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Ecological risk and the exploitation of herbivorous reef fish across Micronesia

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ABSTRACT: Nominally herbivorous fish play a variety of functional roles that are important in maintaining coral reef resilience, yet are major targets of spear fisheries in Micronesia. Although protection is afforded to iconic species in some areas, impacts of the fishery on the ecosystem are poorly understood. The goal of this study was to locate the major potential ecological threats from the fishery by integrating catch data with species-specific metrics of ecological importance and vulnerability to fishing. Region-wide and country-specific grounds for ecological concern were identified. The heavy exploitation of *Naso unicornis* was the most serious regional concern — not only was it the most vulnerable species involved in the fishery, but it plays a low-redundancy functional role (i.e. macroalgal browsing) in the ecosystem. The parrotfishes *Cetoscarus bicolor*, *Scarus rubroviolaceus* and *Chlorurus microrhinos* were also implicated in ecological risks (most noticeable in Palau), and the large proportion of immature catch aggravated the concerns found in Pohnpei. An interview-based assessment of species desirability among fishers highlighted the challenges managers may meet locally in diverting attention away from heavily harvested species. Opportunities to alleviate the ecological risks posed by a significant sector of the Micronesian fisheries were identified. Inducing changes in fishers' targeting behaviour towards opportunistically-caught species may prove feasible in most countries, and if enacted, may reduce fishing pressure in low-redundancy functional roles. The effectiveness of the policy options supported by the present approach in sustaining reef function and resilience has yet to be assessed. However, we anticipate that informing fishers about the implications of their selectivity may achieve tangible progress in conservation of the species. Therefore, policies which moderate catch rates of highly desirable species, as well as efforts to promote more conscious targeting behaviours, may complement the benefits of the existing networks of marine protected areas.

KEY WORDS: Catch-per-unit effort · Fish market surveys · Grazing · Micronesia · Spearfishing

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INTRODUCTION

Herbivorous fish sustain a wealth of key ecosystem functions on coral reefs. Through a variety of feeding modes, they contribute to what has been collectively referred to as the process of 'herbivory' (Hoey & Bellwood 2008, Adam et al. 2011, Lefevre & Bellwood 2011, Welsh & Bellwood 2012) or 'grazing' (van Alystine 1988, Paddack et al. 2006, Cheal et al. 2008, 2010, Ceccarelli et al. 2011), from the system perspective. In this context, grazing is a major force structuring benthic communities (Steneck 1988) and reorganising them into coral-dominated states after physical disturbance (Folke et al. 2004). A substantial amount of gazing can shift the algal community dominance from macroalgae to turfs, and ultimately to encrusting algae (Steneck 1988, Steneck & Dethier 1994); most of which provide suitable substrata for

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settlement of coral larvae (Birkeland 1977, Harrington et al. 2004). In contrast, undergrazed reefs can become increasingly dominated by algal turfs or macroalgae (Hughes et al. 2007, Mumby & Steneck 2008, Diaz-Pulido et al. 2011), which can in turn reduce coral recruitment and recovery (Birrell et al. 2005, Hughes et al. 2007, Mumby et al. 2007).

With a few exceptions (e.g. Peyrot-Clausade et al. 2000, Mapstone et al. 2007), sea urchin populations account for modest contributions to grazing on Pacific reefs (Ogden 1987, Sammarco 1987), while herbivorous fish provide the foundation for the grazing process (Hoey & Bellwood 2008). Parrotfishes (formerly Scaridae, now reclassified as Labridae) (Westneat & Alfaro 2005), unicornfish and surgeonfishes (Acanthuridae), and rabbitfishes (Siganidae) are the most common herbivores within Pacific fish communities (Russ 1984, Bellwood 1995, Jennings & Polunin 1996, Wantiez et al. 1997, Allen & Werner 2002). Feeding continuously throughout the day (Bellwood 1995), and over relatively large spatial scales (due to their roving behaviour), these families (hereafter referred to as roving herbivores) are capable of considerable grazing impact through a range of reef habitats (Fox & Bellwood 2007, Hoey & Bellwood 2008). Although collectively referred to as 'herbivores', these families encompass ~100 species with a variety of feeding modes (Choat et al. 2002, Fox et al. 2009, Hoey & Bellwood 2009, Marshell & Mumby 2012). Increasingly denominated 'nominally herbivorous', species are classified in 4 major functional groups, namely grazers/detritivores, macroalgal browsers, scrapers/small excavators, and large excavators/bioeroders (Green & Bellwood 2009). Not only do these functional groups affect different properties of the substratum, but they may also act complementarily in structuring benthic communities (Burkepile & Hay 2008) and promoting reef recovery after disturbance (Folke et al. 2004).

In Micronesia, as in most of the Pacific Islands and territories, roving herbivores are some of the main components of the catch of artisanal and commercial fisheries (Kitalong & Dalzell 1994, Dalzell et al. 1996, Gillet & Moy 2006, Rhodes et al. 2008). Nocturnal spearfishers are responsible for 75% of the reef fish landed in Micronesia, while a smaller proportion is caught by daytime spearfishers or with barrier nets and hook-and-line (Houk et al. 2012). Roving herbivores comprise >70% of reef fish catches in Palau (S. Bejarano pers. obs.) and 52–73% in Guam, Pohnpei and the Commonwealth of the Northern Mariana Islands (Houk et al. 2012). The strong influence of roving herbivores in speared catches can be explained by their intrinsic social value, but also because their nocturnal quiescence facilitates profitable catches (Johannes 1981). It is also possible that increased fishing pressure is afforded to a wide range of roving-grazer species in response to management measures that protect large, vulnerable carnivorous reef fishes such as groupers (Serranidae), humphead wrasse *Chelinus undulatus*, and green bumphead parrotfish *Bolbometopon muricatum*. Since night-time spearfishing comprises a significant sector of Micronesian reef fisheries, targets key functional groups, and requires improved fisheries policies (Houk et al. 2012), an opportunity exists to investigate the fishery, identify its potential ecological impacts and inform potential management strategies.

As a first step in investigating the roving herbivore fishery, species composition and catch volumes had to be quantified. Although it seems reasonable to expect that spear fishers would concentrate on large-bodied species to maximise income, species of a wide variety of sizes, life histories and functional roles are also harvested (Dalzell et al. 1996, Gillet & Moy 2006, Rhodes et al. 2008, Bellwood et al. 2012). To identify the potential ecological impacts of the fishery, species catch volumes had to be analysed while considering the species' ecological importance and vulnerability to fishing. Roving herbivores are relatively less vulnerable to fishing than other families (Munro 1983, Russ & Alcala 1998, Munro 2007). In fact, in some areas fisheries may sustain high yet variable yields (McClanahan et al. 2008). However, the gregarious behaviour of some species when sleeping (Johannes 1981, Hamilton 2004) and spawning (Hamilton et al. 2008, Sadovy & Colin 2012) makes them easy targets, therefore increasing their vulnerability. Moreover, in places where the large slow-growing carnivores have been removed, herbivores are among the most vulnerable reef fish available (Mumby et al. 2012). Excessive harvesting of roving herbivores, even before reaching overfished stocks, could compromise major processes in reef ecosystems. Yet roving herbivores are amongst the most highly valued food fishes in Micronesia, with certain species attached to cultural customs and lore (e.g. *Bolbometopon muricatum*; Johannes 1981). While it may prove challenging to decrease overall fishing pressure on roving herbivores, it may be possible to manage the fishery to divert fishers' interest from species with the highest grazing impact and vulnerability. In order to inform potential management strategies and allow the acceptance of different policy options to be considered, a detailed assessment of the species desirability among fishers is necessary.

