Contributed Paper

Effects of seascape connectivity on reserve performance along exposed coastlines

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Abstract: *Seascape connectivity (landscape connectivity in the sea) can modify reserve performance in low-energy marine ecosystems (e.g., coral reefs, mangroves, and seagrass), but it is not clear whether similar spatial linkages also shape reserve effectiveness on high-energy, exposed coastlines. We used the surf zones of ocean beaches in eastern Australia as a model system to test how seascape connectivity and reserve attributes combine to shape conservation outcomes. Spatial patterns in fish assemblages were measured using baited remote underwater video stations in 12 marine reserves and 15 fished beaches across 2000 km of exposed coastline. Reserve performance was shaped by both the characteristics of reserves and the spatial properties of the coastal seascapes in which reserves were embedded. Number of fish species and abundance of harvested fishes were highest in surf-zone reserves that encompassed >1.5 km of the surf zone; were located < 100 m to rocky headlands; and included pocket beaches in a heterogeneous seascape. Conservation outcomes for exposed coastlines may, therefore, be enhanced by prioritizing sufficiently large areas of seascapes that are strongly linked to abutting complementary habitats. Our findings have broader implications for coastal conservation planning. Empirical data to describe how the ecological features of high-energy shorelines influence conservation outcomes are lacking, and we suggest that seascape connectivity may have similar ecological effects on reserve performance on both sheltered and exposed coastlines.*

Keywords: conservation, fisheries, landscape ecology, marine reserves, ocean beaches, surf zones

Efectos de la Conectividad de Paisajes Marinos sobre el Desempeño de las Reservas a lo largo de Costas Expuestas

Resumen: *La conectividad entre paisajes marinos puede modificar el desempeño de las reservas en los ecosistemas marinos de baja energía (p. ej.: arrecifes de coral, manglares, pastos marinos), pero no está claro si las conexiones espaciales similares también moldean la efectividad de las reservas en costas expuestas con alta energía. Usamos las zonas de rompimiento de las playas oceánicas en el este de Australia como sistema modelo para probar cómo la conectividad entre paisajes marinos y los atributos de la reserva se combinan para moldear los resultados de la conservación. Los patrones espaciales en los ensamblados de peces se midieron con estaciones remotas de video subacuático con carnada en doce reservas marinas y 15 playas a lo largo de 2000 km de costas expuestas. El desempeño de las reservas estuvo moldeado por las características de las reservas y las propiedades espaciales de los paisajes costeros en los cuales estaban insertadas las reservas. El número de especies de peces y la abundancia de peces recolectados fue mucho mayor en las reservas en las zonas de rompimiento que abarcaban >1.5 km de la zona de rompimiento; estaban localizadas a <100 m de cabos rocosos; e incluían playas pequeñas entre los cabos en un paisaje marino heterogéneo. Los resultados de conservación para las costas expuestas pueden, por lo tanto, mejorarse con la priorización suficiente de grandes áreas de paisajes marinos que están conectados fuertemente con hábitats complementarios colindantes. Nuestros hallazgos tienen consecuencias más generales para la planeación de la conservación costera. Los datos empíricos para describir cómo las características ecológicas de las costas*

con alta energía influyen sobre los resultados de conservación son muy pocos, y sugerimos que la conectividad entre paisajes marinos puede tener efectos ecológicos similares sobre el desempeño de las reservas en costas expuestas y resguardadas.

Palabras Clave: conservación, ecología del paisaje, pesquerías, playas oceánicas, reservas marinas, zonas de rompimiento

摘要: 海洋景观连接度会影响低能量的海洋生态系统 (如珊瑚礁、红树林、海草生态系统) 保护区的保护成效, 但目前尚不清楚高能量、裸露海岸线的保护区成效是否也受到类似空间关联的影响。我们以澳大利亚东部海滩的碎波区为模型, 分析了海洋景观连接度和保护区特性如何共同决定保护成效。我们利用 2000 公里裸露海岸线沿线的 12 个海洋保护区和 15 个钓鱼海滩的诱饵式远程水下视频监控位点, 测定了鱼类群落的空间格局。保护区的特性及其所在海岸线景观的空间特性共同影响着保护区成效。在含有超过 1.5 公里碎波带、距离多岩石的海角不足 100 米, 或是在异质性景观中含有小海滩的碎波带保护区中, 鱼类物种数和渔获量最高。因此, 优先保护那些与毗邻的互补生境紧密相连, 且面积足够大的海洋景观, 可以提高裸露海岸线的保护成效。我们的研究结果对海岸带的保护规划有广泛的意义。目前, 描述高能量海岸线的生态学特性如何影响保护成效的数据仍十分缺乏, 我们提出, 海洋景观连接度对受保护和未受保护海岸线可能有相似的生态学影响并决定保护区的保护成效。【翻译: 胡怡思; 审校: 聂永刚 】

