

Combined effects of urbanization and connectivity on iconic coastal fishes

Elena Vargas-Fonseca¹, Andrew D. Olds^{1*}, Ben L. Gilby¹, Rod M. Connolly², David S. Schoeman¹, Chantal M. Huijbers^{1,2}, Glenn A. Hyndes³ and Thomas A. Schlacher¹

¹School of Science and Engineering, University of the Sunshine Coast, Maroochydore DC, Qld 4558, Australia,
²Australian Rivers Institute – Coast & Estuaries, School of Environment, Griffith University, Gold Coast, Qld 4222, Australia,
³Centre for Marine Ecosystems Research, School of Natural Sciences, Edith Cowan University, Perth, WA 6027, Australia

ABSTRACT

Aim Disturbance and connectivity shape the structure and spatial distribution of animal populations in all ecosystems, but the combined effects of these factors are rarely measured in coastal seascapes. We used surf zones of exposed sandy beaches in eastern Australia as a model seascape to test for combined effects of coastal urbanization and seascape connectivity (i.e. spatial links between surf zones, estuaries and rocky headlands) on fish assemblages.

Location Four hundred kilometres of exposed surf beaches along the eastern coastline of Australia.

Methods Fish assemblages were surveyed from surf zones of 14 ocean-exposed sandy beaches using purpose-built surf baited remote underwater video stations.

Results The degree of coastal urbanization and connectivity were strongly correlated with the spatial distribution of fish species richness and abundance and were of greater importance to surf fishes than local surf conditions. Urbanization was associated with reductions in the abundance of harvested piscivores and fish species richness. Piscivore abundance and species richness were lowest on highly urbanized coastlines, and adjacent to beaches in wilderness areas where recreational fishing is intense. By contrast, seascape connectivity was correlated with the spatial distribution of omnivore and planktivore abundance. Spatial linkages between surf zones and estuaries were also important to two globally threatened guitarfish that are of international conservation significance.

Main conclusions We show for the first time how vulnerable and iconic fish species in surf zones are affected by the presence of coastal cities and the attributes of seascapes in which these cities are embedded. It is possible that greater connectivity may lessen ‘urbanization’ impacts for species with broad diets and strong ecological links to other ecosystems – this offers new perspectives in coastal conservation, for fishes and beyond.

Keywords

coastal management, disturbance, estuaries, landscape ecology, surf zones.

*Correspondence: Andrew D. Olds, School of Science and Engineering, University of the Sunshine Coast, Maroochydore DC, Qld 4558, Australia.
 E-mail: aolds@usc.edu.au

INTRODUCTION

When one tugs at a single thing in nature, they find it attached to the rest of the world.

John Muir

Animals move among habitats in landscapes and seascapes to feed, reproduce and disperse and thereby connect populations, food webs and ecosystems (Loreau *et al.*, 2003; Massol

et al., 2011; Olds *et al.*, 2016). This landscape connectivity is pivotal for the persistence of all organisms and is central to the recovery of ecosystems from disturbance (Cumming, 2011; Kool *et al.*, 2013). It is also an important consideration in conservation because human actions impact landscapes and connectivity in many ways, with wide-ranging, and frequently adverse, effects on both animals and their habitats (Fischer & Lindenmayer, 2007; Tschardtke *et al.*, 2012; Beger *et al.*, 2015). Well-known examples that illustrate the broad

reach of human impacts on connectivity include logging and urban development, which fragment tropical forests and imperil iconic primates and felines (Hardus *et al.*, 2012; Carter *et al.*, 2013); urbanization and hunting, which threaten shorebirds and ungulates at critical points on their migratory paths (Craigie *et al.*, 2010; Runge *et al.*, 2015); and infrastructure and fishing practices, which obstruct fish movement along rivers and among habitats in coastal seascapes (Layman *et al.*, 2007; Darimont *et al.*, 2010).

In coastal waters, the area, quality and configuration of ecosystems can structure the spatial distribution, movement and diversity of animals in seascapes (Grober-Dunsmore *et al.*, 2009; Bostrom *et al.*, 2011). Effects of connectivity on animal populations are particularly well documented for tropical seascapes supporting mangroves, seagrass and coral reefs (Sheaves, 2009; Olds *et al.*, 2016), and temperate regions containing marsh, seagrass and oyster reefs (Kneib, 1997; Micheli & Peterson, 1999). Seascape connectivity (i.e. landscape connectivity in the sea) is also central to the provision of many services that humans expect to receive from coastal environments, including productive fisheries (Nagelkerken *et al.*, 2015), good water quality (Beger *et al.*, 2010), healthy ecosystems (Olds *et al.*, 2016) and shoreline protection (Saunders *et al.*, 2014). Human populations are, however, also concentrated in coastal areas, and our actions (e.g. urbanization, fishing, resource extraction) degrade water quality, fragment habitats and reduce biodiversity in seascapes (Atwood *et al.*, 2015; Graham *et al.*, 2015; Huijbers *et al.*, 2015a). Human disturbances and connectivity may, therefore, exert joint, putatively opposing, effects on animals in coastal seascapes – this hypothesis is rarely tested with empirical data.

Exposed sandy beaches and their surf zones provide a natural laboratory that is ideal to examine what effects coastal cities and seascape connectivity have on animals (Schlacher *et al.*, 2015). These habitats dominate the world's coastlines and comprise approximately 70% of the global interface between the land and the sea (Dugan *et al.*, 2010). Beaches are of immense value to society as prime sites for recreation, development and fishing; they provide critical habitat for species that are of great significance for fisheries and conservation, but are also under stress from escalating human pressures (Defeo *et al.*, 2009; Huijbers *et al.*, 2015b; Schlacher *et al.*, 2016). Effects of urbanization on coastal fauna are geographically widespread and encompass impacts on the distribution and abundance of most taxonomic groups, including invertebrates (Hubbard *et al.*, 2014); fish (Wilber *et al.*, 2003), reptiles (Rizkalla & Savage, 2011), birds (Meager *et al.*, 2012) and mammals (Schmidt *et al.*, 2012). Coastal urbanization similarly affects the spatial distribution of key ecological functions (e.g. carrion removal) on beaches (Huijbers *et al.*, 2015b). Animals on beaches and in the surf are also strongly influenced by spatial linkages with other ecosystems, but these connectivity effects have not been widely studied (Schlacher *et al.*, 2015). Well-known examples that illustrate effects of connectivity on animals at the dune–beach–surf interface include local movements of fish

and birds among habitats (Ayvazian & Hyndes, 1995; Schlacher *et al.*, 2014), regional dispersal of invertebrates and fishes along coastlines (Able *et al.*, 2013; Schoeman *et al.*, 2015) and global migrations of turtles and shorebirds between feeding and nesting locations (Hays, 2008; Runge *et al.*, 2015).

We used the sandy beaches of eastern Australia as a model seascape to test whether and how coastal cities and seascape connectivity affect coastal fish populations. This area contains a strong urbanization gradient known to affect local populations of invertebrates and birds, as well as key ecological functions on beaches (Meager *et al.*, 2012; Noriega *et al.*, 2012; Huijbers *et al.*, 2015b). Seascape connectivity (i.e. spatial links between surf zones, estuaries and rocky headlands) also influences habitat selection and dispersal by birds and fishes across the region (Zeller *et al.*, 1996; Werry *et al.*, 2012; Schlacher *et al.*, 2014). In addition, surf zones of this coastline support numerous iconic fish species that are harvested heavily in local fisheries (e.g. flathead, flounder, whiting) or are the focus of international conservation efforts (e.g. sharks, rays, guitarfish) (White *et al.*, 2013; Jordan & Creese, 2015; Webley *et al.*, 2015). Given the established negative effects of urbanization on local beach invertebrate populations (Noriega *et al.*, 2012), we anticipated that coastal cities would have negative effects on benthic feeding piscivores and zoobenthivores, such as dart (Carangidae), flathead (Platycephalidae) and toadfish (Tetraodontidae). By contrast, connectivity was hypothesized to modify the distribution of omnivorous fishes (i.e. species capable of feeding on a range of resources across multiple habitats) and species that use either estuarine habitats as nurseries or rocky reefs as spawning sites, such as flounder (Paralichthyidae), whiting (Sillaginidae), and sharks, rays and guitarfish (Elasmobranchii).

METHODS

Study seascape

We surveyed fish in the surf zones of 14 exposed sandy beaches in South East Queensland and northern New South Wales, Australia (25°53' S, 153°05' E–28°38' S, 153°36' E), between November and December 2014. Sites were distributed along 400 km of coastline from Rainbow Beach in the north to Byron Bay in the south (Fig. 1) and encompassed a gradient of urbanization from near-wilderness areas (e.g. Stradbroke Island) to highly modified surf beaches fronting coastal cities (e.g. Gold Coast). This coastline contains a wide variety of land uses and supports a heterogeneous seascape that includes exposed sandy beaches, estuaries and rocky headlands (Olds *et al.*, 2012a; Huijbers *et al.*, 2015b). There is considerable variation in the spatial properties of these systems (e.g. estuary size, habitat diversity, urbanization), which makes this region ideal for testing the response of surf fishes to coastal urbanization and seascape connectivity.

