

Habitat type and beach exposure shape fish assemblages in the surf zones of ocean beaches

Hayden P. Borland¹, Thomas A. Schlacher¹, Ben L. Gilby¹, Rod M. Connolly²,
Nicholas A. Yabsley¹, Andrew D. Olds^{1,*}

¹School of Science and Engineering, University of the Sunshine Coast, Maroochydore, QLD 4558, Australia

²Australian Rivers Institute–Coasts & Estuaries, and School of Environment, Griffith University, Gold Coast, QLD 4222, Australia

ABSTRACT: The surf zones of ocean beaches are prime fishing sites and provide habitat for a diversity of fish species. The spatial composition of seascapes shapes fish abundance and diversity in most coastal ecosystems, but it remains untested whether seascape effects operate on ocean beaches. This study used the surf zones of sandy beaches in eastern Australia as a model system to contrast fish assemblages between the 2 main surf habitats (nearshore troughs and offshore bars), and test how habitat partitioning changes with beach exposure, wave conditions, seascape connectivity (i.e. proximity to estuaries and rocky headlands) and tide. Fish were sampled with baited remote underwater video stations from the surf zones of 18 sandy beaches in southern Queensland and northern New South Wales. Habitat type and beach exposure combined to shape fish abundance and diversity in the surf. Fish assemblages always differed between nearshore trough and offshore bar habitats; beach exposure was also important to surf fishes but did not alter the priority effects of habitat partitioning. Beach exposure is an important predictor of faunal assemblages on ocean beaches and is often used as a surrogate in conservation planning. Our results show, however, that surf zones are not single uniform spatial units but are composed of topographically and hydrodynamically distinct habitats that support correspondingly distinct fish assemblages. Because fishing effort also differs between surf habitats, fisheries management and spatial conservation planning need to reflect these spatial nuances in the surf zones of ocean beaches.

KEY WORDS: Surf zone · Fish · Habitat · Exposure · Ocean beach · Coastal conservation planning

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Sandy beaches and their surf zones dominate the global interface between the land and the sea and are prized by society as prime locations for coastal development, tourism and recreation (Dugan et al. 2010, Schlacher et al. 2016). The surf zones of ocean beaches support significant fisheries and provide habitat for a diversity of fish species, which use surf zones as feeding areas, refuges from predators, spawning sites and possibly juvenile nurseries (Defeo 2003, McLachlan & Brown 2006, Rishworth et al. 2014). Despite the diversity and abundance of fishes in global surf zones and the economic value of surf fisheries, we lack basic in-

formation on how fish select and use habitats in surf zones (Layman 2000, Patrick & Strydom 2014). Along many coastlines, fishing pressure on surf fishes is high, and impacts from expanding coastal urbanisation are likely (Defeo et al. 2009, Vargas-Fonseca et al. 2016). Thus, to improve spatial conservation planning and fisheries management, we require empirical data on how the ecological attributes of exposed coastlines shape habitat use in the surf zones of ocean beaches (Schlacher et al. 2015).

The distribution, abundance and diversity of fishes in coastal ecosystems are modified by variations in habitat (e.g. type, quality, area), seascape composition (e.g. habitat context, diversity, connectivity) and

the level of physical exposure to both natural and anthropogenic disturbances (Pittman & McAlpine 2003, Sheaves 2005, Nagelkerken et al. 2015). These attributes combine to structure the composition of fish assemblages in estuaries, kelp forests and coral reefs (Kneib 1997, Connolly & Hindell 2006, Olds et al. 2016). They also shape how fish are distributed in the surf zones of ocean beaches (McLachlan & Brown 2006, Vargas-Fonseca et al. 2016) and modify the abundance, diversity and size of macrofauna on sandy beaches, which alters the availability of food for fish that feed on invertebrates (Crawley et al. 2009, Defeo & McLachlan 2013). Yet the extent to which variation in seascape composition, beach exposure and wave climate (i.e. wave height or period) affect habitat selection by fish in the surf zones of ocean beaches remains to be tested.

Fish move from surf zones to other habitats to feed, spawn and disperse, and fish diversity and abundance often increase with the proximity of surf zones to estuaries and reefs (Ayvazian & Hyndes 1995, Valesini et al. 2004, Vargas-Fonseca et al. 2016). Fish abundance in surf zones is also typically greatest adjacent to low-energy beaches with small waves (<1 m), whereas fish species diversity can be highest in surf zones of moderately exposed beaches (wave heights typically 1–2 m) (Clark 1997, Inui et al. 2010, Patrick & Strydom 2014). Waves shape the morphology of ocean beaches and the bathymetry of their surf zones; wave energy is typically higher over sandbars where waves break, whereas wave velocities and turbulence are often lower in the deeper troughs that separate sandbars (Short & Jackson 2013). Troughs are trench-like shapes that form in the surf zones of dissipative and intermediate beaches due to the action of large waves and currents and the movement of sandbars (McLachlan & Brown 2006, Marin Jarrin & Miller 2016). They provide fish with shelter from breaking waves and offer rich feeding opportunities for species that feed on benthic invertebrates (e.g. whiting; Sillaginidae); conversely, certain piscivores (e.g. tailor; Pomatomidae) forage in the white water associated with waves that break over bars (Layman 2000, Watt-Pringle & Strydom 2003, Janssen et al. 2008). Thus, habitat type (i.e. nearshore trough vs. offshore bar) is predicted to modify the composition of fish assemblages in the surf zones of ocean beaches (McLachlan & Brown 2006). This hypothesis is, however, rarely tested with empirical data, as fish are seldom sampled from offshore bar habitats where large waves break (Marin Jarrin & Miller 2016, Vargas-Fonseca et al. 2016).

