

Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific

AMANDA K. FORD^{a,b,*}, SONIA BEJARANO^a, ALYSSA MARSHELL^c and PETER J. MUMBY^c

^aLeibniz Center for Tropical Marine Ecology (ZMT), Bremen, Germany

^bInstitute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, Netherlands

^cMarine Spatial Ecology Lab, School of Biological Sciences, University of Queensland, St. Lucia, Brisbane, Australia

ABSTRACT

1. *Naso lituratus* (orangespine unicornfish) and *Naso unicornis* (bluespine unicornfish) are widespread species that are heavily targeted in many nearshore fisheries of Pacific Island countries. In addition to providing a critical food and income source, both species fulfil critical ecological functions in the top-down control of coral reef macroalgae; particularly fleshy brown algae (i.e. *Sargassum* spp.) which can out-compete and smother corals.

2. Despite heavy long-term harvesting, there are currently very limited species-specific management measures. This review assesses the biology and ecology of both species, and combines this with the current status of the fisheries in the Pacific, and proposes realistic ecosystem-based species-specific fisheries policies.

3. Although unicornfish populations have displayed continuing resilience to heavy fishing pressure, reports of declining stocks combined with a range of life-history traits (i.e. longevity, habitat-specificity, easily targeted aggregations), indicate that both species are vulnerable to overexploitation. Modern day common fishing practices such as scuba and night-time spearfishing are intensifying their exploitation.

4. The most effective management measure would be fishing effort constraints, including banning modern and unsustainable methods. However, owing to enforcement limitations in Pacific Islands, the most practical approach to management would include a combination of management tools, including periodic sales bans around identified spawning times (i.e. Hawaii; May–June), and size/catch limits.

5. Furthermore, home range data suggest that even with limited knowledge, small MPAs (<1 km²) in structurally complex areas using natural boundaries should accommodate the movement patterns of both species and provide sufficient protection; although MPAs of > 10 km linear distance are recommended for *N. lituratus*.

6. This comprehensive review confirms the pressing need for implementation of the aforementioned management practices to protect these species in regions where they are heavily targeted, and prevent the impairment of their critical ecological function and importance as a food and income source.

Copyright © 2016 John Wiley & Sons, Ltd.

Received 8 June 2015; Revised 12 October 2015; Accepted 14 December 2015

KEY WORDS: *Naso lituratus*; *Naso unicornis*; nearshore fisheries; unicornfish; macroalgae; life-history traits; gear restrictions; management tools

*Correspondence to: Amanda Ford, Leibniz Center for Tropical Marine Ecology (ZMT), Fahrenheitstrasse 6, Bremen 28359, Germany. Email: amanda.ford@zmt-bremen.de

INTRODUCTION

The orangespine unicornfish, *Naso lituratus* (Forster 1801), and the bluespine unicornfish, *Naso unicornis* (Forsskål 1775), are relatively large-bodied acanthurids that are common in a variety of coral reef habitats, where they feed primarily on large fleshy macroalgae such as *Sargassum* spp. (Randall, 2001). Both species genetically belong to the *Naso elegans* sub-clade which comprises unicornfish that are exclusively benthic foragers (Klanten *et al.*, 2004). *Naso lituratus* is widely distributed throughout the Pacific Ocean: from southern Japan to the Great Barrier Reef and New Caledonia, and east to the Hawaiian Islands, French Polynesia, Pitcairn Islands, and Clipperton Island (Randall, 2001). Once regarded as a wide-ranging Indo-Pacific species, morphological analyses confirmed that *N. lituratus* is replaced by *N. elegans* in most of the Indian Ocean (although these sister-species can still hybridize – see, Hobbs *et al.*, 2009) (Klanten *et al.*, 2004). *Naso unicornis* has a widespread distribution throughout the Indo-Pacific: from the Red Sea and East Africa through the Indian Ocean islands and India, east to Micronesia, Hawaii and Pitcairn Islands, French Polynesia, north to southern Japan, and south to the Great Barrier Reef and Lord Howe, Norfolk and Rapa Islands (Randall, 2001).

While the range of *N. unicornis* extends across the Indian Ocean, this review focuses specifically on the Pacific region where both species are culturally and commercially important food fishes, and are consistently among the top few species targeted by fishers (Table 1). Fishermen interviews in Palau highlighted the strong desirability for *N. lituratus* and *N. unicornis*, which were the most popular herbivorous fish, and became the most popular of all fish species during grouper fishery closures (Bejarano *et al.*, 2013, 2014). In Hawaii, *N. unicornis* has been among the top six species in the inshore fisheries for the last two decades, with harvesting continuing to increase every year (Figure 1), which is concerning local stakeholders (Eble *et al.*, 2009). Increased catches of these species may in part be due to shifting pressure as other more vulnerable targets have declined or

succumb to more stringent management, but are also likely to be linked to ongoing fishing gear modernization. Nonetheless, the consistently dominant proportion of the catch that this species comprises indicates a high resilience to long-term fishing pressure. Yet despite this resilience, overexploitation is becoming increasingly apparent across the Pacific region (Table 1), particularly in Micronesia where declines of these species in the snorkelling catch have prompted fishermen to use scuba to access individuals at greater depths (Bejarano *et al.*, 2013; Lindfield *et al.*, 2014).

In addition to their importance as a food and income source, these species have a key ecological function on coral reefs. The role of herbivorous fish in preventing algal phase-shifts on Indo-Pacific reefs is complex. Intense grazing upon algal turfs by key functional groups such as scrapers (e.g. *Scarus* spp.) and grazers (e.g. *Acanthurus* spp.) probably plays a key role in preventing fleshy macroalgae from emerging through the turf (Marshall and Mumby, 2012; Mumby *et al.*, 2013), although the relative role of individual species remains uncertain. However, if fleshy macroalgae do manage to escape grazing at the juvenile stage, then browsing species which feed exclusively on macroalgae are critical to reverse phase-shifts from hard coral to macroalgal domination (Green and Bellwood, 2009). While other browsing species (i.e. siganids and ehippids) have been identified, *N. lituratus* and *N. unicornis* play a disproportionately important role in this group, specifically in removing established brown macroalgal varieties, which are often the dominant group involved in such phase-shifts (Hoey and Bellwood, 2009b; Vergés *et al.*, 2012). As each herbivorous functional group plays a unique role in maintaining coral reef health and resilience, it is important to preserve functionally diverse communities. To achieve this, it is essential to implement management for heavily targeted species such as *N. lituratus* and *N. unicornis* with limited functional redundancy.

Although these unicornfish species are an important food and income source, and fulfil critical key ecological roles, there is a severe lack of explicit species-specific management measures (Table 1). A thorough evaluation of the biology,

Table 1. Relative importance and awareness of overexploitation of *Naso lituratus* and *Naso unicornis* in the fisheries of some Pacific Island countries. Gaps correspond to no available information. Numbers refer to corresponding references for each locality