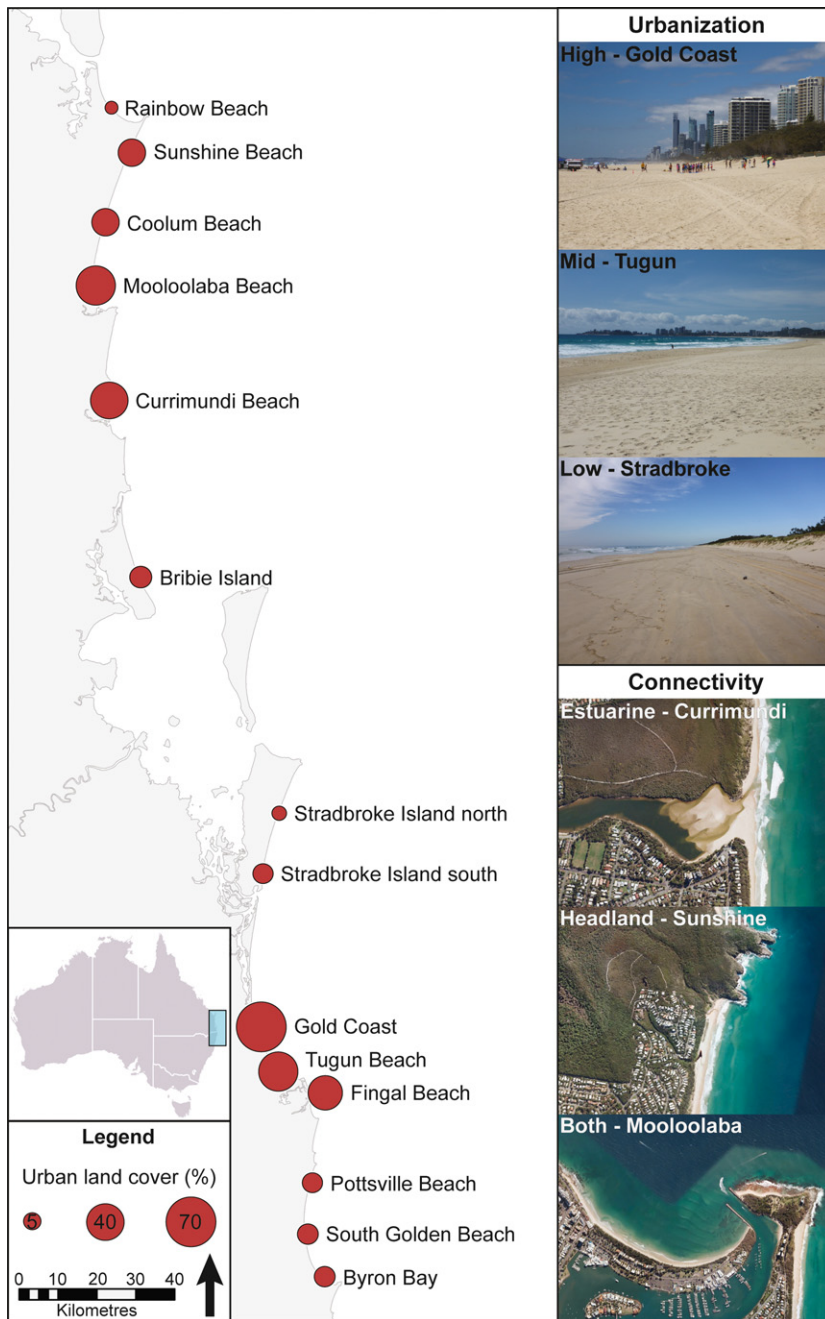


Figure 1 Location of study beaches in eastern Australia. The size of location markers is scaled to the cover of urban land behind each beach. Photographs illustrate the degree of urbanization, and type of connectivity at selected beaches. Colour figure can be viewed at wileyonlinelibrary.com

Coastal urbanization was measured as the cover of urban land (i.e. housing, roads, infrastructure) bordering each beach (refer to Huijbers *et al.*, 2015b) and quantified at two scales that correspond to local home-range movements (kms) and ontogenetic migrations (10s of kms) of coastal fishes in the study area (Olds *et al.*, 2012b; Green *et al.*, 2014). We quantified the intensity of urban development within 4 km² (kms of beachfront) and 133 km² (10s of kms of beachfront) of the centre point of each study beach. The level of seascape connectivity between surf zones and adjacent habitats (i.e. estuaries, rocky headlands) was calculated in ARCGIS (ESRI, Redlands, CA, USA) using three spatial metrics (Wedding *et al.*, 2011) that are expected to affect the

distribution and abundance of fishes in surf zones: (1) distance to the nearest estuary, (2) width of the nearest estuary (mouth width at low tide) and (3) distance to the nearest rocky headland (Ayvazian & Hyndes, 1995; Valesini *et al.*, 2004; Crawley *et al.*, 2006). The composition of surf fish assemblages can be modified by spatial and temporal variation in exposure, wave properties and the density of drifting macrophytes in surf zones (McLachlan & Brown, 2006). We determined latitude, wind speed and direction, wave height and frequency, and macrophyte density at each beach to test whether these influenced fish metrics in addition to the hypothesized effects of cities and connectivity. Macrophyte density was quantified from still frames extracted from video

footage used to census fish abundance; five images were selected from each hour of footage (separated by 15 min), and macrophyte density was estimated using a grid of 18 fixed points overlain on each image (Gilby *et al.*, 2015).

Fish surveys

Fish assemblages in surf zones were surveyed using purpose-built (by the authors) 'surf baited remote underwater video stations' (Surf-BRUVS). Surf-BRUVS consisted of a GoPro Camera (Hero4) attached to a bait bag containing 500 g of chopped pilchards and squid. We used two types of Surf-BRUVS: a mid-water unit, which was attached to a buoy and drifted through surf zones to survey fish at depths of 1–5 m, and a benthic unit, which was attached to a 5 kg weight and surveyed fish and crustaceans on the seafloor at depths of 3–5 m. Cameras were deployed at 200-m intervals along a transect parallel to the beach and seawards of the first line of breakers. Each beach was surveyed on two different days, and on each sampling event, we deployed six mid-water and six benthic Surf-BRUVS per beach. Each surf-BRUVS deployment sampled fish for 1 h, giving a total video sampling time of 24 h per beach and 336 h overall for the study. Surf fish assemblages are characterized by high temporal variation with changes in season, diel period and tidal state (Layman, 2000; Beyst *et al.*, 2002); to standardize for these temporal effects, we restricted sampling to daytime high tides (i.e. within 2 h of high tide) during the austral summer.

Fish abundance, species richness and assemblage composition were quantified from video footage using the standard Max N statistic (Murphy & Jenkins, 2010). Fish were then categorized into four trophic groups (i.e. piscivores, zoobenthivores, omnivores and planktivores; following Baker & Sheaves, 2005; Elliott *et al.*, 2007).

Data analysis

To identify environmental variables that best explained variation in assemblage structure, fish data were examined using global BEST tests in PRIMER (Clarke *et al.*, 2008). Analyses were applied to Bray–Curtis similarity matrices calculated on square-root-transformed abundance data. Canonical analysis of principal coordinates was used to visualize the influence of significant environmental variables on surf zone fish assemblages (Anderson & Willis, 2003). Preliminary BEST results indicated that among the metrics indexing 'coastal urbanization', urban land cover within 133 km² of each beach was more strongly related to biological data (Appendix S1 in Supporting Information). It therefore was adopted as the primary proxy of urbanization in all subsequent analyses.

Variation in the abundance of individual fish species and functional groups across sites was examined for correlation with coastal urbanization, seascape connectivity and surf condition variables using generalized additive models (GAMs) (Hastie & Tibshirani, 1986) with the MGCV package

in R. Analyses examined the spatial distribution of all fish species and functional groups that were recorded at three or more beaches. Model overfitting was reduced by running all possible combinations of \leq four variables and using \leq four model knots (i.e. individual polynomial functions that combine to smooth GAMs) (Zuur *et al.*, 2009). Models were compared using Akaike information criterion corrected for finite sample sizes (AIC_c) with the MUMIN package in R; best-fit models were considered to be those with the lowest AIC_c values, and those with ΔAIC_c within 2 of this model (Burnham & Anderson, 2002). The relative importance of variables in each model was calculated by summing weighted AIC_c values across all models containing the variable of interest; higher important values indicate greater contribution.

