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The ecology of fish in the surf zones of ocean beaches: A global review

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Abstract

The surf zones of ocean beaches provide habitat for a diversity of fishes and are prime sites for recreational angling and commercial net fisheries. Here, we review the global literature (152 studies) on surf fish ecology to better inform fisheries management and coastal conservation planning. These studies suggest that surf zones support diverse fish assemblages, which are characterized by high numerical dominance (10 species typically comprise 95% of catches), but also show that few families are especially common. The composition of assemblages is highly variable, changing with fluctuations in water temperature, wave climate and the biomass of drifting algae or seagrass. Fish use surf zones as feeding habitats and transit routes, but these areas might not be widely used as spawning sites or juvenile nurseries. These systems are under escalating human pressures, most notably from coastal urbanization and recreational angling. Despite the recognized ecological and economic importance of surf-zone fishes, few studies have tested for impacts of urbanization or fishing. The benefits of marine reserves for fish in surf zones are also rarely measured. We suggest that progress will be made by moving from largely descriptive studies to hypothesis-driven research, which is guided by contemporary ecological theory and adapts modern techniques from research in other ecosystems. A key challenge is to obtain empirical data that are needed to improve the effectiveness of fisheries management and underpin conservation planning for coastal waters.

KEYWORDS
coastal conservation, fish, fisheries, ocean beach, surf zone, urbanization

1 | INTRODUCTION

Ocean beaches and their surf zones dominate the world's coastlines, comprising 70% of the global interface between land and sea (Bascom, 1980). These shore habitats are of immense economic and social value as prime sites for coastal development, tourism and recreation (Dugan et al., 2010; Huijbers et al., 2015a). Surf zones (i.e. the area of turbulent waves abutting ocean beaches) attract millions of recreational anglers each year and support significant fisheries (Defeo, 2003; Schlacher et al., 2015). Many fish species are prized by recreational anglers, such as tailor (*Pomatomus saltatrix*, Pomatomidae) and mulloway (*Argyrosomus japonicus*, Sciaenidae) (Griffiths, 1997; Lenanton, Ayvazian, Pearce, Steckis, & Young, 1996), or are harvested in commercial fisheries, for example anchovy (*Thryssa vitrirostris*, Engraulidae), mullet (*Mugil cephalus*, Mugilidae) and trevally (*Trachurus trachurus*, Carangidae) (Broadhurst, Millar, Brand, & Uhlmann, 2008; Cabral, Duque, & Costa, 2003; Mualeque & Santos, 2011). Surf zones are also frequented by numerous threatened elasmobranchs that are promoted as flagships for conservation, including white sharks (*Carcharodon carcharias*, Lamnidae) and guitarfish (*Rhynchobatus australiae*, Rhinobatidae) (Kock et al., 2013; Tobin, Mapleston, Harry, & Espinoza, 2014). Surf fish assemblages are increasingly modified by the effects of fishing, habitat alteration and eutrophication (see reviews by Defeo et al., 2009; Schlacher et al., 2014) (Figure 1).

Research on surf fish began in earnest in the 1960s with descriptive accounts of fish abundance, size and diet (Jones, 1973; Okera, 1978). Research is now geographically widespread and includes studies from the Atlantic, Indian and Pacific Oceans and the Mediterranean Sea (Figure 2). Surprisingly, there is no comprehensive review of the literature on fishes in surf zones, the globe's single largest interface between the sea and the land. To address this shortcoming, we reviewed the published literature on fishes in surf zones by searching the Elsevier Scopus and ISI Web of Knowledge databases using all permutations of the keywords: "surf zone," "sandy," "beach," "nearshore," "fish," "shark," "ray" and "elasmobranch." Our primary goals were to determine global patterns in (i) the distribution and thematic focus of surf fish research; (ii) diversity and abundance of fishes in surf zones; (iii) role of environmental conditions in structuring surf fish assemblages; (iv) ecological functions of surf zones as fish habitat; (v) importance of spatial linkages with other ecosystems; and (vi) human interactions with, and conservation of, fish in the surf zones of ocean beaches. We discuss opportunities to improve fisheries management and conservation planning for coastal waters and identify important knowledge gaps to be targeted in future research.

2 | GLOBAL DISTRIBUTION AND THEMATIC FOCUS OF RESEARCH ON SURF FISHES

We identified 152 studies that reported on surf fishes, of which 130 were in temperate and subtropical waters (Figure 2, Table S1 in Supporting Information). Research on surf fish comes from South Africa (42 studies), Brazil (25), the United States (24), Australia (18), Japan (16), Belgium (5), Portugal (4), Ecuador (2), Indonesia (2), Italy (2), Philippines (2), the United Kingdom (2), France (1), Ghana (1), Mozambique (1), the Netherlands (1), Sierra Leone (1), Sweden (1), Thailand (1) and Uruguay (1) (Figure 2).

Surf fish assemblages were mostly sampled with seine nets (*n* = 114), benthic species using beam trawls and sledges (*n* = 14), omnivores via angling (*n* = 13) and larval fish with specialized ichthyoplankton nets (*n* = 15) (Table S1). Seine netting is an effective means of capturing fish from beaches, but it is ineffective and dangerous in heavy surf or in the deeper sections of many surf zones (i.e. where water depth exceeds 2 m) (McLachlan & Brown, 2006). These limitations restrict the conditions in which sampling can be conducted (e.g. to areas of small waves) and bias survey results by underestimating the abundance of benthic species, large predators and highly mobile taxa (Baker & Sheaves, 2006; Dorenbosch, Grol, de Groene, van Der Velde, & Nagelkerken, 2009). It is for this reason that visual and remote techniques (e.g. drones, baited remote underwater video stations—BRUVS) are commonly used to survey fish in many marine habitats (e.g. estuaries, coral reefs, the open sea) (Gladstone, Lindfield, Coleman, & Kelaher, 2012; Murphy & Jenkins, 2010). Visual methods are not, however, widely used to survey fish in surf zones; to date, they have only been used by two surf-zone studies in eastern Australia (Borland et al., 2017; Vargas-Fonseca et al., 2016).