Region	Relative importance	Signs of overexploitation	Awareness among stakeholders	Laws in place	References
Melanesia (Fiji)	<ul style="list-style-type: none"> - Unicornfish are some of the main species targeted by spear fishers¹ - <i>N. unicornis</i> often preferred food fish³ 	<ul style="list-style-type: none"> - <i>N. lituratus</i> and <i>N. unicornis</i> totally absent in fished areas but comprised 32% of biomass inside 9–10 year old reserves (<i>N. lituratus</i>: 64 to 76 g per 150 m², <i>N. unicornis</i>: 4 to 4093 g per 150 m²)⁵. - Observed a loss of large-bodied herbivores such as <i>N. unicornis</i> after 5 week harvest of closed area, with long-term effects⁴ - Four years after reserves were created, density of <i>N. lituratus</i> > 10 times greater, <i>N. unicornis</i> density improved 3–10 times² 		<ul style="list-style-type: none"> - Minimum size limit 300 mm (FL) for <i>Naso</i> spp.⁶. - Scuba spearfishing banned (but low enforcement)¹ 	<ul style="list-style-type: none"> Gillett and Moy, 2006¹; Friedman <i>et al.</i>, 2009b²; Jupiter and Egli, 2011³; Jupiter <i>et al.</i>, 2012⁴; Rasher <i>et al.</i>, 2013⁵; Fisheries Act [Cap 158] Fiji⁶
Melanesia (New Caledonia)	<ul style="list-style-type: none"> - <i>N. unicornis</i> dominates surgeonfish landings¹ 				<ul style="list-style-type: none"> Dalzell <i>et al.</i>, 1996¹; Wantiez <i>et al.</i>, 1997²
Melanesia (PNG)	<ul style="list-style-type: none"> - <i>Naso</i> spp. form large proportion of surgeonfish landings^{1,2} 		<ul style="list-style-type: none"> - Communities identify night-time spearfishing as a major threat³ 	None	<ul style="list-style-type: none"> Dalzell <i>et al.</i>, 1996¹; Friedman <i>et al.</i>, 2008²; Ford, personal observations 2014³
Melanesia (Solomon Islands)	<ul style="list-style-type: none"> - <i>Naso</i> spp. account for >10% of night-time spearfishery³. - <i>Naso</i> spp. contribute significantly to combined lagoon and outer-reef catch² 		<ul style="list-style-type: none"> - Communities identify night-time spearfishing as a major threat¹ 	<ul style="list-style-type: none"> - Scuba spearfishing banned January 2004¹ 	<ul style="list-style-type: none"> Gillett and Moy, 2006¹; Pinca <i>et al.</i>, 2009²; Hamilton <i>et al.</i>, 2012³
Micronesia (CNMI)		<ul style="list-style-type: none"> - 90% harvested <i>N. unicornis</i> immature¹ - 73% <i>N. unicornis</i> immature¹ - 61% <i>N. lituratus</i> immature¹ 			<ul style="list-style-type: none"> Houk <i>et al.</i>, 2012¹; Lindfield <i>et al.</i>, 2014²
Micronesia (FSM)				<ul style="list-style-type: none"> - Scuba spearfishing banned in Pohnpei¹ 	<ul style="list-style-type: none"> Bejarano <i>et al.</i>, 2013¹; E. Joseph, personal communication 2015²
Micronesia (Guam)	<ul style="list-style-type: none"> - Acanthurids (including <i>N. unicornis</i> and <i>N. lituratus</i>) account for majority of daily catch² - <i>N. unicornis</i> highest acanthurid biomass contribution to snorkel and scuba spearfishery last 20 years (<i>N. lituratus</i> also one of largest contributors)⁴ 	<ul style="list-style-type: none"> - Large proportion of <i>N. unicornis</i> catch immature (39–75%)² - 36% <i>N. lituratus</i> immature³ - Biomass and average length have increased in the scuba spearfishery over the last 20 years (probably due to more focused and deeper effort since other desirable species have declined). However, snorkel fishery mean biomass and length is in decline⁴ - 40% <i>N. unicornis</i> immature⁵ - <i>N. unicornis</i> have undergone long-term declines from the 	<ul style="list-style-type: none"> - Most residents support ban of exploitative fishing methods¹ 	<ul style="list-style-type: none"> - Minimum size limit 16'' (40 cm) in Pohnpei² None⁴ 	<ul style="list-style-type: none"> van Beukering <i>et al.</i>, 2007¹; Houk <i>et al.</i>, 2012²; Bejarano <i>et al.</i>, 2013³; Lindfield <i>et al.</i>, 2014⁴;
Micronesia (Palau)	<ul style="list-style-type: none"> - <i>N. unicornis</i> the single most important commercial reef fish^{2,3} - <i>N. lituratus</i> and <i>N.</i> 		<ul style="list-style-type: none"> - Fishermen have noticed serious decline^{1,2} 	<ul style="list-style-type: none"> - Scuba spearfishing illegal⁵ (but not enforced) 	<ul style="list-style-type: none"> Johannes, 1991¹; Kitalong and Dalzell, 1994²; Johannes <i>et al.</i>, 1999³;

(Continues)

Table 1. (Continued)

Region	Relative importance	Signs of overexploitation	Awareness among stakeholders	Laws in place	References
Polynesia (French Polynesia)	<i>unicornis</i> constitute 34 and 21% acanthurid catch ⁴ - <i>N. unicornis</i> one of the dominant species (up to 54%) in catch from all reef habitats - <i>N. lituratus</i> key part of catches (particularly in lagoon and passages). - <i>N. unicornis</i> consistently in top five species by weight in inshore fishery landings (19251 kg in 2012, 13504 kg in 2011, 15443 kg in 2010) ²	onset of the 1980s ² - 24% <i>N. lituratus</i> immature ⁵			Friedman <i>et al.</i> , 2009a ⁴ ; Bejarano <i>et al.</i> , 2013 ⁵ ; Kronen <i>et al.</i> , 2009
Polynesia (Hawaii)	- <i>N. unicornis</i> consistently in top five species by weight in inshore fishery landings (19251 kg in 2012, 13504 kg in 2011, 15443 kg in 2010) ²	- Declines in overall catch and size of <i>N. unicornis</i> ¹	- Concern over long-term sustainability due to changes in catch ¹	- Minimum size limit for <i>Naso</i> spp. 356 mm ¹ (smaller than female L ₅₀)	Eble <i>et al.</i> , 2009 ¹ ; Annual reports of Division of Aquatic Resources ²
Polynesia (Samoa)	- Unicornfish (and specifically <i>N. unicornis</i>) are commonly caught by spearfishers			- Minimum surgeonfish size limit 200 mm (FL); scuba spearfishery banned	Gillett, 2011
Polynesia (Tonga)	- <i>N. unicornis</i> already commonly marketed by 1978 ¹ - <i>N. unicornis</i> second most abundant (17%) part of scuba night-time spearfishing ^{2,3}				Uchida, 1978 ¹ ; Gillett and Moy, 2006 ² ; Gillett, 2011 ³
Polynesia (Tuvalu)	- Both <i>N. lituratus</i> and <i>N. unicornis</i> are very important in spearfishing catch ^{1,2,3}				Gillett and Moy, 2006 ¹ ; Sauni <i>et al.</i> , 2008 ² ; Gillett, 2011 ³

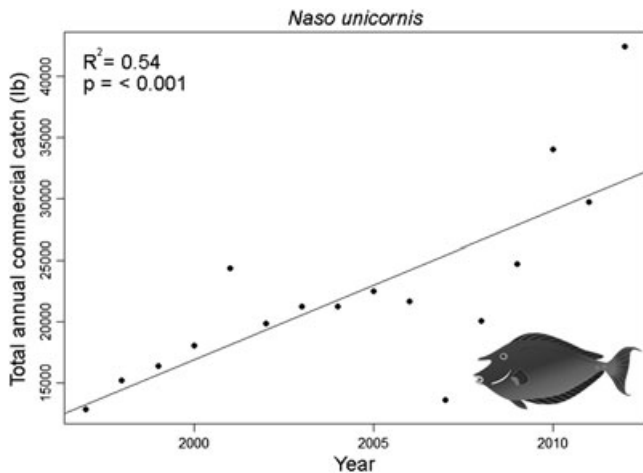


Figure 1. Graph displaying increase in commercial marine fisheries landings of *N. unicornis* in Hawaii 1997–2012. *Naso unicornis* has consistently been within the top six species in the inshore fisheries catch since 1997. Data represent landing reports from licensed fishermen, sourced from: <http://dlnr.hawaii.gov/dar/fishing/commercial-fishing/>.

ecology and fisheries status of both species can identify which traits and factors increase their vulnerability to overexploitation, and consequently which management measures would be most effective. The information within this review aims to support the design of adequate and viable policies that promote sustainable harvesting and maintain key ecological functions.

BIOLOGY, ECOLOGY AND LIFE-HISTORY CHARACTERISTICS

Although population biology indicates two species with overlapping functions should be spaced in terms of resource acquisition, these two species occupy very similar niches. This overlap is permitted because of varying life-history characteristics including home range sizes, mortality and growth rates. While this section discusses these characteristics for the areas where there are available data, it is clear that there is significant spatial variation which is probably driven by latitudinal gradients and local environmental features (Trip *et al.*, 2008; DeMartini *et al.*, 2014; Taylor *et al.*, 2014b).