RESULTS

Coastal urbanization and seascape connectivity were correlated with the spatial distribution of fish abundance, species richness and assemblage composition in surf zones of eastern Australia. Urbanization was correlated with spatial variation in assemblage composition and with reductions in fish species richness and the abundance of harvested piscivores. By contrast, spatial linkages between surf zones and estuaries were correlated with the spatial distribution of omnivore and planktivore abundance, and the abundance of two globally threatened guitarfish that are of international conservation significance.

Urbanization effects

The structure of fish assemblages in surf zones was strongly correlated with the level of coastal urbanization behind beaches, the density of drifting macrophytes in the surf and latitude (BioEnv R value = 0.487, P = 0.01) (Fig. 2, see Appendix S1). Coastal urbanization was of primary importance to the spatial distribution of fish species richness and harvested piscivore abundance (Table 1, Fig. 3, Appendix S2). More fish species and a larger number of harvested piscivorous fishes occurred in surf zones bordering beaches that were moderately urbanized, with 32–45% of abutting land converted to urban development (i.e. housing, roads, infrastructure). By contrast, coastal urbanization did not affect the spatial distribution of zoobenthivores, omnivores or planktivores (Table 1, Fig. 3, Appendix S2).

Coastal urbanization was of greater importance than seascape connectivity, local surf conditions and latitude for the spatial distribution of five harvested fish species, including bluespotted flathead (*Platycephalus caeruleopunctatus*), bartailed flathead (*P. endrachtensis*), dusky flathead (*P. fuscus*), obtuse barracuda (*Sphyrna obtusata*) and swallowtail dart (*Trachinotus coppingeri*) (Table 2, Fig. 4, Appendix S2). The abundance of most of these harvested fish species was greatest near beaches that were moderately urbanized (32–45% urban land cover). By contrast, bluespotted flathead were most abundant near least developed beaches (< 10% urban

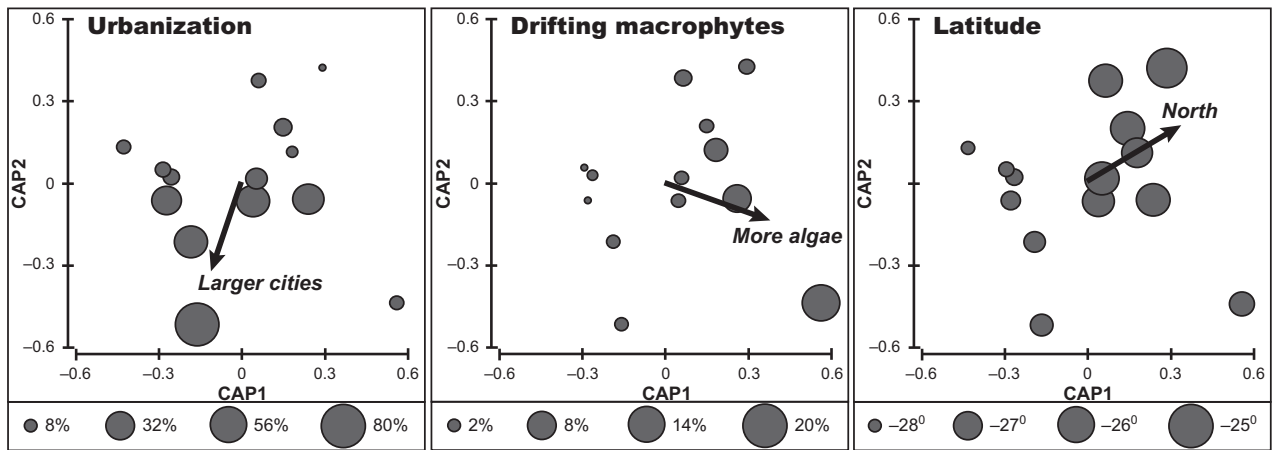


Figure 2 Canonical analysis of principal coordinates (CAPs) illustrating relationships among fish assemblages from surf zones of eastern Australia. Ordination based on Bray–Curtis (square root) dissimilarities with separate bubble plots illustrating gradients in coastal urbanization, cover of drifting macrophytes and latitude across all beaches sampled (vectors depict correlations with canonical axes).

Table 1 Best-fit general additive models (GAMs) relating the species richness and abundance of trophic groups to environmental variables. For linear relations, arrows indicate whether the variable is associated with an increase or decrease in fish abundance. Important values are included in parentheses (larger values indicate stronger correlation with fish abundance).

Richness or group	Variables included in best-fit models				d.f.	R ²	Models
	Rank 1*	Rank 2	Rank 3	Rank 4			
Urbanization effects							
Species richness	Urbanization [†] (1.0) [‡]	Drift macrophyte* (0.9)			7	0.80	3 [§]
Piscivores	Urbanization [†] (0.5)				3	0.16	8
Seascape connectivity effects							
Omnivores	Drift macrophytes [†] (1.0)	Estuary width [†] (0.8)	Distance to estuary [‡] (0.7)	Urbanization [¶]	10	0.79	4
Planktivores	Drift macrophytes [†] (1.0)	Estuary width [‡] (0.5)			5	0.42	5
Latitude effects							
Zoobenthivores	Latitude [†] (0.5)				4	0.26	15

*Variables are ordered (ranked) by their relative important values.

[†]Nonlinear effects result in varied relationships at intermediate values for these factors (see Fig. 3).

[‡]Relative important values were calculated by summing weighted AIC_c values from all models containing the variable.

[§]The number of secondary models within two ΔAIC_c units of best-fit model (see Appendix S2).

[¶]Environmental variables with little or no effect (i.e. with important values < 0.5).

land cover) and swallowtail dart were observed in greatest abundance near urban beaches (75% urban land cover). Bluespotted maskray (*Neotrygon kuhlii*) were also more abundant near least developed beaches, but this was secondary to the influence of seascape connectivity.

Seascape connectivity effects

Seascape connectivity metrics were strongly correlated with the spatial distribution of omnivore and planktivore abundance (Table 1, Fig. 3, Appendix S2). Omnivorous fishes were most abundant in surf zones with moderate levels of drifting macrophytes (7–14% cover), whereas planktivorous fishes were common where macrophytes were denser (> 14% cover). Omnivore abundance was also higher near (< 5 km)

large (> 1 km in width) estuaries, while planktivores were abundant at sites where the closest estuaries were small (< 0.5 km in width).

Seascape connectivity metrics were of greater importance than coastal urbanization, local surf conditions and latitude to the spatial distribution of eight fish species (Table 2, Fig. 4, Appendix S2). The distance of beaches from estuaries was of primary importance to the abundance of bluespotted maskray (*N. kuhlii*) and large-tooth flounder (*Pseudorhombus arsius*); maskray abundance was greatest far from estuaries (> 5 km), while flounder abundance was greater near estuaries (< 5 km). Distance to estuary was similarly important to the distribution of whitespotted guitarfish (*Rhynchobatus australiae*) and yellowtail scad (*Trachurus novaezelandiae*), which were more abundant nearer to estuaries (< 5 km).

