Contributed Paper

Incorporating Surrogate Species and Seascape Connectivity to Improve Marine Conservation Outcomes

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Abstract: *Conservation focuses on maintaining biodiversity and ecosystem functioning, but gaps in our knowledge of species biology and ecological processes often impede progress. For this reason, focal species and habitats are used as surrogates for multispecies conservation, but species-based approaches are not widely adopted in marine ecosystems. Reserves in the Solomon Islands were designed on the basis of local ecological knowledge to conserve bumphead parrotfish (Bolbometopon muricatum) and to protect food security and ecosystem functioning. Bumphead parrotfish are an iconic threatened species and may be a useful surrogate for multispecies conservation. They move across tropical seascapes throughout their life history, in a pattern of habitat use that is shared with many other species. We examined their value as a conservation surrogate and assessed the importance of seascape connectivity (i.e., the physical connectedness of patches in the seascape) among reefs, mangroves, and seagrass to marine reserve performance. Reserves were designed for bumphead parrotfish, but also enhanced the abundance of other species. Integration of local ecological knowledge and seascape connectivity enhanced the abundance of 17 other harvested fish species in local reserves. This result has important implications for ecosystem functioning and local villagers because many of these species perform important ecological processes and provide the foundation for extensive subsistence fisheries. Our findings suggest greater success in maintaining and restoring marine ecosystems may be achieved when they are managed to conserve surrogate species and preserve functional seascape connections.*

Keywords: Coral reef, Coral Triangle, fish, mangroves, marine reserve, seagrass, spatial conservation planning, Solomon Islands

Incorporación de Especies Sustitutas y de Conectividad Marina para Mejorar los Resultados de Conservación

Resumen: *La conservación se enfoca en el mantenimiento de la biodiversidad y del funcionamiento del ecosistema, pero los vacíos en nuestro conocimiento de la biología de las especies y de los procesos ecológicos a menudo impiden progresar. Por esta razón, se utilizan especies y hábitats focales como sustitutos de la conservación multiespecífica, pero los métodos basados en especies no son adoptados ampliamente en ecosistemas marinos. Las reservas en las Islas Salomón fueron diseñadas con base en el conocimiento ecológico local para conservar el pez loro (Bolbometopon muricatum) y para proteger la seguridad alimentaria y el funcionamiento del ecosistema. B. muricatum es una especie amenazada icónica y puede ser un sustituto útil para la conservación multiespecífica. Se mueve por paisajes marinos a lo largo de toda su vida, en un patrón de uso de hábitat compartido con muchas otras especies. Examinamos su valor como un sustituto de conservación y evaluamos la importancia de la conectividad marina (i. e., la conectividad física de parches en el paisaje marino) entre arrecifes, manglares y pasto marino para el funcionamiento de la reserva marina. Las reservas fueron diseñadas para B. muricatum, pero también mejoró la abundancia de otras especies. La integración del conocimiento ecológico local y la conectividad marina mejoraron la abundancia de otras 17 especies de peces en reservas locales. Este resultado tiene implicaciones importantes para el funcionamiento del*

ecosistema y los habitantes locales porque muchas de estas especies realizan procesos ecológicos importantes y proporcionan la base para pesquerías extensivas de subsistencia. Nuestros resultados sugieren que se puede obtener un mayor éxito en el mantenimiento y restauración de ecosistemas marinos cuando son manejados para conservar especies sustitutas y preservar las conexiones marinas funcionales.

Palabras Clave: Arrecife de coral, Islas Salomón, manglares, pasto marino, peces, planificación espacial de conservación reserva marina, Triángulo de Coral

Introduction

Marine ecosystem-based management focuses on maintaining biodiversity, connectivity, and ecosystem functioning (Beger et al. 2010*a*; Foley et al. 2010). Our ability to achieve these goals is, however, often impeded by a lack of information on species biology and ecological processes. Marine spatial planning, therefore, often requires that conservation decisions be made in the absence of vital ecological information (Foley et al. 2010). This necessitates the adoption of surrogates to represent biodiversity or ecosystem functioning (e.g., Mumby et al. 2008). Decision makers consider both habitat (e.g., Harborne et al. 2008) and species (e.g., Beger et al. 2007) targets in the planning process, but the majority of marine studies focus on habitat-based schemes (Zacharias & Roff 2001; Leslie 2005). A broader approach to surrogacy is employed in terrestrial conservation planning, which incorporates a range of species-based approaches and weighting to better conserve vulnerable, diverse, or variable targets (Rodrigues & Brooks 2007; Wilson et al. 2009; Caro 2010). Focal species are adopted to bridge the divide between single and multispecies conservation and may improve conservation outcomes at the ecosystem scale (Caro 2010).