This study used the surf zones of ocean beaches in eastern Australia as a model system to examine habi-

tat partitioning by surf fishes and to test whether habitat use is influenced by beach exposure and seascape connectivity (i.e. spatial linkages with adjacent estuaries and rocky headlands). Given the reported effects of beach exposure and seascape connectivity, and the hypothesised significance of habitat for surf fishes, we anticipated that fish diversity and abundance would be greatest in the trough habitats of moderately exposed beaches.

MATERIALS AND METHODS

Study seascape

Fish assemblages were surveyed in the surf zone of 18 ocean beaches in southern Queensland and northern New South Wales, Australia (Fig. 1), between April and July 2016. These beaches stretch over 300 km of coastline, from Noosa in the north to Kingscliff in the south, and encompass considerable variation in beach exposure, wave conditions and the level of seascape connectivity with other fish habitats (e.g. estuaries, rocky headlands) (Short 2000, 2007, Vargas-Fonseca et al. 2016). To test whether variation in the spatial properties of surf zones modifies how fish use habitats adjacent to ocean beaches, we measured beach exposure, wave properties (i.e. height and period) and tidal conditions daily at each beach and determined the level of seascape connectivity between surf zones and other ecosystems, which provide complementary habitats for fish. The widths of individual beaches and their surf zones were quantified to index beach exposure (Defeo & McLachlan 2013); these variables were measured as distances from high tide lines to swash zones (intertidal subaerial beach width) and from swash zones to the outer breaking waves (surf zone width) using Google Earth (Fig. 1) (following Harris et al. 2011, Patrick & Strydom 2014). The level of seascape connectivity between surf zones and adjacent habitats was calculated in ARCGIS (ESRI) as distances to the nearest estuaries and rocky headlands (Fig. 1) (following Ayvazian & Hyndes 1995, Vargas-Fonseca et al. 2016).

Fish surveys

Surf fish assemblages were surveyed with baited remote underwater video stations (BRUVS), which have been used widely to census fish from reefs, estuaries, the open sea and the surf zones of ocean beaches (Murphy & Jenkins 2010, Gladstone et al.

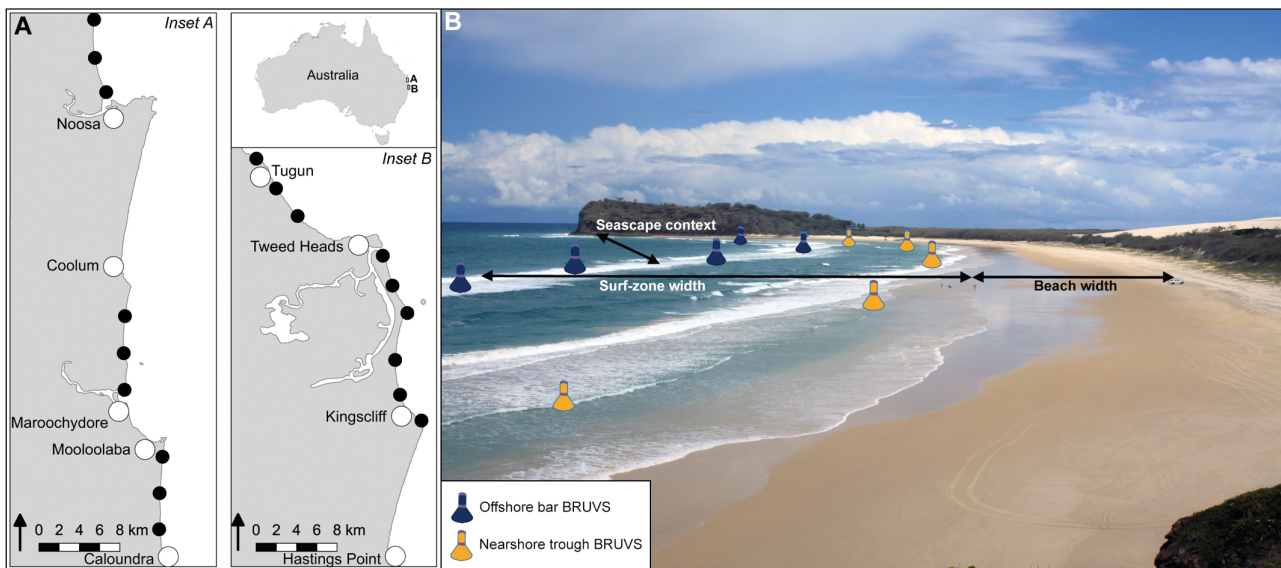


Fig. 1. (A) Study beaches (●) in eastern Australia. (B) Sampling design, showing the distribution of baited remote underwater video stations (BRUVS) in offshore bar and nearshore troughs and displaying how spatial metrics were measured at each location