A sizeable proportion of research on surf fishes is descriptive, dealing with either spatial variation in the composition of fish assemblages among beaches (*n* = 36 studies) or temporal variation in assemblage composition with changes in season, time of day or tide (*n* = 36) (Figure 2, Table S1). These descriptive studies account for almost half of the published literature on surf fishes (i.e. 72/151 studies). Thirty-three per cent (*n* = 50) of studies addressed questions about population ecology (*n* = 29) (e.g. larval recruitment, juvenile nursery habitats; Able, Wuenschel, Grothues, Vasslides, & Rowe, 2013) and trophic ecology (*n* = 21) (e.g. feeding habits, food webs; Bergamino, Lercari, & Defeo, 2011) (Figure 2). Seventeen per cent (*n* = 26) of all surf fish studies tested how variation in local environmental conditions shaped the composition of fish assemblages (Pattrick & Strydom, 2014) (Figure 2). Little research has been carried out on fish movement in surf zones (*n* = 5; Parker, Booth, & Mann, 2013), or effects of habitat modification (*n* = 7; Vargas-Fonseca et al., 2016), fishing (*n* = 7; Clark, Bennett, & Lamberth, 1994) and marine reserves (*n* = 2; Venter & Mann, 2012).

3 | DIVERSITY AND COMPOSITION OF FISH ASSEMBLAGES IN GLOBAL SURF ZONES

Surf fish assemblages are characterized by high variability and numerical dominance of few taxa (Clark, 1997; Rishworth, Strydom, & Potts, 2014). Across all studies for which we could extract data (*n* = 62), the 10 most abundant species in each study made up 95% of the total catch, and the single most abundant species comprised, on average, 44% of all individuals sampled (Figure 3, Table S1). Surf fish assemblages are diverse (mean of 33 species per study), but there is wide variation in the number of species reported from the surf zones of ocean beaches (Figure 3). Low species richness (i.e. <9 species) is reported by studies of short duration or limited spatial coverage or with low replication (Marin Jarrin & Shanks, 2011). By contrast, high species richness (i.e. up to 165 species) is a common finding of studies that sample the same location over multiple years (Suda, Inoue, & Uchida, 2002).

To date, 171 fish families have been reported from surf zones (Figure 4, Table S1). Most families (*n* = 118) are comprised of species that are infrequent visitors to surf zones, such as stone fish (Synanceiidae) (Suda et al., 2002). Many other families (*n* = 43), including turbot (Scopthalmidae), are scarce in most surf zones, but can be common in some locations (Vinagre, Silva, Lara, & Cabral, 2011) (Figure 4). By contrast, few families (*n* = 10), for example mullet and

FIGURE 1 Surf zones support iconic fish species including large elasmobranchs that are of international conservation concern, such as white sharks (a), and heavily harvested bony fishes, such as tailor (b). Fish assemblages in surf zones are impacted by intense recreational fishing (c), commercial netting (d), coastal urbanization (e) and beach modification (f). Photographs by A. Olds, B. Markwell, D. Clark, J. Sears, M. Armistead and W. Gladstone. [Colour figure can be viewed at wileyonlinelibrary.com]

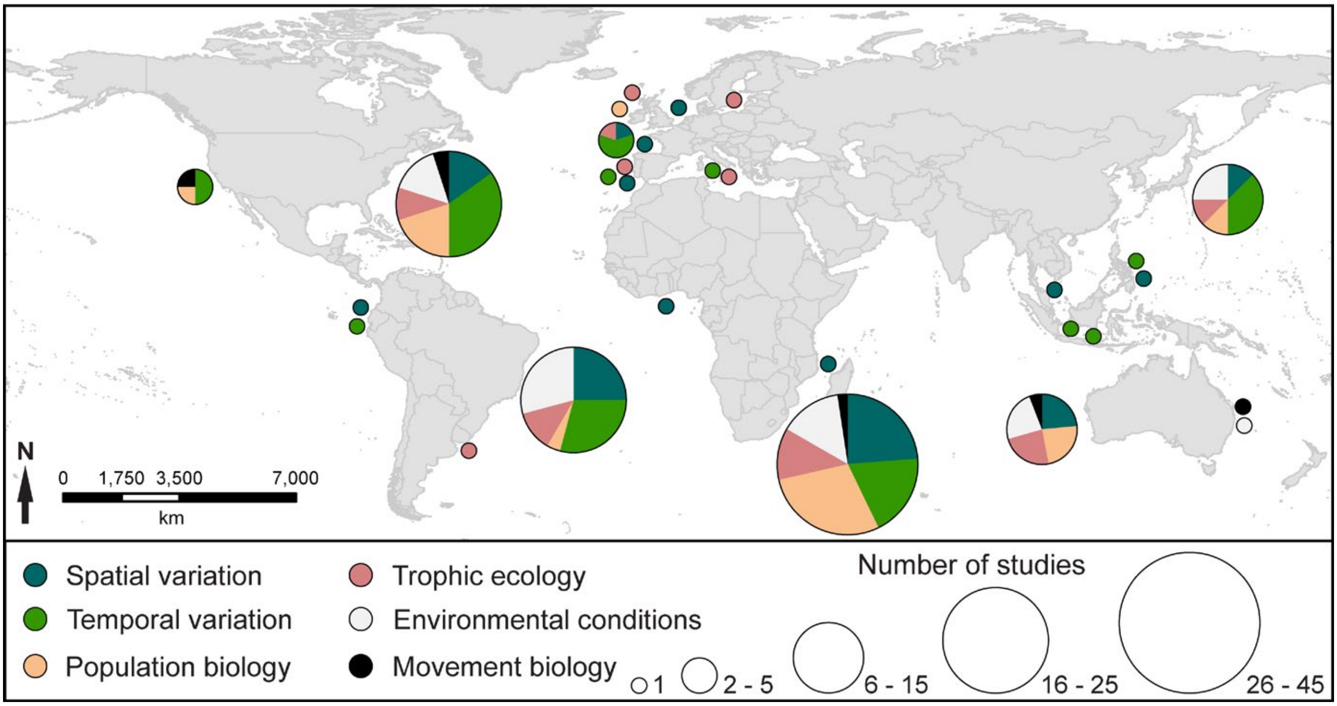

FIGURE 2 Global distribution of fish ecology studies (*n* = 152) from the surf zones of ocean beaches. Pie charts illustrate the thematic focus and number of papers from each country (Table S1). [Colour figure can be viewed at wileyonlinelibrary.com]

herring (Clupeidae), are common and numerically dominate surf fish assemblages (Mikami, Nakane, & Sano, 2012) (Figure 4).

