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REPORT

Hyperstability masks declines in bumphead parrotfish (*Bolbometopon muricatum*) populations

Richard J. Hamilton[1,2] · **Glenn R. Almany**[2,3] · **Don Stevens**[4] · **Michael Bode**[2,5] ·
John Pita[6] · **Nate A. Peterson**[1] · **J. Howard Choat**[7]

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Abstract *Bolbometopon muricatum*, the largest species of parrotfish, is a functionally important species that is characterised by the formation of aggregations for foraging, reproductive, and sleeping behaviours. Aggregations are restricted to shallow reef habitats, the locations of which are often known to local fishers. *Bolbometopon muricatum* fisheries are therefore vulnerable to overfishing and are likely to exhibit hyperstability, the maintenance of high catch per unit effort (CPUE) while population abundance declines. In this study, we provide a clear demonstration of hyperstable dynamics in a commercial *B. muricatum* fishery in Isabel Province, Solomon Islands. Initially, we used participatory mapping to demarcate the Kia fishing grounds into nine zones that had experienced different historic levels of fishing pressure. We then conducted comprehensive underwater visual census (UVC) and CPUE surveys across these zones over a 21-month period in 2012–2013. The individual sites for replicate UVC surveys were selected using a generalised random tessellation stratified variable probability design, while CPUE surveys involved trained provincial fisheries officers and local spearfishers. A comparison of fishery-independent abundance data and fishery-dependent CPUE data indicate extreme hyperstability, with CPUE maintained as *B. muricatum* abundance declines towards zero. Hyperstability may explain the sudden collapses of many *B. muricatum* spear fisheries across the Pacific and highlights the limitations of using data-poor fisheries assessment methods to evaluate the status of commercially valuable coral reef fishes that form predicable aggregations.

Keywords Aggregations · *Bolbometopon muricatum* · Coral reef fisheries · Data-poor assessments · Hyperstability · Collapse

Introduction

The abundance of a target species is a fundamental question in fisheries science, central to sustainable management, and difficult to measure cost-effectively. Abundance is often estimated by fishery-dependent proxies such as catch per unit effort (CPUE) data, which are assumed to have a constant proportional relationship to true abundance (Walters and Martell 2004). However, when the relationship between CPUE and abundance is nonlinear, CPUE will not accurately reflect abundance (Harley et al. 2001). One example of this is hyperstability (Hilborn and Walters 1992), where CPUE is maintained as abundance declines,

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✉ Richard J. Hamilton
rhamilton@tnc.org

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

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

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

[4] Stevens Environmental Statistics, 6200 W. Starr Road, Wasilla, AK 99654, USA

[5] ARC Centre of Excellence for Environmental Decisions, School of BioSciences, University of Melbourne, Parkville, VIC 3010, Australia

[6] The Nature Conservancy, Isabel Environmental Office, Buala, Isabel Province, Solomon Islands

[7] College of Marine and Environmental Studies, James Cook University, Townsville, QLD 4811, Australia

creating an illusion that the present catch rates are sustainable. This is a particular problem with species that form predicable aggregations (Erisman et al. 2011), and aggregation fisheries face the risk of sudden collapse (Sadovy and Domeier 2005; Sadovy de Mitcheson and Erisman 2012). Hyperstability is thought to be one of the reasons behind the collapse of the Atlantic cod fishery, with Atlantic cod increasing their shoaling behaviour as their population numbers declined (Hutchings 1996).

To demonstrate hyperstability, a comparison of CPUE and fishery-independent estimates of abundance is required. Most examples of hyperstability come from temperate fisheries (Harley et al. 2001; Clark 2001; Erisman et al. 2011) where long-term CPUE and fishery-independent data of stock abundance are available. The difficulties of obtaining abundance and CPUE data for many small multispecies tropical fisheries has resulted in a proliferation of data-poor assessment methods that rely on contemporary catch data and limited demographic information (e.g. Froese 2004; Andrew et al. 2007; Prince et al. 2011, 2015; Martell and Froese 2013; Hilborn and Ovando 2014). Under these circumstances, undetected hyperstability may be a problem (Sadovy de Mitcheson and Erisman 2012; Russell et al. 2012), as coral reef fishes form highly predictable aggregations for spawning, feeding, and sleeping (Domeier and Colin 1997; Choat 2012), and tropical fishers have proved to be highly adept in locating and exploiting such aggregations (Hamilton et al. 2012a). Moreover, the ways in which fish and fishers are spatially distributed can have profound impacts on catches and the relationship between CPUE and abundance (Sadovy and Domeier 2005; Pauly et al. 2013).

The likelihood of undetected hyperstability appears to be high in tropical fisheries. Over 200 species of coral reef fishes are known to form predicable aggregations, and the majority of these aggregating species belong to commercially valuable families such as Epinephelidae (groupers), Lutjanidae (snappers), Acanthuridae (surgeonfishes), and Siganidae (rabbitfishes) (Russell et al. 2014). Here, we focus on an iconic coral reef fish, the bumphead parrotfish (*Bolbometopon muricatum*), a species which consistently aggregates for foraging, reproduction, and sleeping (Hamilton and Choat 2012). It is listed as vulnerable on the IUCN Red list and is the largest of the parrotfish, reaching over 50 kg in weight and achieving a maximum age of 40 yr (Hamilton and Choat 2012; Andrews et al. 2015). *Bolbometopon muricatum* plays a key ecological role as a habitat engineer that shapes the functional structure of coral reefs, with an adult capable of removing an average of 5.7 t of carbonate material from reef surfaces per year, of which up to 50% may be in the form of living coral (Bellwood et al. 2003).

Schools of *B. muricatum* often sleep at predicable locations in shallow water, making this species highly vulnerable to capture by nighttime snorkel or SCUBA spearfishers using underwater flashlights to search for sleeping fish (Hamilton and Choat 2012; Lindfield et al. 2014). Where commercial spear fisheries for *B. muricatum* have developed, initial catches are often very high, frequently followed by dramatic declines a decade or so later (Dulvy and Polunin 2004; Hamilton 2005; Kobayashi et al. 2011).

This study examines a night spearfishery for this species over a period of accelerating commercialisation in the Kia District of Isabel Province, Solomon Islands. In the Kia District, spearfishers routinely target nocturnal aggregations of *B. muricatum*, which led us to hypothesise that (1) the Kia *B. muricatum* fishery would display hyperstability, and (2) when assessing aggregation fisheries managers should not rely on data-poor fishery assessment methods, as hyperstability will mask declines in abundance until a point where the fishery collapses. To test for hyperstability, we compared CPUE data with fishery-independent estimates of abundance across nine zones in the Kia District that had experienced different historic levels of spearfishing pressure.

Materials and methods

Study location and environment

The study was conducted in the Kia District at the western end of Isabel Province, Solomon Islands, extending from 7°19′ to 7°39′S over a linear distance of 82 km. The environment is characterised by complex reefs with mangroves and coastal forests. The reef was partitioned into five major habitat types: back reef, fore reef, fringing reef, patch reef, and subtidal reef flats. Habitat types were based on geomorphological maps from the Millennium Coral Reef Mapping Project (Andréfouët et al. 2006) (Fig. 1).