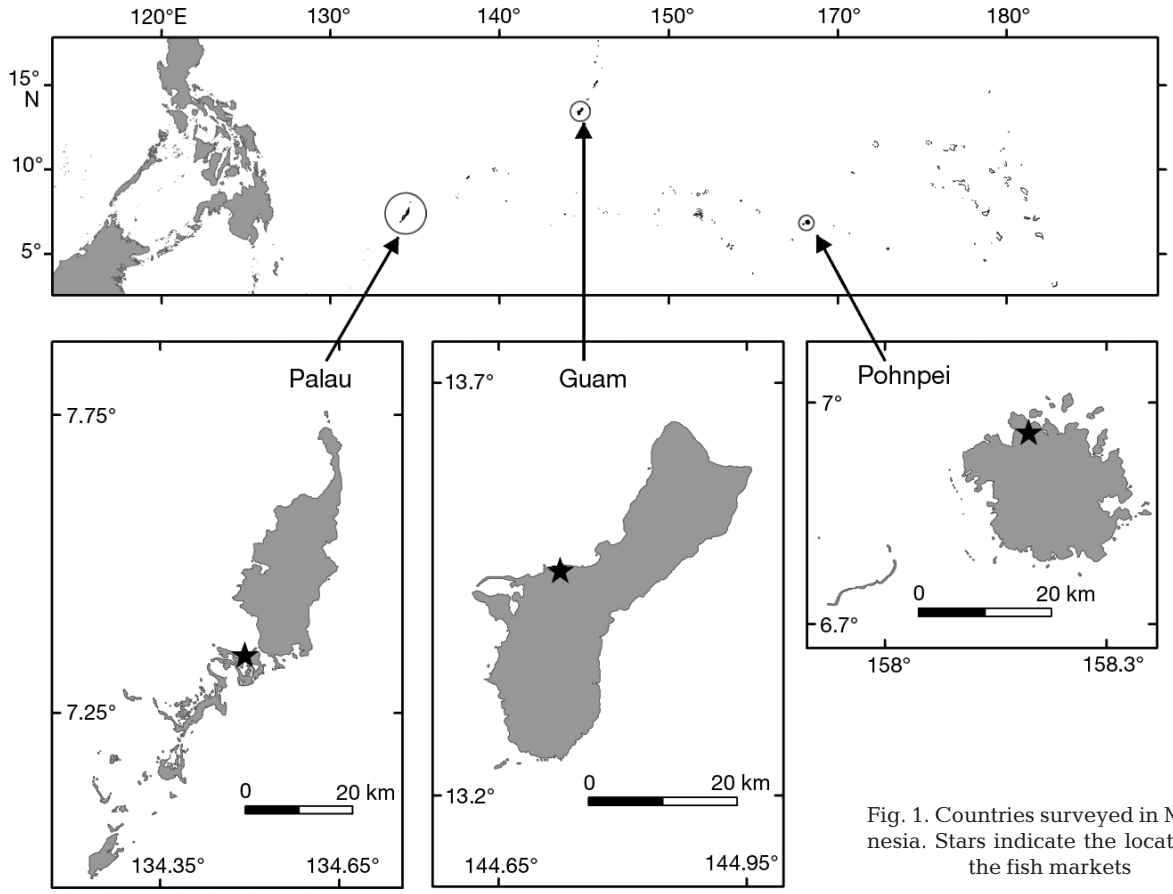

Fig. 1. Countries surveyed in Micronesia. Stars indicate the location of the fish markets

In this study, we evaluated the extent of the spear fishery for roving herbivores in Palau, Pohnpei and Guam. In order to identify the main ecological threats of the fishery, we calculated species-specific metrics of ecological importance (i.e. functional role and potential grazing impact) and vulnerability to fishing, and integrated these with the species' catch volumes. Ecological risks associated with the fishery to particularly vulnerable species with critical functional roles were highlighted. Finally, to identify possible ways to counteract these risks, we conducted a detailed assessment of species desirability among fishers. Opportunities were sought to recommend alternate species that are similar in social or economic value, but are either more sustainable or less critical for the ecosystem function.

MATERIALS AND METHODS

Study area

The commercial sector of the roving-grazer spear fishery was investigated in 3 countries across Micronesia (Fig. 1). Palau, with a population of 19 907, is located 741 km east of the Philippines and 1300 km southwest of Guam. Palau has over 500 km^2 of reefs including a 144 km barrier along the west coast (Golbuu et al. 2005), and a system of 10 marine protected areas spanning various reef habitats. Palauan fishers have been concerned over diminishing stocks of herbivores since the mid 1970s (Kitalong & Dalzell 1994). As a result, a ban on SCUBA-spearfishing, minimum mesh size, and seasonal closures during peak reproductive periods for some species have been enacted (Johannes 1991). Most recently, commerce, possession and export of *Bolbometopon muricatum* was permanently banned (Anonymous 2007, Bureau of Marine Resources). Although 87% of Palauan households have at least one member fishing for subsistence, for sale, or both (Fitzpatrick & Donaldson 2007), only one fish market operates daily as a supplier of reef fish for locals, restaurants and hotels.

Pohnpei, with a population of 34 486, is surrounded by a well developed barrier reef with an extensive lagoon. Thirteen no-take marine sanctuaries exist, but limited protection is afforded to Kitti Municipal-

ity, where much of the commercial fishery focuses (Rhodes et al. 2008). SCUBA-spearfishing and the sale of *Bolbometopon muricatum* are banned under the Conservation and Resource Enforcement Act of 1982. Of the working population in Pohnpei, 11% is dedicated to subsistence and commercial agriculture or fishing. Kolonia Town is the economic and administrative centre of the island, with at least 25 fish markets supplying local consumers, and exports compriseing less than 5% of total marketed catch (Rhodes et al. 2008).

Guam is a US territory with a population of 159358. The island is surrounded by offshore banks, and fringing, patch, submerged, and barrier reefs (Gombos et al. 2007). The nearshore reefs and lagoon comprise 69 km^2, of which 28% are protected within a network of 5 marine reserves (Richmond & Davis 2002). The spearfishery in Guam evolved from a traditional subsistence, predominantly free-diving practice to a commercial and mostly SCUBA-based practice (Hensley & Sherwood 1993). Although the legal use of SCUBA is regarded as one of the main threats to Guam's coral reef fishery, an additional concern is the growing number of immigrants from the federate states of Micronesia who knowingly participate in intensive, frequent and indiscriminate free-dive commercial spearfishing. Guam is virtually free of fishing restrictions, including for herbivorous fish. Although creel surveys have been conducted by the Division of Aquatic and Wildlife Resources (DAWR) since the 1960s, data on spearfishing catches has not been monitored consistently or with sufficient taxonomic detail to quantify the impacts of fishery on individual species of herbivores.

Market-based catch surveys

To quantify catch composition and volume, catch surveys were conducted at the primary fish markets in Kolonia (Pohnpei) from 13–30 April, Hagåtña (Guam) from 6–26 May and Koror (Palau) from 11–26 July of 2009. All markets were of a similar size and capacity. In Pohnpei and Palau, catch surveys were scheduled during the closed season for groupers (1 March–30 April and 1 April–31 July, respectively). In all countries, surveys were timed during new moon periods, when the fishing pressure on herbivorous fish is highest (Rhodes et al. 2008). The frequency, time of day, and duration of the market surveys were adjusted to maximise encounters with nocturnal spearfishers, who land the majority of reef fish. All spearfishing landings in Palau (23), Pohnpei (35) and Guam (15) were surveyed. Each landing was examined for the presence of parrotfish, surgeonfish, unicornfish and rabbitfish, which were separated from the rest of the catch. Individuals were identified to species, weighed to the nearest gram, and their total length (TL) measured to the nearest 0.1 cm. Except for a number of occasions when fishers abstained from disclosing information (~5 per country), effort data was obtained for all landings, by recording the number of fishers associated with each catch and total time spent fishing (including travelling time).

Lacking in this study to estimate the total daily catch of roving herbivores are the volumes extracted for consumption or direct sale to restaurants, schools and hotels. These could not be surveyed due to logistical constraints. Roving-grazer catches originating from net fishing and daytime spearfishing were excluded from the analysis, because these were observed occasionally (n = 2) and only in Palau.

To determine if the catches measured here over 2 wk were representative of the catches observed over larger temporal scales, we compared them to historical data using 95% confidence intervals. Such comparisons were only possible in Palau, where the fish market kept sales records dating back to 2006, with an elementary level of taxonomic detail. *Naso unicornis* was separated from rabbitfish and 'assorted reef fish' (including parrotfishes) until 2010, and parrotfishes were separated from the 'assorted reef fish' in 2011. Outcomes of these comparisons indicated that (1) once the effect of the lunar cycle was accounted for, data collected here were representative of total volume landed in July 2009, (2) the volume of certain species with strong seasonality (e.g. *N. unicornis*) may have been slightly underestimated compared to the typical values of that month (for the last 6 yr), but was not significantly different from volumes sold during the second half of the year during the last 6 yr, (3) the rabbitfish catch volumes measured here were representative of most of the year during the last 6 yr and (4) the observed catch composition and species catch volumes were representative of those logged throughout most of the year. Further detail on the assessment of the representativeness of our catch data can be found in Section 1 of the Supplement at www.int-res.com/articles/suppl/m482p197_supp.pdf.

Catch volume and composition across countries

Catch data were analysed to obtain the mean frequency of occurrence (FO) and mean volumetric

and numeric catch-per-unit effort (hereafter referred to as $CPUE_V$ and $CPUE_N$, respectively), per species per country. FO was calculated per day as the percent of landings where a species was present, and then averaged among all survey days (n = 14). $CPUE_V$ and $CPUE_N$ were calculated per day using Eqs. (1) and (2):

$$CPUE_V = \frac{W}{(T \times F)} \quad (1)$$

$$CPUE_N = \frac{N}{(T \times F)} \quad (2)$$

where W = total weight and N = total number of individuals of a species within a landing; F = number of fishers and T = total fishing time associated with the landing. Mean $CPUE_V$ and $CPUE_N$ were calculated among survey days, including only days when effort data was obtained for all landings (n = 7 d; 9, 8, and 14 catches in Palau, Pohnpei and Guam, respectively). To allow for among-country comparisons, only days of identical moon phase across countries were included. Differences among countries in species composition, FO, $CPUE_V$ and $CPUE_N$ were tested using a permutation multivariate analysis of variance (PERMANOVA). To block their potential confounding effect, landing date and corresponding number of landings were included as covariates when testing differences in the species composition and FO. The landing date and corresponding fishing effort (fishers × hours) were included as covariates when comparing the $CPUE_V$ and $CPUE_N$ among countries.