Fish families that are both common and abundant in surf zones include anchovy (Engraulidae), herring, mullet, mulloway, pipefish and seahorses (Syngnathidae), puffers (Tetraodontidae), silversides (Atherinidae), surf bream (Sparidae), tailor and trevally (Figure 4). Most of these fish families contain species that are well adapted to the high-energy physical conditions of surf zones. Many are silver schooling species with bodies that are fusiform (e.g. mullet), laterally compressed (e.g. trevally) or dorsoventrally flattened (e.g. puffers) (Lauder, 2015;

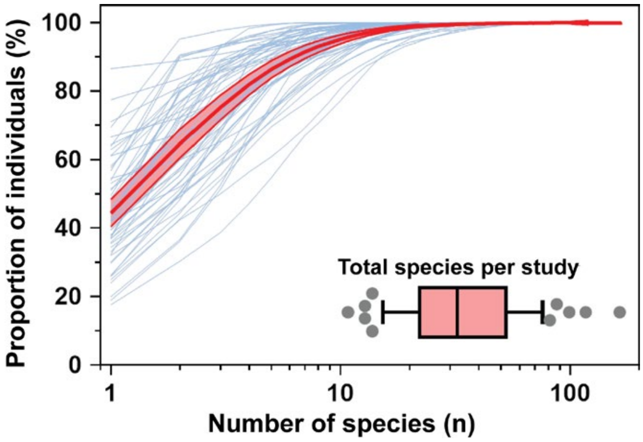

FIGURE 3 Species dominance (k-dominance curves) and species richness (insert bar graph) of fish assemblages from studies in surf zones of ocean beaches (*n* = 62; thin lines are individual studies and thick lines the mean ± 95% confidence limit) (Table S1). [Colour figure can be viewed at wileyonlinelibrary.com]

Webb & Weihs, 1983). Fusiform bodies are streamlined, and lateral compression increases manoeuvrability, whereas dorsoventrally flattening allows fish to bury or remain on the sand surface while waves move over them (Lauder, 2015). These three body plans are likely advantageous for fish in turbulent surf zones (Tatematsu et al., 2014). Pipefish and seahorses are less well adapted to life in the surf; they have thin armoured bodies with small fins and are characterized by their limited mobility and narrow dietary niches; most species live in close association with benthic algae and seagrass (Connolly, Melville, & Keesing, 2002; Kendrick & Hyndes, 2005). Pipefish and seahorses are only likely to be abundant in surf zones when strong winds and waves wash them in from their preferred habitats, or when they arrive with mats of drifting algae (Crawley, Hyndes, & Ayvazian, 2006; Nakane, Suda, & Sano, 2013).

4 | ENVIRONMENTAL DETERMINANTS OF SURF FISH ABUNDANCE AND DIVERSITY

Most studies describe spatio-temporal variation in species abundance or diversity without measuring how these changes relate to variation in environmental conditions (e.g. water quality, wave climate, beach morphology) (Figure 2). A few studies (*n* = 26) have tested for associations between environmental variables and the composition of fish assemblages in surf zones (Figure 2), mostly with the physical or chemical properties of surf zones, including water temperature (*n* = 20), wave climate (*n* = 13), biomass of drifting macrophytes (*n* = 12), salinity (*n* = 11), wind (*n* = 10) and turbidity (*n* = 8) (Figure 5, Table S1). There appears to be a positive effect of water temperature, wind speed and the biomass of drifting macrophytes on fish abundance and diversity (Figure 5). Surf fish abundance and diversity is also often negatively correlated with wave climate (i.e. wave height, period and speed), salinity and turbidity (Figure 5).

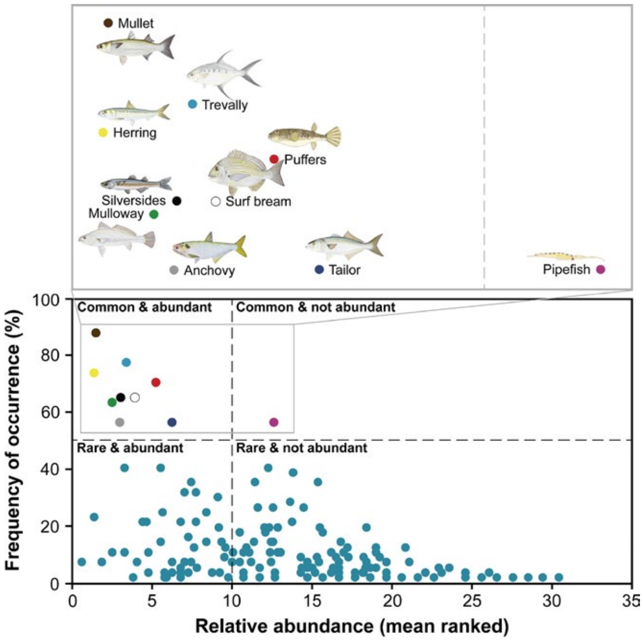

FIGURE 4 Relative abundance and frequency of occurrence of fish families from surf zones globally. Families were ranked by (i) summing all individuals per family in individual studies and (ii) ranking families across all studies (*n* = 58) in terms of the mean abundance (*x*-axis). Frequency of occurrence is the proportion of studies that reported species from each family (*y*-axis) (Table S1). We illustrate "common families" as those that occurred in more than half of all studies and "abundant families" as those that ranked within the top 10 in the global data set. [Colour figure can be viewed at wileyonlinelibrary.com]

Water temperature is positively correlated with fish abundance and diversity in many marine ecosystems (Harborne & Mumby, 2011), and so the widely reported effects of temperature on surf fish assemblages are not surprising (Rodrigues & Vieira, 2012). Positive effects on surf fish assemblages have been reported when water temperatures change by as little as 2°C (e.g. 16–18°C) and as much as 23°C (e.g. 6–29°C), with most studies surmising that this relates to the seasonal occurrence of transient species (Layman, 2000; Nanami & Endo, 2007).