Development of a commercial *B. muricatum* fishery in Kia

Archaeological records from western Isabel (R. Walter personal communication) and oral traditions indicate that *B. muricatum* has been a component of the Kia subsistence fisheries for centuries. Historically, *B. muricatum* was not a particularly sought-after fish, considered rather bland in taste and best eaten alongside more desirable species such as surgeonfishes (Chief Leslie Mikey personal communication). *Bolbometopon muricatum* stocks remained lightly exploited in the Kia District until 2000, being only intermittently targeted by free-diving night spearfishers with underwater flashlights in the 1980s and 1990s when large volumes of fish were required for feasts (Hamilton 2003). The commercialisation of night spearfishing for *B.*

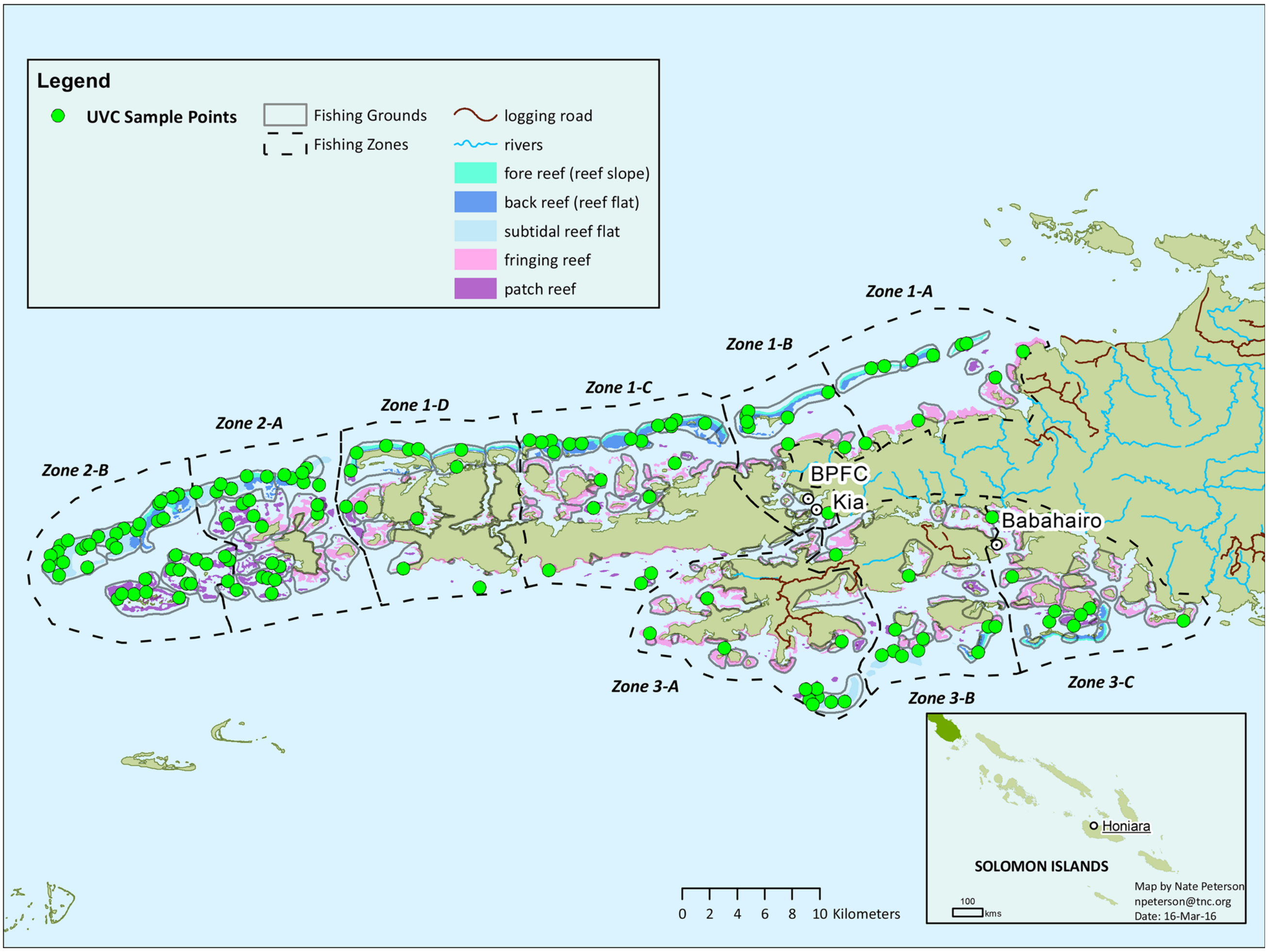

Fig. 1 Locations of the nine subzones, individual fishing grounds, and the distribution of reef habitat types ($N = 5$) within the study area. Features include the locations of the Bahana Provincial Fisheries Centre (BPFC) and Babahairo, the location of the largest community (Kia), and logging roads and rivers. Zone 1 has experienced heavy historical fishing pressure, whereas Zones 2 and 3 have historically been lightly fished. The 150 UVC survey sites selected using a generalised random tessellation stratified (GRTS) variable probability design are also shown (*green dots*)

muricatum commenced in 2001 when the European Union-funded Bahana Provincial Fisheries Centre (BPFC) (Fig. 1) began purchasing reef fish species that had been speared, including *B. muricatum*, for domestic export to the capital, Honiara. Prior to this, the BPFC had a policy of not purchasing fish that were speared (H. Kokoe personal communication). In early 2012, a new, private fisheries centre and storage facility in the nearby community of Babahairo also began to purchase *B. muricatum* (Fig. 1).

In 2001, it was a requirement for provincial fisheries officers at BPFC to keep records of the weights of all fish purchased using standardised data sheets. The total weight of each purchase was recorded, with species-level resolution recorded for some species such as *B. muricatum*. Landings of *B. muricatum* from this period equate to total weight without head and guts. In January 2003, we made copies of all fish purchases ($N = 492$) recorded by BPFC between June 2001 and December 2002, of which 141 purchases included *B. muricatum* (Hamilton 2003).

Definition of fishing zones

To demarcate the entire study area into *B. muricatum* fishing zones that differed in historical fishing intensity, 22 expert *B. muricatum* spearfishers from the Kia ($n = 15$) and Babahairo ($n = 7$) communities were consulted in February 2012 (Fig. 1). Locally recognised experts were selected based on participant observation and snowballing interview techniques (Neis et al. 1999; Hamilton et al. 2012a). Spearfishers used their local knowledge to mark on the base map over 100 fishing grounds where they caught *B. muricatum*. Reefs were named in the local Zabana language, and the map was digitised and provided to fishermen in April 2012. All spearfishers agreed that reefs in

Zone 1 (Fig. 1) had experienced historically high levels of fishing pressure due to the close proximity of outer reefs to processing facilities. From 2000 to 2011, the only fish storage facility in the Kia District was the BPFC, located in the middle of Zone 1. The reefs that made up the westernmost extent of the Kia fishing grounds (Zone 2) were the most distant from the BPFC and have been lightly exploited. Historically, Zone 3 reefs were also lightly exploited, due to the greater distances from outer reefs to the BPFC, and the fact that many spearfishers from the large community of Kia do not have customary rights to fish in Zone 3. An important driver of the distribution of fishing effort was fuel costs.

To test for hyperstability, we aggregated all locally identified fishing grounds into nine spatially distinct subzones: Zones 1-A, 1-B, 1-C, 1-D, Zones 2-A, 2-B, and Zones 3-A, 3-B and 3-C (Fig. 1). The subzones were defined based on local knowledge of historical fishing pressure, biogeography, and the home range of the species. We used geomorphological breaks in the outer reef to subdivide the three primary zones (Zones 1–3) into multiple demographically separate subzones, ensuring that each subzone included a minimum of ten linear kilometres of outer reef, greater than the estimated home range of adult *B. muricatum* (Hamilton 2005; Green et al. 2015).