关键词: 保护, 渔业, 景观生态学, 海洋自然保护区, 海滩, 碎波带

Introduction

Conservation reserves have been implemented globally to restore biodiversity, enhance productivity, and promote the resilience of ecosystems to disturbance (Margules & Pressey 2000; Mellin et al. 2016). Positive conservation outcomes are frequently returned from reserves that are well enforced, have been implemented long enough for populations to recover from harvesting pressure, are larger than the home ranges of focal species, and have been placed in landscapes to optimize performance (Babcock et al. 2010; Edgar et al. 2014; Pressey et al. 2014). There are, however, trade-offs between the ecological benefits of reserves and their perceived socioeconomic costs, which can lead to protection of locations that deliver poor conservation benefits (Halpern et al. 2013; Barr et al. 2016). The likelihood of reserves protecting residual locations may be high in some marine systems, where combined pressures from coastal developers, fishing interests, and mining companies can restrict conservation opportunities to locations that are of limited economic value and low habitat diversity (Ban et al. 2013; Devillers et al. 2015; Gilby et al. 2017).

The performance of marine reserves is typically shaped by the attributes of the species (e.g., longevity and mobility) and ecosystems (e.g., condition and complexity) within their boundaries and the spatial properties of the seascapes in which they are located (Edgar et al. 2014; Olds et al. 2016; Young et al. 2018). Many marine animals move among ecosystems during their lives (e.g., to feed, reproduce, and disperse), and their movements link habitats across coastal seascapes, shape the diversity of animal populations, structure food webs, and modify ecosystem functioning (Bostrom et al. 2011; Hyndes et al. 2014; Olds et al. 2018*a*). These effects of seascape connectivity (i.e., spatial links between ecosystems) can also influence fisheries catches and alter the performance of conservation areas (Harrison et al. 2012; Nagelkerken et al. 2015; Pittman 2018). Positive effects of seascape connectivity on animal abundance, species diversity, and ecosystem functioning in reserves have been reported from the Atlantic, Indian, and Pacific Oceans (Olds et al. 2016), but these benefits of seascape connectivity for reserve performance have been examined only in low-energy ecosystems (e.g., coral reefs, mangrove forests, and seagrass meadows) (e.g., Berkström et al. 2012; Nagelkerken et al. 2012; Pittman et al. 2014). Ecosystems of exposed coastlines differ from low-energy seascapes and are typically characterized by greater wave energy and transient animal populations (Gillanders et al. 2003; Bostrom et al. 2011; Olds et al. 2018*b*). These features may limit the conservation benefits of seascape connectivity, but this hypothesis has not been tested on high-energy coastlines (Vargas-Fonseca et al. 2016). Thus, it is unclear how seascape connectivity should be integrated into conservation plans for exposed coastlines (Olds et al. 2016; McLachlan & Defeo 2017; Pittman 2018).

Ocean beaches and their surf zones dominate the world's exposed coastlines, they comprise approximately 70% of the global interface between land and sea, and are an ideal laboratory for examining how seascape connectivity shapes conservation outcomes on high-energy coastlines (Schlacher et al. 2015; McLachlan & Defeo 2017). These ecosystems are of immense economic and social value to humans as favored sites for development, tourism, and recreation (Defeo et al. 2009; Huijbers et al. 2015*b*). The surf zones of ocean beaches also support substantial commercial net fisheries and are prime locations for recreational angling because they provide important foraging, spawning, and nursery habitats for a diverse range of fishes (Olds et al. 2018*b*). Despite the ecological, social, and economic importance

of surf zones, ocean beaches are often underrepresented in marine reserve networks (Harris et al. 2015; Schlacher et al. 2015). Surf-zone reserves can deliver effective conservation outcomes for heavily harvested species (Bennett & Attwood 1991; Venter & Mann 2012), but their performance is rarely measured (Olds et al. 2018*b*). Empirical data on ecological features that influence reserve effectiveness are, therefore, needed to help improve conservation decisions for ocean beaches.

We used the surf zones of ocean beaches in eastern Australia as a model system to test whether and how conservation effectiveness is influenced by the characteristics (e.g., age and size) and spatial features (e.g., seascape connectivity and beach attributes) of individual reserves. Fishing pressure, seascape connectivity, and beach exposure affect the abundance and diversity of surf fishes along this coastline (Vargas-Fonseca et al. 2016; Borland et al. 2017). We predicted that these spatial properties of beach seascapes would also modify the effectiveness of reserves on exposed coastlines.

Methods

Study Seascape

We surveyed fish assemblages in the surf zones of 27 ocean beaches in southern Queensland and New South Wales, Australia, from June to October 2016. These beaches were distributed along 2000 km of coastline from Fraser Island in the north to Batemans Bay in the south and encompassed all marine reserves designed to conserve ocean beaches on the east coast of Australia (Fig. 1). Twelve beaches were protected in no-take marine reserves, and 15 were open to beach angling.