Biomass of drifting macrophytes (principally algae and seagrass) in surf zones is positively correlated with greater fish abundance and diversity (Crawley et al., 2006; Lenanton, Robertson, & Hansen, 1982). Macrophytes are uprooted from abutting habitats (e.g. reefs, kelp beds, seagrass meadows) and drift into surf zones where they can provide shelter and feeding opportunities for fishes, particularly for species that are able to prey on the invertebrates that drift with macrophytes and use them as habitat (e.g. amphipods) (Hyndes et al., 2014).

Fish abundance and size are negatively correlated with wave height, period and speed, while diversity is usually greatest at intermediate levels of exposure (Clark, 1997; Pattrick & Strydom, 2014). Many fish species are most abundant in the surf zones of low-energy beaches with small waves, but some species can be common in the large surf of ocean beaches (Hyndes, Potter, & Lenanton, 1996; Inui

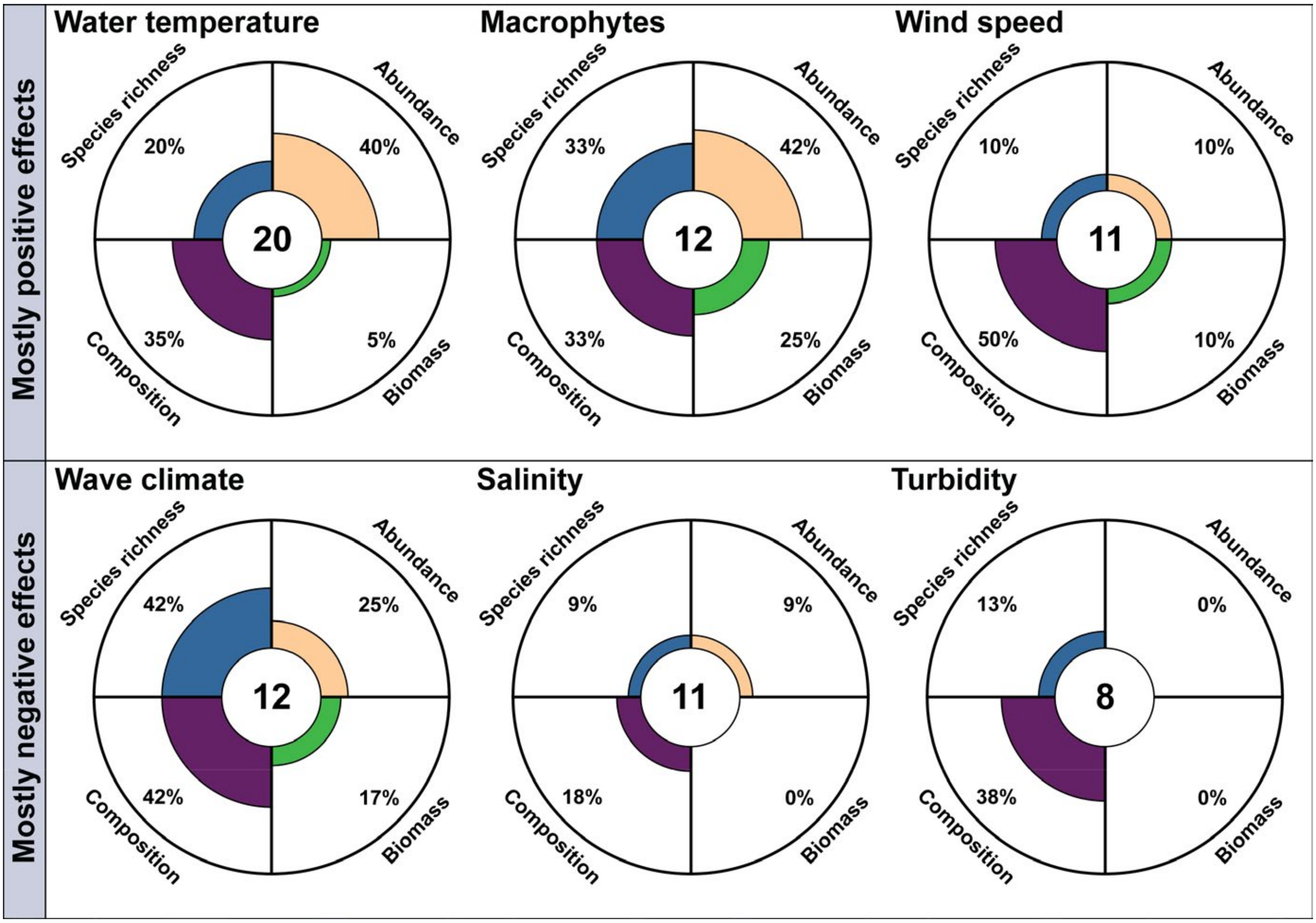

FIGURE 5 Environmental factors identified in the global literature to be associated with changes in surf fish assemblages. Circles provide synopses of research on six environmental factors (i.e. water temperature, macrophytes, wind speed, wave climate, salinity and turbidity). The total number of studies examining each environmental factor is shown in the centre of each circle. Circle quarters represent summaries of correlations with surf fish assemblages (i.e. species richness, abundance, biomass, composition). The proportion of studies reporting significant effects is illustrated by a quadrant's size and is provided as a percentage (e.g. 33% of macrophyte studies report positive effects on fish species richness). [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2010; Valesini, Potter, & Clarke, 2004). Surf zones comprise several microhabitats (e.g. gutters, runnels, sandbars), which experience different wave energy conditions and consequently may support distinct fish assemblages (Layman, 2000; McLachlan & Brown, 2006). Fish diversity and abundance can be greatest in gutters or runnels (but see Borland et al., 2017), which are areas of deeper and less turbulent water that occur away from breaking waves (Janssen, Kleef, Mulder, & Tydeman, 2008; Watt-Pringle & Strydom, 2003). Shallow turbulent waters over sandbars also provide foraging areas for juvenile fishes (Able et al., 2013), support large elasmobranchs that are of conservation concern (Vargas-Fonseca et al., 2016) and sustain high functional diversity (Borland et al., 2017).

