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Use of Habitats as Surrogates of Biodiversity for Efficient Coral Reef Conservation Planning in Pacific Ocean Islands

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Abstract: *Marine protected areas (MPAs) have been highlighted as a means toward effective conservation of coral reefs. New strategies are required to more effectively select MPA locations and increase the pace of their implementation. Many criteria exist to design MPA networks, but generally, it is recommended that networks conserve a diversity of species selected for, among other attributes, their representativeness, rarity, or endemicity. Because knowledge of species' spatial distribution remains scarce, efficient surrogates are urgently needed. We used five different levels of habitat maps and six spatial scales of analysis to identify under which circumstances habitat data used to design MPA networks for Wallis Island provided better representation of species than random choice alone. Protected-area site selections were derived from a rarity-complementarity algorithm. Habitat surrogacy was tested for commercial fish species, all fish species, commercially harvested invertebrates, corals, and algae species. Efficiency of habitat surrogacy varied by species group, type of habitat map, and spatial scale of analysis. Maps with the highest habitat thematic complexity provided better surrogates than simpler maps and were more robust to changes in spatial scales. Surrogates were most efficient for commercial fishes, corals, and algae but not for commercial invertebrates. Conversely, other measurements of species-habitat associations, such as richness congruence and composition similarities provided weak results. We provide, in part, a habitat-mapping methodology for designation of MPAs for Pacific Ocean islands that are characterized by habitat zonations similar to Wallis. Given the increasing availability and affordability of space-borne imagery to map habitats, our approach could appreciably facilitate and improve current approaches to coral reef conservation and enhance MPA implementation.*

Keywords: accumulation curves, biodiversity surrogacy, marine protected area, Millennium Coral Reef Mapping Project, remote sensing, richness congruence, Wallis

Uso de Hábitats como Sustitutos de la Biodiversidad para la Conservación Eficiente de Arrecifes de Coral

Resumen: *Las áreas marinas protegidas (AMPs) han sido resaltadas como un medio para la conservación efectiva de arrecifes de coral. Se requieren nuevas estrategias para seleccionar sitios para AMPS más*

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efectivamente e incrementar el ritmo de su implementación. Existen muchos criterios para diseñar redes de AMP, pero generalmente, se recomienda que las redes conserven una diversidad de especies seleccionadas por, entre otros atributos, su representatividad, su rareza o endemicidad. Debido a que el conocimiento de la distribución espacial es escaso, se requieren sustitutos eficientes urgentemente. Usamos cinco diferentes niveles de mapas de hábitat y seis escalas espaciales de análisis para identificar las circunstancias bajo las cuales los datos de hábitat usados para diseñar redes de AMP en la Isla Wallis aportaron una mejor representación de especies en lugar de la selección aleatoria. Los sitios para las áreas protegidas fueron derivados de un algoritmo de rareza y complementariedad. La sustitución de la biodiversidad fue probada para peces comerciales, todas las especies de peces, los invertebrados capturados comercialmente y especies de corales y algas. La eficiencia de la sustitución de hábitat varió por grupo de especies, tipo de mapa de hábitat y la escala espacial de análisis. Los mapas con la mayor complejidad temática proporcionaron mejores sustitutos que los mapas más simples y fueron más robustos a los cambios en escalas espaciales. Los sustitutos fueron más eficientes para los peces comerciales, corales y algas pero no para los invertebrados comerciales. Por el contrario, otras medidas de las asociaciones de especies-hábitat, como la congruencia de riqueza y las similitudes en composición proporcionaron resultados débiles. Proporcionamos, en parte, una metodología para el mapeo de hábitat para la designación de AMPs en las islas del Océano Pacífico, que se caracterizan por zonaciones de hábitat similares a la Isla Wallis. Debido al incremento en la disponibilidad y asequibilidad de la percepción remota para mapear hábitats, nuestro método podría facilitar y mejorar los métodos actuales para la conservación de arrecifes de coral e impulsar la implementación de AMP.

Palabras Clave: área marina protegida, congruencia de riqueza, curvas de acumulación, percepción remota, Proyecto Milenio de Mapeo de Arrecifes de Coral, sustitución de biodiversidad, Wallis

Introduction

In response to the widespread decline of marine resources worldwide, the international community is supporting increased implementation of marine protected areas (MPAs) (Lubchenco et al. 2003) at levels ranging from customary to governmental (Kareiva 2006). To optimize the implementation process, decision-support tools and high-quality information are needed (Roberts et al. 2003; Bellwood et al. 2004; Sale 2008). Managers often want to define MPA boundaries to include as much biodiversity, from genes to ecosystems, as possible. Unfortunately, comprehensive biological censuses are often scarce, tend to be conducted at small spatial scales, and are time consuming and expensive to conduct (Balmford & Gaston 1999). To date, at the level of terrestrial and marine conservation, species have most commonly been used as estimators of biodiversity (i.e., true surrogates [Sarkar et al. 2005]). Conservation planning initiatives have in turn focused on species-specific conservation criteria such as representativeness, rarity, or endemicity (Margules & Pressey 2000; Roberts et al. 2003). Because knowledge (and availability) of individual species' distribution is still largely unrealistic at large conservation planning scales (>100 km), a practical solution to help conservation projects is to use more easily quantifiable surrogates that have a measurable efficiency (i.e., estimator surrogates [Sarkar et al. 2005]). Terrestrial studies have already largely investigated cross-taxa surrogacy and the value of habitats and environmental factors as estimator surrogates of biodiversity. Results have been mixed, but are often valuable considering the different methods used in measuring surrogacy, the different scales of study and sample units, and the variety of underlying biogeographical patterns (e.g., Howard et al. 1998; Andelman & Fagan 2000; Ferrier 2002; Lund & Rahbek 2002; Sarkar et al. 2005, 2006; Altmoos & Henle 2007; Rodrigues & Brooks 2007; Kremen et al. 2008).

