. bleekeri* (Table 3 and Supporting Information Figure S7). In contrast, the mean BFUA of *C. argus* was low in NTMRs of all ages (22,770 ± 11,200 eggs 500 m^{-2} at its highest) and did not differ significantly from fished

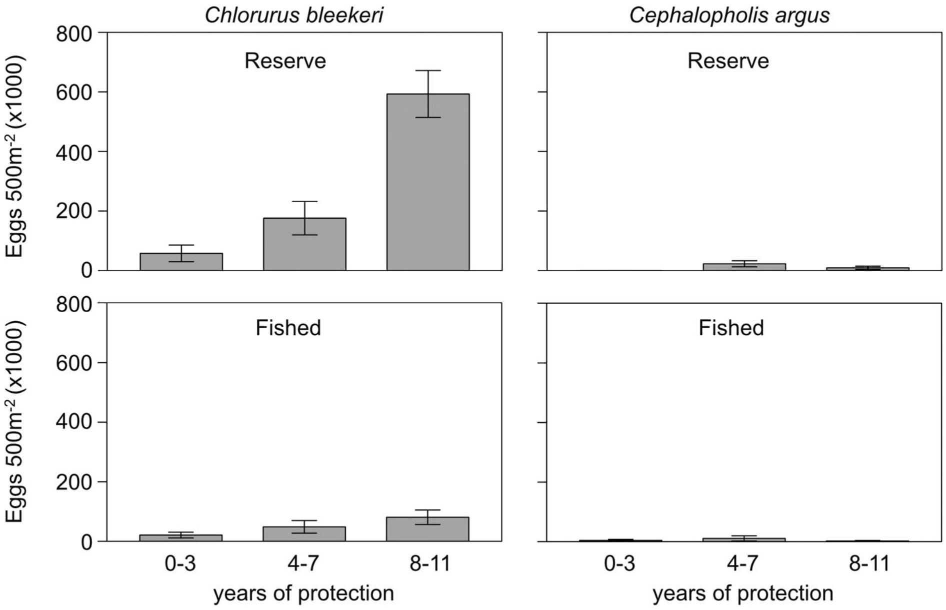

FIGURE 4 Batch fecundity per unit area (BFUA) of mature female *Chlorurus bleekeri* and *Cephalopholis argus* inside NTMRs relative to fished sites (upper and lower rows, respectively) with increasing duration of NTMR protection, inferred from surveys of different NTMRs and paired fished sites (controls) done at one time in the central Philippines. Error bars are s.e.

TABLE 2 Results of two-way ANOVA testing the effect of protection status (NTMR or control) and duration of protection (DOP) on the batch fecundity per unit area of the two study species in the central Philippines

Species	Source	*F*	d.f.	*P*
Chlorurus bleekeri	Status	41.67	1, 198	**<0.001**
	DOP	17.29	2, 198	**<0.001**
	Status × DOP	3.87	2, 198	**0.02**
Cephalopholis argus	Status	1.10	1, 198	0.30
	DOP	0.07	2, 198	0.94
	Status × DOP	0.86	2, 198	0.42

Note: Bold values indicate these are significant (<0.05 alpha level).

TABLE 3 Results of two-way ANCOVA testing the effect of protection status (NTMR or control) and duration of protection (DOP) in the central Philippines on the batch fecundity per unit area of the two study species with live hard coral cover (LHC) or dead substratum cover (DS) as the covariate in the tests

Species	Source	*F*	d.f.	*P*
Chlorurus bleekeri	Status	36.06	2, 197	**<0.001**
	DOP	20.92	2, 197	**<0.001**
	Status × DOP	2.86	1, 197	0.06
	Covariate: LHC	7.67	1, 197	**0.01**
	Status	40.36	2, 197	**<0.001**
	DOP	15.17	2, 197	**<0.001**
	Status × DOP	3.93	1, 197	**0.02**
	Covariate: DS	0.14	1, 197	0.71
Cephalopholis argus	Status	0.64	2, 197	0.42
	DOP	0.17	2, 197	0.85
	Status × DOP	0.92	1, 197	0.40
	Covariate: LHC	2.57	1, 197	0.11
	Status	1.37	2, 197	0.24
	DOP	0.01	2, 197	0.99
	Status × DOP	0.94	1, 197	0.39
	Covariate: DS	0.93	1, 197	0.34

Note: Bold values indicate these are significant (<0.05 alpha level).

controls (Figure 4 and Table 3). There was no significant relationship between NTMR size and the BFUA of any of the two species (Supporting Information Table S7).

3.2.2 | Long-term NTMR protection at Apo Island

Mature females of *C. argus* showed a gradual increase in density inside Apo Island NTMR over 29 years of protection (Figure 5). Mature females had low mean densities in the NTMR during the first 15 years (<0.4 fish 500 m^{-2}) but dominated local population density for most of the following 14 years, peaking at a mean of 1.2 ± 0.3 fish 500 m^{-2} in years 28–29. Secondary males were absent in the NTMR during the first 7 years and had low mean densities (<0.5 fish 500 m^{-2}) beyond this duration of protection. Mature female biomass showed an increase with duration of protection inside Apo Island NTMR, being lower in the first 15 years (usually <0.2 kg 500 m^{-2}) than in the following 14 years, and peaked at a mean of 0.5 ± 0.1 kg 500 m^{-2} in years 28–29 (Figure 5). Secondary males showed an increase in biomass in the NTMR with duration of protection, reaching 0.5 to 0.6 kg 500 m^{-2} from years 16 to 23 duration of protection, dominating local population biomass during those years (Figure 5).