2012, Santana-Garçon et al. 2014, Vargas-Fonseca et al. 2016). BRUVS were deployed from kayaks at 10 sites in the surf zone of each beach, with 5 BRUVS deployed in 200 m intervals along each of 2 transects parallel to the shore (Fig. 1). The first set of BRUVS was deployed in troughs (water depth: 1.0–1.5 m) within 50 m seawards of the swash line. The second set of BRUVS was deployed on the first bar landwards of the outermost line of breakers (water depth: 1.5–2.0 m). BRUVS consisted of a high-definition GoPro camera mounted on a 5 kg weight, which was attached to a bait bag that was held 0.5 m in front of the camera by a PVC pipe (Vargas-Fonseca et al. 2016). BRUVS were baited with 500 g of pilchards *Sardinops sagax*, which are used as a standard bait in BRUVS studies and do not bias fish surveys (Wraith et al. 2013, Gilby et al. 2016, Parker et al. 2016). Each BRUVS deployment lasted 1 h, giving a total video sampling time of 180 h for the study. Surf fish assemblages can be characterised by high temporal variation with changes in season, diel period and tidal state (McLachlan & Brown 2006); to standardise for these temporal effects, we restricted sampling to daytime high tides (i.e. within 2 h of high tide) during the austral winter. Each beach was, however, only surveyed once because previous surveys along this coastline had shown that seascape and wave effects on surf fishes were robust and not affected by short-term temporal variation (Vargas-Fonseca et al. 2016). Fish abundance, species richness and assemblage composition were quantified from video footage using the

standard Max N statistic (Murphy & Jenkins 2010, Vargas-Fonseca et al. 2016). Visibility was consistently high (i.e. >4 m) and exceeded the range at which fish could be identified from video footage. Fish were organised into the following groups: piscivores, zoobenthivores, zooplanktivores, detritivores and harvested fish species (following Elliott et al. 2007, Olds et al. 2012). In southeast Queensland, fish are harvested from troughs (also known as gutters) that occur close to the beach in a commercial net fishery that targets mullet (Mugilidae) and whiting (Sillaginidae) and by recreational anglers targeting bream (Sparidae), dart (Carangidae), flathead (Platycephalidae), tailor (Pomatomidae) and whiting (Vargas-Fonseca et al. 2016).

Data analysis

To test for the effects of habitat type (i.e. nearshore trough vs. offshore bar), beach exposure (i.e. beach and surf zone width), wave properties (i.e. wave height and period), seascape connectivity (i.e. distance to estuaries and rocky headlands) and tidal height on fish assemblages, data were analysed using linkage tree (LINKTREE) analyses. LINKTREE constructs a hierarchical dendrogram to correlate variation in multiple environmental variables with changes in assemblage composition; each division in the dendrogram is characterised by changes in one or more environmental variables that discriminate fish assemblages (Clarke et al. 2008). Tree divisions

and terminal nodes were defined by similarity profile tests ($p < 0.01$, 999 permutations), which identify differences in the composition of assemblages with no *a priori* grouping (Clarke et al. 2008). Analyses were performed using Bray-Curtis (fish data) and Euclidean (environmental attributes) similarity matrices (following Clarke et al. 2008). Fish abundance data were 4th root transformed prior to analysis, and environmental variables were normalised.

To test whether variation in beach exposure or wave properties modified how fish use habitats in the surf zones of ocean beaches, data were analysed with 3-way permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (Anderson 2001). The factors were habitat (a fixed factor with 2 levels), wave properties (a fixed factor with 3 levels) and beach exposure (a fixed factor with 3 levels). Levels for the factors wave properties and beach exposure were identified as natural splits in these data sets by LINKTREE analyses. Non-metric multidimensional scaling (nMDS) ordinations were used to visualise significant factors identified by PERMANOVA (Clarke et al. 2008). PERMANOVA and nMDS analyses were based on Bray-Curtis similarity measures, which were calculated on 4th root transformed fish abundance data. Dufrière-Legendre indicator species analysis was used to identify species that were primarily responsible for differences in fish assemblages between nearshore trough and offshore bar habitats (Dufrière & Legendre 1997). Vectors on the nMDS ordination space display correlations for significant indicator species identified by Dufrière-Legendre indicator species analysis. Finally, to test for effects of habitat type (i.e. nearshore trough vs. offshore bar) on species dominance, species richness and the density of harvested fishes, data were analysed with *k*-dominance curves and *t*-tests.

RESULTS

Surf zone fish assemblages were shaped by the combined effects of habitat, wave period and beach width (Fig. 2). The type of surf zone habitat (i.e. nearshore trough or offshore bar) had the greatest effect on the compo-

sition of fish assemblages (explaining 80.3% of variation). Offshore bar habitats were dominated by zooplanktivores and contained fish from all 4 functional groups (i.e. piscivores, zoobenthivores, zooplanktivores and detritivores). By contrast, nearshore trough habitats were dominated by zoobenthivores and typically comprised fish from 3, or fewer, functional groups. Variation in wave period was of secondary importance to fishes in nearshore trough habitats. Different fish assemblages occurred in trough habitats that had short (<9.7 s), mid (9.8–11.7 s) and long (>11.7 s) period waves (Fig. 2). The functional composition of fish assemblages changed as wave period increased; more functional groups were present in surf zones that experienced shorter wave periods. Beach width was also important in influencing the composition of fish assemblages in nearshore trough habitats. Fish assemblages in trough habitats differed between surf zones adjacent to narrow (<20 m) and wide (>20 m) beaches (Fig. 2). Three fish functional groups (i.e. zoobenthivores, piscivores and