Marine conservation surrogates are not as well studied as those in terrestrial ecosystems, possibly reflecting less biological and ecological information on their utility (Leslie 2005; Caro 2010). Consequently, the findings of marine research often need to be coupled with ecological information acquired from other sources (i.e., local ecological knowledge and customary sea tenure) (Cinner & Aswani 2007). Local ecological knowledge is used in tropical developing nations to inform planning decisions for seascape conservation (Aswani & Hamilton 2004; Weeks et al. 2010). Yet few studies have examined whether combining scientific and local knowledge results in better management outcomes (Hamilton et al. 2012). Marine reserves in Roviana and Vonavona lagoons (Solomon Islands) were designed through integration of local ecological knowledge, existing sea tenure, and marine and social science to conserve bumphead parrotfish (*Bolbometopon muricatum*), protect food security, and maintain ecosystem functioning (Aswani & Hamilton 2004; Aswani et al. 2007). The process of establishing small community-managed local conservation areas is common in the Coral Triangle. In our study area it involved coupling anthropological surveys with GIS to identify and map key nursery

locations to explain how different habitats structure the size distribution of bumphead parrotfish and to identify sensitive locations and habitats in need of protection (e.g., nurseries, spawning, and sleeping aggregation sites); ground truthing this information with biological surveys; identifying locations best suited to successful bumphead parrotfish conservation (i.e., with a greater likelihood for local support) based on secure customary sea tenure; following accepted design principles for marine reserves (i.e., area, spacing, and representation); and maintaining community involvement in the implementation and enforcement of reserves (in the lagoon) and spearfishing bans (to protect vulnerable aggregation sites offshore) (Aswani & Hamilton 2004).

Bumphead parrotfish have high cultural significance, are preferentially targeted by local fishers, are vulnerable to overexploitation, and have declined markedly over their entire distribution (Aswani & Hamilton 2004; Hamilton & Choat 2012). They are large (reaching 139 cm and 52 kg) and important coral predators, bioeroders, and herbivores with a broad distribution across the Indo-Pacific (Hoey & Bellwood 2008; Bellwood & Choat 2011; Bellwood et al. 2012). They functionally connect tropical seascapes through a series of ontogenetic habitat shifts: small juveniles recruit to shallow inner lagoon nurseries, characterized by mangroves, seagrass, algae, and high-relief coral formations; larger juveniles and subadults occur on lagoonal reefs; and adults occur on outer reefs (Aswani & Hamilton 2004; Kobayashi et al. 2011; Hamilton & Choat 2012). Their large size, exploitation, and cultural significance make bumphead parrotfish a flagship (an iconic symbol for conservation) (Aswani & Hamilton 2004; Verissimo et al. 2011). These fish remove carbonate from reefs when feeding and underpin the ecosystem function of bioerosion, which may make them a potential keystone species (actions of which affect many other species) on coral reefs (Bellwood et al. 2003; Bellwood et al. 2012). Their diverse habitat and large area requirements (potentially 5 km as adults and tens of kilometers throughout their life history) (Hamilton 2004) indicate they could also be an important umbrella species (protection of which may also protect many other species) (Roberge & Angelstam 2004; Branton & Richardson 2010). Collectively, these attributes impart high conservation significance to bumphead parrotfish and suggest that they may also be a critical landscape species for conservation (sensu Sanderson et al. 2002). Landscape species (or seascape species in a marine context)

exhibit all the attributes of umbrella, keystone, and flagship species. They use large areas of heterogeneous habitat, exert strong influences on ecosystem functioning, are vulnerable to exploitation, and have high socioeconomic significance (Caro 2010). Consequently, their conservation could also enhance biodiversity, help maintain the functioning of ecosystems, and garner strong support from local communities.

We first determined that bumphead parrotfish were more abundant in reserves than adjacent fished waters and thereby reconfirmed previously identified patterns (Aswani et al. 2007; Aswani & Sabetian 2010). We then assessed whether bumphead parrotfish were an effective surrogate for multispecies conservation by testing our primary hypothesis that fish assemblages would follow patterns in bumphead parrotfish abundance and, therefore, differ between the reserves and adjacent fished locations. Of course fish move across tropical seascapes and use different habitats as juvenile nurseries, for foraging, and spawning (Nagelkerken 2009; Sheaves 2009). This seascape connectivity (i.e., the physical connectedness of patches in a particular seascape) (sensu Pittman et al. 2011) can, therefore, affect fish assemblage composition (Boström et al. 2011; Berkström et al. 2012) and the performance of marine reserves (e.g., Olds et al. 2012,*a*, 2012*b*). To test the effectiveness of the conservation strategy implemented in Roviana and Vonavona lagoons we explicitly accounted for seascape connectivity in the study design by testing the secondary hypothesis that seascape connectivity among seagrasses, mangroves, and coral reefs would enhance the ability of reserves to promote fish abundance (including bumphead parrotfish, which use a range of different habitats through ontogeny). Collectively, these 2 hypotheses focus on the value of bumphead parrotfish as a surrogate for multispecies conservation and the importance of seascape connectivity for tropical marine conservation.