Studies reporting on what constitute effective surrogates in the marine realm are scarce, especially studies with rigorous methodological frameworks as described by Sarkar et al. (2005) and reviewed by Rodrigues and Brooks (2007). Along tropical coastlines, some taxa (e.g., fish species) are weak surrogates of other taxa (e.g., mollusks) (Beger et al. 2003, 2007), and the value of habitats and environmental factors as estimator surrogates is largely unknown, despite their potential as surrogates. Habitats are easier to resolve than species and can be mapped at large spatial scales with the use of space-borne imagery, which limits spatial gaps (Andréfouët 2008). The increasing availability and affordability of remotely sensed habitat maps offer the possibility of designing relevant, spatially explicit management schemes, whereby geomorphological, structural, and benthic cover data, instead of species-level information, guide the decision making process (Friedlander et al. 2003). This approach is based on the simple idea that if enough habitats are included in an MPA network, species using these habitats will by default be included in the protected area, and, ideally, species identified as requiring protection will also be included.

The few studies that have addressed the surrogacy power of marine habitats and habitat maps in representing species-level criteria, sensu Sarkar et al. (2005) (e.g., Stevens & Connolly 2004), suggest, for instance in Australian temperate coastal waters, that >90% of the diversity of fishes, invertebrates, and algal taxa would be represented if >40% of the habitat classes were protected (Ward et al. 1999). In coral reefs environments, the most recent study did not test habitats as estimator surrogates, but rather investigated indirect cross-taxa surrogacy (fish and invertebrate species) in a suite of 11 predefined Caribbean reef habitats (Mumby et al. 2008). This study investigated whether, for a number of habitats selected to represent a given taxon, the same suite of habitats were as effective at representing another taxon. Therefore, the study did not explicitly test the value of a suite of habitats and the value of habitat diversity as an estimator surrogate of biodiversity.

We sought to specifically test the efficiency of reef habitats as estimator surrogates of the diversity of coral reef species in the context of MPA network identification. Both the MPA context and the spatial analysis based on habitat maps provide original approaches to the study of habitat surrogacy in coral reef environments.

Methods

Study Site and Species Data

Wallis, located in the South Pacific (13°16′S, 176°12′W) (Fig. 1), is composed of 79 km^2, 80 km^2, and 140 km^2 of land, lagoon, and reefs, respectively. We based our study-site selection on the island's diversity of habitats (coral, seagrass, algae, sedimentary-dominated habitats, shallow and deep habitats, and sheltered and exposed habitats), which are typical of many coral reef areas worldwide, and the fact that relatively comprehensive data sets of species distribution were available for Wallis.

We conducted censuses of Wallis coral reefs between 2000 and 2007. We used random and random-stratified survey protocols on the basis of wind and wave exposure and coarse geomorphology of the reefs (i.e., barrier reef vs. patch reef vs. fringing reef) at sites distributed all around the island (Fig. 1). With the exception of the commercial fish survey, for which sampling sites were selected on the basis of a coral reef geomorphology map, we did not use any type of habitat map to design the sampling protocol. The censuses focused on fishes, commercially harvest echinoderms and mollusks, macrophytes, and corals.

We collected data on fishes in two independent surveys. The first considered overall fish species diversity (321 species at 38 sites) (Williams et al. 2006), and the second targeted commercial species only (151 species at 42 sites) (Kronen et al. 2009). Williams et al. (2006) and Kronen et al. (2009) detail the sampling methods. In

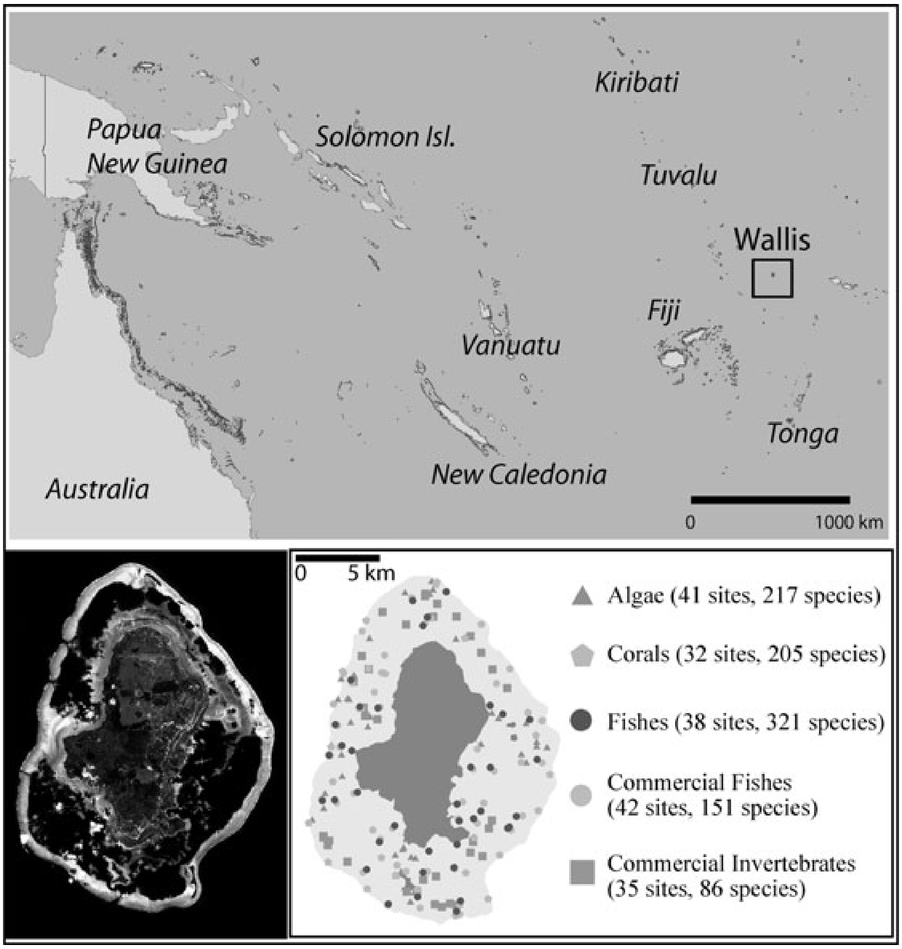

Figure 1. Satellite view (lower left) of Wallis Island and its lagoon (Landsat 7 ETM+) and spatial distribution of species census sites for the five biological groups considered.

short, we used scuba underwater visual censuses (UVC) along 50-m-long transects and independent rotenone surveys to compile overall lists of fish species. The waypoints associated with these data, however, generally indicate the boat position, not transects or sampling locations. Commercial fish data were also collected with scuba UVC along 50-m transects and suffered from similar uncertainty regarding the exact location of surveyed sites.