Our focal marine reserves were in 7 multiuse marine parks: Great Sandy (25^0S, 1 reserve), Moreton Bay (27^0S, 2 reserves), Cape Byron (29^0S, 2 reserves), Solitary Islands (30^0S, 2 reserves), Port Stephens (32^0S, 1 reserve), Jervis Bay (35^0S, 1 reserve), and Batemans Bay (36^0S, 2 reserves). The performance of reserves in these marine parks has been studied, and positive effects have been reported for fish assemblages from reefs (Olds et al. 2012; Coleman et al. 2015), estuaries (McKinley et al. 2011; Gilby et al. 2017), and soft-sediment ecosystems (Malcolm et al. 2016; Henderson et al. 2017). By contrast, the effectiveness of surf-zone reserves has not been tested, but it has been the subject of debate (Jordan & Creese 2015). This debate led to some reserves being opened to beach angling in 2013 and a reduction in the spatial coverage of reserves to <1% of the surf zone in Queensland and New South Wales marine parks (Brooks et al. 2013).

Our study reserves were protected and enforced as no-take zones at the time of survey, and the age (2–10 years), size (0.2–63.9 km^2), and length of surf zone protected (0.8–7.6 km) differed among reserves (Supporting Infor-

Figure 1. Location of reserve and fished study beaches and marine park regions along 2000 km of coastline in eastern Australia.

mation). The ecological attributes of beach seascapes (e.g., beach size, exposure, and seascape connectivity) also differed among reserves, but not between reserves and fished beaches (Supporting Information). The differences in the attributes of reserves made this region ideal

for testing how the spatial features of reserve seascapes shape conservation outcomes on exposed coastlines.

Fish Surveys

We surveyed fish with baited remote underwater video stations (BRUVS). The BRUVS had a camera (Hero 4, Go-Pro, San Mateo) mounted on a 5-kg weight and a bait bag secured 1 m in front of the camera on a PVC pipe (Borland et al. 2017). The bait was 500 g of pilchards (*Sardinops sagax*) (Wraith et al. 2013). We deployed 10 BRUVS in 200-m longshore intervals at each beach. Five units were placed in troughs within 50 m of the swash line (depth 1–2 m), and 5 units were placed on the first bar at the outer line of breakers (depth 2–4 m). This sampling design is used for surveys of assemblages of demersal and pelagic fishes across the entire surf zone (Vargas-Fonseca et al. 2016; Borland et al. 2017). Each BRUVS was deployed for 1 h (total video sampling time 10 h/beach, 270 h overall). Surf-fish assemblages can vary according to season, time of day, and tidal phase (Olds et al. 2018*b*), so we restricted sampling to the austral winter and conducted surveys during daylight hours at high tide (i.e., within 2 h of high tide) (Borland et al. 2017). Surf-fish assemblages are not affected by short-term temporal variation; hence, each beach was only surveyed once (Vargas-Fonseca et al. 2016). Fish abundance and species richness were recorded from video footage with the Max N statistic (i.e., maximum number of individuals of each species observed in 1 h of BRUVS deployment) (Murphy & Jenkins 2010; Gilby et al. 2017).

We classified fish as commonly harvested or of low recreational or commercial value (Borland et al. 2017). In Queensland and New South Wales, recreational anglers and commercial net fishers target fish from several families, including Australian salmon (Arripidae), trevally (Carangidae), mullet (Mugilidae), flathead (Platycephalidae), tailor (Pomatomidae), whiting (Sillaginidae), and surf bream (Sparidae) (Jordan & Creese 2015; Webley et al. 2015).

Classifying Reserve Characteristics and Beach Seascapes

Reserve characteristics (e.g., reserve age, size, and perimeter of reserves bordering surf beaches) were extracted from data published by the Queensland and New South Wales state governments (Gibbes et al. 2014; Jordan & Creese 2015; Martin et al. 2015). The size and perimeter of reserves bordering surf beaches were taken from benthic zoning plans for each marine park with ArcGIS (ESRI, Redlands, California, U.S.A.). Study beaches differed considerably in size, exposure, and level of seascape connectivity with other fish habitats (Vargas-Fonseca et al. 2016). The widths and lengths of individual beaches were measured to quantify variation in beach size and exposure with Google Earth (Harris et al. 2011;

Borland et al. 2017). The level of seascape connectivity between individual surf zones and adjacent habitats was measured in ArcGIS as the distance from each sampling site to the nearest rocky headlands and estuaries (Vargas-Fonseca et al. 2016).