Methods

Seascape Analyses

We surveyed the fish assemblages of coral reef, seagrass, and mangroves in Roviana and Vonavona lagoons between April and June 2011. These lagoons lie within the western province of the Solomon Islands and are part of the Coral Triangle ecoregion, which is recognized as the global center of marine biodiversity with the highest priority for conservation (Veron et al. 2009). The lagoons are formed by raised offshore coral islands and support heterogeneous tropical reef seascapes (Fig. 1), which are managed in a system of small community-based marine reserves (established in 1999 and managed by the Roviana Conservation Foundation) (Aswani et al. 2007). Fish assemblages were surveyed in 3 locations that were no-take marine reserves, adjacent to the villages of Kida, Nusa

Hope, and Olive (established in 2002–2003, protected for 8 years) and 3 unprotected control locations that were paired with each reserve location (Fig. 1). Reserve enforcement can be a problem in the region (Halpern et al. 2013), but the management of the 3 reserves included in this study is regarded as effective at controlling poaching (Aswani et al. 2007; Aswani & Sabetian 2010).

Seascape connectivity was quantified as a categorical variable, and at each location we surveyed one site with adjacent reef and seagrass, one with adjacent reef and mangroves, and one where reef was isolated from both seagrass and mangroves by deep water. Ideally, we would also have surveyed isolated seagrass and mangroves at each location, but these habitats were not present in the reserves surveyed. Sites within each location were selected to minimize differences between reserve and paired control locations, and we verified that fish distributions were not explained by covariation of habitat composition or complexity or distance to the nearest village (Supporting Information).

Seascape connectivity was quantified from existing benthic habitat maps for Roviana and Vonavona lagoons with ArcGIS (ESRI, Redlands, CA, U.S.A.) (sources: James Cook University, Roviana Conservation Foundation, United Nations Environment Program and University of Queensland). Habitats were considered connected based on their proximity to each other. Well-connected reefs were within 250 m of seagrass or mangroves and separated by shallow (<2 m) reef flats. In contrast, isolated reefs were separated from both seagrass and mangroves by deep (>50 m) water and at least 500 m. Seascape studies must be scaled to the mobility of the species of interest (Grober-Dunsmore et al. 2009). Close habitats were, therefore, within the daily home ranges of adult surgeonfish (Acanthuridae), parrotfish (Labridae), emperors (Lethrinidae), snappers (Lutjanidae), goatfish (Mullidae), groupers (Serranidae), rabbitfish (Siganidae), and bream (Sparidae) (Supporting Information), whereas habitats isolated by >500 m and deep water were not. Ideally, home ranges of other species would also be included when selecting a spatial context, but movement data are lacking for other fish in the region.

Fish Assemblages

We used underwater visual census (UVC) to survey fish in coral reef, seagrass, and mangrove areas. This method is standard for the survey of coral reef fishes and is appropriate for examining large mobile species in seagrass (Unsworth et al. 2009) and mangroves (Dorenbosch et al. 2009) where water clarity is sufficient. We followed the standard approach of surveying 5 replicate 50 × 4 m transects in coral reef, seagrass, and mangrove areas at each site. Longer belt transects are often adopted when surveying fish with large home ranges (like adult bumphead parrotfish) (Robbins et al. 2006), but they could not be used here due to the spatially explicit design of our

study, which focussed on quantifying the abundance of juveniles and subadults of this species. Mangroves were surveyed during high tides (when inundated and accessible to fish), and coral and seagrass were surveyed when mangroves were dry and not accessible to investigate the influence of tidal inter habitat movement. Adjacent transects were at least 50-m apart. Each census consisted of a diver swimming parallel to the reef slope, seagrass edge, or mangrove fringe and recording all fish >5 cm total length (TL). Individual fishes were identified to species, and their sizes were estimated. The accuracy of size estimates was evaluated using the standard fish model method. Seagrass and mangroves were sampled when fully inundated (at depths of 0.5–1.5 m), and reefs were surveyed along the adjacent reef slope (at a depth of 5–10 m) when intertidal habitats were dry. We examined the interaction between reserve status, location, and seascape connectivity effects on the composition of fish assemblages and density of individual species. Analyses examining reserve effects on fish assemblages were conducted separately for coral reef, seagrass, and mangrove areas and water depth was standardized among all locations of a particular type.

Data Analyses

Reserve and seascape connectivity effects were evaluated using a modified control-impact design. Analyses examined the interactive effects of seascape connectivity and ecosystem protection through comparison of the 3 reserves and 3 control locations. Assemblage data were examined using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). Three-factor analyses were conducted for reef fish variables, and 2-factor analyses were performed for mangrove and seagrass fish variables. The factors were reserve status (a fixed orthogonal factor with 2 levels), location (a random orthogonal factor with 3 levels), and seascape connectivity (a fixed orthogonal factor with 3 levels, used in reef analyses only). A posteriori pairwise tests were applied to significant factors following PERMANOVA.