Spearfishing pressure across roving-grazer species

Heavily, moderately or rarely harvested species in each country were identified using hierarchical cluster analyses. All species present in the catches of a country were classified based on their FO and $CPUE_V$ and $CPUE_N$. In all cases, Euclidean distance was used as a measure of distance among species, and the group-average algorithm was used to calculate the distance among clusters. Dendrograms were used as visual aids to identify groups of species that were similar in terms of their FO and CPUE. Heavily harvested species were those with relatively high FO and moderate to high $CPUE_V$ and $CPUE_N$; moderately harvested species included those with relatively moderate to high FO and moderate to high $CPUE_V$ and $CPUE_N$; and rarely harvested species corresponded to those with relatively low FO and low $CPUE_V$ and $CPUE_N$.

Identifying ecological risks associated with the roving-grazer fishery

Ecological risks to roving herbivores associated with the fishery were identified in 2 steps. Firstly, for heavily and moderately harvested species, species-specific metrics of ecological importance and vulnerability to fishing were calculated. Secondly, these metrics were analysed in parallel with the species fishing pressure category (assigned in the cluster analysis).

Metrics of ecological importance

For parrotfishes, the metrics of species ecological importance included functional role (sensu Green & Bellwood 2009) and potential grazing impact (PGI). The species PGI was calculated as the product of its daily bite rate (bite rate × length of the feeding day), bite area and fish abundance. Bite rate and bite area depend on fish size (Bonaldo & Bellwood 2008, Lokrantz et al. 2008); however, for the purpose of this study, PGI was calculated using bite rates and bite areas of average-sized individuals of each species found within marine reserves in each country (Table S1 in the Supplement). Mean bite rates were quantified through 7 min observations (n ≥ 10 per species) on forereef habitats. The length of the parrotfish feeding day in Micronesia (10 h) was inferred from that calculated in the Great Barrier Reef (Bellwood 1995), using local sunrise and sunset times (i.e. 05:50 h and 17:50 h in Palau; 06:14 h and 18:08 h in Pohnpei; 06:13 h and 17:57 h in Guam).

Bite area was estimated using species-specific models that describe its allometric relationship with TL (Bejarano 2009). Bite areas (BA) used in the models were calculated as the product of 2 jaw dimensions (gape size and width in contact with the substratum) taken from fished individuals landed at the local markets (n ≥ 20 per species) (Table S1 in the Supplement). Gape size (G) was measured with callipers while applying moderate pressure when separating the lower and upper jaws. Identical pressure was applied when handling all individuals. The width of the individual's mouth likely to be in contact with the substratum during a bite (B_W) was measured using photographs of the contours of upper and lower jaws, imprinted on moulding clay (see Fig. S1 in Section 2 of the Supplement at www.int-res.com/articles/suppl/m482p197_supp.pdf). Here, we used published bite-depth measurements (Bellwood 1995) to determine B_W (Fig. S1). A bite depth of 1.5 mm,

inferred from the mean bite area (169.99 mm^2) and volume (256.04 mm^3) of *Chlorurus microrhinos* (Bellwood 1995) was used for the large excavators/bioeroders (i.e. *Cetoscarus bicolor* and *C. microrhinos*), whereas *Chlorurus sordidus* bite depth (0.1 mm, Bellwood 1995) was used for all scrapers/small excavators.

This method was used as a cost-effective alternative to the conventional technique of measuring parrotfish bite scars directly on the substrate (Bellwood & Choat 1990, Bellwood 1995, Fox & Bellwood 2007, Bonaldo & Bellwood 2009), which met several limitations in this study. Firstly, spearfishing pressure is likely to cause fish to be wary of divers, so observers were often unable to approach individuals closely enough to identify their exact bite location. More importantly, bites often left no visible scars on the substrate, especially when they were taken on algal turfs or on the tip of dead coral branches. Fish abundance was quantified in August 2009 inside marine reserves in each country (n_{Palau} = 6, $n_{Pohnpei}$ = 9, n_{Guam} = 6) using 10 replicate 30 × 4 m transects per site (see Table S1 and Mumby et al. 2013).

Because PGI could not be calculated for siganids and acanthurids, the species functional role (sensu Green & Bellwood 2009) was used as their single metric of ecological importance.

Metrics of vulnerability to fishing

Four life history traits (asymptotic length L_∞, length at first maturity L_m, growth coefficient K and life span LS) were considered informative of the species vulnerability to fishing. Values for these traits were obtained using the FishBase life history tool, customised to perform all calculations based on the maximum TL observed for each species in our study region. The L_∞:K ratio was calculated as a summary metric of vulnerability to fishing, with large values indicating relatively high vulnerability to fishing and low values indicating relative resilience to fishing pressure.

To identify the main concerns rising from the parrotfish spear-fisheries from a functional perspective while accounting for their vulnerability to fishing, species were plotted (as dots) in a bi-dimensional space comprised by the PGI and L_∞:K ratio. Each dot was size-coded to represent the amount of fishing pressure the species received, and colour-coded to indicate the species' functional role. Heavily harvested species, with relatively high vulnerability to fishing and PGI comprised the most concerning risks, whereas low risks were posed by the heavy or moderate harvest of species that were relatively resilient to fishing and capable of modest PGI. High risks were exacerbated if the species involved played a low-redundancy functional role and/or if a large proportion of immature individuals occurred in the catch.

The main risks to acanthurids and siganids associated with the fishery were identified considering the species vulnerability, in parallel with their functional roles (sensu Green & Bellwood 2009) and (when available in the literature) quantitative information of their feeding rates. Risk alleviation strategies, such as diverting attention away from species in the highest risk categories, were recommended.

Interview-based assessment of species desirability

To assess the choices of fishers when targeting roving herbivores, we interviewed 19 fishers in Guam, 25 in Palau and 20 in Pohnpei. Fishers were either associated with surveyed catches or members of the active spearfishing population.

During the interview, card-size photographs of commonly targeted species of roving herbivores were presented. Photographs were organised into 7 groups, and presented to the fishermen sequentially. Each group contained species of the same family and similar maximum length. Fishermen were asked to assign a decision to each photograph as: 'actively targeted', 'caught if seen but not looked for' and 'avoided'. Fishers assigned a ranking number to those species of interest indicating their order of preference, assuming the fish were of optimal size. At the end of each interview, the surveyor was able to identify (1) the preferred species of each size class of a given family, (2) the preferred species of each family and (3) the preferred species of all roving-grazers. Each fisher was asked to provide the main reasons for preferring individual species.

Interview decisions were used to measure the desirability of each species among spearfishers. A preference score from 1 (lowest) to 4 (highest) was assigned to each individual response as follows: (1) = 'I would not catch this species', (2) = 'I would catch it if I see it and it is big', (3) = 'I would catch it if I see it' and (4) = 'I target this species'. Mean desirability scores per species were calculated across fishers' responses in each country. For heavily harvested and highly desirable species, we identified the main reason for preference. Responses were categorised as (1) taste, (2) size, (3) colour or (4) convenience (i.e. easier to catch or more abundant).

Seeking opportunities to mitigate risk by shifting targeting behaviours

For every heavily-exploited roving-grazer implicated in ecological risks, species with similar desirability values were identified. Desirable species were suggested as alternative targets, only if they were relatively more resilient to fishing and had a relatively redundant functional role and modest PGI (in the case of parrotfishes), compared to the risk-bound species. The potential acceptance of shifting fishers' targeting behaviour as a policy instrument was analysed based on the main reasons for preference of the species involved.

RESULTS

Catch volume and composition across countries

Mean $CPUE_V$ and $CPUE_N$ of roving herbivores ranged between 4.3–8.3 kg fisher^{-1} h^{-1} and 8–11.9 ind. fisher^{-1} h^{-1} respectively, but were not significantly different among countries (ANOVA: $F_{2,31}$ = 0.58, p = 0.57; Fig. 2).

A total of 18 acanthurid, 25 scarid and 11 siganid species occurred in the catches (Table 1). Taxonomic composition of the catch, as well as species FO and $CPUE_N$ differed significantly among all countries (PERMANOVA: p = 0.001; Table 2). Significant differences in species $CPUE_V$ occurred between Pohnpei and Guam (PERMANOVA: T_{21} = 2.30, p = 0.001) and between Pohnpei and Palau (PERMANOVA: T_{22} = 1.84, p = 0.003), but not between Palau and Guam (PERMANOVA: T_{22} = 1.84, p = 0.219) (Table 2). The number of landings per day was associated with the species FO and the effort was positively related with the species $CPUE_N$ (Table 2). However, neither the number of daily landings nor the amount of effort was found to interact statistically with the effect of country. Modest increases in effort had, therefore, the same effect on the catch attributes throughout the region surveyed.

Spearfishing pressure across roving-grazer species

Heavily harvested species varied slightly among countries, with the large-bodied *Naso unicornis* being consistently targeted. In Palau, other heavily harvested species included 2 small-bodied surgeonfish *N. lituratus* and *Acanthurus nigricauda*, 4 large-bodied parrotfish *Hipposcarus longiceps*, *Scarus rubroviolaceus*, *Cetoscarus bicolor* and *Chlorurus microrhinos*, and 2 rabbitfish *Siganus argenteus* and *S. punctatus* (see Section 3 of the supplement at www.int-res.com/articles/suppl/m482p197_supp.pdf). Fewer species were heavily harvested in Pohnpei (i.e. *A. nigricauda*, *H. longiceps*, *S. punctatus* and *Siganus doliatus*) and Guam (i.e. *N. lituratus* and *A. lineatus*) and more than 20 other species were rarely to moderately harvested in all countries (see dendrograms for each country in Figs. S2 to S4 in Section 3 of the Supplement).

