#### **ORIGINAL ARTICLE**

# Off-reef planktivorous reef fishes respond positively to decadal-scale no-take marine reserve protection and negatively to benthic habitat change

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#### Abstract

The effects of no-take marine reserve (NTMR) protection and changes in benthic habitat on fusiliers (family Caesionidae) were investigated at four small Philippine offshore islands on time scales of 10-31 years. Fusiliers are highly mobile, schooling, mediumsized planktivorous fish that generally feed "off-reef." For these reasons, and given the small size of the NTMRs (3.6-37.5 ha) in this study, it was predicted that fusilier density would be unlikely to show clear effects of NTMR protection, or to respond to changes in benthic habitat. In contrast to predictions, clear NTMR effects were observed on fusilier density at three of the four NTMRs, with durations of protection from 14 to 31 years. Furthermore, the study provided strong evidence that benthic variables, specifically cover of live hard coral and dead substratum, affect the density of fusiliers. This effect of benthic habitat on density was highlighted by several major environmental disturbances that caused shifts in the benthic habitat from live hard coral to dead substratum. For two of the three most abundant species of fusiliers individually, and for all three of them combined (Pterocaesio pisang + Caesio caerulaurea + Pterocaesio digramma/tessellata), as live hard coral cover decreased, fish density decreased. It is hypothesized that these "off-reef" daytime feeders may have such a strong association with live hard coral cover because they use this habitat as nocturnal sleeping sites. Multivariate analyses indicated that, across all sites and times sampled, cover of live hard coral and dead substratum accounted for 38% of the variation in fish assemblage structure. These results are important as there are very few reports in the published literature of strong effects of NTMR protection or changes in benthic habitat on the density and assemblage structure of fusiliers.

#### KEYWORDS

benthic habitat, Caesionidae, coral reef fishes, fusiliers, no-take marine reserves, Philippines

#### 1 | INTRODUCTION

Marine ecosystems are being degraded worldwide due to anthropogenic and environmental disturbances (Carpenter et al., 2008; Worm et al., 2006). Fishing is one of these disturbances, especially if fishing gradually shifts its targeting from high to low trophic levels, with many fisheries now targeting planktivorous pelagic fish or planktivores (Birkeland & Dayton, 2005; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Pauly et al., 2002). Planktivores are sometimes considered as "forage fish" (Breck, 1993). Forage fish are often prey for other marine animals and are primarily small to medium body-sized schooling species (Alder, Campbell, Karpouzi, Kaschner, & Pauly, 2008). On coral reefs, fisheries for planktivores are mainly small-scale artisanal fisheries, where larger volumes of reef fish landings are commonly

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generated by an increased number of fishers rather than generated by better fishing technologies (Cinner & McClanahan, 2006; Newton, Côté, Pilling, Jennings, & Dulvy, 2007; Zeller, Harper, Zylich, & Pauly, 2015). Over 1,000,000 small-scale artisanal fishermen depend on coral reefs for their livelihoods, with an estimated value of US 5 billion annually (Newton et al., 2007).

Planktivorous fishes (e.g., Clupeiformes-anchovies, herrings, sardines) constitute up to 30% of world fish catches (SOFIA, 2016) and on Indo-Pacific coral reefs they are a major component of total reef fish biomass (Hobson, 1974; Williams & Hatcher, 1983). Coral reef planktivores by definition are species that are closely associated with the reef but primarily feed on plankton, rather than reef-based sources, and can be an important food source for other larger reef fish (e.g., Frisch, Ireland, & Baker, 2014). Thus, planktivores perform an important ecological role of facilitating ecosystem connectivity by energetically coupling resource pools in adjacent habitats (i.e., between pelagic and reef communities; Frisch et al., 2014). Moreover, planktivores may be dependent on the reef for shelter but derive little or no food from it (Bellwood, 1988). Among coral reef fish, Caesionidae, known as fusiliers or caesionids, are common inhabitants of coral reefs of the Indo-West Pacific (Carpenter, 1988, 1990). They often form conspicuous schools that feed on zooplankton in both inshore and exposed outer reef habitats that are periodically exposed to strong currents (Allen & Erdmann, 2008; Friedlander, Brown, Jokiel, Smith, & Rodgers, 2003; Hamner, Jones, Carleton, Hauri, & Williams, 1988). Fusiliers are indirectly related to commercial fisheries, in that they are sometimes used as live bait in tuna pole and line fisheries (Carpenter, 1988). In both commercial and artisanal fisheries, fusiliers are caught as part of a complex multispecies assemblage (Carpenter, 1988). Due to their schooling nature they can be particularly vulnerable to fishing techniques that operate with nets, such as the Philippine muroami drive-net fishing technique (Alcala & Russ, 2002; Carpenter, 1988) that captured around 17,000 tons  $\cdot$  year<sup>-1</sup> of caesionids in the period 1985-1987 (Carpenter, 1988).

Marine ecosystem-based management is now advocated by many scientists and managers (Kellner, Litvin, Hastings, Micheli, & Mumby, 2010). No-take marine reserves (NTMRs) are marine protected areas where fishing is banned permanently (Russ, 2002) and are a popular fisheries management technique within ecosystembased management frameworks. Usually NTMRs are established with one of two broad objectives: to protect biodiversity (Gell & Roberts, 2003) and/or to manage fisheries (Gell & Roberts, 2003; Russ, 2002; Sale et al., 2005). NTMRs have been advocated widely as fisheries management tools (Halpern, Lester, & Kellner, 2010; Harmelin-Vivien et al., 2008; Lubchenco, Palumbi, Gaines, & Andelman, 2003; Russ, 2002). Research has shown that exclusion of fishing in NTMRs protects portions of adult populations (Edgar et al., 2014; Halpern, 2003; Lester et al., 2009; Molloy, McLean, & Côté, 2009) often leading to an increase in biomass, density and size of targeted species (Russ, 2002). Such increases in fish biomass of target species can then lead to the export of biomass across reserve boundaries via larval export (Harrison et al., 2012; Pelc, Warner, Gaines, & Paris, 2010) and adult emigration (Abesamis & Russ, 2005; Francini-Filhoa & Moura, 2008; Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010; Halpern et al., 2010).