Our surveys of commercially harvested echinoderms and mollusks (86 species at 35 sites) followed a complex protocol. First, we used manta-tow broad-scale surveys (approximately 200-m long), followed by smaller-scale surveys to efficiently sample the wide range of species present. Sampling methods are fully detailed in Kronen et al. (2009). Targeted small-scale surveys consisted of searches of reef and benthos in 40 × 1 m transects; reef-front sites; and mother-of-pearl sites. Six replicates were achieved at each of these small-scale sites within a total area ranging between 3000 and 5000 m^2. A single waypoint was entered for each site; thus, exact locations of individual replicates were unknown.

At each survey site, we drew up exhaustive lists of algae species (217 species at 41 sites) during exploration dives conducted around one single marked waypoint (N'Yeurt & Payri 2004). The exact path followed underwater was unknown. We used a method similar to the one we employed for algae to draw up coral species lists (205 species at 32 sites) (Payri et al. 2002; M.P. & F.B., unpublished data).

Habitat Maps

In a remote-sensing context, high-resolution habitat maps are often created with labels that include both geomorphological and benthic information (Andréfouët et al. 2003). This provides a hierarchy of habitat definitions that can thematically range from very coarse (e.g., fringing reef) to very detailed (e.g., diffuse seagrass beds of 10–40% cover; 20-cm-high canopy; mixed community dominated by *Syringodium isoetifolium* and sparse *Thalassia hemprichii*). The level of habitat detail that can accurately be provided depends on image resolution, the geographic domain being processed, image quality, depth of mapping area, water quality, availability of ground-truth data, selected image interpretation techniques, and overall expertise (Andréfouët 2008; Wabnitz et al. 2008). The highest thematic accuracy and precision result in maps with habitat polygons that reveal the highest habitat diversity within the neighborhood of a sampling site.

For Wallis, we used five maps produced from aerial photographs at 2-m resolution. Three of these (maps A, B, and C; Fig. 2) are geomorphological maps. All three maps were derived using the typology of products provided by the Millennium Coral Reef Mapping Project (MCRMP) (Andréfouët et al. 2006). We described habitats in seven thematic classes in maps A and B, whereas habitats were represented in 16 classes in map C (Fig. 2). The latter map corresponded to the reference MCRMP product. For analysis we also used two additional maps (D and E; Fig. 2) derived from benthic data and created with extensive ground-truth data collected in 2005 (Andréfouët & Dirberg 2005). We described 10 coarse benthic classes in map D and 56 precise classes for map E, which integrated information such as depth, exposure, percent cover, macroalgae-seagrass taxonomy and detailed geomorphology (see Supporting Information). This last map best represented the actual diversity of habitats in Wallis. The 56-class map was validated in 2007 with ground-truth points specifically targeting areas around species census sites shown in Fig. 1. An accuracy assessment of the product yielded an overall value of >75% (Andréfouët 2008); most of the errors were due to confusion between habitats that were thematically close (e.g., confusion between sparse- and medium-density seagrass beds).

We ranked the maps as thematically simple (A–C; geomorphological data) to complex (E–D; benthic data). We tested each map for its efficiency as a surrogate of individual species groups with the aim to identify the level of habitat thematic richness required for cost-effective conservation planning for coral reefs.

Data Constraints and Implications for Analysis Design

Although data collection took place during a suite of major field-survey programs, because species censuses were not stratified according to habitat types, not all habitats around the island were fully sampled for all taxa or sampled with similar levels of intensity. Preliminary examination of the data therefore led us to identify two constraints for analysis.

First, because the exact position of sampled sites was uncertain for all surveys, it was impossible in most cases to know unambiguously which mapped habitats were effectively sampled, especially when conducting analyses on the basis of the most highly resolved and complex map (map E). Therefore, we could not conduct analyses precisely at the level of the habitat in which the survey was conducted. We sought to remedy this limitation by devising spatial buffers of at least 25–50 m around each census site. For all analyses in which we used the complex habitat maps, it was thus not possible to assign one specific habitat to a species census site. Rather, we could assign only a cluster of habitats in a so-called neighborhood around the sites.

Second, species censuses sampled a limited number of different habitats because surveys were not conducted and stratified according to the diversity of habitats found in Wallis, a common finding for surveys conducted independently of each other, over long time frames, and