Differences in water chemistry (e.g. salinity, turbidity) and weather conditions (e.g. wind speed) affect the composition of fish assemblages in most coastal ecosystems (Blaber, 2013; Olds et al., 2014; Sheaves, Johnston, & Connolly, 2012), but there is no consensus on how these variables influence fish in the surf zones of beaches. Several studies have described that salinity, turbidity and wind speed can modify the composition of fish assemblages (Lasiak, 1984a; Rodrigues & Vieira, 2012), while numerous others report no effects (Inui et al., 2010; Wilber, Clarke, Burlas, Ruben, & Will, 2003a). Most research was, however, not designed to test for effects on the composition of fish assemblages over broad ranges of either salinity, turbidity or wind speed. Gradients in salinity and turbidity shape the composition of fish assemblages in estuaries (Blaber, 2013) and we predict that future research will show that they are of similar importance to fish in surf zones.

5 | SURF ZONES AS FISH HABITAT

Fish use surf zones as feeding areas, refuges from predators, spawning sites and nursery habitats (Ayvazian & Hyndes, 1995; Layman, 2000; Lenanton et al., 1982; Strydom & D'Hotman, 2005). Well-known examples that illustrate these habitat functions of surf zones include their use as nocturnal feeding areas by mulloway (Griffiths, 1997); refuges from predation and foraging habitats by whiting (*Sillago japonica*, Sillaginidae) (Nakane, Suda, & Hayakawa, 2009); spawning grounds by grunion (*Leuresthes tenuis*, Atherinopsidae) (Griem & Martin, 2000); and juvenile nurseries and feeding areas by tailor (Lenanton et al., 1996) (Figure 6).

5.1 | Foraging habitats

The trophic ecology of surf fishes has been reasonably well studied (*n* = 21), at least by comparison with other the potential roles of surf zones as fish habitat (Bergamino et al., 2011; McLachlan & Brown, 2006). Most species are either planktivores (e.g. silversides), detritivores (e.g. mullet), benthic predators (e.g. trevally) or piscivores (e.g. tailor) (Elliott et al., 2007; Lercari, Bergamino, & Defeo, 2010). By contrast, there are few species of herbivores in the surf zones of ocean beaches.

A rising tide provides access to new food resources for fish that forage in the intertidal zones of beaches, and many species move up the beach at this time to capitalize on the rich diversity of feeding opportunities (sensu Sheaves, 2005; Hyndes et al., 2014). Thus, foraging activity varies with tidal, diel and seasonal changes in food abundance. Small benthic predators (e.g. whiting) feed on intertidal invertebrates when the tide provides access to the beach face (Hyndes et al., 1996; Nakane, Suda, & Sano, 2011). Larger benthic predators (e.g. mulloway) move into surf zones at night to forage on fish and crustaceans (Griffiths, 1996). Piscivores (e.g. tailor) and detritivores (e.g. mullet) feed in surf zones during seasonal migrations to other habitats (Lenanton et al., 1996; Romer & McLachlan, 1986).

5.2 | Refuges from predators

Juvenile fish can be particularly abundant in the gutter habitats of surf zones (e.g. runnels and troughs, which run parallel to beaches and provide areas of deeper, and less turbulent, water between bars), which has led to the hypothesis that these areas might restrict the access, manoeuvrability and foraging efficiency of large predatory fishes (Inoue, Suda, & Sano, 2008). The *refuge-from-predation* hypothesis is a common contention in the surf fish literature, but it has rarely been tested with empirical data (Nakane et al., 2009; Tobin et al., 2014). Predatory fishes can be both diverse and abundant in surf zones (Tobin et al., 2014; Vargas-Fonseca et al., 2016), and predation experiments (*n* = 2), which measure the consumption of tethered prey fish, show that predators can exert heavy mortality on juvenile fish across surf-zone habitats (Gibson & Robb, 1996; Nakane et al., 2009). The results of these studies challenge the notion that surf zones provide juvenile fish with an effective refuge from predators.

The *refuge-from-predation* hypothesis was first conceived as a possible explanation for the high abundance of juvenile fishes in shallow estuarine habitats. It has since been critically examined for seagrass meadows, mangrove forests and intertidal flats (Dorenbosch et al., 2009; Hindell, 2006; Sheaves, 2001) and is often not supported by empirical data (but see Paterson & Whitfield, 2000). Consequently, research in other coastal systems is now concerned with testing how predation shapes the timing and extent of ontogenetic migrations across seascapes (Nagelkerken, Sheaves, Baker, & Connolly, 2015).

5.3 | Spawning sites

Many fish species move through the surf zones of ocean beaches on their spawning migrations from estuaries to marine waters (Gillanders, Able, Brown, Eggleston, & Sheridan, 2003; Ray, 2005). Reproductively ripe and spent individuals of many fish species have been recorded in surf zones, but there is no evidence of actual spawning by these taxa (Lasiak, 1983b, 1984b). In addition, the low numbers of fish eggs and preflexion larvae in surf-zone ichthyoplankton (Strydom, 2003;