Reproduction and recruitment

Naso lituratus and *N. unicornis* form aggregations of thousands of individuals in Palau (Johannes

et al., 1999), which local fishermen have linked to fish containing eggs (Sadovy de Mitcheson and Colin, 2012), thus suggesting this represents spawning behaviour. Both species have spawning periods spanning several months and perhaps throughout the year in Micronesia (Johannes, 1981; Sadovy, 2007; Taylor *et al.*, 2014b), while *N. unicornis* spawning periodicity is highly seasonal in Hawaii, peaking in May and June (DeMartini *et al.*, 2014). This pronounced seasonality may be a result of macroalgal seasonality promoting increased mesenteric fat deposits leading to ripening of the gonads (Montgomery and Galzin, 1993). Larvae of both species have a pelagic duration of 60–90 days, until they reach 4–5 cm and actively swim towards the reef (Planes and Fauvelot, 2002; Lecchini *et al.*, 2005; Irisson and Lecchini, 2008).

Growth and mortality rates

Growth coefficient (K) values of <0.15, 0.15 to 0.3 and >0.3 imply slow, medium and fast growth rates respectively (Froese *et al.*, 2000). Therefore, available data indicate that *N. unicornis* generally display slow to medium growth rates, whereas *N. lituratus* exhibit more rapid initial growth followed by an extended lifespan with little change in size (Figure 2(a), (b); Table 2).

Mortality rates of *N. lituratus* and *N. unicornis* remain largely unknown (Table 2). *Naso lituratus* consistently exhibits higher mortality rates than *N. unicornis* in Guam and Palau, which could be due to fast initial growth being associated with tissue damage and reduced lifespan (Mulligan and Leaman, 1992; Metcalfe and Monaghan, 2001; Lee *et al.*, 2013). Fishing (F) and natural mortality (M) rates tend to be alike for *N. lituratus*, while M is higher than F for *N. unicornis* (Table 2). According to Pauly (1984), fishing mortality should be around 40% of natural mortality for optimal exploitation, implying that *N. lituratus* is overexploited in Palau (Table 2). However, there is a severe lack of data on natural and fishing mortality from other regions and in recent years, making conclusions on the status of the fishery difficult, and which is further complicated by methodological discrepancies between studies.

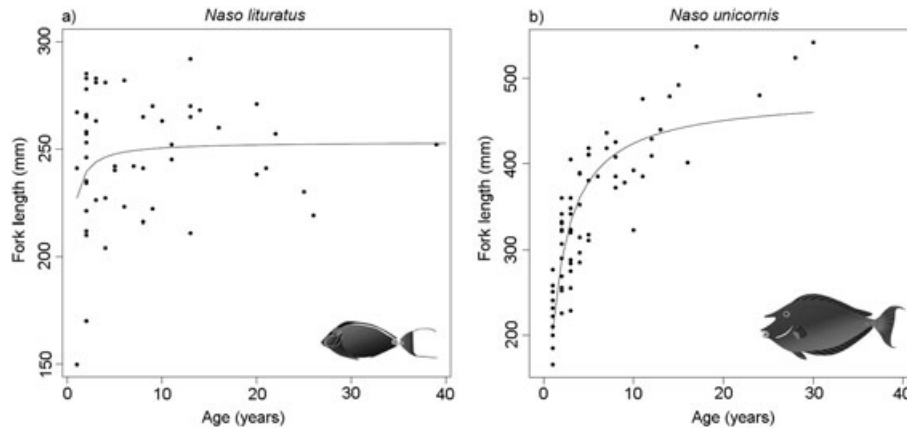


Figure 2. Size-at-age data for *N. lituratus* (a) (n=52) and *N. unicornis* (b) (n=68) from the northern GBR. Length data are based on fork length (FL) (mm). Data provided by JH Choat.

Home ranges and movement patterns

Both *N. lituratus* and *N. unicornis* display strong site attachment, preferring structurally complex areas which provide refuge holes (Meyer, 2003; Meyer and Holland, 2005; Marshall *et al.*, 2011). Relevant information on movements of *N. lituratus* and *N. unicornis* is only available from Guam and Hawaii, where two patterns were identified; commuting and foraging (Meyer and Holland, 2005; Marshall *et al.*, 2011). Commuters make daily crepuscular migrations over several hundred metres between night-time refuge holes and foraging areas, while foragers undertake multiple brief excursions from refuge holes to local foraging areas (10–40 m away). Although all home ranges were relatively small (<0.1 km²), *N. unicornis* in Guam utilized home ranges an order of magnitude larger than in Hawaii (3.2 ha/0.032 km² compared with 0.37 ha/0.0037 km² average) despite both studies investigating similar fringing reef habitats. Generally home ranges correlate with body size (Welsh *et al.*, 2013), yet interestingly within these species the range of smaller *N. lituratus* (fork length: 188–204 mm) extended twofold further (6.8 ha/0.068 km²) than those of *N. unicornis* (fork length: 228–282 mm) in Guam. Commuters were influenced by habitat topography in both studies, using sheltered, shallow habitats for daily migrations. When presented with a system of uninterrupted barrier reefs which offer no restriction to movement through natural boundaries, unicornfish cover

much larger distances (8–12 km in Pohnpei; unpublished data referred to in Taylor *et al.* (2014b)). Home ranges of *N. unicornis* correlate with body size, which is consistent with other acanthurids displaying ontogenetic habitat shifts, allowing larger individuals to optimize foraging once they reach a size at which they may escape predation risk (Dahlgren and Eggleston, 2000; Lecchini *et al.*, 2005; Marshall *et al.*, 2011).

Functional role

Both species target fleshy brown macroalgae which are consumed infrequently by other herbivore species, emphasizing the low functional redundancy of these unicornfish (Robertson and Gaines, 1986; Choat and Robertson, 2002; Choat *et al.*, 2002; Rasher *et al.*, 2013). Coral reef health is impacted by fast-growing algae that out-compete slow-growing corals when corals have been damaged by cyclones or coral bleaching (Hughes *et al.*, 2010). Algae blooms can also occur under additional conditions of eutrophication, iron enrichment, or herbivore depletion, affecting coral growth and recruitment (Mumby *et al.*, 2006; Hughes *et al.*, 2007; Steneck *et al.*, 2014). Coral recruitment can be inhibited by two major categories of algae: (1) algal turfs (Birrell *et al.*, 2005), and (2) fleshy macroalgae – particularly carpeting *Lobophora* spp., and erect *Sargassum* spp., which both reduce coral larval settlement and increase post-settlement mortality (Doropoulos *et al.*, 2014; Webster *et al.*, 2015).

Table 2. Size, maturity, growth and mortality data from the Pacific region for *N. lituratus* (*N. lit*) and *N. unicornis* (*N. uni*). FL = fork length, TL = total length, SL = standard length, Growth (K) and mortality (N, M, F) values are shown as year⁻¹. Gaps correspond to no available information. *Data combined with Guam and Pohnpei. Numbers refer to corresponding references for each locality

Region	Species	L _{max} (mm)	L ₅₀ (mm)	Growth rate (K)	Mortality rates			References
					Total (Z)	Natural (M)	Fishing (F)	
GBR	<i>N. lit</i>	(L _∞ =) 211 TL ²		0.755 ²				Choat and Axe, 1996 ¹ ; Choat and Robertson, 2002 ² ; Wilson, 2004 ³
	<i>N. uni</i>	457 SL ¹ 494 TL ²		0.489 ²	0.27 ³			
Melanesia (New Caledonia)	<i>N. uni</i>	600 FL	Females 145 FL	0.93	0.4			Kulbicki et al., 2005 Taylor et al., 2014b
	<i>N. lit</i>	Females 231 FL Males 251 FL	Males 178 FL					
Micronesia (Guam)	<i>N. uni</i>	Females 520 FL Males 431 FL	Females 292 FL Males 271 FL	0.22	0.16			
	<i>Nlit</i>	Females 250 FL Males 263 FL		1.38	0.33			
Micronesia (FSM – Pohnpei)	<i>N. uni</i>	Females 494 FL Males 496 FL	Females 312 FL Males 269 FL	0.36	0.32			Taylor et al., 2014b
	<i>N. lit</i>	(L _∞ =) 351 FL ¹ , 423 TL ²	241 TL ^{2*}	0.35 ¹	1.683 ¹ 0.414 ³	0.86 ¹ 0.209 ³	0.823 ¹ 0.205 ³	
Polynesia (Hawaii)	<i>N. uni</i>	(L _∞ =) 570 FL ¹ , 683 TL ²	371 TL ^{2*}	0.14 ¹	0.683 ¹ 0.161 ³	0.413 ¹ 0.130 ³	0.27 ¹ 0.031 ³	Eble et al., 2009 ¹ ; DeMartini et al., 2014 ²
	<i>N. uni</i>	Females 596 FL ² , Males 586 FL ²	Females 355 ² , 378 ¹ FL Males 286 ¹ , 301 ² FL	0.17 ¹				