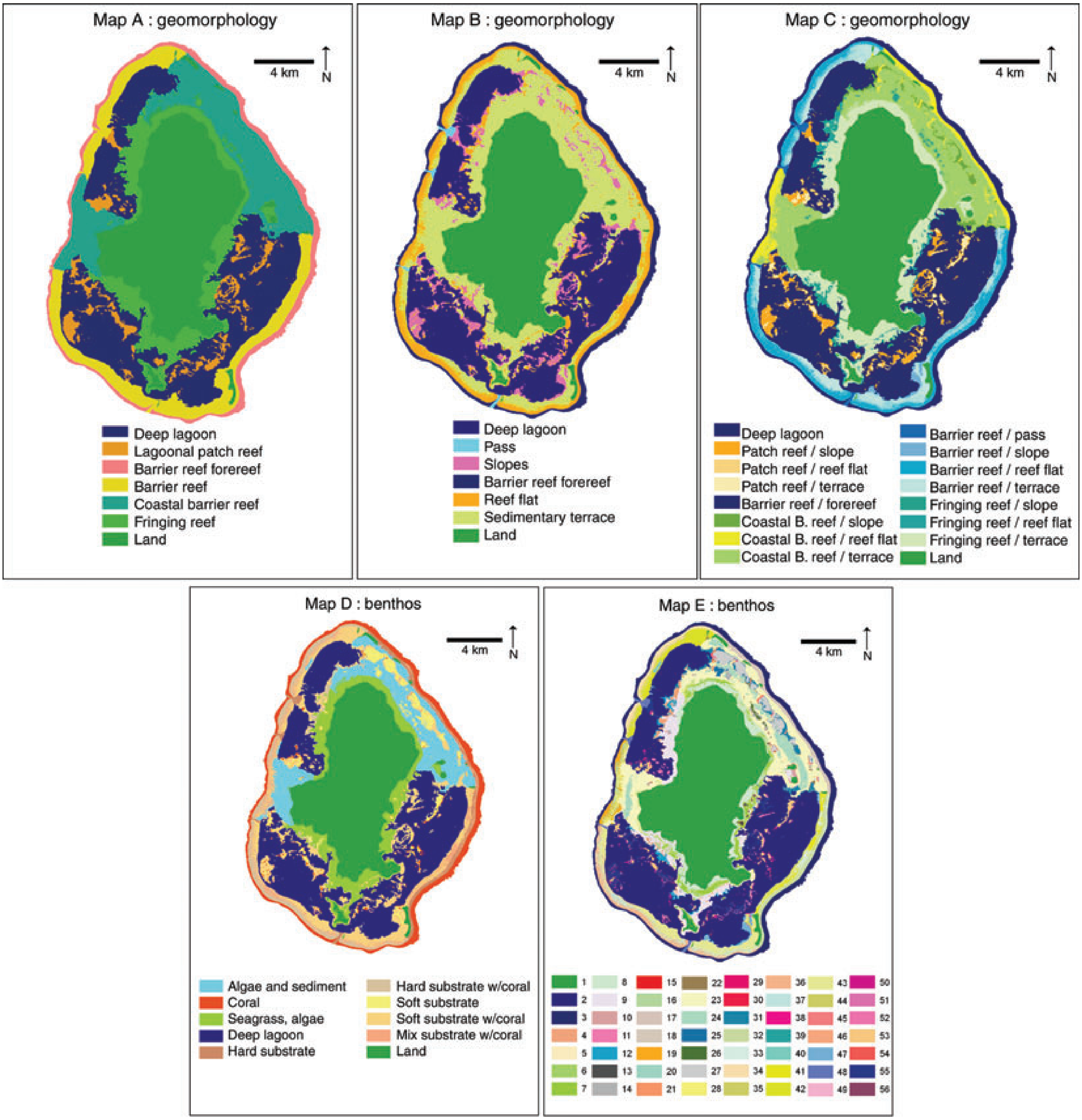

Figure 2. Habitat maps used to test the efficiency of habitats as surrogates of surveyed species groups. Top panels: simple, geomorphological habitat maps. Information provided in maps A and B, when combined, yield map C. Map A is the simplest map and is based on coarse geomorphological categories. Map B, although displaying the same number of classes as map A, reveals more complex habitat patterns. Bottom panels: two, complex, benthic habitat maps. Map D provides a view of the main benthic classes. Map E is a combination of map D and map C, plus additional information on coral growth forms and seagrass-algae taxonomy. The legend for map E's 56 classes is provided online (see Supporting Information).

surveying species that occupy vastly different ecological niches on the reef. In practice, it meant that once overlaid on our habitat maps, the stratification used in each survey emerged as "unbalanced" in terms of inclusion of our habitat categories at different thematic resolutions. For example, in fish surveys coral habitats were overrepresented, whereas seagrass habitats and shallow reef flats were underrepresented.

Given the above uncertainty in survey site locations and the limited coverage of habitat types when looking at point locations only, we opted to run analyses with species census data and clusters of habitats within a given buffer or neighborhood around each census site. We systematized this approach by considering habitats located within a suite of systematically expanding circular neighborhoods around individual species census sites. This is in agreement with recent practices developed to investigate habitat–fish relationships and their spatial patterns, for instance to study the effect of habitat richness and habitat assemblage composition on local fish richness and species assemblage composition (reviewed in Mellin et al. 2009). We used small (25 m, 50 m), medium (100 m, 200 m, 300 m), and large (500 m) radii to screen a wide range of scales because a priori information was available on the most suitable scale of analysis for each taxon (Mellin et al. 2009). By using a cluster of habitats within specified neighborhoods around species census sites, our approach sought to develop a methodology that would make the most efficient use of the greatest number of large disparate data sets for which sampling was not stratified according to habitat information (i.e., survey effort is likely to be different in every habitat).

Surrogacy Analyses

We measured the efficiency of reef habitats as surrogates with three distinct criteria: richness congruence, composition similarity, and representation level. Richness congruence measures whether habitat richness is spatially correlated with species richness for a given spatial scale of analysis. Specifically, we quantified whether the number of species observed at any given census point was related to the number of habitats observed within a given neighborhood. Kendall's rank correlation coefficient (Kendall 1938) was then used to assess the degree of correspondence between the two. This coefficient was chosen because the two test variables did not necessarily need to follow normal distributions and it was corrected for co-occurrences (i.e., instances where two distinct sites have the same number of habitats [or species] within a given neighborhood).

Composition similarity indicates whether given groups of species are associated with certain groups of habitats and the strength of this relationship. We used Mantel tests (Mantel 1967) to determine the correlation between species composition observed at individual census sites and the habitat composition within different-sized neighborhoods around these sites. For the smallest neighborhood (25–50 m) this would have been practically equivalent to investigating whether each habitat had a distinct assemblage of species and how much intrahabitat variation was present. So, in our analysis, the minimum unit was not the habitat; rather, it was the cluster of habitats within the considered neighborhood. This test was performed in two stages. First, two presence–absence matrices were built, one for species and one for habitats. Similarity matrices were then computed with the Bray-Curtis distance, which does not take into account double-zero occurrences. Second, to test the strength of the relationship between habitat and species compositions, we calculated the Pearson correlation coefficient between the two similarity matrices. A high, significant, correlation value suggests that similar habitat compositions are associated with similar species compositions. Conversely, nonsignificant correlation values precluded us from concluding that a relationship existed.