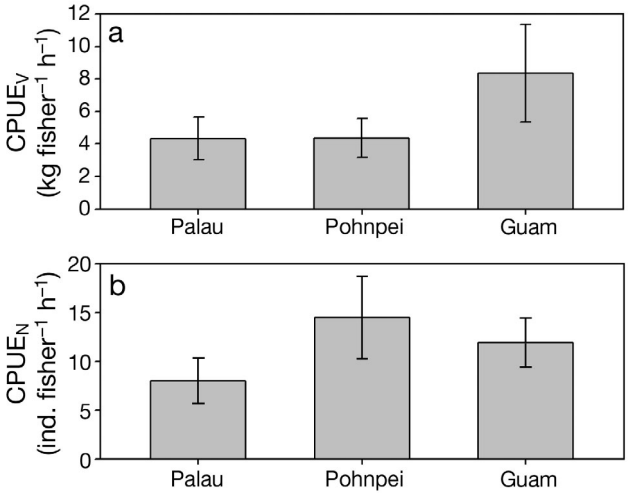

Fig. 2. Mean (a) volumetric and (b) numeric catch-per-unit effort ($CPUE_V$ and $CPUE_N$, respectively) per country

Generalised risks associated with the roving-grazer fishery

The main risk of the fishery across the studied region was the heavy exploitation of *Naso unicornis*. Aside from being the most vulnerable of roving herbivores (L_∞:K = 525), this species plays a relatively low-redundancy functional role in the ecosystem (i.e. macroalgal browsing). The risk of exploiting *N. unicornis* was exacerbated by the considerable proportion of immature individuals caught throughout the region (73% in Pohnpei, 40% in Palau and 39% in Guam; Table 3).

The heavy exploitation of *Hipposcarus longiceps* in Palau and Pohnpei represents a modest but consistent threat to the grazing process (Fig. 3). Although the estimated life history parameters placed *H. longiceps* in a position of moderate vulnerability to fishing compared to other scrapers (L_∞:K = 150), this species was capable of some of the highest PGI within the functional group (e.g.

Table 1. Mean frequency of occurrence (FO, % landings) and catch per unit effort ($CPUE_N$, ind. fisher^{-1} h^{-1}; $CPUE_V$, kg fisher^{-1} h^{-1}) of moderately to heavily harvested herbivores

Family	Palau			Pohnpei			Guam		
Species	FO	$CPUE_N$	$CPUE_V$	FO	$CPUE_N$	$CPUE_V$	FO	$CPUE_N$	$CPUE_V$
Acanthuridae									
Acanthurus blochii	14.1	0.02	0.02	65.7	0.14	0.05	54.2	0.13	0.06
Acanthurus lineatus	2.6	<0.01	<0.01	18.6	0.01	<0.01	70.8	1.12	0.22
Acanthurus maculiceps	62.8	0.10	0.03	–	–	–	–	–	–
Acanthurus nigricauda	75.6	0.67	0.19	85.5	1.75	0.32	66.7	0.25	0.07
Acanthurus olivaceus	–	–	–	1.3	<0.01	<0.01	62.5	0.16	0.03
Acanthurus xanthopterus	3.8	<0.01	<0.01	19.6	0.03	0.02	45.8	0.16	0.08
Naso lituratus	78.2	1.02	0.32	88.2	0.42	0.10	91.7	1.96	0.48
Naso unicornis	79.5	1.89	1.59	87.2	1.21	0.71	100.0	5.18	5.33
Total	89.7	3.81	2.19	100.0	3.77	1.30	100.0	9.17	6.31
Labridae									
Calotomus carolinus	37.2	0.04	0.01	3.1	–	–	12.5	0.01	<0.01
Cetoscarus bicolor	88.5	0.14	0.14	12.7	0.02	0.03	16.7	0.02	0.03
Chlorurus bleekeri	5.1	–	–	52.5	0.64	0.22	–	–	–
Chlorurus frontalis	–	–	–	2.5	–	–	12.5	0.01	<0.01
Chlorurus microrhinos	76.9	0.18	0.17	51.5	0.09	0.05	33.3	0.08	0.07
Chlorurus sordidus	–	–	–	13.8	0.01	<0.01	45.8	0.14	0.03
Hipposcarus longiceps	78.2	1.24	0.73	95.1	1.97	0.92	66.7	0.25	0.33
Scarus altipinnis	2.6	<0.01	<0.01	5.9	0.01	<0.01	58.3	0.41	0.35
Scarus dimidiatus	33.3	0.02	<0.01	55.3	0.31	0.08	–	–	–
Scarus festivus	10.3	0.01	<0.01	1.3	<0.01	<0.01	20.8	0.01	<0.01
Scarus forsteni	37.2	0.09	0.05	–	–	–	58.3	0.09	0.04
Scarus frenatus	33.3	0.03	0.01	1.3	–	–	–	–	–
Scarus ghobban	41.0	0.07	0.10	29.3	0.04	0.02	–	–	–
Scarus prasiognathos	47.4	0.11	0.05	–	–	–	–	–	–
Scarus rubroviolaceus	88.5	0.35	0.27	4.1	0.01	0.01	83.3	0.10	0.10
Scarus schlegeli	44.9	0.03	0.01	4.1	0.03	–	70.8	0.18	0.06
Total	100.0	2.36	1.55	97.9	3.19	1.35	91.7	1.31	1.04
Siganidae									
Siganus argenteus	61.5	0.60	0.12	63.2	0.47	0.08	37.5	0.08	0.02
Siganus canaliculatus	10.3	<0.01	<0.01	–	–	–	–	–	–
Siganus corallinus	42.3	0.07	0.01	–	–	–	–	–	–
Siganus doliatus	50.0	0.15	0.03	86.4	1.09	0.16	–	–	–
Siganus lineatus	6.4	<0.01	<0.01	–	–	–	–	–	–
Siganus puellus	53.8	0.07	0.01	77.6	0.35	0.06	–	–	–
Siganus punctatus	73.1	0.59	0.15	98.8	1.82	0.37	66.7	0.36	0.12
Siganus vulpinus	–	–	–	24.4	0.03	<0.01	–	–	–
Total	76.9	1.49	0.32	98.7	3.81	0.69	75.0	0.45	0.14

0.05% 120 m^2 d^{-1}, in Palau and Pohnpei; Table 3, Fig. 3).

The heavy exploitation of the grazer/detritivore *Siganus punctatus* comprises a moderate threat from the fishery in all 3 countries. Although rabbitfishes were less vulnerable to fishing compared to most roving herbivores, *S. punctatus* was the most vulnerable of the family (L_∞:K = 69).

Risks particular to Palau

The heavy exploitation of *Cetoscarus bicolor*, *Scarus rubroviolaceus* and *Chlorurus microrhinos* represented additional risks associated with the Palau fishery. *C. bicolor* and *S. rubroviolaceus* were the most vulnerable among parrotfishes (L_∞:K = 374, 330, respectively), and had the highest PGI within their functional groups (0.27 and 0.06% 120 m^2 d^{-1}, respectively) (Fig. 3). The risk of exploiting *C. bicolor* in Palau was exacerbated by its relatively low functional redundancy. This was particularly serious given that *C. microrhinos* — another of the few large excavators, with moderate vulnerability to fishing (L_∞:K = 190) and relatively high PGI (0.19% 120 m^2 d^{-1} respectively) — was also heavily harvested in the country (Fig. 3).

Table 2. PERMANOVA results testing for differences among jurisdictions in species composition of the nocturnal spearfishery, as well as in the frequency of occurrence and catch per unit effort (CPUE) of different species. PERMDISP: dispersion test to check for the compliance with the PERMANOVA assumptions

Response variable	Factor	df	*F*	p	Post-hoc contrasts (p-values)
Frequency of occurrence	Number of boats	1	8.2751	0.001	Pohnpei ≠ Guam (0.001)
	Country	2	11.964	0.001	Pohnpei ≠ Palau (0.001)
	Number of boats × Country	2	1.0293	0.425	Guam ≠ Palau (0.001)
	PERMDISP			0.123	
$CPUE_N$ (ind. fisher^{-1} h^{-1})	Effort fisher^{-1} h^{-1}	1	2.8424	0.006	Pohnpei ≠ Guam (0.001)
	Country	2	4.5564	0.001	Pohnpei ≠ Palau (0.011)
	Effort × Country	2	1.0924	0.339	Guam ≠ Palau (0.019)
	PERMDISP			0.657	
$CPUE_V$ (kg fisher^{-1} h^{-1})	Effort fisher^{-1} h^{-1}	1	1.9041	0.070	Pohnpei ≠ Guam (0.001)
	Country	2	3.8218	0.001	Pohnpei ≠ Palau (0.003)
	Effort × Country	2	1.3541	0.141	Guam = Palau (0.219)
	PERMDISP			0.449	