Data Analyses

To test for effects of reserves on surf-fish assemblages, fish data were analyzed with 3-way permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). The factors were reserve status (fixed factor, 2 levels), marine park region (fixed factor, 7 levels), and habitat zone (fixed factor, 2 levels). Significant factors identified by PERMANOVA were displayed with nonmetric multidimensional scaling (nMDS) ordinations (Clarke et al. 2008). The PERMANOVA and nMDS analyses were based on modified Gower ($\log_2$) similarity measures that emphasize differences in the magnitude of variables, such as fish abundance, over differences in composition (Anderson et al. 2011). Dufrêne–Legendre indicator species analysis was used to identify species responsible for differences in assemblage composition between reserves and fished beaches; species are assigned higher indicator scores for treatments in which they are more common and abundant (Dufrêne & Legendre 1997). Vectors on nMDS ordinations display correlations for significant indicator species identified by Dufrêne–Legendre indicator-species analysis. We used generalized linear models to test for reserve effects on fish species richness and abundance of common harvested fish species. We used Tukey's honest significant difference post hoc tests to differentiate significant means and effect-size ratios to display differences in the magnitude of reserve effectiveness between individual reserves (Gilby & Stevens 2014).

To identify the attributes of reserves and beach seascapes that characterized effective marine reserves, environmental data were analyzed with similarity profile (SIMPROF) analysis, which tests for multivariate structure among samples with no a priori grouping (Clarke et al. 2008). Differences in reserve attributes and beach seascapes among reserves were displayed with nMDS. We tested for associations between reserve effectiveness and reserve and beach attributes (Gilby et al. 2017). Similarity matrices for environmental variables were calculated using normalized Euclidean distances. Distance-based linear models (DistLM) were used to quantify how reserve effects on fish were associated with spatial variation in reserve and beach attributes among individual reserves (McArdle & Anderson 2001). Analyses were conducted separately for reserves that supported more harvested fishes than fished beaches, reserves with fewer harvested fishes, and reserves that did not differ from fished beaches. Models were fitted using forward, stepwise, and best selection, and the strongest model was chosen based on corrected Akaike's information criterion (AICc).
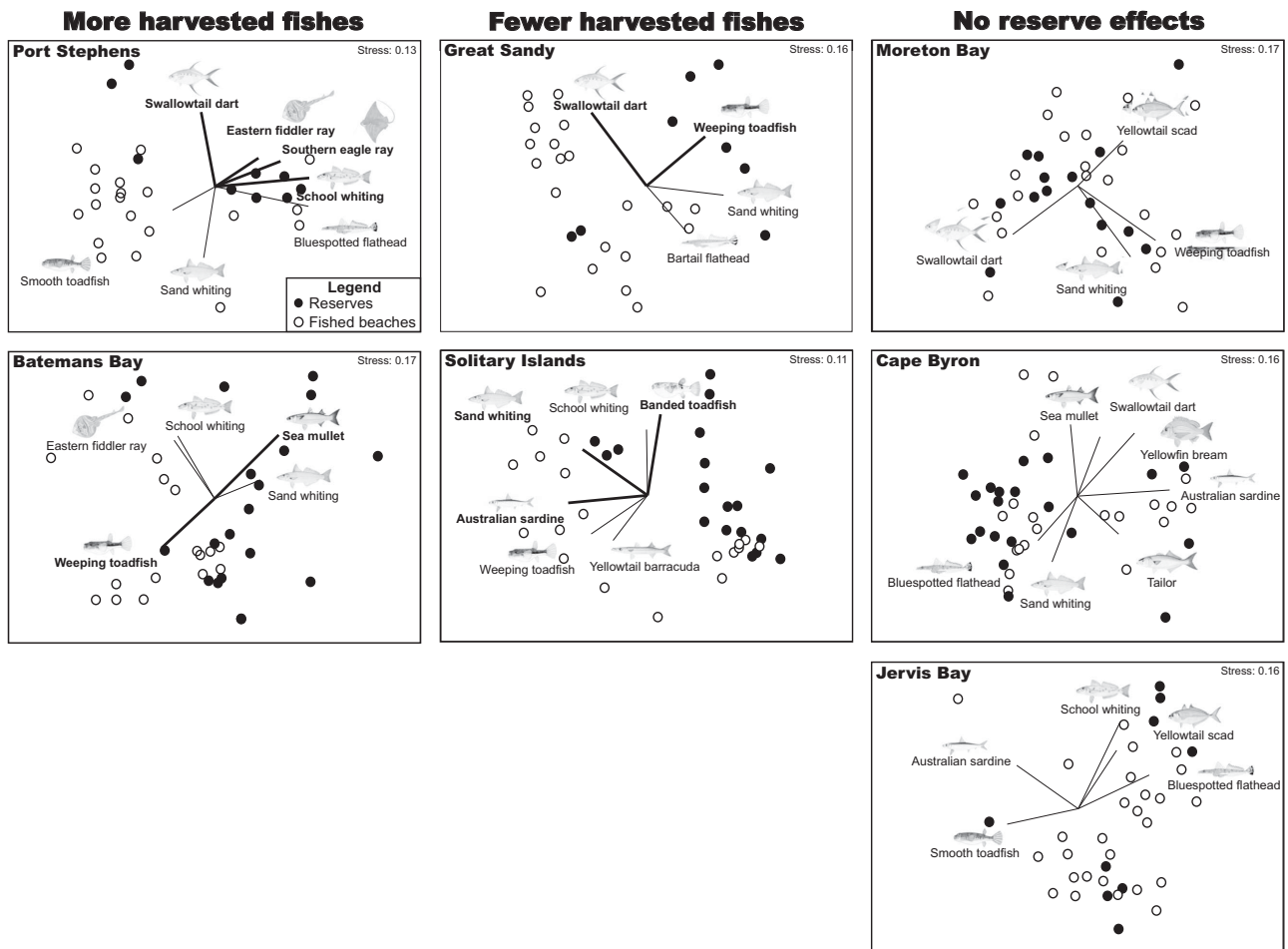
Figure 2. Differences, shown with nonmetric multidimensional scaling ordinations, in surf-fish assemblages between marine reserves and fished beaches. Marine parks grouped by reserve effects (more and fewer harvested fishes and no reserve effects). Vectors show species correlations with each ordination space, and significant indicator species are in bold (Supporting Information).