As highlighted by Sarkar et al. (2005), richness congruence and composition similarity require accurate predictions of species' spatial distributions—probably too difficult to achieve given existing data gaps. Instead, the primary requirement should be that adequate representation of the true surrogates is granted in a network of places selected with estimator surrogates. Therefore, *representation*, here determined via accumulation curves (or surrogate graphs) (Sarkar et al. 2005; Rodrigues & Brooks 2007), was calculated as the proportion of true surrogates (here species) included in a network when designed to incorporate a targeted percentage of estimator surrogates (here habitats). Accumulation curves are increasingly being used to assess empirically the representation level of a true surrogate in a network of protected areas designed with estimator surrogates. The method requires the simulation of a network. In our case, for each species group, all census sites were considered potential conservation sites and thus nodes of a network of MPAs local to Wallis.

The procedure had two steps: (1) we ranked sites according to their habitat composition and measured the level of species representation within them. We then defined conservation targets for both estimator and true surrogates. We considered that a species group's conservation objective had been attained when occurring at least once in the selected network. For habitats, three conservation targets were set alternately: at least one occurrence of each habitat in the selected network; at least 20% of all occurrences (appearing around the sampled sites) included in the final network; and similar to the latter with a 30% threshold (corresponding to the recommendation set forth by the Convention on Biological Diversity [CBD 2006]); (2) we applied a rarity–complementarity-based algorithm (Garson & Sarkar 2002) to these data. This algorithm is regarded as one of the most efficient when attempting to design protected areas that aim to include the maximum diversity of a targeted criterion (e.g., species, habitats) (Sarkar et al. 2004), and previous applications show it performed best when applied to coral reef environments (Beger et al. 2003). We implemented the algorithm by adding sites incrementally to the network, one at a time, according to both presence of the rarest habitats and presence of the largest number of habitats not yet included (to satisfy the complementarity criterion). The algorithm stopped when the conservation target for all habitats had been met.

During the process of adding sites to the network, we monitored the level of species representation (i.e., the proportion of species that achieved their conservation targets and had been included in the network at least once). The rate of species inclusion, or representation, when designing such a network was subsequently compared with the rate of species inclusion obtained when devising a network at random. The random representation value was the upper limit of the confidence interval (CI) resulting from 1000 simulations (mean + 1.96 SE). Graphically, plots of species representation against the number of sites added (or the proportion of habitats that achieved their targets) are called accumulation curves. If the species accumulation curve obtained with the specified habitat criterion was above the random curve, we deemed habitats efficient surrogates for species. We therefore considered surrogacy efficient when a network defined using habitats included species at a faster rate than through random choice alone (Sarkar et al. 2005).

We conducted all three analyses for the different neighborhood sizes and for all five habitat maps. By processing results on the basis of different habitat maps, we circumvented problems associated with a single analysis for which we would have needed to weight individual habitats according to their similarities. There was some level of subjectivity associated with determining how different two habitats may be from each other and from other habitats (e.g., whether two seagrass habitats of different shoot density were more diverse than one coral and one seagrass habitat). Working with different levels of definitions of habitat allowed us to explicitly merge similar habitats (e.g., all seagrass habitats in map E were merged into one single class in map D) and for all habitat configurations to be tested.

Results

Richness congruence was low between habitat and species richness. For analyses conducted at medium size scales and with simple geomorphological maps, coral and fish were weakly correlated with habitats (e.g., for fish at 200 m and geomorphological map B, $\tau = 0.23$; $p = 0.37$). The use of the more complex benthic habitat maps D and E did not improve results. Thus, for Wallis, the conclusion that a sampling site surrounded by a high diversity of habitats in its neighborhood should locally display high species diversity did not hold.

Composition similarities suggested that, in some cases, species and habitat assemblages were linked. Higher correlation coefficients were obtained for medium and large scales (300–500 m) and for the most detailed habitat maps D and E. The highest correlations were never achieved for the smallest scales (25–50 m). Algae provided weak ($r = 0.113$, $p = 0.005$) correlations at 500 m with maps D and E. For corals, "outer slope forereef" communities were clearly different from "lagoon" communities. The link was therefore strong even with the simplest geomorphological map ($r = 0.643$, $p < 0.001$, 50 m). For fish species overall, significant and strong links ($r = 0.587$, $p < 0.001$) were found at the largest scale (500 m) for the most detailed habitat maps D and E. However, the relationship collapsed with commercial species ($r = 0.206$, $p = 0.004$). For any combination of scale and habitat map complexity, invertebrates showed no link with habitat assemblages (e.g., $r = 0.021$, $p = 0.374$ for detailed map E and a neighborhood of 200 m). In short, the type of taxa and complexity of habitat map used in our analyses had a significant effect on the relationship between species composition and habitat composition, but the scale of the analysis did not.

With the detailed benthic habitat map E, for all simulations and cumulative curves (considering one occurrence, 20%, and 30% of habitat occurrences, and at least one occurrence of each species), MPA networks built with benthic habitat data led to better species representation than those devised through random choice alone. We found few differences between results achieved for the three habitats conservation objectives (i.e., one occurrence, 20% and 30% of habitats occurrence), which suggests that the algorithm makes similar decisions on site selections independent of the chosen conservation criteria. Therefore, for purposes of simplicity we only present findings for the 30% level (Figs. 3–5). Use of the most detailed benthic habitat maps always improved species representation over random choice, irrespective of changes in spatial scales. Habitats as classified in the simple map C were efficient as surrogates for algae, corals, and commercial fish species at scales ranging from 50 to 300 m (Fig. 5). Commercial invertebrates were a notable exception; they had poor representation (Figs. 3–5). Commercial fish species were more easily represented than total fish species.