In contrast to the NTMR, mature *C. argus* females were absent in the adjacent fished control site in the first 7 years (Figure 5). After this time, *C. argus* had low mean density (<0.04 fish 500 m^{-2}) and biomass (<0.3 kg 500 m^{-2}) for the next 11 years, then exhibited a weak

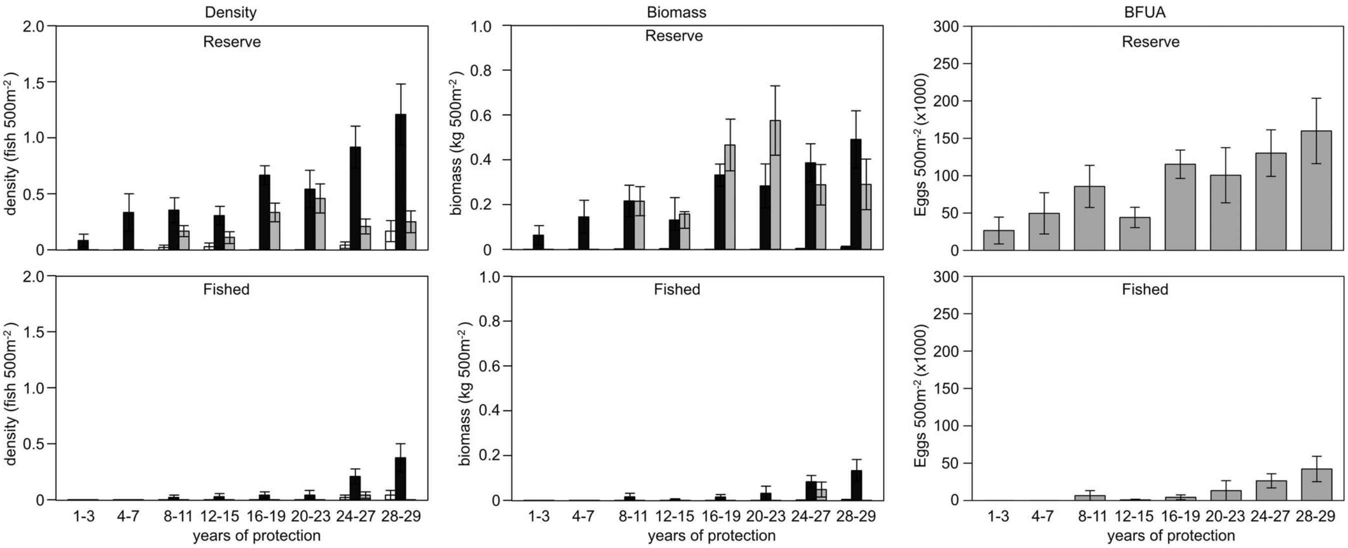

FIGURE 5 Density and biomass of immature, mature female and secondary males and the batch fecundity per unit area (BFUA) of mature females of *Cephalopholis argus* in the NTMR and an adjacent fished site (control) at Apo Island (upper and lower rows, respectively) in the central Philipines, measured by repeated surveys over three decades. Error bars are s.e. (□) Immature; (■) mature female; (▨) secondary male

increase in density (up to 0.4 fish 500 m^{-2}) and biomass (up to 0.5 kg 500 m^{-2}) from years 24 to 29. Secondary males were absent or rare in the fished control site throughout the 29-year period (Figure 5). Immature individuals were rare in both the NTMR and the fished control, suggesting low levels of recruitment of *C. argus* at Apo Island (Figure 5).

Consistent with mature female density and biomass, BFUA of *C. argus* showed a gradual increase in the NTMR with duration of protection, from a mean of 26,630 ± 17,960 eggs 500 m^{-2} in years 1–3 to 159,850 ± 43,740 eggs 500 m^{-2} in years 28–29: a 6-fold increase in reproductive potential (Figure 5). In contrast, BFUA in the adjacent control showed a small increase over the same period and peaked at a mean of 42,230 ± 16,980 eggs 500 m^{-2} in years 28–29.

Two-way repeated measures ANOVA detected significant effects of protection status and duration of protection on the density and biomass of mature females, secondary males and BFUA of *C. argus* at Apo Island (Table 4). The interaction term was not significant in tests involving mature female biomass and BFUA, which was probably due to the weak increase in these variables over time in the fished control (Figure 5). Two-way ANCOVA suggested that neither live hard coral cover nor dead substrate cover was a significant covariate of the density, biomass and BFUA of *C. argus* at Apo Island over the period for which benthic data were available (1993–2011; Supporting Information Figure S8 and Table S8).

3.2.3 | Differentials in reproductive potential

Models that best described trends in density, biomass and BFUA in the space-for-time approach suggested that differentials in these variables between NTMRs and fished controls tended to be larger in

TABLE 4 Results of two-way repeated measures ANOVA testing the effect of protection status (NTMR or control) and duration of protection (DOP) on the density and biomass of immature individuals, mature females and secondary males and the batch fecundity per unit area of *Cephalopholis argus* at Apo Island, central Philippines

Variable/life stage	Source	*F*	d.f.	*P*
Density				
Immature	Status	2.84	1, 263	0.15
	DOP	2.08	21, 263	**<0.01**
	Status × DOP	0.48	21, 263	0.97
Mature female	Status	24.88	1, 263	**<0.01**
	DOP	5.62	21, 263	**<0.001**
	Status × DOP	1.725	21, 263	**0.04**
Secondary male	Status	24.25	1, 263	**<0.01**
	DOP	1.837	21, 263	**0.02**
	Status × DOP	1.885	21, 263	**0.02**
Biomass				
Immature	Status	2.52	1, 263	0.17
	DOP	2.03	21, 263	**0.01**
	Status × DOP	0.56	21, 263	0.94
Mature female	Status	17.20	1, 263	**<0.01**
	DOP	3.19	21, 263	**<0.001**
	Status × DOP	1.21	21, 263	0.26
Secondary male	Status	30.86	1, 263	**<0.01**
	DOP	1.74	21, 263	**0.04**
	Status × DOP	1.817	21, 263	**0.03**
BFUA	Status	40.94	1, 263	**0.001**
	DOP	3.93	21, 263	**<0.001**
	Status × DOP	1.32	21, 263	0.178

Note: Bold values indicate these are significant (<0.05 alpha level).

