Effects of seascape connectivity on reserve performance along exposed coastlines

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Abstract: The spatial properties of landscapes influence numerous ecological attributes on land and in the sea, including the efficacy of conservation areas. In this context, seascape connectivity (landscape connectivity in the sea) has been shown to modify reserve performance in low-energy marine ecosystems (e.g. coral reefs, mangroves, 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 in 12 marine reserves and 15 fished beaches, across two thousand kilometers of exposed coastline, using baited remote underwater video stations. Reserve performance was shaped by both the characteristics of reserves, and the spatial properties of the coastal seascapes in which reserves were embedded. More fish species and a greater abundance of harvested fishes were recorded in surf-zone reserves that had three key attributes: i) they encompassed a sizeable area of surf-zone habitat (> 1.5km of coastline); ii) were located close (< 100m) to rocky headlands; and iii) included pocket beaches in a heterogeneous seascape. Conservation outcomes for exposed coastlines might, therefore, be enhanced by prioritizing sufficiently large areas of seascapes, with strong linkages to abutting complementary habitats. Our findings have broader implications for coastal conservation planning, which is limited by the absence of empirical data to describe how the ecological features of high-energy shorelines influence conservation outcomes, and we suggest that seascape connectivity might have similar ecological effects on reserve performance on both sheltered and exposed coastlines.

Introduction

Conservation initiatives, such as national parks and marine 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 conservation species, and have been strategically placed in landscapes to optimize performance (Edgar et al. 2014; Pressey et al. 2014). There are, however, trade-offs between the ecological benefits of reserves and their perceived socio-economic 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 might be high in some marine systems, including estuaries, ocean beaches, the open ocean and deep sea, 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; Althaus et al. 2017; Gilby et al. 2017).

The performance of marine reserves is typically shaped by the attributes of the species (e.g. longevity, mobility) and ecosystems (e.g. condition, 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 (i.e. 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; Kool et al. 2013; Hyndes et al. 2014; Olds et al. 2018a). These effects of seascape connectivity (i.e. landscape connectivity in the sea) 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 (reviewed by Olds et al. 2016), but these benefits of seascape connectivity for reserve performance have only been examined...
in low-energy ecosystems (e.g. coral reefs, mangrove forests, seagrass meadows) (e.g. Berkström et al. 2012; Nagelkerken et al. 2012; Pittman et al. 2014; Henderson et al. 2017). Exposed coastlines support different ecosystems to low-energy seascapes, and are typically characterized by greater wave energy and transient animal populations (Gillanders et al. 2003; Bostrom et al. 2011; Hyndes et al. 2014; Olds et al. 2018b). These features might 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 not clear 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 coastal development, tourism, and recreation (Defeo et al. 2009; Huijbers et al. 2015b). The surf-zones of ocean beaches also support significant 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 (reviewed by Olds et al. 2018b). Despite the ecological, social and economic importance of surf zones, ocean beaches are often under-represented in marine reserve networks (Harris et al. 2015; Schlacher et al. 2015). Surf zone reserves can deliver effective conservation outcomes for heavily harvested fish species (Bennett & Attwood 1991; Venter & Mann 2012), but their performance is rarely measured (Olds et al. 2018b). Empirical data on ecological features that modify reserve effectiveness are, therefore, needed to help improve conservation decisions for ocean beaches.
This study used the surf zones of ocean beaches in eastern Australia as a model system to test whether, and how, conservation effectiveness is modified by the characteristics of individual reserves (e.g. age, size), and the spatial features of the seascapes (e.g. seascape connectivity, beach attributes) in which reserves are located. Beaches in this region experience high fishing pressure from recreational anglers, which regularly remove large numbers of fish from the surf (Jordan & Creese 2015; Webley et al. 2015). Seascape connectivity (i.e. spatial links between surf zones, estuaries and rocky headlands) and beach exposure also modify the abundance and diversity of surf fishes along this coastline (Vargas-Fonseca et al. 2016). These spatial properties of beach seascapes were, therefore, predicted to 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, between June and October 2016. These beaches were distributed along 2,000 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 fifteen were open to beach angling.
Our focal marine reserves were in seven multi-use marine parks: 1) Great Sandy at 25°S (1 reserve; Martin et al. 2015b); 2) Moreton Bay at 27°S (2 reserves; Gibbes et al. 2014); 3) Cape Byron at 29°S (2 reserves; Kelaher et al. 2015); 4) Solitary Islands at 30°S (2 reserves; Malcolm et al. 2016); 5) Port Stephens at 32°S (1 reserve; Martin et al. 2015a); 6) Jervis Bay at 35°S (1 reserve; Ferguson et al. 2016); and 7) Batemans Bay at 36°S (2 reserves; McKinley et al. 2011). Numerous studies have examined the performance of reserves in these marine parks, and positive effects of conservation have been reported on 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 led to some reserves being opened to beach angling in 2013, and a reduction in the spatial coverage of reserves to < 1% of surf zone habitat in Queensland and New South Wales Marine Parks (Brooks et al. 2013).