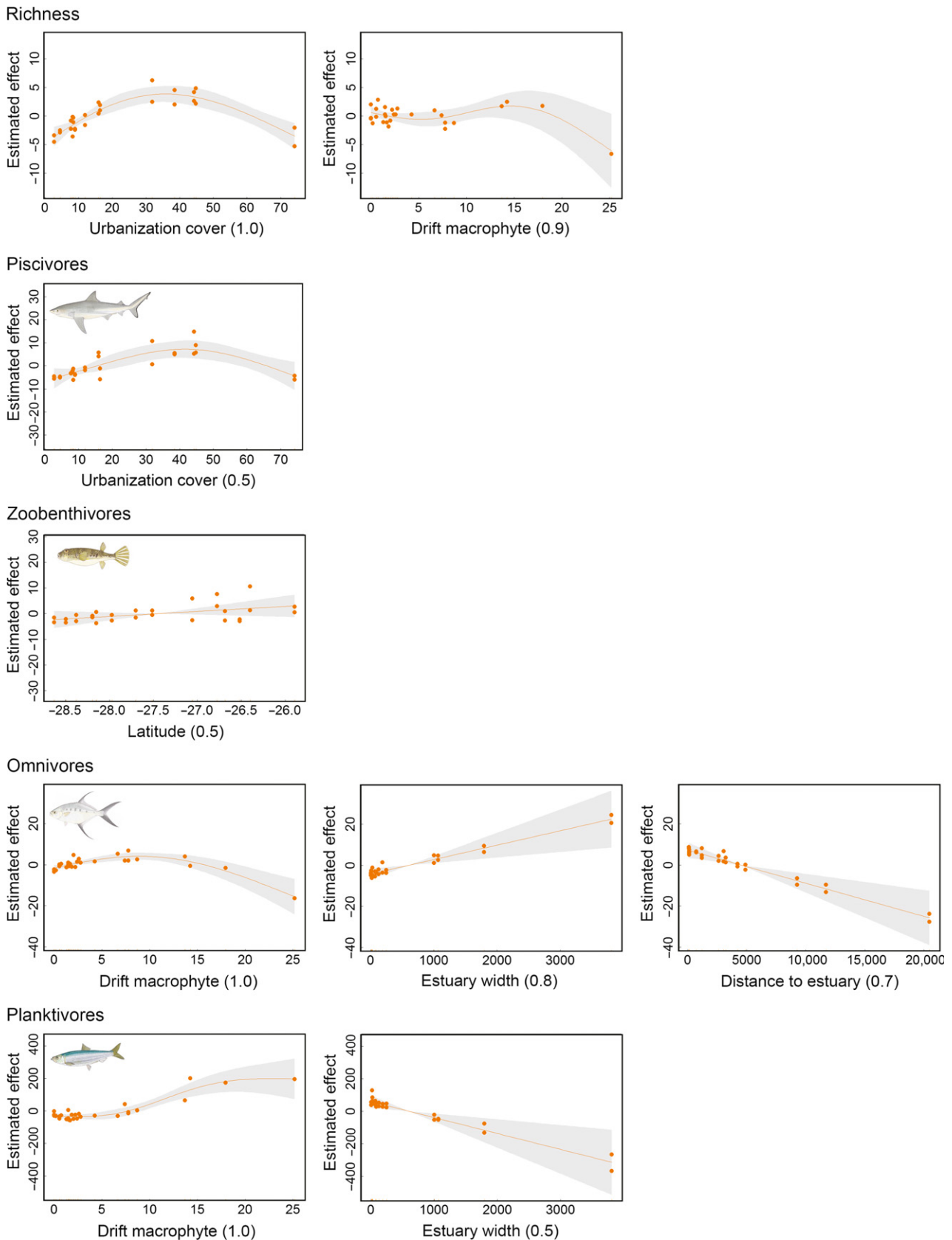


Figure 3 General additive models (GAMs) relating the distribution of species richness and fish trophic groups to significantly important environmental variables. Shaded regions indicate 95% confidence intervals. The relative importance of each variable to GAMs is shown in parentheses (fish illustrations sourced from www.efishalbum.com). Colour figure can be viewed at wileyonlinelibrary.com

Table 2 Best-fit general additive models (GAMs) relating the distribution of common fish species to environmental variables. For linear relations, arrows indicate whether the variable is associated with an increase or decrease in fish abundance. Important values are included in parentheses (larger values indicate stronger correlation with fish abundance).

Species	Variables included in best-fit models				d.f.	R ²	Models
	Rank 1*	Rank 2	Rank 3	Rank 4			
Urbanization effects							
Bluespotted flathead	Urbanization [†] (1.0) [‡]	Distance to headland [↓] (1.0)	Latitude [†] (1.0)	Estuary width [↓] (0.6)	12	0.92	1 [§]
Bartailed flathead	Urbanization [†] (1.0)	Estuary width [†] (0.9)	Drift macrophytes [↓] (0.8)	Latitude [¶]	9	0.75	1
Dusky flathead	Urbanization [†] (0.7)				3	0.24	1
Obtuse barracuda	Urbanization [†] (0.6)	Wave height [¶]	Distance to estuary [¶]		7	0.44	6
Swallowtail dart	Urbanization [†] (0.7)				4	0.23	5
Seascape connectivity effects							
Bluespotted maskray	Distance to estuary [↑] (0.9)	Urbanization [†] (0.8)			7	0.61	4
Large-tooth flounder	Distance to estuary [↓] (0.6)	Estuary width [↑] (0.6)			4	0.37	6
Whitespotted eagle ray	Distance to headland [↑] (0.5)				3	0.15	6
Goldenlined whiting	Distance to headland [↓] (0.8)	Drift macrophytes [¶]			6	0.49	6
Giant shovelnose ray	Distance to headland [↑] (1.0)	Estuary width [†] (1.0)	Wave height [↓] (0.9)		7	0.73	0
Common stingaree	Distance to headland [↑] (0.9)	Estuary width [†] (0.9)	Distance to estuary [¶]		6	0.53	6
Whitespotted guitarfish	Drift macrophytes [↓] (1.0)	Distance to estuary [↓] (0.7)	Distance to headland [↑] (0.6)		8	0.68	3
Yellowtail scad	Drift macrophytes [↓] (1.0)	Distance to headland [↑] (0.9)	Distance to estuary [↓] (0.9)	Estuary width [¶]	11	0.81	1

*Variables are ordered (ranked) by their relative important values.

[†]Nonlinear effects result in varied relationships at intermediate values for these factors (see Fig. 3).

[‡]Relative important values were calculated by summing weighted AIC_c values from all models containing the variable.

[§]The number of secondary models within two ΔAIC_c units of best-fit model (see Appendix S2).

[¶]Environmental variables with little or no effect (i.e. with important values < 0.5).

The abundance of bluespotted flathead, bartailed flathead, giant shovelnose ray (*Glaucostegus typus*) and common stingaree (*Trygonoptera testacea*) peaked at sites where the nearest estuary was small (< 1 km in width), while large-tooth flounder were abundant at sites where the nearest estuary was large (> 1 km in width).

The distance of beaches from rocky headlands was of primary importance to the spatial distribution of whitespotted eagle ray (*Aetobatus narinari*), giant shovelnose ray, goldenlined whiting (*Sillago analis*) and common stingaree (Table 2, Fig. 4, Appendix S1). These taxa were abundant in surf zones that were far from headlands (> 15 km), except for goldenlined whiting, which were common near headlands. Distance to headland was also significant for the abundance of bluespotted flathead, whitespotted guitarfish and yellowtail scad. Bluespotted flathead were abundant nearer to headlands (< 5 km), while whitespotted guitarfish and yellowtail scad were more abundant far from headlands (> 5 km).

The density of drifting macrophytes in the surf was of primary importance to the abundance of whitespotted guitarfish and yellowtail scad (Table 2, Fig. 4, Appendix S1). Macrophyte density was also important for the abundance of bartailed flathead. Whitespotted guitarfish and yellowtail scad were common in surf zones with moderate levels of

drifting macrophytes (7–14% cover), whereas bartailed flathead numbers declined as the density of macrophytes increased.

DISCUSSION

Connectivity and disturbance are critical ecological forces that structure the distribution of animal populations and the composition of assemblages and ecosystems, but joint effects are rarely examined in marine settings (Thrush *et al.*, 2008; Olds *et al.*, 2012c). Here, we show that in eastern Australia, coastal urbanization was strongly correlated with the composition of fish assemblages and fish species richness in surf zones. Urbanization was also related to spatial variation in the abundance of four piscivores that are heavily fished by local recreational anglers (i.e. bartailed, bluespotted and dusky flathead, and swallowtail dart) (Jordan & Creese, 2015; Webley *et al.*, 2015). By contrast, seascape connectivity was correlated with the spatial distribution of omnivore and planktivore abundance. Spatial linkages between surf zones and estuaries were also important to two globally threatened guitarfish (i.e. whitespotted guitarfish and giant shovelnose ray) that are classified as globally threatened by the International Union for Conservation of Nature (White *et al.*, 2013).