Fishery-dependent data collection

In February and April 2012, fisheries centre staff at both BPFC and Babahairo were trained in methods for collecting demographic data from *B. muricatum* catches. Between February 2012 and October 2013, the following information was collected for every *B. muricatum* that passed through the two fisheries centres: name of lead fisher; number of fishermen on a boat; type of boat used; date and location of capture; total length (mm); weight (g); and sex (unknown, female or male). All fish were gutted at fisheries centres, and identification of sex was based on macroscopic examination of gonads, which has been shown to be accurate for *B. muricatum* (Hamilton et al. 2008).

Fisheries centre catch records were periodically double-checked and transcribed by researchers on eight separate occasions between February 2012 and October 2013.

To investigate whether adult catches differed by subzone, we compared the mean catch made by large fishing parties (3–5 individuals operating out of a single boat with 40 hp engine) in all subzones over the study period. Catches made by small fishing parties (1–2 individuals operating from small fibreglass boats with outboard engines 15 hp or less, or any fishing trip conducted from a paddle canoe) were excluded from analysis, since these fishing trips predominantly took place in lagoonal environments in close proximity to the Kia and Babahairo communities, and juvenile *B. muricatum* dominated these catches. The maximum dive time of each fishing trip was considered to be 4 h, based on the lifespan of the batteries used in the underwater torches at this location (Hamilton et al. 2012b). Potential differences in CPUE in each subzone were investigated using Kruskal–Wallis one-way analysis of variance since data were nonparametric. Significant differences identified by this procedure were further explored using Dunn's pairwise multiple comparison procedures in SigmaStat (Systat Software, San Jose, California, USA).

Fishery-independent estimates of adult *B. muricatum* stock abundance

We estimated the current abundance of adult *B. muricatum* for the five reef habitats and nine fishing subzones using a systematic underwater visual census (UVC) programme. Total reef area per subzone was calculated from geomorphological maps of each reef habitat which are based on the Millennium Coral Reef Mapping Project (Andréfouët et al. 2006) (Fig. 1). Individual sites for replicate UVC surveys were selected using a generalised random tessellation stratified (GRTS) variable probability design (Stevens and Olsen 2004). When applied to a spatial population, the GRTS sample selection technique will generally result in more precise estimates than a straightforward random sample, because GRTS controls for the spatial distribution of the sample sites.

The UVC team, comprised of 12 SCUBA divers working from three boats in teams of four, conducted the survey on 14–28 October 2012. A total of 146 UVC surveys were completed across five reef strata (fringing reef, patch reef, back reef, fore reef, and subtidal reef flats) (Fig. 1). UVC teams navigated to sites preselected by the GRTS design using handheld GPS units. Divers, working in teams of two, began their survey at the predefined point and swam with the prevailing current for 20 min. The mean distance covered in a timed swim was 439 m (±115 m SD), and the depths of survey ranged from 2 to 12 m. All shallow surveys were conducted on fringing reefs. One diver recorded the size of each *B. muricatum* observed within a 20-m-wide band, 10 m either side of the diver. The exception was when visibility fell below 10 m as was sometimes the case on lagoonal fringing reefs. The second diver pulled along a floatation device with a GPS unit in a waterproof case set to record a location point every 30 s. The fish recorder's watch was synchronised to the GPS clock and the recorder noted the start and end time of each 20-min survey. GPS tracks of each UVC survey were uploaded into Garmin HomePort enabling calculation of the precise length, and thus area surveyed, of each 20-min UVC survey. The area surveyed differed among surveys due to differences in current speeds. We used biomass (kg) as the unit of abundance for *B. muricatum*, and present UVC data as the mean abundance of *B. muricatum* per square metre of available reef in each subzone, and the total abundance of *B. muricatum* in each subzone.

To estimate current abundance of adults among reef habitats and fishing subzones from UVC survey data, we defined any fish 650 mm total length (TL) or greater as an adult, since this is the size at which 100% of adults reach sexual maturity (Hamilton and Choat 2012). Biomass of each *B. muricatum* was calculated using the allometric weight (W)–length (L) conversion formula $W = aL^b$. The two constants, a and b, were obtained by fitting a power function to a scatter plot of 1976 known length–weight data points for *B. muricatum* captured from the Kia fishing grounds and were $a = 0.0000014272$ and $b = 3.3823$. The power function had an adjusted R^2 of 98.7%. For each UVC survey, we used total area surveyed to calculate adult abundance as kg ha^{-1}.

Total abundance of the entire Kia fishing grounds is the integral of biomass density over the extent of the Kia fishing grounds. If $B(s)$ represents biomass density (g m^{-2}) at point s in the Kia fishing grounds domain K, then total biomass is calculated as $B_{\text{total}} = \int_K B(s)\mathrm{d}s$. We estimated total abundance of the entire Kia fishing grounds by applying the continuous version of the Horvitz–Thompson (HT) theorem (Horvitz and Thompson 1952; Cordy 1993) to the calculated adult *B. muricatum* biomass. The HT estimate of total biomass is given by $\hat{B}_{\text{total}} = \sum_{i=1}^{143} \frac{b(s_i)}{\pi(s_i)}$, where $b(s_i)$ is the calculated biomass density at site i (biomass at the site at divided by the area of the ith transect), and $\pi(s_i)$ is the inclusion probability of that site. The inclusion probability was determined by the sampling design and represents the expected number of sample points per square metre. For this survey, UVC sites on fore reefs, patch reefs and subtidal reef flats were selected with higher inclusion probability (5) than back reef (3) and fringing reef (1), because pilot surveys had indicated that these habitats support the highest biomass of adult *B. muricatum.* The inclusion probability was constant within each reef type.

Testing for hyperstability

We assessed the fishery for hyperstability by analysing the relationship between independently estimated stock abundance and CPUE made by fishing parties in each subzone. In all of the analyses that follow we treat the data from each subzone as independent (although we perform robustness tests on this assumption) because the fishing subzones are larger than the estimated adult home ranges of this species. As a consequence, the dynamics of their adult populations and CPUE will operate independently. The standard statistical signature of hyperstability is a nonlinear concave relationship between the abundance (N_i) and CPUE (U_i):

$$U_i = qN_i^{\beta} \tag{1}$$

where q is a scaling parameter, i identifies the subzone, and $\beta < 1$ indicates hyperstability.

We fitted the parameters (although we are only interested in β) by minimising the residual sum of squares, and estimated confidence intervals by repeatedly fitting Eq. 1 to bootstraps of the data, resampled with replacement at the subzone scale. We repeated the analyses using the estimated total abundance in each subzone, and also the mean density. The former regressor is appropriate if fishers are easily able to find any aggregations in any subzone; the latter is more appropriate if search times are longer in larger zones.

To assess whether our conclusion of hyperstability was sensitive to our definition of subzone, we preformed two additional tests. First, we reran the analysis with abundance and CPUE data for Zone 3-A removed, since this subzone had much greater *B. muricatum* abundance than all other subzones, and may have driven the outcomes of our preliminary analysis. Second, we performed a jackknife robustness test, where we repeated the test for hyperstability on multiple datasets, merging the data of two randomly chosen adjacent fishing subzones. This test retains the demographic independence of the sampling units, while investigating whether a different choice of subzone moved our conclusion away from hyperstability.