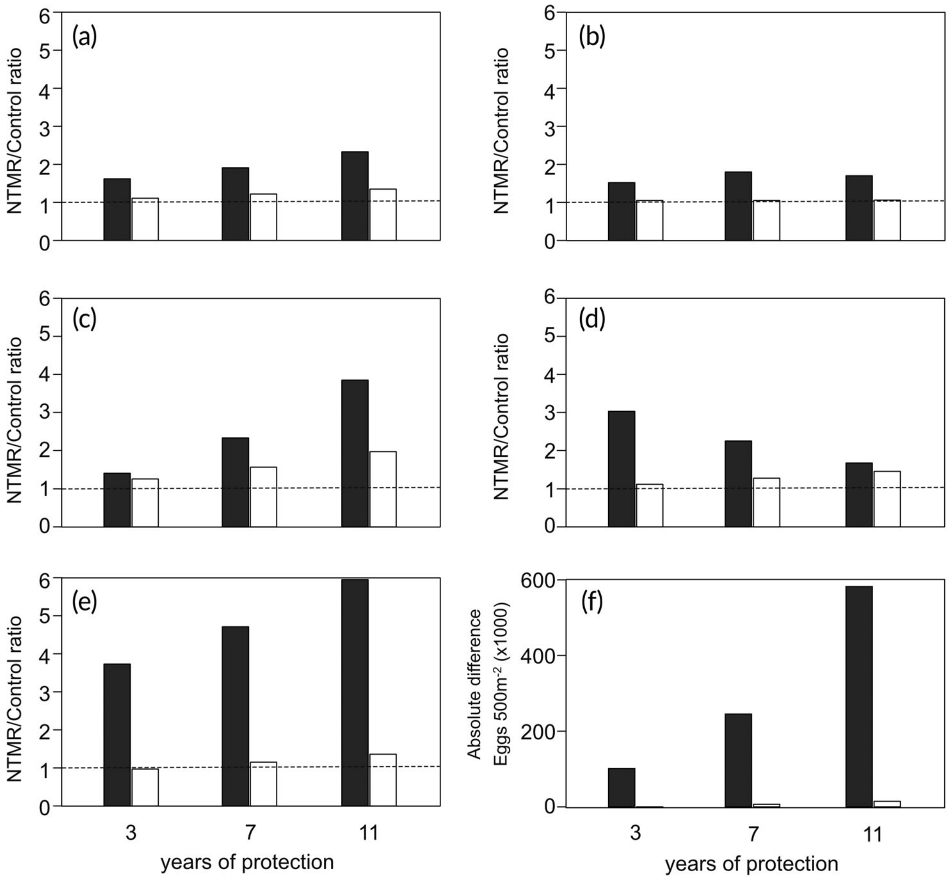

FIGURE 6 NTMR/control ratios for total density (a), mature female density (b), total biomass (c), mature female biomass (d), batch fecundity per unit area (BFUA) (e) and absolute difference in BFUA between NTMR and controls (f) in *Chlorurus bleekeri* and *Cephalopholis argus* for different durations of NTMR protection in the central Philippines derived from best-fit models fitted to space-for-time data (see Supporting Information Figures S9 and S10). The broken horizontal line indicates a 1:1 ratio (no difference between NTMR and control). (■) *Chlorurus bleekeri*; (□) *Cephalopholis argus*

C. bleekeri than in *C. argus* within the first 11 years of NTMR protection (Figure 6). However, there was considerable inherent uncertainty (large 95% confidence intervals) in the modelled trends of *C. bleekeri* due to the relatively low sample sizes and variability in the magnitude of response variables (Supporting Information Figures S9 and S10, and Table S9). In *C. argus*, differentials were nonexistent (NTMR/control ratios = 1) or relatively small (1.9-fold higher total biomass in NTMRs at most) over the 11-year duration of NTMR protection that was considered (Figure 6). All differentials in the *C. bleekeri* were higher at greater durations of protection, except for mature female biomass, where they tended to decrease in older NTMRs (Figure 6d). This decreasing trend was due to the slightly higher mature female biomass in controls adjacent to older NTMRs (Figure 3). The models predicted that BFUA in *C. bleekeri* would be 6.0 times greater in NTMRs than controls by year 11 of protection, which equates to approximately 582,000 more eggs produced 500 m^{-2} within the NTMR (Figure 6e,f). Furthermore, BFUA ratios in *C. bleekeri* were larger than density and biomass ratios at any point in time.

Modelled trends in the density, biomass and BFUA of *C. argus* at Apo Island had less inherent uncertainty (narrower 95% confidence intervals) than those predicted from the space-for-time data (Supporting Information Figure S11 and Table S10). The models suggested gradually increasing ratios for total density, mature female density and mature female biomass (Figure 7a,b). Total biomass ratios in *C. argus* increased strongly from year 3 to year 15 of protection and exceeded all other density and biomass ratios throughout most of the period. This increase was driven by the disproportionately greater biomass contribution of fewer, but much larger, secondary males starting in year 11 (Figure 5). BFUA ratios in *C. argus* were always greater than density and biomass ratios, except total biomass, but decreased over time from 3.2-fold higher in the reserve in year 3 to just 2.4-fold higher in the reserve by year 29 (Figure 7c). However, the absolute difference in BFUA between the NTMR and control doubled over the same period (Figure 7d), with *C. argus* estimated to produce approximately 113,000 more eggs 500 m^{-2} inside Apo Island NTMR by year 29.