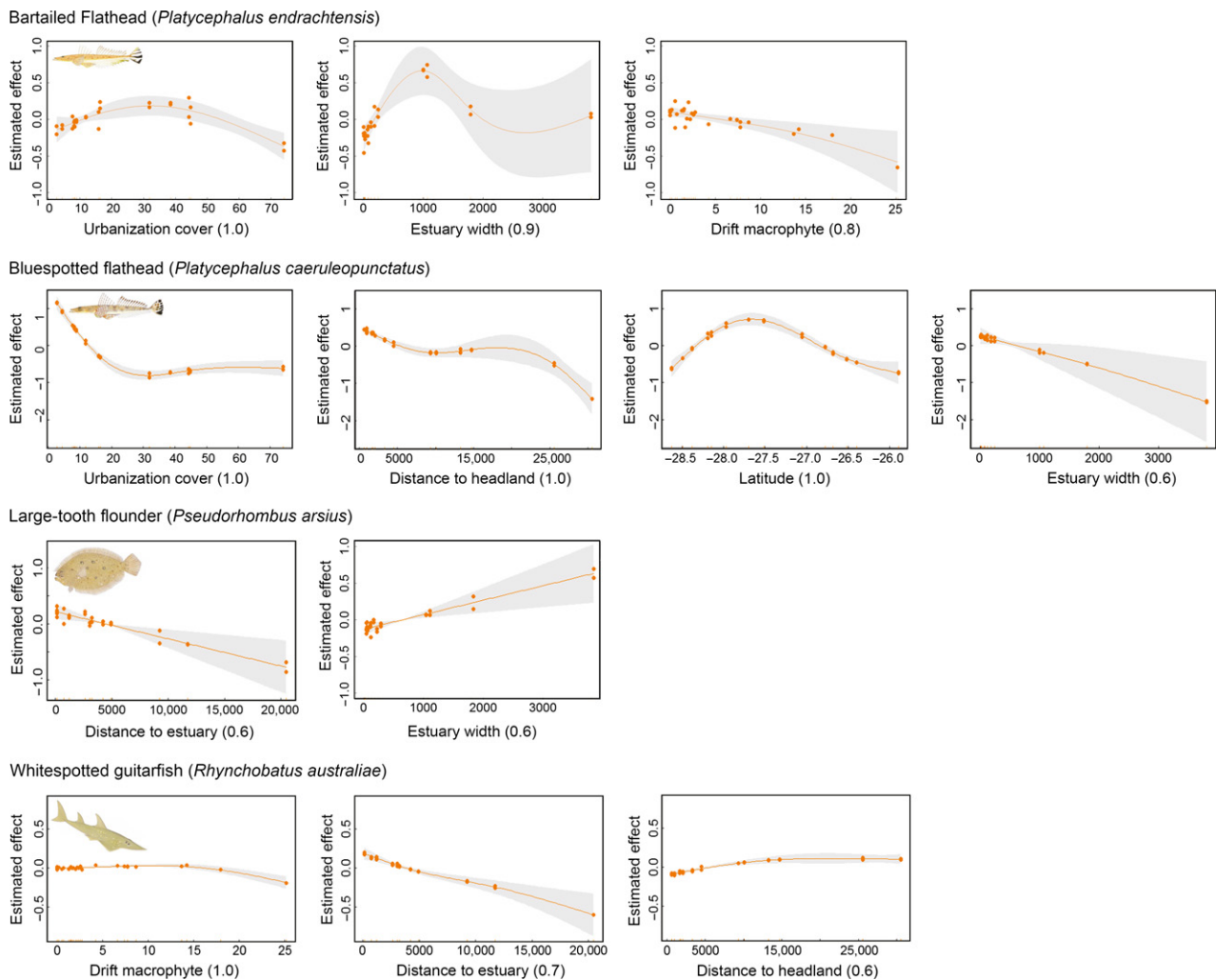


Figure 4 General additive models (GAMs) relating the distribution of three harvested species: bartailed flathead (*Platycephalus endrachtensis*) bluespotted flathead (*Platycephalus caeruleopunctatus*) and large-tooth flounder (*Pseudorhombus arsius*), and the globally threatened whitespotted guitarfish (*Rhynchobatus australiae*) to significantly important environmental variables. Shaded regions indicate 95% confidence intervals. The relative importance of each variable to GAMs is shown in parentheses (fish illustrations sourced from www.efishalbum.com). Colour figure can be viewed at wileyonlinelibrary.com

Urbanization and fishing effects

Fish assemblages in surf zones abutting coastal cities were affected by the degree of coastal urbanization. Species richness and piscivore abundance were consistently lowest in the surf zones of highly urban beaches (e.g. Gold Coast, Mooloolaba). The effect of urbanization on predatory fishes primarily reflects low densities of four mesopredators (bartailed, bluespotted and dusky flathead, and obtuse barracuda) in surf zones fronting coastal cities. These fish are all medium-sized predators that feed on benthic invertebrates and smaller fishes (Baker & Sheaves, 2006; Olds *et al.*, 2012a), suggesting that urbanization chiefly impacts coastal food webs from the bottom up (i.e. predators are impacted by reductions in the abundance or diversity of their prey). Bottom-up effects of urbanization on surf zone food webs may operate through five complementary mechanisms, which are common, intense

and widespread on beaches bordering the most urbanized coastlines: (1) human traffic (i.e. swimmers, boats), (2) beach grooming, (3) beach nourishment, (4) sensorial pollution (i.e. artificial light, noise) and (5) contamination (i.e. plastics, nutrients, chemicals) (Defeo *et al.*, 2009; Huijbers *et al.*, 2015b; Schlacher *et al.*, 2016). The effects of urbanization on fish assemblages in this study likely result from a combination of these stressors, which operate in concert to reduce water quality in surf zones, decrease feeding options for predatory fishes and physically deter animals from impacted areas. Beach grooming and storm-water run-off impact water quality along urbanized coastlines by increasing turbidity and concentrations of dissolved nutrients and chemical contaminants (Huijbers *et al.*, 2015a). Human traffic (on foot, in boats or 4WDs), shoreline grooming, beach nourishment and pollution (chemical, noise, light) also reduce the diversity and abundance of invertebrate and fish

populations in coastal seascapes (Wilber *et al.*, 2003; Noriega *et al.*, 2012). Furthermore, sensorial pollution and chemical pollution trigger behavioural response from predatory fishes (and their prey), and fish tend to avoid areas where water quality is poor, or noise or artificial light are concentrated (Davies *et al.*, 2014; Hawkins *et al.*, 2015). Artificial light has, however, also been shown to increase the abundance of predatory and prey fishes in estuaries (Becker *et al.*, 2013).

Effects of urbanization were, however, not always negative, as swallowtail dart were slightly more abundant in surf zones abutting the largest coastal cities. This result runs counter to our expectation and suggests that dart may actually benefit in some way from urbanization. Dart are zoobenthivores with home ranges that are an order of magnitude larger than any of the species that were affected negatively by urbanization (McPhee *et al.*, 1999). They roam widely along exposed coastlines and, therefore, are likely to move through the surf zones of urban beaches frequently, where they may benefit from reduced competition with, or predation by, other mesopredators that are less common in these areas.

Surf-fish assemblages also differed among beaches that had lower levels of urbanization landwards of the surf zone. Fish species richness, piscivore numbers and the abundance of three mid-sized predators (bartailed and dusky flathead, and obtuse barracuda) were lower in the surf zones of near-wilderness areas (e.g. Bribie, Rainbow, Stradbroke) than those of beaches that were moderately urbanized (e.g. Currimundi, Fingal, Tugun). These fish species and functional groups were largely absent from the surf zones of highly urban beaches, and so this result seems at odds with our a priori model for negative bottom-up effects of coastal cities. There is, however, another top-down mechanism through which humans directly impact surf-fish populations. Surf fishing is common from beaches in the study area; fishing effort can be intense and is concentrated in near-wilderness areas that people use for recreation (e.g. holidaying, camping, fishing competitions) (Jordan & Creese, 2015; Webley *et al.*, 2015). Recreational anglers catch a wide range of mesopredators (i.e. fish that readily consume the baits favoured by anglers use) from surf beaches, but the potential ecological impacts of this practice are rarely tested with empirical data (Lewin *et al.*, 2006; Defeo *et al.*, 2009). Therefore, it is not particularly surprising that piscivore numbers and fish species richness were lower adjacent to the beaches of wilderness areas, where surf fishing is concentrated. The surf beaches supporting low fish abundance and species richness are all open to 4WD vehicles, which considerably extends the ecological footprint of surf anglers in these areas.

The impacts of urbanization and beach fishing on surf-fish communities have not been widely studied (Defeo *et al.*, 2009; Dugan *et al.*, 2010). Our findings suggest that bottom-up effects of coastal urbanization likely combine with top-down effects of beach fishing to structure surf-fish assemblages, but further research is required to elucidate how these mechanisms interact to modulate regional patterns in fish diversity and abundance.

Seascape connectivity effects

Spatial linkages with estuaries were correlated with the distribution of eight fish species in the surf. These correlations were positive for seven species (bartailed flathead, bluespotted flathead, large-tooth flounder, yellowtail scad, common stingaree, giant shovelnose ray and whitespotted guitarfish), and negative for bluespotted maskray. All of these species use estuarine habitats at some point during their lives. Bartailed flathead, bluespotted flathead and large-tooth flounder use estuaries as juvenile nurseries; their distribution in surf zones is, therefore, potentially structured by the spatial extent of ontogenetic migrations from estuaries to coastal waters (Connolly *et al.*, 2009; Moore *et al.*, 2010; Barnes *et al.*, 2011; Mohammadikia *et al.*, 2014). Yellowtail scad and the four elasmobranch species (giant shovelnose ray, whitespotted guitarfish, common stingaree and bluespotted maskray) use a range of coastal habitats; both juveniles and adults of these species are common in estuaries, but it is not clear why individuals move among ecosystems in coastal seascapes (Stewart & Ferrell, 2001; Van Den Broek *et al.*, 2011; Weigmann & Thiel, 2013; White *et al.*, 2014). Coastal waters near estuaries are highly productive and typically support an abundance of small fish and invertebrates, which provide food for predatory fishes (Schlacher & Connolly, 2009). Flathead, flounder and scad are piscivores (Blaber & Bulman, 1987; Connolly *et al.*, 2009; Barnes *et al.*, 2011), while guitarfish, rays and stingarees are predators of benthic invertebrates (Marshall *et al.*, 2008; White *et al.*, 2013; Pardo *et al.*, 2015); greater numbers of these species in surf zones near estuaries might, therefore, reflect the spatial distribution of their prey.