Fusiliers are under-studied in the NTMR literature. Russ and Alcala (1989) and Alcala and Russ (1990) reported a 60% decline in fusilier density when a 10-year-old NTMR at Sumilon Island, Philippines, was subjected to intense fishing with explosives and drive nets for 18 months. Fusilier density recovered in the Sumilon NTMR when fishing ceased for the next 5 years (Russ & Alcala, 1998a.b). In the same study, fusilier density was reported to double during 8 years of effective NTMR protection at Apo NTMR (Russ & Alcala, 1998a,b). Fusiliers might be expected not to respond strongly in a positive way to NTMR protection due to their mobility, off-reef feeding habits and life-history characteristics (relatively short life span, high natural mortality and early reproduction) that make them resilient to fishing pressure (Abesamis, Green, Russ, & Jadloc, 2014; Carpenter, 1988). Their high mobility relative to the small size of many community-based NTMRs established in the Philippines (e.g., 5-30 ha; Weeks, Russ, Alcala, & White, 2010) would suggest high flux rates across NTMR boundaries and thus reduced probability of clear increases in density due to NTMR protection (Abesamis, Russ, & Alcala, 2006; DeMartini, 1993).

Many coral reef fish species depend on coral cover for food, shelter from predators and recruitment habitat (Jones, McCormick, Srinivasan, & Eagle, 2004; McClanahan et al., 2012). In addition, coral cover and topographic complexity are critical components of the benthic habitat that can affect the structure of fish assemblages (Carpenter, Miclat, Albaladejo, & Corpuz, 1981; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011; Pratchett et al., 2008; Syms & Jones, 2000). Environmental disturbances are often associated with events that decrease coral cover and habitat complexity, with such decreases often negatively affecting the density, species richness and assemblage structure of coral reef fishes (Carpenter et al., 1981; Emslie, Cheal, & Johns, 2014; Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015; Graham et al., 2006; Jones et al., 2004; Pratchett et al., 2008; Wilson, Graham, Pratchett, Jones, & Polunin, 2006; Wilson et al., 2008, 2010). Species that are highly dependent on live coral cover (i.e., species that require live coral for food or habitat) are especially vulnerable to coral loss and typically display major declines when live hard coral is reduced below a certain threshold (Emslie et al., 2014; Graham et al., 2006, 2015; Jones et al., 2004; Myers & Ambrose, 2009; Pratchett et al., 2008; Wilson et al., 2006, 2008, 2010).

Many studies have addressed how reef fish species that are targeted by fisheries, and are economically important or are highly dependent on coral cover, are affected by coral loss, but no such studies exist for fusiliers. Responses of reef planktivores, such as pomacentrids and anthiids, generally report an overall negative response in density and species richness as live coral cover and structural complexity is reduced (Graham et al., 2006; Wilson et al., 2006). The dependence of fusiliers on benthic cover has not been addressed before, and thus represents a critical knowledge gap. No, or weak, responses to changes in benthic cover are predicted for fusiliers due to their off-reef feeding habits and low dependence on the reef for daytime

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**FIGURE 1** Map showing the location of the study islands Apo, Sumilon, Mantigue and Selinog in the Central Philippines. Each island had a no-take marine reserve and a fished (control) site

shelter (Carpenter, 1988; Hamner et al., 1988). However, fusiliers may still respond to benthic change if they are dependent on the benthos to provide sleeping sites at night.

In the present study, we examine the relative effects of longterm (decadal-scale) NTMR protection and benthic habitat on fusilier density in four small NTMRs and at four adjacent control (fished) sites located in the Central Philippines. Long-term monitoring data (31 years) for fish and corals in NTMR and fished (control) sites where NTMR status and benthic structure have varied over time provide a unique opportunity for assessing the effects of NTMRs and of changes to benthos on fusiliers. The Central Philippines has experienced a number of environmental (e.g., typhoons and coral bleaching) and anthropogenic (e.g., destructive fishing techniques) disturbances that have reduced live coral cover on various occasions throughout the study. This renders a "natural long-term experiment" that allows us to answer two specific research questions:

- 1. Does NTMR protection affect the density of fusiliers over time?
- 2. Do changes in benthic cover caused by environmental and anthropogenic disturbances affect the density of fusiliers?

We predict that NTMR protection will result in little or no increases in fusilier density over time, due to the high mobility and "off-reef" feeding habits of fusiliers, and the relatively small size of the NTMRs (3.6–37.5 ha). We further predict that environmental disturbances that decrease live coral cover will not affect, or have little effect on, fusilier density due to the low dependence of these fish on coral reefs for food and daytime shelter.

#### 2 | MATERIAL AND METHODS

## 2.1 | Study sites, history of protection and environmental disturbances

This study was undertaken at four small, Central Philippine islands: Apo, Sumilon, Mantigue and Selinog (Figure 1) during the period 1983-2014. The islands varied in size (Table 1) and geomorphology (calcareous and granite). Community managed NTMRs were established at each island. The four NTMRs ranged in size from 3.6-37.5 ha and had relatively good compliance throughout the study period (Table 1; Alcala & Russ, 2006), with the exception of some years at Sumilon Reserve. The history of protection and disturbances differs at each island (Table 1). Apo and Sumilon sites were sampled almost annually (26 times in 31 years) (Table 1). Sampling of Mantigue and Selinog islands began in 1999 before NTMR implementation and these islands were surveyed opportunistically, four and five times, respectively, during the period 1999-2009. On each of the four islands, NTMR and paired control (fished) sites were sampled. Both fish and benthic cover were sampled at all islands. NTMR and control (fished) sites often had different benthic characteristics, with NTMRs often placed in areas of high coral cover and steep reef slopes and many control sites having to be placed in areas of lower coral cover and gradual reef slope (Table 1).

