THE NATURE CONSERVANCY'S MAPPING OCEAN WEALTH PROJECT:

MODELLING AND MAPPING FISHING PRESSURE AND THE CURRENT AND POTENTIAL STANDING STOCK OF CORAL-REEF FISHES IN FIVE JURISDICTIONS OF MICRONESIA

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Cover photographs:

Left: *Plectropomus leopardus* (leopard coral trout) is an important fishery species from many reefs in Micronesia. © Mark Priest.

Right: A wide variety of fishing techniques are used in Micronesia, including this use of a cast net in Guam. © Mark Priest.

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Summary

Marine ecosystem goods and services, such as protein provision, are being affected by a range of anthropogenic stressors, and maintaining their integrity represents an important goal of conservation and management. Consequently, there is a need for a greater effort to incorporate ecosystem services into policy making at a range of scales. In response to this need, The Nature Conservancy (TNC) has established the Mapping Ocean Wealth Project to quantitatively describe what global oceans provide today, and facilitate better decision making.

Within a larger project framework, TNC contracted the University of Queensland (Australia) to undertake Phase 1 of the effort to map coral reef fisheries. The key aims of this work were to model and map fishing pressure, model and map the current value of coral reef fisheries (current fish standing stock), and assess the potential benefit of conservation and management measures, such as the potential standing stock on a reef if fishing was managed through the establishment of no-take reserves or other fisheries management tools. The research at UQ also aimed to identify options for using the resulting maps and models for marine spatial planning, and to assist with the preparation of practical tools summarizing the findings of the research and its potential applications. Phase 1 modelled and mapped these variables (fishing pressure, current and potential standing stock) across five jurisdictions of Micronesia (the Republic of Palau, the Federated States of Micronesia, the Territory of Guam, the Commonwealth of the Northern Marianas, and the Republic of the Marshall Islands). Micronesia represented a tractable spatial scale to explore the mapping and modelling approaches, and the project results will complement on-going conservation and management initiatives in the region. Furthermore, fisheries are of significant economic importance in the region. The final products were delivered in January 2016, with the aim of extending to a global scale in a funding-dependent Phase 2 later in the year. This report outlines the methods used to achieve the mapping and modelling aims of Phase 1, shows the results of the statistical models, and includes the resulting maps.

Through the generous provision of fish survey data from a range of sources, the Phase 1 project had access to >1,100 fish surveys from all five jurisdictions. Data from locations where surveys were conducted by more than one data source suggests that the data are comparable, and can be pooled to obtain robust, region-wide models. The first step was to statistically model fishing pressure, which used fishery-independent data on parrotfish mean size from the fish surveys. This approach builds on a growing literature suggesting that the size of larger parrotfishes represents an excellent indicator of fishing pressure. Data on parrotfish sizes across all jurisdictions were modelled in relation to 22 potential predictor variables, including human population size, distance to markets, and oceanic temperature and productivity. When controlling for biophysical gradients, the model demonstrated that fishing was best predicted by distance to the nearest port and human population pressure within 200 km. This model was then used to extrapolate relative fishing pressure (specifically the total cumulative impact of fishing on the fish assemblage, which may be decoupled from current fishing effort) to all sites across the region, and generate a continuous map. However, the values of fishing pressure (and standing stock) were generally restricted to forereef slopes, reflecting that the fish survey data were collected in this particular habitat type. This map represents the first continuous assessment of fishing pressure across the region.

Estimates of fishing pressure were then used as a key data layer, along with 16 other potential environmental variables, to model current standing stock at an independent set of sites where additional survey fish data were available. The metric of standing stock was the total biomass of 19 key fisheries species from a range of taxa and trophic groups that were surveyed in all data sources and are found across the region, and are a good proxy of standing stock of all species. The model demonstrated that standing stock increased with increasing oceanic productivity, upstream larval supply, depth, and coral cover, and decreased with increasing sea surface temperature and fishing

pressure. As for fishing pressure, this model was then used to extrapolate estimates of current standing stock across the region to generate a previously unavailable map of fish biomass. Finally, the model of current standing stock was adjusted to represent a potential management scenario (fishing pressure reduced to zero to simulate the establishment of a no-take reserve or other fisheries management tool) to allow the production of a map estimating patterns of potential standing stock across the region. Using the maps of predicted current and potential standing stock also allowed the project to generate a map of the expected percentage gain in biomass following the cessation of fishing. These data suggest that the current standing stock of these 19 species alone might increase by a regional total of ~12,200 metric tonnes following the cessation of fishing. In addition to models and maps of the total biomass of all 19 species, maps of current standing stock and potential gain following the cessation of fishing were also produced for the species separated by trophic group: herbivores, invertivores, and piscivores. All maps were produced at a resolution of 100 x 100 m cells (1 hectare).

Summaries of the map products from the project provide a snapshot of the status of fishing and fisheries in Micronesia. These summary figures clearly show the impact of human populations on fish stocks, with generally lower biomasses on reefs close to relatively heavily populated islands, and more intact fish assemblages on more remote reefs. The summaries also demonstrate the variation within the region with, for example, the reefs around Guam clearly more heavily impacted than the reefs of the Marshall Islands. The data were also summarised following calculation of the ratio of current to potential standing stock. This metric has been proposed as providing important insights into the status of fisheries, and potentially benthic dynamics. Although the majority of reefs in Micronesia appear to be relatively functionally intact (current biomass >50% of potential biomass), the exact thresholds where loss of fishes alters ecosystem processes are not well defined in the region. We also used published relationships between the ratio of current to potential biomass and the time to recover to a fully functioning fish assemblage (current biomass >90% of potential biomass). Many of the reefs in the region would take decades (maximum time ~50 years) to reach this state, which highlights the importance of establishing no-take reserves or other fisheries management tools as soon as possible.

Along with mapping aspects of ocean wealth (e.g. harvestable protein), it is anticipated that the products of the Phase 1 project will be useful for on-going marine spatial planning in Micronesia. For example, the Micronesia Challenge aims to conserve 30% of the region’s marine resources by 2020, and we anticipate that the maps of fishing pressure and standing stock can be used as previously unavailable data layers within analyses to plan protected area networks. These opportunities, and other possible uses of the project products, were discussed at two workshops during Phase 1 and are outlined in detail in a separate report.

1. Introduction

1.1 The Mapping Ocean Wealth Project

There is an increasing interest in conserving the ecosystem goods and services provided by ecological systems, such as carbon sequestration and storage, production of livestock on natural grasslands, and water provision (Naidoo et al. 2008). The world's oceans are a particularly important target within this conservation effort, since they provide a wealth of ecosystem goods and services including coastal protection (Koch et al. 2009), protein provision (Holmlund and Hammer 1999), tourism opportunities (Hall 2001), water filtration (Breitburg et al. 2000), and carbon storage (McLeod et al. 2011). However, these goods and services are being threatened by a range of anthropogenic stressors (Halpern et al. 2008), and there are widespread concerns about the health of marine ecosystems such as coral reefs (Bellwood et al. 2004), mangroves (Valiela et al. 2001), and seagrass beds (Waycott et al. 2009).

Despite a growing literature on marine ecosystem services, and how they are being affected by a range of threats, there have been relatively limited attempts to translate this science into the engineering, financial and policy language that could drive changes in the way we evaluate and manage nature. However, this translation of research findings is critical to help decision-makers, development organizations, industry, and community members make effective planning decisions about coastal areas (Arkema et al. 2015). Consequently, The Nature Conservancy (TNC) has established the Mapping Ocean Wealth Project[1] to quantitatively describe what global oceans provide today, in order to facilitate better future investments and decision making (Spalding 2014). Critically, the term 'mapping ocean wealth' describes a process moving from looking at ecosystem services as broad global averages to considering specific local details, allowing nature to be evaluated as an asset and incorporating its benefits into all coastal planning decisions. Furthermore, this wealth is broadly defined to cover monetary value, but also captures other facets of the value of marine areas to society. For example, the oceans have significant cultural importance (Moberg and Folke 1999) and provide food security (Pauly et al. 2005).

The ultimate aim is to work with others to change the way the world sees the ocean, and relies on multiple partnerships. The early planning work on Mapping Ocean Wealth has already benefited from governmental, academic, development, and conservation partner input. Furthermore the project is collaborating with the Global Partnership for Oceans, a growing alliance of over 140 governments, international organizations, civil society groups, and private-sector interests committed to addressing the threats to the health, productivity, and resilience of the ocean. This broad range of stakeholders is critical to generate an explicit understanding of how and where 'ocean wealth' is built, stored, and generated. In turn, the project recognizes that locally accurate, spatially explicit quantification of ocean wealth needs to use metrics that can be understood and utilized by different decision-makers in a variety of socio-economic settings, and which can be assimilated into existing and new coastal and ocean management. For example, engineers may require maps and models explaining the variation of wave attenuation by shallow reefs, fisheries managers may want to understand the differing potential impacts of marine no-take reserves and other fisheries management tools, and coastal planners need to know potential tourism revenues from different habitats and locations.

In summary, the Mapping Ocean Wealth project aims to have two policy components (Spalding 2014): (1) to provide general advice across the policy landscape to influence science, and scientific

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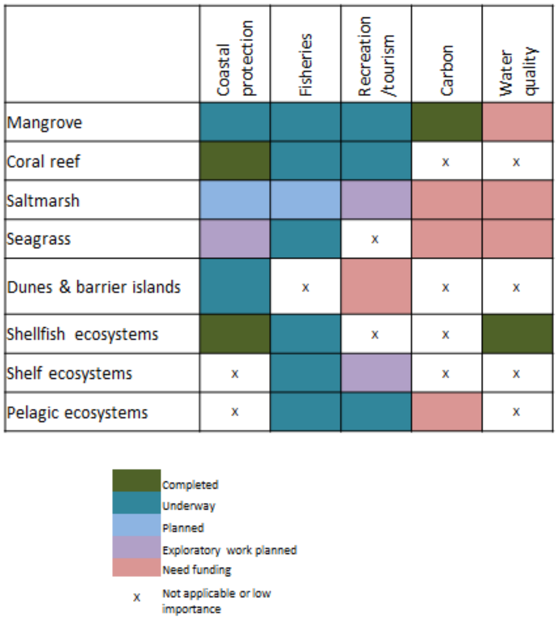
[1] http://www.nature.org/ourinitiatives/habitats/oceanscoasts/mapping-ocean-wealth.xml

outputs and communications, in multiple sectors and across scales; and (2) to focus on two key areas of policy where the project can have a direct and dramatic influence over a relatively short time-frame. Specifically, the general advice aims will be: (1) to review the science proposed and underway through the Mapping Ocean Wealth project and its partners, and advise on key audiences, information needs and outputs to help shape the research agenda and its outputs; (2) maintain a watching brief on multiple national and global policy forums and look for opportunities to incorporate or otherwise highlight ecosystem service valuation; (3) identify key drivers of loss of ecosystem benefits and policy options to reduce the risk; (4) undertake a sector review of utilization, dependency or impact on marine ecosystem services; and (5) identify incentives and potential barriers to mainstreaming of ecosystem benefits and enable conditions and engagement strategy needed to promote their adoption. The key policy options are: (1) influencing the global development agenda, and notably the UN Post 2015 Development Agenda; and (2) influencing the international conservation community, including the Convention on Biological Diversity (CBD), and the global protected areas community, notably through the recognition and detailed incorporation of ecosystem service quantification into the CBD Strategic Plan and Aichi targets for conservation and restoration.

1.2 Modelling and mapping coral reef fisheries

The Mapping Ocean Wealth project is focusing on a matrix of eight marine habitats and five ecosystem goods and services, although there is prioritisation across this matrix and progress is varied (Fig. 1). TNC has contracted the University of Queensland (UQ), Brisbane, Australia to undertake Phase 1 of the effort to map coral reef fisheries. Coral reefs provide critically important ecosystem goods and services to hundreds of millions of people who live in coastal communities worldwide, particularly fisheries, coastal protection, tourism, and recreation (Burke et al. 2011). For example, reef fisheries provide important sources of protein and livelihoods to millions of people worldwide, and have been estimated to be worth ~US$6 billion each year (Cesar et al. 2003). However, the ecosystem services provided by coral reefs are difficult to quantify and integrate into marine conservation and management, and the need to quantify and map ecosystem services has been identified as a priority for building stronger scientific support for coral reef management (Aswani et al. 2015).



	Coastal protection	Fisheries	Recreation /tourism	Carbon	Water quality
Mangrove	🟦	🟦	🟦	🟩	🟥
Coral reef	🟩	🟦	🟦	x	x
Saltmarsh	▨	▨	🟪	🟥	🟥
Seagrass	🟪	🟦	x	🟥	🟥
Dunes & barrier islands	🟦	x	🟥	x	x
Shellfish ecosystems	🟩	🟦	x	x	🟩
Shelf ecosystems	x	🟦	🟪	x	x
Pelagic ecosystems	x	🟦	🟦	🟥	x

🟩 Completed
🟦 Underway
▨ Planned
🟪 Exploratory work planned
🟥 Need funding
x Not applicable or low importance

Fig. 1. Matrix of habitats and ecosystem services being considered by the Mapping Ocean Wealth project, and details of priority areas and progress.

The Phase 1 project to map coral reef fisheries was co-ordinated through the research groups of Professor Peter Mumby (Marine Spatial Ecology Lab) and Professor Hugh Possingham (Centre of Excellence for Environmental Decisions), and led to the appointment of Dr Alastair Harborne to lead the research. This work also included input from TNC's Mapping Ocean Wealth project team (Alison Green, Mark Spalding, and Philine zu Ermgassen), TNC's regional GIS specialist (Nate Peterson), and other researchers and resource managers. The key aims of this work were to model and map the current value of coral reef fisheries (current fish standing stock), model and map current fishing pressure, and assess the potential benefit of conservation and management measures, such as the potential standing stock that could be found on a reef is fishing was managed through establishment of a marine no-take reserve or other fisheries management tool. The research at UQ also aimed to identify options for using the resulting maps and models for marine spatial planning, including protected area network design and identifying options for return on investments for different fisheries management actions. Finally, the work on coral reef fisheries aimed to assist the preparation of practical tools for field managers, which will summarise and explain the findings of the research, and its potential applications.

1.3 Modelling and mapping coral reef fisheries in Micronesia

The coral reef fisheries project began with a workshop at UQ in November 2014, involving many of the personnel involved in the research (Fig. 2). This workshop reviewed the aims of the project to assess fisheries on coral reefs, and assessed what could be achieved within Phase 1 (up to January 2016) ahead of a subsequent, funding-dependent Phase 2.

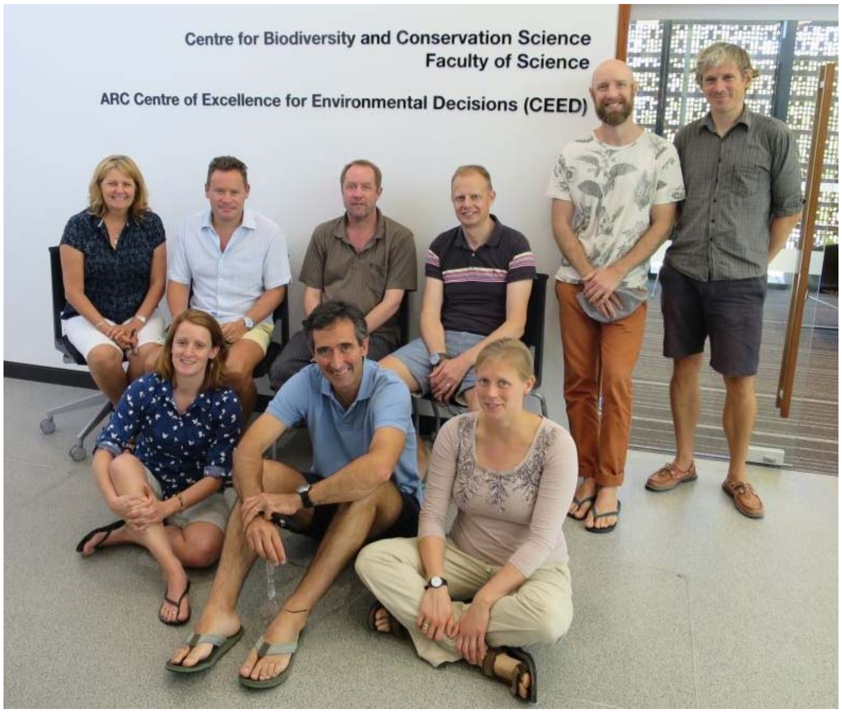


Fig. 2. Participants at the UQ workshop, November 2014. Back row (l-r): Alison Green (TNC), Peter Mumby (UQ), Hugh Possingham (UQ), Alastair Harborne (UQ), Eddie Game (TNC), Yves-Marie Bozec (UQ). Front row (l-r): Alice Rogers (UQ), Mark Spalding (TNC), Philine zu Ermgassen (TNC).

A key output of this workshop was a decision to focus Phase 1 of the project on coral-reef fisheries in Micronesia. Note that Phase 1 focused on fin-fish fisheries because of data availability, although it is known that invertebrates are also a valuable component of Pacific fisheries (Dalzell et al. 1996). Mapping reef fisheries represents a trade-off between wanting maps and models at spatial scales that are as large as possible, but recognising that consistent and detailed data sets are rarely available at scales beyond national or regional boundaries. A focus on Micronesia represented a compromise between these factors. Micronesia represents a relatively large biogeographic province, and thus the project has provided map and models for multiple countries and allowed for regional, national, and sub-national marine spatial planning and decision making. However, it was still tractable to generate accurate and relatively fine-scale maps of key variables (e.g. wave exposure, extent of marine protected areas, and ocean productivity). Furthermore, Micronesia is already a target site for TNC to aid marine spatial planning, and consequently a focal site for the Mapping Ocean Wealth project (along with the Coral Triangle, Gulf of California, mid-Atlantic, and the

Cayman Islands). Finally, the project was able to both assist and benefit from on-going efforts to conserve at least 30% of the marine resources in the region as part of the ‘Micronesia Challenge’ (Houk et al. 2015). The Micronesia Challenge has strong political support, and is empowering scientists and managers to assess reefs and threats to their health, and develop conservation strategies (Houk et al. 2015).

The ultimate aim of the coral reef fisheries component of the Mapping Ocean Wealth project remains to map the values of this ecosystem service at a global scale. However, Phase 1 provided an important first stage in this effort by providing a ‘blueprint’ of how fishing pressure and standing stock may be mapped at large scales. Furthermore, it identified critically important variables to generate informative maps and models, and this will help guide research efforts at the global scale. Phase 1 also initiated research into how maps and models of reef fisheries can be most effectively incorporated into marine spatial planning and decision making. Finally, the work in Micronesia has provided critically important data layers, tools, and case studies to managers in five jurisdiction of the region to assist conservation and management initiatives at a range of spatial scales.

In summary, the aims of Phase 1 were:

- A model and map of each of the following for Micronesia:
    - Fishing pressure
    - Current standing stock
    - Potential standing stock
- Identify options for using these maps for reef conservation and management (e.g. marine spatial planning, return on investment of different conservation and management strategies);
- Provide assistance for preparing practical tools for field managers to summarize and explain the project results and potential applications;
- Provide a technical report to explain the methods used, and disseminate the associated data layers and modelling codes;
- Provide technical advice for using the maps and models for coral reef conservation and management in at least one jurisdiction in Micronesia;
- Identify options and approaches for expanding this work to develop global-scale maps;
- Provide a detailed work-plan to identify how to modify approaches for assessing reef fisheries in other regions.

This document represents a final technical report and provides a background to the project and the region, outlines the research methodology in detail, and provides an overview of the results and their relevance to marine conservation in Micronesia. The map products are also appended to this report.

2. Background information on Micronesia

2.1 The reefs of Micronesia

Phase 1 of the project to map coral reef fisheries and their value encompassed five jurisdictions of Micronesia, namely the Republic of Palau, the Federated States of Micronesia (FSM), the Territory of Guam, the Commonwealth of the Northern Marianas (CNMI), and the Republic of the Marshall Islands (RMI) (Fig. 3).

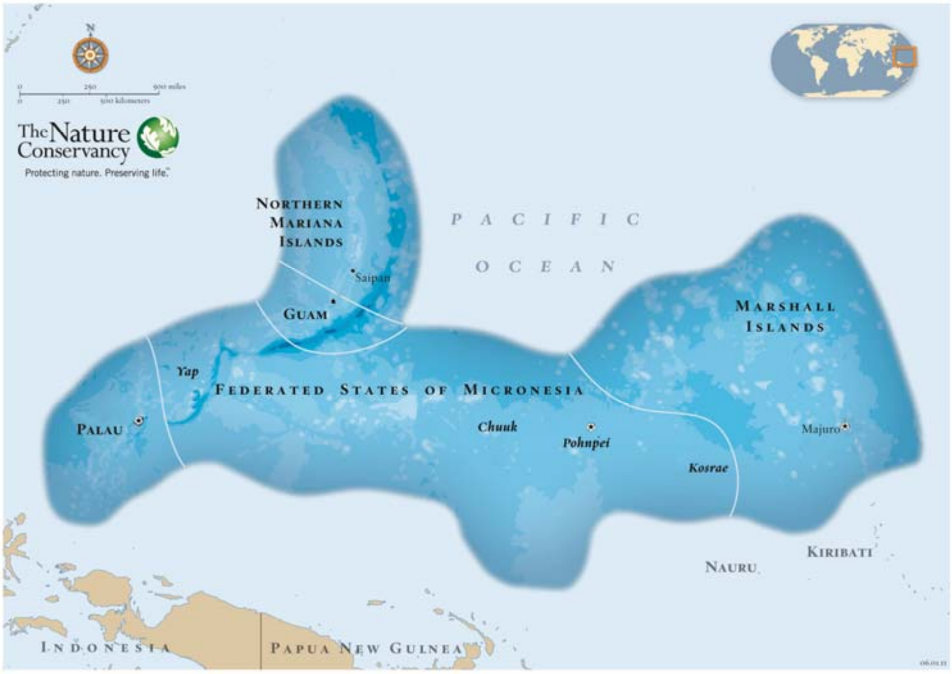


Fig. 3. The geographic area encompassed by Phase 1 of the mapping coral reef fisheries component within the Mapping Ocean Wealth project.

A comprehensive review of the reefs of Micronesia is beyond the scope of this report, and readers are referred to more detailed studies (e.g. UNEP/IUCN 1988, Price and Maragos 2000). The reefs of Micronesia are typically found around two major island types, namely high (volcanic origin) islands and atolls (Dalzell et al. 1996). The high islands may be surrounded by a fringing reef system with limited lagoon and back reef habitats (e.g. Guam and Kosrae), or by barrier reefs systems with extensive lagoon and back reef habitat (e.g. Yap and Pohnpei) (Taylor et al. 2014b). In addition there are examples of atolls with a single low island (sedimentary origin) with fringing reefs but no lagoon, such as Satawal in the FSM (Taylor et al. 2014b), and drowned atolls.

Environmental drivers, such as temperature, wave exposure, and oceanic productivity, vary widely across the Pacific (Gove et al. 2013). As in other regions, these environmental gradients affect coral assemblages, with high wave exposure sites in the Northern Mariana Islands having non-constructional reefs with small corals, while larger corals and constructional reefs occur at more sheltered sites (Houk and van Woesik 2010). Island geomorphology and the extent of watersheds can also affect reef zonation (Houk and van Woesik 2010). Ecological processes are relatively poorly studied on Micronesian reefs compared to locations such as the Great Barrier Reef in Australia, but there are increasing efforts to understand the biotic and abiotic drivers of reef condition and resilience (Mumby et al. 2013, Doropoulos et al. 2014). Like many reefs, fish grazing pressure is a key determinant of resilience (Mumby et al. 2013), and predictive models of Pacific coral cover trajectories are emerging (Ortiz et al. 2014). Such models are important for understanding the future condition of Micronesian reefs given the range of local and global stressors, including climate-change driven coral bleaching (van Woesik et al. 2012), fishing pressure and pollution (Houk and van Woesik 2010, Houk et al. 2015), sedimentation (Shafer Nelson et al. 2016), and trophic cascades following the reduction of functionally important fish guilds (Houk and Musburger 2013).

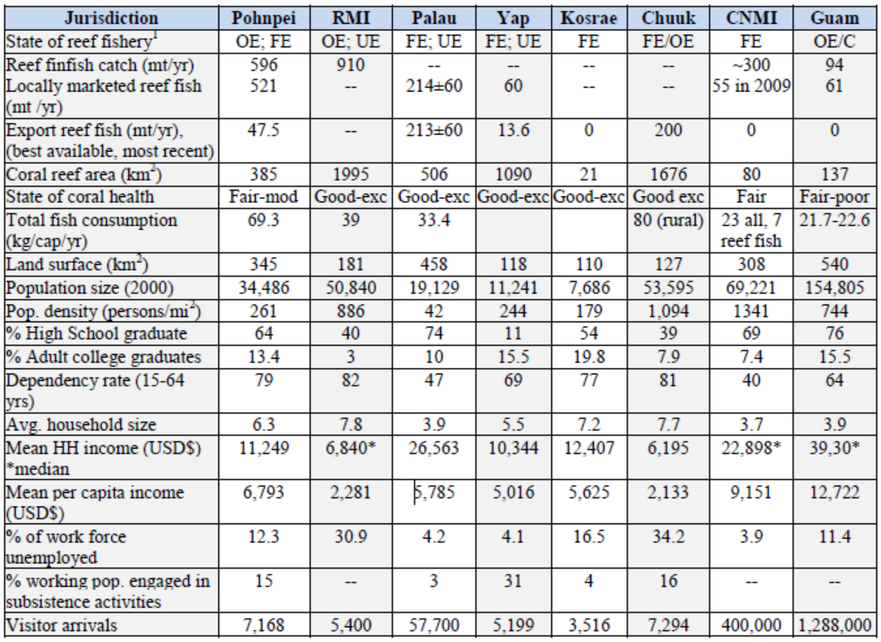
2.2 Fishing on Micronesian reefs

This project focused on reef fisheries that are critical for livelihoods and food security, and did not consider the widely roaming tuna fleets that are an important component of commercial fisheries in the region (Zeller et al. 2015). Tuna fisheries are often found close to reefs, but the distribution of these pelagic species is controlled by different drivers than those affecting the abundance of reef fishes. Although the project described in this report focuses on reef fishes, another component of the Mapping Ocean Wealth project is considering some pelagic fisheries.

Coral reef fisheries of the region can be separated into subsistence and commercial components, with subsistence particularly prevalent on remote islands and atolls (Dalzell et al. 1996) and representing 60% of coastal fisheries catches in Palau (Lingard et al. 2011). Reef fisheries encompass a variety of techniques in Micronesia, but commercial catches are predominantly from nocturnal spearing (Houk et al. 2012b). Gillnetting, throw nets, hook-and-line, and traps are also used (Dalzell et al. 1996, Houk et al. 2012b, Cuetos-Bueno and Houk 2015). SCUBA spearfishing is legal in some parts of Micronesia, and is used to land a significant proportion of the commercial catch in Guam (Houk et al. 2012b).

Reef fisheries are vital to the economies of the jurisdictions of Micronesia, with total fisheries production being >100,000 t yr^{-1} and worth ~US$262 million in the mid 1990's (Dalzell et al. 1996). Consequently there is a growing literature considering catch rates, the status of different fisheries, and management strategies. It is clear that the status of fisheries varies significantly across the region, driven by a range of socio-economic factors (Rhodes et al. 2011, Table 1). For example, the high population density and poor reef health in Guam mean that the fisheries are either overfished or have collapsed. Conversely, less populous jurisdictions such as Yap still have large area of relatively under-exploited fish stocks living on healthy reefs.