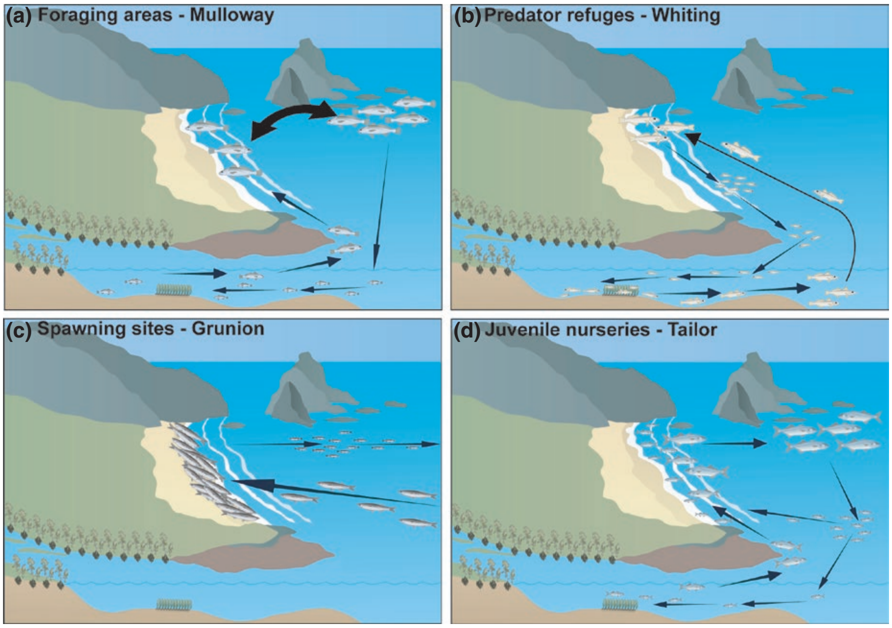

FIGURE 6 Conceptual diagram illustrating the diverse functions of surf zones as habitat for fishes and the importance of spatial connections to other coastal ecosystems. Mulloway move into surf zones at night from nearby rocky reefs and estuaries to feed on benthic invertebrates (a). Whiting migrate to surf zones from estuaries and use these areas as refuges from predators and feeding grounds (b). Grunion migrate to surf zones from coastal waters to spawn on exposed beaches (c). Tailor use surf zones as juvenile nurseries and feeding areas and as dispersal routes on spawning migrations from estuaries to rocky headlands (d) (symbols courtesy of the IAN, ian.umces.edu/symbols/). [Colour figure can be viewed at wileyonlinelibrary.com]

Whitfield, 1989) suggest that most coastal fish species spawn further offshore (Pattrick & Strydom, 2008).

Empirical evidence of spawning in surf zones of beaches is limited to two genera: grunion (*Leuresthes* spp., Atherinopsidae) and surf smelt (*Hypomesus* spp., Osmeridae). Grunion undertake mass spawning migrations to deposit their eggs into the exposed face of surf beaches in California and Mexico (Griem & Martin, 2000). Surf smelt migrate *en masse* to spawn in the shallow swash areas of surf beaches in the United States and Japan (Quinn et al., 2012). Spawning in shallow water, or on the beach face, can be a risky strategy for fish (i.e. greater risk of stranding, egg desiccation and predation from beach invertebrates), but it also affords eggs with advantages (i.e. warmer temperatures and high oxygenation) that aid their development (Martin & Swiderski, 2001). The high turbulence of exposed surf zones also makes these areas hazardous for spawning fishes and possibly limits the extent to which they are used for this purpose (Hyndes & Potter, 1997).

5.4 | Juvenile nursery habitats

Many studies have postulated that surf zones function as nursery habitats for fish because assemblages are frequently dominated by larvae and juveniles of species that differ to those in nearby coastal habitats (Able et al., 2013; Lasiak, 1981; Whitfield & Pattrick, 2015). Surf zones also support an abundance of post-larvae and early juveniles of estuary-associated fish species, which suggests that these habitats may function as settlement sites or interim nurseries for some fish species (Whitfield, 1989). To function as a nursery for juvenile fish, it is, however, not sufficient to simply support an abundance of juveniles: effective nursery habitats must also promote fish growth and survival and allow individuals to migrate to adult habitats and reproduce (Beck et al., 2001). These criteria can be difficult to test even in sheltered estuaries (Nagelkerken et al., 2015) and are particularly challenging to address in the dynamic conditions of exposed surf zones. Data on juvenile abundance and growth ($n = 6$) suggest that surf zones might be alternative nurseries to estuaries for certain mullet (*Liza richardsonii* and *Mugil curema*, Mugilidae), trevally (*Trachinotus carolinus*, Carangidae), surf bream (*Diplodus capensis*, *Lithognathus mormyrus* and *Rhabdosargus globiceps*, Sparidae), grunts (*Pomadasys olivaceus*, Haemulidae) and salmon (*Oncorhynchus tshawytscha*, Salmonidae) (Able et al., 2013; Lasiak, 1981, 1983a; Marin Jarrin & Miller, 2013; Rishworth, Strydom, & Potts, 2015; Whitfield & Pattrick, 2015). The strongest evidence that surf zones provide a nursery function is available for tailor, which can be abundant and grow rapidly in surf zones before migrating to other locations as adults (Able et al., 2013; Whitfield & Pattrick, 2015).

Given that the nursery functions of surf zones have rarely been measured by testing for effects on juvenile growth, survival and ontogenetic migration, there is much work to be done before we can confirm whether surf zones represent effective nurseries for juvenile fish. Surf zones are, however, just one of the many habitats that are used by fish species that migrate among different ecosystems in coastal seascapes (Gillanders et al., 2003; Ray, 2005). Their value as a nursery for fish should therefore not be viewed in isolation from the other ecosystems to which they are functionally linked by fish migration (sensu Whitfield, 1989; Nagelkerken et al., 2015).

6 | SURF ZONES ARE LINKED TO OTHER COASTAL ECOSYSTEMS

Fish assemblages in the surf zones of ocean beaches are influenced by the effects of spatial linkages with other ecosystems (Ayvazian & Hyndes, 1995; Schlacher et al., 2015). Fish move from surf zones to other habitats (e.g. estuaries, coral and rocky reefs) to feed, spawn and disperse (Vargas-Fonseca et al., 2016). The post-larvae of some estuary-associated marine fishes also recruit to surf zones before moving into estuaries (Whitfield, 1989). These movements modify spatial patterns in fish abundance and diversity across coastal seascapes (Gillanders et al., 2003) (Figure 6). Surf zones are also functionally linked to estuaries, seagrass meadows and reefs through the translocation of organic material (seagrass, algae, carrion), which provides food for invertebrates and fish (Crawley, Hyndes, Vanderklift, Revill, & Nichols, 2009; Hyndes et al., 2014; Schlacher & Connolly, 2009).

