Marine Biology (1995) 122:527–536

S. G. Ayvazian · G. A. Hyndes

Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna?

Received: 15 December 1994/Accepted: 20 January 1995

Abstract Nearshore fish faunas from 32 sites along 1500 km coastline of temperate south-western Australia were sampled by seine net between 1991 and 1992 to examine the species composition in sandy surf zones along this region, and to determine whether it is influenced by adjacent nearshore habitats and the warm southward flowing Leeuwin Current. Although the ichthyofauna was diverse, with 95 species from 47 families recorded, it was numerically dominated by only a few species. Species of Atherinidae, Mugilidae, Tetraodontidae, Clupeidae and Pomatomidae, such as *Atherinomorus ogilbyi*, *Leptatherina presbyteroides*, *Mugil cephalus*, *Aldrichetta forsteri*, *Torquigener pleurogramma*, *Hyperlophus vittatus*, *Spratelloides robustus* and *Pomatomus saltatrix*, were often common to these surf zones. When the species composition of the surf zones was compared with that found in adjacent nearshore habitats, 38 and 42% of the species were shared with reefs and seagrass beds, respectively, and 22% were present in all three habitats. Classification and ordination demonstrated that the faunal composition on the west coast was distinct from that on the south coast, and within each of these regions there were discrete assemblages. There was a marked decline in the number of species on the south coast, with 20 to 66 species reported from the six west-coast assemblages and 11 to 16 species collected from the four south-coast assemblages. A high proportion of resident species was found in the surf zones on both coasts; however, there was a smaller contribution of transient species on the south coast than on the west coast. This decline in transient species was associated with the absence of tropical species on the latter coast. Benthic invertevores were dominant on both coasts, while trophic diversity decreased and the proportion of zooplanktivores increased on the south coast. These differences in the characteristics of the fish fauna between the two coasts can be related to the presence of seagrass beds and limestone patch reef adjacent to sandy surf-zone areas on the west coast which provide more microhabitats for fish. The presence of inshore limestone reefs along the west coast moderates wave energy, producing more sheltered and temporally stable surf zones. The lower number of species on the south coast can also be attributed to the reduced influence of the Leeuwin Current. This southward flowing current acts as a mechanism for the dispersal of tropical species which display no regular association with the surf zones on the lower west coast.

Communicated by G.F. Humphrey, Sydney

S.G. Ayvazian (✉)[1]
Department of Zoology, The University of Western Australia, Nedlands, Western Australia 6009, Australia

G.A. Hyndes
School of Biological and Environmental Sciences, Murdoch University, Murdoch, Western Australia 6150, Australia

Present address:
[1] Western Australian Marine Research Laboratory, P.O. Box 20, North Beach, Western Australia 6020, Australia

Introduction

The surf zones of sandy beaches are physically dynamic environments which provide little habitat complexity for fishes (Robertson and Lenanton 1984). Although the fish faunas of surf zones have not received the same attention as those in estuarine or seagrass environments, due to the difficulty of sampling and the perception that they contain a depauperate fauna (see Brown and McLachlan 1990), these nearshore environments can support significant fish populations (Lasiak 1981, 1984a, b; Lenanton et al. 1982). The fish faunas associated with these regions are dominated by a small number of numerically abundant species, which are generally represented by juveniles (Lasiak 1981, 1984a, b; Lenanton 1982; Robertson and Lenanton

1984). The high proportion of juvenile fishes suggests that, for many species of marine fishes, nearshore sandy beach environments provide an important alternative nursery habitat to estuaries (Brown and McLachlan 1990).

The utilisation of the surf zones by large numbers of juvenile fishes is almost certainly due to the presence in these areas of rich food resources in the form of zooplankton and the protection from predation provided by the shallowness, turbidity and turbulence of these waters (Lasiak 1986). Furthermore, the large wracks of detached macrophytes that often accummulate in these nearshore regions provide food and shelter for the juveniles of some species of fish (Lenanton et al. 1982; Robertson and Lenanton 1984). However, the spatial and temporal instability of surf zones, which results from variable physical features such as wind and wave exposure, produces a dynamic fish assemblage (Romer 1990), with most juvenile fishes using these regions either seasonally or opportunistically (Lasiak 1984a, b). The changing features of this habitat and the mobility of juvenile fishes greatly influences the composition of the fish communities in these regions.

The proximity of nearshore sandy-beach habitats to reefs and seagrass beds in south-western Australia may also influence the species composition in these surf-zone areas. The lower west coast of Australia contains extensive limestone reefs and seagrass beds in both nearshore and offshore regions, which contrasts with the situation on the south coast where the lack of these features exposes the inshore coastal waters to prevailing weather conditions. Studies on the fish faunas associated with surf zones (Robertson and Lenanton 1984), limestone reefs (Howard 1989; Hutchins 1994) and seagrass beds (Scott 1981; Kirkman et al. 1991) in south-western Australia have shown a number of abundant species to be present in each of these three habitat types. In addition to regional differences in habitats, the Leeuwin Current, a warm, southward-flowing current on the outer continental shelf of the west coast of Australia, facilitates the dispersal of tropical reef dwelling fish species to the temperate waters of the lower west and south coasts (Hutchins 1991), and influences the catches of commercial teleost species (Lenanton et al. 1991). Since the Leeuwin Current is stronger on the west than on the south coast (Creswell 1990), it is likely to influence more strongly the distribution of some fish species in the surf zone regions of the former coast.