Coral recruitment is essential for reef recovery after disturbances, highlighting the critical need for key functional herbivores to facilitate coral settlement. Moreover, contact between adult corals and fleshy macroalgae can reduce coral growth rates and fecundity (Tanner, 1995; Foster et al., 2008; Ferrari et al., 2012). The impacts of algae on corals can drive a fundamental phase-shift in community structure on reefs from coral- to algal-domination (Done, 1992). While other functional groups (grazers, scrapers/small excavators, large excavators/bioeroders) are essential for controlling algal turfs, browsers such as *N. lituratus* and *N. unicornis* are responsible for removing established macroalgae (Green and Bellwood, 2009).

Sargassum spp. are one of the most common brown fleshy macroalgae on Indo-Pacific reefs, and can cover >50% of the substrate in shallow inshore reefs (Bellwood et al., 2006; Wismer et al., 2009). *Naso lituratus* and *N. unicornis* play a large role in controlling *Sargassum* spp. even in highly diverse fish assemblages, emphasizing the importance of looking beyond biodiversity when considering functional capacity (Hoey, 2010; Hoey and Bellwood, 2010). For example, despite accounting for only 32% of the biomass within Fijian MPAs, *N. lituratus* and *N. unicornis* were responsible for 94% of feeding on transplanted brown macroalgae (Rasher et al., 2013). Correspondingly, at Lizard Island on the Great Barrier Reef (GBR), *N. unicornis* was responsible for 89.8% of observed bites on *Sargassum* spp., and further south at Orpheus Island, it was one of only three species (from a total of 43 herbivorous fish species present on the reef) that removed *Sargassum* spp. (Hoey and Bellwood, 2009b; Hoey, 2010). In addition to *Sargassum* spp. both species also graze on the chemically-rich brown alga *Dictyota bartayresiana*, which has been found to induce bleaching and to suppress photosynthetic efficiency of *Porites* spp. (Rasher and Hay, 2010; Rasher et al., 2013).

Importantly, a disparity may exist between biomass estimates and the functional impact of these species due to their recognized wariness to divers, and hence census-based assessments may have failed to capture their exact contribution to herbivory (Kulbicki, 1998). Herbivorous fish

density on the GBR, for example, does not reflect browsing rates as herbivory is disproportionately driven by both unicornfish which were scarcely encountered in visual surveys (Hoey and Bellwood, 2009a, b). In video observations in the species-rich reefs of Indonesia, *N. lituratus* and *N. unicornis* accounted for up to 64 and 83% respectively of bites on *Sargassum* spp. at different reefs, although neither species was observed in visual diver surveys (Plass-Johnson *et al.*, 2015). Such inconsistencies emphasize the difficulty in quantifying ecosystem processes using merely biomass estimates as both species may remain underrepresented. However, it is evident that there is low functional redundancy surrounding these species, and that depleted stocks could have a significant impact on benthic coral reef community structure.

FISHERY (PRACTICE AND STATUS) ACROSS THE PACIFIC

Although both species are currently found in the 'Least Concern' category of the IUCN Red list (McIlwain *et al.*, 2012a, b), a separate reclassification of the status of parrotfish and surgeonfish within the coral triangle area suggested that both *N. lituratus* and *N. unicornis* are 'Near Threatened' (Comeros-Raynal *et al.*, 2012). Despite their apparent regional-scale resilience, various factors contribute to their impending vulnerability; related to life-history characteristics and the way the fishery is practised.

Fishing practices

Handline and spearfishing are the more traditional methods employed by fishermen in Micronesia, Melanesia and Polynesia, with night-time spearfishing being the most effective for *N. lituratus*, *N. unicornis* and other large herbivores. Relatively recent availability of underwater flashlights throughout the region has led to night-time spearfishing becoming frequently practised across the Pacific (Rhodes *et al.*, 2008; Hamilton *et al.*, 2012). Given that this modern fishing method provides easy access to inactive fish, even when they are sheltering, it facilitates disproportionately

high catch rates. Night-time spearfishing is now commonly practised across most of the Pacific, despite many local fishermen being aware that this method is contributing to the decline of key species (Gillett and Moy, 2006). However, data on night-time spearfishing catches are primarily available from Micronesia, where this fishery contributes >75% of marketed reef fish (Houk *et al.*, 2012). Guam boasts the highest catch per unit effort (CPUE) compared with Pohnpei and Palau, most likely as a consequence of the currently unrestricted scuba spearfishery (Bejarano *et al.*, 2013). The use of scuba has also become popular among spearfishers throughout the Pacific region (Gillett and Moy, 2006), enabling fishermen to exploit deeper and previously inaccessible waters (Lindfield *et al.*, 2014). Scuba spearfishing remains legal in many parts of the Pacific, and even in areas where it is banned (e.g. Pohnpei, Palau, Fiji, Samoa – see Table 1), there is little catch monitoring or enforcement. In addition to gear modernizations leading to unsustainable practices, there is concern over the large proportion of immature individuals in catches. For example, across Micronesia 39–73% of *N. unicornis*, and 24–61% of *N. lituratus* individuals caught are immature (Bejarano *et al.*, 2013), and specifically in the Commonwealth of the Northern Mariana Islands (CNMI) and Guam, 90% and 75% (respectively) of harvested *N. unicornis* are immature (Houk *et al.*, 2012).

Vulnerable life-history characteristics

Unicornfish populations have remained relatively resilient to long-term fishing pressure in the Pacific, although both species exhibit life-history characteristics which make them vulnerable to overexploitation. First, both species form large aggregations, which despite being short-lived, allow fisherman to obtain large catches at predictable times and places (Johannes, 1981; Johannes *et al.*, 1999). For example, fishers in Palau targeting *N. unicornis* aggregations can catch >250 kg in a single trip (Sadovy de Mitcheson and Colin, 2012). In addition, predictable spawning seasonality (i.e. in Hawaii) also restricts reproduction to a limited period annually. Second, unicornfish life-history

characteristics such as habitat specificity, slow growth and extended longevity all increase their vulnerability to overfishing (Roberts and Hawkins, 1999); and when comparing these characteristics between the species suggest that *N. unicornis* populations are more vulnerable to overfishing than *N. lituratus* (Table 2). Furthermore, late maturation (particularly females) and large body size were found to be strong predictors of parrotfish vulnerabilities (Taylor *et al.*, 2014a), and *N. unicornis* displays similar values (i.e. $L_{50} > 250$ mm, $L_{max} > 400$ mm fork length; Table 2) to the most vulnerable species measured. Third, high catches of immature individuals in the Pacific may act synergistically with high unicornfish recruitment mortality rates (Doherty *et al.*, 2004), resulting in serious consequences for natural replenishment of unicornfish populations. However, large individuals are also vulnerable to exploitation owing to life-history characteristics and gear modernization. For example, as a consequence of ontogenetic habitat shifts, deeper reefs are primarily characterized by larger individuals, and thus scuba spearfishing is specifically exploiting the more fecund and functionally important individuals (Birkeland and Dayton, 2005; Lokrantz *et al.*, 2008). Furthermore, while smaller unicornfish are likely to find abundant suitable refugia in shallower habitats, larger individuals remain conspicuous and are more vulnerable to night-time spearfishers. Unicornfish are also more vulnerable to being caught in reefs with low topographic complexity which offer less refuge, indicating that these species are susceptible to disturbances such as storms and destructive fishing methods which destroy three-dimensional reef structure. Finally, although smaller, faster growing *N. lituratus*, have larger home ranges and higher natural mortality rates than *N. unicornis*, and should be a more sustainable fishing target, mortality data from Palau indicates that they are overexploited, while *N. unicornis* remains stable (Moore *et al.*, 2014; Table 2).