Table 3. Metrics of grazing, vulnerability, and fishing pressure per species (moderately to heavily harvested in at least one country). PGI = potential grazing impact; FR = functional role (sensu Green & Bellwood 2009): dark green = grazers/detritivores (G/D), light green = browsers (BR), red = large excavators/bioeroders (LE/BIO), orange = scrapers/small excavators (SC/SE). L_m = length at first maturity (cm TL); L_∞ = asymptotic length (cm TL); LS = life span (yr); L_∞:K = vulnerability metric where K = growth coefficient of von Bertalanfy growth function. Note that although *Calotomus carolinus* was moderately harvested in Palau, it was excluded from this table because no bite rate data (and therefore no PGI) were available for this species. np = species not present in the country; nh = species not harvested in the country

Family	FR	PGI (% 120 m^2 d^{-1})			Life history trait			L_∞:K	% immature ind. in catch		
Species		Palau	Pohnpei	Guam	L_m	L_∞	LS		Palau	Pohnpei	Guam
Acanthuridae											
Acanthurus blochii	G/D				24.2	42.5	15.8	236.1	0	22	7
Acanthurus lineatus	G/D				16.2	28.6	5.4	54.0	0	2	0
Acanthurus maculiceps	G/D				19.3	33.0	10.2	117.9	0	nh	nh
Acanthurus nigricauda	G/D				20.0	34.3	9.5	114.3	0	11	0
Acanthurus olivaceus	G/D				18.1	30.8	7.5	81.1	nh	0	0
Acanthurus xanthopterus	G/D				25.9	45.8	5.0	80.4	0	5.0	10
Naso lituratus	BR				24.1	42.3	8.1	120.9	24	61	36
Naso unicornis	BR				37.1	68.3	22.0	525.4	40	73	39
Labridae											
Cetoscarus bicolor	LE/BIO	0.272	0.005	0.011	29.2	52.3	20.5	373.6	21	7	0
Chlorurus microrhinos	SC/SE	0.180	0.106	0.189	28.8	51.5	10.6	190.7	30	35	12
Chlorurus sordidus	SC/SE	0.217	0.486	0.261	17.9	30.4	4.9	52.4	nh	0	0
Chlorurus bleekeri	SC/SE	0.004	0.014	np	21.2	36.6	7.9	21.9	0	3	
Hipposcarus longiceps	SC/SE	0.046	0.046	0.002	29.3	52.5	8.2	150.0	26	37	3
Scarus rubroviolaceus	SC/SE	0.055	0.003	0.034	31.1	56.1	16.9	330.0	34	60	14
Scarus prasiognathos	SC/SE	0.015	np	np	26.5	46.9	11.0	180.4	20		
Scarus altipinnis	SC/SE	0.003	0.003	0.006	26.5	46.9	13.6	223.3	0	22	6
Scarus ghobban	SC/SE	0.002	0.002	0.002	32.7	59.4	8.5	174.7	15	78	nh
Scarus dimidiatus	SC/SE	0.022	0.023	np	20.7	35.6	6.6	82.8	0	4	
Scarus schlegeli	SC/SE	0.030	0.024	0.071	21.2	36.6	15.8	203.3	0	0	0
Scarus forsteni	SC/SE	0.009	0.009	0.011	22.8	39.7	8.9	124.1	0	nh	0
Scarus frenatus	SC/SE	0.003	0.002	np	20.7	35.7	4.7	58.5	0	0	
Siganidae											
Siganus argenteus	G/D				22.3	38.7	4.7	63.4	18	32	4
Siganus corallinus	G/D				19.1	32.6	5.8	66.5	10	nh	np
Siganus doliatus	G/D				17.7	29.9	4.2	44.6	np	10	nh
Siganus puellus	G/D				19.0	32.5	5.2	59.1	0	4	np
Siganus punctatus	G/D				20.8	35.8	5.5	68.8	9	22	0

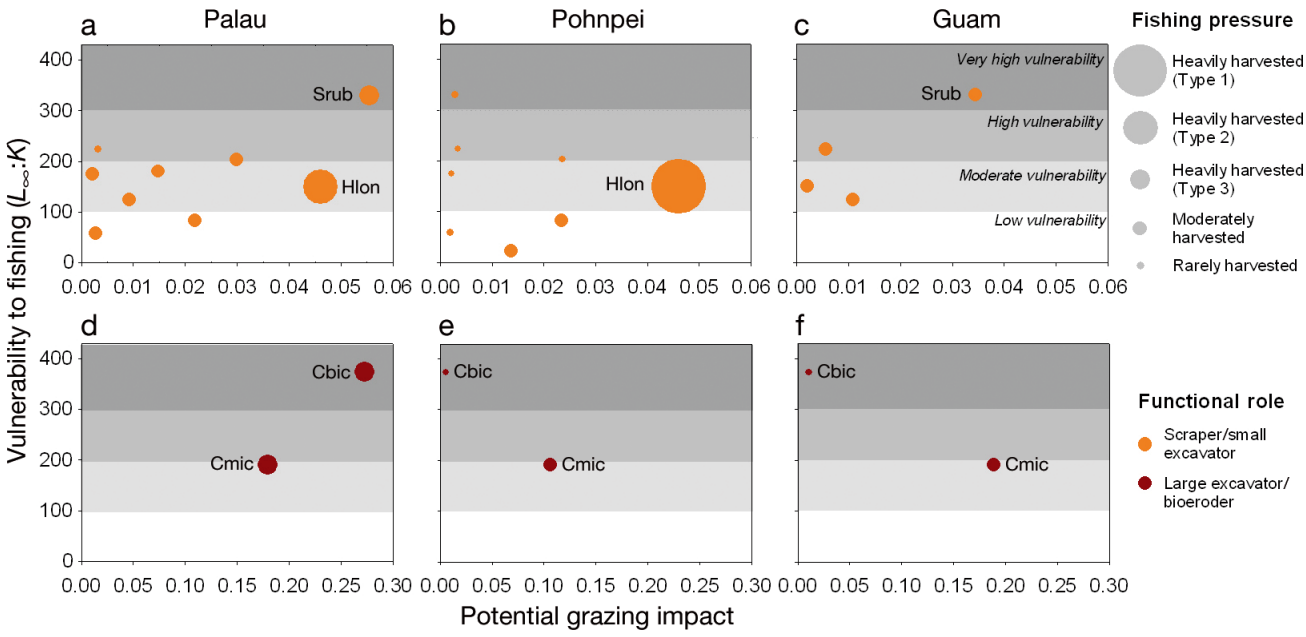

Fig. 3. Location of each parrotfish species in a bi-dimensional space comprised by the potential grazing impact and vulnerability to fishing (L_∞:K ratio). Sphere size indicates fishing pressure (from heavily to rarely harvested); sphere colour indicates the functional group (scraper/small excavator and large excavator/bioeroder). Species associated with risks are highlighted: Srub: *Scarus rubroviolaceus*; Hlon: *Hipposcarus longiceps*; Cbic: *Cetoscarus bicolor*; Cmic: *Chlorurus microrhinos*

Risks particular to Pohnpei

Pohnpei catches had the most species under the length at first maturity (18), and also the largest percentages of immature individuals per species (up to 78% for *Scarus ghobban*) compared to other countries (Table 3). From a vulnerability and functional-role perspective, the high proportion of immature individuals in the catch may aggravate the impacts of the fishery on the macroalgal browsers *Naso unicornis* and *N. lituratus* (Table 3).

Risks particular to Guam

The moderate harvest of *Scarus rubroviolaceus* was a potential concern in Guam, due to its vulnerability and high PGI (Fig. 3).

Interview-based targeting behaviour and species desirability

Spearfisher's behaviour and species desirability differed among countries (Figs. 4 to 6). In Palau, a relatively small group of species (10) were targeted, whereas most other species were either avoided (16), or caught only if individuals had reached what fishers considered to be 'a good size' (i.e. > ~25 cm TL; 15 species) (Figs. 4 to 6). Fishers in Guam targeted 13 species, avoided catching 5 species, caught 11 species opportunistically and caught 8 species only if individuals had reached a 'good size' (Figs. 4 to 6). In contrast, fishers in Pohnpei actively targeted the most species (16); the remainder were caught opportunistically (26) and none were actively avoided (Figs. 4 to 6).