All islands surveyed were subject to intensive fishing from artisanal and subsistence fishermen using hook-and-line, traps, gill nets and spears before implementation of NTMRs (Alcala & Russ, 2006). Continuous protection from fishing was enforced in all NTMRs, with the exception of Sumilon Reserve, which had a complex history of

site	Apo Island	Sumilon Island	Mantigue Island	Selinog Island
reserve size (ha)	22.5	37.5	6	3.6
year of reserve establishment	1982, legal in 1986	1974	2000	2000
sampling years	1983-2014 (except: 1984, 1986-1987, 1989,1996, 2002)	1983-2014 (except: 1984, 1986-1987, 1989,1996, 2002)	1999, 2001, 2003, 2007	1999–2003, 2009
destructive fishing <sup>a</sup> (years)		Sumilon Reserve (1984-1986)		
environmental disturbances (years)	coral bleaching (1998) Apo Reserve typhoons (2011, 2012)	coral bleaching and crown-of- thorn starfish outbreak (1998) Sumilon Non-Reserve typhoon (2012)	coral bleaching (1998)	coral bleaching (1998)
initial live coral cover (%) ± SE				
reserve	65.6 ± 5.9	50.94 ± 5.22	28.58 ± 1.88	17.17 ± 1.47
non- reserve	25 (no SE)	26.75 ± 1.45	31.00 ± 3.02	13.00 ± 1.04

**TABLE 1**Description of Apo, Sumilon,Mantigue and Selinog Islands

<sup>a</sup>Explosive fishing and *Muroami*.

protection (Table 1). Full NTMR protection from fishing was enforced continuously from 1982 for Apo and from 2000 at Mantigue and Selinog (Table 1). Destructive fishing (using explosives and drive nets) occurred at Sumilon Reserve during 1984–1986 and then was subject to partial protection, allowing only hook-and-line fishing, during 1995–1999. Sumilon Non-Reserve received full protection from fishing in 1987–1991 and partial protection (hook-and-line fishing only) in 2009–2014.

Exposure to anthropogenic and environmental disturbances that affected the cover of live hard coral differed between NTMRs and their paired fished control sites. Anthropogenic disturbances (i.e., destructive fishing practices) affected the benthos at Sumilon Reserve significantly during 1984–1986. At Apo, destructive fishing was banned in the mid-1980s. The massive 1998 coral-bleaching event affected all islands and at Sumilon Reserve a crown-of-thorn starfish outbreak decreased the live coral cover in the same year. In addition, Sumilon Non-Reserve and Apo Reserve sites were impacted by typhoons in 2011 and 2012, decreasing live hard coral cover and structural complexity significantly (Russ, Bergseth, Rizzari, & Alcala, 2015; Russ, Questel, Rizzari, & Alcala, 2015). Uneven sampling of the four islands was unavoidable over the course of 30+ years of monitoring due to these extreme weather events precluding monitoring during certain years.

#### 2.2 | Study species

Density estimates were made for nine species of fusiliers (family Caesionidae; Table 2) at all NTMR and paired control sites in all years. Individual fish lengths (total length: TL) were not estimated and juveniles (<5 cm TL) were not counted. Fusiliers are considered reef planktivores, closely associated with the reef but feeding primarily on plankton (Bellwood, 1988). Caesionids are medium-sized perciforms found only in the tropical Indo-Pacific (Carpenter, 1988). They have different species-specific coloration on their fins and scales, with many species characterized by bright yellow stripes and patches (Carpenter, 1988). Fusiliers are synchronous schooling fishes and specialized for planktivorous feeding. Genetically, caesionids are related to the family Lutjanidae or tropical snappers. They have ascending jaws with a reduction in dentition that allows jaw protrusion for engulfing planktonic prey (Carpenter, 1988; Hobson, 1991). Considered as diurnal reef planktivores, they feed on plankton produced in and around coral reefs by eddies and upwellings (Andrews & Gentien, 1982; Hamner et al., 1988; Wolanski, Jupp, & Pickard, 1986).

**TABLE 2**List of nine species of fusiliers surveyed at Apo,Sumilon, Mantigue and Selinog sites. The three most abundantspecies are in bold

species	
Pterocaesio digramma*	Caesio caerulaurea
Pterocaesio pisang	Caesio cuning
Pterocaesio randilli	Caesio lunare
Pterocaesio tessellata <sup>*</sup>	Caesio teres
Pterocaesio tile	

\*Indicates species that were pooled for statistical analyses due to initial difficulty in identification.

Fusiliers are primarily reef inhabitants, although they often range over soft bottoms while swimming from reef to reef (Carpenter, 1988). During the day, fusiliers are found in the water column, feeding on plankton off-reef (Hamner et al., 1988). Fish abundances depend on the species and locations (Williams, Russ, & Doherty, 1986). Fusiliers were estimated to account for 14–60% of all the reef fish biomass at Apo and Sumilon islands (Alcala & Russ, 2002; Bellwood, 1988; Russ & Alcala, 1998a,b). Fusiliers are caught by drive-nets, traps, gill nets and hook-and-line (Carpenter, 1988; Russ & Alcala, 1998a,b). Caesionids are also important baitfish in many areas when reefs are in proximity to tuna fisheries. In the Philippines they are caught by artisanal and subsistence fishermen (Alcala & Russ, 2002; Russ & Alcala, 1998a,b) and constitute a common component of reef fish catch in the country.

#### 2.3 | Fish surveys

Underwater visual censuses (UVC) were undertaken on the reef slope (3-17 m) at NTMR and paired control (fished) sites at four islands in the Central Philippines (Apo, Sumilon, Mantigue and Selinog). Data were collected as part of a census of 18 reef fish families (178 species). For this study, nine species of the most common fusiliers (family Caesionidae; Table 2) were analysed. At each island, fish density and benthic cover data were collected from NTMR and fished sites simultaneously in November or December of most years. Six replicates for each site (NTMR or fished) were placed within 5-10 m of the previous locations, except for Apo Non-Reserve in 1983 where replicates were placed slightly differently from other years. Benthic data were not collected in some years (1988, 1990, 1991 and 1992) at Apo Island and Sumilon Non-Reserve. For statistical analyses, these years were excluded. Using UVC, fish density was quantified at NTMR and fished, control sites. Each of the six replicates consisted of 50  $\times$  20 m transects (1,000 m<sup>2</sup> area), with fusiliers recorded as individuals per 1,000 m<sup>2</sup>. The observer (G. R. Russ), the sites and the UVC method were kept constant throughout the whole study period (1983-2014).