In aggregative fisheries, CPUE remains high at low abundance because individuals congregate in high densities in predictable locations and/or times. Such aggregations are likely to merge as populations decline, remaining large but less common. The result will likely be that, as abundance decreases, CPUE will not change much on average (i.e., classical hyperstability), but it will become more variable. Successful fishing expeditions will still encounter large (perhaps even larger) aggregations and high CPUE, but at particularly low abundances some expeditions will fail to find any aggregations. To examine this assumption, we calculated the variance of the CPUE within each of the subzones and then fit a linear regression to the data to assess whether the relationship showed any trend.

Results

Catch data

2001–2002

Between June 2001 and December 2002, the BPFC purchased 34,017 kg of fish (Fig. 2). The BPFC began to

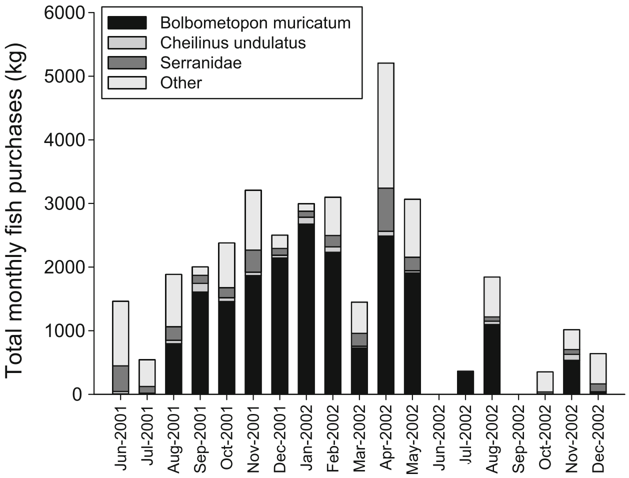

Fig. 2 Total monthly purchases made by the BPFC between June 2001 and December 2002. Smaller landings from June 2002 onwards reflect low fishing effort which was a result of irregular shipping services between Kia and Honiara during this period

purchase speared reef fish from August 2001, with *B. muricatum* making up the bulk of total monthly catches. A total of 20,365 kg of gutted and beheaded *B. muricatum* were purchased between August 2001 and December 2002, ranging 1–584 kg per landing. During this period, the BPFC produced and sold ice, and some spearfishers would travel with ice and coolers to uninhabited islands in the Kia fishing grounds (Fig. 1) and camp and fish for several nights (J. Pita personal observation). Since we did not know which purchases in the 2001–2002 period represented catches from single or multiple nights, we were unable to calculate nightly CPUE rates from these data.

2012–2013

Over 21 months, 2606 individual *B. muricatum* that were captured from within the Kia fishing grounds (Fig. 1.) were purchased by the BPFC and the private fisheries centre at Babahairo. The total catch (whole fish) weighed 31,920 kg. Adult *B. muricatum* ($\geq$650 mm TL) made up 82% of the catch numerically, and 96% of biomass. This represented 293 fishing trips. Large fishing parties made 165 fishing trips, and 128 fishing trips were made by small fishing parties. Small fishing parties tended to focus on fringing reefs close to the Kia and Babahairo communities, whereas large fishing parties fished over the entire Kia fishing grounds and rarely fished on lagoonal fringing reefs that are dominated by juvenile *B. muricatum*. All catches were made in a single night, as the fishery centres did not produce ice during this period. We were able to precisely map the total weight of all adult *B. muricatum* that were captured on different fishing grounds (Fig. 3). Most adult fish were captured from outer reef habitats including fore reef slopes in Zones 1 and 3, and patch reef and subtidal reef flat habitats in Zone 2. This spatial catch distribution confirms that adult *B. muricatum* were most associated with exposed outer reef habitats (Fig. 3). Large fishing parties obtained high mean CPUE of *B. muricatum* in all fishing subzones (Table 1). A Mann–Whitney rank sum test showed that the mean CPUE achieved by large fishing parties was significantly different among subzones ($P < 0.001$); post hoc tests showed that Zones 2-A and 2-B had significantly greater mean CPUE than Zone 1-B.

Fishery-independent abundance estimates—UVC survey results

A total of 146 UVC belt transects were completed throughout the study area covering the nine fishing subzones and five reef habitat types (Fig. 1). Four sites selected for UVC by the GRTS sampling protocol were not surveyed because of poor visibility. Of the 365 individual *B. muricatum* recorded from the UVC surveys, 88% ($N = 321$) were adults, and individuals <500 mm TL were only recorded on fringing reefs located within lagoonal habitats.

Estimates of mean and total adult abundance in each subzone are shown in Table 2. Notable observations from the UVC surveys (Fig. 4) include: (1) the virtual absence of *B. muricatum* adults from the extensive fore reef (reef slope) habitats in Zones 1-C and 1-D, and (2) the contrastingly large numbers of adults observed in Zone 2 and Zones 3-A and 3-B. The current spatial distribution of adult abundance among the fishing zones appears to reflect historical differences in fishing pressure (Table 2), with consistently high fishing pressure over the last decade only on Zone 1 reefs, those in close proximity to the BPFC, the only centre operational throughout the entire study period (2001–2013).

Hyperstability

A comparison of the estimates of relative abundance and relative CPUE clearly indicates a hyperstable fishery (Fig. 5). The CPUE changed very little as abundance declined towards zero, and the parameter β is consequently much lower than one. The use of either total abundance per subzone [$\beta = 0.014$, 95% confidence interval (CI): (0, 0.3)] or mean abundance m^{-2} of available reef area per subzone [$\beta = 0.013$, 95% CI (0, 0.25)] as the regressor did not alter the conclusion of hyperstability. The variance in CPUE data was significantly higher in subzones that had low abundances [Fig. 6; linear trend of variance in per tonne fish: $b = -4.11$, 95% CI (-6.55, 1.28)], supporting the conclusion of hyperstability.