The proximity of surf zones to rocky headlands was correlated with the spatial distribution of seven fish species, five of which were also affected by the characteristics of estuaries. This correlation was positive for two species (bluespotted flathead and *goldenlined* whiting), and negative for five species (yellowtail scad, common stingaree, whitespotted eagle ray, giant shovelnose ray and whitespotted guitarfish). It is not clear why bluespotted flathead and *goldenlined* whiting were present in greater abundance near rocky headlands; both species use estuaries as nurseries and are typically most abundant over sandy substrates that are isolated from rocky reef structure (Hyndes *et al.*, 1996; Krüeck *et al.*, 2009; Moore *et al.*, 2010). It is also not obvious why the abundance of yellowtail scad and the four elasmobranch species (giant shovelnose ray, whitespotted guitarfish, common stingaree, common stingaree, whitespotted eagle ray) would increase with isolation from rocky headlands. These species use a range of coastal habitats throughout their lives and are not likely to deliberately avoid surf zones that abut rocky headlands (Stewart & Ferrell, 2001; Pierce *et al.*, 2011; Van Den Broek *et al.*, 2011; White *et al.*, 2014). Correlations between fish abundance and headland proximity might, therefore, reflect underlying spatial variation in other environmental variables that we did not measure. For example,

rocky headlands occur in exposed coastal locations that regularly experience strong winds and large waves, and exposure shapes the hydrology (e.g. wave height and period), morphology (e.g. beach width and slope) and sediment characteristics (e.g. grain size) of surf beaches and modifies the composition of benthic invertebrate assemblages (Dexter, 1992; Defeo & McLachlan, 2013). These effects of exposure influence the availability of food and habitat for fishes and can alter the composition of fish assemblages (Clark, 1997), but this hypothesis has rarely been tested with empirical data.

The density of drifting macrophytes in the water column was negatively correlated with the abundance of three fish species (bartailed flathead, yellowtail scad and whitespotted guitarfish), all of which were also affected by spatial linkages with estuaries and rocky headlands. These species may avoid areas of high macrophyte accumulation because drifting macrophytes reduce water clarity and accumulations restrict access to the underlying substrate, which limits the foraging efficiency of visual piscivores (e.g. flathead and scad) and benthic carnivores (e.g. guitarfish) (Wilber *et al.*, 2003; Crawley *et al.*, 2006). Drifting macrophytes are a temporary feature in coastal waters, but surf zones that regularly accumulate macrophytes typically support different fish and benthic invertebrate assemblages to areas that do not (Crawley *et al.*, 2006). In this study, drifting macrophytes were dominated by four genera of brown algae (*Colpomenia*, *Dictyota*, *Hinckia* and *Sargassum*) that are exported to surf beaches across South East Queensland from estuaries, rocky shores and offshore reefs (EHMP, 2010). Spatial linkages with these adjacent 'source' habitats might affect the frequency of macrophyte accumulation in surf zones. Gaining a better understanding of how connectivity affects the spatial ecology of surf fish, therefore, requires data on both direct effects of linkages on fish movement and indirect effects of algal subsidies on fish trophic ecology (Hyndes *et al.*, 2014).

The spatial patterning of habitats in seascapes plays a pivotal role in structuring species distributions across all marine ecosystems (Grober-Dunsmore *et al.*, 2009; Bostrom *et al.*, 2011; Olds *et al.*, 2016), but consequences of seascape connectivity for surf fishes are rarely examined empirically (Schlacher *et al.*, 2015). Many studies report on the migration of fishes from estuaries to offshore habitats (e.g. reefs, continental shelves, open sea) (Gillanders *et al.*, 2003; Sheaves, 2009; Nagelkerken *et al.*, 2015), but few have quantified the ecological effects of connectivity between estuaries and surf zones and beyond (Schlacher *et al.*, 2015; Olds *et al.*, 2016). Two notable exceptions (Ayvazian & Hyndes, 1995; Valesini *et al.*, 2004) report positive effects of spatial linkages with estuaries and reefs on fish species richness in surf zones along the west coast of Australia. Our results extend the geographic scope of this work and suggest that seascape connectivity may be of broad relevance to the ecology and distribution of fish in surf zones. Moreover, our findings show that the abundance of most surf-fish species was correlated with a combination of seascape features. Best-fit models explained between 15%

and 92% of variation in fish abundance, but model performance was relatively poor (< 50% of variance explained) for six species (Table 2). Regional variation in exposure, beach morphology and the proximity of surf zones to offshore habitats (e.g. reefs, for which no accurate maps exist) likely contributed to this unexplained variation. To improve our understanding of the spatial ecology of surf fishes, we must quantify how exposure and beach morphology interact with seascape connectivity to shape fish assemblages in the coastal zone.

Implications for conservation

Most species that were impacted negatively by intense urbanization use estuaries as nursery habitats (Baker & Sheaves, 2006; Moore *et al.*, 2010; Olds *et al.*, 2012a), suggesting that impacts from coastal development might also reduce the role of connectivity for other species with this life history strategy (Adams *et al.*, 2009; Werry *et al.*, 2012). Spatial linkages between surf zones and estuaries were, however, correlated with the distribution of eight other fish species, including two globally threatened guitarfish that are of international conservation significance (White *et al.*, 2013). This finding demonstrates that urbanization does not diminish the role of connectivity for all taxa (particularly omnivorous species with catholic diets) (sensu Brown *et al.*, 2015) and implies that species with diverse feeding strategies and strong links to other ecosystems may in fact be better placed to cope with pressures from coastal development (sensu Layman *et al.*, 2007; Sheaves & Johnston, 2008). To improve precision and representation in coastal conservation planning, we require empirical data on the scale over which seascape connectivity mediates the distribution of animal populations and ecological functions in dune–beach–surf systems.

CONCLUSION

In this study, we show how coastal urbanization and seascape connectivity (i.e. spatial linkages among habitats in seascapes) combine to shape the spatial distribution of vulnerable and iconic fish species in surf zones. Moreover, our findings suggest that greater connectivity may reduce impacts from coastal development on species with broad dietary niches and strong links to other ecosystems. Connectivity has been shown to promote resistance to, and recovery from, disturbance in coral reef and estuarine seascapes (Mumby & Hastings, 2008; Olds *et al.*, 2012c), but our results highlight the need for caution when considering the management implications of spatial linkages in seascapes. To optimize spatial conservation planning for diversity, productivity and resilience, we require a clearer understanding of how and where connectivity mediates disturbance effects on coastal populations and ecosystems. Identifying the mechanisms through which coastal cities affect fish assemblages in adjacent surf zones, and quantifying how such impacts are influenced by the spatial patterning of seascapes, will be key to

improving conservation planning and environmental management actions on sandy shorelines globally.

ACKNOWLEDGEMENTS

This work was funded by the Seaworld Research and Rescue Foundation, the Foundation for National Parks and Wildlife, Paddy Pallin Foundation and the Australian Government's Collaborative Research Network (CRN) programme. We thank H. Faddy, I. Franks, N. Ortodossi, N. Yabsley and A. Zylstra for help in the field.