Table 1. Characteristics of the major islands within Micronesia. OE = overfished; FE = fully exploited; UE = under exploited; C = collapsed. Table taken from Rhodes et al. (2011), and the authors report that the information represents the best and most recent data available at the time.



Jurisdiction	Pohnpei	RMI	Palau	Yap	Kosrae	Chuuk	CNMI	Guam
State of reef fishery[1]	OE; FE	OE; UE	FE; UE	FE; UE	FE	FE/OE	FE	OE/C
Reef finfish catch (mt/yr)	596	910	--	--	--	--	~300	94
Locally marketed reef fish (mt /yr)	521	--	214±60	60	--	--	55 in 2009	61
Export reef fish (mt/yr), (best available, most recent)	47.5	--	213±60	13.6	0	200	0	0
Coral reef area (km^2)	385	1995	506	1090	21	1676	80	137
State of coral health	Fair-mod	Good-exc	Good-exc	Good-exc	Good-exc	Good exc	Fair	Fair-poor
Total fish consumption (kg/cap/yr)	69.3	39	33.4			80 (rural)	23 all, 7 reef fish	21.7-22.6
Land surface (km^2)	345	181	458	118	110	127	308	540
Population size (2000)	34,486	50,840	19,129	11,241	7,686	53,595	69,221	154,805
Pop. density (persons/mi^2)	261	886	42	244	179	1,094	1341	744
% High School graduate	64	40	74	11	54	39	69	76
% Adult college graduates	13.4	3	10	15.5	19.8	7.9	7.4	15.5
Dependency rate (15-64 yrs)	79	82	47	69	77	81	40	64
Avg. household size	6.3	7.8	3.9	5.5	7.2	7.7	3.7	3.9
Mean HH income (USD$) *median	11,249	6,840*	26,563	10,344	12,407	6,195	22,898*	39,30*
Mean per capita income (USD$)	6,793	2,281	5,785	5,016	5,625	2,133	9,151	12,722
% of work force unemployed	12.3	30.9	4.2	4.1	16.5	34.2	3.9	11.4
% working pop. engaged in subsistence activities	15	--	3	31	4	16	--	--
Visitor arrivals	7,168	5,400	57,700	5,199	3,516	7,294	400,000	1,288,000

The collapse of Guam's fisheries is reflected in a global analysis of fishing pressure on tropical islands, where a sustainable fishery is considered to extract 5 mt km^{-2} yr^{-1} (Fig. 4) (Newton et al. 2007). The entire fishery in Palau is considered fully exploited, and catches are potentially unsustainable. The fisheries in FSM, RMI, and CNMI appear to be either fully exploited or underexploited, and catches appear to be sustainable. This intra-regional variation has also been examined in more detail by reconstructing catches from 1950 to 2010 across the Pacific (Zeller et al. 2015). These reconstructions indicate that catches have decreased over this time period in Guam and CNMI, but have increased by up to 306% in FSM, RMI, and Palau. These reconstructions also suggested that peak catches varied significantly among jurisdictions, with catches declining since these times because of overexploitation: Guam (1953), CNMI (1964), FSM (1994), Palau (2002), and RMI (2007) (Zeller et al. 2015). For example a detailed reconstruction of the fisheries of CNMI highlights that catches are likely to have declined significantly from the 1950s, with fisherfolk progressing from basic equipment in shallow water to nocturnal spearing, leading to fish populations declining near human populations and fishing increasingly occurring on remoter reefs (Cuetos-Bueno and Houk 2015). Additional catch data trends are also available for Guam (Hensley and Sherwood 1993, Myers 1993) and Palau (Lingard et al. 2011).

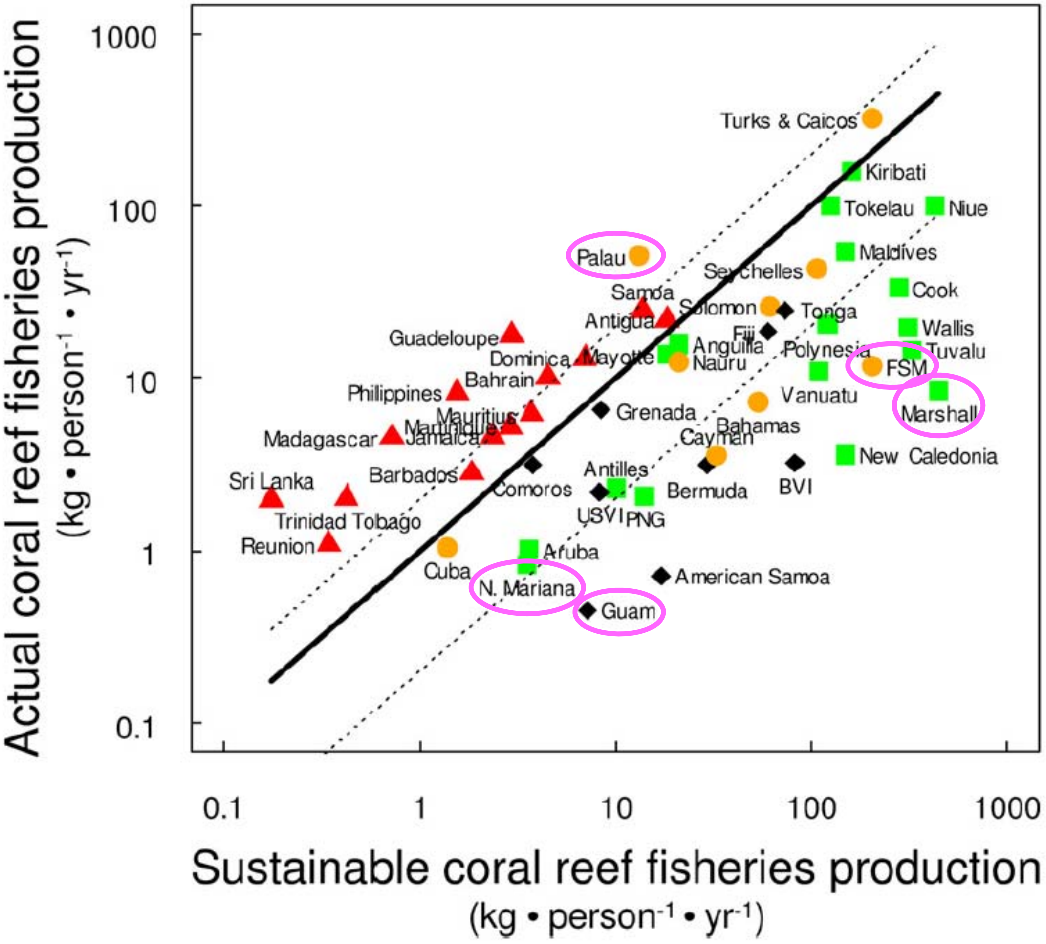


Fig. 4. Graph of sustainable versus actual fisheries production for island fisheries globally. Line represents where current and sustainable fisheries production = 5 mt km^{-2} yr^{-1}. Islands above and to the left of the line have unstainable ecological footprints. Green = underexploited; red = overexploited; orange = fully exploited; black = collapsed. Pink circles show the Micronesian jurisdictions considered in the Phase 1 project. From Newton et al. (2007).

National and regional assessments of fisheries are inevitably limited by data availability (Adams et al. 1997, Zeller et al. 2015), and smaller-scale studies provide more detail for individual islands. Throughout the Pacific, surgeonfishes, parrotfishes, and groupers are the most important targets of the commonest fishing technique (spearing) (Gillett and Moy 2006). For example, a study of the fisheries of CNMI, Guam, Yap, and Pohnpei, documented over 150 species being landed, but surgeonfishes, unicornfishes, and parrotfishes dominated catches, with other herbivores and the carnivores *Monotaxis grandoculis*, *Lethrinus harak*, and *Caranx melampygus* also common (Rhodes et al. 2008, Houk et al. 2012b). Roving herbivores also dominate catches in Palau (Bejarano et al. 2013), and catches in the region may increase significantly during seasonal closures of the grouper fishery (Rhodes et al. 2008, Bejarano Chavarro et al. 2014). In addition to spearfishing of larger herbivores, there are major cultural events in Guam associated with annual harvesting of juvenile rabbitfishes using minnow and cast nets (Kami and Ikehara 1976).

This focus on targeting herbivores, which have a key functional role on reefs by grazing macroalgae, has led to concerns about the overexploitation of this group of species and the implications for benthic dynamics. For example, *Naso unicornis* is heavily exploited, vulnerable to fishing, and has a functional role (macroalgal browsing) that is not fulfilled by many other species (Bejarano et al. 2013). Functionally important, larger-bodied parrotfish and the large wrasse *Cheilinus undulatus* are also scarce on heavily fished reefs, including on deeper slopes in Guam where spearfishing using SCUBA is permitted (Lindfield et al. 2014). In addition to changing the abundance of herbivorous fishes, fishing can change the social demography of parrotfishes in the region, with increasing fishing pressure reducing the length at which fishes undergo sex change (Taylor 2014). There are also concerns about the sustainability and ecological impacts of other parts of the fishery, such as the overexploitation of slow-growing grouper that are heavily targeted by fishers and are particularly susceptible at their spawning aggregation sites (Newton et al. 2007, Rhodes and Tupper 2007).

2.3 Fisheries management in Micronesia

Some reefs of Micronesia, particularly around remote islands, have more intact fish assemblages than many other areas of the world, at least partly caused by traditional community management (Adams et al. 1997). However, it is clear that there has been a shift towards open access resource exploitation and unsustainable fishing on many reefs across the region, with fishing increasingly targeting lower trophic levels and smaller individuals (Houk et al. 2012b). Furthermore, there are concerns about the impacts of climate change on reef fisheries, with predicted decreases of up to 20% by 2050 in the Pacific (Bell et al. 2013). Consequently, there is a growing interest in fisheries management, epitomised by the ‘Micronesia Challenge’ that aims to effectively conserve 30% of the marine resources of the region (Houk et al. 2015).

Conservation and management of reef fisheries frequently focuses on marine no-take reserves (e.g. Halpern 2003). Designating no-fishing areas has repeatedly been demonstrated to increase fish abundance, size, and diversity, as documented in a wealth of empirical studies, meta-analyses, and reviews (e.g. Mosquera et al. 2000, Halpern and Warner 2002, Russ 2002, Micheli et al. 2004). Furthermore, no-take reserves may also increase ‘spillover’ of larval and adult fish into surrounding, fished areas (Roberts et al. 2001, Abesamis et al. 2006, Harrison et al. 2012), and have additional benefits for reducing macroalgal cover, increasing coral cover and recruitment, and reducing the abundance of invasive species (Mumby et al. 2006, Mumby et al. 2007, Mumby and Harborne 2010, Mumby et al. 2011). These potential benefits to reef health, along with direct mitigation of local and global stressors, are critical to maintaining fisheries because of the links between coral cover and fish abundance and diversity (e.g. Jones et al. 2004). The multifaceted benefits mean that marine protected areas and no-take reserves have been established around many islands in Micronesia, including Palau, Pohnpei, and Guam, although their enforcement and effectiveness varies (Rhodes et al. 2008, Mumby et al. 2013, Lindfield et al. 2014).

Alongside the establishment of permanent no-take reserves, gear and seasonal restrictions can aid fisheries management, and are used relatively widely in Micronesia. Although the majority of reefs remain open to unrestricted harvest (Houk et al. 2012b), islands such as Pohnpei have a long-standing seasonal ban on sales of grouper to protect spawning aggregations (Rhodes and Tupper 2007) and SCUBA fishing is banned in many jurisdictions (Bejarano Chavarro et al. 2014, Cuetos-Bueno and Houk 2015). Some islands also have species-specific bans on highly prized, vulnerable species such as the bumphead parrotfish, *Bolbometopon muricatum* (Houk et al. 2012b, Bejarano Chavarro et al. 2014). The use of gear restrictions is an attractive option where the prevalent techniques target functionally important species that are critical to reef resilience following climate-change induced coral mortality (Cinner et al. 2009). Especially when the establishment of no-take reserves is impractical, banning traps or spearing could significantly reduce the mortality rates of herbivores such as parrotfishes (Cinner et al. 2009).

Such efforts to establish gear restrictions could be particularly productive in Micronesia, given the number of fisherfolk using spears and high catches of herbivores, although reducing use of a traditional technique and changing the desirability of which species are harvested will be difficult (Rhodes et al. 2008, Bejarano et al. 2013). However, in a review of spearfishing in the Pacific, the ban of its use on SCUBA was judged to the single most important management measure related to this gear type (Gillett and Moy 2006), and this conclusion is supported by field studies (Lindfield et al. 2014). Such changes, and other complementary initiatives to alter catch sizes and quotas, will need to be enacted at local, national, and regional scales in order to be successful (Gillett and Moy 2006, Houk et al. 2012b).

3. Methods and data used in the Phase 1 project

3.1 Methodological overview

The major products of Phase 1, namely the models and maps of fishing pressure and current and potential standing stocks throughout Micronesia, utilised a range of data inputs and were interlinked (Fig. 5). Details of the fish survey data and predictive data layers are provided in subsequent sections and appendices, but the first step was to model fishing pressure using size-based metrics derived from fish survey data in relation to environmental (e.g. wave exposure) and socio-economic (e.g. population density) variables. Modelling fishing pressure used data that were independent of the data used to model standing stock in order to ensure robust statistical models (i.e. the same data were not used to derive fishing pressure and then fishing pressure used to model standing stock in that data set). The model of fishing pressure was limited to locations where fish survey data were available, but it was used to extrapolate values across the region using continuous data layers of each significant explanatory variable, thus deriving a continuous map of fishing pressure. A future aim is for the relative patterns of fishing pressure within the region to be corroborated using fisheries-dependent data, and possibly local knowledge.

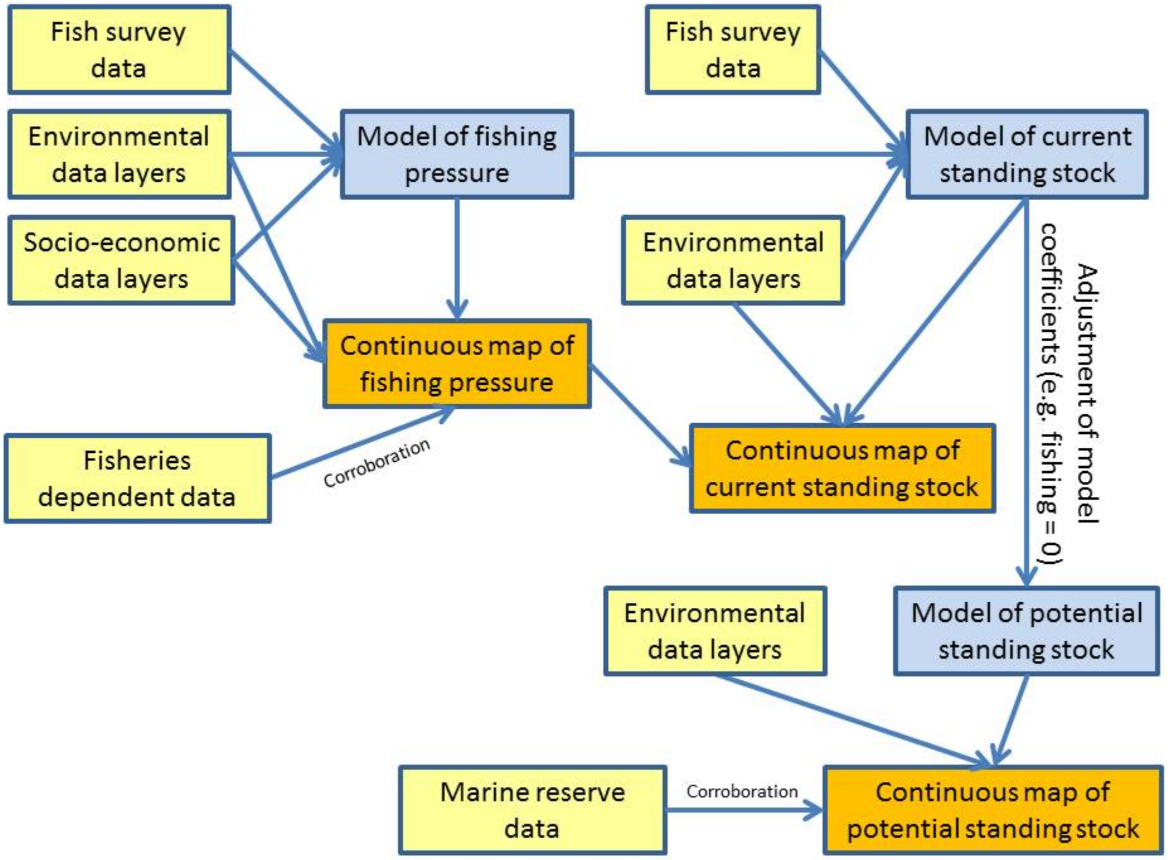


Fig. 5. Overview of the methodology for modelling and mapping the fishing pressure and fish standing stocks in Micronesia. Yellow boxes represent input data, blue boxes represent output models, and orange boxes represent output maps.

The predicted values of fishing pressure at each site where fish survey data are available were then a key input into the model of current standing stock. Predicted fishing pressure was combined with environmental data (e.g. island geomorphology) to model the biomass of the fish assemblage as recorded during fish surveys. Similarly to fishing pressure, the model was combined with the continuous data layers of fishing pressure and environmental variables to extrapolate values of current standing stock throughout Micronesia and derive a continuous map. Finally, the coefficients of the model of current standing stock can be adjusted to estimate potential standing stock under different conservation and management initiatives. This report includes a map derived from perhaps the most obvious conservation scenario, namely with fishing pressure hypothetically reduced to zero, simulating the effects of a no-take reserve or other fisheries management tool. However, other approaches could potentially be modelled, such as increasing coral cover, or the models could be used to simulate some of the potential effects of climate change (increasing sea surface temperatures). This adjusted model or models can then be combined with all significant environmental data layers to generate a continuous map of potential standing stock under different management scenarios. Because of their hypothetical nature, these maps are difficult to validate but data from no-take reserves and remote areas may provide some corroborative evidence of the potential (unfished) standing stock on some reefs in the region.

Note that this approach, the variables to be included, and preliminary results were discussed at a Micronesian workshop in September 2015 to obtain expert input into the plans for Phase 1, answer questions regarding the products and their use, and engage stakeholders in Mapping Ocean Wealth. The results of this workshop can be found in a separate report (Green et al. 2016).

3.2. Approach to modelling fishing pressure

Researchers typically use fishery-dependent (e.g. catch data) or fishery-independent (e.g. underwater fish censuses) to assess fishing pressure. While some catch data are available from Micronesia, they lacked the spatial resolution, widespread coverage, and species-level detail required for the models and maps produced by the Phase 1 project. Furthermore, there are widespread concerns about the reliability of many fisheries-dependent data sets, which often underestimate catches and may not even give reliable trends in catches (Pauly and Zeller 2014).

While fishery-dependent data may be useful for corroborating the maps and models of fishing pressure, the Phase 1 project focused on using fishery-independent data derived from surveys of fish assemblages at sites in Micronesia. Where survey data are available there are myriad different options for inferring fishing pressure, and many approaches have been discussed in the general fisheries literature (e.g. Jennings 2005, Shin et al. 2005, Shin et al. 2010). The use of indicators of fishing pressure has subsequently extended into coral reef fisheries and has included maximum size or age at female maturation as an indicator of vulnerability (Jennings et al. 1999, Stallings 2009, Taylor et al. 2014a), and measuring fishing impacts by the calculation of size-spectra (Graham et al. 2005), average length of caught fish (Kronen et al. 2010), mean length, trophic level and density of large fishes (Guillemot et al. 2014), and length-based metrics from the major fishery target species (Ault et al. 1998, Ault et al. 2005, Ault et al. 2008, Ault et al. 2014).

Recently, there has been a growing interest in the derivation of metrics of fishing pressure from surveys of herbivorous species, particularly parrotfishes. Although parrotfish are typically targeted only after more valuable species, such as grouper, are extirpated (Mumby et al. 2012), parrotfish are increasingly found in catches from reefs and some species are particularly important in Micronesian catches (Houk et al. 2012b). Consequently, large-bodied parrotfishes are often rare on heavily fished reefs, with assemblages shifting towards smaller-bodied species, and these changes in species structure and decreasing mean size have been highlighted as a potential indicator of over-exploitation (Clua and Legendre 2008). Working across the Caribbean, Vallès and Oxenford (2014) demonstrated that mean parrotfish weight, but not density or total biomass, was a better metric of fishing pressure than the biomass of some commercially important species. In subsequent research, average parrotfish weight was shown to vary linearly with fishing pressure at smaller spatial scales, as required by a good indicator, and be a preferred metric compared to those derived from commercially targeted species (Vallès et al. 2015). These results are consistent with research in Micronesia, where mean length of either all parrotfishes combined or individual species was highly correlated with fishing pressure at multiple spatial scales, and this variable was the most the sensitive to increased human extraction (Taylor et al. 2014b). However, some of the variation in mean parrotfish size will be driven by environmental variables (Taylor et al. 2014b), and therefore putative environmental variables of mean parrotfish size (e.g. island geomorphology) were included in the fishing pressure models, along with anthropogenic metrics such as human population density and distance to markets.

A further advantage of using parrotfish-derived metrics is that, unlike groupers, parrotfish are rarely totally absent under very high fishing pressure regimes, thus allowing for mean length or weight to be calculated at all sites. Deriving accurate estimates of mean length from fish surveys is also robust to survey technique and the taxonomic expertise of the observer, as it simply requires counts and sizes of each individual identified as a parrotfish and does not need standardising to a fixed area. Finally, because of their global functional importance as grazers of macroalgae (e.g. Bellwood et al. 2004), parrotfishes data are usually recorded in surveys, providing a wealth of data for analysis.

Based on this literature, the Phase 1 project used mean size and weight of parrotfishes as a key indicator of fishing pressure. As recommended in previous studies (Shin et al. 2010, Vallès et al. 2015), mean parrotfish size or weight was calculated from fishes larger than 15 cm to make the analyses robust to inter-observer differences (e.g. some surveys may ignore small juveniles) and variability in recruitment not linked to fishing (e.g. some sites may have large numbers of small individuals because of naturally high recruitment rates or surveys coinciding with recruitment events). Furthermore, records of the bumphead parrotfish, *Bolbometopon muricatum* were excluded from these analyses because they can skew metrics as they so much larger than other species (maximum length 130 cm, Froese and Pauly 2010), are difficult to survey accurately because they form large, widely roving schools, and are absent from the Marshall Islands (Froese and Pauly 2010).

Critically, the maps of fishing pressure generated by the Phase 1 project represent relative, unitless patterns of estimated total exploitation impact, as opposed to absolute fishing rates as measured by metrics such as catch per unit effort. This distinction is important because the Phase 1 project highlights areas that have been heavily impacted by fishing (small mean size of parrotfishes), rather than identifying areas that are currently being heavily fished. Highly impacted sites may also be currently heavily fished, but equally these sites may be lightly fished because catches are limited and fisherfolk have moved to more profitable locations. However, light fishing pressure may be sufficient to limit any recovery of heavily impacted sites. Equally, some sites may currently be heavily fished, but have little evidence of fishing impact (large mean size of parrotfishes) because the site has only recently been targeted by fisherfolk.

3.3. Fish survey data sets

The derivation of the maps and models produced by Phase 1 was entirely parameterised using existing fish survey data. Thanks to the generosity of numerous sources, we obtained data from numerous sites across all five jurisdictions of Micronesia (Table 2, Fig. 6).

The data sets vary in geographical location, date of collection, survey technique, and taxonomic resolution (Table 2, and each set is described in more detail in Appendix 1). These characteristics mean that each set was used for different purposes (Table 2), and the full rationale for their use is described in Appendix 1. Briefly, Peter Mumby's data set was used as a key data set for modelling fishing pressure based on the mean size and weight of parrotfishes because it focused on herbivorous species. The Peter Mumby data set does not include any data from CNMI, but the NOAA CRED data set includes temporal replicates of multiple sites in this jurisdiction, and one of the replicates (2011) was used to parameterise the fishing pressure model. The 2014 NOAA CRED replicates were used for the standing stock model. The remaining data sets were typically split to provide data to both the fishing pressure and standing stock models, particularly where there were geographic gaps in the Peter Mumby data set (Table 2). The models of standing stock were then developed using the remaining data from the remaining data (i.e. the other sites surveyed and not used in the fishing pressure model). The Micronesia Challenge data set was only be used to parameterise the models of standing stock because the size data for each fish, which are required for deriving size-based metrics in the fishing pressure model, were not available to the Phase 1 project. All data were converted into standardised Microsoft Access databases to aid data analysis.

Table 2. Summary of fish survey data sets available to the project, and whether they were used to model fishing pressure and / or standing stock. Numbers represent the number of sites used from each data set in each model. UVC = underwater visual census. CNMI = Commonwealth of the Northern Marianas, FSM = Federated States of Micronesia, RMI = Republic of the Marshall Islands.

Source	**Sites from**	**Dates**	**Technique**	**Species**	**Fishing model**	**Standing stock model**
Peter Mumby	• Palau • Guam • Pohnpei	2009-2012	UVC belt transects	All species of parrotfish, surgeonfish, and rabbitfish	54	-
Maria Beger	• Marshall Islands (3 atolls)	2014	UVC belt transects	All non-cryptic species. 372 species from 39 families	15	14
Brett Taylor	• Guam • 7 islands in FSM	2011-2012	Video belt transects	143 taxa from 22 families	37	57
NOAA CRED	• Guam • 12 islands in CNMI	2011, 2014	Stationary point counts	All non-cryptic species. >480 taxa from 53 families	297	414
Micronesia Challenge	• 4 islands in FSM • 3 islands in CNMI • 3 atolls in RMI	2011-2015	Stationary point counts	157 taxa from 22 families[a]	-	79
PICRC	• Palau	2014	UVC belt transects	Focused on 35 key species from 11 families	2	26
Alison Green	• Helen Reef (Palau)	2000	UVC belt transects	All non-cryptic species. 245 species from 27 families	2	2
PROCFish	• Palau • 2 islands in FSM • 3 atolls in RMI	2006-2007	Distance-based UVC transects	Most non-cryptic species. 313 species from 30 families	63	65
Total					470	657

[a] Only site-level biomass data available to the Phase 1 project.

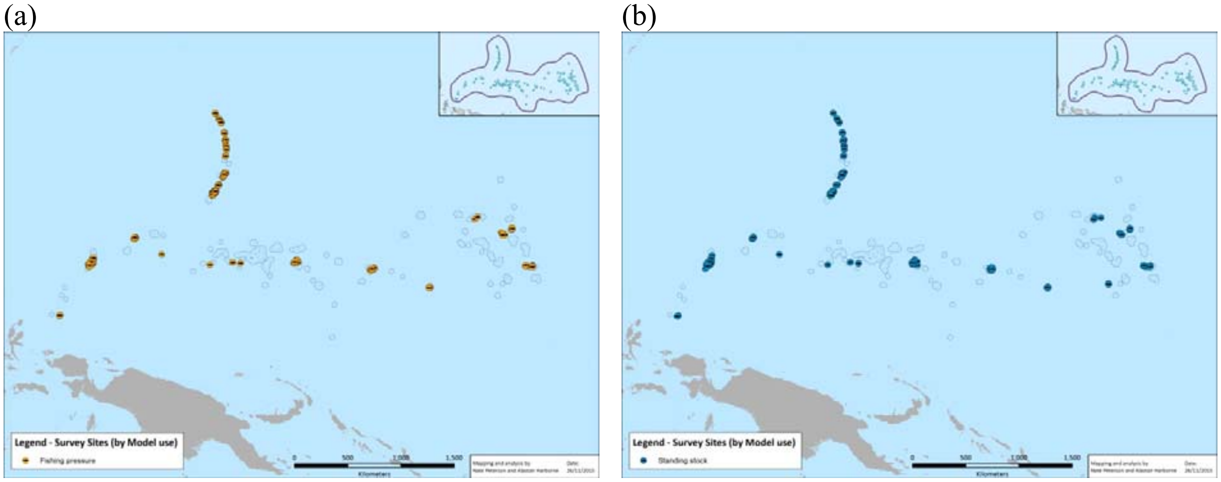

(a) (b)

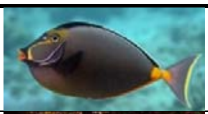
Fig 6. Location of survey sites used in (a) fishing pressure model and (b) standing stock model.