All reserves were protected, and enforced, as no-take zones at the time of survey, but there was considerable variation in the age (2–10 years) and size (0.2–63.9 km²) of reserves, and the length of surf zone protected (0.8–7.6 km) (Appendix S1, Supporting Information). The ecological attributes of beach seascapes (e.g. beach size, exposure, seascape connectivity) also differed among reserves, but not between reserves and fished beaches (Appendix S1). These differences in the attributes of reserves make this region ideal for testing how the spatial features of reserves, and reserve seascapes, shape conservation performance for surf fishes.
**Fish surveys**

Fish were surveyed with Baited Remote Underwater Video Stations (BRUVS). BRUVS consisted of a GoPro camera (Hero 4) mounted on a 5 kg weight, with a bait bag secured 1 m in front of the camera on a PVC pipe (Borland et al. 2017). BRUVS were baited with 500 g of pilchards (*Sardinops sagax*) (Wraith et al. 2013). We deployed ten BRUVS in 200 m longshore intervals at each beach; 5 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 has been shown to represent assemblages of both demersal and pelagic fish species across the entire surf zone (Vargas-Fonseca et al. 2016; Borland et al. 2017). Each BRUVS deployment sampled fish for 1 h, giving a total video sampling time of 10 h per beach and 270 h overall for the study. Surf fish assemblages can vary according to season, time of day, and tidal phase (Olds et al. 2018b); to standardize for these temporal effects, we restricted sampling to the austral winter, and conducted surveys during daylight hours at high tide (i.e. within 2h of high tide) (Borland et al. 2017). Previous surveys have shown that 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 using the Max N statistic, which is the maximum number of individuals of each species observed in one hour of BRUVS deployment (Murphy & Jenkins 2010; Gilby et al. 2017).
Fish were classified as being commonly harvested or being of low recreational or commercial value (Borland et al. 2017). In Queensland and New South Wales, surf fishes are harvested by recreational anglers and commercial net fishers targeting several families: 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, 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. 2015b). The size and perimeter of reserves bordering surf beaches was measured from benthic zoning plans for each marine park using ArcGIS (ESRI, Redlands, CA, USA). Study beaches differed considerably in beach size, exposure, and the 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, using 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 analysis

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 with 2 levels), marine park region (fixed factor with 7 levels) and habitat zone (fixed factor with 2 levels). Significant factors identified by PERMANOVA were displayed with non-metric multidimensional scaling (nMDS) ordinations (Clarke et al. 2008). PERMANOVA and nMDS analyses were based on Modified Gower (Log2) similarity measures, which 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. Generalized Linear Models (GLMs) were then used to test for reserve effects on fish species richness and the abundance of common harvested fish families. Tukey’s HSD post hoc tests were used to differentiate significant means, and effect-size ratios were used 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 between...
reserves with: (1) more harvested fishes; (2) fewer harvested fishes; and (3) assemblages that did not differ from fished beaches were displayed with nMDS. We tested for associations between reserve effectiveness and both reserve and beach attributes (Gilby et al. 2017). Similarity matrices for environmental variables were calculated using normalized Euclidean distances. Finally, 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 with: (1) more harvested fishes; (2) fewer harvested fishes; and (3) no difference to fished beaches. Models were fitted using forward, stepwise and BEST selection, and the strongest model was chosen using corrected Akaike’s information criterion (AICc).

Results

Reserve effectiveness

Reserve status significantly influenced the structure of fish assemblages in four of the seven marine parks (Fig. 2, Appendix S2). 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 (Appendix S2).

Marine reserves in the Port Stephens and Batemans Bay regions supported more individuals of numerous 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, Appendix S3). No fish species were good indicators of fished beaches in Port Stephens. Similarly, sea mullet (*Mugil cephalus*), a fished species, was a good indicator of reserves in Batemans Bay, whereas weeping toadfish (*Torquigener pleurogramma*), a species not harvested, was a good indicator of fished beaches (Fig. 2).

Marine reserves in the Great Sandy and Solitary Islands regions were numerically dominated by species that are 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 two harvested species, sand whiting (*Sillago ciliata*) and Australian sardines (*Sardinops sagax*), were good indicators of fished beaches (Fig. 2). The fish assemblages of marine reserves in the Moreton Bay, Cape Byron and Jervis Bay regions did not differ from those of fished beaches (Fig. 2).