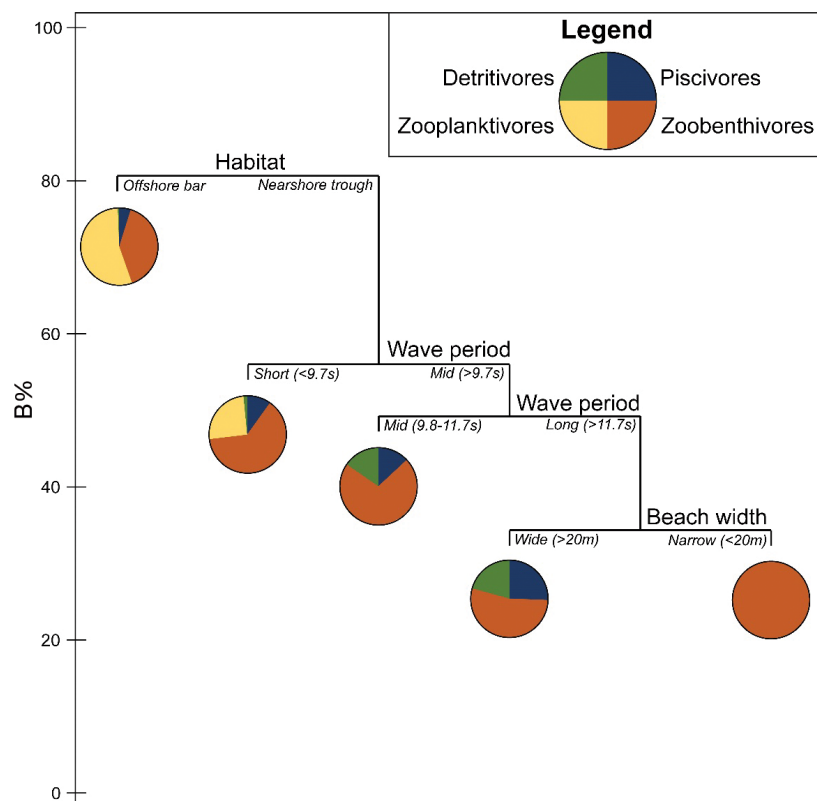


Fig. 2. Linkage tree displaying combined effects of habitat, wave period and beach width on surf fish assemblages. Tree divisions and terminal nodes were defined by similarity profile tests ($p < 0.01$) and correspond to variation in environmental attributes above each division. B%: relative importance of environmental attributes to fish assemblage composition. Pie charts display the functional group composition of fish assemblages in each type of surf zone habitat

detritivores) were present in trough habitats adjacent to wide beaches, but only zoobenthivores occurred in trough habitats abutting narrow beaches. None of the other environmental attributes (i.e. wave height, tidal height, surf zone width, proximity to estuaries, distance to rocky headlands) were significantly correlated with variation in the composition of surf fish assemblages.

The effect of habitat on fish assemblages was consistent across all surf zones and was not modified by variation in either wave period or beach width (Fig. 3, Tables 1 & 2). Surf fish assemblages always differed between nearshore trough and offshore bar habitats; however, variation in wave period and beach width also shaped the composition of fish assemblages within both nearshore trough and offshore bar habitats (Fig. 3, Tables 1 & 2). Three species — weeping toadfish *Torquigener pleurogramma* (Tetraodontidae), whitespotted guitarfish *Rhynchobatus australiae* (Rhynchobatidae) and bluespot maskray *Neotrygon kuhlii* (Dasyatidae) — were good indicators of fish assemblages in offshore bar habitats and were more abundant in these than in nearshore trough habitats (Fig. 3, Table 3). By contrast, 2 species — swallowtail dart *Trachinotus coppingeri* (Carangidae) and yellowfin bream *Acanthopagrus australis* (Sparidae) — were good indicators of fish assemblages in nearshore trough habitats and were more abundant in these than in offshore bar habitats (Fig. 3, Table 3).

Overall, fish assemblages in offshore bar habitats were characterised by lower dominance (Fig. 4) and supported more fish species (*t*-test; *n* = 90; *p* = 0.027) and more harvested fishes (*t*-test; *n* = 90; *p* = 0.041) than those in nearshore trough habitats.

DISCUSSION

The composition of fish assemblages in most marine ecosystems is determined by the condition, availability and context of habitats, which are modified by the physical and biological features of landscapes (e.g. seascape connectivity, habitat exposure, disturbance regime) (Sheaves 2009, Nagelkerken et al. 2015, Pittman & Olds 2015). This study shows that habitat type can have a greater influence on the composition of fish assemblages in surf zones than seascape connectivity, beach exposure, wave conditions or tide. This is an important finding because these other ecological attributes of surf zones (i.e. connectivity, exposure, wave conditions, tide) are known to affect the composition of fish assemblages, but the role of habitat in shaping surf fish abundance and