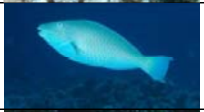
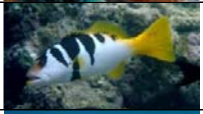
3.4. Modelling current standing stock

One of the challenges of modelling during the Phase 1 project was that the different data sets had to be pooled to allow for extrapolation across the region to generate continuous map layers. Comparability among data sets caused by variations in survey techniques is examined in the next section, but an additional issue was that each data set surveyed different groups of species (e.g. virtually all species were counted in the NOAA CRED surveys, but only 35 target species were consistently recorded during PICRC surveys). All data sets counted parrotfishes to species or family level, so mean parrotfish length or biomass could be derived from any site. However, models of standing stock needed to reflect differences caused by fishing and environmental gradients, not variations in survey techniques (e.g. grouper were absent from the data set because they have been extirpated, rather than because they weren't counted). Furthermore, biogeographic patterns of fish distributions within the region mean that a species seen on a reef in one jurisdiction may be absent elsewhere, or replaced by a different species. Consequently, if a species is not present in one jurisdiction because of biogeography, but it was included in metrics of standing stock, then standing stock would be modelled as being low (biomass of that species = 0). In fact, total standing stock could be much higher than modelled because the niche of that species is fulfilled by another, locally abundant species that is in turn absent from other reefs.

In order to model standing stock consistently across the region, the Phase 1 project identified 19 taxa that are recorded in all data sets used to model standing stock, are relatively abundant, and occur in each of the five jurisdictions according to biogeographic data (Froese and Pauly 2010) (Table 3). These species are also relatively large, and therefore make a significant contribution to the biomass of fishes at each site, unlike many of the smaller species from some of the diverse families that are poorly represented in the key species list (e.g. small-bodied wrasses, butterflyfishes, and damselfishes). Although reducing the data sets to these key species involved using only a subset of the data available, it did ensure consistent estimates of current standing stock across the region and among data sets. Furthermore, because the 19 key taxa represent a range of families, trophic levels, and attractiveness to fisherfolk, the biomass of these key taxa represents a good proxy of the total biomass recorded by each data set (Fig. 7). It is also important to note that because of the use of a shortlist of key species, the final models and maps of current standing stock produced by the Phase 1 project only predict standing stock of those species, not total standing stock. However, because the key species represent a good proxy of total standing biomass, the resulting maps should indicate patterns of variability in total standing stock in Micronesia.

Table 3. Details of the 19 key species used to model standing stock in Micronesia. Trophic group follows Sandin and Williams (2010). Vulnerability index taken from Abesamis et al. (2014) where available.

Family	Species	Common name	Photograph	Trophic group	Vulnerability index
Acanthuridae	*Naso lituratus*	Orange-spine surgeonfish		Primary Consumer	Low - moderate
Acanthuridae	*Naso unicornis*	Blue-spine unicornfish		Primary Consumer	High
Carangidae	*Caranx melampygus*	Bluefin trevally		Piscivore	Moderate - high

Kyphosidae	*Kyphosus spp.*	Chub or drummer		Primary Consumer	-
Labridae	*Cheilinus undulatus*	Humphead wrasse		Secondary Consumer	High – very high
Lethrinidae	*Lethrinus obsoletus*	Orange-striped emperor		Secondary Consumer	-
Lethrinidae	*Lethrinus olivaceus*	Longface emperor		Piscivore	Moderate
Lutjanidae	*Lutjanus bohar*	Two-spot red snapper		Piscivore	High – very high
Lutjanidae	*Lutjanus gibbus*	Humpback red snapper		Secondary Consumer	-
Scaridae	*Cetoscarus bicolor*	Bicolour parrotfish		Primary Consumer	High – very high
Scaridae	*Chlorurus microrhinos*	Steephead parrotfish		Primary Consumer	Moderate
Scaridae	*Chlorurus sordidus*	Bullethead parrotfish		Primary Consumer	Low
Scaridae	*Hipposcarus longiceps*	Pacific longnose parrotfish		Primary Consumer	Low - moderate
Scaridae	*Scarus rubroviolaceus*	Redlip parrotfish		Primary Consumer	-
Serranidae	*Epinephelus fuscoguttatus*	Brown-marbled grouper		Piscivore	Moderate - high
Serranidae	*Epinephelus polyphekadion*	Camouflage grouper		Piscivore	-
Serranidae	*Plectropomus laevis*	Black-saddled coral grouper		Piscivore	High – very high
Siganidae	*Siganus argenteus*	Forktail rabbitfish		Primary Consumer	-
Siganidae	*Siganus punctatus*	Gold-spotted rabbitfish		Primary Consumer	-

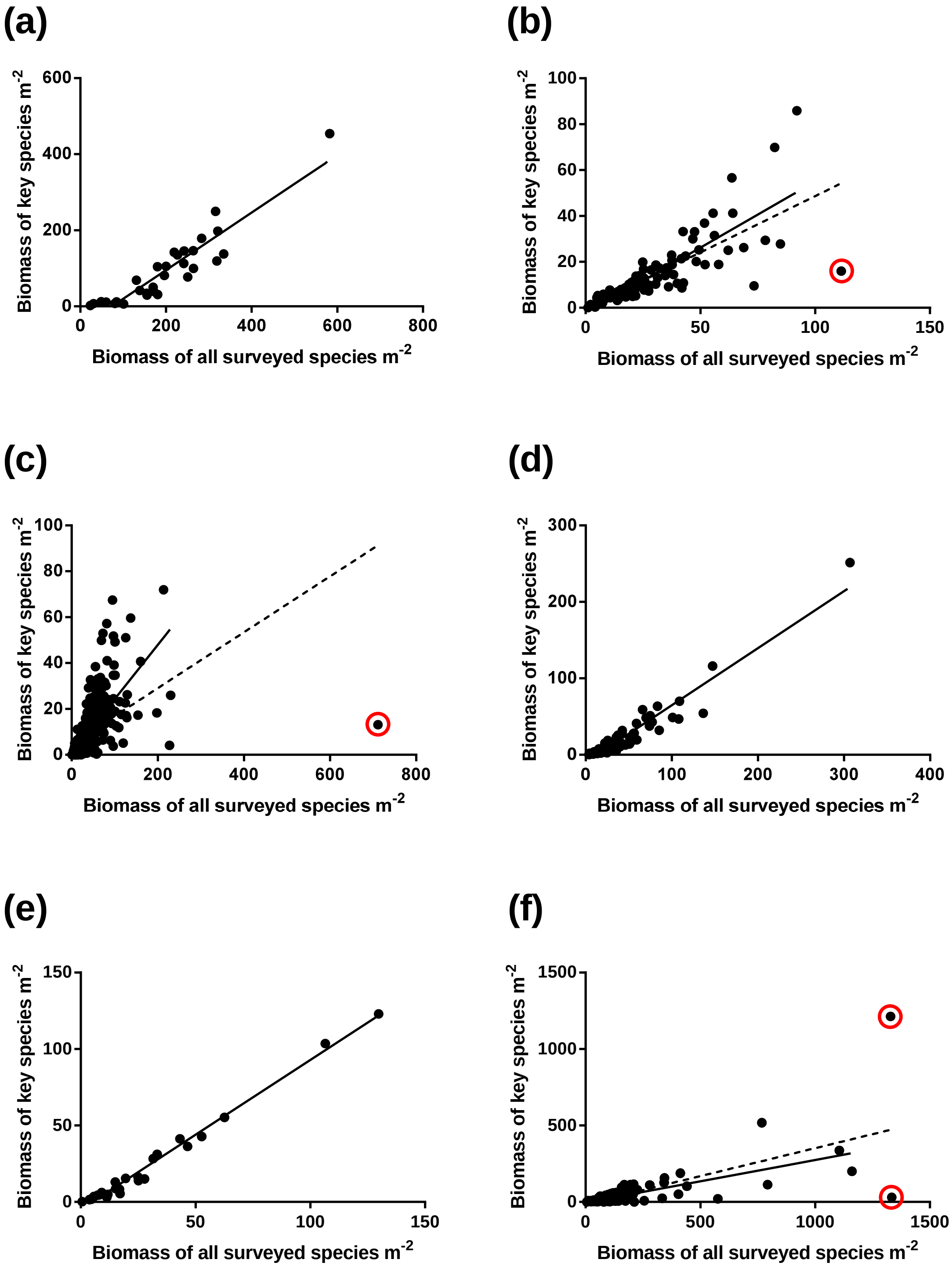


Fig. 7. Scatter plots of site-level data comparing the biomass for all species recorded to the biomass for only the 19 species considered by the Phase 1 project. Data sets and Pearson correlation coefficients (solid line) are: (a) Maria Beger (0.925), (b) Brett Taylor (0.825), (c) NOAA CRED (0.697), (d) Micronesian Challenge (0.957), (e) PICRC (0.993), and (f) PROCFISH (0.777). Alison Green (0.913) not shown because of limited number of sites. Dotted lines represent correlations including outliers (red circles) where correlation coefficients are (b) 0.764, (c) 0.506, and (f) 0.694. Outliers are caused by large shoals of (b) *Platax orbicularis*, (c) *Caranx sexfasciatus*, and (f) *Bolbometopon muricatum* (lower) and *Lutjanus gibbus* (upper).

3.5. Data comparability

Pooling of fish survey data sets is inevitable for large-scale analyses, and there are numerous examples in the literature of where this has been done successfully (Paddack et al. 2009, Mora et al. 2011, MacNeil et al. 2015). The Phase 1 project pooled data by converting the results of each fish survey to standard units (g m^{-2}) and focusing on a standardised list of 19 key species. Furthermore, there are studies suggesting that results are comparable between belt transects and stationary point counts (Watson and Quinn 1997, Samoilys and Carlos 2000). These results are supported by comparing transects and stationary point counts during collection of the Micronesian Challenge data used in the Phase 1 project (Peter Houk, unpublished data). There is also some evidence that video-based data (here the Brett Taylor database) are comparable to visual censuses, unless working with more cryptic species (Holmes et al. 2013). Furthermore, all the data sets used within the Phase 1 project are from quantitative counts within defined areas, facilitating the calculation of fish densities or biomasses per standardised unit area. Such comparisons would be very difficult if any of the data had been collected by techniques not conducted in well-defined areas (e.g. random swims). Finally, the method of data collection was explicitly incorporated as an explanatory variable into the models of fishing pressure and standing stock to account for any systematic inter-technique differences (see Section 3.7).

Despite this theoretical justification for pooling the data sets, it was prudent to compare the data where possible. Some of the data sets collected data at the same locations, and this allows for some assessment of data comparability (Appendix 2).

3.6. Mapping Micronesian reefs

Establishing the extent of reef areas within Micronesia was critical for the Phase 1 project, and the project used the maps generated by the Millennium Coral Reef Mapping (MCRM) Project. The MCRM Project utilised a global compilation of Landsat 7 ETM+ images to produce consistent map products to assist local, regional, and global research and management applications (Andréfouët et al. 2006). The MCRM project uses a thematically rich habitat classification scheme, and level 4 of this scheme was appropriate for differentiating habitats for the Phase 1 project. Firstly, habitats that would be included in the modelling and mapping work were identified (Table 4). Only habitats that were well represented in the fish survey data sets could be reliably modelled, which were typically fringing or barrier forereef slopes. These models cannot be reliably extended into other habitats because of the potential for significant inter-habitat variations in how fish assemblages respond to fishing and environmental gradients (Houk et al. 2012a). For example, since the data were predominantly from forereef slopes, the resulting models cannot be used to predict fishing pressure or standing stock on reef crests or patch reefs. However, it may be appropriate to extrapolate the maps to some habitats not well represented in the fish surveys because of perceived similarities in biophysical parameters, but these habitats were identified with a caveat that the extrapolation may not be reliable (labelled as ‘Possibly’ in Table 4).

One of the key explanatory variables used in the models of fishing pressure was human population size divided by the area of fishable reef (see Section 3.7), because previous studies have demonstrated that large populations fishing small areas of reefs have more significant impacts on fish assemblages (e.g. Stallings 2009, Cinner et al. 2013). Fishing by local populations is not limited to the habitats that were modelled, so the Phase 1 project identified all reef habitats that are likely to be fished (Table 4). The total area of these fishable habitats was used in calculations of human population pressure.

Table 4. Millennium Coral Reef Mapping (MCRM) Project level 4 marine classes. Each class may either be represented by models of fishing pressure and standing stock (with two levels of certainty, ‘Yes’ or ‘Possibly’), or not parameterised by these models (‘No’). In addition, only some habitat classes were considered in calculations of human population per unit area of fishable reef (i.e. a ‘fished reef’ habitat). wc = with constructions.

MCRM habitat	Modelled?	Fished reef?	MCRM habitat	Modelled?	Fished reef?
Bay exposed fringing	Yes	Yes	Forereef	Yes	Yes
Bridge	Possibly	Yes	Forereef or terrace	Yes	Yes
Channel	No	No	Inner slope	No	Yes
Deep drowned reef flat	Possibly	Yes	Lagoon pinnacle	Possibly	Yes
Deep lagoon	No	No	Pass	No	Yes
Deep lagoon wc	No	No	Pass reef flat	No	Yes
Deep terrace	Possibly	Yes	Pinnacle	Possibly	Yes
Deep terrace wc	Possibly	Yes	Reef flat	No	Yes
Diffuse fringing	No	Yes	Reticulated fringing	Yes	Yes
Drowned bank	Possibly	Yes	Ridge and fossil crest	No	Yes
Drowned inner slope	No	Yes	Shallow lagoon	No	No
Drowned lagoon	No	No	Shallow lagoon wc	No	No
Drowned pass	No	No	Shallow lagoonal terrace	No	Yes
Drowned patch	Possibly	Yes	Shallow terrace	No	Yes
Drowned rim	Possibly	Yes	Shallow terrace wc	No	Yes
Enclosed basin	No	No	Shelf slope	No	Yes
Enclosed lagoon	No	No	Subtidal reef flat	No	Yes
Enclosed lagoon or basin	No	No	Undetermined envelope	Yes	Yes
Enclosed lagoon wc	No	Yes	Uplifted reef flat	No	Yes
Faro reef flat	No	No			

The MCRM Project maps are vector coverages, with habitats represented by polygons of varying size. However, to accurately model the reefs of Micronesia, the Phase 1 project required a raster (grid) coverage of identically sized cells. Rasterising a vector map requires a spatial resolution to be specified, which represents a trade-off of tractability versus accuracy. For example, as the cells become larger, there are fewer of them across the region and this improves computation times. However, small areas of reef may be lost as they are grouped with surrounding lagoonal habitat. Smaller cells allow for a more accurate representation of the habitat distributions and allow the models to represent more subtle gradients in environmental factors, but computation time is increased. Furthermore, very small cells may not be well parameterised because of the limitations of the explanatory data sets. Experimentation indicated that 100 x 100 m (1 hectare) cells represent an appropriate grid size that retains habitat detail, but is computationally tractable (Fig. 8a). In contrast, 1000 x 1000 m cells lose a lot of habitat detail (Fig. 8b). Consequently, all maps products from the Phase 1 project are at a 1 hectare resolution.

It is important to note that other habitats not considered by the Phase 1 project, such as lagoons, may have significant fish stocks and be heavily exploited by fisherfolk. Rather than being unimportant, their exclusion in the Phase 1 project is a function of a lack of data to parameterise the models adequately. However, the modelling and mapping techniques described in this report could be extended to other habitats, at regional, national, or sub-national scales if additional data were available.

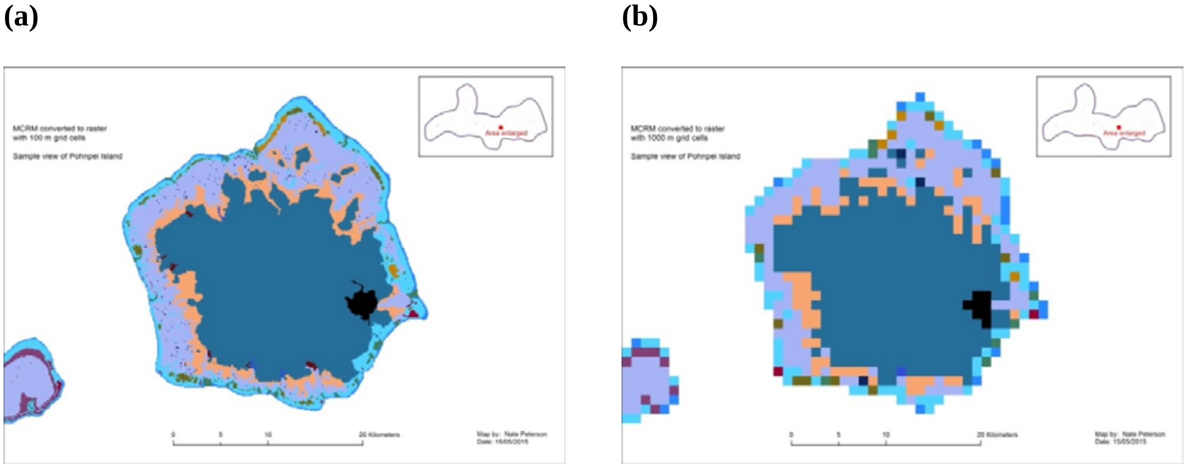


Fig. 8. The MCRM Project map of Pohnpei rasterized into (a) 100 x 100 m and (b) 1000 x 1000 m cells. The Phase 1 project used the 100 x 100 m resolution.

3.7. Derivation of explanatory variables

The response variables at each fish survey site, particularly parrotfish mean size and current standing stock, were modelled against a range of explanatory variables to assess the significant factors driving their variability. These models were then used to extrapolate fishing pressure and standing stock across the appropriate habitat types (see Section 3.6) in the five jurisdictions of Micronesia. Consequently, the Phase 1 project required continuous data layers of numerous potentially important explanatory variables (Table 5 and 6, Fig. 9). Their derivation is described in detail in Appendix 3.

Note that two explanatory variables (coral cover and depth) are available from the *in situ* fish surveys, and were included in models of fishing pressure and standing stock, but could not be mapped continuously in Micronesia. Unfortunately there is not a high-resolution bathymetric data layer for Micronesia, and deriving a continuous data layer for coral cover required information on a complex range of variables including recruitment, grazing pressure, wave exposure, and the frequency of cyclones and bleaching events (Williams et al. 2015b). These data, and an understanding of how they interact to affect coral cover and the resilience of reefs, are not available. Therefore, coral cover and depth were modelled to assess whether they are important, but during the mapping extrapolation across unsurveyed cells this parameter were represented by the mean value from all the fish survey sites (i.e. no measurable spatial variability).

Table 5. Variables used to model mean parrotfish size at each survey site, including brief details of their derivation.

Variable	Description	Derivation
Coral cover	Coral cover at collection site	From data set
Depth	Depth of data collection	From data set
Distance to pass	Distance to the nearest reef pass (gap through the reef)	MCRM
Distance to port	Distance to nearest major port	Expert knowledge of fish processing ports
Export	Degree to which each jurisdiction exports fish	Expert knowledge
Habitat type	Habitat type at location (Table 4)	MCRM
Habitat category	Whether site is in the 'Yes' or 'Possible' category in Table 4.	From MCMP
Human population pressure at 20 km	Number of people within 20 km divided by area of fishable reef	Online data on human populations and MCRM
Human population pressure at 200 km	Number of people within 200 km divided by area of fishable reef	Online data on human populations and MCRM
Island geomorphology	Geomorphology at location (e.g. atoll, fringing reef around island)	MCRM
Latitude	Latitude of survey site	From data set
Longitude	Longitude of survey site	From data set
Oceanic net primary productivity (NPP)	Mean net primary productivity from monthly data 2010-2014	Satellite data
Protected status	Whether site is in a well- or partially enforced no-take reserve	Database of marine reserves and expert knowledge
Sea surface temperature (SST)	Mean temperature of the coldest month from 2008-2012 (Kelvin)	Satellite data
Socio-economic development 1	Categorisation of the socio-economic situation in each jurisdiction	Component 1 of a PCA of a range of socio-economic variables
Socio-economic developemnt 2	Categorisation of the socio-economic situation in each jurisdiction	Component 2 of a PCA of a range of socio-economic variables
Survey method	UVC, stationary point count or video (Table 2).	From data set
Tourist pressure within 20 km	Number of tourists within 20 km	Online estimates of tourist numbers per jurisdiction, distributed in proportion to indigenous population
Tourist pressure within 200 km	Number of tourists within 20 km	Online estimates of tourist numbers per jurisdiction, distributed in proportion to indigenous population
Wave exposure	Wave exposure based on fetch and mean wind data from 2005-2009	Satellite data and fetch from MCRM
Year	Year of data collection	From data set

Table 6. Variables used to model total biomass of the 19 key species at each survey site, including brief details of their derivation and whether they were included in the final model.

Variable	**Description**	**Derivation**
Coral cover	Coral cover at collection site	From data set
Depth	Depth of data collection	From data set
Distance to pass	Distance to the nearest reef pass (gap through the reef)	MCRM
Fishing pressure	Predicted fishing pressure on 0-1 scale	From project model
Habitat type	Habitat type at location (Table 4)	MCRM
Habitat category	Whether site is in the 'Yes' or 'Possible' category in Table 4.	From MCMP
Island geomorphology	Geomorphology at location (e.g. atoll, fringing reef around island)	MCRM
Latitude	Latitude of survey site	From data set
Longitude	Longitude of survey site	From data set
Number of larvae	Estimate of relative number of larvae arriving at each reef	Biophysical model of ocean currents
Number of larvae from upstream	Estimate of relative number of larvae arriving at each reef from upstream sources only	Biophysical model of ocean currents
Oceanic net primary productivity (NPP)	Mean net primary productivity from monthly data 2010-2014	Satellite data
Protected status	Whether site is in a well- or partially enforced no-take reserve	Database of marine reserves and expert knowledge
Sea surface temperature (SST)	Mean temperature of the coldest month from 2008-2012 (Kelvin)	Satellite data
Survey method	UVC, stationary point count or video (Table 2).	From data set
Wave exposure	Wave exposure based on fetch and mean wind data from 2005-2009	Satellite data and fetch from MCRM
Year	Year of data collection	From data set

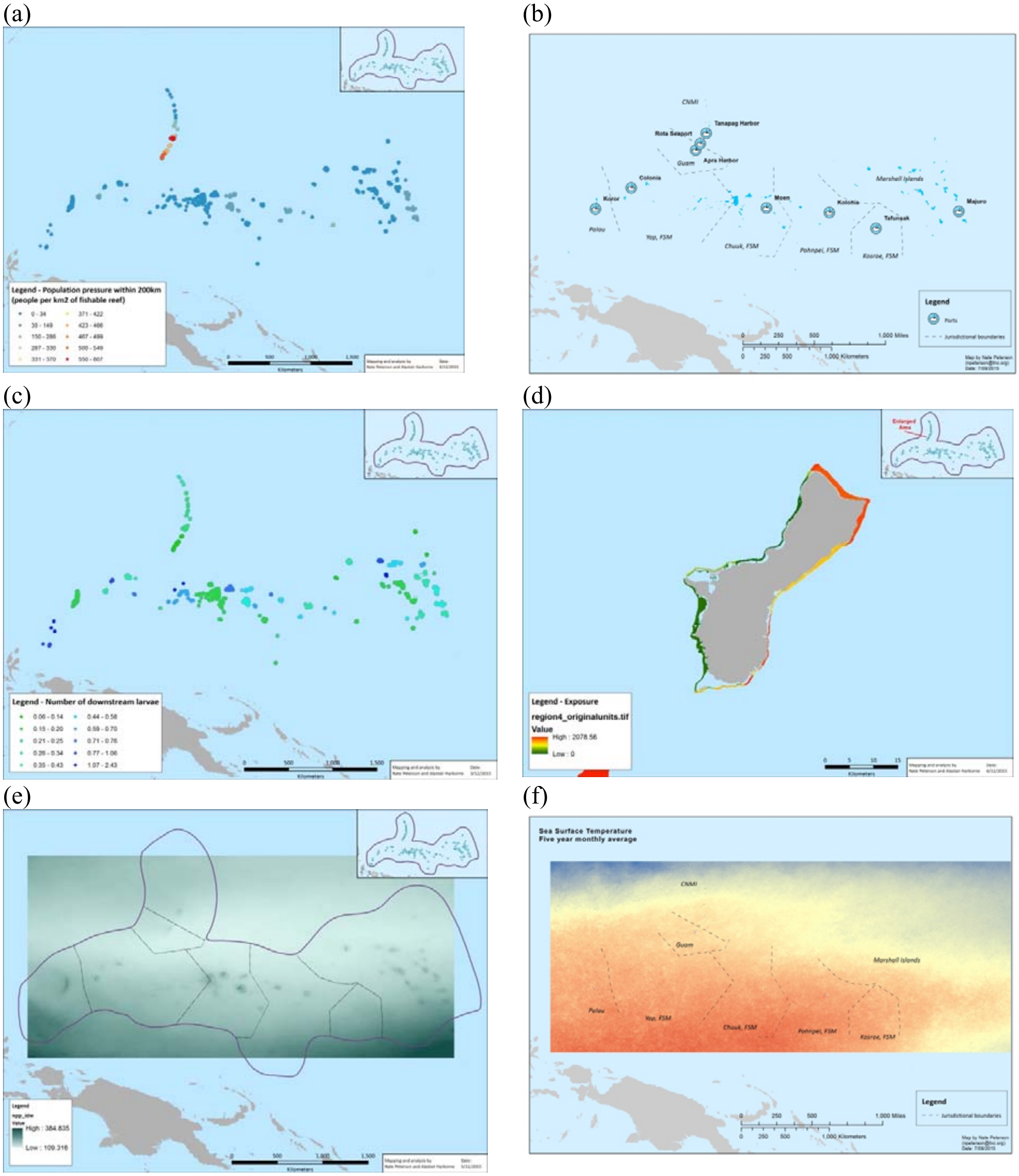


Fig. 9. Distribution of some of the key social and biophysical gradients within Micronesia. (a) Population pressure within 200 km of each 1 ha cell, (b) site of major ports, (c) relative number of larvae arriving at each reef patch from a different patch, (d) wave exposure around Guam, (e) net primary productivity, and (f) sea surface temperature.

3.8. Additional considerations for modelling potential standing stock

As described previously, the map and model of potential standing stock represents a hypothetical data layer of the potential standing stock of fish at any location with no fishing. The map of potential standing stock represents a target carrying capacity that might be reached within a well-enforced no-take reserve, or following implementation of another fisheries management tool, after a sufficiently long time has elapsed to allow fish abundances to recover. However, there are myriad factors that will alter the carrying capacity, such as habitat quality that may be altered by disturbances (Abesamis et al. 2014), and this map should be viewed as only indicative of which reefs may be able to support higher biomasses of fishes in the absence of fishing or other stressors. As for the current standing stock data layers, note that the map shows the potential standing stock of the 19 key species, not the entire assemblage. However, the potential standing stock of these 19 species is a proxy of total potential standing stock.