REFERENCES

- Able, K.W., Wuenschel, M.J., Grothues, T.M., Vasslides, J.M. & Rowe, P.M. (2013) Do surf zones in New Jersey provide "nursery" habitat for southern fishes? *Environmental Biology of Fishes*, **96**, 661–675.
- Adams, A.J., Wolfe, R.K. & Layman, C.A. (2009) Preliminary examination of how human-driven freshwater flow alteration affects trophic ecology of juvenile snook (*Centropomus undecimalis*) in estuarine creeks. *Estuaries and Coasts*, **32**, 819–828.
- Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, **84**, 511–525.
- Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays, G.C., Fourqurean, J.W. & Macreadie, P.I. (2015) Predators help protect carbon stocks in blue carbon ecosystems. *Nature Climate Change*, **5**, 1038–1045.
- Ayvazian, S.G. & Hyndes, G.A. (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? *Marine Biology*, **122**, 527–536.
- Baker, R. & Sheaves, M. (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. *Marine Ecology Progress Series*, **291**, 197–213.
- Baker, R. & Sheaves, M. (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. *Marine Ecology Progress Series*, **323**, 75–82.
- Barnes, L.M., Leclerc, M., Gray, C.A. & Williamson, J.E. (2011) Dietary niche differentiation of five sympatric species of Platycephalidae. *Environmental Biology of Fishes*, **90**, 429–441.
- Becker, A., Whitfield, A.K., Cowley, P.D., Järnegren, J. & Næsje, T.F. (2013) Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology*, **50**, 43–50.
- Beger, M., Grantham, H.S., Pressey, R.L., Wilson, K.A., Peterson, E.L., Dorfman, D., Mumby, P.J., Lourival, R., Brumbaugh, D.R. & Possingham, H.P. (2010) Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biological Conservation*, **143**, 565–575.
- Beger, M., McGowan, J., Treml, E.A., Green, A.L., White, A.T., Wolff, N.H., Klein, C.J., Mumby, P.J. & Possingham, H.P. (2015) Integrating regional conservation priorities for multiple objectives into national policy. *Nature Communications*, **6**, 8208.
- Beyst, B., Vanaverbeke, J., Vincx, M. & Mees, J. (2002) Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*, **225**, 263–274.
- Blaber, S.J.M. & Bulman, C.M. (1987) Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology*, **95**, 345–356.
- Bostrom, C., Pittman, S.J., Simenstad, C. & Kneib, R.T. (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series*, **427**, 191–217.
- Brown, M.B., Schlacher, T.A., Schoeman, D.S., Weston, M.A., Huijbers, C.M., Olds, A.D. & Connolly, R.M. (2015) Invasive carnivores alter ecological function and enhance complementarity in scavenger assemblages on ocean beaches. *Ecology*, **96**, 2715–2725.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference*. Springer, New York, NY.
- Carter, N.H., Gurung, B., Viña, A., Campa Iii, H., Karki, J.B. & Liu, J. (2013) Assessing spatiotemporal changes in tiger habitat across different land management regimes. *Ecosphere*, **4**, 1–19.
- Clark, B.M. (1997) Variation in surf-zone fish community structure across a wave-exposure gradient. *Estuarine, Coastal and Shelf Science*, **44**, 659–674.
- Clarke, K.R., Somerfield, P.J. & Gorley, R.N. (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology*, **366**, 56–69.
- Connolly, R.M., Schlacher, T.A. & Gaston, T.F. (2009) Stable isotope evidence for trophic subsidy of coastal benthic fisheries by river discharge plumes off small estuaries. *Marine Biology Research*, **5**, 164–171.
- Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Ben, C., Green, R.E. & Hutton, J.M. (2010) Large mammal population declines in Africa's protected areas. *Biological Conservation*, **143**, 2221–2228.
- Crawley, K.R., Hyndes, G.A. & Ayvazian, S.G. (2006) Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches. *Marine Ecology Progress Series*, **307**, 233–246.
- Cumming, G.S. (2011) Spatial resilience: integrating landscape ecology, resilience, and sustainability. *Landscape Ecology*, **26**, 899–909.
- Darimont, C.T., Bryan, H.M., Carlson, S.M., Hocking, M.D., Macduffee, M., Paquet, P.C., Price, M.H.H., Reimchen, T.E., Reynolds, J.D. & Wilmers, C.C. (2010) Salmon for terrestrial protected areas. *Conservation Letters*, **3**, 379–389.

- Davies, T.W., Duffy, J.P., Bennie, J. & Gaston, K.J. (2014) The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment*, **12**, 347–355.
- 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, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M. & Scapini, F. (2009) Threats to sandy beach ecosystems: a review. *Estuarine, Coastal and Shelf Science*, **81**, 1–12.
- Dexter, D.M. (1992) Sandy beach community structure: the role of exposure and latitude. *Journal of Biogeography*, **19**, 59–66.
- Dugan, J.E., Defeo, O., Jaramillo, E., Jones, A.R., Lastra, M., Nel, R., Peterson, C.H., Scapini, F., Schlacher, T.A. & Schoeman, D.S. (2010) Give beach ecosystems their day in the sun. *Science*, **329**, 1146.
- EHMP (2010) *Coastal algal blooms of South East Queensland: a field guide*. South East Queensland Healthy Waterways Partnership, Brisbane, Australia.
- Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G. & Harrison, T.D. (2007) The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries*, **8**, 241–268.
- Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.
- Gilby, B.L., Maxwell, P.S., Tibberts, I.R. & Stevens, T. (2015) Bottom-up factors for algal productivity outweigh no-fishing marine protected area effects in a marginal coral reef system. *Ecosystems*, **18**, 1056–1069.
- Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B. & Sheridan, P.F. (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series*, **247**, 281–295.
- Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, **518**, 94–97.
- Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J. & White, A.T. (2014) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, **90**, 1215–1247.
- Grober-Dunsmore, R., Pittman, S.J., Caldwell, C., Kendall, M.S. & Frazer, T.K. (2009) A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. *Ecological connectivity among tropical coastal ecosystems* (ed. by I. Nagelkerken), pp. 493–530. Springer, Heidelberg.
- Hardus, M.E., Lameira, A.R., Menken, S.B.J. & Wich, S.A. (2012) Effects of logging on orangutan behavior. *Biological Conservation*, **146**, 177–187.
- Hastie, T. & Tibshirani, R. (1986) Generalized additive models. *Statistical Science*, **1**, 297–318.
- Hawkins, A.D., Pembroke, A.E. & Popper, A.N. (2015) Information gaps in understanding the effects of noise on fishes and invertebrates. *Reviews in Fish Biology and Fisheries*, **25**, 39–64.
- Hays, G.C. (2008) Sea turtles: a review of some key recent discoveries and remaining questions. *Journal of Experimental Marine Biology and Ecology*, **356**, 1–7.
- Hubbard, D.M., Dugan, J.E., Schooler, N.K. & Viola, S.M. (2014) Local extirpations and regional declines of endemic upper beach invertebrates in southern California. *Estuarine, Coastal and Shelf Science*, **150**, 67–75.
- Huijbers, C.M., Connolly, R.M., Pitt, K.A., Schoeman, D.S., Schlacher, T.A., Burfeind, D.D., Steele, C., Olds, A.D., Maxwell, P.S., Babcock, R.C. & Rissik, D. (2015a) Conservation benefits of marine reserves are undiminished near coastal rivers and cities. *Conservation Letters*, **8**, 312–319.
- Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.W. & Connolly, R.M. (2015b) Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. *Diversity and Distributions*, **21**, 55–63.
- Hyndes, G.A., Potter, I.C. & Lenanton, R.C.J. (1996) Habitat partitioning by whiting species (Sillaginidae) in coastal waters. *Environmental Biology of Fishes*, **45**, 21–40.
- Hyndes, G.A., Nagelkerken, I., McLeod, R.J., Connolly, R.M., Lavery, P.S. & Vanderklift, M.A. (2014) Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biological Reviews*, **89**, 232–254.
- 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.
- Kneib, R. (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology Annual Review*, **35**, 163–220.
- Kool, J.T., Moilanen, A. & Treml, E.A. (2013) Population connectivity: recent advances and new perspectives. *Landscape Ecology*, **28**, 165–185.
- Krüeck, N.C., Chargulaf, C.A., Saint-Paul, U. & Tibbetts, I.R. (2009) Early post-settlement habitat and diet shifts and the nursery function of tidepools during *Sillago* spp. recruitment in Moreton Bay, Australia. *Marine Ecology Progress Series*, **384**, 207–219.
- Layman, C.A. (2000) Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia barrier islands. *Estuarine, Coastal and Shelf Science*, **51**, 201–213.
- Layman, C.A., Quattrochi, J.P., Peyer, C.M. & Allgeier, J.E. (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters*, **10**, 937–944.
- Lewin, W.C., Arlinghaus, R. & Mehner, T. (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science*, **14**, 305–367.