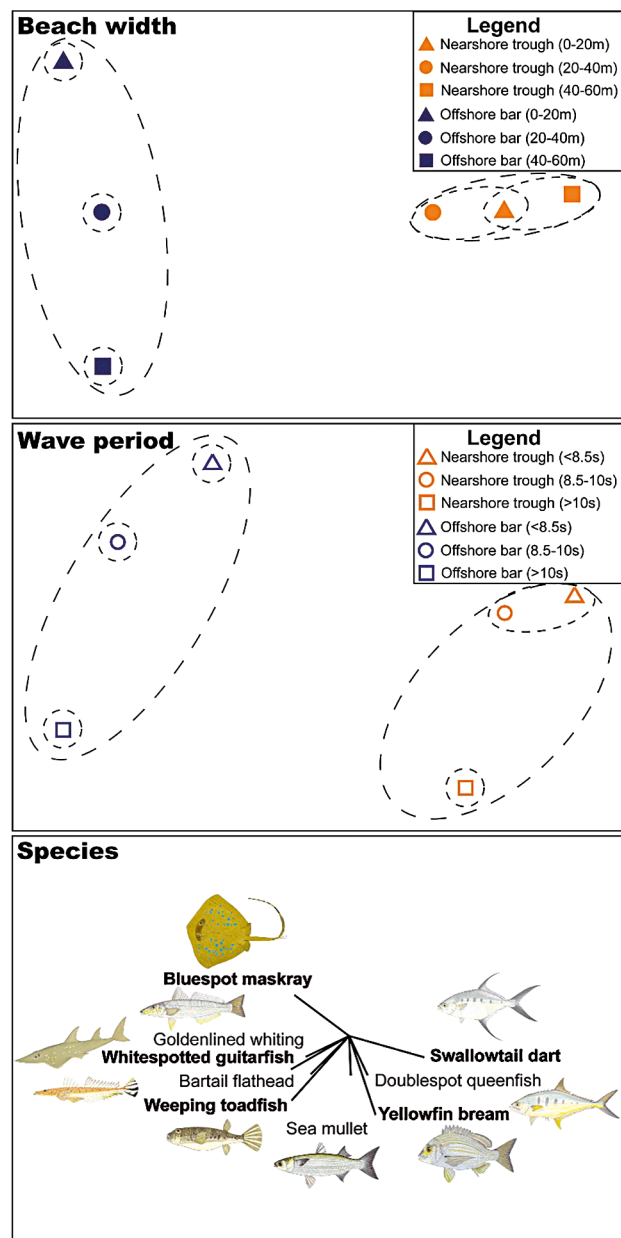


Fig. 3. Non-metric multidimensional scaling ordinations displaying relationships among surf fish assemblages in both habitat types (nearshore trough and offshore bar) at each level of beach width and wave period. Points represent multivariate centroids for each treatment. Dashed lines over ordinations delineate coherent groups (*p* < 0.05) defined by pairwise tests following permutational multivariate analysis of variance. Vectors display species correlations with the ordination space; taxa in **bold** are significant indicator species (Table 2)

diversity has rarely been tested (McLachlan & Brown 2006, Pattrick & Strydom 2014, Marin Jarrin & Miller 2016, Vargas-Fonseca et al. 2016). By highlighting the role of habitat for surf fishes, this work makes an important contribution to fisheries management and

Table 1. Three-way permutational multivariate analysis of variance examining the effects of habitat type, wave period and beach width on the structure of surf zone fish assemblages. Values in **bold** are significant at $p < 0.05$

Source of variation	df	F-value	p-value
Habitat type (H)	1	35.15	0.001
Wave period (WP)	2	2.91	0.003
Beach width (BW)	2	7.24	0.001
H × WP	2	2.51	0.006
H × BW	2	1.88	0.045
WP × BW	4	1.41	0.112
H × WP × BW	4	1.11	0.312

Table 2. Pairwise test results (following permutational multivariate analysis of variance) examining effects of environmental variables (habitat, wave period, beach width) on the composition of surf zone fish assemblages. Values in **bold** are significant at $p < 0.05$

Pairwise comparison	p-value
Habitat type (nearshore trough vs. offshore bar)	
Wave period	
Short (<9.7 s)	0.001
Mid (9.8–11.7 s)	0.001
Long (>11.7 s)	0.001
Beach width	
Narrow (<20 m)	0.001
Mid (20–40 m)	0.001
Wide (>40 m)	0.001
Wave period (short vs. mid vs. long)	
Nearshore trough	
Short vs. mid	0.489
Short vs. long	0.001
Mid vs. long	0.003
Offshore bar	
Short vs. mid	0.005
Short vs. long	0.001
Mid vs. long	0.008
Beach width (narrow vs. mid vs. wide)	
Nearshore trough	
Narrow vs. mid	0.074
Narrow vs. wide	0.100
Mid vs. wide	0.008
Offshore bar	
Narrow vs. mid	0.038
Narrow vs. wide	0.045
Mid vs. wide	0.029

spatial conservation planning for ocean beaches, which is currently limited to utilising variations in the morphology and exposure of beaches as surrogates for animal diversity and abundance (Harris et al. 2011, Defeo & McLachlan 2013, Schlacher & Thompson 2013).

Fish assemblages differed between nearshore trough and offshore bar habitats in the surf zones of ocean beaches. These habitat effects were strong and remained consistent despite considerable variation in beach exposure (beach width: 4.7–66.5 m; wave period: 6.1–12.0 s; wave height: 0.2–1.5 m). It is widely believed that surf fishes use nearshore troughs as foraging habitats and as refuges from breaking waves, and several authors have shown that species richness and abundance can be high in these areas (Watt-Pringle & Strydom 2003, Janssen et al. 2008, Marin Jarrin & Miller 2016). Fish diversity and abundance were not, however, always greatest in nearshore trough habitats. Instead, offshore bar and nearshore trough habitats supported distinct fish assemblages that differed in terms of both species dominance and functional composition. Offshore bar habitats supported more species, were comprised of zooplanktivores, piscivores, zoobenthivores, and detritivores, and were dominated by weeping toadfish *Torquigener pleurogramma*, whitespotted guitarfish *Rhynchobatus australiae* and bluespot maskray *Neotrygon kuhlii*. By contrast, nearshore trough habitats supported fewer species, were primarily comprised of zoobenthivores, and were dominated by swallowtail dart *Trachinotus coppingeri* and yellowfin bream *Acanthopagrus australis*. Species that are targeted by recreational anglers and commercial net fisheries were common in both bar (e.g. goldenlined whiting *Sillago analis*, bartailed flathead *Platycephalus endrachtensis*) and trough (e.g. swallowtail dart *T. coppingeri*, yellowfin bream *A. australis*) habitats but were always most abundant over offshore bars. Surf fish are, however, usually only caught from troughs that occur close to the beach (Bennett 1991, Clark et al. 1994), which suggests that any impacts from surf