Results

Reserve Effectiveness

Reserve status significantly influenced the structure of fish assemblages in 4 of the 7 marine parks (Fig. 2 & Supporting Information). Fish assemblages differed between reserve and fished beaches in the Great Sandy, Solitary Islands, Port Stephens, and Batemans Bay regions, but not in the Moreton Bay, Cape Byron, or Jervis Bay regions (Fig. 2). Reserve effects were consistent across all surf-zone habitats (Supporting Information).

Marine reserves in Port Stephens and Batemans Bay supported more individuals of harvested species. Harvested species that were good indicators of reserves in Port Stephens (i.e., more abundant in these than in fished areas) included school whiting (*Sillago flindersi*), swallowtail dart (*Trachinotus coppingeri*), yellowtail barracuda (*Sphyraena obtusata*), eastern fiddler ray (*Trygonorrhina fasciata*), and southern eagle ray (*Myliobatis*

tenuicaudatus) (Fig. 2 & Supporting Information). No fish species were good indicators of fished beaches in Port Stephens. Sea mullet (*Mugil cephalus*), a fished species, was a good indicator of reserves in Batemans Bay, whereas weeping toadfish (*Torquigener pleurogramma*), a nonharvested species, was a good indicator of fished beaches (Fig. 2). Great Sandy and Solitary Islands reserves were dominated by species not harvested in surf fisheries. Weeping toadfish were good indicators of reserves in Great Sandy, whereas swallowtail dart, a harvested species, was a good indicator of fished beaches (Fig. 2). Similarly, banded toadfish (*Marilyna pleurosticta*) was a good indicator of reserves in the Solitary Islands, whereas harvested sand whiting (*Sillago ciliata*) and Australian sardines (*S. sagax*) were good indicators of fished beaches (Fig. 2). Fish assemblages of marine reserves in Moreton Bay, Cape Byron, and Jervis Bay did not differ from those of fished beaches (Fig. 2).
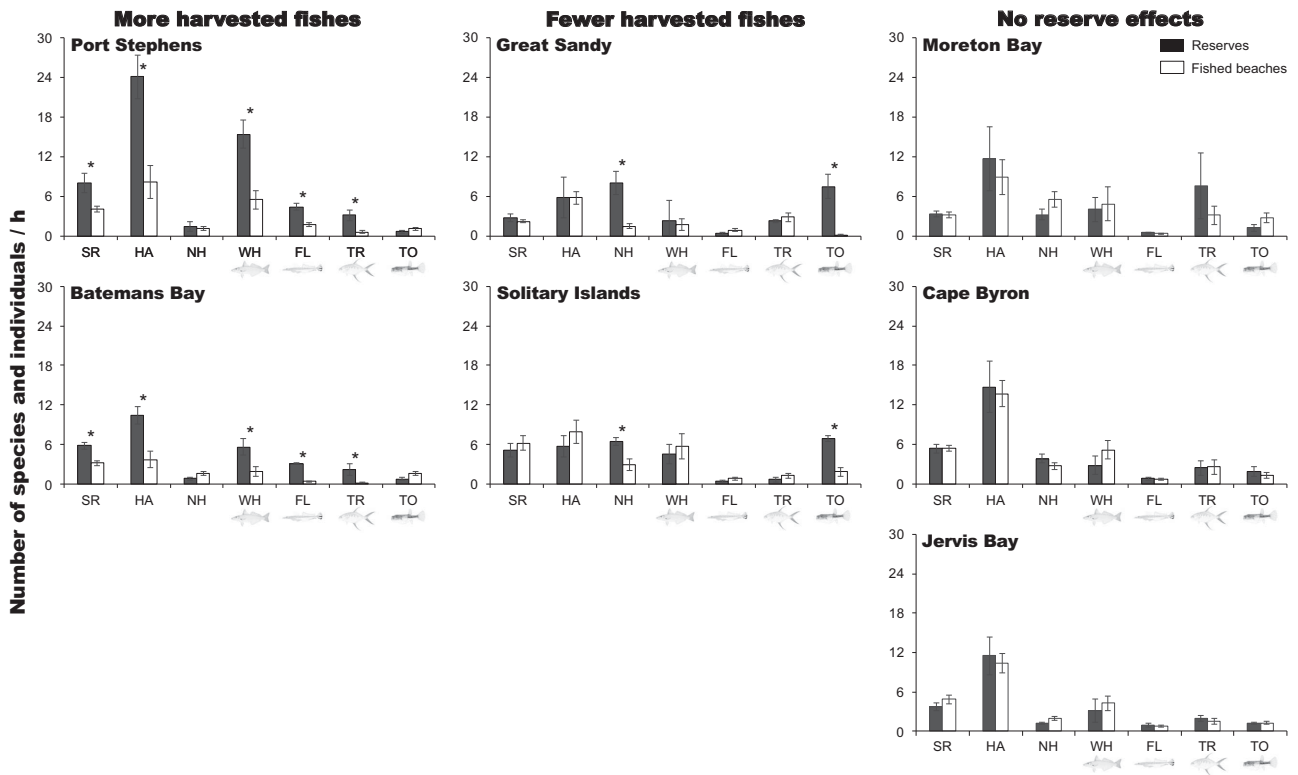
Figure 3. Mean (SE) number of species (SR) and number of individuals per hour of harvested fish (HA), nonharvested fish (NH), whiting (Sillaginidae) (WH), flathead (Platycephalidae) (FL), trevally (Carangidae) (TR), and toadfish (Tetraodontidae) (TO) in marine reserves and adjacent to fished beaches (, significant differences between reserve and unprotected locations based on Tukey's honest significant difference).*