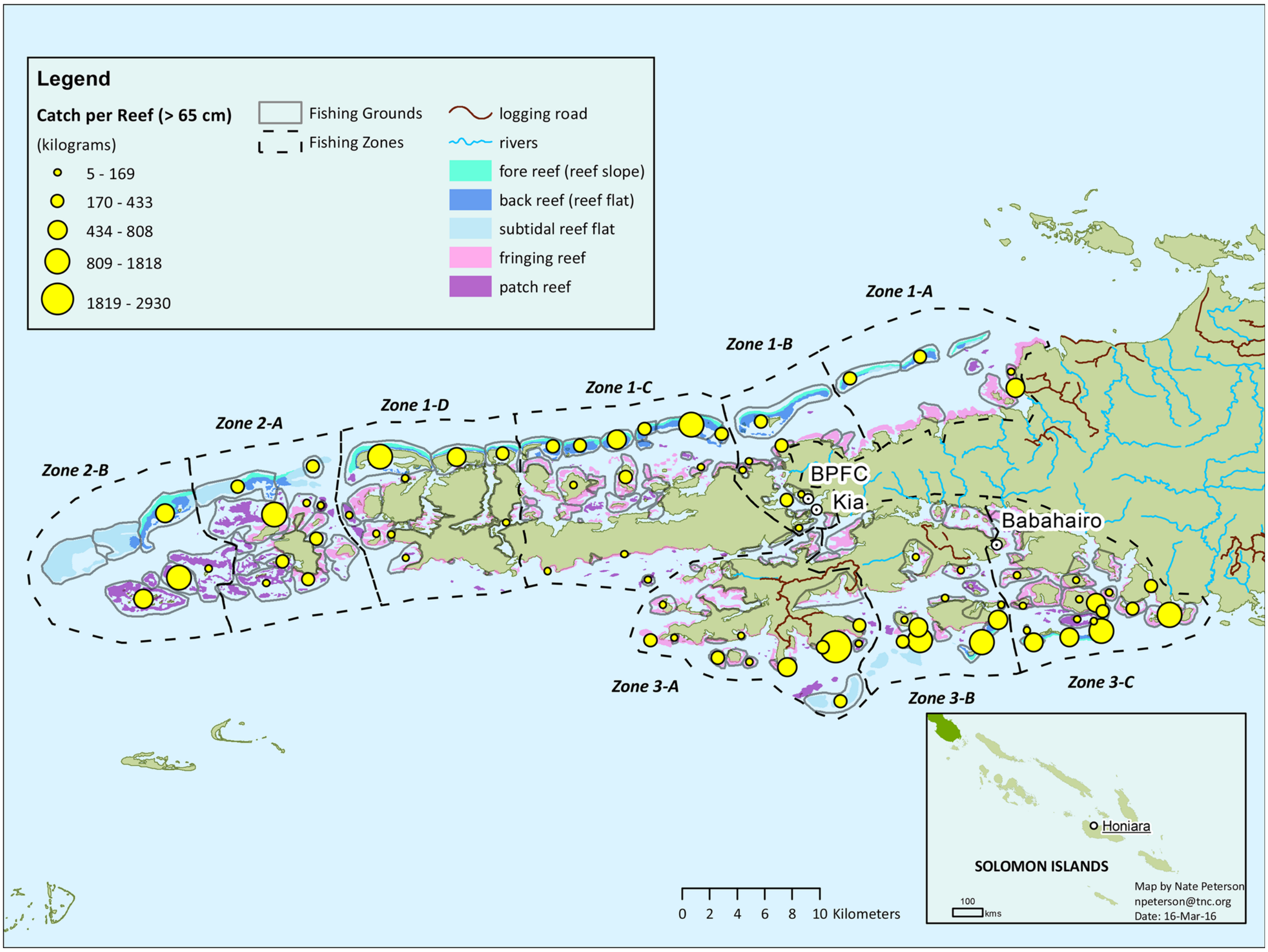

Fig. 3 Total weight (kg) of adult (≥650 mm TL) *Bolbometopon muricatum* captured from each fishing ground during the 293 fishing trips recorded in 2012–2013

Table 1 Mean catch per unit effort of a large fishing party in a single night in each of the zones

Zone	Number of fishing trips	Mean catch (kg)	Standard deviation (kg)
1-A	7	156	189
1-B	10	72	69
1-C	28	127	145
1-D	16	189	137
2-A	14	211	110
2-B	11	244	135
3-A	38	101	63
3-B	16	92	64
3-C	25	156	110

This conclusion does not depend on our definition of fishing subzones. Removing the subzone with the highest *B. muricatum* abundance from the analysis (Zone 3-A) did not influence our conclusion of hyperstability (Fig. 7), and all of the jackknife-merged datasets also exhibited hyperstability, at approximately the same level as the full dataset ($0.007 > \beta > 0.03$).

Discussion

The primary focus of this study was to assess whether fishery-dependent data could be used to determine the status of a commercially targeted coral reef species, in which hyperstability was a potential issue. We were particularly interested in evaluating this in the context of a

Table 2 Mean and total estimated adult ($\geq$650 mm TL) *Bolbometopon muricatum* abundance (kg) in each of the subzones from underwater visual censuses conducted in October 2012

Zone	Historical fishing pressure	Reef area (km^2)	Mean abundance (kg/m^2) (SE)	Total abundance (kg) (SE)
Zone 1-A	High	6.95	0.0033 (0.0024)	22,794 (16,569)
Zone 1-B	High	8.92	0.0021 (0.0010)	18,467 (8784)
Zone 1-C	High	12.03	0.0001 (0.0001)	1266 (902)
Zone 1-D	High	9.12	0.0002 (0.0002)	1729 (1449)
Zone 2-A	Low	11.82	0.0041 (0.0012)	47,913 (14,450)
Zone 2-B	Low	12.23	0.0042 (0.0014)	51,697 (16,700)
Zone 3-A	Low	8.61	0.0172 (0.0057)	148,261 (48,807)
Zone 3-B	Low	8.61	0.0047 (0.0027)	40,086 (23,191)
Zone 3-C	Low	9.02	0.0009 (0.0006)	7795 (5488)
Total		87.31	0.0039 (0.0007)	340,008 (61,750)

Qualitative historical (2001–2002) fishing pressure and total area of reef (fore reef, back reef, subtidal reef flat, fringing reef and patch reef) is shown for each fishing subzone