From 1983 to 1998 at Sumilon and Apo, fusiliers were placed into log4 abundance categories (no. fish  $\cdot$  1,000 m<sup>-2</sup>) to quantify fish densities (Russ & Alcala, 1998a,b): Category 1 = 1 fish, Category 2 = 2-4 fish, Category 3 = 5-16 fish, Category 4 = 17-64 fish, Category 5 = 65-256 fish, Category 6 = 257-1,024 fish, Category 7 = 1,025-4,096 fish. From 1999 onwards, actual counts of fish per 1,000 m<sup>2</sup> were made. To obtain estimates of actual numbers per replicate from the log4 abundance categories for the period 1983-1998, the modal number of fish per abundance category was estimated from the actual count data collected from 1999 to 2014 (16 years). Actual count frequencies were placed into log4 abundance categories (1-7) and frequency distributions were examined. The modal value of each distribution was taken as the best estimate of density. If more than one mode was observed, then the values were averaged and rounded to the nearest unit. While using a more recent time frame to inform what approximate densities were in log4 abundance categories developed in a prior time frame may not be completely representative marine ecology

of fish population trends, we opted for this approach as opposed to the only other alternative—using log4 abundance categories throughout—as we feel abundance estimates were more reliable (see Russ, Questel, et al., 2015). The actual densities calculated from abundance categories were species specific, with the exception that counts for *Pterocaesio digramma* and *Pterocaesio tessellata* were pooled due to the uncertainty of initial identification (Table 2).

Length data were not recorded as fusiliers school in the water column, and schools generally consist of fish of a narrow size range, often close to the adult size. Further, most fusilier recruits (e.g., <10 cm TL) tend to stay near the benthos, sometimes even schooling with other fish such as damselfish of similar size. It should be noted that juvenile fish <10 cm TL were not counted in this study. Fusiliers also have very rapid initial growth in length and probably attain a size ready to join schools in the water column rapidly. For these reasons, we are confident that the major effects of marine reserve protection, and particularly benthic change, were detectable in terms of fish density.

#### 2.4 | Benthic surveys

For the period of 1983–1998, benthic habitat was surveyed using the transect point-intercept method in the same areas as fish surveys and immediately after the fish surveys. A benthic survey consisted of estimating the substratum cover at 20-cm intervals along a 50-m transect tape laid on the bottom. In Apo Reserve and Non-Reserve and Sumilon Non-Reserve in some years (1988, 1990, 1991 and 1992) benthic cover data were not collected. Eight benthic categories were recorded: (i) branching and table coral, (ii) massive and encrusting coral, (iii) soft coral (SC), (iv) rubble (R), (v) sand (S), (vi) hard dead substratum (HDS), (vii) macroalgae and (viii) other. Percent cover of benthos was estimated as the frequency of occurrence of each category on 100 points along the 50-m transect.

From the period 1999 to 2014, benthic cover was estimated within the entire  $50 \times 20$  m transect area used to census fish. Each transect was divided into ten  $10 \times 10$  m quadrats and the percent cover of each benthic category was estimated visually to the nearest 5%. An average was made across all quadrats, calculating the percent cover within each  $50 \times 20$  m transect area (Russ, Stockwell, & Alcala, 2005). This method provided a more robust benthic cover estimate over the entire 1,000 m<sup>2</sup> fish transect in comparison with the line intercept method. For statistical purposes, a number of benthic categories were combined into a hard coral category (HC; i and ii above) and total dead substrate (DS; iv, v and vi above). A structural complexity index (SCI) was estimated for each transect, on a scale of 0–4, with 0 = flat and 4 = highly complex.

#### 2.5 | Data analysis

Demonstration of an NTMR effect on fusilier density requires a significant NTMR status × time interaction plus an increasing density of fusiliers in the NTMR relative to the fished control site over time. Firstly, densities of the three most abundant species (*Pterocaesio pisang* + *Caesio caerulaurea* + *Pterocaesio digramma/tessellata*) were ILEY— marine ecology

pooled together (number of fish per 1,000 m<sup>2</sup>) and were plotted against duration of protection (in years). In addition, densities of P. pisang and C. caerulaurea were plotted individually against duration of protection in order to examine species-specific NTMR effects. Sumilon was the only island where duration of NTMR protection did not correspond to chronological time, due to its complex protection history (Table 1). Firstly, at Sumilon Non-Reserve, years when the site was closed to fishing were excluded from the graphical plots. Secondly, for both Sumilon Reserve and Non-Reserve, fish densities were only considered from 1995 to 2008, because these years represented 14 years of uninterrupted protection. Finally, typhoon and post-typhoon years (2011, 2012 and 2013) were also excluded from the graphical plots for Apo Reserve and Sumilon Non-Reserve in order to obtain more realistic long-term estimates of the NTMR effect on fusilier density over time. Standard errors could not be estimated for years prior to 1999 as modal points from log-abundance categories were used to estimate fusilier density. Standard errors are only displayed from 1999 onwards. Additionally, cover of live hard coral (HC; branching, massive and encrusting coral combined), dead benthic substrata (DS; sand, rubble and hard dead substrata combined), soft coral (SC) and a structural complexity index (SCI) were included in statistical analyses and were also plotted against chronological time. Both fish and benthic substrata categories were plotted together in order to observe variation in patterns of fusilier density in relation to changes in the benthic cover in NTMR and paired fished control sites. Trends in both fusilier density and benthic cover were fitted with polynomials to emphasize temporal relationships between fish and benthos over time.