Table 3. Dufrene-Legendre indicator species analysis contrasting fish assemblages between nearshore trough and offshore bar habitats. Values in **bold** are significant at $p < 0.01$

Common name	Scientific name	Primary habitat	Indicator value	p-value
Swallowtail dart	<i>Trachinotus coppingeri</i>	Nearshore trough	0.70	0.001
Yellowfin bream	<i>Acanthopagrus australis</i>	Nearshore trough	0.27	0.001
Weeping toadfish	<i>Torquigener pleurogramma</i>	Offshore bar	0.38	0.001
Whitespotted guitarfish	<i>Rhynchobatus australiae</i>	Offshore bar	0.11	0.004
Bluespot maskray	<i>Neotrygon kuhlii</i>	Offshore bar	0.10	0.007

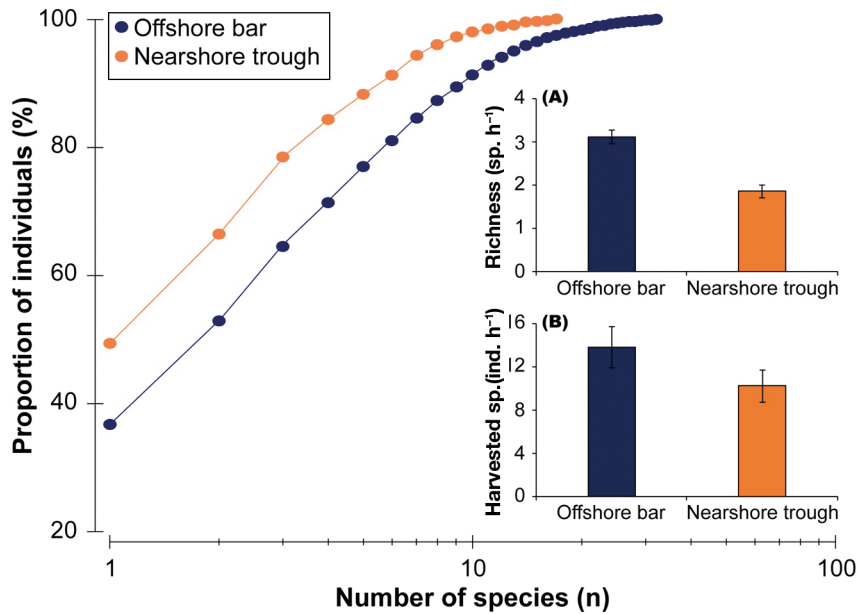


Fig. 4. Differences in species dominance (k -dominance curves), species richness (inset A) and density of harvested fishes (inset B) between offshore bar and nearshore trough habitats

fishing might be concentrated in nearshore trough habitats.

Offshore bar habitats are often characterised by breaking waves and comparatively shallow water depths (Davidson-Arnott 2013). Visibility is also frequently greater in offshore bar habitats than in nearshore troughs, which likely improves the foraging efficiency of visual zoobenthivores (e.g. weeping toadfish *T. pleurogramma*, whitespotted guitarfish *R. australiae*) and piscivores (e.g. bartailed flathead *P. endrachtensis*) (Hyndes et al. 1996, Able et al. 2013, White et al. 2014, Vargas-Fonseca et al. 2016). Plankton (e.g. diatoms, mysids, crab and fish larvae) can also be abundant over offshore bars, particularly just behind the area where waves begin to break, where they provide diverse feeding opportunities for zooplanktivores (e.g. scad, Carangidae) and detritivores that graze on surf diatoms (e.g. mullet, Mugilidae) (Romer & McLachlan 1986, Watt-Pringle & Strydom 2003, Johnson 2015, Marin Jarrin et al. 2016). Nearshore troughs are characterised by comparatively low wave energy and deeper water (Short & Jackson 2013). These areas support an abundance of benthic invertebrates (e.g. polychaetes, bivalves, crabs) and frequently accumulate drifting macrophytes and epifaunal amphipods, which provide food for zoobenthivores (e.g. swallowtail dart *T. coppingeri*, yellowfin bream *A. australis*) (Layman 2000, Inoue et al. 2008, Crawley et al. 2009, Parker & Booth 2015). Most research on surf fishes is limited to sampling fish assem-

blages from shallow troughs that occur close to the beach. To date, only 2 other studies (Marin Jarrin & Miller 2016, Vargas-Fonseca et al. 2016) have surveyed fish from offshore surf bars, and more empirical data are needed to improve our understanding of how fish use habitats within the surf zones of ocean beaches.