Discussion

Our results (Figs. 3–5) demonstrate the value of using maps of coral reef habitats for designing representative MPA networks that target species representation, despite our results indicating low congruence and composition similarities for Wallis, particularly for algae and invertebrates. The fact that invertebrate census data predominantly focused on commercial species may explain the poor results obtained for this group. Another likely

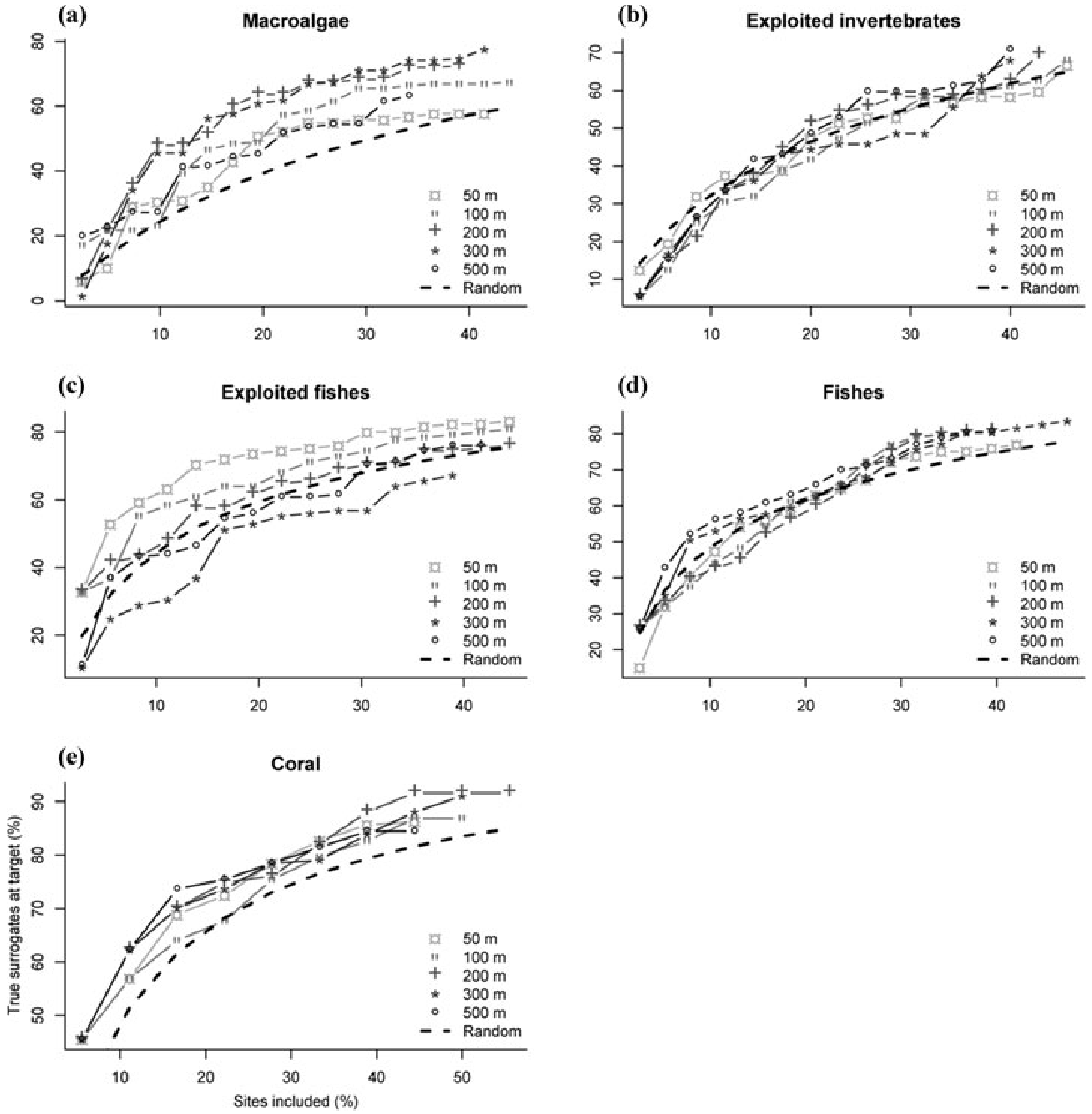

Figure 3. Accumulation curves for marine protected area networks designed with the most complex benthic habitat map (map E; Fig. 2): (a, e) macroalgae and coral species, repsectively; (b, c) fish and invertebrate species harvested commercially, respectively; (d) all fish species combined. The dashed curve represents the 95% upper limit of the confidence interval generated by 1000 simulation runs selecting sites at random. Habitat surrogacy curves that are based on the rarity-complementarity algorithm we used are in different colors for each neighborhood radius size. Habitats are efficient surrogates if the surrogacy curve is above the dashed curve.

explanation is that benthic invertebrates' distributions depend on habitat factors occurring at spatial scales we did not consider (i.e., of a few meters or less). In addition to further investigating the points raised so far, future work should also examine responses according to the specific composition of this broad commercial group, for instance looking at holothuroids (sea cucumbers), echinoids (sea urchins), and mollusks separately.

Overall, poor congruence and positive representation results may seem contradictory at first. However, the representation capacity of an estimator surrogate depends on the reserve selection algorithm used to prioritize sites. On the basis of the rarity-complementarity algorithm we used (Garson & Sarkar 2002), final selected sites may not necessarily include habitats with the most diverse fauna individually, but instead include the most complementary set of habitats required to protect maximal species diversity overall. Thus, poor congruence is not incompatible with effective representation and surrogacy, and evaluating the efficiency of an estimator