To partition the effects of NTMR protection and benthic habitat change on fusilier density, we used generalized linear mixed models (GLMMs) with a negative binomial error distribution. Predictor variables included effects of NTMR status, time (duration of protection), and benthic variables (i.e., HC, SC, DS, SCI) on fusilier density. Separate GLMMs were performed for Apo, Sumilon and Selinog Islands for each of the three most abundant species as well as these species combined. Separate analyses were performed for each island, as opposed to an analysis with all islands combined, because of the contrasting differences in reserve history and duration of sampling at each island (see Table 1). For Selinog only P. pisang was analysed and Mantigue Island was not included in the GLMM analyses due to the small number of years surveyed (only four times in 10 years). NTMR status, time, and benthic variables were treated as fixed effects, while replicate transects were treated as a random effect. GLMMs were fitted using the Ime4 package in R (R Core Team, 2012). Model selection for GLMMs was based on minimization of the Akaike information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). The top three models based on AICc values are presented, detailing changes in AICc with respect to the top-ranked model. The relative support for one model was determined by calculating the differences between its AICc and the smallest AICc ( $\Delta$ AICc) and scaling these differences into model weights (wAICc). Second- and third-ranked models were included for variables that were highly significant, but not included in the top-ranked model.

The assemblage structure of fusiliers was examined using a nonmetric multidimensional scaling (nMDS) analysis based on Bray-Curtis dissimilarities in which data were square-root transformed to downweight abundant species. Variation in benthic characteristics was examined using nMDS based on Euclidean distances in which data were normalized and natural log-transformed to improve the spread of the data. Both analyses were conducted on mean values at each location within each year (i.e., the six replicate transects were averaged within each site within each year). nMDS analyses were performed in PRIMER v. 6 (Clarke & Gorley, 2006; Clarke & Warwick, 2001). Variability in benthic composition among sites was related to the composition of the fusilier assemblage structure using permutational distance-based linear modeling (DISTLM; Anderson, 2001; McArdle & Anderson, 2001) with 999 permutations, as implemented in PERMANOVA+ of PRIMER v. 6 (Anderson, Gorley, & Clarke, 2008). DISTLM is a multivariate regression routine where a resemblance matrix of a response



**FIGURE 2** Mean density of the three most abundant fusilier species combined (no. fish  $\cdot$  1,000 m<sup>-2</sup>) inside the no-take marine reserve (NTMR; black circles, solid lines) and at a fished control site (white circles, broken lines) versus duration of protection (years) at Sumilon Island. (a): Mean density of the three most abundant species combined versus duration of protection (years) for 1983–2014. Fished control site plot does not include years where typhoons occurred. (b): Mean density of the three most abundant species combined versus duration of protection for the period 1995–2008 (14 years of continuous protection). Polynomials are fitted to data from both reserve and fished control sites and error bars represent standard errors. Note that standard errors could not be estimated for years prior to 1999 as modal points were used to estimate fusilier density (see Material and Methods section)

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location	model	df	logLik	AICc	ΔAICc	wAICc
Аро						
Pterocaesio pisang	DS + SCI + status + time	7	-1,491.53	2,997.60	0.00	0.14
	DS + status + time	6	-1,493.28	2,999.00	1.36	0.07
	DS + HC + SCI + status + time	8	-1,491.46	2,999.60	2.02	0.05
Caesio caerulaurea	HC + status × time	7	-1,125.57	2,265.70	0.00	0.23
	HC + SCI + status × time	8	-1,125.42	2,267.50	1.86	0.09
	DS + HC + status × time	8	-1,125.51	2,267.70	2.04	0.08
Pterocaesio digramma/tessellata	status	4	-610.27	1,228.70	0.00	0.07
	HC + status	5	-609.28	1,228.90	0.12	0.07
	HC + SCI + status	6	-608.31	1,229.00	0.28	0.06
species combined	DS + SCI + status × time	8	-1,549.70	3,116.10	0.00	0.12
	HC + SC + SCI + status × time	9	-1,548.77	3,116.40	0.32	0.10
	DS + HC + SCI + status × time	9	-1,548.84	3,116.60	0.46	0.09
Sumilon						
Pterocaesio pisang	HC + status × time	7	-1,838.72	3,691.90	0.00	0.13
	HC + SC + status × time	8	-1,838.50	3,693.60	1.70	0.06
	DS + HC + status × time	8	-1,838.51	3,693.60	1.72	0.05
Caesio caerulaurea	DS + SCI + time	6	-1,439.25	2,890.90	0.00	0.09
	DS + SCI + status + time	7	-1,438.83	2,892.10	1.28	0.05
	SCI	4	-1,442.05	2,892.30	1.41	0.05
Pterocaesio digramma/tessellata	null	3	-940.73	1,887.60	0.00	0.08
	time	4	-939.78	1,887.70	0.16	0.07
	status	4	-940.23	1,888.60	1.08	0.05
species combined	HC + status × time	7	-1,894.43	3,803.30	0.00	0.19
	HC + SCI + status × time	8	-1,894.34	3,805.30	1.96	0.07
	status × time	6	-1,896.54	3,805.40	2.10	0.07
Selinog						
Pterocaesio pisang	DS + HC	5	-197.02	405.40	0.00	0.13
	DS + HC + SC	6	-196.04	406.10	0.64	0.09
	HC + SC	5	-197.63	406.60	1.20	0.07

**TABLE 3** Optimal generalized linear mixed models (GLMMs) for predicting fusilier density for the three most abundant species of fusiliers individually and all of them combined at Apo, Sumilon and Selinog Islands

Models presented are those with the three lowest values of the Akaike information criterion corrected for small samples sizes (AICc) from GLMMs that evaluated the influence of no-take marine reserve protection status (i.e., fished or no-take marine reserve), time, and percent cover of hard coral (HC), dead substrate (DS), soft coral (SC) and structural complexity index (SCI). The top-ranked model is the one with the lowest AICc. Bold text in the top model indicates the significant predictor variables at an alpha value of 0.05. Shown are degrees of freedom (*df*), model maximum log-likelihood (logLik), AICc, change in AICc with respect to the top-ranked model ( $\Delta$ AICc), and AICc weights (wAICc).

data set (i.e., fusilier assemblage structure) is regressed against a set of explanatory variables (i.e., benthic characteristics). The variables included in the final DISTLM-model were selected using the *step-wise* selection procedure (Anderson et al., 2008).