The effects of this seascape connectivity are particularly well documented for fish assemblages in estuarine and coral reef seascapes (Nagelkerken et al., 2015; Olds et al., 2016), but their potential consequences for surf fishes are rarely tested with empirical data (Schlacher et al., 2015). Research into the ecological effects of seascape connectivity on surf fish assemblages ($n = 5$) has demonstrated that spatial linkages with estuaries and reefs can affect fish abundance and species richness in surf zones (Ayvazian & Hyndes, 1995; Valesini et al., 2004; Vargas-Fonseca et al., 2016). The translocation of uprooted kelp fronds to ocean beaches provides food for fish (principally from amphipods that travel with kelp) and modifies fish diet and abundance in the surf zones of ocean beaches (Crawley et al., 2006, 2009). All of these studies are geographically limited to Australian surf zones. Thus, research needs to be expanded to other biogeographic regions to test the broader relevance of seascape connectivity for fish in surf zones.

7 | HUMANS AND SURF FISHES: HABITAT MODIFICATION, FISHING AND CONSERVATION

Beaches are focal points for coastal development, recreation and fishing (Schlacher et al., 2014) (Figure 1). The cumulative impacts of human use (e.g. walking on dunes, 4WDs on the beach), shoreline modification (e.g. grooming, nourishment, armouring) and contamination (e.g. nutrients, sediments, toxicants) modify the abundance of fauna on beaches that border coastal cities (Defeo et al., 2009; Huijbers et al., 2015a; Schlacher et al., 2016). Data on anthropogenic effects on surf fishes are limited to impacts from urbanization ($n = 1$), beach nourishment ($n = 3$) and artificial shoreline structures ($n = 3$). The single study to examine the effects of coastal urbanization on surf fish assemblages (Vargas-Fonseca et al., 2016) reported that fish diversity and abundance of piscivorous fishes were lowest in the surf zones of highly urban beaches in Australia. Beach nourishment studies either report no significant effects on fish assemblages (Ross & Lancaster, 2002) or describe impacts to fish abundance, diversity and diet (Manning, Peterson, & Fegley, 2013; Wilber, Clarke, Ray, & Burlas, 2003b). Studies on the effects of artificial structures either report no impact of jetties or breakwaters on fish assemblages (Mikami et al., 2012; Rodrigues & Vieira, 2012) or outline changes to fish abundance and diversity that are attributed to the construction of groins (Tatematsu et al., 2014).

Ocean beaches attract millions of recreational anglers each year and are focal points for commercial netting (Cabral et al., 2003; Clark et al., 1994; McLachlan & Brown, 2006). Large predators are also routinely removed from surf zones in shark control programmes aimed at improving swimmer safety (Gibbs & Warren, 2015). Angling, netting and shark control programmes harvest fish from different guilds and might have altered the diversity and trophic composition of surf fish assemblages, but surprisingly little research has been carried out to investigate their impact in surf zones globally ($n = 7$).

Fishing has changed the abundance, diversity and composition of surf fish assemblages in Australia, Brazil, Portugal and South Africa (Cabral et al., 2003; Clark et al., 1994; Franco, Ramos Chaves, Castel-Branco, & Neves Dos Santos, 2016; Mualeque & Santos, 2011; Parker et al., 2013). Two studies correlate changes in fishing practices with variation in fish abundance over multiple years (7 years, Bennett, 1991, 20 years, Rishworth et al., 2014). Both report evidence of overfishing in South African surf zones, including a reduction in fish abundance and a shift in dominance to smaller fishes at lower trophic levels (Rishworth et al., 2014). It appears that fishing can modify fish assemblages in the surf; however, we do not know whether different forms of fishing (e.g. recreational angling, commercial netting, shark control programmes) exert distinct impacts.

There are also limited data to show how surf fish assemblages respond to fisheries management actions (e.g. size limits, catch quotes, closed seasons) that are enacted to minimize impacts of fishing on surf fishes. South African fisheries for tailor provide a prominent example of management success. Tailor fishing was banned after catches declined from 12.5 to 5 fish per 100 hr of fishing between 1956 and 1973 (van der Elst, 1976). Tailor populations recovered by 1988 and recreational angling and commercial fisheries recommenced (Mann, 2000).

Marine reserves are a common, and effective, tool for conserving biodiversity and ecosystem functioning (Lester et al., 2009; Olds et al., 2016). Reserves that prohibit fishing can promote the density, body size and biomass of harvested fishes (Huijbers et al., 2015b). Despite their widespread success in other ecosystems, only two studies have examined the effects of marine reserves on fish in surf zones (Bennett & Attwood, 1991; Venter & Mann, 2012). These studies assessed the effectiveness of the De Hoop and Dwesa-Cwebe reserves in South Africa, and both report higher fish abundance and diversity inside marine reserves than in nearby fished areas. These results require broader testing to confirm whether marine reserves provide effective conservation for fish in other surf zones, and to improve planning decisions about coastal conservation.

8 | FUTURE DIRECTIONS

The inventory of fish species from global surf zones is incomplete (Figure 2). As fish are surveyed from other ocean beaches and new sampling techniques become more widely adopted (e.g. BRUVS, drones) (Vargas-Fonseca et al., 2016), we predict that many more fish species and families will be reported from the surf zones of ocean beaches (Research Priority 1; Table 1). Surprisingly, few studies have examined how surf fish assemblages are modified by environmental conditions (e.g. wave climate, water quality and drifting macrophytes) (Research Priority 2; Table 1). Beach morphology, exposure and coastal hydrodynamics can also affect fish assemblages in the surf (Borland et al., 2017; Pattrick & Strydom, 2014). The abundance, diversity and size of macrofauna on beaches are shaped, globally, by tidal range, sediment grain size and both the width and slope of beaches (Defeo & McLachlan, 2013; Schlacher & Thompson, 2013). These morphological features of beaches are modified by sediment supply, tides and wave exposure and alter the availability of both food (e.g. invertebrate prey) and habitat (e.g. gutters, runnels, bars) for surf fishes, but it is not clear to what extent they influence the composition of surf fish assemblages (Research Priority 3; Table 1).