4 | DISCUSSION

Our results indicate that with sufficient time, NTMRs can significantly enhance the reproductive potential of fishery-targeted protogynous coral reef fishes. The inferred rate of development and magnitude of this effect in Philippine NTMRs differed between the parrotfish (*C. bleekeri*) and the grouper (*C. argus*). The space-for-time substitution approach showed that NTMRs may significantly increase the density, biomass and BFUA of the parrotfish, but not the grouper, within approximately a decade (11 years) of protection. Enhancement of reproductive potential in the grouper was evident at Apo Island NTMR where increases in density, biomass and BFUA were more pronounced after year 15 through year 29 of the monitoring period. These findings are consistent with the age of female sexual maturity

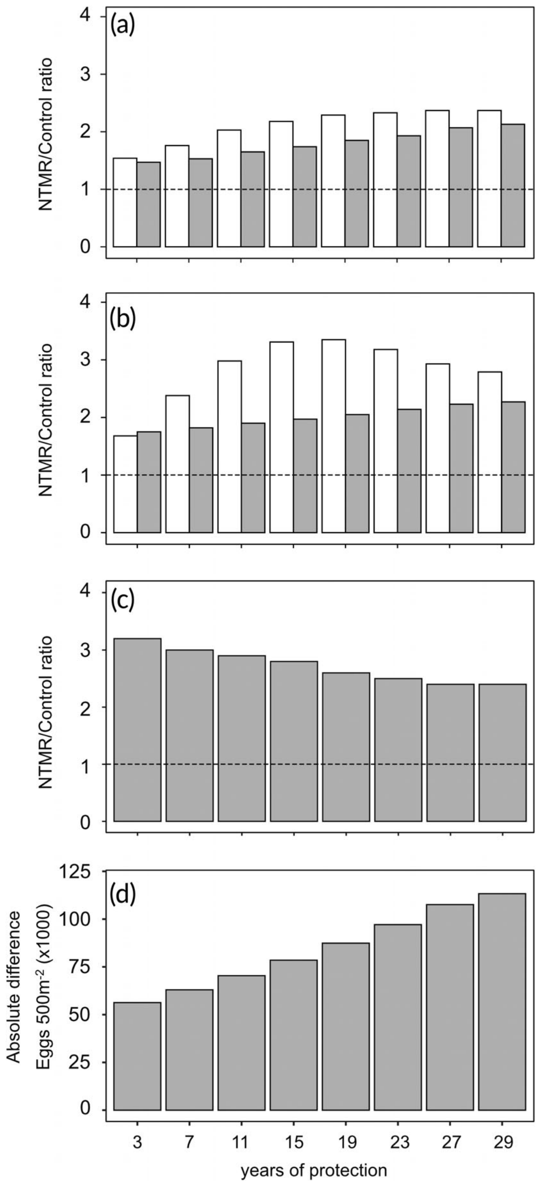

FIGURE 7 NTMR/control ratios for total density and mature female density (a), total biomass and mature female biomass (b), batch fecundity per unit area (BFUA) (c) and absolute difference in BFUA between the NTMR and control (d) in *Cephalopholis argus* for different durations of NTMR protection derived from best-fit models fitted to long-term data from Apo Island (see Supporting Information Figure S11), central Philippines. The broken horizontal line indicates a 1:1 ratio (no difference between NTMR and control). (a) (□) Total and (▨) mature females. (b) (□) Total and (▨) mature females

estimated by the present study, with the parrotfish maturing much earlier (~6 months) than the grouper (~4 years). Sex change was also estimated to occur much earlier in the parrotfish (~3 years) than the grouper (~13 years). At their highest, the differentials in BFUA (*i.e.*, NTMR/control ratios) inferred from space-for-time substitution were greater in the parrotfish (6.0 times greater in NTMRs) than those actually measured over real time for the grouper at Apo Island (3.2 times greater in the NTMR), despite the longer duration of protection that was examined in the latter. This result was probably driven more by faster population recovery and higher natural abundance of the parrotfish than differences in individual female fecundity among species. Similarly, while both species showed an increase in the absolute difference in BFUA between NTMR and fished sites, the difference increased much more rapidly in *C. bleekeri* (a 6-fold increase over 11 years) than in *C. argus* at Apo Island (a 2-fold increase over 29 years) (Figures 6f and 7d).

The rates of local population recovery documented here are consistent with the decadal time scales of full recovery in coral reef fishes inside NTMRs suggested by previous studies (Babcock *et al*., 2010; MacNeil *et al*., 2015; McClanahan, 2000; Russ & Alcala, 2004, 2010). The results also conform to general predictions about population recovery in reef fishes based on their intrinsic productivity, where the nominal herbivore (*C. bleekeri*) is commonly expected to recover earlier than the carnivore (*C. argus*) (Abesamis *et al*., 2014; but see McClanahan & Humphries, 2012). But apart from intrinsic factors, population recovery can be influenced by fishing intensity, disturbances, metapopulation structure, recruitment rates, trophic interactions, habitat quality, and the effectiveness of NTMRs and other fisheries management measures (Babcock *et al*., 2010; Jennings, 2001; MacNeil *et al*., 2015). Thus, it is not surprising that recovery rates within NTMRs, and therefore the development of reproductive potential within their boundaries, can greatly differ between locations across a large range of spatial scales. For example, parrotfish assemblages in Kenyan NTMRs were estimated to attain full recovery in 20–25 years (McClanahan *et al*., 2007), contrasting with our results and those of previous work by Stockwell *et al*. (2009) that suggested full recovery of parrotfish populations inside NTMRs in the central Philippines within 10 years. On the Great Barrier Reef (GBR, Australia), mean density of groupers (*Plectropomus* spp.) inside new NTMRs increased by 31%–75% within just 2 years of establishment (Russ *et al*., 2008), which contrasts with our findings for *C. argus*, likely due to species-specific differences in life history traits and reproductive modes. Russ and Alcala (2004, 2010) estimated that it will take up to 40 years for the assemblage of large predatory reef fishes (including *C. argus*) to fully recover inside Apo Island NTMR, with low recruitment rates and high harvesting pressure in surrounding reefs possibly slowing down recovery. In contrast, the time required for full recovery of large predatory reef fishes at nearby Sumilon NTMR was estimated to be 15–20 years (Russ & Alcala, 2004, 2010). In extreme cases of overfishing, protection by NTMRs may not result in local population recovery. This was often the case in a large, heavily fished reef system in the central Philippines (Danajon Bank) that exhibited signs of system-wide population declines, yet a number of NTMRs there appeared to have slowed down the declines within their boundaries (Bayley *et al*., 2020). In that particular case, the NTMRs may still generate differentials in reproductive potential but are unlikely to sustain recruitment subsidies or reverse population declines in the reef system.