Opportunities to mitigate risk by shifting targeting behaviours

Opportunities to channel fishers' interest towards alternative species that could safely absorb the fishing pressure otherwise set on *Naso unicornis* were not clear. *Naso lituratus* and *Acanthurus xanthopterus* were similar to *N. unicornis* in desirability throughout the region (Fig. 4). *N. lituratus* was not recommended as an option to replace *N. unicornis*, however, mainly because of its low functional redundancy. *A. xanthopterus* was predicted to be relatively resilient to fishing among acanthurids and had relatively high functional redundancy as a grazer/detritivore; however, fishers were likely to oppose the possibility of targeting it instead of *N. unicornis*, since *N. unicornis* was predominantly

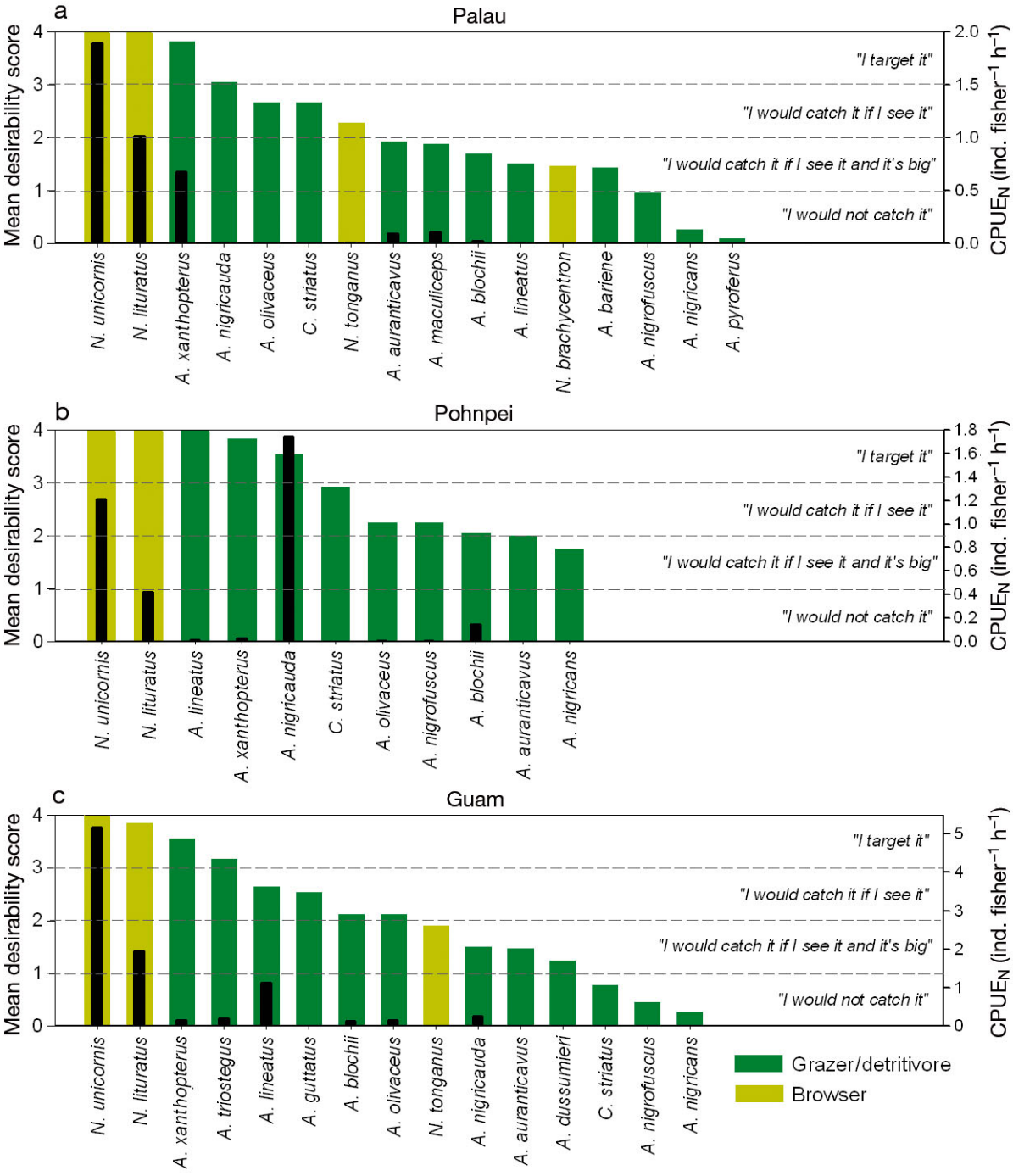

Fig. 4. Mean desirability score of different acanthurid species *Acanthurus*, *Ctenochaetus* and *Naso* spp. (see Table 1) (coloured bars, left *y*-axis) and mean $CPUE_N$ (ind. fisher^{-1} h^{-1}) (solid black bars, right *y*-axis) in (a) Palau, (b) Pohnpei and (c) Guam. Colours of bars indicate the different functional roles

valued for its taste (60–100% of responses) rather than for size or convenience, thus complicating its exchangeability.

Opportunities to alleviate the impact of the spearfishery on *Hipposcarus longiceps* could be offered by *Scarus ghobban* in Palau, *Chlorurus bleekeri* in Pohnpei and *Scarus festivus* in Guam (Fig. 5). Although most of these species have relatively low PGI (Table 3), *S. ghobban* would be the least recommended based on its vulnerability to fishing (L_∞:K = 175). Substituting *H. longiceps* with the non-schooling species *C. bleekeri* or *S. festivus* may prove challenging from an ecological perspective. Large schooling aggregations are common

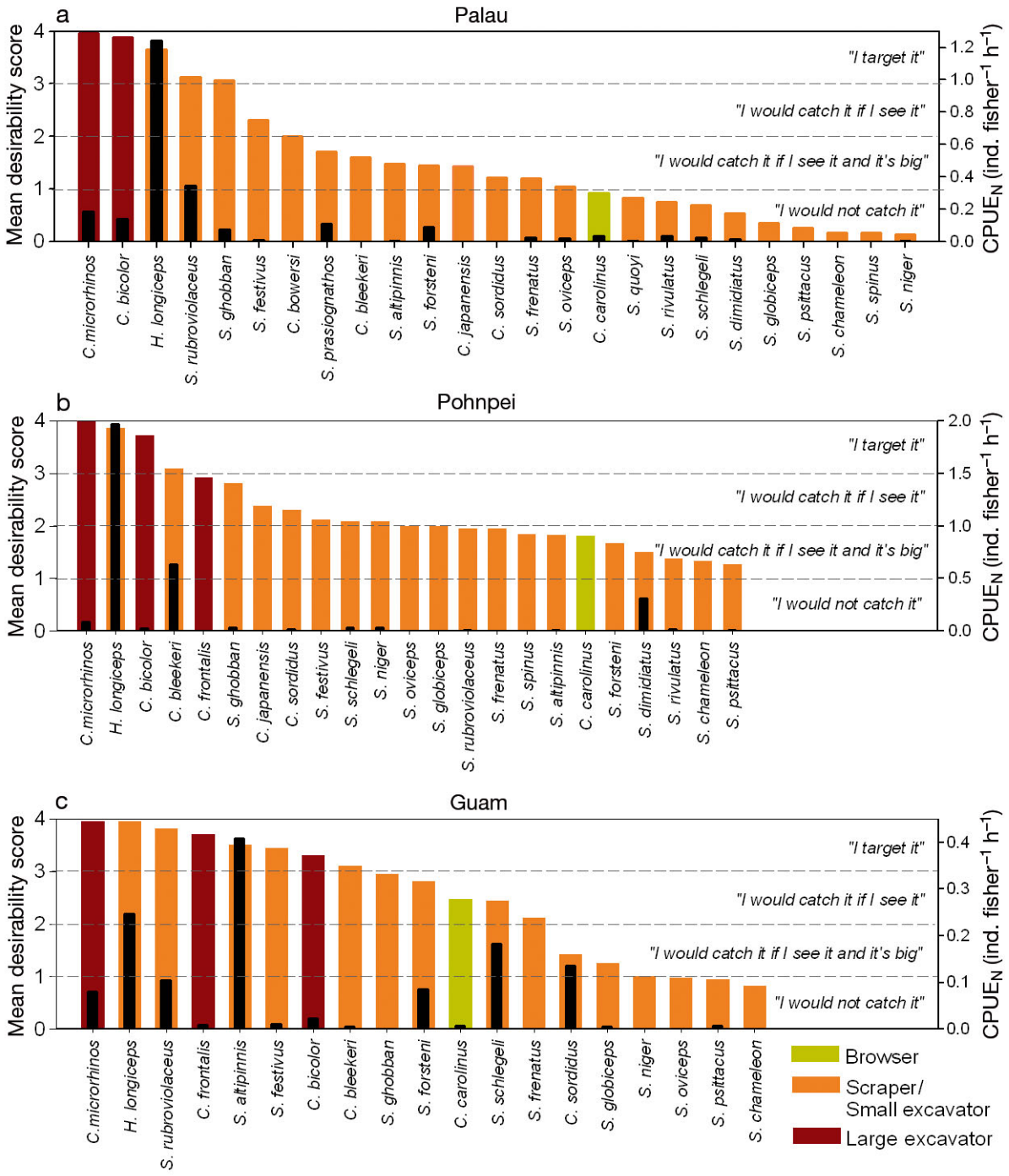

Fig. 5. Mean desirability score of different parrotfish species *Calotomus*, *Cetoscarus*, *Chlorurus* (includes *C. bowersi*, *C. japanensis*, *C. frontalis*), *Hipposcarus* and *Scarus* spp. (see Table 1) (coloured bars, left *y*-axis) and mean $CPUE_N$ (ind. fisher^{-1} h^{-1}) (solid black bars, right *y*-axis) in (a) Palau, (b) Pohnpei and (c) Guam. Colours of bars indicate the different functional roles

in *H. longiceps* (Welsh & Bellwood 2012) and may confer increased catchability on this species, thus making it an ideal target. Finding an alternative to *H. longiceps* may prove the most challenging in Palau and Pohnpei, where this species was mostly valued for taste (54% and 60% of responses, respectively). Similar-sized alternatives may meet less resistance among fishers in Guam, where *H. longiceps* was mostly valued because of its size (54% of responses).