The time needed for fishes to fully recover in no-take reserves and reach a putative carrying capacity is an important research topic (Abesamis et al. 2014), encompassing complex questions of variability among fish families (McClanahan et al. 2007), predator-prey interactions that may lead to some species decreasing in abundance because of increasing abundances of carnivores (Micheli et al. 2004), and increasing abundances of herbivores increasing habitat quality by grazing macroalgae (Mumby and Harborne 2010). Noticeable differences in fish stocks are often visible within a few years (Halpern and Warner 2002, Russ et al. 2008), but up to 40 years may be needed for some predatory fishes (Russ and Alcala 2004). Providing additional insight into the recovery of species under scenarios of fishing cessation is beyond the scope of the Phase 1 project, but we provide broad spatial estimates of when standing stock might recover using estimates of the ratio of current to potential standing stock and recent, generic insights into the recovery of reef fishes (MacNeil et al. 2015). Furthermore, data on trajectories of recovery within no-take reserves in the region (e.g. PICRC data on no-take reserve effectiveness) may be used in future to better parameterise these recovery rates for the reefs of Micronesia.

3.9. Statistical analyses

For models of both fishing pressure and standing stock, the final data set consists of univariate response variables (e.g. mean size of parrotfishes), and a large number of categorical and continuous explanatory variables. Furthermore, the relationships among explanatory and response variables may be curvilinear and include significant interactions that are difficult to predict *a priori*. Consequently, the Phase 1 project used boosted regression trees (BRTs) during the modelling process. Explaining the mathematical basis of BRTs is beyond the scope of this report, and readers are referred to Elith et al. (2008) for an excellent introduction to the topic. Briefly, BRT relates a response variable to explanatory variables by recursive binary splits (e.g. sites with high and low human populations) using an adaptive algorithm. BRT essentially creates an additive regression model and the relationships between the variables are visualised in a series of intuitively obvious graphs. Critically, BRTs have many advantages that were useful for the Phase 1 project including handling different types of predictors, accommodating missing data, being insensitive to outliers, fitting complex nonlinear relationships, automatically handling interactions, and being robust to fitting a large number of explanatory variables (Elith et al. 2008). Finally, models can easily be used to predict values at other locations, as required to transition from the models based on fish survey data to continuous regional maps of fishing pressure and standing stock. Random variables are harder to include in BRTs than in generalized linear mixed-effect models, and the Phase 1 project accounted for the clustering of fish survey sites by investigating spatial autocorrelation in the data (see Stuart-Smith et al. 2013 for a description and justification of this approach).

Within the Phase 1 project, all the variables (Tables 5 and 6) were first tested for correlations. Variables were then removed so that there were no inter-variable correlations >0.7. The remaining variables were then included within the BRT, along with a variable comprising of random numbers. This variable was included as a guide to which variables were most 'significant' (Soykan et al. 2014): variables which had less explanatory power than this random number were removed from the model to generate a final, minimal model including only the most important variables. BRT parameters (learning rate, tree complexity, and bag fraction) were calculated for each model by testing each model across a series of values, and then using the values that gave the lowest model deviance (Elith et al. 2008). Model performance was assessed using the amount of deviance explained and the correlation between observed and model-predicted values.

4. Results of the Phase 1 project

4.1. Fishing pressure model

The model of parrotfish mean size (log transformed to improve normality of residuals) involved a range of variables (Table 5), but latitude was removed because it was strongly correlated with sea surface temperature, the tourist variables were removed because they were strongly correlated with human population pressure, and the second principle component axis of socio-economic development was removed because it was strongly correlated with primary productivity and sea surface temperature. The boosted regression tree analysis resulted in a series of partial dependency plots that can be interpreted in exactly the same way as a regression line on a traditional scatterplot (Fig. 10).

This model was then used to predict fishing pressure in every 1 ha cell considered by the project. Predictions were made from the model by classifying the significant variables (Fig. 10) into three categories. Firstly, distance to port and human population pressure were considered to relate entirely to fishing pressure (higher fishing pressure close to ports and population centres). Predictive values unique to each 1 ha cell were used for each of these variables. In contrast, sea surface temperature, coral cover, exposure, longitude, depth, and year were considered to be either environmental drivers of parrotfish size (e.g. parrotfish are bigger where there is higher coral cover) or functions of the data set (data collected in different years). The values of these variables in every 1 ha cell were set to their mean. This ensured that the predictions only represented the effects of fishing on parrotfish size, and not environmental gradients, as required for the map of fishing pressure. Actual values of each variable in each cell would have been used if the aim was to predict actual mean parrotfish size: but here the project only wanted to investigate the effect of fishing on parrotfish size. The final category was for the variable distance to pass, which was assessed as reflecting both human and environmental inputs. The most parsimonious explanation for the relationship between distance to pass and mean parrotfish size (Fig. 10) is that size increases close to passes because of the increased water flow and hence increased productivity, and increases far from passes because fisherfolk prefer to fish close to access points onto the reef (i.e. where they are likely to transit from the lagoon onto the forereef). Distance to pass has previously been demonstrated to be an important influence on parrotfish abundances in the region (Taylor et al. 2014a). The small peak in mean parrotfish size when distance to pass is ~10 km is less easy to explain, but is less significant than the peaks at small or large distances and was assumed to be caused by human influences. To only model the effects of fishing on parrotfish size, the Phase 1 project used a hybrid relationship between parrotfish size and distance to pass in order to maintain the human component but remove the environmental component (Fig. 11).

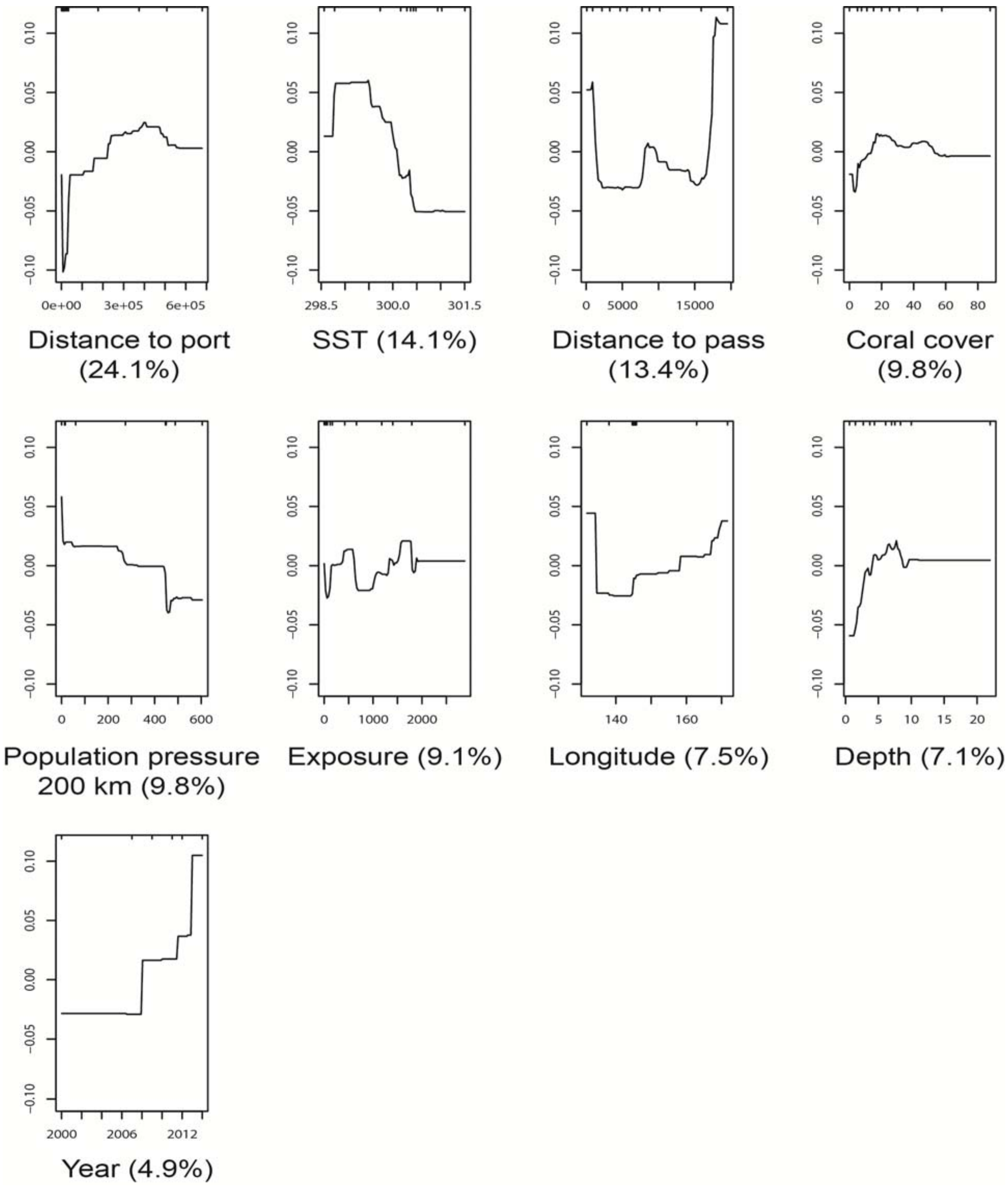


Fig. 10. Relationships between each significant variable and mean parrotfish size (increasing values on y axis, which is equal to decreasing fishing pressure) as modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log parrotfish size on the y axis are normalised.

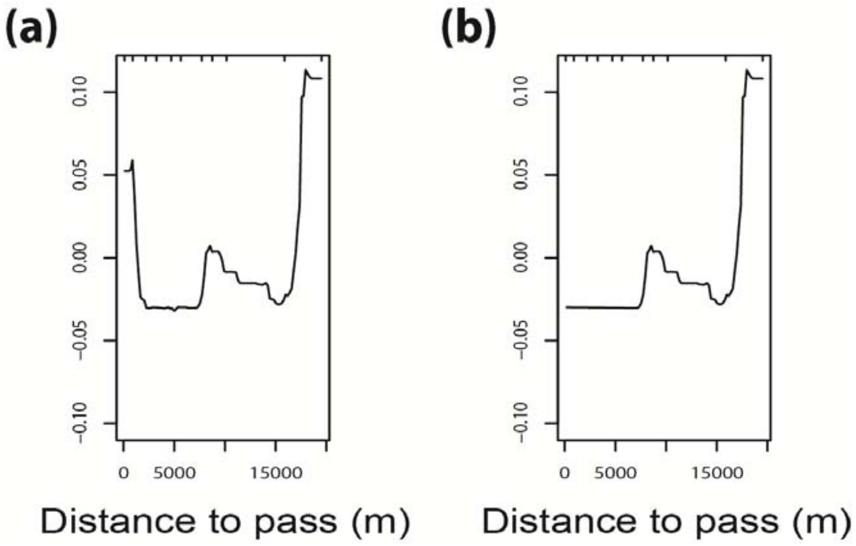
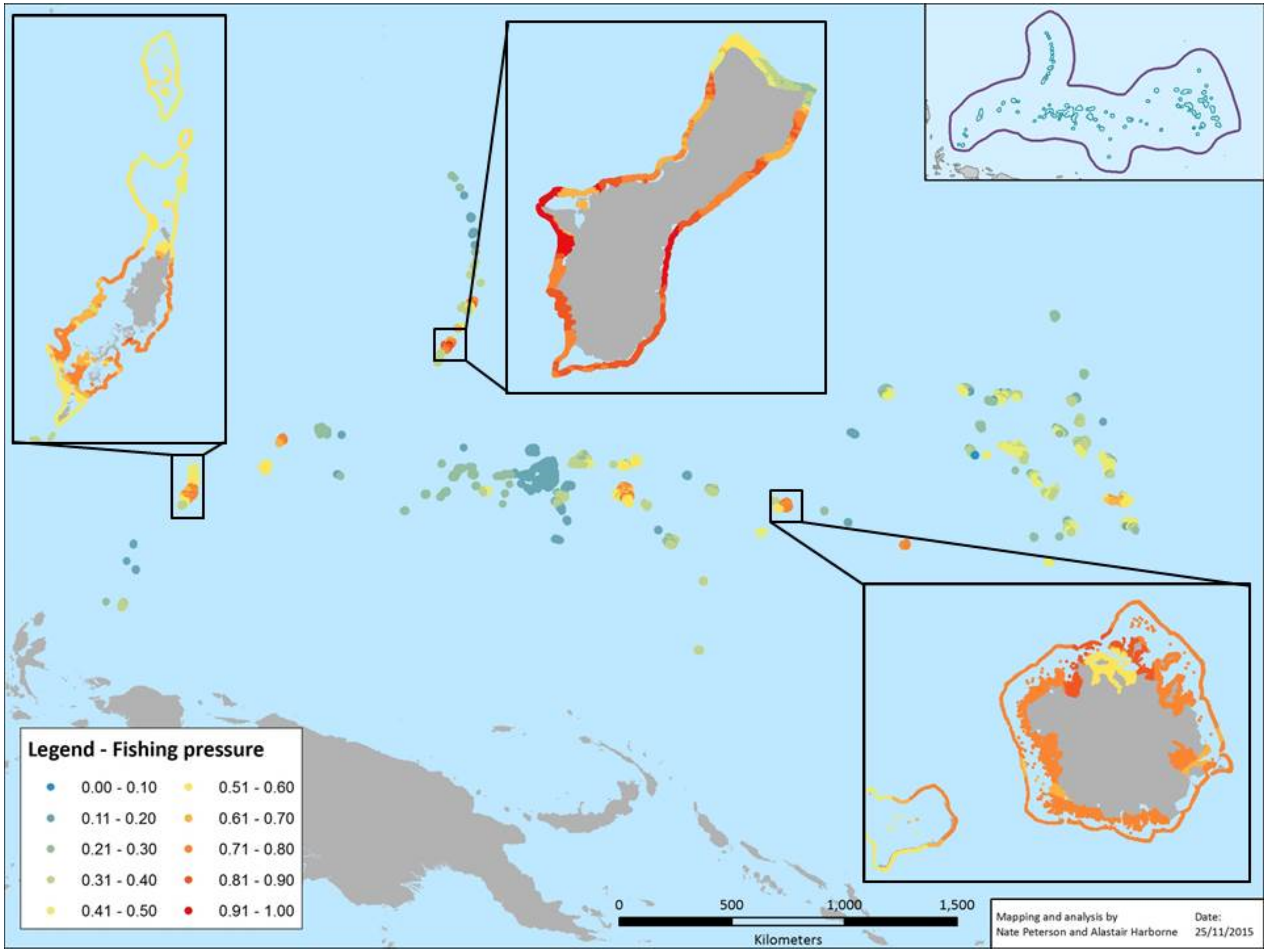


Fig. 11. Changes made to (a) modelled relationship between distance to pass and mean parrotfish size to produce (b) hybrid relationship used to predict fishing pressure by only incorporating the human effect on parrotfish size.

The fishing pressure model explained 36% of the variability in the data set, and the correlation between observed and predicted values was 0.602. This exploratory power is considered acceptable given the challenges of the project: combining multiple data sets across a large geographic area and using a relatively crude fishery-independent metric of fishing pressure. There was significant (Moran's I; *P*=0.041) spatial autocorrelation among the residuals of the BRT model, but this correlation was negative. This means that residuals at sites close together are more dissimilar than residuals among more distant sites (Stuart-Smith et al. 2013), which is the opposite of what would be expected if the effects of spatial structure in the location of data collection sites was affecting model performance.

Following predictions of parrotfish sizes in each 1 ha cell, the predicted log transformed values of parrotfish size were rescaled to range from 0 (lowest fishing pressure in the region) to 1 (highest fishing pressure in the region) (Map 1). Note that this range covers an extremely broad range from highly fished reefs close to population centres through to virtually untouched remote atolls. Consequently, even small numerical increases in fishing pressure may be significant for considering fisheries management options. Furthermore, space limits mean that only three larger-scale maps are presented as insets on the regional-scale map. However, the digital map files allow users to zoom in on any island or sub-region within Micronesia and view the data at the 1 ha resolution.



Map 1. Regional map of predicted relative fishing pressure, including larger-scale insets of fishing pressure around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).

4.2 Interpretation of the fishing pressure model

The final model for fishing pressure (Fig. 10) shows that parrotfish size typically increased (decreasing fishing pressure) with increasing distance from the nearest port and decreasing population pressure within 200 km, which is consistent with a number of previous studies that have examined the impacts of humans on fish stocks (e.g. Cinner et al. 2013). The predicted increase in parrotfish size very close to ports may be a statistical artefact, or may represent a reluctance of fisherfolk to fish close to port entrances, perhaps because of concerns about pollution, small fishing boats needing to avoid larger shipping entering the ports, or increased enforcement of fishing restrictions. Although care must be taken to avoid over-interpreting curvilinear relationships in BRT models, there do appear to be some population pressure thresholds that may be significant within Micronesia. Thus there appears to be a noticeable drop in parrotfish size between reefs with almost zero population pressure and reefs exposed to small population pressures. This threshold suggests that only the remotest reefs in the region have virtually unexploited fish stocks. A second threshold seems to occur at a population pressure of ~450 people per km^2 of reef, suggesting that highly populated areas have disproportionally significant fishing impacts that may be exacerbated by the effects of other stressors such as pollution and coastal development.

Parrotfish size was also affected by environmental gradients, and tended to be higher on cooler, deeper reefs with medium to high coral cover. The impact of temperature on fish size is attracting increasing research attention because of the potential impacts of climate change, and there is now a relatively well-established expectation that fish size will decrease with increasing temperature because of changes in distribution and physiological stress (Daufresne et al. 2009, Sheridan and Bickford 2011, Cheung et al. 2013). The effect of coral cover on fish abundance is long-established, because of fish using corals for functions such as hiding from predators (Bell and Galzin 1984). However, the relationship between coral cover and fish size is less well known. We suggest that the increase in parrotfish size with increasing coral cover may be caused by smaller-bodied species being excluded from high coral cover areas because of a lack of food. Larger-bodied species will still be present because they are able to forage more widely, and find food sources between coral patches. Although there is some research on the effects of coral cover on parrotfish foraging (Nash et al. 2012), this hypothesis requires further testing.

Water movement can have significant effects on fish assemblages (Fulton et al. 2005), but the relationship between wave exposure and parrotfish size was not clear in the fishing pressure model. However, there is some suggestion that mean size increases with increasing exposure, perhaps because only larger species can function in areas with high water movement. More sophisticated models of wave energy may be able to elucidate this relationship more clearly. However, very turbulent water on the shallowest reefs may exclude some species, leading to a more abundant and varied assemblage below a depth of ~5 m. Parrotfish sizes tended to be higher to the east and west of the region, perhaps because of biogeographical patterns. Year was a significant factor in the model, presumably because less exploited areas were generally surveyed more recently.

Note that although marine reserve status was not included in the final model, this does not mean that reserves are not locally effective in the region. Rather, their effects are not clear at a regional scale because of factors such as the large biophysical gradients across Micronesia, the varying age and enforcement of reserves, and potentially having a larger effect on variables other than parrotfish size (e.g. total biomass of fished species). Marine reserves have repeatedly been demonstrated to be effective for increasing fish biomass compared to nearby fished reefs (Mosquera et al. 2000, Russ 2002, Halpern 2003), and the marine reserve effect is likely to become clearer in the future.

4.3. Current standing stock model

The model of total biomass of the 19 key species (log transformed to improve normality of residuals) involved a range of variables (Table 6), but latitude was removed because it was strongly correlated with sea surface temperature. The boosted regression tree analysis resulted in a series of partial dependency plots that can be interpreted in exactly the same way as a regression line on a traditional scatterplot (Fig. 12). This model was then used to predict the biomass of the current standing stock of these 19 species in every 1 ha cell considered by the project (Map 2). Values specific to each reef cell were used for every variable, except for mean values of coral cover and depth because of the lack of region-wide data layers of the variables (see Appendix 3). The fishing pressure model explained 52% of the variability in the data set, and the correlation between observed and predicted values was 0.721. This exploratory power is considered acceptable given the challenges of combining multiple data sets across a large geographic area. There was no significant (Moran's I; P=0.129) spatial autocorrelation among the residuals of the BRT model.

4.4. Interpretation of the current standing stock model results

The final model for current standing stock (Fig. 12) shows that the biomass of the 19 key species tended to be highest in more productive waters. This is consistent with ecological theory that higher primary productivity enriches food webs at higher trophic levels, and has previously been reported as a strong driver of fish biomass across the Pacific (Williams et al. 2015a). Within reefs, the presence of passes through the reef can also increase productivity because of higher water flow, and biomass was negatively correlated with increasing distance from a pass. As for mean parrotfish size, standing stock was negatively correlated with sea surface temperature, although there appeared to be a slight increase in biomass at the warmest temperatures. Biomass was also increased by a greater supply of larvae from upstream sources, which suggests a potential, assemblage-scale role of increasing larval supply on fish abundances. There has been much debate about the role of larval supply on fish demographics (Hixon 2011), but the data from Micronesia support species-scale studies that demonstrate higher adult abundances at sites with high larval supply (Doherty and Fowler 1994). Furthermore, the relationship between larval supply and biomass is consistent with expectations that biomass will increase linearly with increasing larval supply at relatively low levels, but then will asymptote when larval supply as density-dependent processes regulate population sizes (Hixon et al. 2012). The role of self-recruitment in determining fish biomass was difficult to assess in this study because of the limitations of the biophysical model, but has been demonstrated in other studies to be an important source of recruits, and is a particularly critical consideration in protected area network planning (Harrison et al. 2012).

Biomass was higher as depth increased to ~25 m and on sheltered reefs, presumably because some species avoid turbulent and physiologically challenging shallow reefs (Fulton et al. 2005, Harborne 2013). Biomass was highest on reefs with medium to high coral cover, reflecting the long-established link between fish and live corals that provide refuge, feeding, and settlement microhabitats (Bell and Galzin 1984, Coker et al. 2014). Biomass also appeared to higher on the westernmost reefs within the region. This longitudinal gradient is likely to reflect biogeographic patterns in fish biomass, possibly linked to the proximity of western reefs to the large reef areas of the Coral Triangle that may enhance larval supply. Increasing fishing pressure decreased total biomass, as expected given the well-established impact of fishing on reef fisheries (Friedlander and DeMartini 2002, Mora 2008). Stationary point counts tended to underestimate fish biomass compared to visual or video belt transects. Year was a significant factor in the model, presumably because of the order in which the reefs were surveyed (higher in years when less exploited areas were surveyed).

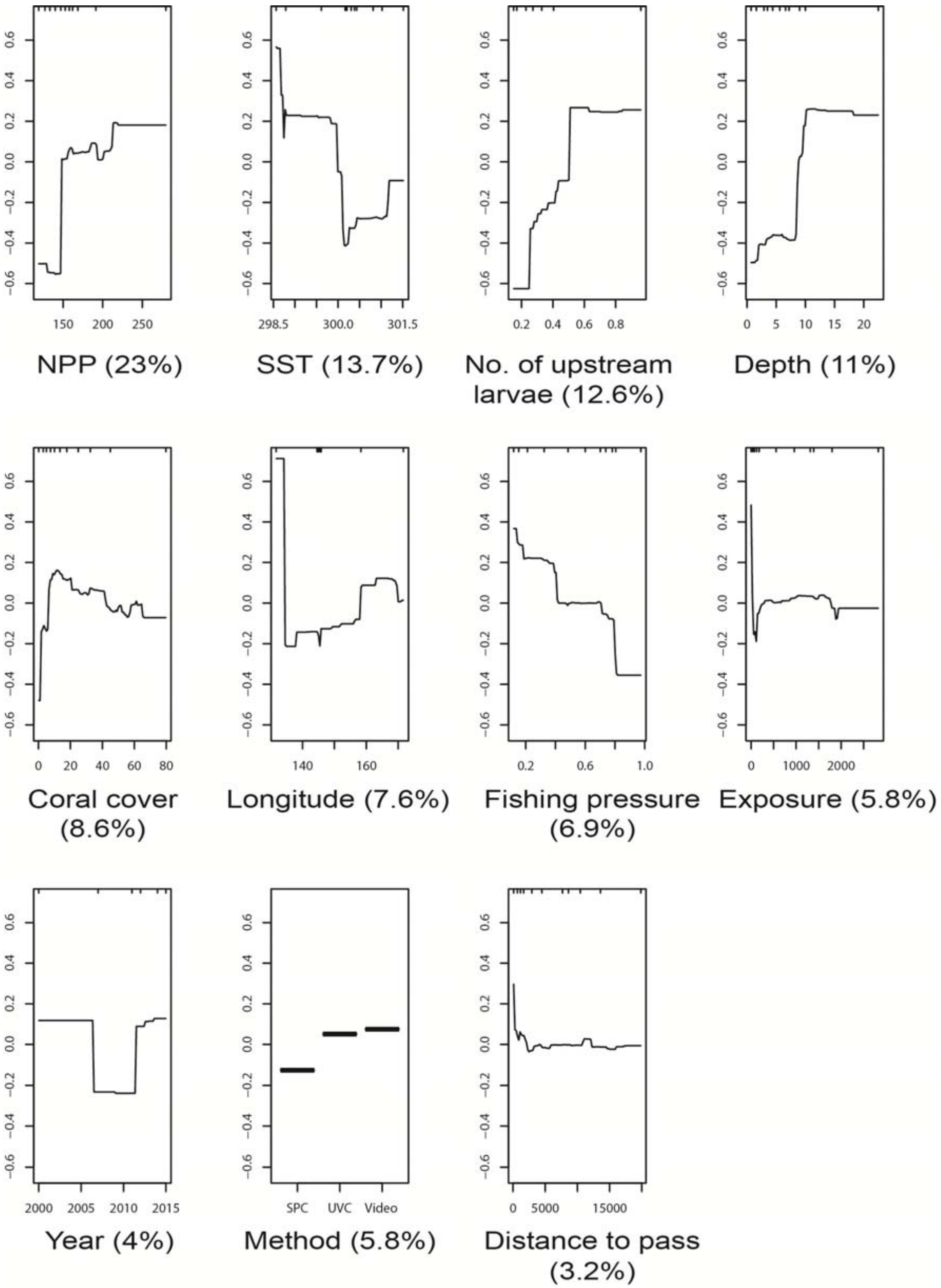
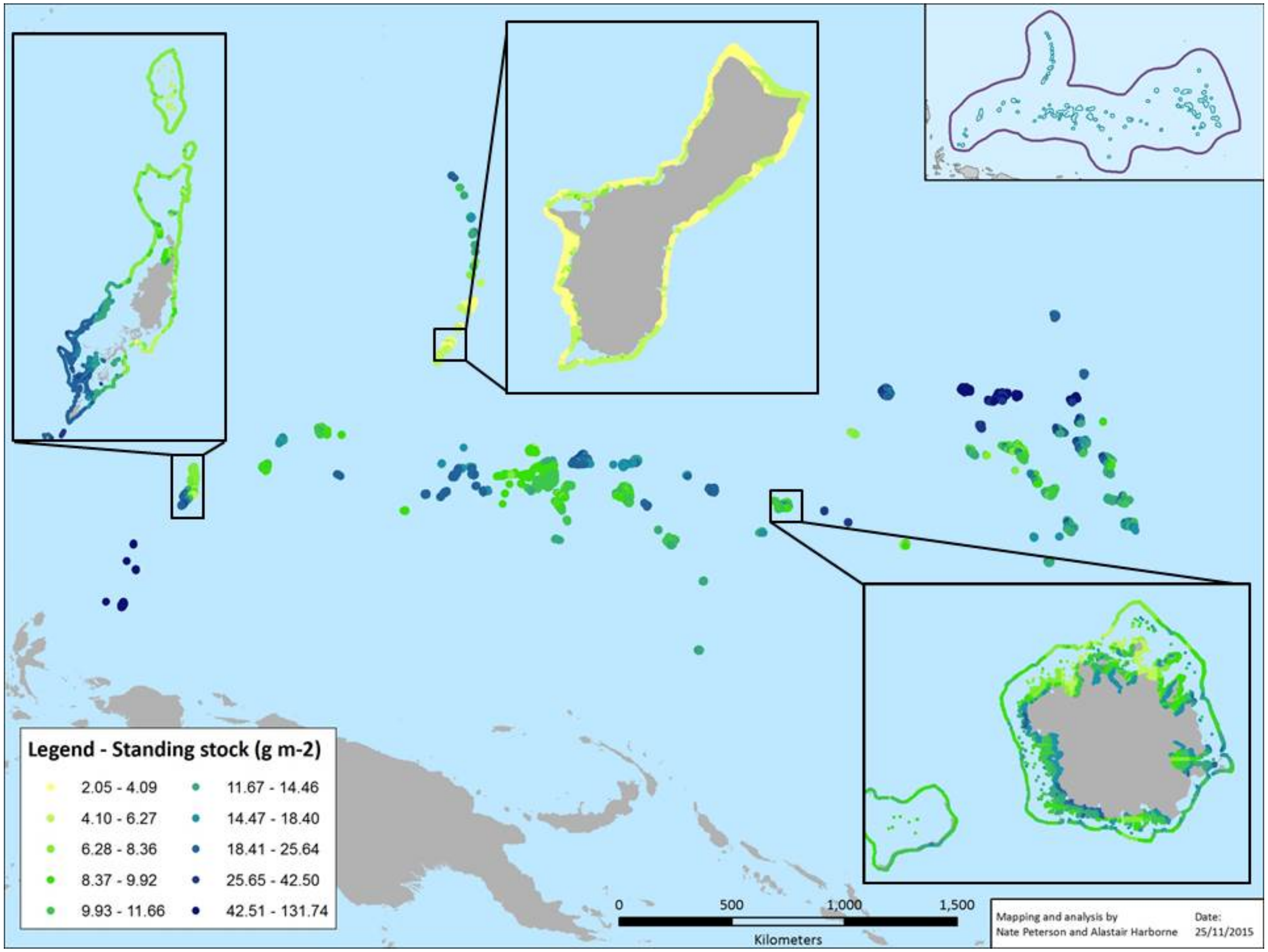


Fig. 12. Relationships between each significant variable and total biomass of 19 key species (y axis) modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log biomass on the y axis are normalised.