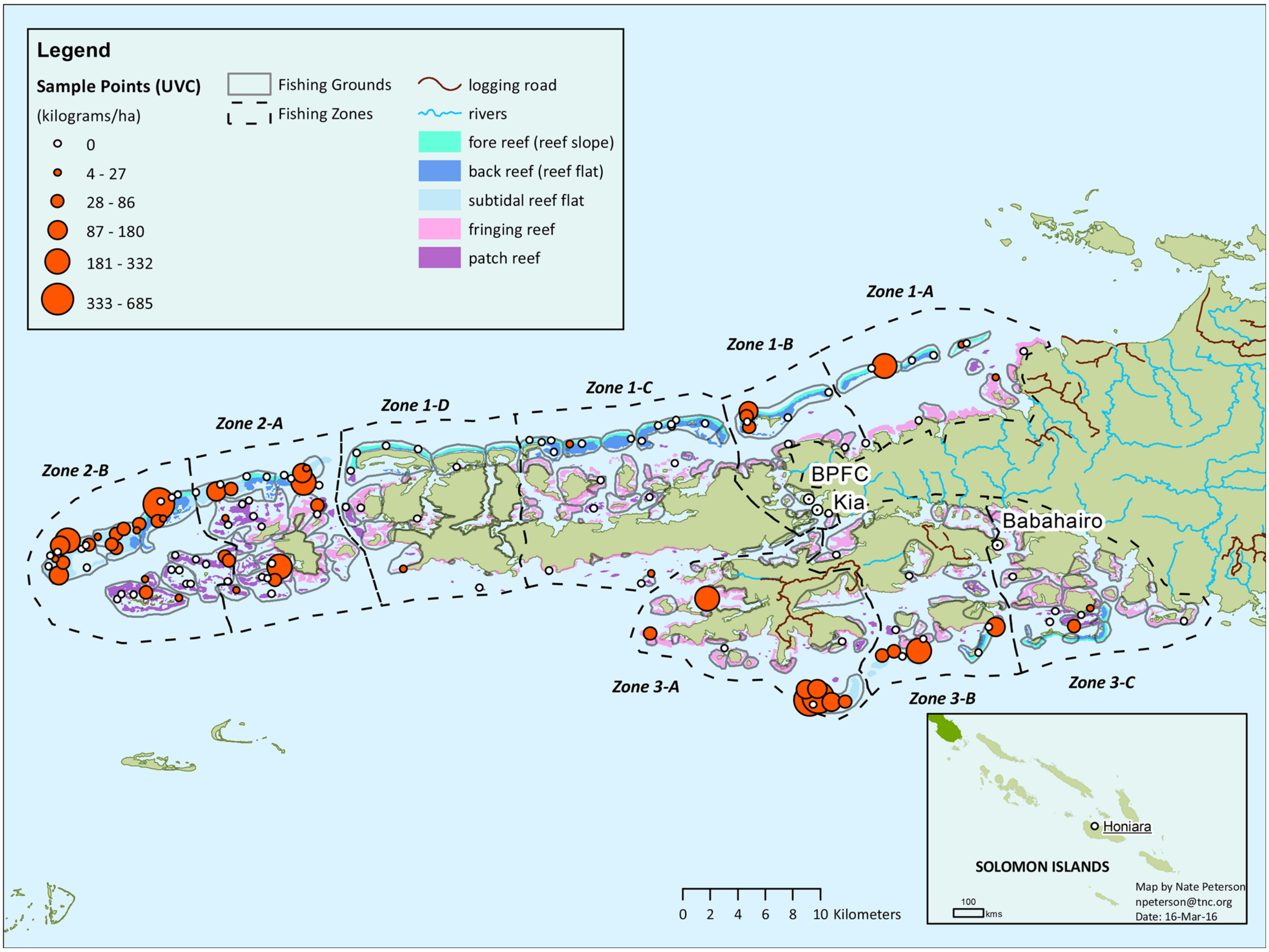

Fig. 4 Biomass (kg ha^{-1}) of adult ($\geq$650 mm TL) *Bolbometopon muricatum* observed at each UVC survey point in October 2012

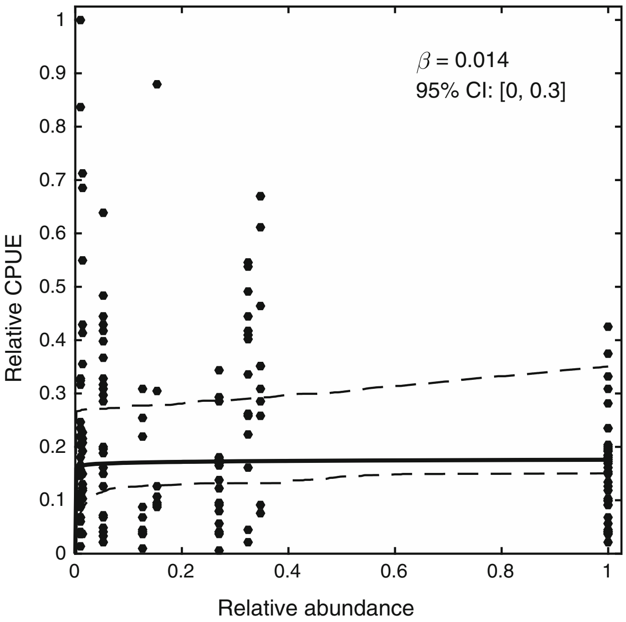

Fig. 5 Relationship between catch per unit effort (CPUE) and fishery-independent abundance (kg) across all fishing subzones. Both datasets have been standardised relative to the largest observation. Each *point* indicates a CPUE estimate within a subzone with estimated total abundance. *Solid line* shows the best-fit power-law relationship, and the *dashed lines* show 95% bootstrap confidence bounds

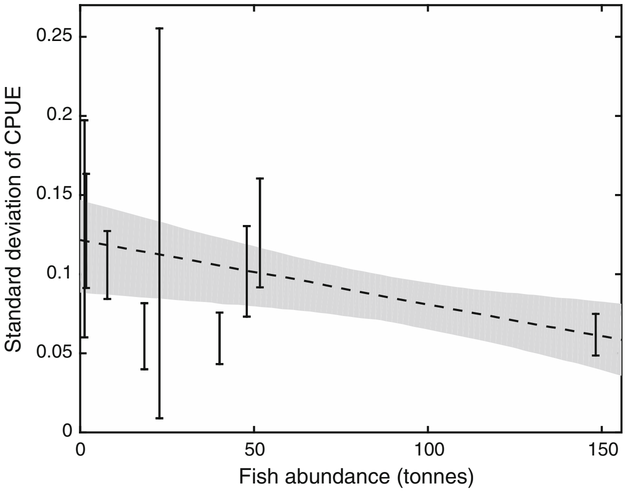

Fig. 6 Relationship between the standard deviation of catch per unit effort (CPUE) and estimates of total fish biomass (*t*) in each fishing subzone. Confidence intervals of the standard deviation were constructed using bootstrap resampling of CPUE within each subzone. *Dashed line* shows best-fit linear relationship, with the shaded area indicating 95% confidence bounds

data-poor setting, where fisheries-dependent data are invariably collected over a short timeframe. We used spatial rather than temporal analyses (Richards and Schnute 1986) to determine impacts of fishing and the extent to

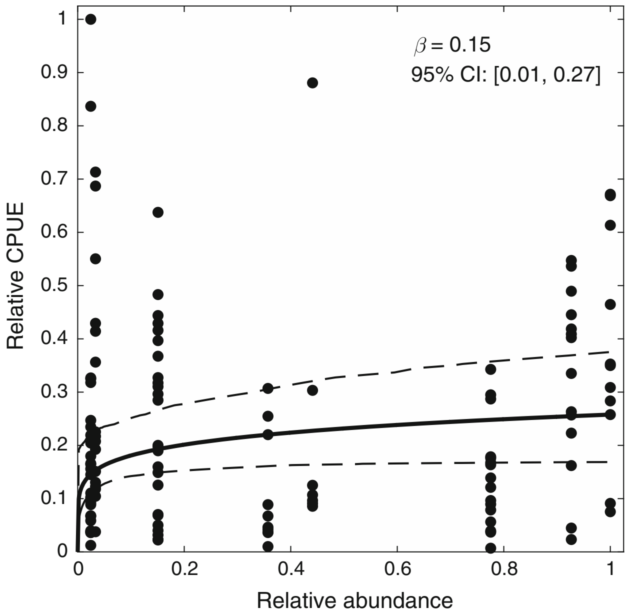

Fig. 7 Relationship between catch per unit effort (CPUE) and fishery-independent abundance (kg) across eight fishing subzones, excluding subzone 3-A which had high *B. muricatum* abundance. Both datasets have been standardised relative to the largest observation. Each *point* indicates a CPUE estimate within a subzone with estimated total abundance. *Solid line* shows the best-fit power-law relationship, with the *dashed lines* showing 95% bootstrap confidence bounds

which hyperstability compromised appropriate fisheries management decisions.

Fishery-independent estimates of abundance of *B. muricatum* in the fishing subzones appear to reflect the historical patterns of fishing pressure, with very low abundance of adults on the extensive system of exposed reef slopes of Zones 1-C and 1-D on the western margin of Isabel. However, CPUE was effectively the same across the nine subzones as abundance declined towards zero, indicating extreme hyperstability in this fishery.

In this example, hyperstability is a product of the behaviour of both fish and fishers. Adult *B. muricatum* form diurnal schools for foraging, and spearfishers are able to obtain very high catches by targeting resting schools at night. School size can remain constant or increase, while target species' abundance decreases in both pelagic (Brierley and Cox 2015) and demersal fish species (Hutchings 1996; Pauly et al. 2013). We propose that when the numbers in sleeping schools are depleted by spearfishing, the surviving smaller schools will merge to maintain foraging school sizes. Such aggregations will be less common in heavily fished zones. The result will be that, as abundance decreases, CPUE will not change on average but will become more variable. Successful fishing expeditions will still encounter large (perhaps even larger) aggregations and high CPUE, but at particularly low abundances some expeditions will only locate the odd individual and fail to find any aggregations. This proposal is supported by our catch data, which shows greater variance at low abundances. Indeed the highest CPUE for a fishing party occurred in the heavily fished subzone 1-C, when 647 kg of *B. muricatum* were captured from a single school in one night.