With *Bolbometopon muricatum* fishing permanently banned in Palau, virtually no alternative targets are likely to be easily recommended to supplant *Chlorurus microrhinos*, *Scarus rubroviolaceus*, and

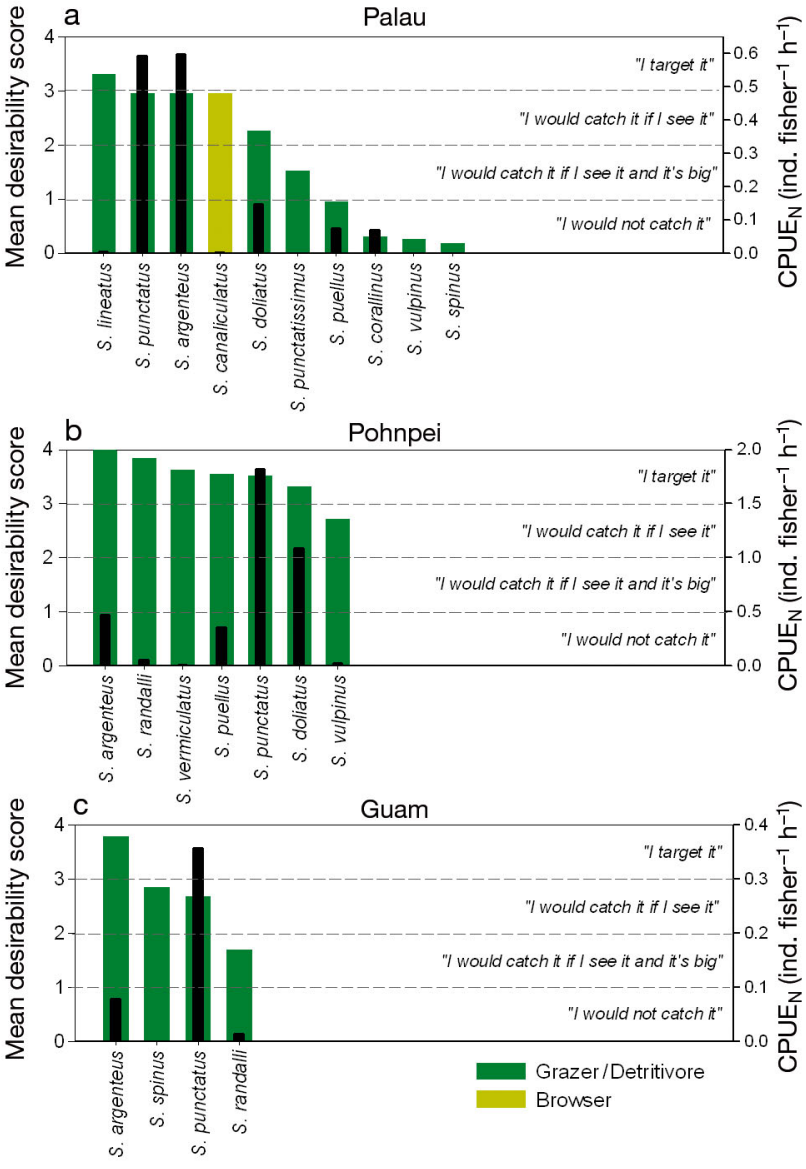

Fig. 6. Mean desirability score of different rabbitfish species *Siganus* spp. (coloured bars, left *y*-axis) and mean CPUE$_N$ (ind. fisher^{-1} h^{-1}) (solid black bars, right *y*-axis) in (a) Palau, (b) Pohnpei and (c) Guam. Colours of bars indicate the different functional roles

Cetoscarus bicolor in the fishery. These are among the largest parrotfishes, with size being the main driver of fishers' selectivity for these species (69, 60 and 57% of responses, respectively). Prioritising these 3 parrotfish species for protection is not straightforward; *C. bicolor* and *S. rubroviolaceus* warrant protection from a vulnerability perspective, whereas *C. bicolor* and *C. microrhinos* need to be managed from a functional perspective.

Based on vulnerability to fishing, *Siganus doliatus* was more resilient to fishing, compared to *S. punctatus* (Table 3). However, due to the paucity of information on the PGI of *S. doliatus*, it is uncertain whether this species could absorb increased fishing pressure without impairing the grazing process. Suggesting an exchange of *S. punctatus* for alternative targets may prove especially difficult in Palau, where this species was largely appreciated primarily because of its taste (60% of responses).

DISCUSSION

Managers are increasingly adopting an ecosystem-based approach to fisheries management in an effort to maintain ecosystem function and resilience in the face of climate change (Pikitch et al. 2004). We found ecological concerns associated with the exploitation of 6 roving-grazer species that play a variety of functional roles in Micronesia (i.e. *Naso unicornis*, *Cetoscarus bicolor*, *Chlorurus microrhinos*, *Hipposcarus longiceps*, *Scarus rubroviolaceus* and *Siganus punctatus*). Voluntary shifts in fishers' behaviour might alleviate some of these risks, particularly for species that are caught opportunistically (e.g. *Naso tonganus*, *N. brachycentron* and *Chlorurus frontalis*). Opportunities to recommend alternative targets to replace the most desirable targets (e.g. *N. unicornis*, *C. microrhinos* and *C. bicolor*) were scarce, suggesting that control by regulation rather than voluntary choices might be required.

Based on this analysis, fishing pressure should be most urgently directed away from *Naso unicornis*, *Hipposcarus longiceps* and *Siganus punctatus* in all 3 countries. In Palau, efforts should also be directed to reduce the fishing pressure on *Cetoscarus bicolor*, *Scarus rubroviolaceus* and *Chlorurus microrhinos.* Moreover, in Guam the fishery for *S. rubroviolaceus* also warrants vigilance. In all countries it is imperative to avoid immature catches for the abovementioned species.

The concerns associated with the exploitation of *Naso unicornis* support previous studies where fishermen acknowledged significant declines of this species over the last 50 yr (Kitalong & Dalzell 1994).

Although *N. unicornis* is particularly wary of divers and rarely observed feeding, stationary video cameras have recorded it as being one of the only species capable of effectively reducing the biomass of adult *Sargassum* spp. (Hoey & Bellwood 2009). From a functional perspective, diminished populations of this vulnerable browser may hinder the capacity of Micronesian reefs to revert from adverse changes generating macroalgal dominance. Given the high value of *N. unicornis* among fishers, recommending *Acanthurus xanthopterus* as an alternative species was found to be unfeasible. Such a switch in target may be further complicated by the fact that these species occupy different habitats. While *N. unicornis* is a cosmopolitan species distributed across reef flats, reef crests, patch reefs, forereefs and outer terraces (up to 25 m) (Caillart et al. 1994, Hoey & Bellwood 2009, Marshell et al. 2011), *A. xanthopterus* is confined to deeper outer slopes (below 25 m) (Caillart et al. 1994), thus making it harder to catch. A potentially useful management measure aimed to preserve the browsing function might be to implement temporary closures of *N. unicornis* fishing when natural disturbances that may result in large-scale coral mortality emerge locally. However, short-term management of this type will only succeed if densities of *N. unicornis* are routinely maintained at levels that are demographically relevant and sensitive to a short-term change in fishing mortality. No obvious herbivore may be unequivocally suggested as an alternative target. Moreover, a proposed shift in target may meet resistance among spearfishers, given that the value of *N. unicornis* is mainly in its taste. However, given that 8% of the fishers interviewed in Palau explicitly declared being supportive of management measures to protect this species, policies might be welcomed at least by the minority of the spearfishing population.

Regulating the fishery of *Hipposcarus longiceps*, *Cetoscarus bicolor*, *Scarus rubroviolaceus* and *Chlorurus microrhinos* will most likely meet challenges, given that spearfishers ranked these as their preferred parrotfish species. From both a vulnerability and functional perspective, risks associated with the exploitation of *C. bicolor* require perhaps the most urgent attention. Reducing the excavating/bioeroding function of *C. bicolor* will result in impairment of the potential for dead coral removal, clearing new areas of substratum for coral colonization, favouring the growth of coralline algae, and recycling of sediments (Steneck 1988, Choat 1991, Folke et al. 2004, Hoey & Bellwood 2008). From a functional perspective, special attention should be given to *H. longiceps* catches. Although this species has been catalogued as having a relatively high-redundancy functional role (i.e. scraping/small excavating; Green & Bellwood 2009), individuals took up to 50% of total bites on the calcified alga *Halimeda* spp. and consumed at least another 9 macroalgal species in experimental assays (Mantyka & Bellwood 2007a,b). Therefore, risks associated with *H. longiceps* may not be limited to the loss of turf scraping function, but also the potential loss of macroalgal removal.

Because this study aimed to identify risks among all harvested roving herbivores, metrics of parrotfish ecological importance were calculated at a species-level, rather than at a size-class level. Consequently, intra-specific variability in PGI due to body size was unaccounted for. A further step to refine parrotfish PGI calculations (and corresponding exploitation risks) should consider that grazing impact may increase non-linearly with body size (Lokrantz et al. 2008). Such an increase implies that a severe loss of functional performance may be expected from overfishing large individuals (Bellwood et al. 2003, 2012, Lokrantz et al. 2008).

Failing to reflect the variability caused by the substratum characteristics, jaw-based estimates of parrotfish bite area could arguably be less accurate than direct scar measurements, thus compromising our PGI estimates. However, bite areas obtained with both methods were comparable. The bite size of *Chlorurus microrhinos* (46–58 cm TL) ranged from 1.45–1.94 cm^2 on the Great Barrier Reef (Bellwood 1995), whereas in the present study the modelled bite area for similar sized *C. microrhino*s ranged from 1.16–1.47 cm^2. Similar bite sizes were obtained from direct scar (Bellwood 1995) and jaw measurements for *Chlorurus sordidus* (0.20–0.23 cm^2 vs. 0.13–0.23 cm^2 in this study) and *Scarus rivulatus* (0.44 vs. 0.30–0.34 cm^2 in this study) (Table S2 in the Supplement).