- Loreau, M., Mouquet, N. & Holt, R.D. (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, **6**, 673–679.
- Marshall, A.D., Kyne, P.M. & Bennett, M.B. (2008) Comparing the diet of two sympatric urolophid elasmobranchs (*Trygonoptera testacea* Müller & Henle and *Urolophus kapalensis* Yearsley & Last): evidence of ontogenetic shifts and possible resource partitioning. *Journal of Fish Biology*, **72**, 883–898.
- Massol, F., Gravel, D., Mouquet, N., Cadotte, M.W., Fukami, T. & Leibold, M.A. (2011) Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*, **14**, 313–323.
- McLachlan, A. & Brown, A.C. (2006) Surf-zone fauna. *Ecology of sandy shores* (ed. by A. McLachlan and A.C. Brown), pp. 197–213. Elsevier, Burlington, MA, USA.
- McPhee, D.P., Sawynok, B., Warburton, K. & Hobbs, S.J. (1999) Movements of the surf zone carangid *Trachinotus coppingeri* (Gunther, 1884) in Queensland and northern New South Wales. *Proceedings of the Royal Society of Queensland*, **108**, 89–97.
- Meager, J.J., Schlacher, T.A. & Nielsen, T. (2012) Humans alter habitat selection of birds on ocean-exposed sandy beaches. *Diversity and Distributions*, **18**, 294–306.
- Micheli, F. & Peterson, C.H. (1999) Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology*, **13**, 869–881.
- Mohammadikia, D., Kamrani, E., Taherizadeh, M.R., Soleymani, A., Farokhi, E. & Momeni, M. (2014) Age and growth of flathead, *Platycephalus indicus* from the Persian Gulf (Bandar Abbas, Iran). *Journal of the Marine Biological Association of the United Kingdom*, **94**, 1063–1071.
- Moore, C.H., Van Niel, K. & Harvey, E.S. (2010) The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. *Ecography*, **34**, 425–435.
- Mumby, P.J. & Hastings, A. (2008) The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology*, **45**, 854–862.
- Murphy, H. & Jenkins, G. (2010) Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. *Marine and Freshwater Research*, **61**, 236–252.
- Nagelkerken, I., Sheaves, M., Baker, R. & Connolly, R.M. (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*, **16**, 362–371.
- Noriega, R., Schlacher, T.A. & Smeuninx, B. (2012) Reductions in ghost crab populations reflect urbanization of beaches and dunes. *Journal of Coastal Research*, **28**, 123–131.
- Olds, A.D., Connolly, R.M., Pitt, K.A. & Maxwell, P.S. (2012a) Primacy of seascape connectivity effects in structuring reef fish assemblages. *Marine Ecology Progress Series*, **462**, 191–203.
- Olds, A.D., Connolly, R.M., Pitt, K.A. & Maxwell, P.S. (2012b) Habitat connectivity improves reserve performance. *Conservation Letters*, **5**, 56–63.
- Olds, A.D., Pitt, K.A., Maxwell, P.S. & Connolly, R.M. (2012c) Synergistic effects of reserves and connectivity on ecological resilience. *Journal of Applied Ecology*, **49**, 1195–1203.
- Olds, A.D., Connolly, R.M., Pitt, K.A., Pittman, S.J., Maxwell, P.S., Huijbers, C.M., Moore, B.R., Albert, S., Rissik, D., Babcock, R.C. & Schlacher, T.A. (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography*, **25**, 3–15.
- Pardo, S.A., Burgess, K.B., Teixeira, D. & Bennett, M.B. (2015) Local-scale resource partitioning by stingrays on an intertidal flat. *Marine Ecology Progress Series*, **533**, 205–218.
- Pierce, S.J., Scott-Holland, T.B. & Bennett, M.B. (2011) Community composition of elasmobranch fishes utilizing intertidal sand flats in Moreton Bay, Queensland, Australia. *Pacific Science*, **65**, 235–247.
- Rizkalla, C.E. & Savage, A. (2011) Impact of seawalls on loggerhead sea turtle (*Caretta caretta*) nesting and hatching success. *Journal of Coastal Research*, **27**, 166–173.
- Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015) Protected areas and global conservation of migratory birds. *Science*, **350**, 1255–1258.
- Saunders, M.I., Leon, J.X., Callaghan, D.P., Roelfsema, C.M., Hamylton, S., Brown, C.J., Baldcock, T., Golshani, A., Phinn, S.R., Lovelock, C.E., Hoegh-Guldberg, O., Woodroffe, C.D. & Mumby, P.J. (2014) Interdependency of tropical marine ecosystems in response to climate change. *Nature Climate Change*, **4**, 724–729.
- Schlacher, T.A. & Connolly, R.M. (2009) Land–ocean coupling of carbon and nitrogen fluxes on sandy beaches. *Ecosystems*, **12**, 311–321.
- Schlacher, T.A., Meager, J.J. & Nielsen, T. (2014) Habitat selection in birds feeding on ocean shores: landscape effects are important in the choice of foraging sites by oystercatchers. *Marine Ecology*, **35**, 67–76.
- Schlacher, T.A., Weston, M.A., Schoeman, D.S., Olds, A.D., Huijbers, C.M. & Connolly, R.M. (2015) Golden opportunities: a horizon scan to expand sandy beach ecology. *Estuarine, Coastal and Shelf Science*, **157**, 1–6.
- Schlacher, T.A., Lucrezi, S., Connolly, R.M., Peterson, C.H., Gilby, B.L., Maslo, B., Olds, A.D., Walker, S.J., Leon, J.X., Huijbers, C.M., Weston, M.A., Turra, A., Hyndes, G.A., Holt, R.A. & Schoeman, D.S. (2016) Human threats to sandy beaches: a meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuarine, Coastal and Shelf Science*, **169**, 56–73.
- Schmidt, J.A., McCleery, R., Seavey, J.R., Cameron Devitt, S.E. & Schmidt, P.M. (2012) Impacts of a half century of sea-level rise and development on an endangered mammal. *Global Change Biology*, **18**, 3536–3542.
- Schoeman, D.S., Schlacher, T.A., Jones, A.R., Murray, A., Huijbers, C.M., Olds, A.D. & Connolly, R.M. (2015) Edging along a warming coast: a range extension for a common sandy beach crab. *PLoS One*, **10**, e0141976.

- Sheaves, M. (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series*, **391**, 107–115.
- Sheaves, M. & Johnston, R. (2008) Influence of marine and freshwater connectivity on the dynamics of subtropical estuarine wetland fish metapopulations. *Marine Ecology Progress Series*, **357**, 225–243.
- Stewart, J. & Ferrell, D.J. (2001) Age, growth, and commercial landings of yellowtail scad (*Trachurus novaezelandiae*) and blue mackerel (*Scomber australasicus*) off the coast of New South Wales, Australia. *New Zealand Journal of Marine and Freshwater Research*, **35**, 541–551.
- Thrush, S.F., Halliday, J., Hewitt, J.E. & Lohrer, A.M. (2008) The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries. *Ecological Applications*, **18**, 12–21.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A. *et al.* (2012) Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biological Reviews*, **87**, 661–685.
- 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? *Estuarine, Coastal and Shelf Science*, **60**, 737–754.
- Van Den Broek, J., Peach, M. & Booth, D.J. (2011) The reproductive biology of the common stingaree *Trygonoptera testacea* (Urolophidae) in eastern Australia. *Australian Zoologist*, **35**, 627–632.
- Webley, J., McInnes, K., Teixeira, D., Lawson, A. & Quinn, R. (2015) *Queensland statewide recreational fishing survey 2013–14*. Department of Agriculture and Fisheries, Queensland Government, Brisbane.
- Wedding, L.M., Lepczyk, C.A., Pittman, S.J., Friedlander, A.M. & Jorgensen, S. (2011) Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. *Marine Ecology Progress Series*, **427**, 219–232.
- Weigmann, S. & Thiel, R. (2013) Predicting the spatial distribution of the blue-spotted maskray *Neotrygon kuhlii* (Myliobatiformes, Dasyatidae) on the Australian North and Northwest Shelf comparing two different methods of habitat modeling. *Journal of Ichthyology*, **53**, 628–640.
- Werry, J.M., Lee, S.Y., Lemckert, C.J. & Otway, N.M. (2012) Natural or artificial? Habitat-use by the bull shark, *Carcharhinus leucas*. *PLoS One*, **7**, e49796.
- White, J., Heupel, M.R., Simpfendorfer, C.A. & Tobin, A.J. (2013) Shark-like batoids in pacific fisheries: prevalence and conservation concerns. *Endangered Species Research*, **19**, 277–284.
- White, J., Simpfendorfer, C.A., Tobin, A.J. & Heupel, M.R. (2014) Spatial ecology of shark-like batoids in a large coastal embayment. *Environmental Biology of Fishes*, **97**, 773–786.
- Wilber, D.H., Clarke, D.G., Ray, G.L. & Burlas, M. (2003) Response of surf zone fish to beach nourishment operations on the northern coast of New Jersey, USA. *Marine Ecology Progress Series*, **250**, 231–246.
- Zeller, B.M., Pollock, B.R. & Williams, L.E. (1996) Aspects of the life history and management of tailor (*Pomatomus saltatrix*) in Queensland. *Marine and Freshwater Research*, **47**, 323–329.
- Zuur, A.F., Ieno, N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer, Berlin.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of results from multivariate analyses.

Appendix S2. Summary of results from general additive models.

BIOSKETCH

The research team is based at the University of the Sunshine Coast (Queensland, Australia) and conducts applied and theoretical research in the fields of spatial ecology, conservation biology and marine climate-change ecology. This work has resulted from close collaboration with researchers at Griffith University and Edith Cowan University.

Author contributions: A.O. and T.S. conceived and designed the study; A.O. and E.V. conducted the fieldwork; A.O., B.G. and E.V. analysed the data. All authors contributed to interpreting the results, and writing and revising the manuscript. <http://www.usc.edu.au/connect/research/animal-and-marine-ecology/marine-and-coastal-ecology>.

Editor: Jeremy VanDerWal