Canonical analysis of principal coordinates (CAP) was used to visualize significant factors following PERMANOVA (Anderson & Willis 2003). All multivariate analyses were based on modified Gower (log base 2) similarity measures, which exclude joint absences, strongly emphasize differences in species abundance, and are appropriate for dealing with multivariate heterogeneity of variance (Anderson et al. 2011). We used the PERMANOVA+ add-on package for PRIMER to perform these analyses. Fish density data were log transformed to produce homogenous variances and analyzed with analysis of variance (ANOVA). Analyses were based on the design adopted for PERMANOVA tests. Tukey's HSD post hoc tests were used to differentiate significant means. The accuracy of fish size estimation was verified using

one-way ANOVA, which confirmed that size estimates made on each assessment event did not differ (i.e., $p > 0.05$) from the known size of fish models. The size of reef fish species with distributions that correlated with seascape connectivity to mangroves or seagrass was then compared between reefs and adjacent habitats with nonparametric tests. Nonparametric analyses were adopted because there were vastly different numbers of fish in the different habitats, and transformation of the data failed to homogenise variance. Mann-Whitney U tests were used for species that were only recorded in 2 habitats. Kruskal–Wallis tests were used for species that were recorded in all 3 habitats.

Results

Reserve and Connectivity Effects

Bumphead parrotfish were more abundant on reserve reefs near seagrass than on similar fished reefs (Fig. 2, Supporting Information). Juveniles were recorded in shallow mangrove, seagrass, and reef, but their abundance was always greater in reserve seagrass near reef than in similar fished seagrass (Fig. 2, Supporting Information). Overall, bumphead parrotfish abundance was also greater on reserve than fished reefs at Olive and Nusa Hope, but not at Kida (Supporting Information).

Reserves affected the composition of fish assemblages only on reefs located close to seagrass or mangroves (Fig. 3, Supporting Information). These differences were driven primarily by variation in the abundance of rabbitfish (Siganidae), snappers (Lutjanidae), and sweetlip (Haemulidae) (Supporting Information).

Reserves influenced the composition of fish assemblages in seagrass and mangroves near reefs (Fig. 3, Supporting Information). Assemblage composition also varied among locations, but this did not influence reserve effects on seagrass or mangrove fish (Supporting Information). These differences were driven mainly by variation in the abundance of snappers and sweetlip in mangroves and emperors (Lethrinidae), parrotfish (Scaridae), and rabbitfish (Siganidae) in seagrass (Supporting Information).