Status of the fishery in the Pacific

Reports from the last two decades have highlighted a growing concern over the fishing pressure exerted

on *N. lituratus* and *N. unicornis* populations in Micronesia (Table 1). Bejarano *et al.* (2013) referred to the exploitation of *N. unicornis* as one of Micronesia's most serious fisheries management concerns, and observed that *N. lituratus* is also heavily harvested. *Naso unicornis* is one of the most highly prized fish in Palau, and has been referred to as Palau's single most commercially important fish for many years despite fishermen recognizing that catches were already seriously declining over two decades ago (Johannes, 1991; Johannes *et al.*, 1999). In Pohnpei, Guam and Yap, acanthurids (in particular *N. unicornis*, but also *N. lituratus*) account for the majority of the daily catch (Houk *et al.*, 2012). However, exploitation is also conspicuous beyond Micronesia (Table 1); for example, concerns have been raised over a recent increase in commercial fishing pressure on *N. unicornis* in Hawaii (Figure 1; Eble *et al.*, 2009). In addition, *N. lituratus* represents a highly valuable catch for the aquarium trade. Between 2005–2009 the species was worth USD 122 090 in West Hawai'i alone, with approximately 29 859 individuals caught (Walsh *et al.*, 2010). In areas where these species are most heavily targeted (i.e. Micronesia), there are currently no bag limits or closed seasons for either unicornfish species.

IMPROVING MANAGEMENT

Naso lituratus and *N. unicornis* populations are heavily targeted by both subsistence and commercial fishing, and the aquarium trade across many regions of the Pacific. These species may have remained relatively resilient among coral reef fish owing to their biology: for example, overharvested stocks are replenished by distant populations due to a long pelagic larval duration and high connectivity (Horne *et al.*, 2008, 2013; Lindfield *et al.*, 2014). However, both species are heavily exploited, of high socio-economic and ecological value, and large proportions of immature individuals are caught. Therefore, a thorough revision of species-specific management strategies is warranted. Conserving the function of browsing herbivores has become a priority as it may provide

reefs with the best chance to resist and recover from increasingly erratic future disturbances (Graham *et al.*, 2013; Rasher *et al.*, 2013).

Gear- and effort-based restrictions

For large-scale and long-term sustainable harvesting, the foremost step would be banning the unsustainable practices of both night-time and scuba spearfishing in areas where they remain legal, and investing special effort into optimizing enforcement of the bans that are already implemented. Many local stakeholders throughout the Pacific agree that both scuba and night-time spearfishing are unsustainable and encourage overexploitation of fish stocks (Johannes, 1991; Gillett and Moy, 2006; van Beukering *et al.*, 2007; Rhodes *et al.*, 2008; Stoffle and Allen, 2012; Ford, personal observation 2014), as well as endangering fishermen as they take increasing risks to improve their catch (e.g. scuba spearfishers). Potential caveats for gear- and effort-based management include the large effort required from resource and enforcement agencies to patrol over wide areas, and the associated high profitability and low investment (particularly with night-time spearfishing). Without compensation or alternative livelihoods, fishermen will be unlikely to adopt more sustainable methods that are less profitable (Cinner *et al.*, 2009). However, conveying the importance and justification of these forms of management to local communities, and empowering and training local stakeholders, can encourage self-regulation within communities. Furthermore, while it is challenging to prove that fish were caught using unsustainable methods compared with daytime spearfishing on snorkel, new legislation could be promoted which makes it illegal for fishermen to have scuba gear or underwater flashlights on the same boat or vehicle as their catch (Gillett and Moy, 2006; Lindfield *et al.*, 2014). There is some consensus that fishermen should be encouraged to move away from spearfishing entirely because of the strong association of this method with species key to maintaining coral reef health (Cinner *et al.*, 2009). Where it is feasible (at larger market areas), management could also consider incorporating

licensing of fishers to restrict the number of people selling these species, and catch quotas could restrict the number of fish that individuals can catch and sell (Houk *et al.*, 2012). Restrictions could also be placed on aquarium fishers which could be limited to specifically target abundant pelagic juveniles owing to their high post-recruitment mortality (Doherty *et al.*, 2004).

Size limits

Management of fisheries often focuses on discouraging fishermen from removing small individuals, and thus promoting reproductive capacity of stocks. Minimum size limits have been imposed in a few countries (Table 1). However, not only are these limits difficult to enforce, but they may not offer adequate protection. In Hawaii, the legal minimum size limit for *N. unicornis* (356 mm) will prevent males being fished before maturity, but does not guarantee maturation of females before capture (Eble *et al.*, 2009; DeMartini *et al.*, 2014). In other areas (e.g. Samoa) small minimum size limits correspond to all surgeonfish and are thus unlikely to protect maturation of larger species such as *N. unicornis*, although a lack of data from regions throughout the Pacific makes this difficult to ascertain. While minimum size limits promote reproductive capacity, maximum size limits can promote stock recovery by protecting the largest and thus most fecund and functionally important individuals (Froese, 2004, Birkeland and Dayton, 2005). Coral reefs harbouring high fish biomass remain functionally impaired if they are dominated by small individuals as grazing impact can be non-linearly related to body size (Mumby *et al.*, 2006; Lokrantz *et al.*, 2008). As both unicornfish species are predominantly harvested via a highly selective fishing method (i.e. spearfishing), size limits could theoretically be established. However, while the growth profile of *N. unicornis* supports the implementation of size limits (as size can be extrapolated to age and maturity), they would be futile for *N. lituratus* individuals that reach asymptotic length very early, often within two years (Taylor *et al.*, 2014b). As with gear- and effort-based restrictions, enforcing size limits is

highly challenging for subsistence fishing, but has potential to be self-regulated at the local level if awareness of the importance is well conveyed. Furthermore, there is a strong potential for size limit enforcement at local fish markets by empowering and training local stakeholders.

Marine protected areas (MPAs)

While limited resources mean that fishing effort constraints are often challenging in many coral reef areas, or for all species, MPAs provide an alternative, albeit suboptimal, option under such circumstances (Brown and Mumby, 2014). While site attachment, small home ranges, and a preference for structurally complex habitats increase vulnerability (Roberts and Hawkins, 1999), they also indicate that both species are ideal candidates for protection through small MPAs using natural boundaries such as sandy areas. Both species comprised 32% of the herbivorous fish biomass inside adjacent 9–10 year old reserves in Fiji despite being absent from adjacent fished areas (Rasher *et al.*, 2013). The increased biomass of *N. lituratus* and *N. unicornis* was considered to be primarily responsible for driving macroalgal cover from between 49 and 91% cover (predominantly brown algae) in fished areas down to 1–3% inside reserves. Furthermore, biomass of *N. unicornis* improved as much as 300 times (up to 9.63 kg 500 m⁻²) inside 8–11 year old small (6–20 ha) reserves compared with fished areas (0.03 kg 500 m⁻²) in the central Philippines, actually showing the greatest improvement of the various species measured (Stockwell *et al.*, 2009). Correspondingly, macroalgal cover and reserve age were strongly negatively correlated. Density also improved within five year old reserves in New Caledonia for both *N. lituratus* (>10 times greater) and *N. unicornis* (3–10 times greater) (Wantiez *et al.*, 1997). There is therefore robust evidence that MPAs have a positive effect on both population density and individual size of these species, and consequently on the ecosystem.