It is difficult to assess the ecological implications of the heavy exploitation of *Siganus punctatus* in all 3 countries until the feeding habits of this species are studied in detail. Rabbitfishes dominated the total catch volumes in Pohnpei where fishers caught the largest proportion of immature individuals. Although from a functional perspective immature rabbitfish are likely to have less functional contribution due to their smaller size, exploiting them exacerbates the risk of losing reproductive potential from the population, and may ultimately hinder the adult grazing potential. In Guam, the percentage of immature siganids observed in the catch was relatively low. However, this does not account for the seasonal fish-

ery of juveniles (mañahak) which poses an important post-recruitment bottleneck for rabbitfishes (Kami & Ikehara 1976), including *Siganus spinus* and *S. argenteus* (S. Bejarano pers. obs.). The mañahak fishery remained outside the scope of this paper, thus its ecological impacts remain poorly understood.

In the recently explored context of the ecological roles of rabbitfish, Fox et al. (2009) hypothesised that while some species seek shelter on the reef, they are functionally active in off-reef locations. The impacts of the fishery on the function of these species (e.g. *Siganus lineatus*) may, therefore, need to be considered when managing other ecosystems (e.g. seagrasses, mangroves). However, most rabbitfishes play a significant role in macroalgal to epilithic algal phase-shift reversals on reefs (Bellwood et al. 2006), with certain species (e.g. *Siganus doliatus*) acting as important *Sargassum* consumers across habitats (Fox & Bellwood 2008), and pairing species (e.g. *Siganus corallinus*, *S. puellus* and *S. vulpinus*) selectively exploiting crevices that are inaccessible to other reef fish (Fox & Bellwood 2013). The relative resilience of rabbitfish to fishing does not justify discarding ecological risks associated with the spear fishery. In Palau and Pohnpei, catch levels of *S. doliatus* and *S. puellus* were moderate, but need to be monitored to help maintain the macroalgal removal capacity of the former, and the uniqueness in niche-exploitation of the latter. We anticipate that rabbitfish regulations would meet less resistance among Palau fishers, who ranked these species as caught opportunistically, than among Pohnpei fishers who classified these among of their preferred targets.

Life history parameters considered here were calculated per species for the studied region, thus failing to account for intra-specific or geographic variations in vulnerability to fishing. Length at first maturity, for example, may differ between male and female *Naso unicornis* (Eble et al. 2009). Therefore, more detailed fishing-related risks could be identified by calculating the L_m for different sexes, and determining if these are being differentially affected by undersized catches. Moreover, age and length at first maturity vary geographically in response to different rates of natural mortality (Gust 2004) and degrees of fishing pressure (Trippel 1995, Rochet & Trenkel 2003). Combining the catch data reported here with country-specific demographic information of the species involved in the fishery may provide further assistance for managers in species prioritisation.

Inducing changes in fishers' targeting behaviour may appear to be a challenging task compared to using conventional policy options with a widely-understood rationale. Enacting periodic closures of designated areas (Cinner et al. 2006) or gear-based management measures (McClanahan & Mangi 2004) as well as fortifying traditional management schemes (Johannes 1981, McClanahan et al. 1997), or enhancing the existing networks of marine protected areas are some of these options. Each entails a particular cost and a set of advantages and shortcomings in preserving reef resources which fall beyond the scope of this paper.

Shifting targeting behaviour in fishers requires them to be adequately informed about the potential ecological risks of their selectivity for roving-grazers. Commercial fishers are likely to oppose such initiatives due to their economic interest and the high desirability of the species involved. Compromises may be reached by diverting attention from species caught opportunistically in all countries. Further opportunities to reduce fishing pressure on low-redundancy functional groups may be found, for example, in diverting fishers' attention away from *Naso tonganus* and *N. brachycentron, Chlorurus frontalis,* and *Siganus corallinus*, *S. puellus* and *S. vulpinus*.

The intricate ecological implications of reducing the abundance of certain functional groups on Pacific reefs remains to be empirically tested. Moreover, there is much to be learned about the role of fisheries in decreasing species diversity and disturbing the feeding complementarity within the roving-grazer trophic guild (Burkepile & Hay 2008, 2011) and within functional groups (Fox & Bellwood 2013). Although the impairment of the grazing process seems to have less severe consequences in Pacific than Caribbean reefs (Roff & Mumby 2012), evidence has been found in Guam of key benthic colonisation processes being clearly affected by the suppression of herbivory (Belliveau & Paul 2002). Although a relatively high functional redundancy may favour the resilience of Pacific reefs (Bellwood et al. 2004, Roff & Mumby 2012), there is low redundancy within functional roles (e.g. Fox & Bellwood 2013). Therefore, risks of phase-shifts are by no means improbable where overfishing contributes to a disequilibrium between algal production and consumption.

Caveats and future research needs

Risks identified here were outlined based on one of the most significant sectors of the roving-grazer fishery: commercial spearfishing. Potential ecological impacts of the subsistence spear fishery, as well

as risks associated with catches derived from other gear (e.g. barrier nets or fish traps) and sold directly to smaller markets, families, restaurants or hotels need to be quantified in the future.

Reported values of per capita fish consumption in Micronesia (reviewed by Rhodes et al. 2011), and specifically in Palau (33 kg person^{-1} yr^{-1}), Pohnpei (69 kg person^{-1} yr^{-1}), and Guam (22 kg person^{-1} yr^{-1}), indicate that subsistence fishing makes up a significant proportion of the annual catches in all 3 countries. Estimated subsistence fisheries production in Palau (500–1100 t yr^{-1} including non-reef fish; Kitalong & Dalzell 1994) and Pohnpei (87 t yr^{-1} including only reef fish; Rhodes et al. 2011), also suggest that non-marketed catches could represent a considerable addition to the total volumes considered here. While the exclusion of subsistence and direct-sale catches implied an underestimation of the total catch volumes in all countries, this is unlikely to have invalidated the identified risks. Interviews with fishers, as well as with restaurant and market managers, suggest that species that were heavily harvested for market sale were also preferred by consumers and subsistence fishers. Therefore, minor differences may be expected in species composition between marketed and non-marketed catches. In most interviews, fishers indicated that in general, smaller individuals were caught for consumption. Thus, the proportion of catch below L_m as calculated from market catches may be an underestimate of the true proportion of undersized fish harvested in all countries.

Roving-grazer catches obtained with barrier nets are less frequently marketed compared to speared catches in Palau, likely because fishing journeys are synchronised with falling spring tides and schools travelling from reef flats to deeper water (Johannes 1981). Because *Hipposcarus longiceps* is usually targeted by net fishers (S. Bejarano pers. obs.), catch volumes and associated ecological risks were likely underestimated in Palau, and require further examination. In Guam, catches landed by free-diving spearfishers in smaller markets could not be consistently surveyed due to logistic constraints. However, regular inspections indicated that free-diving catches were drastically different from SCUBA catches in volume, size and species composition. Investigating the targeting behaviour and catches of free-divers in Guam may lead to the recognition of further ecological risks.

Potential bias was introduced in the catch data presented here by timing our surveys during new-moon periods and closed grouper seasons. Catch volumes landed during more illuminated periods of the lunar cycle may be lower in all countries. In Palau and Pohnpei, catch volumes are representative of the times of year when access to groupers is restricted. Several grouper species constitute important targets of spearfishers in both countries (Dalzell et al. 1996, Rhodes & Tupper 2007). Therefore, some changes in the species and size composition of the roving-grazer catch during the open grouper season may be expected (authors' unpubl. data). Although there is no seasonal grouper closure in Guam, groupers are scarce on Guam's reefs (Hensley & Sherwood 1993). Therefore, our Guam data may be reflecting SCUBA-speared catches that are likely to remain more stable throughout the year.

Because of the temporal scale of our surveys, this study comprises a snapshot of the roving-grazer spear fishery in all 3 countries. A detailed assessment of the representativeness of our 2 wk surveys (see details in Section 1 of the Supplement at www.int-res.com/articles/suppl/m482p197_supp.pdf) indicated that extrapolation to larger temporal scales must be subject to a number considerations. Total roving-grazer catch volumes may fluctuate throughout the year, and this may be more evident in species with strong seasonality (i.e. *Naso unicornis*). The temporal variations in the catch and associated ecological risks remain a subject requiring attention.

Concluding remarks

This study is simply a first step towards developing a true ecosystem-based fisheries policy for herbivores on coral reefs. A more comprehensive approach would set catch limits to individual species or functional groups, based on (1) a clear understanding of the contribution of the species to grazing, (2) the importance of grazing in preventing undesirable community shifts after disturbance, and (3) a demographic analysis of the response of a given reef fish species to fishing mortality. At this point we have used available data on herbivore behaviour, and considered vulnerability based on life history characteristics. There is still much to be learned about the importance of having a diverse herbivore assemblage (Burkepile & Hay 2008), and establishing critical levels of grazing for system resilience.

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