The differentials (NTMR/control ratios) in egg output that were reported here (Figures 6e and 7c) are relatively modest and comparable to other studies of tropical and temperate reef fishes. For example, the relative egg output of kelp rockfishes (*Sebastes* spp.) was estimated to be about 3 to 4.5 times greater inside than outside two NTMRs in central California that had been protected for about

10–20 years (Paddack & Estes, 2000). Across three inshore island groups on the GBR, the BFUA of a coral reef snapper (*Lutjanus carponotatus*) was found to be 2.5 times higher on average inside NTMRs after 15 years of protection (Evans *et al*., 2008). Similarly, egg production per unit area in a coral reef grouper (*Plectropomus leopardus*) was estimated to be 2.5 times higher in NTMRs in the central GBR (Carter *et al*., 2017). However, differentials in the same species were found to be only 21% higher in NTMRs in the southern GBR and 56% lower in NTMRs in the northern GBR, suggesting significant geographic variation over a large latitudinal gradient (Carter *et al*., 2017). Much higher differentials in reproductive potential have been documented in the Poor Knights Islands (New Zealand) where the relative fecundity of a temperate reef snapper (*Pagrus auratus*) was estimated to be 11–18 times higher in the NTMR, although this was probably due to immigration of large adults into the NTMR and not true population recovery (Denny *et al*., 2004). Large differentials in reproductive potential may also occur when species are subject to heavy fishing pressure outside of managed areas. Kamukuru and Mgaya (2004) showed that unlike areas within a marine park in Tanzania, sexually mature coral reef snapper (*Lutjanus fulviflamma*) were not recorded in adjacent intensely-fished areas, indicating very high differentials in reproductive potential between managed and fished sites. This situation is similar to that of *C. argus* in Apo Island during the first 7 years of NTMR protection when mature females were inferred to be absent in the fished control (Figure 5) but our analytical approach of eliminating zeros in the data before modelling differentials de-emphasized this absence.

The differentials in BFUA of *C. bleekeri* in the space-for-time analysis and *C. argus* at Apo Island were often greater than the differentials in the density of mature females, total density and total biomass (the latter only true for *C. bleekeri*), which can be attributed to the hyperallometric scaling of fecundity with body size (or age for *C. argus*; Supporting Information Figure S3) found in these species, which is common in fishes (Supporting Information Figures S1 and S6; Hixon *et al*., 2014; Barneche *et al*., 2018). However, the differentials in the BFUA of *C. argus* at Apo Island were exceeded by differentials in its total biomass during the latter half of the 29-year monitoring period due to increased contribution of secondary males to biomass in the NTMR (Figure 7). The substantial contribution of larger females to egg production and the substantial contribution of secondary males to total biomass underscore the limitations of density or biomass as proxies for egg output and highlight the importance of considering key species-specific sexual parameters when estimating the reproductive potential of protogynous reef fishes. The importance of key sexual parameters was also demonstrated by Carter *et al*. (2017), who found that the reproductive potential of *Plectropomus leopardus* was lowest on southern reefs of the GBR despite higher densities there compared to northern and central reefs. This was due to a male-biased sex ratio, lower female fecundity for a given size and lower spawning frequency of *P. leopardus* on southern reefs (Carter *et al*., 2014a,b, 2017).

The decline in the BFUA ratio of *C. argus* at Apo Island over time (Figure 7c) needs discussion as it appears to contradict the general conclusion that NTMRs can enhance reef fish reproductive potential. This decrease was likely driven by spillover of *C. argus* from the NTMR to the adjacent control, which may also have been facilitated by the gradual improvement of coral habitat over time in the control (Russ *et al*., 2021; Russ & Alcala, 1996). The decline is consistent with a general prediction made 25 years ago by Russ and Alcala (1996) that the density ratio of fish between Apo Island NTMR and the nearby control would decrease over time if spillover occurred. Data collected by Russ and Alcala (1996) during the first 11 years of NTMR protection confirmed this prediction, showing that the density ratio of large predatory reef fishes (including *C. argus*) decreased in the latter part of this relatively short period as their density increased exponentially in the control. In the present study, we documented exponential increases in the density, biomass and BFUA of mature female *C. argus* in the control over a much longer period (29 years) (Supporting Information Figure S11 and Table S10). However, the exponential trend in the BFUA of the control caused a decline in the corresponding ratio, which may have been largely driven by the hyperallometric scaling of reproductive output not only with fish size, but also with fish age (Supporting Information Figures S3b and S6c). Nonetheless, the absolute difference in the BFUA of *C. argus* between the NTMR and the control doubled over 29 years, strongly suggesting a real build-up of reproductive potential in Apo Island NTMR despite spillover.