Marine reserves in the Port Stephens and Batemans Bay regions supported more fish species and a greater abundance of harvested fishes, particularly whiting (Sillaginidae), flathead (Platycephalidae), and trevally (Carangidae) (Fig. 3, Appendix S3). The effects of these reserves on harvested fishes were between two and three times larger than for other reserves (Appendix S3). By contrast, reserves in the Great Sandy and Solitary Islands regions had the greatest influence on the abundance of non-harvested fishes, particularly toadfish (Tetraodontidae) (Fig. 3, Appendix S3). The effect of these reserves on toadfish were up to 17 times larger than for other reserves (Appendix S3).

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Effects of reserve attributes and seascape connectivity on conservation performance

Reserves that supported more fish species and a greater abundance of harvested fishes (i.e. Port Stephens and Batemans Bay) were characterized by different attributes to other reserves (Fig. 4, Appendix S4). They encompassed a larger area of surf zone habitat (i.e. more of these reserves bordered beaches), and included short, narrow, pocket beaches that were close to rocky headlands (Fig. 4).

Several seascape attributes significantly influenced fish assemblages within reserves. In reserves with more harvested fishes, the length of surf zone habitat and the proximity of beaches to nearby rocky headlands were features 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 the area of surf zone habitat conserved were important for fish in reserves that did not differ from fished beaches (Table 1, Fig. 4).

Discussion

The performance of conservation areas depends on the characteristics of individual reserves, and the spatial properties of the landscapes, and seascapes, they conserve (Edgar et al. 2014; Pressey et al. 2014). Reserve effectiveness is positively correlated with

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reserve size and age, and is also shaped by the level of seascape connectivity among coastal ecosystems (Lester et al. 2009; Babcock et al. 2010; Huijbers et al. 2015a). Positive effects of seascape connectivity have been reported widely from reserves in low-energy seasapes, but until now have not been tested on high-energy exposed coastlines (reviewed by Olds et al. 2016; Pittman 2018). Our findings show that conservation outcomes on exposed ocean beaches are also shaped by both the characteristics of reserves, and the spatial properties of the seasapes in which they are 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 concur with the conclusions of other research on the conservation benefits of seascape connectivity in low-energy ecosystems (Olds et al. 2016; Young et al. 2018). For example, seascape connectivity (quantified as habitat isolation at the scale of 100s -1000s m) influences the magnitude of reserve effects on fish abundance, diversity and ecological functions in seagrass meadows (Valentine et al. 2008; Henderson et al. 2017), mangrove forests (Olds et al. 2013; Martin et al. 2015b) 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 seasapes.

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). Variation 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; Defeo & McLachlan 2013; Meager & Schlacher 2013; Borland et al. 2017). These metrics have helped to improve 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 et al. 2016). In this study, we show 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 habitat, and conserved narrow pocket beaches close to rocky headlands, were most successful at promoting the diversity and abundance of harvested fishes. There are three mechanisms through which these spatial features of ocean beaches might affect reserve performance: (1) habitat heterogeneity; (2) food availability; and (3) 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 is washed into beaches to provide food for fishes and invertebrates (Crawley et al. 2009). Finally, headlands are major barriers to fish migrating 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 results from a combination of these spatial effects on exposed coastlines (Vargas-Fonseca et al. 2016; McLachlan & Defeo 2017; Olds et al. 2018b).

The effects of marine reserves on harvested fishes reflect the distribution of whiting, flathead, trevally, barracuda and mullet, which were up to three 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, these findings concur with the results of the two 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, however, and 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 that were dominated by toadfishes, and not a high abundance or diversity of harvested fishes, conserved only a small area of surf-zone habitat in the center of long beaches. These reserves might not provide effective conservation for harvested fishes due to their small size, or because they are isolated 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. 2015a). Reserves in the center of long beaches are also isolated from other coastal habitats, limiting both habitat heterogeneity and the feeding opportunities that are available for fishes in these seascapes (Vargas-Fonseca et al. 2016; Olds et al. 2018b). These reserves might, therefore, have been established in residual locations, possibly in response to heavy lobbying from fishers (Brooks et al. 2013; Jordan & Creese 2015). Nevertheless, our results show that the fish assemblages of exposed coastlines can 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 both headlands and estuaries.