As for bumphead parrotfish, seascape connectivity enhanced marine reserve effects on the abundance of 17 other fish species (Supporting Information). Seagrass-reef connectivity improved reserve effects on the abundance of 8 species (Supporting Information). Maori wrasse (*Cheilinus undulatus*) were always more abundant in reserves than fished locations with adjacent seagrass and reef (e.g., Fig. 2, Supporting Information). Paddletail snapper (*Lutjanus gibbus*), manyspotted sweetlip (*Plectorhinchus chaetodonoides*), lined sweetlip (*Prochilodus lineatus*), and bluebarred parrotfish (*Scarus ghobban*) were more abundant on reserve
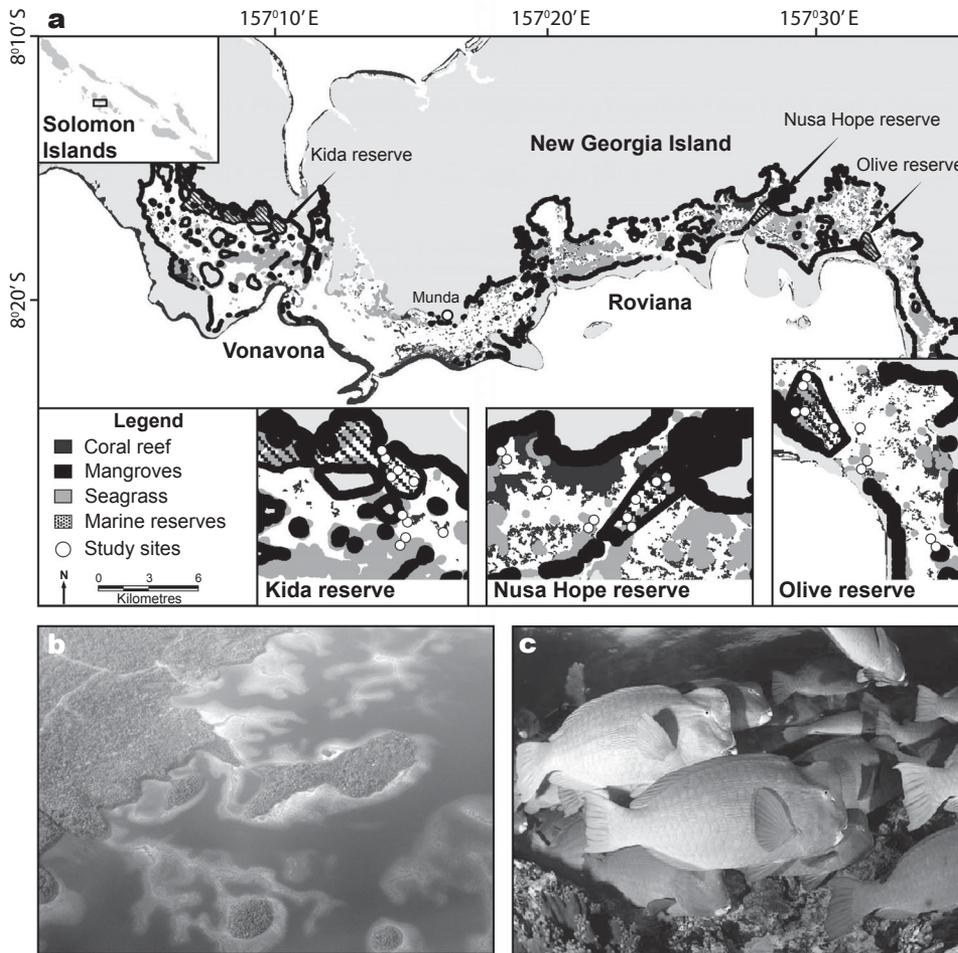
Figure 1. (a) Surveyed marine reserves and habitats in Roviana and Vonavona lagoons, Solomon Islands, (b) their diverse seascapes of coral reefs, seagrass, and mangroves (photo by A.D.O.), and (c) bumphead parrotfish (B. muricatum) (photo by A. Plummer).
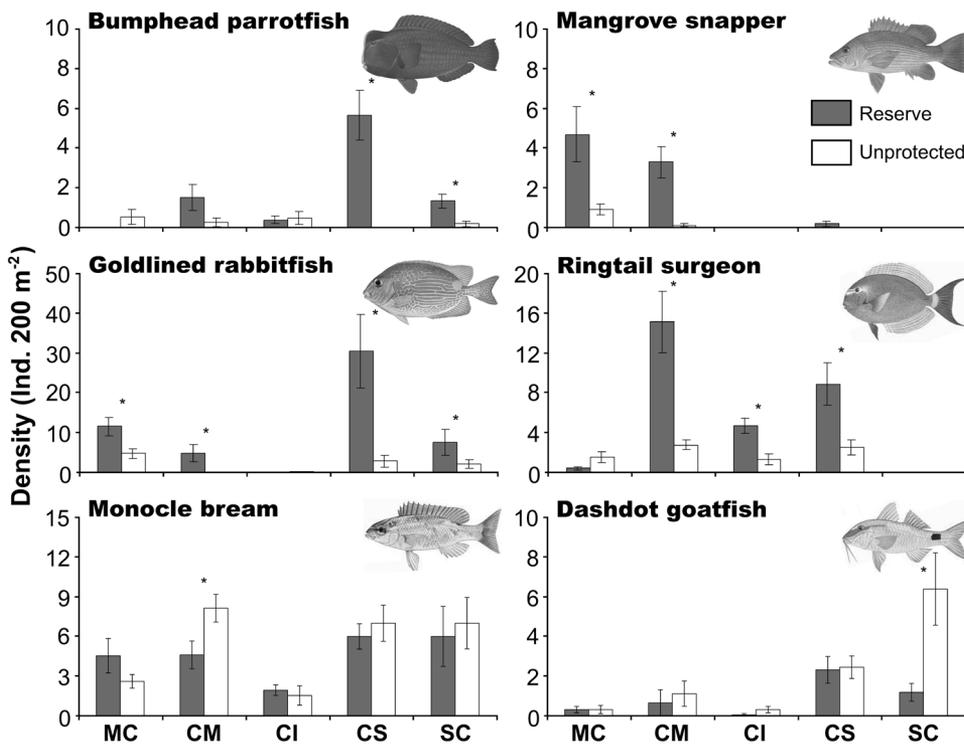