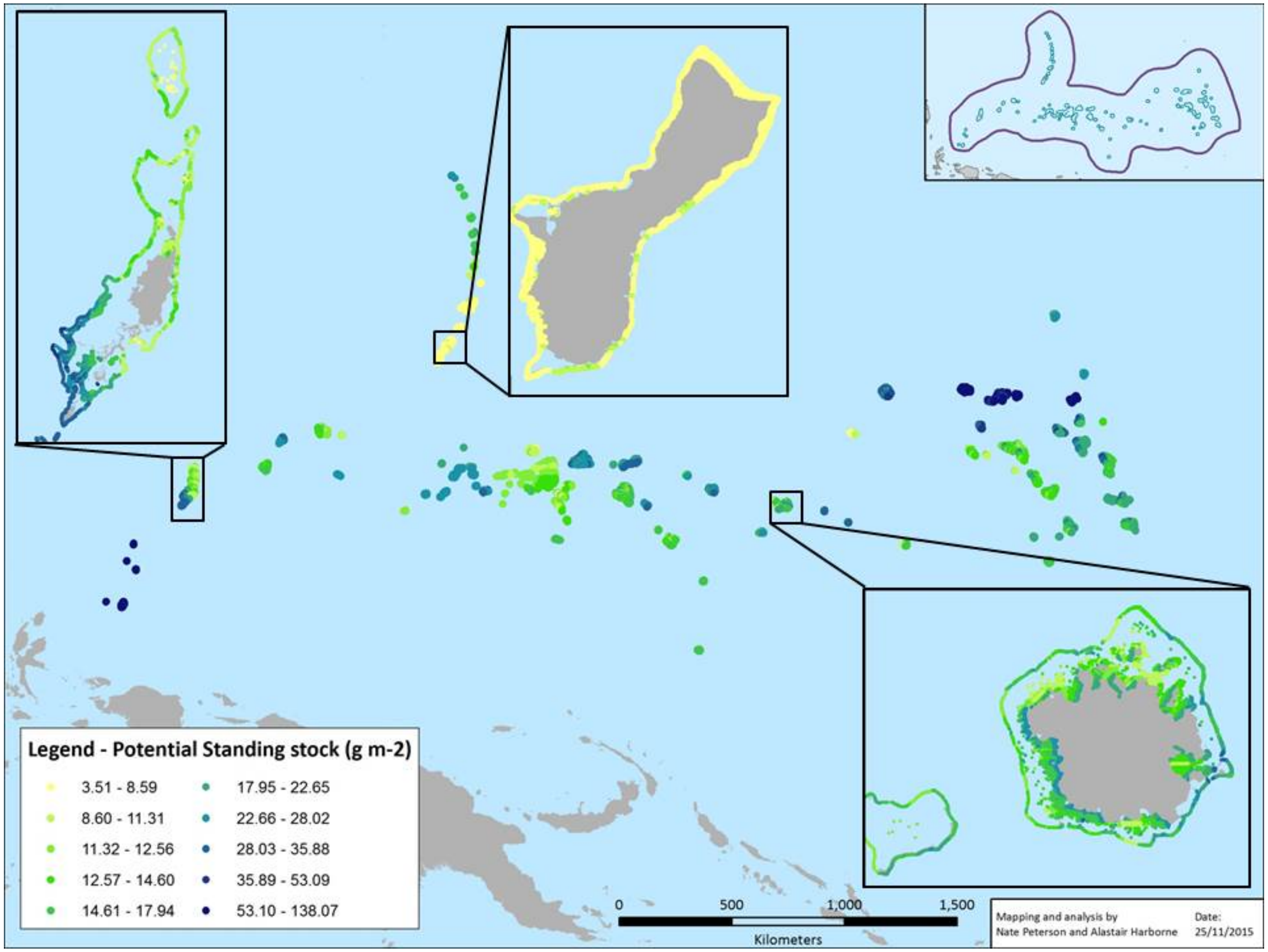


Map 2. Regional map of predicted current standing stock of 19 key fish species, including larger-scale insets of the biomass around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).

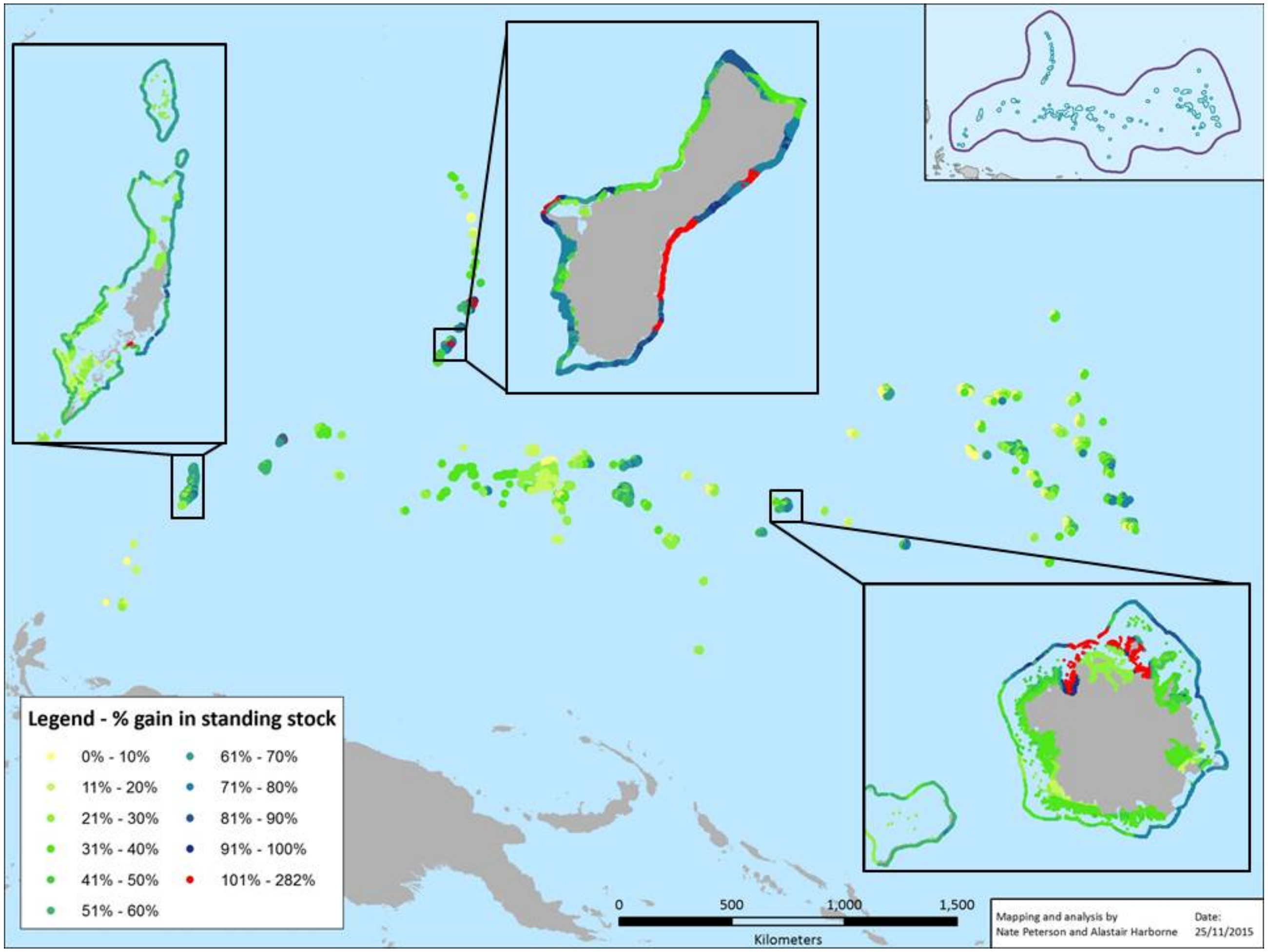
4.5. Generating a map of potential standing stock

The map of potential standing stock represents a hypothetical data layer of the potential standing stock of fish at any location with no fishing pressure (Map 3). It was created by predicting the standing stock in each 1 ha cell with fishing pressure set to 0 (as opposed to the value actually predicted by the fishing pressure model). The map of potential standing stock represents a carrying capacity that might be reached within a well-enforced no-take reserve. However, equivalent layers can be created by predicting standing stock with increased coral cover or SST (e.g. the impacts of climate change). Because of the complex ecological processes on reefs, this map should be viewed as only indicative of which reefs may be able to support higher biomasses of fishes in the absence of fishing or other stressors. Note that, as for the current standing stock data layers, the map only shows the potential standing stock of the 19 key species, not the entire assemblage. However, the potential standing stock of these 19 species is a good proxy of total potential standing stock.

The difference between the values for current and potential standing stock was calculated for every 1 ha cell in order to produce an estimated potential gain in absolute biomass if fishing pressure was reduced to 0. This value was also used to generate a map of the potential percentage gain in biomass under a scenario where fishing pressure was reduced to 0 (Map 4). By summing the absolute predicted gain in biomass, we suggest that the standing stock of these 19 species alone would increase by ~12,200 metric tonnes following the cessation of fishing.



Map 3. Regional map of predicted potential standing stock of 19 key fish species if there was zero fishing, including larger-scale insets of the biomass around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).



Map 4. Regional map of predicted potential percentage gain of standing stock of 19 key fish species if there was zero fishing, including larger-scale insets of the gain around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).

4.6. Models of current and potential standing stock for each fish trophic group

Using an identical model structure to that described for total biomass (Table 6), the models were rerun for the response values of total biomass (log transformed) of each trophic group (primary consumers [herbivores], secondary consumers [predominantly invertivores], and piscivores). The trophic group model performances were: primary consumer model explained 50% of the variability in the data set, and the correlation between observed and predicted values was 0.708; secondary consumer model explained 35% of the variability in the data set, and the correlation between observed and predicted values was 0.567; piscivore model explained 45% of the variability in the data set, and the correlation between observed and predicted values was 0.669. These models (Figs 13-15) were then used to map the predicted current standing stock of each trophic group (Maps 5-7). Finally, fishing pressure was then set to 0 in order to calculate potential standing stock of each trophic group and map the predicted potential percentage gains (Maps 8-10).

The models for each trophic group are qualitatively similar to the model for total standing stock, but with some interesting differences. The biomass of primary consumers is particularly sensitive to the number of upstream larvae, possibly reflecting the importance of larval supply to herbivore dynamics. The negative impact of fishing pressure was also stronger in the model of primary consumers, which reflects the importance of herbivores in Micronesian fisheries. The effect of temperature is also less significant for herbivores, perhaps reflecting the complex effects of temperature on both these fishes and their food resources.

The model for secondary consumers is least robust because of the small number of species, and should be interpreted with care. Perhaps most noticeably, the biomass of this group was correlated with geomorphology, with increased biomass at reefs on atolls or around islands with extensive lagoonal areas. The inclusion of this variable may reflect the importance of mangrove and seagrass nursery habitats to these species, which can significantly enrich local populations (Nagelkerken 2009).

The biomass of piscivores was most clearly correlated with water temperature, reflecting the sensitivity of species such as grouper to increased temperatures (Johansen et al. 2014). In contrast to the other trophic groups, piscivores were more abundant on windward (high exposure) reefs. As for secondary consumers, there was some evidence that nursery areas are important for piscivores. Finally, although increasing fishing pressure generally decreased the abundance of piscivores as expected, piscivore biomass was slightly lower when fishing pressure was ~0 compared to when fishing pressure was ~0.1. This may be an artefact in the data, or may reflect that some fishing, which typically targets the apex predators (e.g. sharks and the largest grouper), may increase the abundance of smaller piscivores by removing their predators. This meso-predator release has been documented in many marine systems (Myers et al. 2007), but has only received limited attention on coral reefs. However, on remote reef systems, high piscivore biomass has been documented to drive prey assemblages with fewer large prey and greater numbers of prey from small size classes (Friedlander et al. 2010).

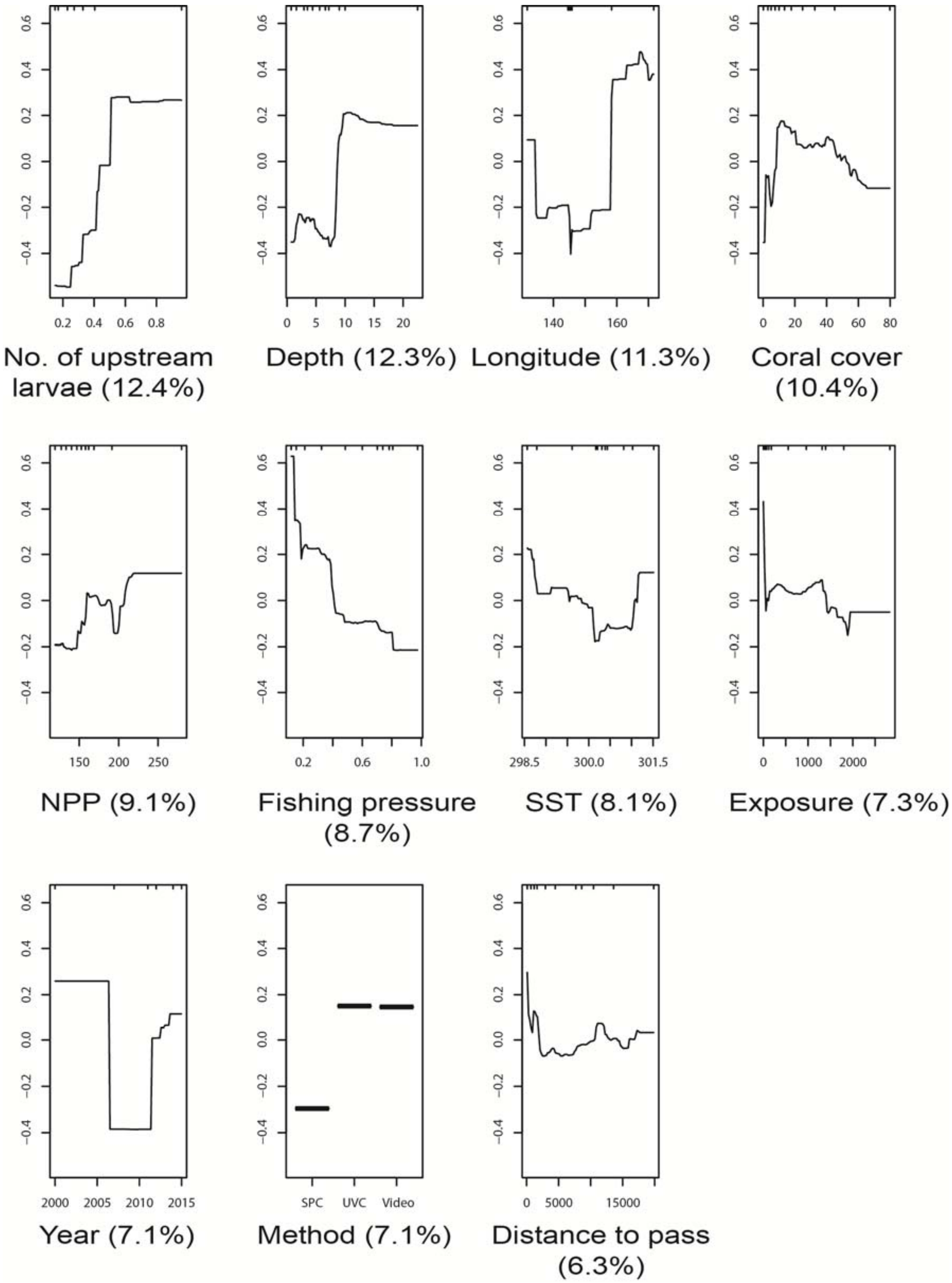


Fig. 13. Relationships between each significant variable and total biomass of 10 key primary consumers (herbivores) (y axis) modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log biomass on the y axis are normalised.

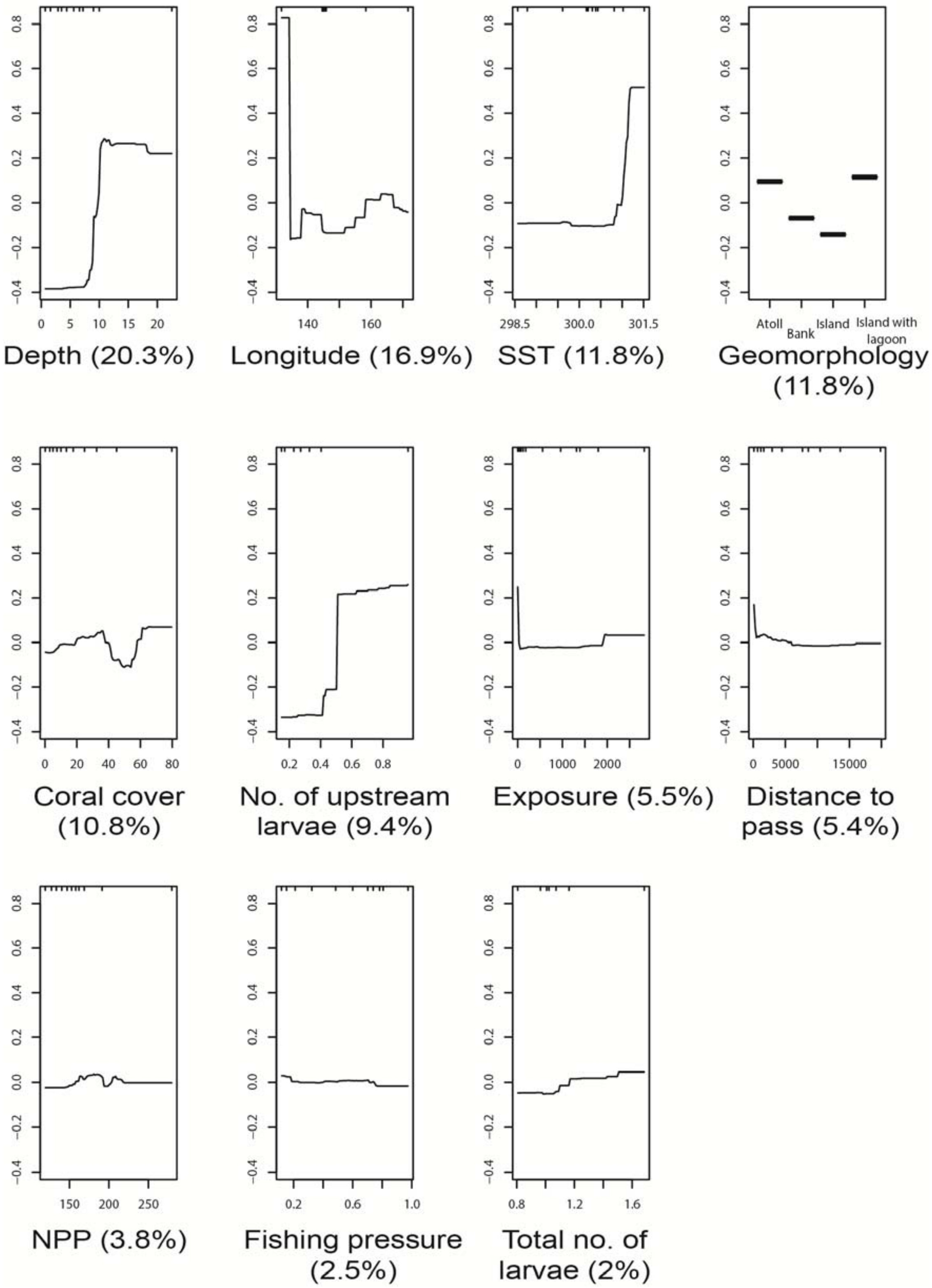


Fig. 14. Relationships between each significant variable and total biomass of 3 key secondary consumers (invertivores) (y axis) modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log biomass on the y axis are normalised.