We surveyed all marine reserves that conserve ocean beaches on the east coast of Australia, but this included only twelve surf zones that were 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 twelve ocean beaches, but encompassed only 33 km of beachfront (i.e. <1% of this habitat) across seven 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 two reserves in each marine park, and might 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. 2018b), it would have been beneficial to sample fish from multiple beaches inside each reserve, multiple reserves in each marine park, and from 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 by better characterizing the potential confounding impacts of spatial heterogeneity on surf fish assemblages (Beck 1997; Underwood 1997). Furthermore, this approach would have enabled us to test 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.
This study shows, 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 demonstrate that spatial linkages between exposed surf zones and rocky headlands modify conservation outcomes over similar scales (i.e. 100 s of metres) to the reported benefits of seascape connectivity on sheltered coastlines. We find 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 surf-zone habitat (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 better integrate spatial linkages between prominent features of exposed coastlines.

Acknowledgments

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Literature Cited


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Jordan A, Creese R 2015. Ecological background to the assessment of shore-based recreational fishing on ocean beaches and rocky headlands in sanctuary zones in mainland NSW marine parks. NSW Department of Primary Industries, Nelson Bay, Australia.


Lenanton RCJ, Ayvazian SG, Pearce AF, Steckis RA, Young GC. 1996. Tailor (Pomatomus saltatrix) off Western Australia: where does it spawn and how are the larvae distributed? Marine and Freshwater Research 47:337-346.


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Whitfield AK, Panfilii J, Durand JD. 2012. A global review of the cosmopolitan flathead mullet Mugil cephalus Linnaeus 1758 (Teleostei: Mugilidae), with emphasis on the biology, genetics, ecology and fisheries aspects of this apparent species complex. Reviews in Fish Biology and Fisheries 22:641-681.


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Table 1 Results of distance-based linear models (DISTLM) relating the environmental and conservation attributes of reserves with: (1) more harvested fishes; (2) fewer harvested fishes; and (3) no difference to fished beaches, with the composition of fish assemblages. Models fitted using forward, stepwise and BEST selection and evaluated using Akaike’s information criterion (see Table S8).

<table>
<thead>
<tr>
<th>Reserve effectiveness</th>
<th>Pseudo-$F$</th>
<th>$P$</th>
<th>Prop. of variance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>More harvested fishes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reserve bordering beach (km)</td>
<td>6.53</td>
<td>0.001</td>
<td>0.189</td>
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<tr>
<td>Proximity to headland (km)</td>
<td>2.80</td>
<td>0.040</td>
<td>0.076</td>
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<tr>
<td><strong>Fewer harvested fishes</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Proximity to estuary (km)</td>
<td>2.25</td>
<td>0.042</td>
<td>0.074</td>
</tr>
<tr>
<td><strong>No reserve effects</strong></td>
<td></td>
<td></td>
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<tr>
<td>Reserve area $(\text{km}^2)$</td>
<td>4.49</td>
<td>0.001</td>
<td>0.085</td>
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<tr>
<td>Beach width (m)</td>
<td>4.06</td>
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<tr>
<td>Reserve bordering beach (km)</td>
<td>2.91</td>
<td>0.008</td>
<td>0.053</td>
</tr>
</tbody>
</table>
Figure 1 Location of reserve and fished study beaches, and of marine park regions, along 2,000 km of coastline in eastern Australia.
Figure 2 Non-metric multidimensional scaling (nMDS) ordinations displaying differences in surf fish assemblages between marine reserves (green dots) and fished beaches (blue dots) in each marine park region. Fish assemblages differ significantly between reserves and fished beaches in Port Stephens, Batemans Bay, Great Sandy and Solitary Islands, but not in Moreton Bay, Cape Byron or Jervis Bay (Appendix S1). Reserves support more harvested species in Port Stephens and Batemans Bay, but not in Great Sandy or Solitary Islands. Vectors display species correlations with each ordination space; taxa in bold are significant indicator species (Appendix S2).
Figure 3 Species richness and the density of harvested fish, non-harvested fish, whiting (Sillaginidae), flathead (Platycephalidae), trevally (Carangidae) and toadfish (Tetraodontidae) in marine reserves and adjacent to fished beaches (mean ± SE). SR, species richness; HA, harvested fish; NH, non-harvested fish; WH, whiting; FL, flathead; TR, trevally; TO, toadfish. *Represent significant differences between reserve and unprotected locations (identified by Tukey’s HSD post hoc tests).
Figure 4 Non-metric multidimensional scaling (nMDS) ordination displaying differences in the attributes of reserves with: (1) more harvested fishes; (2) fewer harvested fishes; and (3) no difference to fished beaches. Dashed lines delineate coherent groups (p < 0.01) defined by similarity profile tests. Vectors display 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 (Appendix S3). Inset photos illustrate the reserve and seascape attributes and of selected conservation areas.