Figure 2. Densities of 6 fish species (mean and SE) across all reserve and unprotected mangrove, coral reef, and seagrass areas (MC, mangroves near coral; CM, coral near mangroves; CI, coral isolated; CS, coral near seagrass; SC, seagrass near coral; ∗, significant differences between reserve and unprotected locations). Bumphead parrotfish and goldlined rabbitfish illustrations copyright R.Swainston/anima.net.au (used with permission). All other fish illustrations sourced from www.efishalbum.com.
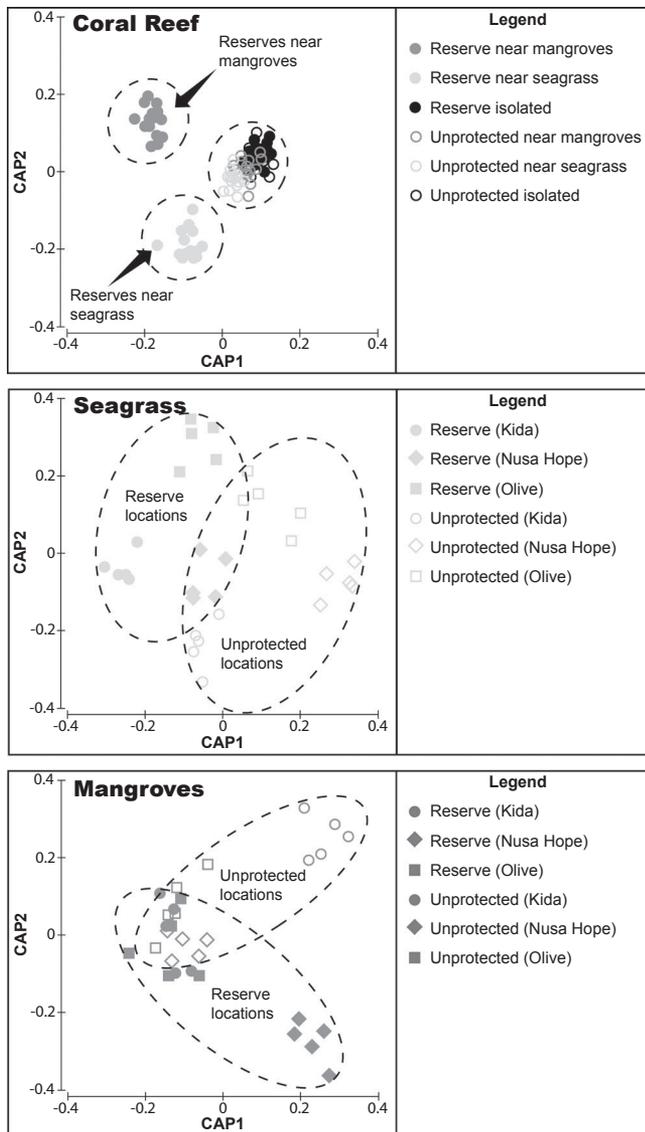
Figure 3. Constrained canonical analyses of principal coordinates (CAP) illustrating relationships among fish assemblages on reserve and unprotected coral reefs at each level of connectivity with mangroves and seagrass, in reserve and unprotected seagrass, and in reserve and unprotected mangroves. Ordinations based on modified Gower (log 2) dissimilarities. Dashed lines over ordinations delineate coherent groups (p < 0.05) defined by pairwise tests following permutational multivariate analysis of variance (PERMANOVA).

than fished reefs near seagrass (Supporting Information). Grass emperor (*Lethrinus laticaudis*) and whitespotted rabbitfish (*Siganus canaliculatus*) were also more abundant in reserve than fished seagrass near reef (Supporting Information).

Mangrove-reef connectivity increased reserve effects on the abundance of 6 species (Supporting Information). Redfin emperor (*Lethrinus erythropterus*), man-

grove snapper (*Lutjanus argentimaculatus*), blackspot snapper (*Lutjanus fulviflamma*), giant sweetlip (*Plectorhinchus albovittatus*), and brown sweetlip (*Plectorhinchus gibbosus*) were always more abundant in reserves than fished locations with adjacent mangroves and reef (e.g., Fig. 2, Supporting Information). Blacktail snapper (*Lutjanus fulvus*) were more abundant in reserve than fished mangroves near reef and on reserve reefs, regardless of their proximity to mangroves (Supporting Information).

Seascape connectivity between reefs and both seagrass and mangroves increased reserve effects on the abundance of 4 species (Supporting Information). Anchor tuskfish (*Choerodon anchorago*), thumbprint emperor (*Lethrinus harak*), barred rabbitfish (*Siganus doliatus*), and goldlined rabbitfish (*Siganus lineatus*) were more abundant in reserves than fished locations with adjacent seagrass and reef or adjacent mangroves and reef (e.g., Fig. 2, Supporting Information). In contrast, lined bristletooth (*Ctenochaetus striatus*) and white-ringed surgeonfish (*Acanthurus* spp.) were more abundant on reserve than fished reefs, regardless of their proximity to seagrass or mangroves (e.g., Fig. 2, Supporting Information).

Three species were more abundant in fished locations than reserves. This pattern held for monocle bream (*Scolopsis* spp.) on reefs near mangroves and dashdot goatfish (*Parapeneus barberinus*) and ornate emperor (*Lethrinus ornatus*) on seagrass near reefs (e.g., Fig. 2, Supporting Information).

Variation in Fish Size Among Coral Reef, Seagrass, and Mangroves

Fifteen of the species with abundances that were enhanced by the interaction between reserve and seascape connectivity effects were also larger on reefs than in adjacent seagrass or mangroves (Supporting Information). Six species were smaller in seagrass than adjacent reef (e.g., maori wrasse), 5 species were smaller in mangroves than adjacent reef (e.g., brown sweetlip), and 4 species were smallest in seagrass, larger in mangroves, and largest on adjacent reef (e.g., thumbprint emperor) (Fig. 4, Supporting Information). These size differences were independent of reserve effects.