Kia spearfishers' spatial knowledge of nocturnal sleeping sites was a primary driver of hyperstability in this fishery, as they were able to pinpoint specific locations in their preferred fishing grounds where *B. muricatum* schools could often be found. Publication of these sites was resisted. This detailed local knowledge has resulted in a spearfishery that operates by spot-checking. Fishermen will travel to an outer reef area that is a known *B. muricatum* sleeping site and rapidly search the area for 10–15 min. If unsuccessful, they will move to the next site until sleeping *B. muricatum* schools are encountered. Fishers report that any resting *B. muricatum* that escape the initial pass through the area tend to remain in the same location, and can often be captured in subsequent passes through the area. As a result, the interaction between fish aggregation and fisher searching behaviour results in high CPUE even when overall abundance is low.

While the comparison between fishery-independent abundance data and fishery-dependent CPUE strongly supports our conclusion of hyperstability, alternative explanations are possible. Our analysis assumes localised movement in foraging and reproductive schools. However, if adult *B. muricatum* in our study area are highly mobile, our demarcation of the study area into nine subzones could be artificial. This would be exacerbated if adults moved between the subzones, for example during spawning migrations. We argue against this explanation for the following reasons. First, spawning of *B. muricatum* in the study area occurs monthly throughout the year and reflects a lunar periodicity (R Hamilton personal observation), whereas the UVC survey was designed to take place outside the lunar spawning period. Second, all females captured during the 2012–2013 period were checked for hydrated oocytes, a sign of imminent spawning (Domeier 2012), and females with hydrated oocytes were captured from multiple distant reefs on the same day in our study area, which supports the conclusion that in this area spawning occurs within schools at localised sites (Hamilton and Choat 2012), implying limited or no movement of schools for spawning. Third, there is direct evidence of limited adult movement from an ultrasonic telemetry study at another site in the Solomon Islands (Roviana Lagoon) where a 690-mm TL *B. muricatum* that was tracked for three consecutive days covered a linear reef area of 7.6 km (Hamilton 2005). Finally, there is increasing evidence that even large excavating parrotfish have very limited movement patterns (Welsh and Bellwood 2012).

If the Isabel *B. muricatum* fishery was evaluated solely based on current (2012–2013) fishery-dependent catch data, it would be deemed sustainable. Adult fish dominated the catch, and CPUE was high in all fishing subzones, even those that have been exploited for a long period of time; these are standard predictors of a healthy fishery. Furthermore, no spearfishers ever reported a fishing trip that did not yield at least one *B. muricatum*, and the consensus among spearfishers was that their fishery was healthy. However, our comparison of CPUE and fishery-independent UVC abundance data paints a less optimistic picture, with CPUE data failing to detect marked differences in abundances that existed between fishing grounds that had experienced high and low levels of historical fishing pressure. Our finding of hyperstability in *B. muricatum* highlights the limitations of using data-poor fisheries assessment methods (Froese 2004; Andrew et al. 2007; Prince et al. 2011; Martell and Froese 2013; Hilborn and Ovando 2014) for commercially valuable coral reef fishes that form aggregations.

A cautionary tale for *B. muricatum* fisheries across the species' Indo-Pacific range comes from examining the rapid rise and fall of the *B. muricatum* fishery in Roviana Lagoon, Western Solomon Islands (Hamilton 2005). When a commercial spearfishery developed in the early 1980s, maximum catches of *B. muricatum* exceeded 70 fish per boat per night. Catches of adults from outer reefs and passage environments declined rapidly in the 1990s, with spearfishers subsequently redirecting their efforts to the remaining juvenile populations which were restricted to the lagoon environments (Hamilton 2005). During this period, the water quality of Roviana Lagoon also declined due to widespread commercial logging on the mainland of New Georgia (Halpern et al. 2013). Recognition of these declines led to efforts to protect *B. muricatum* through the establishment of small community-based marine protected areas in Roviana Lagoon (Aswani and Hamilton 2004). Despite these management attempts, local knowledge surveys revealed that in 2014 the maximum catches of *B. muricatum* in Roviana Lagoon were less than five individuals (A. Hughes personal communication). Since maximum catches have fallen to <10% of the maximum historical catches, the Roviana Lagoon *B. muricatum* fishery can be classified as collapsed (Pauly et al. 2013).

Although rarely documented with empirical data, anecdotal information indicates that the Roviana Lagoon scenario has played out across many locations in the Pacific, with large *B. muricatum* catches obtained when commercial night spearfishing commences, followed by abrupt declines several decades later (Dulvy and Polunin 2004; Kobayashi et al. 2011; Hamilton and Choat 2012;

Polloi et al. 2014). Adding to the vulnerability of this species is its late maturity at a large size (Hamilton et al. 2008) and the restriction of juvenile recruitment to lagoonal fringing reef environments with high coral cover that are sensitive to the effect of poor land-based practices (R Hamilton, personal observation).

How then, does one monitor and manage a fishery that initially provides a lucrative return to small-scale fishers, but is highly susceptible to sudden collapse? When hyperstability is suspected, there appear to be no monitoring shortcuts, and fishery scientists need to consider collecting both fishery-dependent and fishery-independent data (Erisman et al. 2011). Fishery-dependent and fishery-independent data should be collected at fine spatial scales, including the collection of demographic parameters from the fishery (Taylor and Choat 2014), and drawing on local knowledge, participatory mapping, and the support of local fishers whenever possible (Almany et al. 2010). As this study shows, independent estimates of spatial variation in abundance can be contrasted with site-specific CPUE data in areas that have experienced spatially variable levels of harvest. Key features of our study that enabled collection of relevant data were (1) development of a commercial fishery and establishing basic monitoring protocols, (2) support from nongovernmental organizations and government agencies to provide training and monitoring infrastructure, and (3) a group of scientists with both a detailed biological knowledge of the fishery species and familiarity with the social and cultural setting of the fishery. While it is clearly not possible to use this model for all coral reef fisheries, it is feasible for large species that attract commercialisation, the same species that are most threatened by collapse.

For effective management of *B. muricatum* fisheries, there is a need to consider the role of external market drivers (Brewer et al. 2009, 2013) and to develop precautionary approaches that account for all life stages of the species. Governments and donor agencies should be aware that unless the establishment of rural fisheries centres go hand-in-hand with effective management measures, improvement in rural livelihoods is likely to come at the expense of aggregating species that have high intrinsic vulnerability to overfishing (Sadovy and Domeier 2005; Hamilton et al. 2012b). The history of the BPFC in Kia exemplifies this point. In August 2001, the BPFC made the decision to begin purchasing fish that had been speared, and Kia fishers immediately redirected their attention to nocturnal aggregations of *B. muricatum*. Overnight a species that had not been a prized subsistence food fish became a lucrative source of revenue.

Practical management options for *B. muricatum* that would be applicable across much of its range include (1) establishing networks of large marine protected areas on outer reefs, (2) protecting nursery habitats on lagoonal reefs that are adjacent to adult habitat, and (3) enforcing a 65-cm size limit which would protect immature fish and limit the amount of commercial fishing in lagoons. In areas where *B. muricatum* populations are already overfished communities and governments should consider placing moratoriums on harvesting to allow overexploited *B. muricatum* populations the chance to recover. Some of these management recommendations are beginning to be adopted across the Pacific. For example, a moratorium on all *B. muricatum* fishing was instituted in Palau in 2006 and is currently still in place (Polloi et al. 2014; S Victor, personal communication) and in September 2015 tribal leaders from the Mwanus Endras Asi Resource Development Network in Manus Province, Papua New Guinea (Almany et al. 2015) initiated discussions with their communities regarding banning commercial night spearfishing across their 50,000 ha seascape (Manuai Matawai, personal communication). Finally, in northern Isabel Province where this study was conducted, several commercial logging licences have recently been declined, in part due to a growing appreciation among customary land owners of the importance of preserving remaining *B. muricatum* nursery habitat that fringes the last unlogged islands in northwest Isabel (J. Pita personal observation).