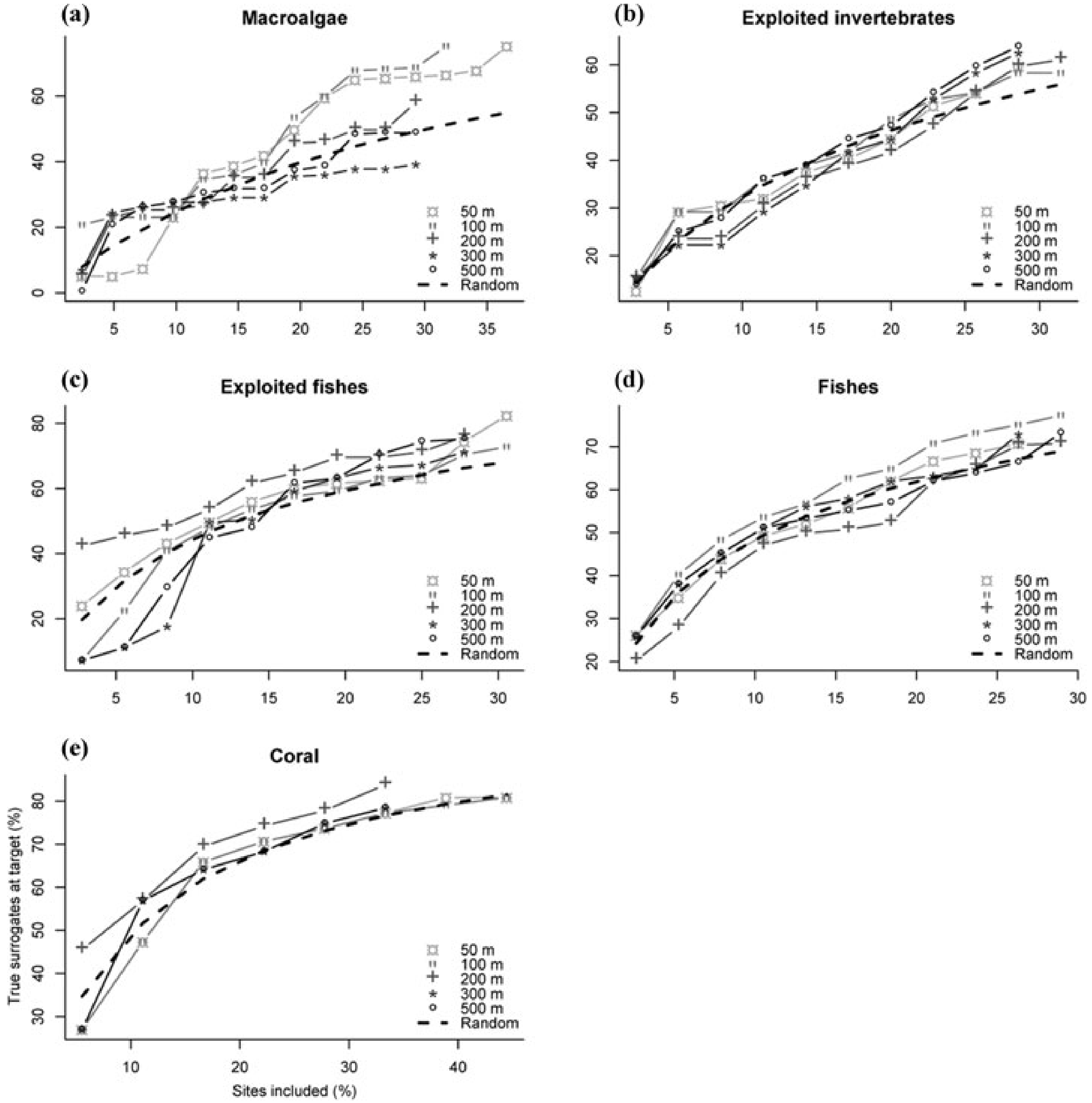

Figure 4. Accumulation curves for marine protected area networks simulated with habitats described at the coarsest geomorphological level (map A; Fig. 2). Species' accumulation curves below the dashed "random" line (i.e., networks designed at random) show species groups for which habitats are efficient surrogates (for comparative purposes, see Fig. 3).

surrogate solely on the basis of richness correlations would be misleading.

Our results further show that composition similarities and representation levels improved with increasing habitat map complexity. In practical terms then, mapping efforts need to be conducted at a relatively fine thematic scale for habitat maps to optimally inform conservation planning. In terms of costs, for Wallis, a 56-class map required a high-resolution image (2 × 2 m pixels), 10 days of fieldwork for two scientists, and 2 weeks of desktop work. In comparison, each biological survey required 1–2 weeks of fieldwork for four to six taxonomic specialists, and significant additional lab-based identification work. Also, unlike the habitat surveys, none of the species censuses were spatially exhaustive. However, useful results in a conservation planning context are possible with intermediate resolution maps if only those are available (Fig. 5). Production of accurate geomorphological products requires only a few hours of desktop work and no fieldwork—albeit for a trained scientist with good knowledge of reef geomorphology. Such maps are now available for most of the world's reef regions (Andréfouët et al. 2006), and on the basis of our results (Fig. 5), these products should provide valid means of protecting biodiversity. As such, they could offer very cost-effective solutions for many countries.