Home range data indicate that MPAs can be small (<1 km² – Meyer, 2003; Meyer and Holland, 2005; Marshall *et al.*, 2011), but ideally should extend 10 and 2 km linear distance

(between natural boundaries in the longest dimension) for *N. lituratus* and *N. unicornis* respectively, accounting for areas extending over more than twice the home range size in all directions (Green *et al.*, 2014). While strong site-attachment can reduce adult spill-over from reserves, increased juvenile recruitment to local fishing areas will still benefit local fishermen (Moffitt *et al.*, 2009; Harrison *et al.*, 2012). Designs of MPAs should restrict reserve spacing to a maximum of 15 km, and movements between critical habitats for various life-history strategies should be accounted for (Green *et al.*, 2014). MPAs should also take into account that these species undergo ontogenetic habitat shifts which have implications for management on local scales, as closures focusing on specific habitats would protect particular life stages. To allow for true replenishment of overfished populations, highly dispersive reef species such as *N. unicornis* (Horne *et al.*, 2008) would need protection using networks of MPAs at regional scales (Taylor *et al.*, 2014b).

Seasonal/periodic closures

Seasonal closures and sales bans around spawning periods have been implemented for other targeted reef fish, particularly serranids (Beets and Friedlander, 1999; Russell, 2001; Rhodes *et al.*, 2008). When a peak spawning season is observed, such as May–June for *N. unicornis* in Hawaii, seasonal closures and sales bans would be highly effective (DeMartini *et al.*, 2014). When spawning occurs over several months or year-round, several short-term closures over peak monthly spawning have potential (e.g. GBR grouper fishery – Sadovy de Mitcheson and Colin, 2012). For example, *N. unicornis* has been observed to synchronize spawning times with the lunar cycle year-round in Palau (Johannes, 1981), indicating that short-term closures around new and full moons could be beneficial and may also protect these species during the highest fishing pressure (i.e. at new moon, see Rhodes *et al.*, 2008). A more recent study by Taylor *et al.* (2014b) found no relationship with the lunar cycle in other areas of Micronesia, but did identify peaks in spawning months for both species; *N. lituratus* peaked

through March–November in Guam, and April in Pohnpei, while *N. unicornis* spawning was limited through May–October in Guam, and in Pohnpei reproductively active individuals were found in all months except February, October and December. These results indicate that the fisheries could benefit from periodic closures and sales bans through March–September. There is an urgent need for conclusive reproductive data from other regions within these species' ranges. To this end, local knowledge of spawning behaviour and locations can contribute substantially to research and management (Haggan *et al.*, 2007).

Though there is potential for periodic closures, as is traditional in Melanesia, managers must address the prospective functional loss in the system after harvest openings. During a five-week harvest of one MPA in Fiji, there was a significant decrease in *N. unicornis* (-1303 kg ha^{-1} four weeks into harvest), and a concomitant increase in small roving grazers with reduced functional capacity (Jupiter *et al.*, 2012). These effects remained evident for one year after the area was closed to fishing again, emphasizing that a single intensive harvest can quickly undo the positive effects of long-term protection. Although managers can consider temporary closures of the fisheries immediately following a disturbance when macroalgal blooms are most likely to occur, these are unlikely to be beneficial unless pre-disturbance stock levels remain at a sufficient level for their browsing functional impact to be maintained. Managers should therefore consider also closing appropriate small areas over extended periods of time in order to act as 'egg-banks', allowing the highly dispersive exported larvae to repopulate over widespread reefs.

Alternative species

Interviews of local fishermen in Micronesia highlighted that it would be challenging to encourage a switch from *N. unicornis* to another more sustainable target species with higher functional redundancy (Bejarano *et al.*, 2013). According to fishermen desirability, *N. lituratus* would be one of the only species that could alleviate pressure on *N. unicornis*, yet this would

not provide a viable alternative due to (i) already being heavily targeted, and (ii) having correspondingly low functional redundancy. In places where protection is most difficult to enforce, catch levels of other macroalgal feeders (e.g. siganids) should not be overlooked.

Monitoring and research

This comprehensive review has highlighted that a severe lack of data exists, coupled with an obvious spatial disparity on key life-history characteristics which are critical for developing management tools. Mortality estimates must be conducted across more locations to enable managers to investigate trends and exploitation of populations and to define maximum sustainable yields. The apparent compensatory density dependence response of these species to harvesting requires further studies to determine maximum size limits and yields that promote optimal population growth responses. Owing to demographic variability, it is essential that local data is used to develop management within each region. For example, differences in reproduction highlight that size limits must be developed specifically within each region to ensure that minimum size limits are greater than the L_{50} value of the local population.

CONCLUDING REMARKS

Naso lituratus and *N. unicornis* represent two essential species in both the context of their contribution to Pacific Island fisheries, and their function as macroalgal browsers on coral reefs, for which there is very low redundancy. Although these species appear to have remained relatively resilient in many regions, the steep decline of other desirable species heralds a high risk of collapse. Of special concern is the ongoing modernization of fishing gears, which will likely continue to increase catch rates. If *N. lituratus* and *N. unicornis* stocks continue to be heavily exploited, severe economic repercussions can be expected for large human populations who rely on them as a food and income source. Serious consequences are also highly likely if their abundance is reduced far enough to impair their function, or if pathways of

larval connectivity are not maintained. For more long-term sustainability, attention should be focused on implementing species-specific management strategies and promoting more sustainable targeting of fish through increasing community awareness of fishing impacts. Furthermore, when resources are available, locally sourced socio-ecological data must be used to establish appropriate local management strategies owing to demographic variation of species traits as well as socio-cultural differences. Inevitable difficulties implementing and enforcing restrictions in the region indicate that ultimately a combination of different management tools and actions will be most effective.

ACKNOWLEDGEMENTS

PJM would like to thank the ARC for funding. AKF would like to thank Mark Vermeij for his comments on the original thesis, and Howard Choat for providing the size-at-age data for each species. AKF and SB would like to thank the German Ministry for Research and Education (BMBF) and the European Union for funding the REPICORE project (grant number 01LN1303A) through the 'Nachwuchsgruppen Globaler Wandel 4 + 1'. Finally, the authors would like to thank the editor and the reviewers for their useful contributions and comments for this manuscript.

REFERENCES

- Beets J, Friedlander A. 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environmental Biology of Fishes* **55**: 91–98.
- Bejarano S, Golbuu Y, Sapolu T, Mumby P. 2013. Ecological risk and the exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress Series* **482**: 197–215.
- Bejarano S, Mumby PJ, Golbuu Y. 2014. Changes in the spear fishery of herbivores associated with closed grouper season in Palau, Micronesia. *Animal Conservation* **17**: 133–143.
- Bellwood DR, Hughes TP, Hoey AS. 2006. Sleeping functional group drives coral-reef recovery. *Current Biology* **16**: 2434–2439.
- Birkeland C, Dayton PK. 2005. The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution* **20**: 356–358.
- Birrell CL, McCook LJ, Willis BL. 2005. Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* **51**: 408–414.
- Brown CJ, Mumby PJ. 2014. Trade-offs between fisheries and the conservation of ecosystem function are defined by management strategy. *Frontiers in Ecology and the Environment* **12**: 324–329.
- Choat JH, Axe LM. 1996. Growth and longevity in acanthurid fishes; an analysis of otolith increments. *Oceanographic Literature Review* **43**: 1263–1264.
- Choat JH, Robertson DR. 2002. Age-based studies on coral reef fishes. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem*, Sale PF (ed.). Academic Press: San Diego, CA; 57–80.
- Choat JH, Clements K, Robbins W. 2002. The trophic status of herbivorous fishes on coral reefs. *Marine Biology* **140**: 613–623.
- Cinner JE, McClanahan TR, Graham NA, Pratchett MS, Wilson SK, Raina JB. 2009. Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. *Journal of Applied Ecology* **46**: 724–732.
- Comeros-Raynal MT, Choat JH, Polidoro BA, Clements KD, Abesamis R, Craig MT, Erdi Özuardi M, McIlwain J, Muljadi A, Myers RF, et al. 2012. The likelihood of extinction of iconic and dominant herbivores and detritivores of coral reefs: the parrotfishes and surgeonfishes. *PloS One* **7**: e39825.
- Dahlgren CP, Eggleston DB. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* **81**: 2227–2240.
- Dalzell P, Adams TJH, Polunin NVC. 1996. Coastal fisheries in the Pacific Islands. *Oceanography and Marine Biology: An Annual Review* **34**: 395–531.
- DeMartini EE, Langston RC, Eble JA. 2014. Spawning seasonality and body sizes at sexual maturity in the bluespine unicornfish, *Naso unicornis* (Acanthuridae). *Ichthyological Research* **61**: 243–251.
- Doherty PJ, Dufour V, Galzin R, Hixon MA, Meekan MG, Planes S. 2004. High mortality during settlement is a population bottleneck for tropical surgeonfish. *Ecology* **85**: 2422–2428.
- Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* **247**: 121–132.
- Doropoulos C, Roff G, Zupan M, Nestor V, Isechal AL, Mumby PJ. 2014. Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. *Coral Reefs* **33**: 613–623.
- Eble JA, Langston R, Bowen B. 2009. Growth and reproduction of Hawaiian Kala, *Naso unicornis*. In *Fisheries Local Action Strategy, Final Report, Division of Aquatic Resources*, Hawai'i: Honolulu.
- Ferrari R, Gonzalez-Rivero M, Ortiz JC, Mumby PJ. 2012. Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. *Coral Reefs* **31**: 683–692.
- Foster N, Box S, Mumby P. 2008. Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastraea annularis*. *Marine Ecology Progress Series* **367**: 143–152.
- Friedman K, Kronen M, Pinca S, Magron F, Boblin P, Pakoa K, Awiva R, Chapman L. 2008. *Papua New Guinea country report: profiles and results from survey work at Andra, Tsoilaunung, Sideia and Panapompom*. PROCFish/C/CoFish. Secretariat of the Pacific Community: Noumea, New Caledonia.