Discussion

Conservation planning for Roviana and Vonavona lagoons focused on conserving bumphead parrotfish, protecting food security, and ecosystem functioning (Aswani & Hamilton 2004). We found that reserves designed for bumphead parrotfish conservation also effectively enhanced the abundance of other species. Our results showed that the incorporation of seascape connectivity improved the benefits of reserves for 17 other fish species. This finding indicates that bumphead
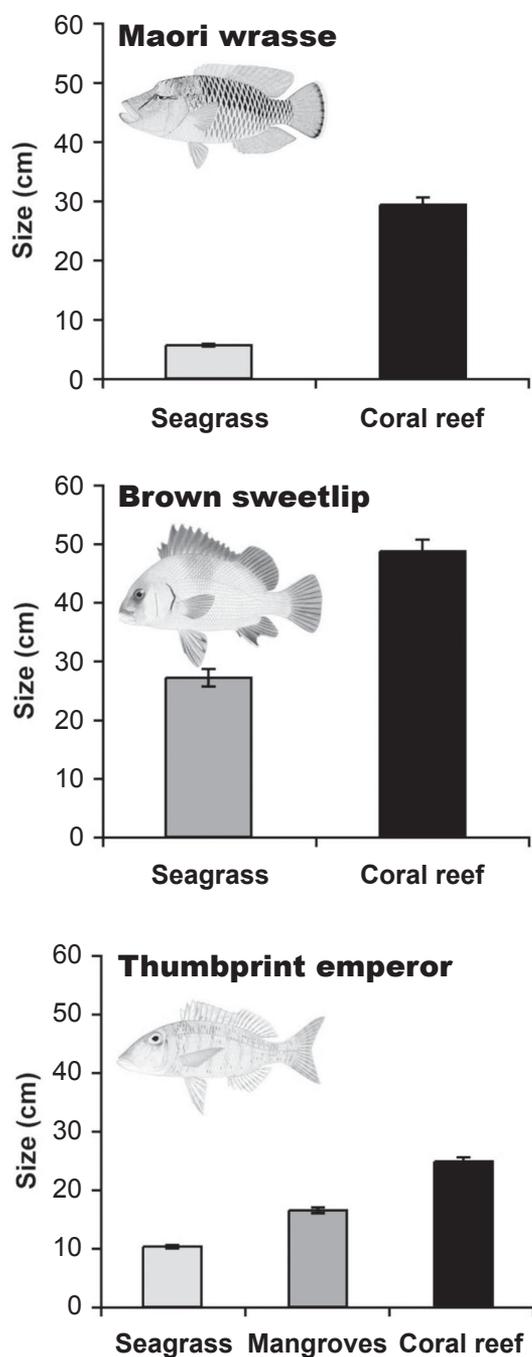
Figure 4. Size of 3 fish species (mean and SE) in mangrove, coral reef, and seagrass areas. Fish illustrations sourced from www.efishalbum.com.

parrotfish can be a valuable surrogate species for multispecies conservation. It also illustrates the role that local ecological knowledge can play in informing conservation planning decisions and underscores the importance of incorporating seascape connectivity in tropical marine conservation. Given the value of bumphead parrotfish as a flagship species (Aswani & Hamilton 2004) and potential keystone species (Bellwood et al. 2003), this finding suggests that programs directed at their conservation

may also help promote fish diversity, maintain ecosystem functioning, and garner support from local communities.

We focused on marine reserves in a lagoon system. Consequently, the local utility of bumphead parrotfish as a surrogate species likely relates to their habitat use through ontogeny rather than the requirements of adults. Adults have large home ranges (≥ 5 km) on offshore reefs and, therefore, are potentially best managed with alternative strategies to marine reserves (e.g., spearfishing bans and protection of aggregation sites) (Hamilton 2004), as were implemented in the study area (Aswani & Hamilton 2004). In contrast, ontogenetic migrations of juveniles and subadults encompass lagoon areas that are important to many other species. Indeed, juveniles were recorded in shallow mangrove and seagrass (particularly where interspersed with coral patches) and subadults were located on lagoonal reefs.

Due to the compressed and heterogeneous seascapes of the study area, ontogenetic migration between juvenile and adult habitats can occur over relatively small distances (i.e., 100–1000s of meters) and within the small (i.e., 1.5–5.5 km^2) locally managed marine reserves. Similar strategies for seascape conservation might, therefore, find success elsewhere in the Coral Triangle (where seascapes are equally diverse and compressed), but larger reserves would be necessary in locations that support wider lagoons (e.g., the Great Barrier Reef). Consequently, a surrogate-based approach to conservation planning would require the scaling of reserve size to match the habitat requirements of a species through ontogeny, which likely follows habitat diversity and connectivity in the underlying seascape. It might, therefore, be simpler to focus directly on prioritising seascape connectivity when designing marine reserves. Indeed, seascape connectivity metrics can be easily extracted from benthic habitat maps (where available) (Pittman et al. 2011) and readily incorporated into the conservation planning process (Beger et al. 2010b).