We acknowledge that the general approach used in this study to infer patterns of reproductive potential between NTMRs and fished areas has significant limitations. A major issue is that spatial variability in environmental and anthropogenic conditions can influence life history traits and demographic patterns in coral reef fishes. Indeed, previous studies have shown that factors such as local density, habitat quality and fishing intensity can affect female maturation, sex change, reproductive modes and fecundity in protogynous reef fishes (Carter *et al*., 2014a, 2014b; Hamilton *et al*., 2007; Hawkins & Roberts, 2003; Taylor, 2014). The present study does not consider any of these factors in a manner that can provide insights to how local ecological conditions may influence the trajectory of development of reproductive potential in NTMRs or fished areas. Another issue pertains to BFUA itself as a measure of relative reproductive potential because of its rather simplistic assumption of simultaneous spawning of all mature female fish within a given area at one time. BFUA ignores any temporal (daily, monthly, interannual) or site-specific variability in the actual number of female fish that participate during spawning events and does not account for the duration of the breeding period and the frequency of spawning (both of which are likely to differ between *C. bleekeri* and *C. argus*; Supporting Information Figures S4 and S5). This issue is of concern because reef fishes can exhibit intraspecific variation in spawning behaviour (*e.g*., ranging from pair spawning to group spawning) even within the same site and certain sites may be preferred for spawning more than others (Choat, 2012; Kuwamura *et al*., 2009; Warner, 1987). At best, BFUA can serve only as an initial indicator of probable differences in reef fish reproductive potential among sites and through time, and should be cross-validated by other approaches if possible.

Increased reproductive output of targeted species within NTMRs is commonly expected to result in recruitment subsidies that could enhance fisheries (Harrison *et al*., 2012; Pelc *et al*., 2010), but for NTMRs to become effective sources of viable recruits, female fish within their boundaries must export not just a much greater number of eggs but also a greater number of high-quality eggs. Thus, another way to investigate the potential recruitment subsidy effect of NTMRs is to test the hypothesis that female fish inside NTMRs produce higher quality eggs compared to fished sites. This is a promising area for future research because egg quality in fishes has been linked to female condition, body size and age, as well as food availability and water temperature (Brooks *et al*., 1997; Carter *et al*., 2015; Donelson *et al*., 2010; Hixon *et al*., 2014; Kjørsvik *et al*., 1990; Pankhurst & Munday, 2011), which are factors that can operate at more localized scales relevant to NTMRs. Furthermore, direct sampling of newly spawned and fertilized fish eggs in the wild is feasible (Bowling, 2014; Partridge *et al*., 2017) and may be more acceptable to local stakeholders than destructive sampling of female fish inside NTMRs to measure egg output. Relating egg quality parameters such as size, lipid content, development rates and hatching success (Kjørsvik *et al*., 1990) to local demographic and environmental patterns such as fish density, size, age and sex structure, spawning behaviour and reef habitat conditions inside and outside NTMRs could generate deeper insights into the ecological processes that are most influential in determining the strength of recruitment subsidies from NTMRs.

This is one of the few studies to investigate the development of reproductive potential in protogynous coral reef fishes within NTMRs and the first to do so in the context of Philippine reef fisheries. In general, the study emphasizes the importance of long-term protection of NTMRs to generate larval subsidies and the contrasting time scales at which this effect may occur depending on the life history traits of the species. In multispecies reef fisheries typical of developing countries, the more intrinsically productive reef fish species could play a crucial role in maintaining fish yields, as well as accelerating the achievement of food security through earlier provision of substantial recruitment subsidies from NTMRs. The study also highlighted the limitations of current methods to estimate reproductive potential in reef fish species with highly complex sexual life history patterns, signalling the need for more innovative studies that address the drivers of fisheries enhancement through larval subsidies from NTMRs. Estimates of location-specific reproductive outputs of reef fishes and evaluations of the quality of eggs spawned in different localities would also provide valuable insights on the impact of NTMRs on the life history features of resident fish.

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AUTHOR CONTRIBUTIONS

Conceptualization: A.A.B. and R.A.A. Data generation: A.A.B., R.A.A., G.R.R., B.L.S. and J.R.L. Data analysis: A.A.B., R.A.A. and J.R.L. Funding acquisition: R.A.A., B.L.S. and G.R.R. Methodology: A.A.B., R.A.A., G.R.R., B.L.S. and J.R.L. Project administration: A.A.B. and R.A.A. Writing – original draft: A.A.B. and R.A.A. Writing – review and editing: A.A.B., R.A.A., G.R.R., J.R.L. and B.L.S.

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REFERENCES

Aalto, E. A., Micheli, F., Boch, C. A., Espinoza Montes, J. A., Woodson, C. B., & De Leo, G. A. (2019). Catastrophic mortality, Allee effects, and marine protected areas. *The American Naturalist*, *193*, 391–408.

Abesamis, R. A., Green, A. L., Russ, G. R., & Jadloc, C. R. L. (2014). The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. *Reviews in Fish Biology and Fisheries*, *24*, 1033–1063.

Adams, S., Mapstone, B. D., Russ, G. R., & Davies, C. R. (2000). Geographic variation in the sex ratio, sex specific size, and age structure of *Plectropomus leopardus* (Serranidae) populations between reefs open and closed to fishing on the Great Barrier Reef. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 1448–1458.

Alcala, A. C., & Russ, G. R. (2006). No-take marine reserves and reef fisheries management in The Philippines: a new people power revolution. *Ambio: A Journal of Human Environment*, *35*, 245–254.

Alonzo, S. H., & Mangel, M. (2004). The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fishery Bulletin*, *102*, 1–13.

Alonzo, S. H., & Mangel, M. (2005). Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. *Fishery Bulletin*, *103*, 229–245.

Babcock, C. R., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., … Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences*, *107*, 18256–18261.