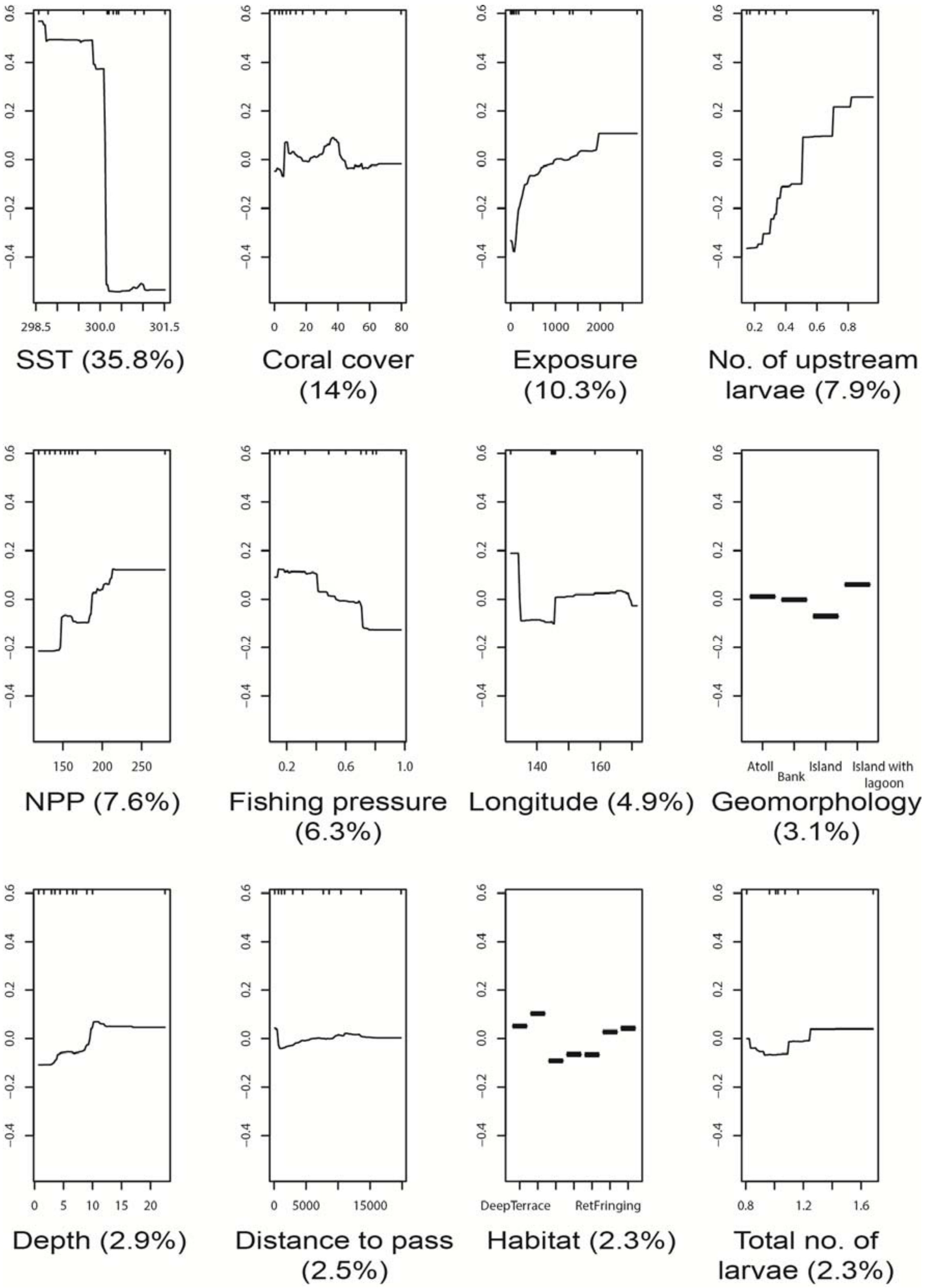
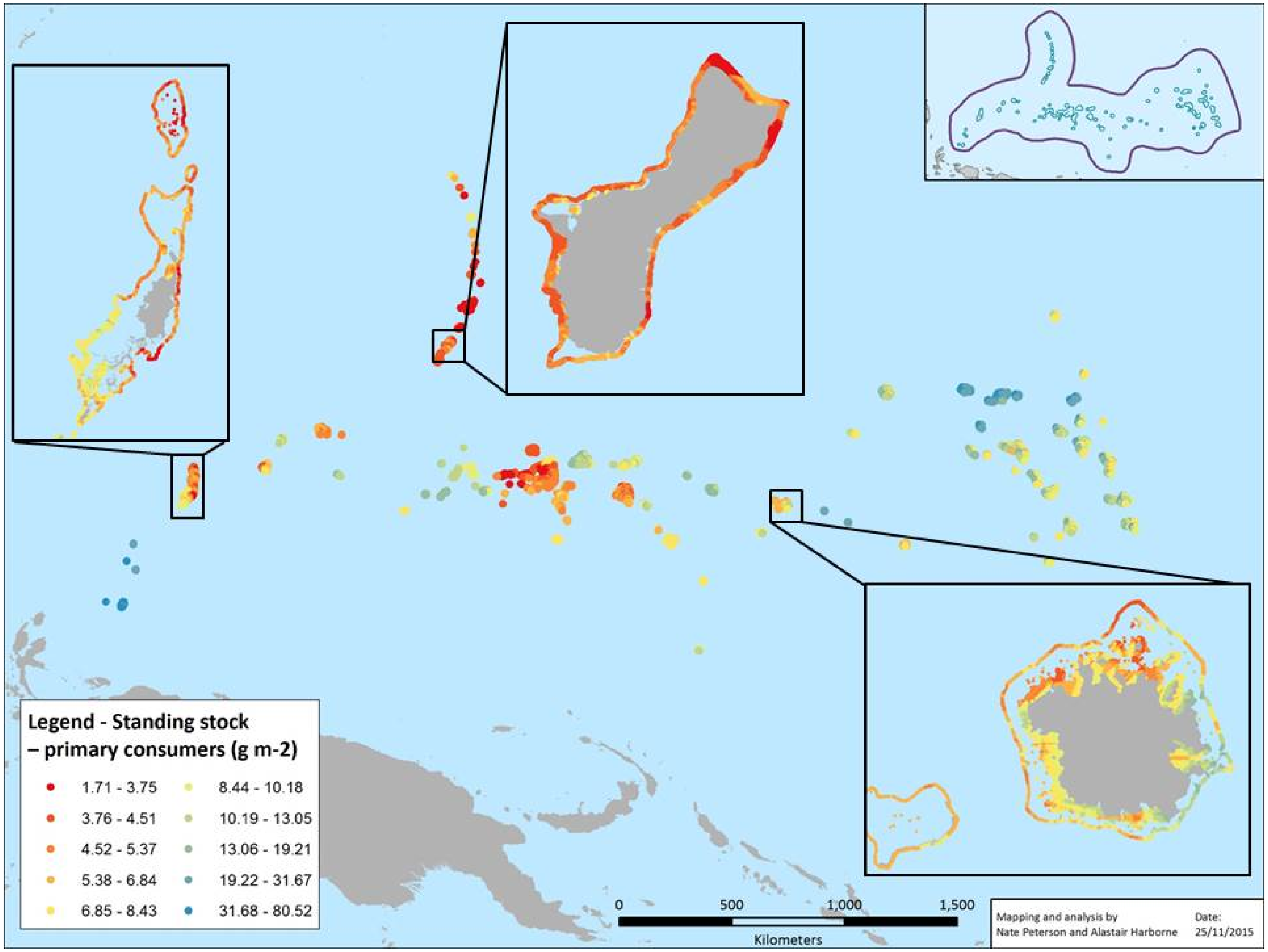
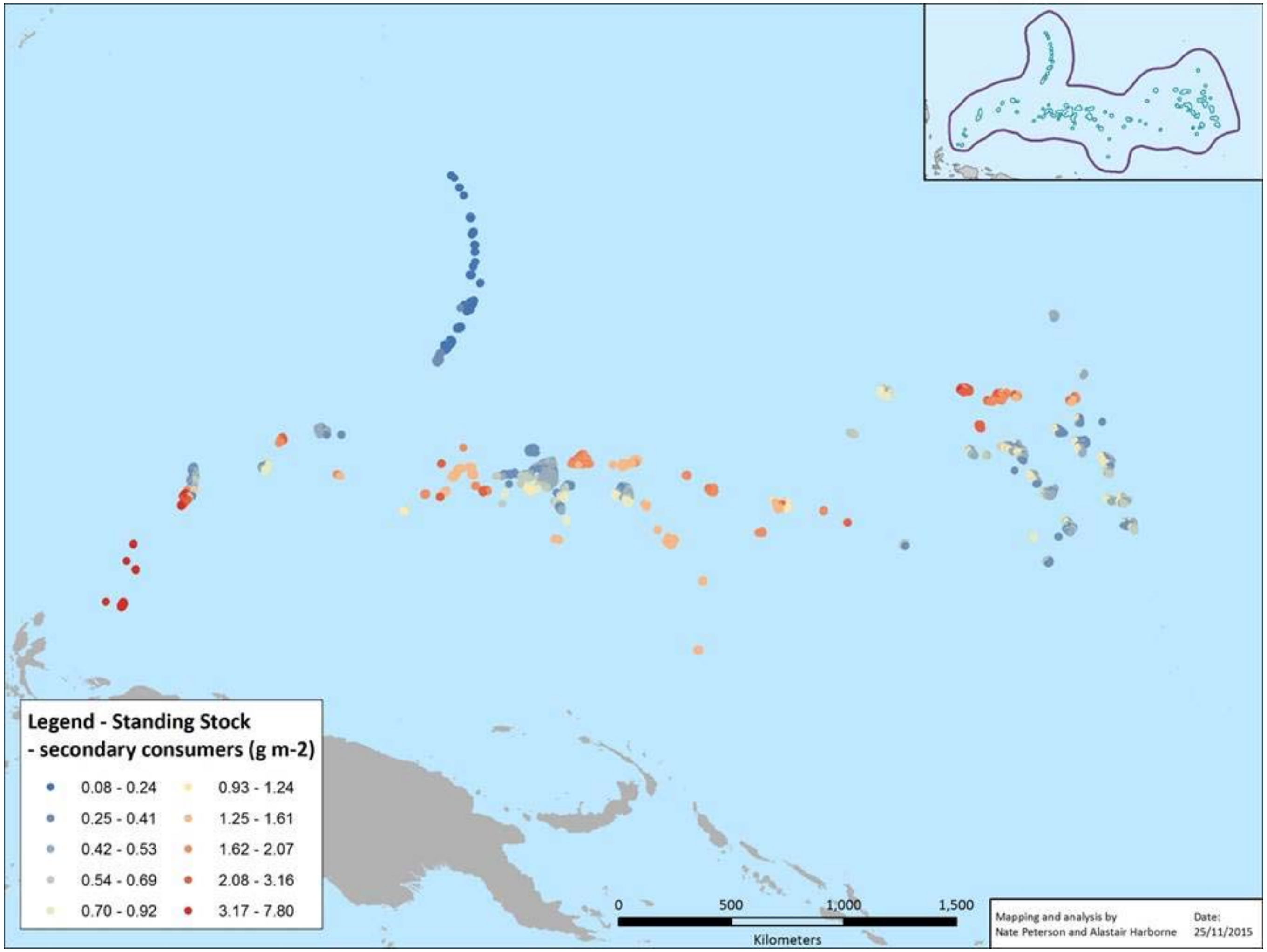


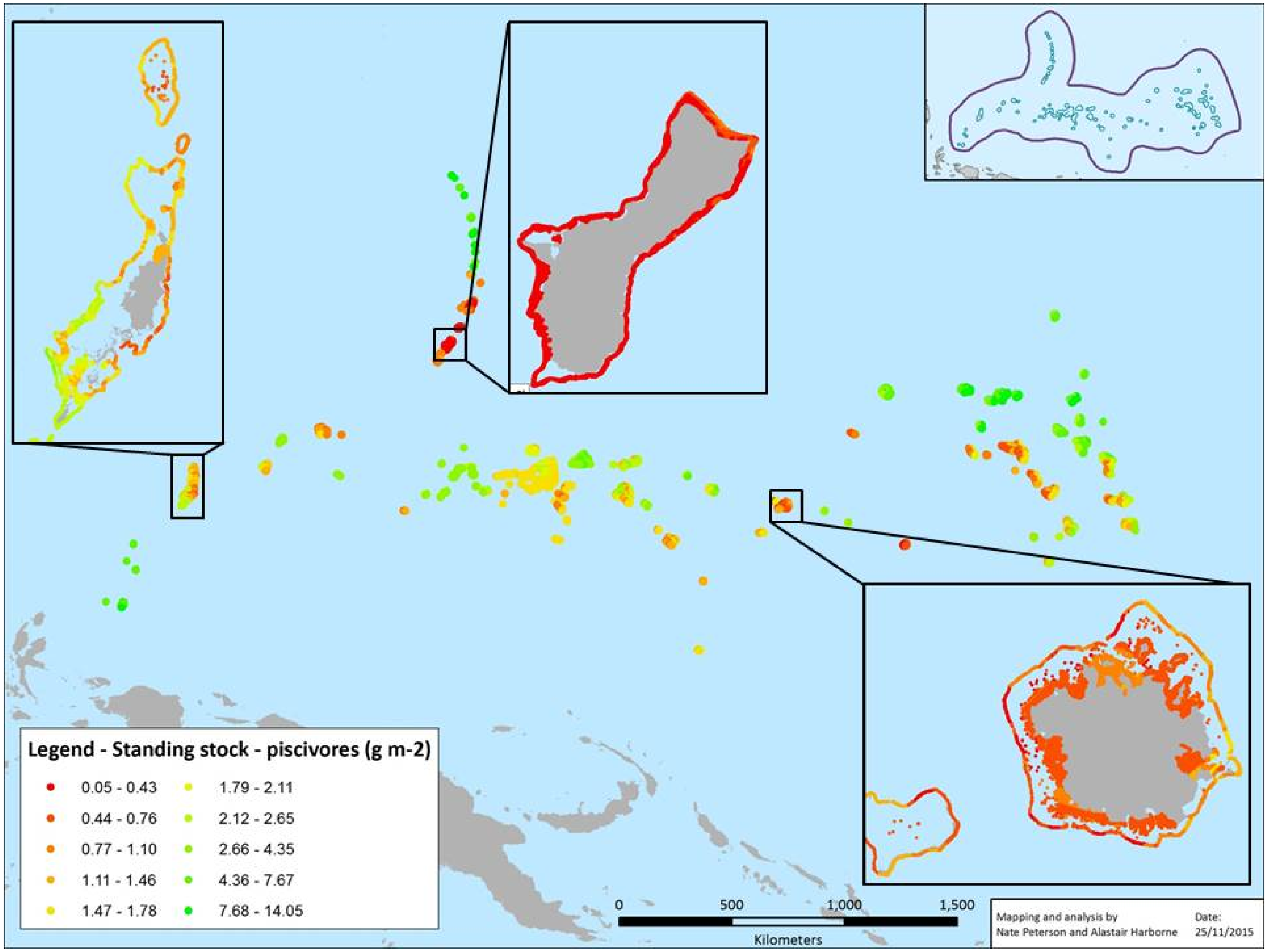
Fig. 15. Relationships between each significant variable and total biomass of 6 key piscivores (y axis) modelled by boosted regression trees. Values represent how much of the explained deviance was explained by each variable. Values of log biomass on the y axis are normalised.



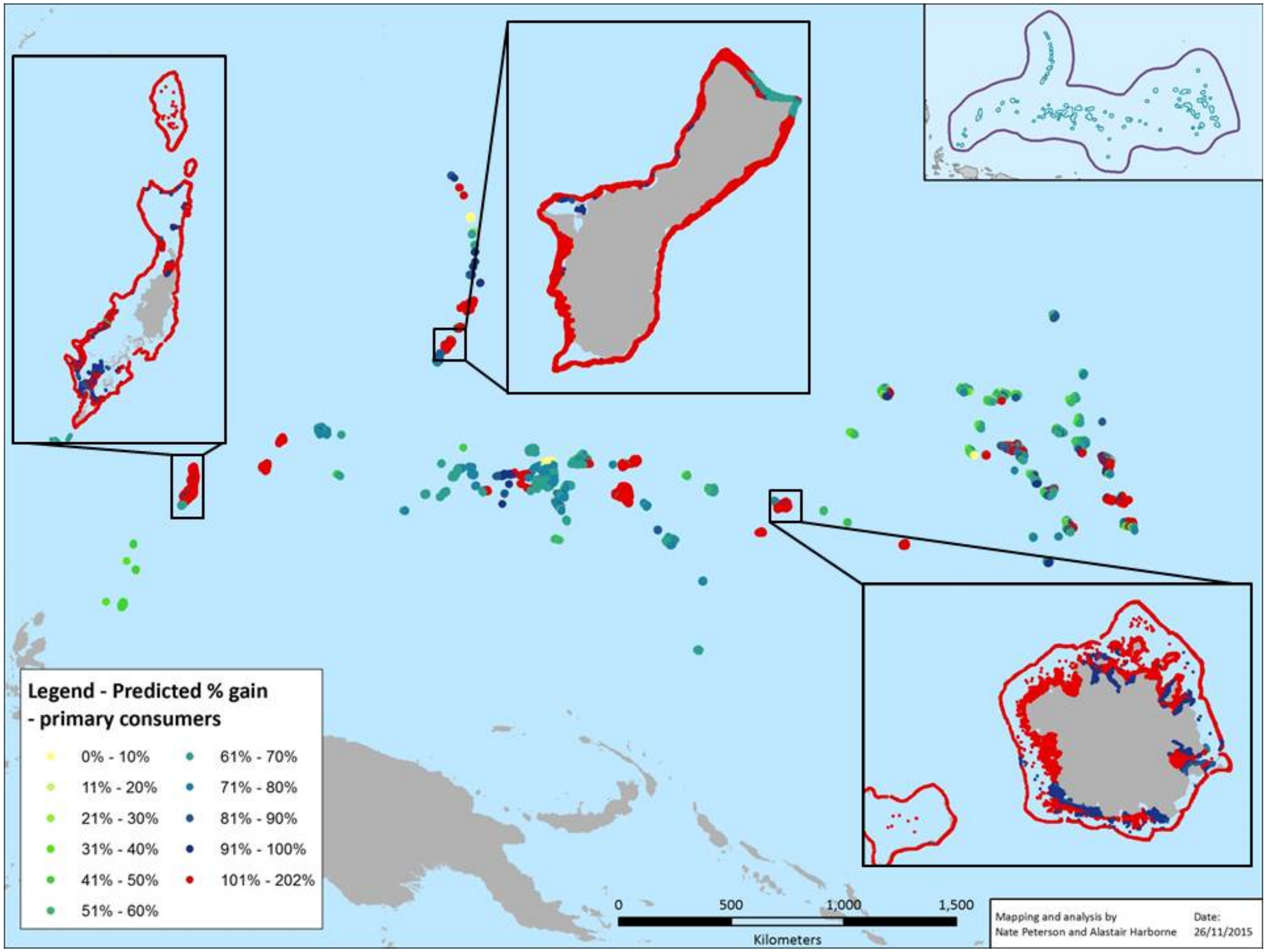
Map 5. Regional map of predicted current standing stock of 10 primary consumers (herbivores), including larger-scale insets of the biomass around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).



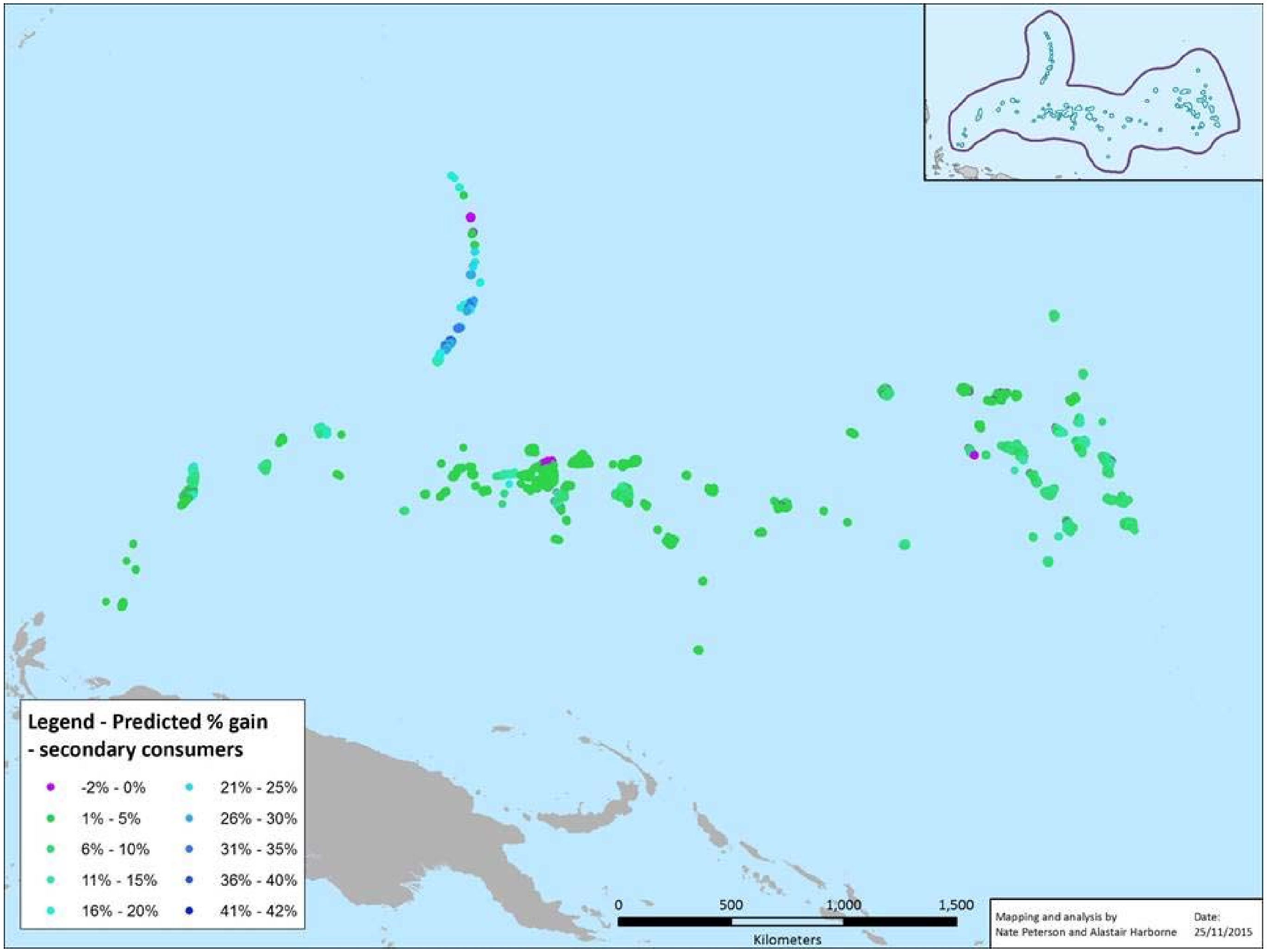
Map 6. Regional map of predicted current standing stock of 3 key secondary consumers (invertivores). Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).



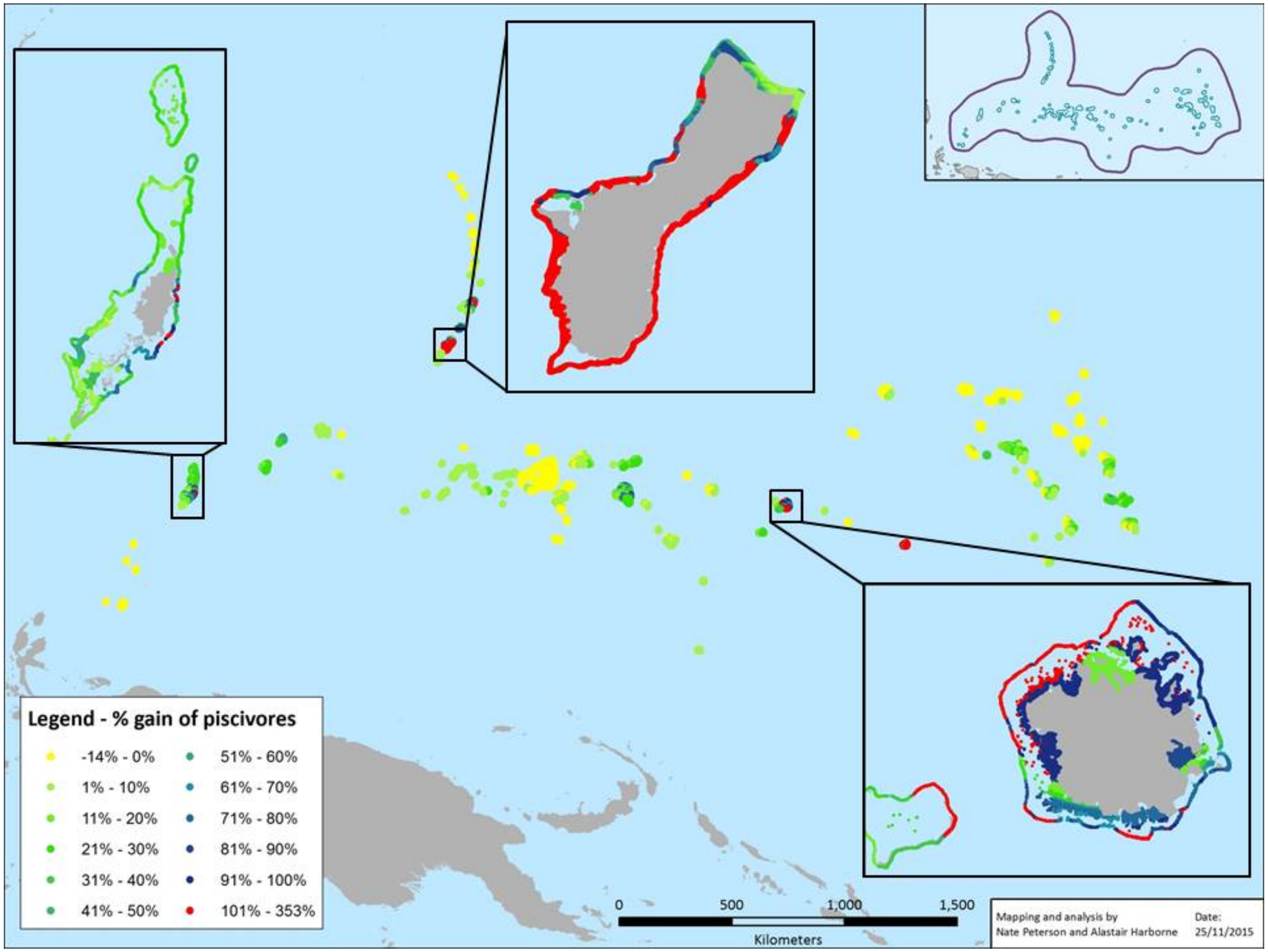
Map 7. Regional map of predicted current standing stock of 6 key piscivores, including larger-scale insets of the biomass around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).



Map 8. Regional map of predicted potential percentage gain of standing stock of 10 primary consumers (herbivores) if there was zero fishing, including larger-scale insets of the gain around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).



Map 9. Regional map of predicted current standing stock of 3 key secondary consumers (invertivores). Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).



Map 10. Regional map of predicted potential percentage gain of standing stock of 6 key piscivores if there was zero fishing, including larger-scale insets of the gain around Palau, Guam, and Pohnpei. Map shows predicted values for both well-parameterised and possibly well-parameterised habitat types (see Table 4 for explanation).

5. Summary of patterns highlighted in the maps

The maps of fishing pressure, current standing stock, and potential standing stock under a zero fishing pressure scenario demonstrate patterns at a range of scales. For example, fishing pressure decreases north through CNMI with increasing distance from the populous islands of Saipan and Guam, fishing pressure is highest around Koror in Palau, and fishing pressure is generally low in RMI with the exception of close to Majuro. Current standing stock is then generally higher where fishing pressure is lower, but also reflects the various biophysical gradients within the model. Finally, potential gains in standing stock are highest where fishing pressure is highest (e.g. Guam), but is constrained by biophysical gradients.

Summaries of each map (Fig. 17) provide a snapshot of the conditions in each jurisdiction (and each state within FSM). Clear differences are visible in the metrics among each jurisdiction or state with, for example, the reefs around Guam typically having high fishing pressure and low standing stock. The summary statistics are further split for populous (reefs within 20 km of the populous islands or atolls of Palau, Guam, Rota, Aguijan, Tinian, Saipan, Yap, Chuuk, Pohnpei, Kosrae, Majuro, and Kwajalein) and remote areas (>20 km from these population centres). Remote reefs typically have much lower fishing pressure and higher current standing stocks, but a lower potential gain under zero fishing pressure scenarios.

The maps of fishing pressure and standing stock also facilitated the calculation of the ratio of current standing stock to potential (unexploited) standing stock. Ratios were calculated using back-transformed predicted values of current and potential biomass, as recommended by MacNeil et al. (2015). This metric has been suggested as a useful metric of fishery status and whether benthic communities are approaching critical dynamic thresholds (McClanahan et al. 2011, MacNeil et al. 2015). For example, when this ratio falls below 0.5 it is possible that this is approaching an unsustainable fishery and potentially some thresholds of ecosystem processes. Conversely, reefs where this ratio is >0.9 are considered to be virtually intact and with effectively no impacts on reef functioning (MacNeil et al. 2015). Although the majority of reefs in Micronesia appear to be above the 0.5 threshold (Fig. 18), this should be interpreted with caution because whether these thresholds are similar in Micronesia and other parts of the world is not clear. Consequently, impacts on reef functions may occur when current stocks are at higher proportions of potential biomass.

A global analysis of reef fish stock has provided an estimated relationship between the ratio of current to potential biomass and time to "recovery", defined as reaching 90% of potential biomass (Fig. 16) (MacNeil et al. 2015). The project used this relationship to estimate the time it would take each 1 ha cell to reach this threshold of 0.9 of potential biomass (Fig. 18). For many reefs in the region, reefs may not recover following the cessation of fishing for decades (maximum was ~50 years), underscoring the need to establish fisheries management initiatives as soon as possible.

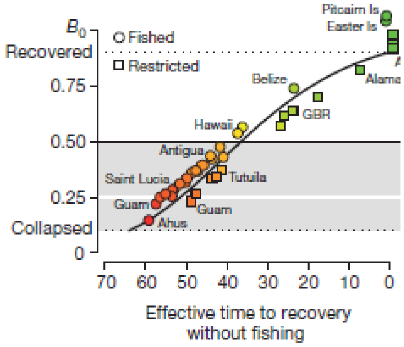


Fig. 16. The relationship between time to recovery (90% of potential biomass) following cessation of fishing and current fishery status. Points highlight reef sites used to parameterise the relationship.