#### 3 | RESULTS

#### 3.1 | Effect of NTMR protection on fusilier density

NTMR protection affected fusilier density positively in some islands, but given the high variations in density estimates over time, reserve effects were sometimes difficult to detect. NTMR effects were observed on the density of the three most abundant species of fusiliers combined at Sumilon Island (Figure 2; Table 3). In addition, NTMR effects were observed for *Caesio caerulaurea* at Apo (Figure 3a; Table 3) and *Pterocaesio pisang* at Selinog (Figure 3b; Table 3). In all three cases, fusilier density increased over time in NTMRs relative to fished areas; however, some inter-year variability was observed. Over 14 years of protection at Sumilon Reserve, an increase in density of the three most abundant species combined within the NTMR was observed, with a slight decrease in density from 15 to 20 years of NTMR protection (Figure 2a). Density in the control site at Sumilon rose slightly



**FIGURE 3** (a): Mean density (no. fish  $\cdot$  1,000 m<sup>-2</sup>) of *Caesio caerulaurea* inside the no-take marine reserve (NTMR; black circles, solid lines) and at a fished control site (white circles, broken lines) versus duration of protection (years) at Apo Island. (b): Mean density (no. fish  $\cdot$  1,000 m<sup>-2</sup>) of *Pterocaesio pisang* inside the NTMR (black circles, solid lines) and at a fished control site (white circles, broken lines) versus duration of protection (years) at Selinog Island. Polynomials are fitted to data from both reserve and fished control sites and error bars represent standard errors. Note that standard errors could not be estimated for years prior to 1999 as modal points were used to estimate fusilier density (see Material and Methods section)

with time, but remained relatively stable (Figure 2a). From 1995 to 2008, when NTMR protection was well enforced, an NTMR effect on fusilier density was observed (Figure 2b). Although similar initial densities for both NTMR and fished sites were observed, after 14 years of uninterrupted protection, density had increased in the NTMR relative to the fished control site by a factor of 2 (Figure 2b). Significant interactions between NTMR status and time were detected at Sumilon for both time periods and were included in one of the three top-ranked models (Table 3).

At Apo, similar densities of *C. caerulaurea* were observed initially at NTMR and control sites (Figure 3a). The density of this species increased significantly during long-term NTMR protection, with a slight decrease during the coral-bleaching event years (1997–1998–15 and 16 years of protection) relative to the fished control site (Figure 3a). Density in the NTMR increased to be three to four times higher than in the fished site at Apo (Figure 3a). A significant NTMR status × time interaction was detected for *C. caerulaurea* at Apo Island (Table 3). At Selinog Reserve, density of *P. pisang* increased over 10 years in the NTMR relative to the fished control site (Figure 3b). Density in the NTMR increased to be up to three times higher than in the fished site at Selinog (Figure 3b). However, a significant NTMR status × time interaction in the GLMM top model was not observed at Selinog, possibly due to the short duration of observation or high inter-year variability (Figure 3b; Table 3).

### 3.2 | Effects of anthropogenic and environmental disturbances to the benthos on fusilier density

Changes in the benthos, namely cover of live HC, was a significant and important predictor of the density of the three most abundant species of fusiliers (Table 3). At Apo Reserve, temporal patterns of HC cover and fusilier density were very similar, with similar oscillations of coral cover and fusilier density observed during the study period (Figure 4a). From 1995 to 1998 HC cover decreased due to the coral bleaching event (~20% of HC loss) and fish density decreased threefold from 1993 to 1998 (Figure 4a). Subsequently, live HC cover recovered from ~45% to ~65% (1998-2009) following the bleaching, and fish density increased from ~500 to ~1,500 individuals  $\cdot$  1,000 m<sup>-2</sup>. Live HC cover in Apo Reserve decreased from ~60% to ~1-2% from 2009 to 2012 due to two typhoons and fish density decreased 15-fold (~1,500 to ~100 fish  $\cdot$  1,000 m  $^{-2})$  (Figure 4a). In contrast, at the Apo fished site, a significant increase (~10% to ~60% cover) in HC cover from 1999 to 2014 was accompanied by an increase in fusilier density from 1997 to 2006, but then fusilier density declined from 2007 to 2014 even though HC cover kept increasing (Figure 4b).

At Sumilon Reserve no clear relationship with cover of HC and density of the three most abundant species combined was observed (Figure 4c). As HC cover declined sharply between 1983 and 1985 due to use of destructive fishing techniques in Sumilon Reserve, fusilier density declined also, but this was likely caused primarily by direct fishing effects. As HC cover recovered from 1985 to 1994, fusilier density increased to 1991 but then declined from 1992 to 1995 (Figure 4c). For the remainder of the study, fusilier density oscillated and showed no clear relationship to HC cover (Figure 4c). In contrast, at the Sumilon fished site there was a concordance between percent cover of HC and fusilier density (Figure 4d; Table 3). In the 1983–2008 period, stable HC cover and fish densities were observed (Figure 4d). Both HC cover and fusilier density decreased between 2009 and 2014 due to the 2012 typhoon (Figure 4d).

An examination of two "case studies" in specific time periods at specific sites highlights the close relationship between changes in HC cover caused by environmental disturbances and fusilier density. Sumilon Reserve was heavily affected by destructive fishing techniques (explosives and drive nets) in 1983–1985 after 10 years of NTMR protection. Destructive fishing techniques decreased HC cover by almost half (~30% HC in 1983 to ~15% in 1985), resulting in a decrease of *Pterocaesio pisang* density of almost 65% (Figure 5a). Furthermore, after explosive fishing and *muroami* drive net activities ceased, both fish densities and HC cover increased substantially, to almost pre-disturbance levels, after a period of 6 years (1985–1991;



FIGURE 4 Temporal variations in mean density of the three most abundant species of fusiliers combined and cover of hard coral at Apo Reserve (a), Apo fished (b), Sumilon reserve (c), and Sumilon fished (d) sites from 1983 to 2014. Black circles represent mean density of the three most abundant species of fusiliers combined (no. fish • 1,000 m<sup>-2</sup>). White circles represent percent cover of live hard coral. Polynomials are fitted to fish (solid lines) and hard coral cover (dotted lines). Error bars are standard errors. Note that standard errors could not be estimated for years prior to 1999 as modal points were used to estimate fusilier density (see Material and Methods section). Under the x-axis, the white arrow indicates the 1998 coral bleaching event, the grey arrow indicates the typhoon event and the black arrow indicates destructive fishing

Figure 5a). The direct effects of fishing and reduction in HC cover on the density of P. pisang could not be partitioned adequately at Sumilon Reserve. However, at Apo Reserve, HC cover decreased sharply after the typhoons in 2012 and 2013. This was accompanied by a strong decline in P. pisang density (Figure 5b) to almost negligible levels, despite fishing still being banned in this reserve. Combined, these two case studies strongly indicate a clear effect of live HC cover on the density of P. pisang.