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. S. (2018). Fish reproductive- energy output increases disproportionately with body size. *Science*, *360*, 642–645.

Bayley, D. T. I., Purvis, A., Nellas, A. C., Arias, M., & Koldewey, H. J. (2020). Measuring the long-term success of small-scale marine protected areas in a Philippine reef fishery. *Coral Reefs*, *39*, 1591–1604.

Bowling, T. (2014). Bumphead parrotfish: a family first? Scaridae. *Proceedings of the World Aquaculture Society*. World Aquaculture Society, Adelaide, Australia, 814 p.

Brooks, S., Tyler, C. R., & Sumpter, J. P. (1997). Egg quality in fish: what makes a good egg? *Reviews in Fish Biology and Fisheries*, *7*, 387–416.

Cabral, R. B., Aliño, P. M., Balingit, A. C. M., Alis, C. M., Arceo, H. O., Nañola, C. L., Jr., … Partners, M. S. N. (2014). The Philippine Marine Protected Area (MPA) database. *Philippine Science Letters*, *7*, 300–308.

Carter, A. B., Russ, G. R., Tobin, A. J., Williams, A. J., Davies, C. R., & Mapstone, B. D. (2014a). Spatial variation in the effects of size and age on reproductive dynamics of common coral trout *Plectropomus leopardus*. *Journal of Fish Biology*, *84*, 1074–1098.

Carter, A. B., Davies, C. R., Mapstone, B. D., Russ, G. R., Tobin, A. J., & Williams, A. J. (2014b). Effects of region, demography, and protection from fishing on batch fecundity of common coral trout (*Plectropomus leopardus*). *Coral Reefs*, *33*, 751–763.

Carter, A. B., Carton, A. G., McCormick, M. I., Tobin, A. J., & Williams, A. J. (2015). Maternal size, not age, influences egg quality of a wild, protogynous coral reef fish *Plectropomus leopardus*. *Marine Ecology Progress Series*, *529*, 249–263.

Carter, A. B., Davies, C. R., Emslie, M. J., Mapstone, B. D., Russ, G. R., Tobin, A. J., & Williams, A. J. (2017). Reproductive benefits of no-take marine reserves vary with region for an exploited coral reef fish. *Scientific Reports*, *7*, 1–12.

Chan, N. C. S., Connolly, S. R., & Mapstone, B. D. (2012). Effects of sex change on the implications of marine reserves for fisheries. *Ecological Applications*, *22*, 778–791.

Choat, J. H. (2012). Spawning aggregations in reef fishes; ecological and evolutionary processes. In Y. Sadovy de Mitcheson & P. Colin (Eds.), *Reef fish spawning aggregations: Biology, research and management*. Fish & Fisheries Series 35 (pp. 85–116). Dordrecht, The Netherlands: Springer.

Claydon, J. A. B., McCormick, M. I., & Jones, G. P. (2014). Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns. *Journal of Fish Biology*, *84*, 1136–1163.

Clements, K. D., German, D. P., Piché, J., Tribollet, A., & Choat, J. H. (2017). Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society*, *120*, 729–751.

Denny, C. M., Willis, T. J., & Babcock, R. C. (2004). Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Marine Ecology Progress Series*, *272*, 183–190.

Donelson, J. M., Munday, P. L., McCormick, M. I., Pankhurst, N. W., & Pankhurst, P. M. (2010). Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. *Marine Ecology Progress Series*, *401*, 233–243.

Easter, E. E., Andreani, M. S., Hamilton, S. L., Steele, M. A., Pang, S., & White, J. W. (2020). Influence of protogynous sex change on recovery of fish populations within marine protected areas. *Ecological Applications*, *30*, e02070.

Evans, R. D., Russ, G. R., & Kritzer, J. P. (2008). Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia. *Coral Reefs*, *27*, 179–189.

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*. 2nd. Ed., Singapore: Sage Publications.

Goñi, R., Hilborn, R., Díaz, D., Mallol, S., & Adlerstein, S. (2010). Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology Progress Series*, *400*, 233–243.

Halpern, B. S., Gaines, S. D., & Warner, R. R. (2004). Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications*, *14*, 1248–1256.

Hamilton, S. L., Caselle, J. E., Standish, J. D., Schroeder, D. M., Love, M. S., Rosales-Casian, J. A., & Sosa-Nishizaki, O. (2007). Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecological Applications*, *17*, 2268–2280.

Harrison, H. B., Williamson, D. H., Evans, R. D., Almany, G. R., Thorrold, S. R., Russ, G. R., … Jones, G. P. (2012). Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology*, *22*, 1023–1028.

Hawkins, J. P., & Roberts, C. M. (2003). Effects of fishing on sex-changing Caribbean parrotfishes. *Biological Conservation*, *115*, 213–226.

Heppell, S. S., Heppell, S. A., Coleman, F. C., & Koenig, C. C. (2006). Models to compare management options for a protogynous fish. *Ecological Applications*, *16*, 238–249.

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, *71*, 2171–2185.

Hunter, J. R., Lo, N. C., & Leong, R. J. (1985). Batch fecundity in multiple spawning fishes. *NOAA Technical Report NMFS*, *36*, 67–77.

Jennings, S. (2001). Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries*, *10*, 209–231.

Kamukuru, A. T., & Mgaya, Y. D. (2004). Effects of exploitation on reproductive capacity of blackspot snapper, *Lutjanus fulviflamma* (Pisces: Lutjanidae) in Mafia Island, Tanzania. *African Journal of Ecology*, *42*, 270–280.

Kerwath, S. E., Winker, H., Götz, A., & Attwood, C. G. (2013). Marine protected area improves yield without disadvantaging fishers. *Nature Communications*, *4*, 1–6.

Kjørsvik, E., Mangor-Jensen, A., & Holmefjord, I. (1990). Egg quality in fishes. *Advances in Marine Biology*, *26*, 71–113.