Seascape connectivity among seagrass, mangroves, and coral reefs in Roviana and Vonavona lagoons enhanced the ability of marine reserves to promote fish abundance. This finding corroborates the results of other studies showing that seascape connectivity can improve the potential of marine reserves to enhance fish populations (e.g., Olds et al. 2012a). It also supports the case for greater incorporation of spatial ecology into ecosystem-based management (Massol et al. 2011) and management of reefs and adjacent areas as functional seascapes (Adam et al. 2011; Olds et al. 2012b). We detected an effect of seascape connectivity on reserve performance at a similar scale (i.e., 100–1000s of meters) to that reported elsewhere in the western Pacific Ocean (Olds et al. 2013) and Caribbean Sea (Nagelkerken et al. 2012). This corresponds to the scale of tidal and diel feeding fish movements and some ontogenetic habitat shifts (e.g., Boström et al. 2011; Olds et al. 2012c) but is less than the scale of larval dispersal (i.e., 10s of kilometers) (e.g., Harrison

et al. 2012; Almany et al. 2013). Indeed, differences in fish size among habitats suggest that the importance of seascape connectivity may reflect ontogenetic migration (sensu Nagelkerken 2009), but it is also influenced by diel and tidal inter habitat movement.

Seascape connectivity between reefs and adjacent habitats is clearly important for the effectiveness of inshore reserves, but it was not beneficial for all species studied. Seascape connectivity-reserve effects did not influence the abundance of 118 species in this study. These species either do not migrate among habitats or are less likely to be targeted by local fishers. Broader inter reef connectivity (e.g., through larval dispersal or spawning migrations) and the conservation of isolated and offshore reefs may be more critical for such species (e.g., Beger et al. 2010*b*; Mellin et al. 2010; Harrison et al. 2012). We must strive, therefore, to better incorporate the range of connectivity types into marine conservation. There are of course many drawbacks to prioritizing connectivity in conservation, and its potential value must always be considered in light of these and other conservation targets (Beger et al. 2010*a*; Olds et al. 2013).

Seascape effects on reserve performance may be evident in the contrasting results of other studies in Roviana Lagoon, which detected strong reserve effects on parrotfish abundance (Aswani et al. 2007; Aswani & Sabetian 2010) and negligible effects on fish abundance at the family and functional group levels (Halpern et al. 2013) from the same reserve (Nusa Hope). These contrasting results may reflect variation in the ecology or fishing pressure on different species within particular families. When considered together with the findings of this study, however, they also suggest that due to the spatially heterogeneous influence of seascape connectivity on reserve performance, it can really matter how and where reserves are monitored to assess their effectiveness. For example, we examined reefs that were both close to and isolated from adjacent seagrass and mangroves and detected only strong reserve effects on reefs near adjacent habitat. If only isolated reefs were examined we may, therefore, have concluded that the reserves were not particularly effective. Consequently, the design and monitoring of similar conservation efforts must consider the context of habitats within the seascape.

This result has important implications for local villagers because the majority of these fish species are harvested extensively in subsistence fisheries and contribute the bulk of protein to the diet of local people (Brewer et al. 2009; Aswani & Sabetian 2010). However, our findings also raise important questions for local reserve managers and for marine spatial conservation more broadly. For example, can the boundaries of any underperforming local reserves be modified to better incorporate seascape connectivity, and can separate adjacent reserves that incorporate different habitats deliver the same overall outcome? There is certainly local interest in optimizing reserve de-

sign, and it would seem logical to modify reserve boundaries to better incorporate seascape connectivity, where possible. The potential for adjacent reserves, which support different habitats, to fulfill the same function, however, remains to be tested. Interestingly, ontogenetic migration takes fish from lagoon habitats to offshore reefs and, therefore, from existing reserves into adjacent fished waters. Consequently, the effectiveness of local reserves highlights the importance of establishing lagoon reserves to facilitate adult movement offshore and improve the potential for capturing juvenile recruitment into inshore nursery habitats (Nagelkerken 2009). Both functions will likely be enhanced where inshore reserves are established near oceanic passages in heterogeneous seascapes that incorporate reefs, seagrass, and mangroves.

Our findings show that seascape connectivity enhanced the abundance of bumphead parrotfish in marine reserves. By increasing the abundance of this potential keystone species, local reserves may also augment the key ecosystem functions of bioerosion and herbivory on coral reefs. We found that the incorporation of seascape connectivity and surrogate species ecology also improved the ability of reserves to promote the abundance of 17 other fish species. This finding has important implications for local villagers because most of these species provide the focus for local subsistence fisheries. Our results highlight the potential benefits of incorporating seascape connectivity and surrogate species in marine conservation. We suggest that by managing marine ecosystems to preserve functional seascape connections one might expect better success in maintaining fish communities and the functioning of ecosystems.

Acknowledgments

Supporting Information

Testing potential alternative explanations (Appendix S1), summary of fish home range studies (Appendix S2), reserve and connectivity effects on fish abundance (Appendix S3), reserve and connectivity effects on fish assemblages (Appendix S4), and effects of habitat on fish

size (Appendix S5) are available online. The authors are solely 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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