Variation in beach exposure, seascape connectivity and tidal height did not modify the effects of habitat on surf fishes, but beach exposure (as indexed by both beach width and wave period) was important in structuring the composition of fish assemblages within both offshore bar and nearshore trough habitats. Exposure is widely considered one of the most important attributes of ocean beaches, as it shapes the abundance, diversity, biomass and size of macrofauna on beaches (Defeo & McLachlan 2013)

and modifies the composition of fish assemblages in surf zones (McLachlan & Brown 2006). Fish diversity is often greatest in the surf zones of intermediate beaches, which are moderately exposed to the prevailing swell, although both species richness and abundance have been negatively correlated with wave period, height and speed (Clark 1997, Inui et al. 2010, Patrick & Strydom 2014). Variation in the morphological features of beaches (e.g. width and slope) is also strongly correlated with changes in the composition of macrofaunal assemblages (Harris et al. 2011, Defeo & McLachlan 2013) and therefore the availability of food for benthic feeding fishes.

This study shows how habitat type and beach exposure combine to shape fish abundance and diversity in the surf zones of ocean beaches. Nearshore trough and offshore bar habitats support distinct fish assemblages, and these differences are not modified by variation in beach exposure and wave conditions. The importance of exposure to faunal assemblages on ocean beaches is widely appreciated, but in this study, the role of exposure for surf fishes was secondary to the priority effects of habitat. This work demonstrates the importance of habitat to surf fishes and has significant implications for fisheries management and conservation planning on exposed coastlines. Fishing effort on ocean beaches is concentrated in nearshore trough habitats, which are therefore likely to require a different type of spatial management than offshore bar habitats. Marine spatial plan-

ning for ocean beaches is, however, currently limited to using beach morphology and exposure as surrogates for animal diversity and abundance, and we suggest that this approach must be broadened to incorporate the priority effects of habitat for surf fishes.

Acknowledgements. This work was funded by the Seaworld Research and Rescue Foundation, the Foundation for National Parks and Wildlife, the Paddy Pallin Foundation and the Australian Government's Collaborative Research Network programme. We thank I. Kelly, A. Moses, N. Ortodossi and A. Rummell for help in the field.

LITERATURE CITED

- Able KW, Wuenschel MJ, Grothues TM, Vasslides JM, Rowe PM (2013) Do surf zones in New Jersey provide 'nursery' habitat for southern fishes? *Environ Biol Fishes* 96: 661–675
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Ayvazian SG, Hyndes GA (1995) Surf-zone fish assemblages in south-western Australia: Do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Mar Biol* 122:527–536
- Bennett BA (1991) Long-term trends in the catches by shore anglers in False Bay. *Trans R Soc S Afr* 47:683–690
- Clark BM (1997) Variation in surf-zone fish community structure across a wave-exposure gradient. *Estuar Coast Shelf Sci* 44:659–674
- Clark BM, Bennett BA, Lamberth SJ (1994) A comparison of the ichthyofauna of two estuaries and their adjacent surf zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. *S Afr J Anim Sci* 14:121–131
- Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *J Exp Mar Biol Ecol* 366:56–69
- Connolly R, Hindell J (2006) Review of nekton patterns and ecological processes in seagrass landscapes. *Estuar Coast Shelf Sci* 68:433–444
- Crawley KR, Hyndes GA, Vanderklift MA, Revill AT, Nichols PD (2009) Allochthonous brown algae are the primary food source for consumers in a temperate, coastal environment. *Mar Ecol Prog Ser* 376:33–44
- Davidson-Arnott RGD (2013) Nearshore bars. In: Shroder J (ed) *Treatise on geomorphology*. Academic Press, San Diego, CA, p 130–148
- Defeo O (2003) Marine invertebrate fisheries in sandy beaches: an overview. *J Coast Res* SI35:56–65
- Defeo O, McLachlan A (2013) Global patterns in sandy beach macrofauna: species richness, abundance, biomass and body size. *Geomorphology* 199:106–114
- Defeo O, McLachlan A, Schoeman DS, Schlacher TA and others (2009) Threats to sandy beach ecosystems: a review. *Estuar Coast Shelf Sci* 81:1–12
- Dufrène M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Dugan JE, Defeo O, Jaramillo E, Jones AR and others (2010) Give beach ecosystems their day in the sun. *Science* 329: 1146
- Elliott M, Whitfield AK, Potter IC, Blaber SJM, Cyrus DP, Nordlie FG, Harrison TD (2007) The guild approach to categorizing estuarine fish assemblages: a global review. *Fish Fish* 8:241–268
- Gilby BL, Tibbetts IR, Olds AD, Maxwell PS, Stevens T (2016) Seascape context and predators override water quality effects on inshore coral reef fish communities. *Coral Reefs* 35:979–990
- Gladstone W, Lindfield S, Coleman M, Kelaher B (2012) Optimisation of baited remote underwater video sampling designs for estuarine fish assemblages. *J Exp Mar Biol Ecol* 429:28–35
- Harris L, Nel R, Schoeman D (2011) Mapping beach morphodynamics remotely: a novel application tested on South African sandy shores. *Estuar Coast Shelf Sci* 92:78–89
- Hyndes GA, Potter IC, Lenanton RCJ (1996) Habitat partitioning by whiting species (Sillaginidae) in coastal waters. *Environ Biol Fishes* 45:21–40
- Inoue T, Suda Y, Sano M (2008) Surf zone fishes in an exposed sandy beach at Sanrimatsubara, Japan: Does fish assemblage structure differ among microhabitats? *Estuar Coast Shelf Sci* 77:1–11
- Inui R, Nishida T, Onikura N, Eguchi K, Kawagishi M, Nakatani M, Oikawa S (2010) Physical factors influencing immature-fish communities in the surf zones of sandy beaches in northwestern Kyushu Island, Japan. *Estuar Coast Shelf Sci* 86:467–476
- Janssen GM, Kleef H, Mulder S, Tydeman P (2008) Pilot assessment of depth related distribution of macrofauna in surf zone along Dutch coast and its implications for coastal management. *Mar Ecol* 29:186–194
- Johnson WS (2015) Suprabenthic species distributions relative to small-scale bathymetric features along the Virginia coast, USA. *Mar Biol Res* 11:1009–1020
- Kneib R (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanogr Mar Biol Annu Rev* 35: 163–220
- Layman CA (2000) Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia barrier islands. *Estuar Coast Shelf Sci* 51:201–213
- Marin Jarrin JR, Miller JA (2016) Spatial variability of the surf zone fish and macroinvertebrate community within dissipative sandy beaches in Oregon, USA. *Mar Ecol* 37: 1027–1035
- Marin Jarrin JR, Miño Quezada SL, Dominguez-Granda LE, Guartatanga Argudo SM, De Grunauer MDPCR (2016) Spatio-temporal variability of the surf-zone fauna of two Ecuadorian sandy beaches. *Mar Freshw Res* 67:566–577
- McLachlan A, Brown AC (2006) Surf-zone fauna. In: McLachlan A, Brown AC (eds) *The ecology of sandy shores*. Academic Press, Burlington, MA, p 197–213
- Murphy H, Jenkins G (2010) Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. *Mar Freshw Res* 61:236–252
- Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish Fish* 16:362–371
- Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012) Habitat connectivity improves reserve performance. *Conserv Lett* 5:56–63
- Olds AD, Connolly RM, Pitt KA, Pittman SJ and others (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. *Glob Ecol Biogeogr* 25:3–15