Equation of the line used in the Phase 1 project was:
Time to recovery = (-173.607(current ratio^3)) + (225.572*(current ratio^2)) - (149.639*current ratio)+77.042*

From MacNeil et al. (2015)

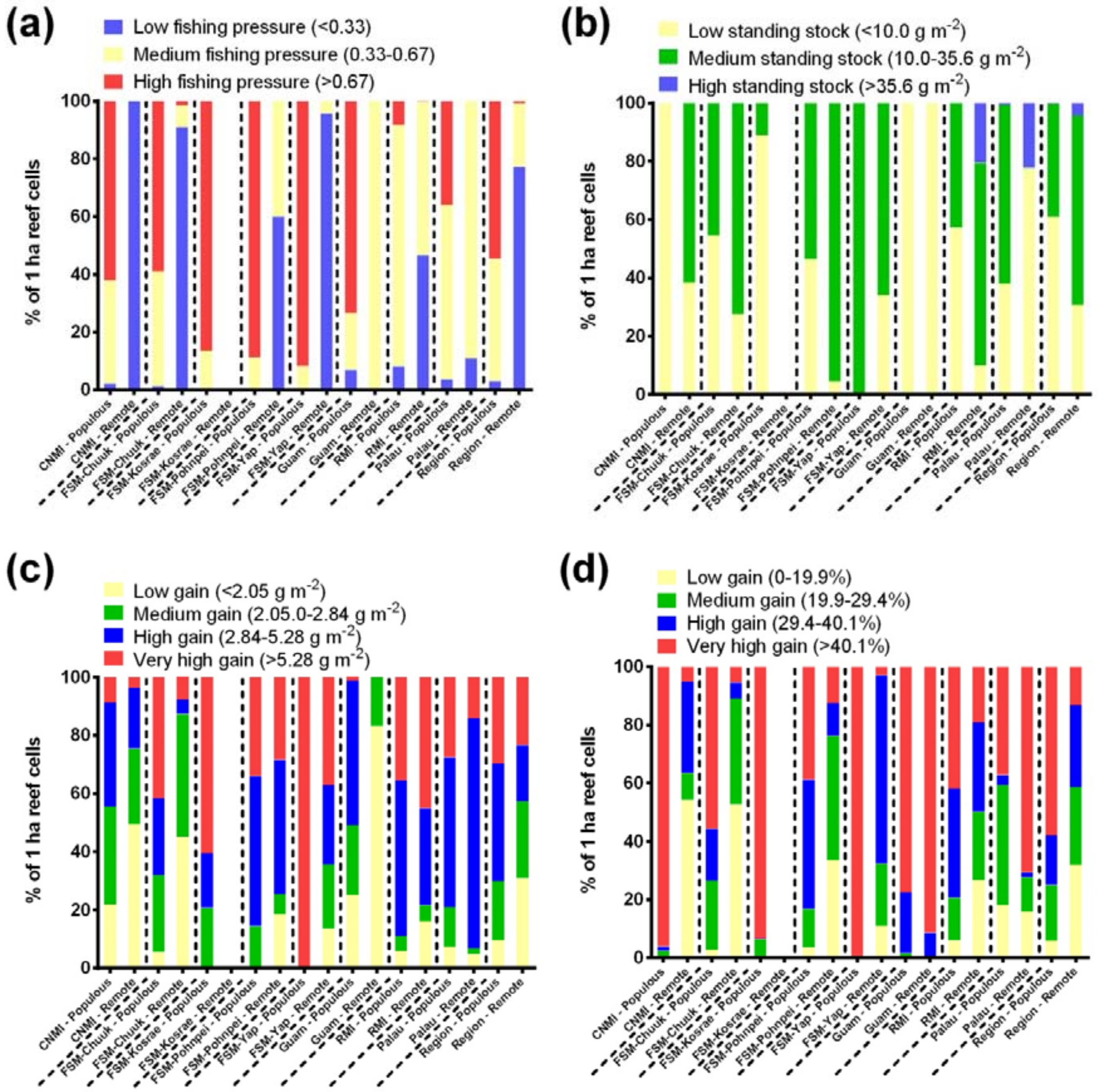


Fig. 17. Summary plots of the proportion of 1 ha reefs cells separated by (a) fishing pressure, (b) current standing stock, (c) potential absolute gain in standing stock under a 0 fishing pressure scenario, and (d) potential percentage gain in standing stock under a 0 fishing pressure scenario. Values are separated by jurisdiction (and states in FSM) and by remote (within 20 km of the most populated islands) and populous (>20 km from the most populated islands) areas. Categories in (c) and (d) are defined by 25%, 50%, and 75% quantiles.

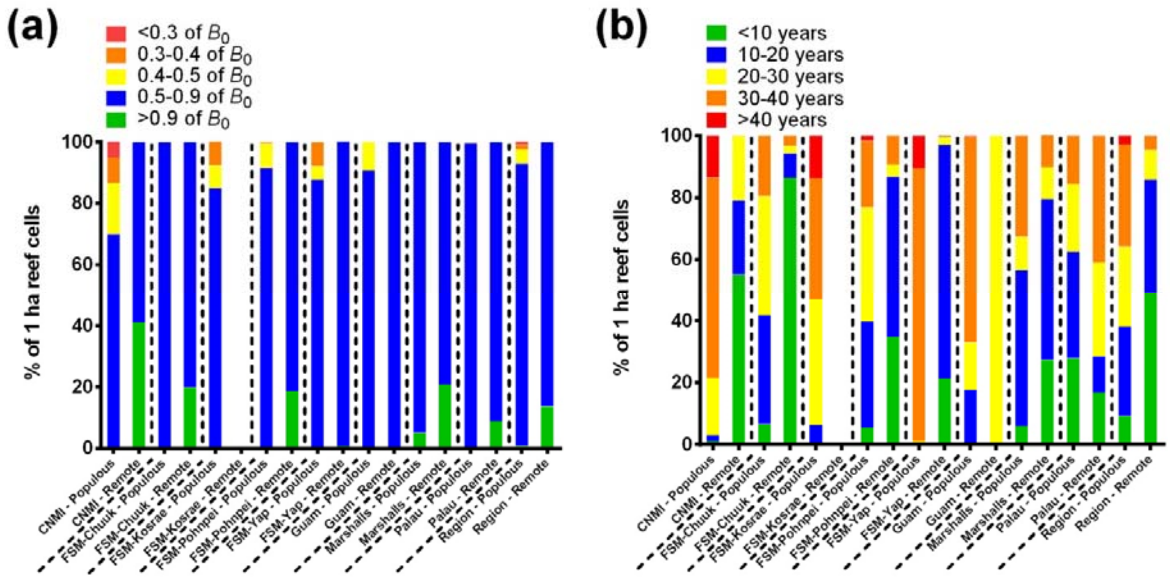


Fig. 18. Summary plots of the proportion of 1 ha reefs cells separated by (a) ratio of current standing stock to potential biomass (B_0), and (b) time to recover to 90% of B_0. Values are separated by jurisdiction (and states in FSM) and by remote (within 20 km of the most populated islands) and populous (>20 km from the most populated islands) areas.

6. Potential use of map products in marine spatial planning

Maps of fishing pressure and fish standing stock implicitly represent aspects of ocean wealth, as they represent protein that has been, or could be, harvested. These maps may also have multiple uses for conservation and management. For example, we anticipate that the Phase 1 project products will be particularly useful for marine spatial planning, such as designing protected area networks. A detailed outline of how the products of the Phase 1 project can be used in planning and implementing conservation and management initiatives in Micronesia is available in a separate report resulting from meetings at the University of Queensland and in Palau (Green et al. 2016).

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Appendix 1: Details of each data set

Peter Mumby data set

This data set was collected by Peter Mumby (Marine Spatial Ecology Lab, University of Queensland, Australia) and colleagues as part of research to investigate the impacts of herbivore fishing (Bejarano et al. 2013) and indicators of resilience on Micronesian reefs (Mumby et al. 2013). Surveys were conducted in Palau, Guam, and Pohnpei, using underwater visual censuses along ten, 30 x 4 m belt transects on reef slopes (typically between 7-10 m depth) to count and size (nearest cm) each target fish. All parrotfishes, rabbitfishes, and wide-ranging surgeonfishes (principally species of the genus *Naso*) were censused during laying of the transect, and the remaining, territorial surgeonfish species were censused on a second pass along the transect. Although the data set contains some data on predatory species (e.g. grouper) from two 5 min roving surveys at each site, the focus of the surveys was herbivorous species. Photo-quadrats were used to estimate coral cover at each site.

Since this data set is focused on herbivorous species, it was only used for modelling fishing pressure and not for standing stock.

Maria Beger data set

This data set was collected by Maria Beger (Centre of Excellence for Environmental Decisions, University of Queensland, Australia) and colleagues as part of research to monitor and understand fish assemblages in the Marshall Islands. Surveys were conducted on three atolls using underwater visual censuses along three, 50 x 5 m belt transects on reef slopes (replicated at 3 and 10 m depth) to count and size (nearest cm) each fish. All non-cryptic fishes were identified, counted, and sized (nearest cm), and 372 species were identified. Coral cover was estimated along each transect.

A random sample of sites from the Maria Beger data set were used in the model of fishing pressure to ensure model coverage across all five jurisdictions. The remaining sites in the Maria Beger data set were used in the models of standing stock.

Brett Taylor data set

This data set was collected by Brett Taylor (then at the School of Marine and Tropical Biology, James Cook University, Australia) and colleagues as part of research to investigate the effects of fishing pressure on multiple aspects of parrotfish assemblages (Taylor 2014, Taylor and Choat 2014, Taylor et al. 2014a, Taylor et al. 2014b). Surveys were collected in Guam and seven locations in FSM, using diver-operated stereo-video. At each site, 16 replicate timed-swim belt transects (5 m wide x 3 min long, averaging 315 m^2) were stratified at two depths (6–10 and 18–22 m), and fish were counted if they were within 8 m in front and 2.5 m either side of the camera trajectory. Fishes were identified and sized (nearest mm) using the EventMeasure software[2]. Fishes that could not be sized because of their orientation on the video frame were assumed to be the mean size of that particular species and life phase. Not all species were recorded, but the data set contains records of 143 taxa from 22 families, including the majority of families that are commercially or ecologically important. Mean live coral cover was estimated visually at each site from five replicate locations along each transect on a 1–5 scale. For comparability to the other data sets, these measures of coral

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[2] www.seagis.com.au

cover were converted to estimated coral cover by assuming 1 = 5%, 2 = 20%, 3 = 40%, 4 = 62.5%, and 5 = 87.5%.

A random sample of sites from the Brett Taylor data set were used in the model of fishing pressure to ensure model coverage across all five jurisdictions. The remaining sites in the Brett Taylor data set were used in the models of standing stock.

NOAA Coral Reef Ecosystem Division (CRED) data set

This data set was collected by NOAA CRED[3] as part of a monitoring program, known as the Pacific Reef Assessment and Monitoring Program (Pacific RAMP), which is tasked with documenting and understanding the status and trends of coral reef ecosystems in the U.S. Pacific (Heenan et al. 2014). In addition to monitoring work, the wider data set has been used to examine human and environmental drivers on Pacific fish assemblages (Williams et al. 2011, Richards et al. 2012, Williams et al. 2015a, Williams et al. 2015b). The only data from this data set that are relevant to the Phase 1 project are from the Mariana Archipelago. Surveys have been conducted at 12 islands in CNMI, plus Guam on three different occasions from 2009-2014. Sites were stratified in hardbottom habitats around each island and occurred in three depth zones (0–6 m; 6–18 m; 18–30 m). Only reef slope data were used in the Phase 1 project. At each site, a pair of divers laid a 30 m transect along a depth contour. Divers surveyed fishes using a paired stationary point count method: the two divers conducted simultaneous counts in adjacent visually estimated 15 m diameter cylinders extending from the substrate to the limits of vertical visibility. Each SPC consisted of two components: a 5-minute species enumeration period in which divers recorded all species present in or moving through their cylinder, followed by a tallying portion, in which divers systematically recorded the number and size (nearest cm) of all fishes of each taxon on their list. The divers' goal was to get a near instantaneous record of all fishes present within their cylinder, including many cryptic species. A total of >480 taxa from 53 families are included in the data set. On completing the fish count, divers also estimated coral cover within the SPC cylinders. At each site, data from the two adjacent cylinders were pooled into a mean value for both fish abundance and coral cover.

This data set represents the major set of surveys in the CNMI where fish sizes are available, and lengths are necessary for deriving size-based metrics of fishing pressure. The 2009 data from the NOAA CRED data set did not include benthic data and were not used in the Phase 1 project. The 2011 data in the NOAA CRED data set were used to model fishing pressure, and the 2014 sites were used in the models of standing stock.

Micronesia Challenge data set

This data set was collected by researchers in Micronesia[4] as part of a regional effort to assess, monitor, and conserve reefs as part of the Micronesia Challenge (Houk et al. 2015). Data are available from three islands in CNMI, four islands in FSM, and three atolls in the Marshall Islands. At each site, five 50 m transects were used to measure fishes at 8–10 m on outer reefs and at 3–5 m for inner reefs (matching zones of optimal coral growth). The size (nearest 5 cm) and abundance of fishes were estimated from 12 stationary-point counts conducted at equal intervals along the transects. At each point, the count was within a 5 m circular radius for a period of 3 minutes. The focus was on species targeted for food, and data are available for 157 taxa in 22 families. Coral cover was assessed using a photo-quadrat technique, with 50 photos taken at 1 m intervals along

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[3] Contact: Ivor Williams, Pacific Islands Fisheries Science Center, National Marine Fisheries Service, NOAA, Hawaii
[4] Contact: Peter Houk, University of Guam Marine Laboratory, Guam

each 50 m transect line. Within each photo, benthic substrates were evaluated under five randomly allocated crosses.

Although the Micronesia Challenge data set includes fish sizes and densities, only site-level data on the biomass of each taxa were available to the Phase 1 project. Consequently, size-based metrics cannot be derived. Therefore, this data set was used only to parameterise models of standing stock.

PICRC data set

This data set was collected by the Palau International Coral Reef Center (PICRC)[5] as part of on-going efforts to monitor reef health around Palau and assess the effectiveness of marine protected areas. Data will be used from reef slopes (at 3 and 10 m) for 14 of the long-term monitoring sites and inside and outside six of the protected areas (at 8 m) around the main islands of Palau. At each site, fish are counted (nearest cm) along five, 5 x 50 m belt transects. The number of taxa identified during each transect depended on the observer, but during all surveys 35 ecologically and economically taxa from 11 families were recorded. Coral cover was estimated from photo quadrats at each site.

Since the Peter Mumby data set provides size-based data on herbivorous fishes for Palau, the PICRC data set was mainly used for modelling standing stock. Most of the sites surveyed by PICRC were visited on multiple occasions, and only replicates when benthic data were also collected (2014) were used in the Phase 1 project.

Alison Green data set

This data set was collected by Alison Green as part of a multi-disciplinary team in 2000 assessing the marine resources of remote Helen Reef, Palau, in order to assess the health of the reefs and compare it to data from 1992, establish a monitoring programme, and provide management recommendations (Birkeland et al. 2002). The fish component of this project surveyed reef slope sites at 10 m around the reef. Fish surveys were conducted using visual censuses along five, 50 m transects at each site. Transect width was 3 m for most species, with two exceptions. Damselfishes were counted along a 1 m wide belt. Several very large species (e.g. humphead wrasse, *Cheilinus undulatus*, and bumphead parrotfish, *Bolbometopon muricatum*) were counted along most of the width of the reef slope (20 m wide). Fishes were surveyed by making three passes along the transects, counting different groups of families in each pass. The first count was of large, highly mobile species, which are most likely to be disturbed by the passage of a diver (such as large parrotfishes, wrasses, snappers, and emperors). The second count was of medium sized mobile families (including most surgeonfishes, butterflyfishes and wrasses), and the third count was of small, site-attached species least disturbed by the passage of a diver (mostly damselfishes). The size of each fish (nearest cm) was recorded. All non-cryptic fishes were recorded, and the data set contains 245 taxa from 27 families. Coral cover at each site was estimated using video transects and plotless *in situ* measurements of coral densities.

Helen Reef is a remote atoll, and therefore the Alison Green data are interesting as an example of presumably low fishing pressure and high standing stock away from the main island in Palau. Therefore, two of the four sites were used in the model of fishing pressure, and the other two were used in the model of standing stock.

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[5] Contacts: Marine Gouezo and Yimnang Golbuu, Palau International Coral Reef Center, Palau

PROCFish data set

This data set was collected by the Pacific Regional Oceanic and Coastal Fisheries Development Programme (PROCFish) and the Pacific Regional Coastal Fisheries Development Programme (CoFish)[6], to provide the first comprehensive, multi-country baseline comparative assessment of reef fisheries in the Pacific Island region (Pinca et al. 2012, D'agata et al. 2014). Data provided to the Phase 1 project cover sites in Palau, two islands in the FSM, and three atolls in the RMI. Surveys used in the Phase 1 project were conducted from 2.2-14.7 m in four different habitat types (deep terrace, forereef, pinnacle, and lagoonal pinnacle). To survey fishes, distance sampling underwater visual census (Bozec et al. 2011) was used, where species name, abundance, body length and distance of each fish or group of fishes from a 50 m transect are recorded up to the distance of maximum visibility. However, the Phase 1 project only included data on fishes within a distance of 5 m on each side of the transect, in order to maximise comparability with the other data sets. Two divers surveyed the transect, with each diver surveying an adjoining 50 x 5 m transect (total area 500 m^2). Most non-cryptic species were surveyed, resulting in data from 313 species from 30 families. Coral cover was estimated using the medium scale approach (Clua et al. 2006), which involves semi-quantitative estimates of cover in 20, 5 x 5 m quadrats.

A random sample of sites from the PROCFish data set were used in the model of fishing pressure to ensure model coverage across all five jurisdictions. The remaining sites in the PROCFish data set were used in the models of standing stock.

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[6] Contact: Laurent Vigliola, Institut de Recherche pour le Développement, New Caledonia

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Appendix 2: Details of data compatibility testing

Some of the data sets collected data at the same locations, and this allows for some assessment of data comparability (Fig. A1). The results of these data comparability analyses are outlined in the subsequent sections, and generally support the conclusion that the data sets can be pooled for the modelling fishing pressure and standing stock. However, reef fish assemblages can be patchy at small spatial and temporal scales, and consequently if comparisons are weak this does not necessarily suggest that the data cannot be pooled. Rather, it suggests that there may have been significant differences in the timing or location of the surveys. Alternatively, there may potentially be systematic differences among the data sets. It is because this latter explanation may be true that survey methodology will be included as an explanatory variable in the models of fishing pressure and standing stock.

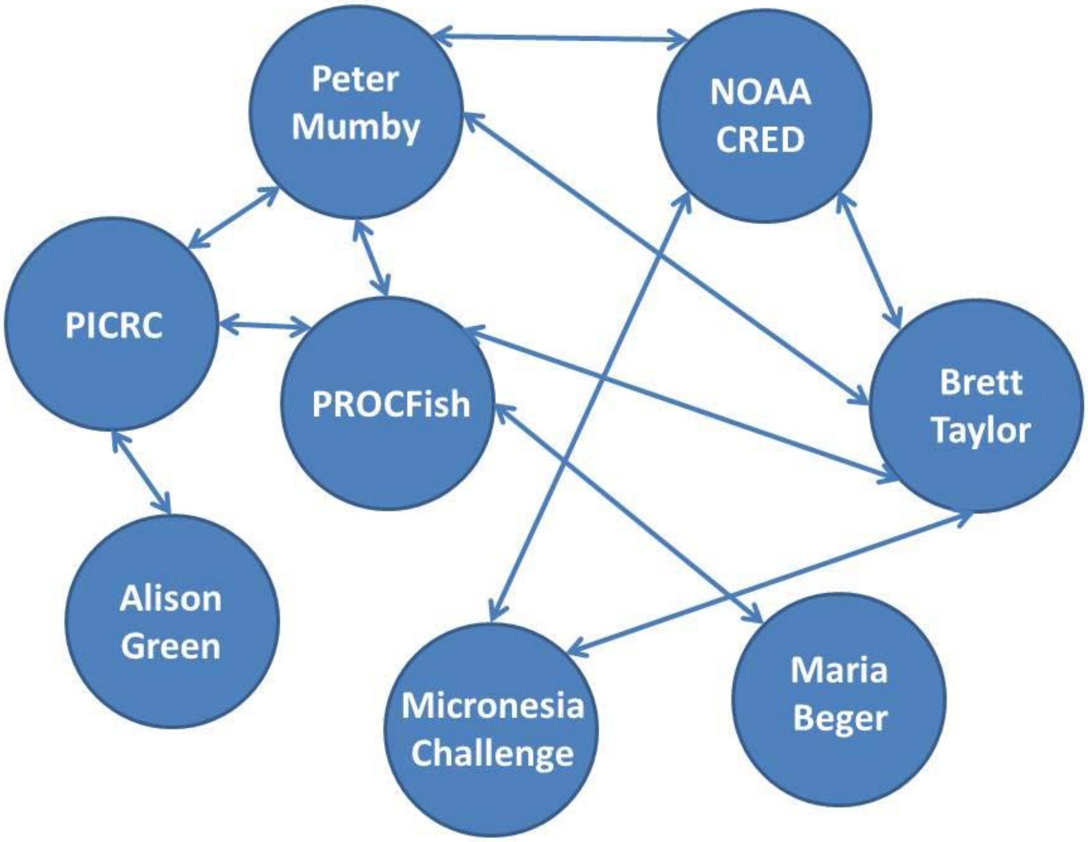

Fig. A1. Schematic overview of the inter-data set comparisons (double-headed arrows) that are possible among data sources available to the Phase 1 project.

Peter Mumby versus NOAA CRED

Both the Peter Mumby and NOAA CRED data sets surveyed a series of sites around Guam in 2009. Across all sites, the mean sizes (21.8 cm and 20.2 cm respectively) and biomasses (271.7 versus 201.0 g respectively) of all parrotfishes >15 cm and not including *Bolbometopon muricatum* were similar. Furthermore, four specific sites were surveyed in both data sets and, although having low statistical power, the patterns in mean sizes and biomasses were the same in both data sets (Fig. A2).

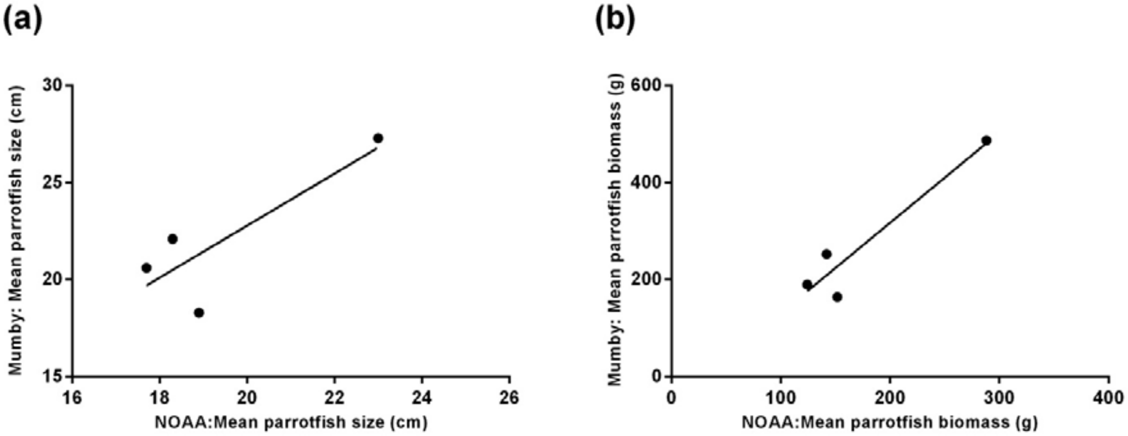

Fig. A2. Comparison of (a) mean size and (b) mean biomass of parrotfishes (>15 cm) at four sites surveyed by both the NOAA CRED and Peter Mumby data sets in Guam in 2009. Pearson correlation coefficients are 0.843 (not significant, *P*>0.05) and 0.951 (significant, *P*=0.048) respectively.

NOAA CRED versus Brett Taylor

Both the NOAA CRED and Brett Taylor data sets surveyed a series of sites around Guam in 2011. Across all sites, the mean sizes (22.7 cm and 20.3 cm respectively) and biomasses (201.0 versus 227.6 g respectively) of all parrotfishes >15 cm and not including *Bolbometopon muricatum* were reasonably similar. However, there was no significant relationship (*P*>0.05) between these two data sets at a site-level scale (Pearson correlation coefficients -0.045 and 0.126 respectively).

NOAA CRED versus Micronesia Challenge

Both the NOAA CRED and Micronesia Challenge data sets include recent surveys at four islands in the Northern Marianas. Although size data for individual fishes are not available for the Micronesia Challenge data, the mean total biomass of all 19 key species at all survey sites per island can be compared (Fig. A3). The pattern of increasing biomass from Tinian to Aguijan was similar in both data sets, and is consistent with likely fishing pressures. For example, Aguijan has no resident population, while the other three islands have populations > 3,200 (Williams et al. 2011).

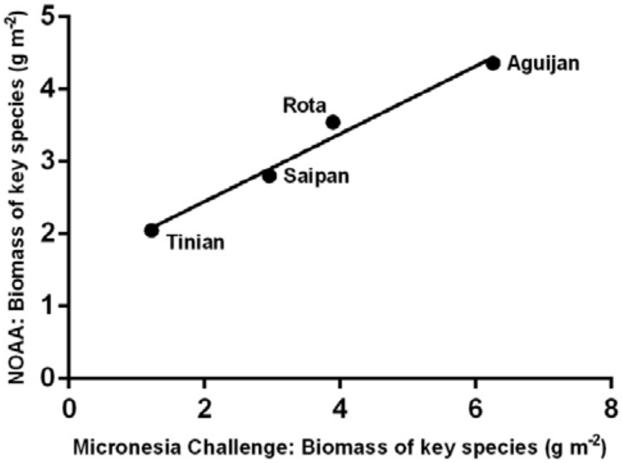

Fig. A3. Comparison of the biomass of the 19 keys species at four Northern Marianas Islands as measured by the Micronesia Challenge and NOAA CRED data sets. Pearson correlation coefficient is 0.990 (significant, *P*=0.010).

Brett Taylor versus Micronesia Challenge

Both the Brett Taylor and Micronesia Challenge data sets surveyed Kosrae, Pohnpei, and Yap. Although size data for individual fishes are not available for the Micronesia Challenge data, the mean total biomass of all 19 key species at all survey sites per island can be compared. There was no significant correlation (*P*>0.05) between these three points in both data sets (Pearson correlation coefficients -0.203).

Peter Mumby versus PICRC

Both the Peter Mumby and PICRC data sets contain size data for parrotfishes in 2009 and 2012, although not from the same sites. However, even when data are pooled from the different sites, the mean sizes and mean biomasses of parrotfishes are comparable at a national scale. In 2009, mean size of parrotfishes >15 cm and not including *Bolbometopon muricatum* for the Peter Mumby and PICRC data sets were 23.4 cm and 25.3 cm respectively. The values for 2012 were 24.4 cm and 23.8 cm respectively, and were 24.0 cm and 24.8 cm for both years combined. Biomass values were 339. 3 g and 427.2 g (2009), 355.7 g and 350.0 g (2012), and 349.5 g and 398.3 g (both years combined). Note that Guam is recognised as having a higher fishing pressure than Palau, and this is supported by mean parrotfish lengths being ~24 cm compared to ~21 cm in Guam (see previous comparison data).

Peter Mumby versus Brett Taylor

Both the Peter Mumby and Brett Taylor data sets contain parrotfish size data for Guam and Pohnpei, although not at the same sites or at the same time. However, when the data are pooled at the island scale, the mean size and biomass of parrotfishes >15 cm and not including *Bolbometopon muricatum* are comparable. Around Guam, parrotfish mean size was 21.8 cm (Peter Mumby) and 20.3 cm (Brett Taylor), and mean biomass was 271.7 g (Peter Mumby) and 227.6 g (Brett Taylor). Around Pohnpei, parrotfish mean size was 24.5 cm (Peter Mumby) and 22.6 cm (Brett Taylor), and mean biomass was 367.8 g (Peter Mumby) and 319.3 g (Brett Taylor). The mean size of parrotfishes increased by 2-3 cm from Guam to Pohnpei, which is consistent with the larger fishing pressure in Guam (19-1383 people per km^{-2} of reef) compared to Pohnpei (0-382 people per km^{-2} of reef) (Taylor et al. 2014).

Alison Green versus PICRC

The PICRC data set includes surveys from Helen Reef that was previously surveyed by Alison Green. The 2000 surveys led to the establishment of a marine reserve, and this is reflected in an increase in mean parrotfish size (2000: 25.3 cm vs 2014: 30.1 cm). The mean biomass of the 19 key species used for standing stock estimates was more comparable (Green: 205.1 g m^{-2}; PICRC 129.2 g m^{-2}).

PROCFish versus Peter Mumby, Maria Beger, Brett Taylor, and PICRC

The PROCFish data were collected at a range of sites, allowing for multiple comparisons. In Palau, mean parrotfish size was 21.2 cm (250.6 g) from the PROCFish data, and 23.0 (305.2 g) in the Peter Mumby data set and 21.0 (249.0 g) in the PICRC data set. In Yap, the PROCFish estimates of mean parrotfish size were similar to those from the Brett Taylor data set (PROCFish: 24.3 cm, 346.1 g; Taylor: 22.6 cm, 308.0 g). In RMI, there was a sizeable discrepancy in mean parrotfish size compared to the data set of Maria Beger (PROCFish: 24.2 cm, 426.8 g; Beger: 33.0 cm, 993.9 g), perhaps because the latter surveys were conducted in more remote atolls.