- Friedman K, Kronen M, Pinca S, Lasi F, Pakoa K, Awira R, Boblin P, Tardy E, Chapman LB, Magron F. 2009a. *Palau Country Report: Profiles and results from survey work at Ngarchelong, Ngatpang, Airai and Koror*. PROCFish/C/CoFish. Secretariat of the Pacific Community: Noumea, New Caledonia.
- Friedman K, Kronen M, Vunisea A, Pinca S, Pakoa K, Magron F, Chapman L, Sauni S, Vigliola L, Tardy E, Labrosse P. 2009b. *Fiji Islands country report: Profiles and results from survey work at Dromuna, Muavuso, Mali and Lakeba*. PROCFish/C/CoFish. Secretariat of the Pacific Community: Noumea, New Caledonia.
- Froese R. 2004. Keep it simple: three indicators to deal with overfishing. *Fish and Fisheries* **5**: 86–91.
- Froese R, Palomares MLD, Pauly D. 2000. Estimation of life history key facts of fishes. In *FishBase 2000: Concepts, Design and Data Sources (no. 1594)*, R. Froese and D. Pauly (eds). ICLARM: Makati City, Philippines; 167–175.
- Gillett R. 2011. *Fisheries of the Pacific Islands regional and national information*, RAP Public: FAO Regional Office for Asia and the Pacific: Bangkok, Thailand.
- Gillett R, Moy W. 2006. *Spearfishing in the Pacific Islands; current status and management issues*, 19FAO. Fish Code Review: FAO, Rome.
- Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norström AV, Nyström M. 2013. Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment* **11**: 541–548.
- Green AL, Bellwood DR. 2009. Monitoring functional groups of herbivorous fishes as indicators for coral reef resilience. In *A practical guide for coral reef managers in the Asia Pacific Region*, IUCN: Gland, Switzerland Available online at: http://cmsdata.iucn.org/downloads/resilience_herbivorous_monitoring.pdf.
- Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT. 2014. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*. DOI: 10.1111/brv.12155.
- Haggan N, Neis B, Baird IG. 2007. *Fishers' Knowledge in Fisheries Science and Management*, 35–40UNESCO Publishing: Paris.
- Hamilton RJ, Giningele M, Aswani S, Ecochard JL. 2012. Fishing in the dark-local knowledge, night spearfishing and spawning aggregations in the Western Solomon Islands. *Biological Conservation* **145**: 246–257.
- Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, van Herwerden L, Planes S, Srinivasan M, et al. 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* **22**: 1023–1028.
- Hobbs J-PA, Frisch AJ, Allen GR, van Herwerden L. 2009. Marine hybrid hotspot at Indo-Pacific biogeographic border. *Biology Letters* **5**: 258–261.
- Hoey AS. 2010. Size matters: macroalgal height influences the feeding response of coral reef herbivores. *Marine Ecology Progress Series* **411**: 299–302.
- Hoey AS, Bellwood DR. 2009a. Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* **12**: 1316–1328.
- Hoey AS, Bellwood DR. 2009b. Among-habitat variation in herbivory on *Sargassum* spp. on a mid-shelf reef in the northern Great Barrier Reef. *Marine Biology* **157**: 189–200.
- Hoey AS, Bellwood DR. 2010. Cross-shelf variation in browsing intensity on the Great Barrier Reef. *Coral Reefs* **29**: 499–508.
- Horne JB, van Herwerden L, Choat JH, Robertson DR. 2008. High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution* **49**: 629–638.
- Horne JB, van Herwerden L, Abellana S, McIlwain JL. 2013. Observations of migrant exchange and mixing in a coral reef fish metapopulation link scales of marine population connectivity. *The Journal of Heredity* **104**: 532–546.
- Houk P, Rhodes K, Cuetos-Bueno J, Lindfield S, Fread V, McIlwain JL. 2012. Commercial coral-reef fisheries across Micronesia: a need for improving management. *Coral Reefs* **31**: 13–26.
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschanivskyj N, Pratchett MS, Steneck RS, Willis B. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**: 360–365.
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* **25**: 633–642.
- Irisson J-O, Lecchini D. 2008. *In situ* observation of settlement behaviour in larvae of coral reef fishes at night. *Journal of Fish Biology* **72**: 2707–2713.
- Johannes RE. 1981. *Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia*, University of California Press: Berkeley, CA.
- Johannes RE. 1991. Some suggested management initiatives in Palau's nearshore fisheries, and the relevance of traditional management. Palau Marine Resources Division Technical Report 91.
- Johannes RE, Squire L, Graham T, Sadovy Y, Renguul H. 1999. Spawning aggregations of Groupers (Serranidae) in Palau. In *The Conservancy Marine Conservation Report No 1*, The Nature Conservancy: Brisbane.
- Jupiter SD, Egli DP. 2011. Ecosystem-based management in Fiji: successes and challenges after five years of implementation. *Journal of Marine Biology*, vol. 2011, Article ID 940765, 14 pp. DOI: 10.1155/2011/940765.
- Jupiter SD, Weeks R, Jenkins AP, Egli DP, Cakacaka A. 2012. Effects of a single intensive harvest event on fish populations inside a customary marine closure. *Coral Reefs* **31**: 321–334.
- Kitalong A, Dalzell P. 1994. *A preliminary assessment of the status of inshore coral reef fish stocks in Palau - Inshore Fisheries Research Project Technical Document No. 6*, South Pacific Commission: Noumea, New Caledonia.
- Klanten SO, van Herwerden L, Choat JH, Blair D. 2004. Patterns of lineage diversification in the genus *Naso* (Acanthuridae). *Molecular Phylogenetics and Evolution* **32**: 221–235.
- Kronen M, Boblin P, Friedman K, Pinca S, Magron F, Awira R, Pakoa K, Lasi F, Tardy E, Vigliola L, Chapman L. 2009. *New Caledonia country report: Profile and results from survey work at Ouassé, Thio, Luengoni, Oundjo and Moindou*. PROCFish/C/CoFish. Secretariat of the Pacific Community: Noumea, New Caledonia.
- Kulbicki M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual

- censuses. *Journal of Experimental Marine Biology and Ecology* **222**: 11–30.
- Kulbicki M, Guillemot N, Amand M. 2005. A general approach to length–weight relationships for New Caledonian lagoon fishes. *Cybium* **29**: 235–252.
- Lecchini D, Planes S, Galzin R. 2005. Experimental assessment of sensory modalities of coral-reef fish larvae in the recognition of their settlement habitat. *Behavioral Ecology and Sociobiology* **58**: 18–26.
- Lee W-S, Monaghan P, Metcalfe NB. 2013. Experimental demonstration of the growth rate–lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280** (1752): 20122370.
- Lindfield SJ, McIlwain JL, Harvey ES. 2014. Depth refuge and the impacts of SCUBA spearfishing on coral reef fishes. *PLoS One* **9**: e92628.
- Lokrantz J, Nyström M, Thyresson M, Johansson C. 2008. The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* **27**: 967–974.
- Marshall A, Mumby PJ. 2012. Revisiting the functional roles of the surgeonfish *Acanthurus nigrofusus* and *Ctenochaetus striatus*. *Coral Reefs* **31**: 1093–1101.
- Marshall A, Mills JS, Rhodes KL, McIlwain J. 2011. Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. *Coral Reefs* **30**: 631–642.
- McIlwain J, Choat J, Abesamis R, Clements K, Myers R, Nanola C, Rocha L, Russell B, Stockwell B. 2012a. *Naso lituratus*. The IUCN Red List of Threatened Species. Version 2014. Available at: <http://www.iucnredlist.org/details/177950/0> [Accessed September 2014]
- McIlwain J, Choat J, Abesamis R, Clements K, Myers R, Nanola C, Rocha L, Russell B, Stockwell B. 2012b. *Naso unicornis*. The IUCN Red List of Threatened Species. Version 2014. Available at: <http://www.iucnredlist.org/details/summary/177970/0> [Accessed September 2014]
- Metcalfe NB, Monaghan P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* **16**: 254–260.
- Meyer CG. 2003. An empirical evaluation of the design and function of a small marine reserve (Waikīki Marine Life Conservation District). PhD thesis, Department of Zoology, University of Hawai'i, USA.
- Meyer CG, Holland KN. 2005. Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes* **73**: 201–210.
- Moffitt EA, Botsford LW, Kaplan DM, O'Farrell MR. 2009. Marine reserve networks for species that move within a home range. *Ecological Applications* **19**: 1835–1847.
- Montgomery WL, Galzin R. 1993. Seasonality in gonads, fat deposits and condition of tropical surgeonfishes (Teleostei: Acanthuridae). *Marine Biology* **115**: 529–536.
- Moore B, Rechellul P, Victor S. 2014. *Creel survey and demographic assessments of coastal finfish fisheries of southern Palau*. Secretariat of the Pacific Community, Noumea: New Caledonia 48 pp.
- Mulligan TJ, Leaman BM. 1992. Length-at-age analysis: can you get what you see? *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 632–643.
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, *et al.* 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science (New York)* **311**: 98–101.
- Mumby PJ, Bejarano S, Golbuu Y, Steneck RS, Arnold SN, van Woesik R, Friedlander AM. 2013. Empirical relationships among resilience indicators on Micronesian reefs. *Coral Reefs* **32**: 213–226.
- Pauly D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews No. 8. Manila, Philippines.
- Pinca S, Vunisea A, Lasi F, Friedman K, Kronen M, Awira R, Boblin P, Tardy E, Chapman L, Magron F. 2009. *Solomon Islands country report: Profiles and results from survey work at Nggela, Marau, Rarumana and Chubikopi*. PROCFish/C/CoFish. Secretariat of the Pacific Community: Noumea, New Caledonia.
- Planes S, Fauvelot C. 2002. Isolation by distance and vicariance drive genetic structure of a coral reef fish in the Pacific Ocean. *Evolution* **56**: 378–399.
- Plass-Johnson JG, Ferse SC, Jompa J, Wild C, Teichberg M. 2015. Fish herbivory as a key ecological function in a heavily degraded coral reef system. *Limnology and Oceanography* **60**: 1382–1391.
- Randall JE. 2001. *Surgeonfishes of the World*, Mutual Publishing and Bishop Museum Press: Hawaii, USA.
- Rasher DB, Hay ME. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. Proceedings of the National Academy of Sciences of the United States of America **107**: 9683–9688.
- Rasher DB, Hoey AS, Hay ME. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* **94**: 1347–1358.
- Rhodes KL, Tupper MH, Wichimel CB. 2008. Characterization and management of the commercial sector of the Pohnpei coral reef fishery, Micronesia. *Coral Reefs* **27**: 443–454.
- Roberts CM, Hawkins JP. 1999. Extinction risk in the sea. *Trends in Ecology & Evolution* **14**: 241–246.
- Robertson DR, Gaines SD. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* **67**: 1372–1383.
- Russell M. 2001. *Spawning aggregations of reef fishes on the Great Barrier Reef: implications for management*, Great Barrier Reef Marine Park Authority: Townsville, Australia.
- Sadovy Y. 2007. Report on current status and exploitation history of reef fish spawning aggregations in Palau. *Western Pacific Fishery Survey Series: Society for the Conservation of Reef Fish Aggregations* **3**: 1–40.
- Sadovy de Mitcheson Y, Colin PL (eds). 2012. *Reef Fish Spawning Aggregations: Biology, Research and Management*. Springer: Netherlands.
- Sauni S, Kronen M, Pinca S, Sauni L, Friedman KJ, Chapman LB, Magron F. 2008. *Tuvalu country report: profiles and results from survey work at Funafuti, Nukufetau, Vaitupu and Niutao*. PROCFish/C/CoFish. Secretariat of the Pacific Community: Noumea, New Caledonia.
- Steneck R, Arnold S, Mumby P. 2014. Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors. *Marine Ecology Progress Series* **506**: 115–127.
- Stockwell B, Jadloc C, Abesamis R, Alcalá A, Russ G. 2009. Trophic and benthic responses to no-take marine reserve

- protection in the Philippines. *Marine Ecology Progress Series* **389**: 1–15.
- Stoffle BW, Allen SD. 2012. The Sociocultural Importance of Spearfishing in Hawai'i. US Department of Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-PIFSC-31, pp 38.
- Tanner JE. 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* **190**: 151–168.
- Taylor BM, Houk P, Russ GR, Choat JH. 2014a. Life histories predict vulnerability to overexploitation of parrotfishes. *Coral Reefs* **33**: 869–878.
- Taylor BM, Rhodes KL, Marshall A, McIlwain JL. 2014b. Age-based demographic and reproductive assessment of orangespine *Naso lituratus* and bluespine *Naso unicornis* unicornfishes. *Journal of Fish Biology* **85**: 901–916.
- Trip EL, Choat JH, Wilson DT, Robertson DR. 2008. Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Marine Ecology Progress Series* **373**: 97–109.
- Uchida RN. 1978. Fisheries information for Western Samoa and the Kingdom of Tonga. In *Southwest Fisheries Center Administrative Report 26H*, Hawai'i: Honolulu.
- van Beukering P, Haider W, Longland M, Cesar H, Sablan J, Shjegstad S, Beardmore B, Liu Y, Omega Garces G. 2007. The economic value of Guam's coral reefs. Mangilao, Technical Report no. 116, University of Guam Laboratory.
- Vergés A, Bennett S, Bellwood DR. 2012. Diversity among macroalgae-consuming fishes on coral reefs: a transcontinental comparison. *PLoS One* **7**: e45543.
- Walsh W, Cotton S, Carman B, Livnat L, Osada K, Barnett C, Tissot B, Stevenson T, Wiggins C, Tarnas D. 2010. Report on the findings and recommendations of effectiveness of the West Hawai'i Regional Fishery Management Area. Report to the Twenty-Fifth Legislature Regular Session of 2010. Department of Land and Natural Resources State of Hawai'i.
- Wantiez L, Thollot P, Kulbicki M. 1997. Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs* **16**: 215–224.
- Webster FJ, Babcock RC, van Keulen M, Loneragan NR. 2015. Macroalgae inhibits larval settlement and increases recruit mortality at Ningaloo Reef, Western Australia. *PLoS One*. DOI: 10.1371/journal.pone.0124162.
- Welsh JQ, Goatley CHR, Bellwood DR. 2013. The ontogeny of home ranges: evidence from coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20132066.
- Wilson SK. 2004. Growth, mortality and turnover rates of a small detritivorous fish. *Marine Ecology Progress Series* **284**: 253–259.
- Wismer S, Hoey A, Bellwood DR. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Marine Ecology Progress Series* **29**: 499–508.