Kuwamura, T., Sagawa, T., & Suzuki, S. (2009). Interspecific variation in spawning time and male mating tactics of the parrotfishes on a fringing coral reef at Iriomote Island, Okinawa. *Ichthyological Research*, *56*, 354–362.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., … Warner, R. R. (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, *384*, 33–46.

Longenecker, K., & Langston, R. (2016). *The jungle histology atlas of gonad stages in coral- reef fishes*. Honolulu, HI: Bishop Museum.

Lowe, J. R., Russ, G. R., Bucol, A. A., Abesamis, A. A., & Choat, J. H. (2021). Geographic variability in the gonadal development and sexual ontogeny of *Hemigymnus*, *Cheilinus*, and *Oxycheilinus* wrasses among indo-Pacific coral reefs. *Journal of Fish Biology*, 1–16. https://doi.org/10.1111/jfb.14842.

MacNeil, M. A., Graham, N. A., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., … McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, *520*, 341–344.

Marshall, D. J., Gaines, S., Warner, R., Barneche, D. R., & Bode, M. (2019). Underestimating the benefits of marine protected areas for the replenishment of fished populations. *Frontiers in Ecology and the Environment*, *17*, 407–413.

McClanahan, T. R. (2000). Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation*, *94*, 191–198.

McClanahan, T. R., & Graham, N. A. J. (2005). Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. *Marine Ecology Progress Series*, *294*, 241–248.

McClanahan, T. R., Graham, N. A., Calnan, J. M., & MacNeil, M. A. (2007). Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications*, *17*, 1055–1067.

McClanahan, T. R., & Humphries, A. T. (2012). Differential and slow life-history responses of fishes to coral reef closures. *Marine Ecology Progress Series*, *469*, 121–131.

McClure, E. M., Hoey, A. S., Sievers, K. T., Abesamis, R. A., & Russ, G. R. (2020). Relative influence of environmental factors and fishing on coral reef fish assemblages. *Conservation Biology*, *35*, 976–990. https://doi.org/10.1111/cobi.13636.

McGovern, J. C., Wyanski, D. M., Pashuk, O., Manooch, C. S., & Sedberry, G. R. (1998). Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976–1995. *Fishery Bulletin*, *96*, 797–807.

Munday, P., White, J. W., & Warner, R. (2006). A social basis for the development of primary males in a sex-changing fish. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 2845–2851.

Nañola, C. L., Aliño, P. M., & Carpenter, K. E. (2011). Exploitation-related reef fish species richness depletion in the epicenter of marine biodiversity. *Environmental Biology of Fishes*, *90*, 405–420.

Paddack, M. J., & Estes, J. A. (2000). Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecological Applications*, *10*, 855–870.

Pankhurst, N. W., & Munday, P. L. (2011). Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research*, *62*, 1015–1026.

Partridge, G. J., Ginbey, B. M., Woolley, L. D., Fairclough, D. V., Crisafulli, B., Chaplin, J., … Jenkins, G. I. (2017). Development of techniques for the collection and culture of wild-caught fertilised snapper (*Chrysophrys auratus*) eggs for stock enhancement purposes. *Fisheries Research*, *186*, 524–530.

Pelc, R. A., Warner, R. R., Gaines, S. D., & Paris, C. B. (2010). Detecting larval export from marine reserves. *Proceedings of the National Academy of Sciences*, *107*, 18266–18271.

Petersen, C. W., Warner, R. R., Cohen, S., Hess, H. C., & Sewell, A. T. (1992). Variable pelagic fertilization success: implications for mate choice and spatial patterns of mating. *Ecology*, *73*, 391–401.

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from: https://www.R-project.org/.

Russ, G. R., & Alcala, A. C. (1996). Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series*, *132*, 1–9.

Russ, G. R., & Alcala, A. C. (2004). Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia*, *138*, 622–627.

Russ, G. R., & Alcala, A. C. (2010). Decadal-scale rebuilding of predator biomass in Philippine marine reserves. *Oecologia*, *163*, 1103–1106.

Russ, G. R., Cheal, A. J., Dolman, A. M., Emslie, M. J., Evans, R. D., Miller, I., … Williamson, D. H. (2008). Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Current Biology*, *18*, R514–R515.

Russ, G. R., Questel, S.-L. A., Rizzari, J. R., & Alcala, A. C. (2015). The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. *Marine Biology*, *162*, 2029–2045.

Russ, G. R., Rizzari, J. R., Abesamis, R. A., & Alcala, A. C. (2021). Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications*, *31*, e02224. https://doi.org/10.1002/eap.2224.

Sadovy de Mitcheson, Y., & Liu, M. (2008). Functional hermaphroditism in teleosts. *Fish and Fisheries*, *9*, 1–43.

Schemmel, E. M., Donovan, M. K., Wiggins, C., Anzivino, M., & Friedlander, A. M. (2016). Reproductive life history of the introduced peacock grouper *Cephalopholis argus* in Hawaii. *Journal of Fish Biology*, *89*, 1271–1284.

Stockwell, B., Jadloc, C. R. L., Abesamis, R. A., Alcala, A. C., & Russ, G. R. (2009). Trophic and benthic responses to no-take marine reserve protection in the Philippines. *Marine Ecology Progress Series*, *389*, 1–15.

Taylor, B. M. (2014). Drivers of protogynous sex change differ across spatial scales. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132423.

Warner, R. R. (1987). Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. *Animal Behaviour*, *35*, 1470–1478.

Warner, R. R. (1988). Sex change in fishes: hypotheses, evidence, and objections. *Environmental Biology of Fishes*, *22*, 81–90.

Warner, R. R., & Hoffman, S. G. (1980). Local population size is a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). *Evolution*, *34*, 508–518.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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