References

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Williams, I. D., B. L. Richards, S. A. Sandin, J. K. Baum, R. E. Schroeder, M. O. Nadon, B. Zgliczynski, P. Craig, J. L. McIlwain, and R. E. Brainard. 2011. Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific. Journal of Marine Biology 2011:Article ID 826234.

Appendix 3: Details of explanatory variables

Coral cover

Coral cover provides fishes with food (Pratchett 2005), refuge from predators and water flow (Hixon and Beets 1993, Johansen et al. 2008), and nesting sites (Robertson and Sheldon 1979). Consequently, numerous studies have linked coral cover to fish abundance (Bell and Galzin 1984, Jones et al. 2004, Gratwicke and Speight 2005), and it may be important for determining standing stock. Furthermore, aspects of parrotfish biology are linked to coral cover (Nash et al. 2012), and therefore it will be included in models of fishing pressure since it will be derived from the mean size of parrotfishes. Coral cover was estimated *in situ* during all fish surveys. However, coral cover cannot be reliably modelled continuously across all five focal jurisdictions in Micronesia. Therefore, predictions for the continuous maps of fishing pressure and standing stocks were calculated using mean coral cover measured across the region (21.7%) for all cells.

Depth

While rarely affecting fish assemblages directly, depth is a proxy for numerous environmental gradients such as light intensity, temperature, and salinity that may affect fishes. Fishermen may also change their targeted species and gears depending on depth, and deeper waters may offer a refuge to highly targeted species (Lindfield et al. 2014). Depth was measured during *in situ* surveys, but there is no continuous, high-resolution bathymetric data layer available for Micronesia. Therefore, predictions for the continuous maps of fishing pressure and standing stocks were calculated using mean survey site depth (6.0 m) for all cells.

Distance to pass

The distance to a natural or artificial pass through the reef may affect fishing pressure by providing greater access to sites close to breaks in the reef. Furthermore, higher water movement and productivity associated with hydrological fluxes through these channels may affect fish assemblage structure (Houk et al. 2012a, Taylor et al. 2014a). Therefore, the distance of each reef site to the nearest pass was included in models of both fishing pressure and standing stock. Level 4 of the MCRM project classification scheme (Andréfouët et al. 2006) includes a habitat class for pass, and so this variable was calculated as the Euclidean distance of the reef site to the nearest pass in the reef. To ensure that all distances were relevant to the behaviour of fishers distances were truncated at 20 km, which is slightly further than the average distance travelled by fishers in the region (~17 km; Sonia Bejarano, unpublished data). This truncation also ensured that there were no situations where large distances were returned because there was no pass present on a given island or atoll (i.e. no situations where meaningless distances were returned because the algorithm was measuring from a reef cell on one island or atoll to a pass on a different island or atoll).

Distance to port

The distance from a reef to the nearest market for selling and processing fish can be an important determinant of fishing pressure at local and global scales, particularly among reefs with low local population densities (Brewer et al. 2012, Brewer et al. 2013, Cinner et al. 2013). Distance to market may even have a curvilinear relationships to fish biomass, with biomass increasing exponentially at distances over 14 km from a market (Cinner et al. 2013). This response variable was estimated as the Euclidean distance between each reef cell and the nearest major population centre (Koror on

Palau, Apra Harbor on Guam, Rota Seaport and Tanapag Harbor in CNMI, Colonia on Yap, Moen on Chuuk, Kolonia on Pohnpei, Tafunsak on Kosrae, and Majouro in the RMI).

Export

In some jurisdictions, the export of coral reef fishes can be an important driver of fishing pressure (where coolers of coral reef fishes are exported by air for markets and off island family members in other jurisdictions). The importance of these exports as drivers of fishing pressure depends on the current status of coral reef fish populations (i.e. if there are still enough fish to catch for export) and the access to airports. This variable was included in the fishing pressure model by developing a semi-quantitative scale for these exports using expert opinion, where every reef cell was ranked as 0, except for cells within 20 km of the main islands in some jurisdictions. These island were ranked as follows:

- Main islands in Pohnpei and Yap were ranked as 1 (low);
- Koror in Palau was ranked as 2 (medium); and
- Main island in Chuuk was ranked as 3 (high).

Consequently, this variable allows for reef cells close to these islands to potentially be more heavily fished than other reef cells because of the additional pressure of catch for export.

Fishing pressure

The model and map of fishing pressure (Section 4.1) was a key response variable in the model of standing stocks.

Habitat type

Habitat type is well established as influencing fish assemblages (e.g. Alevizon et al. 1985), and has been demonstrated as an important factor affecting fishes in Micronesia (Houk et al. 2012a, Pinca et al. 2012). Although the majority of the sites modelled and mapped are from a single habitat class in the MCRM project classification scheme (forereef), some other habitats are included in the project (Section 3.6). Therefore, habitat identity was included in the models of both fishing pressure and standing stock.

Habitat category

The fish survey data are drawn from habitat types that are either well parameterised with many replicates or less well parameterised because of a limited number of replicates. These habitats were distinguished as definitely being well modelled, or only possibly being well modelled (see Section 3.6). This uncertainly was included in the models of fishing pressure and standing stock using a categorical variable (well modelled, possibly well modelled) in order to allow the model to account for any systematic differences between these two groups of habitats.

Human population pressure

The size of local human populations has repeatedly been demonstrated to be an excellent proxy of fishing pressure on reefs (e.g. Mora 2008, Stallings 2009, Mora et al. 2011, Cinner et al. 2013). Therefore, it was anticipated to be a key variable in the model of fishing pressure in Micronesia. Standardised, rasterized, global data sets of human populations are available online, and the Phase 1 project used data from SEDAC, the Socioeconomic Data and Applications Center (SEDAC), which part of the Earth Observing System Data and Information System (EOSDIS) of NASA[7]. The project used the Global Rural-Urban Mapping Project (GRUMP) 2000 data layer, which provides estimated population sizes within at a resolution of 30 arc-seconds (~1km). Full details of the derivation of this data layer is provided in Balk et al. (2010), but it is generated using population counts and night-time light intensities.

The impact of human population sizes on reef fisheries is dependent on the reef area available, and the Phase 1 project followed other studies in calculating population size per square km of fishable reef (Stallings 2009, Houk et al. 2012b, Taylor et al. 2014b, Williams et al. 2015). For many islands within the region, it may be appropriate to consider human populations at the island scale (i.e. on a small island, demand for fish from local reefs is likely to be driven by the population on the whole island). However, on larger islands (e.g. Palau, Guam, and Chuuk) areas closer to population centres are likely to be more heavily fished than more remote areas. Defining the area included in assessing human populations affecting a survey site was informed by previous studies that have estimated populations within 5 km^2 (Stallings 2009, Cinner et al. 2013), a radius of 15 km (Williams et al. 2008), and a radius of 25 km (Halpern et al. 2008, Mora et al. 2011). Furthermore, interviews with fisherfolk in Palau, Pohnpei, and Guam suggest that on average they travel ~17 km to fish (Sonia Bejarano, unpublished data). Therefore, the project considered human populations within 20 km of each fish survey site, and divided this figure by the area of reef within the same distance, resulting in a metric of human population pressure per km^2. In addition, we followed Williams et al. (2015) and calculated population pressure per km^2 of reef within 200 km as a metric of the potential for a reef to be fished by more distant populations that are increasingly using larger, faster boats that are able to fish more widely.

Island geomorphology

Island geomorphology in Micronesia (whether they are high islands with fringing or barrier reefs, atolls, or low islands) is an important factor influencing herbivorous fish assemblages on surrounding reefs (Taylor 2014, Taylor et al. 2014b). Geomorphology may also be an important driver of total fish biomass at Pacific-wide and global scales (Pinca et al. 2012, Cinner et al. 2013). Although the mechanism underpinning this pattern is unknown, it is likely to be at least partially driven by the availability of lagoonal nursery habitats (Taylor 2014). Because of larger tidal ranges, inshore nursery habitats, particularly mangroves, appear to be less important to fish populations than in the Caribbean (Igulu et al. 2014). However, mangroves are important for some Pacific fish species (Paillon et al. 2014), and lagoonal habitats support habitats utilised by a range of juvenile species (Dorenbosch et al. 2006, Tupper 2007, Bellwood and Choat 2011). Geomorphology may also be a significant factor in models of finfish catches (Kronen et al. 2010).

For the Phase 1 project, geomorphology for each island was derived from levels 2 and 3 of the MCRM project classification scheme (Andréfouët et al. 2006). Level 2 distinguishes oceanic atolls, oceanic banks and ocean uplifted / filled atolls (low islands), and oceanic islands (high islands). The classification scheme does not distinguish among islands with and without lagoons, and those with lagoons (particularly Palau, Pohnpei, Chuuk, and Yap) were classified by hand. Level 3 was used to separate drowned atolls and those atolls with islands.

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[7] http://sedac.ciesin.columbia.edu/

Latitude and longitude

The reef fishes of Micronesia are recognised as being located within a single biogeographic region in the central Pacific (Kulbicki et al. 2013). Consequently, biogeography of fishes is unlikely to be a major confounding factor in the analyses, as it might be when working across biogeographic regions. However, the region is not homogeneous and some species are absent from some jurisdictions, such as the bumphead parrotfish *Bolbometopon muricatum* not having being recorded in the Marshall Islands (Froese and Pauly 2010). Furthermore, the distribution and abundance of some parrotfishes differs between the Mariana and Caroline Island groups (Taylor et al. 2014b), as might be expected across the range of any species (Sagarin et al. 2006). Latitude and longitude may also be a significant factor in models of finfish catches (Kronen et al. 2010). Therefore, latitude and longitude were included in the models of both fishing pressure and standing stock to account for any biogeographic variation in fish assemblages and fishing effort across the region.

Number of larvae

The importance of larval supply on the abundance of reef fishes has been a hotly debated topic , leading to a large literature on the relative importance of pre- and post-settlement processes (see Hixon 2011 for an overview of this debate). The debate is now generally less polarised, with the importance of pre- and post-settlement processes apparently varying among species and in space and time. To investigate the importance of larval supply in predicting fish standing stocks, we used a biophysical model of larval supply throughout the area (see Mora et al. 2012 for a full description of the model)[8]. Briefly, patches of reef habitat were identified (Fig. A4), and then ‘virtual larvae’ were released within a computer simulation of oceanic conditions. Larval release was at the midpoint of each season (i.e. 2 February, 5 May, 6 August, and 11 November) and across six years (2004–2009), for a total of 24 simulations. Virtual larvae were tracked for 100 days, a duration encompassing the majority of pelagic larval durations in tropical reef fishes, and where they ‘settle’ was recorded (either back to the same reef, to a different reef, or lost into oceanic water). These data generate a connectivity matrix, showing the proportion of larvae moving from each patch to every other patch.

This connectivity matrix was used to determine two metrics of larval supply. Firstly, total arrivals at each location were calculated by summing the arrivals from every patch, after adjusting the values to account for patch size (i.e. a large patch will receive more larvae, but this value needs to be adjusted to arrivals per unit area). Secondly, the number of self-recruiting arrivals at each patch (arrivals originating and settling at the same patch) were removed to calculate the number of arrivals from upstream sources. This second metric was calculated because local-retention patterns tend not to be reliable when extracted from biophysical models because they ignore all local processes (e.g. tides, local-scale eddies, and near-shore turbulence). Note that these metrics are not estimates of actual numbers of larvae arriving at each patch, but are values representing the relative strength of fluxes of larvae among patches. Furthermore, the metrics are the same for every location within each patch. Therefore, the larval arrival metrics for each modelled patch were assigned to every reef cell that was located within that patch. These metrics were only used for the standing stock model as larval supply is unlikely to affect mean parrotfish size, as considered by the fishing pressure model.

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[8] Data supplied by Eric Treml, University of Melbourne

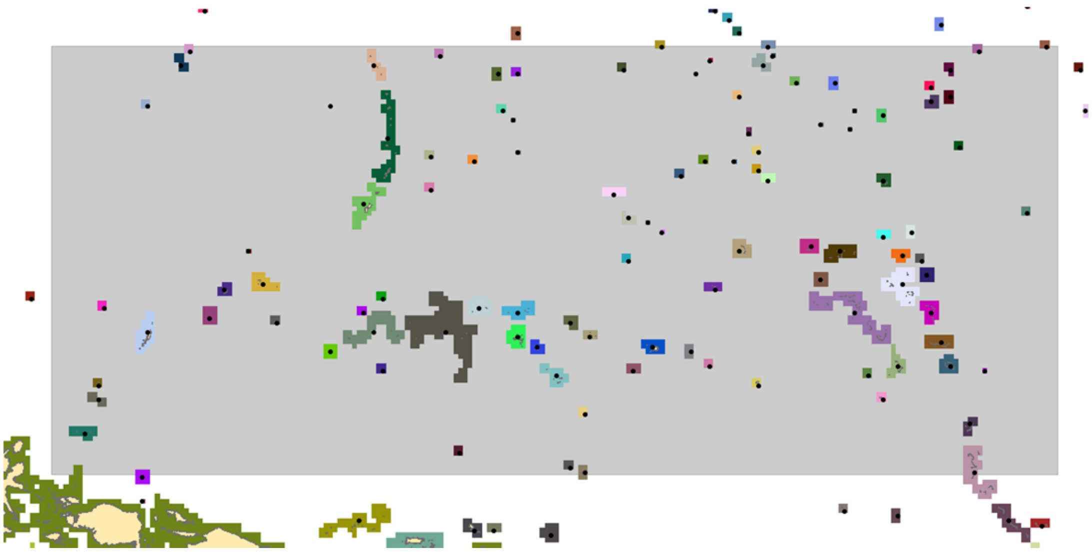

Fig. A4. Location of reef patches included in the larval supply model used in the Phase 1 project. Virtual larvae were released from each patch at the location of the black circle. Additional releases occurred from outside this region, simulating larvae that arrive from, for example, reefs in Papua New Guinea,

Oceanic net primary productivity

The primary productivity of benthic communities varies at small scales because of changes in wave exposure, light intensity, and nutrient concentrations (Hatcher 1988, 1990). This variation in primary productivity can influence herbivorous fish assemblage structure (Mumby et al. 2013), and the total biomass of reef fishes (Williams et al. 2015). Therefore, oceanic productivity was included in the models of fishing pressure and standing stock. High-resolution measures of productivity across the entire region are not possible, and the Phase 1 project used remotely sensed data on chlorophyll-*a* as a proxy of primary productivity on reefs. Although these chlorophyll-*a* data do not discriminate small-scale variations in productivity within islands, they do capture larger-scale patterns in productivity across the region (Gove et al. 2013). Mean monthly chlorophyll-*a* data from 2010-2014 at a resolution of ~350 km^2 was obtained from an online source[9]. Remotely sensed estimate of productivity of over reefs are confounded by bottom reflectance, so only data from pelagic areas around each reef were used. These areas were identified using the protocol described in Gove et al. (2013): productivity data was excluded where they intersected with any polygon delineated by the MCMP, and then the productivity value for each reef cell was derived as the value contained within the nearest, entirely pelagic data cell.

Protected status

A large literature demonstrates that marine protected areas can effectively reduce fishing pressure and fundamentally change fish assemblages (e.g. Mosquera et al. 2000, Halpern and Warner 2002, Russ 2002, Micheli et al. 2004). Consequently, whether a fish survey site is inside or outside a protected area was included within the model of reef fishing pressure. Although whether fishing is allowed at a given site or not will be captured within the fishing pressure data layer, protected status was also be included in the model of standing stock to account for any differential effects on parrotfishes compared to other species (i.e. the fishing pressure model only considers fishing of parrotfish, which may not be affected by reserve status, while the standing stock model considers a

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[9] http://www.science.oregonstate.edu/ocean.productivity/index.php

range of other species that may be more significantly affected).Regional data layers of the extent of marine protected areas were available within the region, but included both well-enforced no-take reserves, areas with only limited regulations (e.g. no commercial fishing), and ‘paper parks’. Therefore, expert opinion was used to refine this data layer and classify only no-take reserves as either ineffective (essentially comparable to areas open to fishing), partly effective (some enforcement of regulations), or effective (well enforced).

Sea surface temperature

As ectotherms, temperature is the primary abiotic factor influencing the physiological performance of fish (Brett 1971). Temperature will also affect the productivity of algae (Hatcher 1990), and thus potentially the demographics of herbivorous fishes. Consequently, general patterns of variability in sea surface temperature were included in the models of fishing pressure and standing stock. Sea surface temperature data were obtained online from the Coral Reef Temperature Anomaly Database (CoRTAD)[10], and used data from 2008-2012 at a 4 km resolution. The metric of sea surface temperature followed Williams et al. (2015), namely the mean temperature from the coldest month of each year (i.e. the lower climatological mean) at each reef location. The final metric was calculated as the mean temperature of the coldest month over the five year period from 2008-2012.

Socio-economic development

The socio-economic status of an island can affect fishing pressure, with the potential for a decrease in fishing in areas with higher levels of socio-economic development (Brewer et al. 2012). Therefore, this variable was included in the model of fishing pressure. Socio-economic status could not be assessed for each island in the region, but was derived at a jurisdiction level using standardised data from online sources[11,12] (Table A1).

Table A1. The jurisdiction-scale, raw socio-economic data used in the Phase 1 project.

	CNMI	Guam	FSM	Palau	RMI
Population density (people per km^2 of land)	112.8103	297.3989	149.8803	46.32898	398.8453
Median age (years)	31.6	29.9	23.8	33	22.5
Population growth rate (%)	2.18	0.54	-0.46	0.38	1.66
Birth rate (per 1000 people)	18.32	16.82	20.54	11.05	25.6
Death rate (per 1000 people)	3.71	5.12	4.23	7.99	4.21
Urban population (%)	89.2	94.5	22.4	87.1	72.7
Life expectancy (years)	77.82	78.98	72.62	72.87	72.84
GDP ($ million)	1232	4600	315	269	193
GDP growth rate (%)	4.5	0.6	0.1	8	0.5
GDP per capita ($)	13300	30500	3000	16300	3300
Unemployment rate (%)	11.2	8.4	16.2	4.2	36

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[10] http://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0126774

[11] http://databank.worldbank.org/data/reports.aspx?source=world-development-indicators

[12] https://www.cia.gov/library/publications/the-world-factbook/

Rather than use each variable separately, they were combined into a composite index using principle components analysis (PCA, Fig. A5). This analysis separated the jurisdictions with, for example, Palau, CNMI, and Guam having a higher median age, GDP, and life expectancy (negative scores on PC1) compared to FSM and RMI. Similarly, FSM and RMI have higher unemployment and population growth rates than the other three jurisdictions (positive scores on PC1). Finally, Palau is separated from CNMI and Guam by having a lower life expectancy (more positive values on PC2).

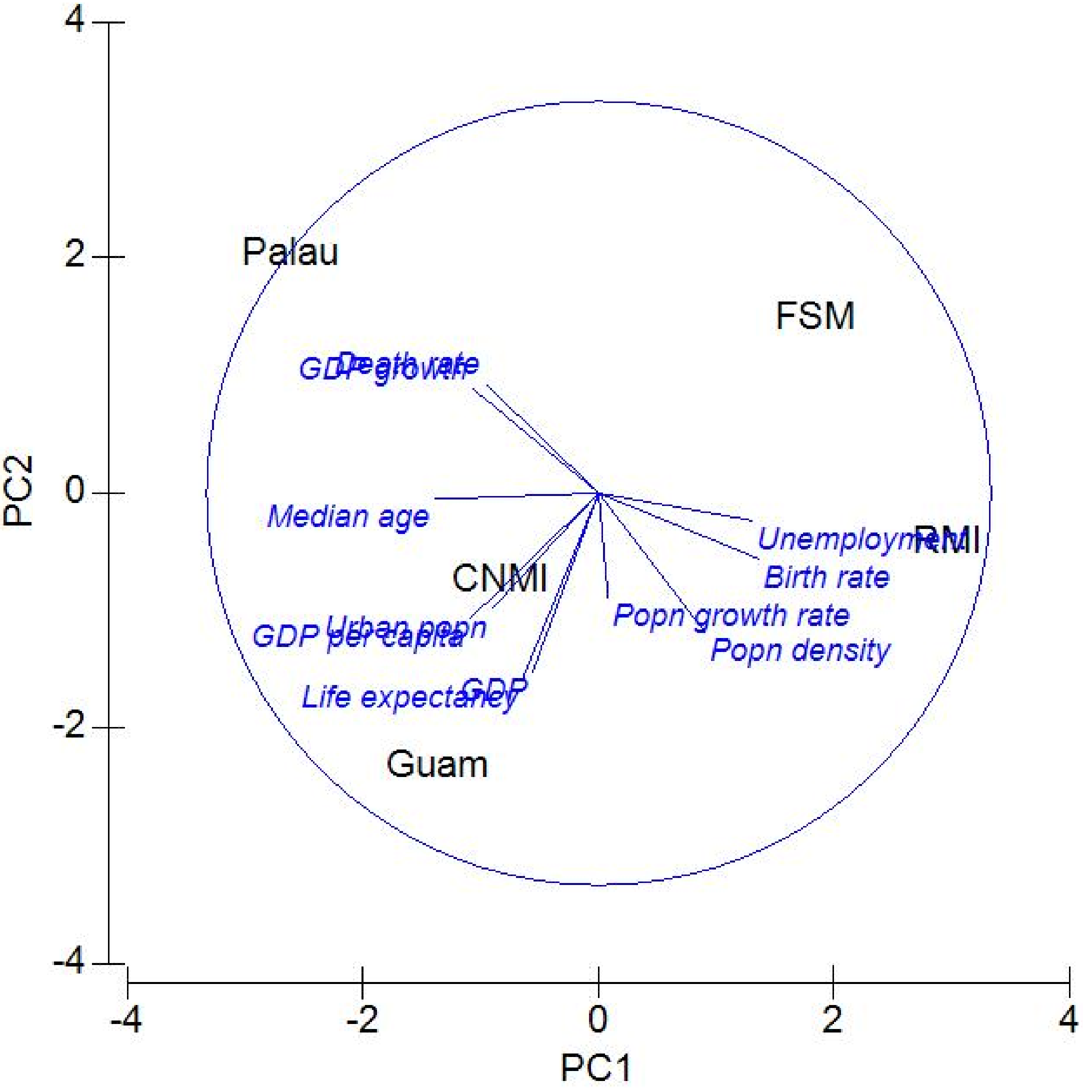

Fig. A5. Position of each jurisdiction on the first two axes (PC1 and PC2) of a principle components analysis of the raw socio-economic data.

These first two axes were used as the two metrics of socio-economic development for reef cells (Table A2). However, these values were only applied to reef cells within 20 km of the islands with major populations (Palau, Guam , Rota, Aguijan , Tinian, Saipan, Yap, Chuuk, Pohnpei, Kosrae, Majuro, and Kwajalein Atoll). The socio-economic situation at more remote islands with limited populations do not necessarily reflect the situation on these populous islands, and indeed these remote islands are more likely to be more socio-economically similar to each other than nearby population centres. Because no socio-economic data were available for these remote islands, values for these reefs cells were not included ('missing data').

Table A2. PCA scores for the first two axes for socio-economic development in each of the five jurisdictions. Values were used as metrics 'Socio-economic development 1' and 'Socio-economic development 2' for reefs cells within 20 km of a populous island.

Jurisdiction	PC1	PC2
CNMI	-0.8323	-0.7463
FSM	1.8414	1.4773
Guam	-1.3719	-2.3273
Palau	-2.6103	2.0203
RMI	2.9730	-0.4240

Survey method

There is some evidence of comparability among data sets (see Section 3.3), but the method of data collection (underwater visual census, stationary point counts, or video belt transects) was included in the models of both fishing pressure and standing stock to account for any systematic inter-technique variability. Where data source was a significant variable, values of fishing pressure or standing stock across the region were predicted across the continuous maps as if collected using underwater visual census (belt transects) as this is the method used to collect a majority of the data sets.

Tourist pressure

The number of tourists arriving in each jurisdiction varies widely across Micronesia, and potentially accentuates the impact of local populations on fish stocks. Across the entire region, reliable tourist arrival data are only available at the jurisdiction level[13] (Table A3). These data were compared to total jurisdiction population predictions from the SEDAC data layer (see section on Human population pressure) to generate a tourist to local population ratio. This ratio was then used to change the 'Human population pressure' metrics at 20 and 200 km for each cell (i.e. Human population pressure values were multiplied by 4.134 in CNMI and by 0.320 in FSM). This assumes that tourist numbers are distributed around the jurisdiction in the same proportion as local populations, which seems likely as most tourists spend at least some time in the population centres. Consequently, this calculation leads to an estimate of the total number of tourists per km^2 of reef within 20 and 200 km of each reef cell.

Table A3. Total number of annual tourist arrivals into each jurisdiction, and the tourist to local population ratios.

Jurisdiction	2011 tourist arrivals	Local population	Tourist to population ratio
CNMI	336000	81275	4.134
FSM	35000	109411	0.320
Guam	1160000	152423	7.610
Palau	109000	19290	5.651
RMI	4600	52066	0.088

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[13] http://data.worldbank.org/indicator/ST.INT.ARVL

Wave exposure

Wave exposure can have significant effects on fish assemblages since the morphologies of some species are better adapted to dealing with high levels of water movement (Fulton et al. 2005), and it can have significant effects on benthic habitat type (Chollett and Mumby 2012). High wave exposure can also increase the productivity of algae, influencing the abundance of herbivorous fishes (Mumby et al. 2013). High wave exposure can also limit fishing boat access, reducing fishing pressure (Houk et al. 2012b, Chollett et al. 2014, Taylor et al. 2014b). Therefore, wave exposure was included in models of both fishing pressure and standing stock.

Exposure was calculated using linear wave theory, which has successfully been used to predict habitat distribution and benthic beta-diversity on reefs (Harborne et al. 2006, Chollett and Mumby 2012). Full details of the method are described elsewhere (Ekebom et al. 2003), including their application to reefs (Harborne et al. 2006, Chollett and Mumby 2012), and are only described briefly here. Firstly, average weekly wind speed and direction for each ~25 km^2 cell across the region was obtained from QuikSCAT satellite scatterometer data (from 2005 to 2009), available online[14]. These data were then used to calculate mean wind speed in each 25 km^2 cell in each of eight directions (N, NE, E, SE, S, SW, W, and NW), and the proportion of time the wind blew from that direction. The fetch to the nearest land mass or reef crest in each of eight directions (N, NE, E, SE, S, SW, W, and NW) from each reef cell was then calculated using bespoke MATLAB code. The wave exposure in each direction was then calculated using fetch, mean wind speed and direction data, and linear wave exposure equations (Ekebom et al. 2003). An estimate of total wave exposure was calculated by summing the eight individual estimates of wave energy, weighted by the proportion of time the wind blows from each direction. Because of the lack of detailed bathymetric data needed to attenuate wave exposure with increasing water depth, surface wave exposure was used. However, this metric is likely to be a good estimate of the exposure experienced in each cell since this project focuses on shallow-water habitats.

Year

With the exception of inside marine protected areas, fishing typically increases over time with continually increasing impacts on fish assemblages. Inevitably, the large data set assembled for this project was not collected simultaneously, but the majority of the data was collected recently (<7 years). However, the year of collection was included in the models of both fishing pressure and standing stock to account for any temporal variation in fish assemblages. Where year was a significant variable, values of fishing pressure or standing stock across the region were predicted across the continuous maps using the mean year of data collection.

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