- Parker D, Booth AJ (2015) Aspects of the biology and life history of largespot pompano, *Trachinotus botla*, in South Africa. *Mar Freshw Res* 66:247–255
- Parker D, Winker H, Bernard ATF, Heyns-Veale ER, Langlois TJ, Harvey ES, Götz A (2016) Insights from baited video sampling of temperate reef fishes: How biased are angling surveys? *Fish Res* 179:191–201
- Patrick P, Strydom NA (2014) The effects of exposure in sandy beach surf zones on larval fishes. *J Fish Biol* 84: 1354–1376
- Pittman SJ, McAlpine CA (2003) Movements of marine fish and decapod crustaceans: process, theory and application. *Adv Mar Biol* 44:205–294
- Pittman SJ, Olds AD (2015) Seascape ecology of fishes on coral reefs. In: Mora C (ed) *Ecology of fishes on coral reefs*. Cambridge University Press, Cambridge, p 274–282
- Rishworth GM, Strydom NA, Potts W (2014) Fish utilization of surf-zones. Are they changing? A case study of the sheltered, warm-temperate King's Beach. *Afr Zool* 49:5–21
- Romer GS, McLachlan A (1986) Mullet grazing on surf diatom accumulations. *J Fish Biol* 28:93–104
- Santana-Garcon J, Newman SJ, Harvey ES (2014) Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. *J Exp Mar Biol Ecol* 452:82–90
- Schlacher TA, Thompson L (2013) Spatial structure on ocean-exposed sandy beaches: faunal zonation metrics and their variability. *Mar Ecol Prog Ser* 478:43–55
- Schlacher TA, Weston MA, Schoeman DS, Olds AD, Huijbers CM, Connolly RM (2015) Golden opportunities: a horizon scan to expand sandy beach ecology. *Estuar Coast Shelf Sci* 157:1–6
- Schlacher TA, Lucrezi S, Connolly RM, Peterson CH and others (2016) Human threats to sandy beaches: a meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuar Coast Shelf Sci* 169:56–73
- Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. *Mar Ecol Prog Ser* 302:293–305
- Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar Ecol Prog Ser* 391: 107–115
- Short AD (2000) *Beaches of the Queensland coast: Cooktown to Coolangatta*. Sydney University Press, Sydney
- Short AD (2007) *Beaches of the New South Wales coast: a guide to their nature, characteristics, surf and safety*. Sydney University Press, Sydney
- Short AD, Jackson DWT (2013) Beach morphodynamics. In: Shroder J (ed) *Treatise on geomorphology*. Academic Press, San Diego, CA, p 106–129
- Valesini F, Potter I, Clarke K (2004) To what extent are the fish compositions at nearshore sites along a heterogeneous coast related to habitat type? *Estuar Coast Shelf Sci* 60:737–754
- Vargas-Fonseca E, Olds AD, Gilby BL, Connolly RM and others (2016) Combined effects of urbanization and connectivity on iconic coastal fishes. *Divers Distrib* 22: 1328–1341
- Watt-Pringle P, Strydom NA (2003) Habitat use by larval fishes in a temperate South African surf zone. *Estuar Coast Shelf Sci* 58:765–774
- White J, Simpfendorfer CA, Tobin AJ, Heupel MR (2014) Spatial ecology of shark-like batoids in a large coastal embayment. *Environ Biol Fishes* 97:773–786
- Wraith J, Lynch T, Minchinton TE, Broad A, Davis AR (2013) Bait type affects fish assemblages and feeding guilds observed at baited remote underwater video stations. *Mar Ecol Prog Ser* 477:189–199

Editorial responsibility: Konstantinos Stergiou, Thessaloniki, Greece

Submitted: November 25, 2016; Accepted: March 9, 2017
Proofs received from author(s): April 5, 2017