The species composition of the surf zone fish fauna at sites distributed along the 1500 km coastline of south-western Australia have been examined, and each species classified into life history, trophic and geographic range categories in order to explore the relationships between these characteristics and surf-zone habitats. These data were used to test the hypothesis that species composition and the proportions of life history, trophic and geographic categories differ between the west and south coasts as a result of the greater complexity of habitats and the presence of the Leeuwin Current on the west coast.

Materials and methods

Site descriptions

The wave energy reaching the shoreline on the south-western coast of Australia is moderated by local wave refraction and diffraction patterns (Hegge 1994). Furthermore, along the lower west coast, an extensive limestone offshore reef-chain dissipates $\simeq 40\%$ of the offshore wave energy (Steedman and Associates 1977). The attenuation rates are higher along sections of the west coast, particularly where extensive reefs outcrop close to shore. This results in low modal wave heights commonly ranging between 0.5 and 1.0 m at the shoreline. Wave energy is generally greater along the south coast (range up to 6.0 m) than on the west coast, with few localised features such as headlands and reefs to provide limited shelter (I. Eliot personal communication). The sites in this study represent a range of moderate to low-energy sandy beaches where modal wave heights are <1.0 m.

The presence of extensive polytypic seagrass meadows is a second persistent and unique feature of the lower west coast and parts of the south coast of Western Australian (Kirkman and Walker 1989). Along the lower west coast, the presence of reefs running parallel to the shore has formed shallow (4 to 10 m deep) embayments (up to 10 km wide) in which seagrasses proliferate (Searle and Semeniuk 1985; Sanderson and Eliot 1995). Seagrass meadows are not as prominent along the south coast, occurring principally in estuaries and embayments which are sheltered from extreme sea conditions.

Thirty-two surf zone sites were sampled at beaches along the south-western coast of Australia covering $\simeq 1500$ km between Geraldton (28°47′S; 114°35′) and Esperance (33°37′S; 121°55′: Fig. 1). The west coast sites extended from Sites 1 to 16 and the south coast sites extended from Sites 17 to 23 (Fig. 1).

Sampling methods

The fish faunas were sampled from all sites, except one in Warnbro Sound and three in Shoalwater Bay, using a 41.5 m long seine net with 19 m wings (25 mm mesh) and a 3.5 m bunt (9.5 mm mesh) which was deployed from a small dinghy. The seine net sampled a maximum depth of 1.5 m and covered an area of 274 m^2. Samples were taken from each site in late summer and winter 1991 and 1992. Sampling at the four sites in Warnbro Sound and Shoalwater Bay was carried out using a 21.5 m-long seine net with 10 m wings (6 m of 9 mm mesh and 4 m of 6 mm mesh) and a 1.5 m bunt (6 mm mesh). The net sampled to a depth of 1.5 m and swept an area of 116 m^2. Each site was sampled during winter 1991 and summer 1991/1992. Triplicate seine hauls were taken during the day at each site for both sampling methods.

At the time of sampling, water temperatures and salinities were recorded from the surf zone at each site to the nearest 1 C° and 1‰, respectively.

Fish identification, distribution, life-history classification and trophic levels

The number of each species in each sample was recorded. Each fish species was placed in one of the following life-history categories,

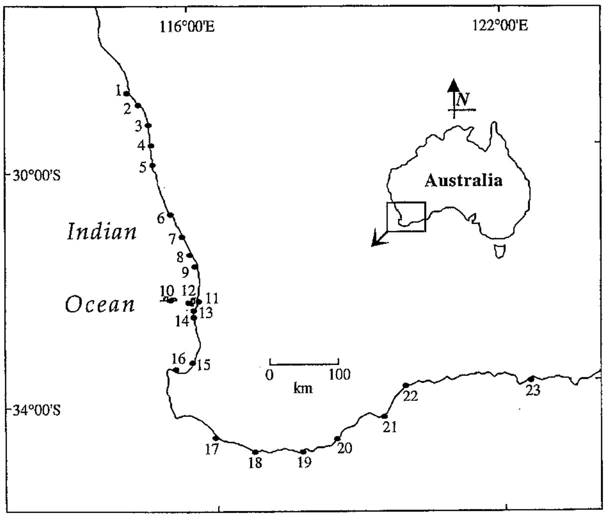

Fig. 1 Location of sampling sites along coast of south-western Australia

based on the way in which each uses the surf zones, either: resident (R)-species which spend their entire life cycle associated with nearshore marine environment; nursery (N)-species which use the nearshore environment as a nursery ground; or transient (T)-species which appear irregularly, have no apparent nearshore requirement, and/or are beyond their normal distribution range (Lenanton 1982; Hutchins and Swainston 1986; Potter et al. 1990, personal observations). Nine trophic categories were used: zooplanktivores (Z); benthic microinvertevores (BI); benthic macroinvertevores (BM); benthic micro/macroinvertevores (BI/BM); benthic macroinvertevores/piscivores (BM/P); piscivores (P); piscivores/zooplanktivores (P/Z); herbivores (H); and omnivores (O) (Scott et al. 1974; Grant 1982; Hutchins and Swainston 1986; Kuiter 1993). Geographic distributions were described as: temperate species and temperate extending into tropical regions (Te); tropical species and tropical extending into temperate regions (Tr); and circum-Australian species (C) (Hutchins and Swainston 1986; Allen and Swainston 1988; Hutchins 1994).