Marine reserves in Port Stephens and Batemans Bay supported more fish species and a greater abundance of harvested fishes, particularly whiting, flathead, and trevally (Fig. 3 & Supporting Information). The effects of these reserves on harvested fishes were 2–3 times larger than for other reserves (Supporting Information). By contrast, Great Sandy and Solitary Islands reserves had the greatest influence on the abundance of nonharvested fishes, particularly toadfish (Fig. 3 & Supporting Information). The effect of these reserves on toadfish was up to 17 times larger than for other reserves (Supporting Information).

Effects of Reserve Attributes and Connectivity

Attributes of reserves that supported more fish species and a greater abundance of harvested fishes (i.e., Port Stephens and Batemans Bay) differed from those of other reserves (Fig. 4 & Supporting Information). They encompassed more surf zone (i.e., more of these reserves bordered beaches) and included short, narrow beaches close to rocky headlands (Fig. 4).

Several seascape attributes significantly influenced fish assemblages within reserves. In reserves with more harvested fishes, the length of the surf zone and the proximity of beaches to rocky headlands were significantly associated with fish assemblages (Table 1 & Fig. 4). By contrast, the proximity of beaches to estuaries was important for fish in reserves with fewer harvested fishes, whereas reserve area, beach width, and area of surf zone conserved were important for fish in reserves that did not differ from fished beaches (Table 1 & Fig. 4).

Discussion

Conservation outcomes on exposed ocean beaches were shaped by reserve characteristics and the spatial properties of the seascapes in which reserves were embedded. Effective marine reserves, which supported a greater abundance and diversity of harvested fishes, were larger (i.e., conserved over 1.5 km of beach frontage) and were well connected to adjacent fish habitats (i.e., were within 100 m of rocky headlands). These results are consistent with the conservation benefits of seascape connectivity in low-energy ecosystems (Olds et al. 2016; Young et al. 2018). For example, seascape connectivity (quantified at the scale of hundreds to thousands of meters) influences the effects of reserve on fish abundance, diversity,

Table 1. Reserve characteristics and seascape attributes correlated with reserve effectiveness in distance-based linear models.*

Reserve effectiveness and attributes	Pseudo F	p	Proportion of variance explained
More harvested fishes			
reserve bordering beach (km)	6.53	0.001	0.189
proximity to headland (km)	2.80	0.040	0.076
Fewer harvested fishes			
proximity to estuary (km)	2.25	0.042	0.074
No difference to fished beaches			
reserve area (km^2)	4.49	0.001	0.085
beach width (m)	4.06	0.003	0.070
reserve bordering beach (km)	2.91	0.008	0.053