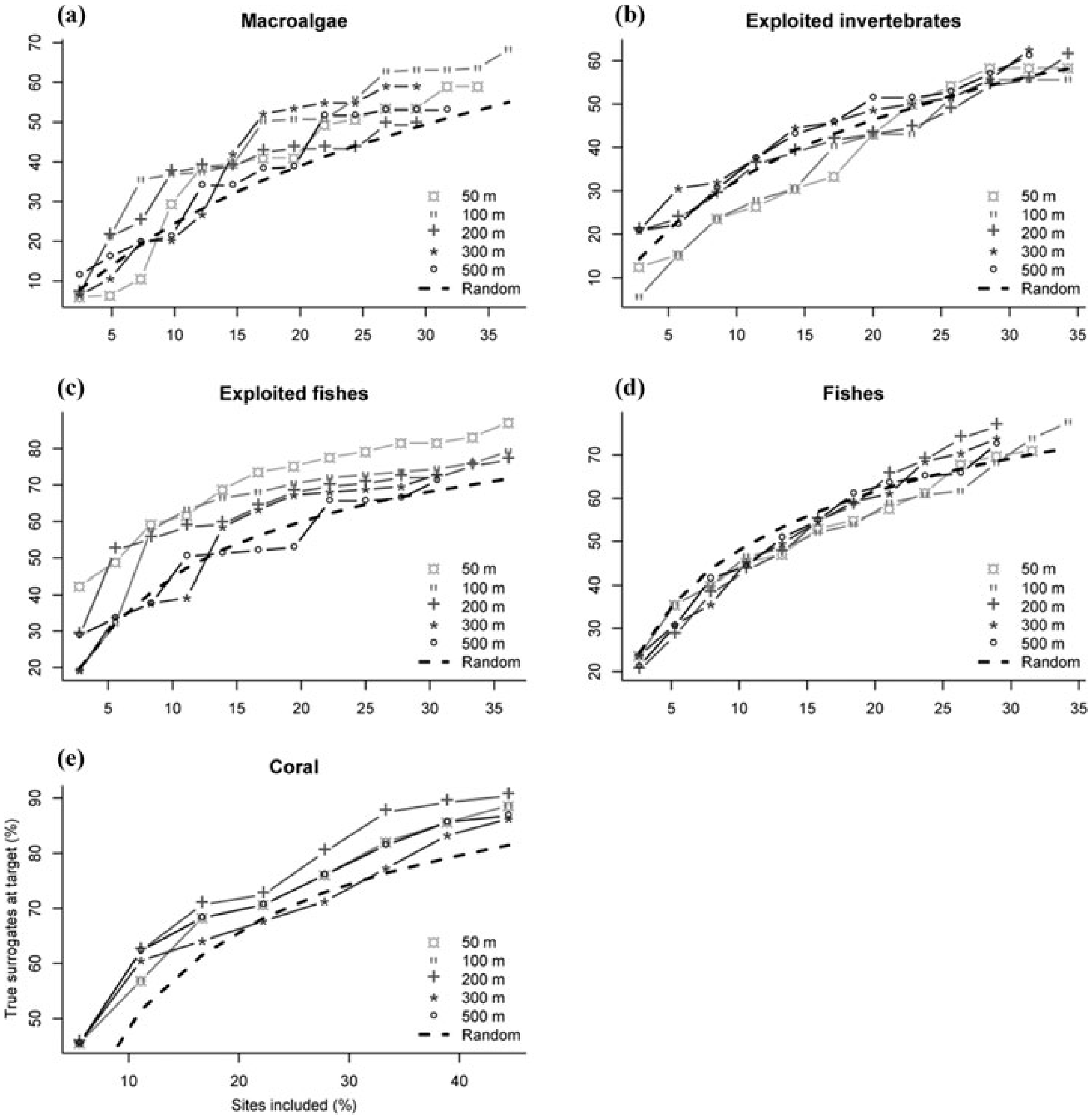

Figure 5. Accumulation curves for marine protected area networks simulated with a habitat map derived from detailed geomorphological data only (map C).

The geomorphological habitat maps we present for Wallis were based on the MCRMP typology. To date, all Pacific Ocean islands have been mapped in this way. After initial comparison between Wallis and islands with similar geomorphological classes, it was possible to cautiously infer to what extent our results could be generalized. Specifically, many islands of the Society, Gambier, and Australes archipelagos (French Polynesia), Cook Islands, Samoa, American Samoa, Tonga, Fiji, New Caledonia, Solomon Islands, Mircronesia, Palau, and Papua New Guinea display similar reef zonations to Wallis. Conversely, Vanuatu, the main Hawaiian Islands, and Mariana Islands are vastly dominated by small fringing reefs directly exposed to the ocean, a situation that does not occur in Wallis Island. Atolls in Tuamotu Archipelago, Cook Islands, Kiribati, Tokelau, Tuvalu, Marshall Islands, and the northwestern Hawaiian Islands also do not match Wallis' geomorphological zonations. Of course, transferability of our findings to similar geomorphological areas warrants further precise investigation. Such an analysis should consider the location of Wallis along the biogeographical Indo-Pacific diversity gradient (halfway between the center of biodiversity in the Indo-Pacific, at least for corals and reef fish and the relatively poor areas of eastern Polynesia). However, more detailed comparisons and further tests of the validity of our results for these other sites will be difficult given the paucity of island sites that possess multitaxa lists of species as complete as for Wallis.

Identification of the "right" level of habitat mapping complexity and the scale of analysis for a given objective are certainly necessary to understand surrogacy and achieve optimized MPA networks. This study is the first to address these issues for coral reefs with a spatially explicit design. Authors of the most recent study to have evaluated coral reef habitats as surrogates (Mumby et al. 2008), did not consider surrogate efficacy in the context of attempting to achieve various levels of biodiversity conservation within MPA networks. Moreover, the analysis only included one benthic habitat typology (thematically close to our map D) and did not take into account different spatial scales of variability (i.e., they did not "address the spatial variability of habitat distribution"). Mumby et al.'s (2008) assessment of habitat surrogacy was indirect because habitats were used as a function of transfer for taxonomic (or other criteria) surrogacy (their table 5) and the habitats' efficiency as surrogates was computed with a "brute force" complementarity algorithm. Thus, it would be interesting to test the surrogacy value of habitats in the Bahamas within the analysis' framework we established here. However, in contrast with the Bahamas study, our Wallis study did not investigate surrogacy of ecosystem services and ecological functional groups.

Our results corroborate findings that the use of habitat maps is a promising way to cost-effectively design MPA networks for coral reef environments (Wabnitz et al. 2009). Pending availability of resources and time, biological censuses to enhance and complement habitat data sets are to be encouraged, especially if they are designed to cover a wealth of habitat and habitat diversity configurations, as well as the integration and processing of all existing biological data (Williams et al. 2002). We advocate for similar simulations to be run for different reef areas worldwide to confirm our findings, particularly in the Caribbean and Red Sea, where habitat assemblages and geomorphology differ from Indo-Pacific reefs. Such simulations and comparisons would lead to a better understanding of how habitat data, mapping, and representation criteria can contribute to more informed decision making in marine conservation planning.

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Supporting Information

The legend of map E (Appendix S1) and in situ photographs illustrating the different habitats (Appendix S2 [six figures]) are available as part of the on-line article. The corresponding author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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