It is widely believed that fish use surf zones as habitat for feeding, seeking refuge from predators and spawning and as juvenile nurseries, but these hypothesized habitat functions of surf zones are rarely tested with empirical data (Able et al., 2013; Tobin et al., 2014; Vargas-Fonseca et al., 2016). Translocated organic material (seagrass, algae, carrion) provides food for invertebrates and fish in surf zones (Crawley et al., 2009); these trophic subsidies are widespread on ocean beaches, but their role in coastal food webs is not well documented. Stable isotope analysis (see reviews by Hyndes et al., 2014; Layman et al., 2015) will be useful for tracing sources of fish nutrition and understanding food webs in surf zones (Research Priority 4; Table 1). The abundance of predators and heavy predation on small fishes in surf zones indicate that these habitats may not provide juvenile fish with a particularly effective refuge from predators (Nakane et al., 2009; Tobin et al., 2014). Predation might therefore modify fish abundance and movement, but it is not clear where predators occur in surf zones or whether particular microhabitats (e.g. wrack, sand bars) provide any form of reprieve from predation (Research Priority 5; Table 1). Empirical evidence of spawning is rare and limited to grunion and surf smelt, which spawn largely on beaches (Martin & Swiderski, 2001). Consequently, it has been suggested that surf zones might not make suitable spawning sites for many fishes (Hyndes & Potter, 1997); this hypothesis requires further testing (Research Priority 6; Table 1). Similarly, few studies have attempted to assess whether surf zones function as nurseries for juvenile fish (sensu Beck et al., 2001; Nagelkerken et al., 2015). Juvenile fish can be abundant and grow in surf zones (Able et al., 2013), but we do not know the proportion of juveniles of any species that survive and migrate to adult habitats to reproduce (Research Priority 6; Table 1). Nevertheless, fish move into surf zones from other habitats and this connectivity structures fish populations, food webs and ecosystem functions across coastal seascapes (Olds et al., 2016). It is not clear, however, whether these

TABLE 1 Priority questions for research on the ecology of fishes from surf zones of ocean beaches. Cited studies provide examples of potential approaches for examining each question

Priority research questions
1. Unexplored biodiversity: What fish species, families and life stages are found in assemblages from surf zones that have not yet been sampled? (e.g. Vargas-Fonseca et al., 2016).
2. Environmental conditions: Which combination of environmental factors (e.g. wave climate, water quality, drifting macrophytes) is most influential in structuring fish assemblages in the surf zones of ocean beaches? (e.g. Clark, 1997).
3. Beach and seabed morphology: What is the role of bathymetry, exposure and coastal hydrodynamics in shaping fish assemblages in surf zones? (e.g. Borland et al., 2017).
4. Trophic ecology: What is the relative contribution of imported organic material (e.g. macrophytes, carrion) and local production (e.g. phytoplankton) to food webs in the surf? (e.g. Bergamino et al., 2011).
5. Predators and predation: How abundant and diverse are large predators in surf zones, and how does predation shape fish assemblages in surf zones? (e.g. Nakane et al., 2009).
6. Spawning and nursery habitats: Are surf zones used as spawning sites by fish other than grunion and surf smelt, and are these areas effective as nurseries for juvenile fishes? (e.g. Able et al., 2013).
7. Seascape connectivity: Ocean beaches exchange individuals and matter with adjoining ecosystems, but does this connectivity have prominent functional effects on fish assemblages in the surf? (e.g. Vargas-Fonseca et al., 2016).
8. Urbanization impacts: How severe and widespread are the ecological impacts of coastal development on surf-zone ecosystems? (e.g. Wilber et al., 2003b).
9. Fishing effects: How have different types of fishing modified the diversity, abundance and composition of fish assemblages in surf zones? Are these fisheries sustainable, and which species are at particular risk from harvesting? (e.g. Rishworth et al., 2014).
10. Spatial conservation: What combination of reserve features (e.g. size, age, spacing) and seascape characteristics (e.g. habitat diversity, connectivity) promotes conservation performance in surf zones? (e.g. Olds et al., 2016).

functional effects of connectivity are prominent features of global surf zones (Research Priority 7; Table 1).

Most ocean beaches have been modified by human actions (e.g. urbanization, shoreline modification, pollution, fishing) (Defeo et al., 2009; Schlacher et al., 2014). The potential ecological consequences of these activities for surf fish are rarely considered in ecological impact assessments or fisheries management. Consequently, it is not clear whether the ecological effects of coastal development are severe in surf zones (Research Priority 8; Table 1). Furthermore, intense fishing pressure leads to significant reductions in fish abundance, biomass and diversity, but there are no published data that can be used to determine what level of fishing effort is sustainable or which species are particularly at risk from harvesting in surf zones (Research Priority 9; Table 1). Marine reserves have been implemented globally to conserve biodiversity and protect threatened species (Huijbers et al., 2015b), but modern principles of conservation planning are rarely applied to ocean beaches (Harris, Nel, Holness, & Schoeman, 2015) and empirical data on reserve effectiveness are needed to improve conservation decisions for ocean beaches (Research Priority 10; Table 1).

9 | CONCLUSIONS

Despite the prominent ecological, economic and social roles of ocean beaches, we lack basic information on the biology of many surf-zone fishes. Most research is purely descriptive, and surprisingly little is known about why fish use surf zones as habitat. Moreover, it is not clear how the habitat values of surf zones for fishes change with variation in the physical properties of surf zones (e.g. water chemistry, wave height, beach morphology, bathymetry), or in response to impacts from heavy fishing pressure and coastal urbanization. Consequently, there are many opportunities for research on the ecology of fish from ocean beaches. Working in tumultuous surf zones presents unique challenges for researchers and their equipment, and more efficient technologies are thus required to improve the accuracy and safety of studies of surf biota. To advance our understanding of surf fish assemblages, we must draw on ecological theory and experimental techniques that are applied to study fish in other coastal ecosystems. The chief priorities for research are to obtain data on the ecological effects of fishing and coastal urbanization, and to identify features that promote marine reserve performance; this is critical for optimizing marine spatial planning on exposed coastlines.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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