Models fitted using forward, stepwise, and best selection and evaluated using Akaike's information criterion (Supporting Information).
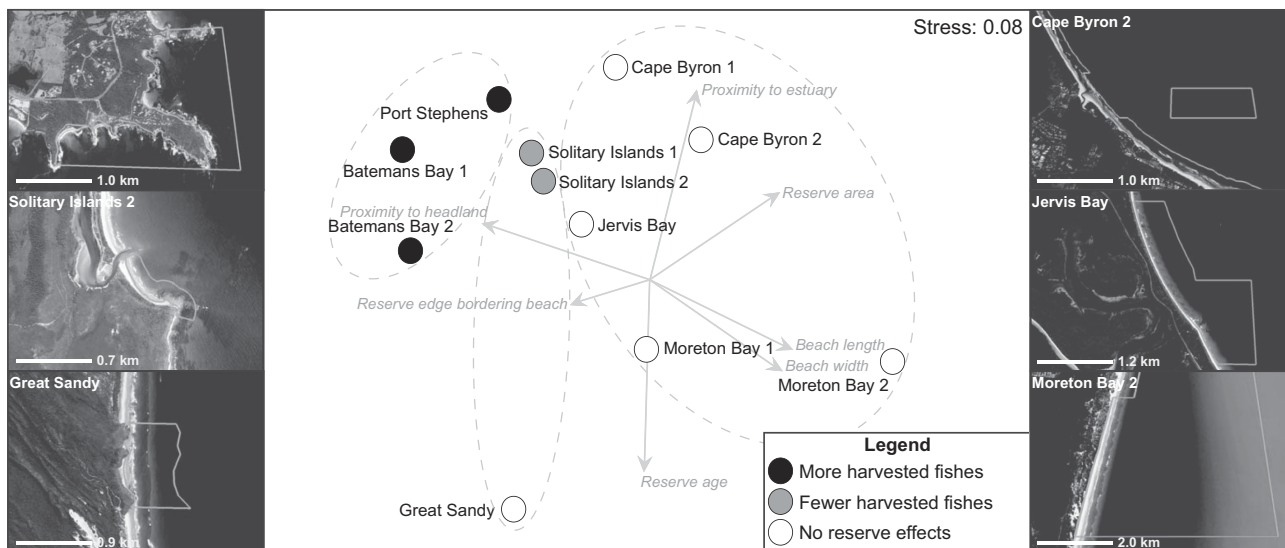
Figure 4. Nonmetric multidimensional scaling ordination showing differences in the attributes of reserves with more and fewer harvested fishes and with no difference to fished beaches (dashed lines, significant groups; vectors, correlations between attributes and the ordination space). For example, reserves with more harvested fishes were closer to headlands and had a larger perimeter bordering surf beaches (Supporting Information). Photos illustrate the reserve and seascape attributes of selected conservation areas.

and ecological function in seagrass meadows (Valentine et al. 2008; Henderson et al. 2017), mangrove forests (Olds et al. 2013; Martin et al. 2015), and coral reefs (Huntington et al. 2010; Nagelkerken et al. 2012) in the Caribbean Sea, Florida Keys, and western Pacific Ocean. Thus, the benefits of seascape connectivity for conservation are geographically widespread (Olds et al. 2016) and affect comparable components of fish assemblages (e.g., diversity and abundance of harvested fishes) over similar spatial scales in both high-energy exposed coastlines and low-energy seascapes.

Exposed coastlines are often underrepresented in conservation because of economic and social pressures and the absence of empirical data linking the ecological features of ocean beaches and rocky shores to reserve performance (Banks & Skilleter 2007; Harris et al. 2015). Variations in exposure, wave energy, and microhabitat

complexity have been used as surrogates for animal diversity and abundance in conservation plans for exposed coastlines (Blamey & Branch 2009; Meager & Schlacher 2013; McLachlan & Defeo 2017). These metrics have improved conservation decisions, but do not represent ocean beaches and rocky shores as highly connected habitat patches in high-energy seascapes (Hyndes et al. 2014; Vargas-Fonseca et al. 2016). We showed how spatial linkages with prominent rocky headlands can shape conservation performance on adjacent ocean beaches, and this extends the options for conservation prioritization on exposed coastlines from habitat to seascape-scale metrics. Reserves that encompassed a large area of surf zone and conserved narrow beaches close to rocky headlands were most successful at promoting diversity and abundance of harvested fishes. These spatial features of ocean beaches may affect reserve

performance because they affect habitat heterogeneity, food availability, and biomass accumulation. Headlands are prominent features of exposed coastlines, and many fish move between surf zones and rocky headlands to feed, shelter, and reproduce (Vargas-Fonseca et al. 2016). Surf-zone food webs are also linked to rocky headlands via translocated algae, which are washed onto beaches and provide food for fishes and invertebrates (Crawley et al. 2009). Finally, headlands are major barriers to fish migration along exposed coastlines and can accumulate a large biomass and diversity of fishes (Lenanton et al. 1996). The high abundance and diversity of harvested fishes inside effective reserves likely result from a combination of these spatial effects on exposed coastlines (Vargas-Fonseca et al. 2016; McLachlan & Defeo 2017; Olds et al. 2018*b*).