#### Effect of NTMR protection and benthic habitat 3.3 on fusilier assemblage structure

The benthic structure of the NTMRs at each island differed from their paired control (fished) sites (Figure 6a). Reserve sites were characterized by a higher percentage of hard coral cover and high structural complexity, whereas fished sites were characterized by low hard coral cover and structural complexity, and high cover of dead substratum (Figure 6a). An exception was Apo Non-Reserve, which had high soft coral cover from 1983 to 1998. These differences remained relatively consistent over time. The only exceptions to this occurred at Apo Reserve and Sumilon Non-Reserve (Fished) when typhoons in 2012-2013 caused dramatic increases in cover of dead substratum (Figure 6a) and at Apo Non-Reserve (Fished) as SC cover declined and was replaced by HC cover from 1999 to 2014 (Figure 4b and 6a). Fusilier assemblage structure was distinct among the eight sites, generally reflecting the distinctness of the benthos, and this remained relatively stable over time (Figure 6b). The only clear temporal changes in assemblage structure occurred at Apo Reserve and Sumilon Non-Reserve following the typhoons in 2012-2014 (Figure 6b). DISTLM identified cover of hard coral, dead substratum, soft coral, and structural complexity as the best benthic predictors of observed patterns in fusilier assemblage structure (Table 4). The model incorporating all four variables (hard coral, dead substratum, soft coral and structural complexity) performed better (based on AICc) than models containing one, two or three of the benthic variables. Although results from GLMMs indicated some significant status and time (years of protection) effects, analysis by nMDS indicated that these patterns are also driven by benthic characteristics of the sites themselves.

#### DISCUSSION 4

Duration of protection significantly affected the density of fusiliers at three of the four small NTMRs studied in the Central Philippines. Furthermore, the structure of the benthic habitat, in particular cover of live hard coral, which presumably provides suitable sleeping sites



**FIGURE 5** Temporal variations in mean density of *Pterocaesio pisang* and cover of live hard coral at Sumilon Reserve from 1983 to 1991 (a) and Apo Reserve from 2009 to 2014 (b). Black circles represent mean density of *P. pisang* (no. fish  $\cdot$  1,000 m<sup>-2</sup>). White circles represent percent cover of hard coral. Polynomials are fitted to fish (solid lines) and benthic (dotted lines) data. Error bars are standard errors. Note that standard errors could not be estimated for years prior to 1999 as modal points were used to estimate fusilier density (see Material and Methods section)

and shelter for these fish, was a major driver of fusilier density. These results demonstrate a relationship between medium-sized, schooling, off-reef feeding planktivores, and the benthos, particularly live hard coral cover. This is an important finding because of the lack of previous studies on the relationship between fusilier density and changes in benthic cover. These conclusions, that NTMR protection and live hard coral cover affect the density of fusiliers at these offshore Philippine islands, appear to be robust as they are based on 31 years of almost annual surveys of both NTMR and fished sites that have been subjected to a series of environmental and anthropogenic disturbances that provided a unique "natural experiment."

#### 4.1 | Response of fusiliers to NTMR protection

One of the expected effects inside NTMRs is the increase in density of target species over time (Russ, 2002). Thus, this should be observed inside old, well-enforced NTMRs (Edgar et al., 2014; Graham, Chabanet, et al., 2011; Graham, Nash, & Kool, 2011; Halpern, 2003; Lester et al., 2009; Molloy et al., 2009). Fishing is a major driver of density of targeted reef fish populations on coral reefs (Jennings & Polunin, 1996; Newton et al., 2007; Polunin & Roberts, 1996). Given that harvest rates (but not necessarily absolute yields) of fusiliers in Apo and Sumilon Islands are relatively moderate (Abesamis et al., 2014; Russ & Alcala, 1998a,b), these fish are mobile, "off-reef" feeders, and all NTMRs were small relative to the potential mobility of the fish, NTMR effects on fusiliers at these locations were not expected. However, "reserve effects" were observed on fusilier densities in three of the four Philippine NTMRs in this study, although some temporal variability was observed. Fusilier densities increased inside NTMRs relative to fished (control) sites over time in Sumilon, Apo and Selinog NTMRs. These findings are consistent with those of Russ and Alcala (1998a,b), who reported significant increases in fusilier density inside Apo (1983–1991) and Sumilon (1985–1991) NTMRs.

The decreases in fusilier density inside Sumilon Reserve in 1983-1985 were also reported by Russ and Alcala (1989, 1998a,b) and Alcala and Russ (1990). These studies reported that decreases in fusilier density were linked to periods of cessation of protection in Sumilon Reserve when high levels of fishing mortality occurred. This very high level of fishing pressure was caused by use of destructive fishing techniques, explosives and *muroami* drive nets, applied in a "pulse" fishing exercise (Russ & Alcala, 1989). A more recent study (Abesamis et al., 2014) concluded that caesionids at these Philippine islands have a relatively low vulnerability to fishing compared to other target species, due to their schooling, highly mobile and off-reef feeding behavior. However, fusiliers at these islands are still subject to enough fishing pressure from traps and gill nets (Carpenter, 1988; Russ & Alcala, 1998a,b) to detect recovery inside well-protected, long-term, small NTMRs.