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References

Almany GR, Hamilton RJ, Matawai M, Kichawen P (2015) Local benefits from community actions: small managed areas can help rebuild and sustain some coastal fisheries. SPC Tradit Mar Resour Manag Knowl Bull 35:3–17

Almany GR, Hamilton RJ, Williamson DH, Evans RD, Jones GP, Matawai M, Potuku T, Rhodes KL, Russ GR, Sawynok B (2010) Getting communities involved in marine protected area research: two case studies from Papua New Guinea and Australia. Coral Reefs 29:567–576

Andréfouët S, Muller-Karger FE, Robinson JA, Kranenburg CJ, Torres-Pulliza D, Spraggins SA, Murch B (2006) Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. Proc 10th Int Coral Reef Symp 2:1732–1745

Andrew NL, Bene C, Hall SJ, Allison EH, Heck S, Ratner BD (2007) Diagnosis and management of small-scale fisheries in developing countries. Fish Fish 8:227–240

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

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

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

Brewer TD, Cinner JE, Green A, Pandolfi JM (2009) Thresholds and multiple scale interaction of environment, resource use, and market proximity on reef fishery resources in the Solomon Islands. Biol Conserv 142:1797–1807

Brewer TD, Cinner JE, Green A, Pressey RL (2013) Effects of human population density and proximity to markets on coral reef fishes vulnerable to extinction by fishing. Conserv Biol 27:443–452

Brierley AS, Cox MJ (2015) Fewer but not smaller schools in declining fish and krill populations. Curr Biol 25:75–79

Clark M (2001) Are deepwater fisheries sustainable?—the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. Fish Res 51:123–135

Choat JH (2012) Spawning aggregations in reef fishes; ecological and evolutionary processes. In: Sadovy de Mitcheson YS, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, vol 35. Springer Fish and Fisheries Series, Springer Science + Business Media, pp 85–116

Cordy CB (1993) An extension of the Horvitz–Thompson theorem to point sampling from a continuous universe. Stat Probab Lett 18:353–362

Domeier ML (2012) Revisiting spawning aggregations: definitions and challenges. In: Sadovy de Mitcheson YS, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, vol 35. Springer Fish and Fisheries Series, Springer Science + Business Media, pp 1–20

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed. Bull Mar Sci 60:698–726

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

Erisman BE, Allen LG, Claisse JT, Pondella DJ, Miller EF, Murray JH (2011) The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can J Fish Aquat Sci 68:1705–1716

Froese R (2004) Keep it simple: three indicators to deal with overfishing. Fish Fish 5:86–91

Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev 90:1215–1247

Halpern BS, Selkoe KA, White C, Albert S, Aswani S, Lauer M (2013) Marine protected areas and resilience to sedimentation in the Solomon Islands. Coral Reefs 32:61–69

Hamilton R (2003) A report on the current status of exploited reef fish aggregations in the Solomon Islands and Papua New Guinea–Choiseul, Ysabel, Bougainville and Manus Provinces. Western Pacific Fisher Survey Series, Society for the conservation of reef fish aggregations. www.scrfa.org, p 52

Hamilton RJ (2005) The demographics of bumphead Parrotfish (*Bolbometopon muricatum*) in lightly and heavily fished regions of the Western Solomon Islands. Ph.D. Thesis, University of Otago, Dunedin, New Zealand, p 273

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

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

Hamilton R, Sadovy de Mitcheson YS, Aguilar-Perera A (2012a) The role of local ecological knowledge in the conservation and management of reef fish spawning aggregations. In: Sadovy de Mitcheson YS, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, vol 35. Springer Fish and Fisheries Series, Springer Science + Business Media, pp 331–370

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

Harley SJ, Myers RA, Dunn A (2001) Is catch-per-unit-effort proportional to abundance? Can J Fish Aquat Sci 58:1760–1772

Hilborn R, Walters CJ (eds) (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, London

Hilborn R, Ovando D (2014) Reflections on the success of traditional fisheries management. ICES J Mar Sci 71:1040–1046

Horvitz DG, Thompson DJ (1952) A generalization of sampling without replacement from a finite universe. J Am Stat Assoc 47:663–685

Hutchings JA (1996) Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can J Fish Aquat Sci 53:943–962

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

Lindfield SJ, McIlwain JL, Harvey ES (2014) Depth refuge and the impacts of SCUBA spearfishing on coral reef fishes. PLoS One 9:e92628

Martell S, Froese R (2013) A simple method for estimating MSY from catch and resilience. Fish Fish 14:504–514

Neis B, Felt LF, Haedrich RL, Schneider DC (1999) An interdisciplinary method for collecting and integrating fishers' ecological knowledge into resource management. In: Newell D, Ommer R (eds) Fishing places, fishing people: issues and traditions in Canadian small-scale fisheries. University of Toronto Press, Toronto, pp 217–238

Pauly D, Hilborn R, Branch TA (2013) Fisheries: does catch reflect abundance? Nature 494:303–306

Polloi K, Golbuu Y, Merep G, Koshiba S, Friedlander A, Koike H (2014) An assessment of Maml and Kemedukl in Palau and management recommendations. In: The nature conservancy micronesia program technical report No. 14-07, p 33

Prince JD, Dowling NA, Davies CR, Campbell RA, Kolody DS (2011) A simple cost-effective and scale-less empirical approach to harvest strategies. ICES J Mar Sci 68:947–960

Prince J, Hordyk A, Valencia SR, Loneragan N, Sainsbury K (2015) Revisiting the concept of Beverton-Holt life-history invariants with the aim of informing data-poor fisheries assessment. ICES J Mar Sci 72:194–203

Richards LJ, Schnute JT (1986) An experimental and statistical approach to the question: is CPUE an index of abundance? Can J Fish Aquat Sci 43:1214–1227

Russell MW, Luckhurst BE, Lindeman KC (2012) Management of spawning aggregations. In: Sadovy de Mitcheson YS, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, vol 35. Springer Fish and Fisheries Series, Springer Science + Business Media, pp 371–404

Russell MW, Sadovy de Mitcheson Y, Erisman BE, Hamilton RJ, Luckhurst BE, Nemeth RS (2014) Status report—world's fish aggregations 2014. Science and conservation of fish aggregations. International Coral Reef Initiative, California, USA

Sadovy de Mitcheson YS, Erisman B (2012) Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. In: Sadovy de Mitcheson YS, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, vol 35. Springer Fish and Fisheries Series, Springer Science + Business Media, pp 225–284

Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254–262

Stevens DL, Olsen AR (2004) Spatially balanced sampling of natural resources. J Am Stat Assoc 99:262–278

Taylor BM, Choat JH (2014) Comparative demography of commercially important parrotfish species from Micronesia. J Fish Biol 84:383–402

Walters C, Martell SJD (2004) Fisheries ecology and management. Princeton University Press, Princeton

Welsh JQ, Bellwood DR (2012) Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. Coral Reefs 31:55–65