The effects of marine reserves on harvested fishes reflect the distribution of whiting, flathead, trevally, barracuda, and mullet, which were up to 3 times more abundant in effective reserves. These fish species are harvested regularly from surf zones by recreational anglers and commercial net fisheries (Jordan & Creese 2015; Borland et al. 2017). Most have small home ranges, but some can roam widely along exposed coastlines to feed or spawn (e.g., trevally and mullet) (Hyndes et al. 1996; Whitfield et al. 2012; Vargas-Fonseca et al. 2016). Thus, our findings concur with the results of 2 previous studies that examined reserve performance on ocean beaches (Bennett & Attwood 1991; Venter & Mann 2012) and show that surf-zone reserves provide effective conservation for harvested fish species with small home ranges.

Not all reserves were effective; some promoted the abundance of species that have no fisheries value. Toadfishes, which have small home ranges and are not targeted in surf fisheries (Piah & Bucher 2014; Vargas-Fonseca et al. 2016), were up to 17 times more abundant in some reserves. Reserves dominated by toadfishes conserved only a small area of surf zones in the center of long beaches. These reserves may not provide effective conservation for harvested fishes due to their small size or isolation from other coastal habitats. Fish can move readily across the boundaries of small reserves and into adjacent waters, where they are frequently the target of heavy fishing pressure (Lester et al. 2009; Huijbers et al. 2015*a*). Reserves in the center of long beaches are also isolated from other coastal habitats, limiting both habitat heterogeneity and available feeding opportunities (Vargas-Fonseca et al. 2016; Olds et al. 2018*b*). These reserves may, therefore, have been established in residual locations, possibly in response to heavy lobbying from fishers (Brooks et al. 2013; Jordan & Creese 2015). Nevertheless, we found that the fish assemblages of exposed coastlines could be shaped by the complementary effects of different seascape attributes. To conserve the full diversity of fishes, and other organisms, in the surf zones of ocean beaches it will, therefore, be important to adequately represent underlying heterogeneity in the attributes of coastal seascapes, including linkages with headlands and estuaries.

We surveyed all marine reserves that conserve ocean beaches on the east coast of Australia, but this included only 12 surf zones closed to fishing. The number of surf-zone reserves was therefore limited, as was the size of reserves and the seascapes in which these were located. Reserves protected fish in the surf zones of 12 ocean beaches, but encompassed only 33 km of beachfront (i.e., <1% of beaches) across 7 marine parks. These attributes of reserves constrained our experimental design by restricting sampling to only a single beach in each reserve and a maximum of 2 reserves in each marine park and may have limited our capacity to detect effects of some reserve and seascape attributes on conservation performance. Given that the fish assemblages of surf zones can be characterized by high variability (McLachlan & Defeo 2017; Olds et al. 2018*b*), it would have been beneficial to sample fish from multiple beaches inside each reserve, multiple reserves in each marine park, and multiple fished beaches to serve as controls for both reserve and marine park effects. This type of nested, and spatially balanced, experimental design would have significantly improved the power of our analyses and the generality of our results (Beck 1997; Underwood 1997). Furthermore, this approach would have enabled us to examine how a wider variety of seascape attributes combine to influence reserve performance (Olds et al. 2016; Pittman 2018) and is therefore recommended for future research when permitted by the design constraints of marine-reserve networks.

We determined, for the first time, how seascape connectivity and reserve attributes combine to shape conservation performance on exposed coastlines. The importance of seascape connectivity for conservation is widely appreciated, and we demonstrated that spatial linkages between exposed surf zones and rocky headlands modify conservation outcomes over similar scales (i.e., hundreds of meters) to the reported benefits of seascape connectivity on sheltered coastlines. We found that effective surf-zone reserves conserve small pocket beaches that are close to adjacent rocky headlands (i.e., < 100 m) and encompass a relatively large area of the surf zone (i.e., >1.5 km of beach frontage), which fringes both ocean beaches and rocky headlands. This is a significant contribution to coastal conservation planning, which is limited by the absence of empirical data that links ecological features of seascapes with reserve effectiveness. We suggest that conservation performance for coastal seascapes will be improved by optimizing reserve design to incorporate ocean beaches and their surf zones and by improving integration of spatial linkages between prominent features of exposed coastlines.

Acknowledgments

Supporting Information

Differences in the characteristics of focal reserves and the ecological attributes of ocean beaches (Appendix S1), effects of marine park region and reserve status on fish assemblages (Appendix S2), effects of marine reserves on fish abundance and species richness (Appendix S3), and differences in characteristics and ecological attributes of reserves types (Appendix S4) 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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