Positive NTMR effects on similar medium-sized planktivorous reef fish have been recorded for Naso vlamingii (family Acanthuridae) at Apo NTMR (Abesamis & Russ, 2005). A significant increase in N. vlamingii density was observed inside the Apo NTMR relative to the fished control site after 20 years of protection. This suggests that NTMR effects are more likely to be detected for schooling, mobile planktivores, even in small NTMRs, when NTMRs are well protected for long periods. Finally, NTMR effects on planktivorous, schooling and medium-bodysized reef fish reported here are consistent with the global review of NTMR effects on planktivorous reef fish by Soler et al. (2015). These authors reported a meta-analysis of 79 marine protected areas worldwide, and showed that the biomass of planktivorous reef fish was, on average, around two times higher in NTMRs relative to adjacent fished areas. It should be noted that in some instances the putative effects of marine reserves (i.e., no fishing) could be confounded with loss of live coral habitat because of fishing practices that reduce habitat, such as the explosives and drive nets in Sumilon Reserve in 1984.

# 4.2 | Response of fusiliers to changes in benthic cover due to environmental and anthropogenic disturbances

Benthic habitat of coral reefs is important to many reef fish species as they rely on it for feeding, reproduction, recruitment and shelter. Responses of reef fish assemblages to benthic change have



FIGURE 6 Non-metric multidimensional scaling analysis performed on distance matrices for (a): benthic cover and (b): the density of nine species of fusiliers. Note that Pterocaesio digramma and P. tessellata are combined due to initial difficulty in identification. Fished sites are black shapes and reserve sites are grev shapes. Solid black circles represent years when typhoons hit Apo reserve and Sumilon fished sites and dotted black circles represent a shift from soft coral dominance to hard coral dominance from 1999 to 2014 at the Apo fished site. APOF = Apo fished; APOR = Apo reserve; SUMF = Sumilon fished; SUMR = Sumilon reserve; MANF = Mantigue fished; MANR = Mantigue reserve; SELF = Selinog fished; SELR = Selinog reserve

been reviewed extensively (e.g., Chong-Seng, Mannering, Pratchett, Bellwood, & Graham, 2012; Graham et al., 2006, 2015; Pratchett et al., 2008, 2011; Wilson et al., 2006, 2008, 2010). Coral cover and topographic complexity are identified as critical and distinct benthic components that shape coral reef fish assemblages (e.g., Pratchett et al., 2008, 2011), and are declining due to both local and global human activities (e.g., Carpenter et al., 2008). Studies report that reductions of up to 40% in density of reef fish highly dependent on live coral cover are common following major disturbances that reduce live coral cover substantially (Emslie et al., 2014; Graham et al., 2006, 2015; Jones et al., 2004; McClanahan et al., 2012; Pratchett et al., 2008, 2011; Wilson et al., 2006, 2008). Note however that some species of coral reef fish, such as goatfish and parrotfish, may increase in local density when benthic communities shift from hard coral to dead substratum (Russ, Bergseth, et al., 2015; Russ, Questel, et al., 2015). This present study has, somewhat uniquely, reported similar responses of reef fish species that are schooling,

mobile and feed "off-reef" to benthic disturbances that reduced hard coral cover.

Literature that relates caesionid density to changes in coral cover is non-existent, this study being the first to report such a link. Most fusiliers are dependent on coral reefs at settlement and recruitment, where they remain in restricted areas close to the substrate to avoid predation (Carpenter, 1988). In addition, fusiliers sleep at night and may hide in the reef, often in crevices and under coral heads (Carpenter, 1988). These links between fusiliers and benthic cover may partly explain the consistent correlation of fusilier density with coral cover and high structural complexity observed in this study (see also Graham et al., 2006; Gratwicke & Speight, 2005; Willis & Anderson, 2003).

Fusiliers form the dominant component by weight of fish catch in benthic fish traps at Sumilon Island (Alcala & Russ, 1990). Fish surveys were only conducted during daylight hours due to logistical difficulties and safety guidelines. However, if one uses night-time and day-time probabilities of entering benthic fish traps (bamboo traps, Y—marine ecology

**TABLE 4** Summary of results from distance-based linear models based on Akaike information criterion corrected for small sample sizes (AICc)

model	AICc	R <sup>2</sup>	pseudo-F	p-value
HC, DS, SC, SCI	696.86	.31	5.25	.001
DS, SC, SCI	700.23	.27	2.03	.09
SC, SCI	700.32	.26	15.97	.001
SCI	713.59	.14	16.69	.001

HC = cover of hard coral; DS = cover of dead substrate; SC = cover of soft coral; SCI = structural complexity index.

 $\sim 2 \times 1.5 \times 0.6$  m, mesh size  $\sim 1$  cm) as a proxy for when fusiliers are more likely near the benthos, one can infer a higher probability of being near the benthos at night. In a smaller related study, the observer (G. R. Russ) visually monitored entry and exit of Pterocaesio pisang for 47 traps at close to dawn and dusk each day over the period 19 January 1984 to 25 January 1984 on the fished side of Sumilon Island. The number of P. pisang in the same 47 traps was counted visually on 1 February 1984, after a further 6 days of fishing, without dawn and dusk estimates of numbers made. The ratio of entry to exit of fish traps by P. pisang at night at Sumilon Island was 2.36. The ratio of entry to exit of traps during the day was 0.91. This suggests that this species of fusilier was 2.6 times more likely to enter a trap at night than during the day. After a further 6 days of fishing by these traps, six of 47 traps contained 50 or more P. pisang (range 50-95). This suggests that this species not only tends to enter traps more often at night, but that fish may enter traps as schools of at least 50-100 fish at one time. These observations, whilst circumstantial, are consistent with the suggestion that fusiliers seek sleeping sites in the benthos at night, and may seek such shelter as schools, rather than as individual fish.

#### 5 | CONCLUSIONS

No-take marine reserve protection resulted in increased density of fusiliers on small, offshore Philippine islands over decadal time scales. Such results are somewhat surprising, given that these fish are highly mobile relative to the size of the NTMRs, feed "off-reef" and are subject to moderate harvest levels at these islands. Cover of live hard coral was also a strong driver of density of fusilier species in this study. Environmental disturbances that occurred inside and outside NTMRs, and the longterm nature of the study (31 years), made the relationship between fusiliers and benthos clear. The study is the first to provide evidence of the relationship between live hard coral cover and fusilier density.

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