Data analysis

The numbers of each species at each site were expressed as densities, i.e. number of individuals 100 m^{-2}. The mean density of each species was calculated for each sample followed by averaging the mean density over seasons and years to produce the overall mean density. The overall mean density for each species has been presented as low density (1 to 9 individuals 100 m^{-2}), moderate density (10 to 99 individuals 100 m^{-2}) and high density ($\geq$ 100 individuals 100 m^{-2}). Four seine areas were sampled along both the east facing side of Garden Island and along the northern side of Rottnest Island. The overall mean densities of each species were averaged for Garden Island and for Rottnest Island to produce regional values. In Shoalwater Bay, the 21.5 m seine net was used at three sites and the 41.5 m seine net was used at one site, and the overall mean density per species were averaged for these sites. Preliminary trials indicated that a similar suite of species was caught by both seine nets.

The species composition at each site was classified using the flexible unweighted pair-group using arithmetic averages (UPGMA, $\beta = -0.1$) and ordinated using hybrid multi-dimensional scaling (HMDS) on the pattern-analysis package (PATN, Belbin 1988). Prior to classification, the densities of each species were log-transformed. The Bray–Curtis dissimilarity measure was used to produce the association matrix.

Results

Physical parameters

Water temperatures measured in the surf zones ranged between 18.3 and 27.0 °C (mean = 21.8 °C) at sites along the lower west and south coasts of Western Australia during the summer months in 1991 and 1992, and declined to between 12.5 and 19.5 °C (average = 16.1 °C) during the winter months of 1991 and 1992. The average salinity value over the entire sampling region was 32.5‰ during summer and 33.4‰ in winter.

Species composition

Ninety-two species of teleosts and three species of elasmobranchs from 47 families were caught by seine netting (Table 1). Classification separated the sites into two broad groupings comprising the west- and south-coast sites (Fig. 2). The west-coast sites were separated further into six distinct groupings. Groups A–D consisted of sites which were generally distributed along the central west coast. Groups A (Sites 1, 2, 9) and D (Sites 4, 5, 6, 7, 8) each consisted of several sites, while B (Site 3) and C (Site 15) each represented a single site. Groups E (Sites 11, 13, 14) and F (Sites 10, 12, 16) represented sites in embayments (Sites 11, 13, 16) and islands (Sites 10 and 12) on the lower west coast. The south-coast cluster separated into four groups, where Group G (Site 17) represented the most western site and Groups H (Sites 18, 22), I (Sites 20, 21) and J (Sites 19, 23) comprised two sites each.

The results of multi-dimensional scaling closely mirrored the associations of sites demonstrated by classification. There was an overall affinity of west-coast Beach Groups A to F to lie above the south-coast Groups G to J on Vectors 2 and 3 (Fig. 2).

Due to the distinct groupings derived from classification and ordination, each of these groups (A to J) have been considered as separate fish assemblages (Table 1). In general, there was a decrease in the number of species recorded from assemblages both north and south-east of Assemblages E and F. The number of species recorded from Assemblages E and F were 66 and 49, respectively, while the number of species collected from west-coast Assemblages A to D ranged between 20 and 43, and the four south-coast Assemblages G through J possessed the most depauperate fauna, ranging between 11 and 16 species (Table 1).

Aldrichetta forsteri, *Sillago bassensis* and *Lesuerina sp.* were collected from all ten assemblages, while *Mugil cephalus* and *Leptatherina presbyteroides* were each present in all but one assemblage (Table 1). A further 23 species were present in at least one assemblage on

Table 1 Species composition of Fish Assemblages A through J along west and south coasts of Western Australia, and life-history, trophic level and geographic-range categories of each species. Relative density: * = low density (1–9 fish/100 m^2); ** = moderate density (10–99 fish/100 m^2); *** = high density (≥ 100 fish 100 m^{-2}) (*Life-history categories*: *R* resident; *N* nursery juveniles; *T* transient. *Trophic level*: *Z* zooplanktivore; *BI* benthic microinvertevore; *BM* benthic macroinvertevore; *P* piscivore; *H* herbivore; *O* omnivore. *Geographic range*: *Te* temperate; *Tr* tropical; *C* circum-Australia)

Species	Assemblage										Life history	Trophic level	Geographic range
	west coast						south coast						
	A	B	C	D	E	F	G	H	I	J			
Aldrichetta forsteri	*	*	**	*	*	*	*	*	*	*	N	O	Te
Sillago bassensis	*	*	*	*	*	*	**	*	*	*	N	BM	Te
Lesuerina sp.	*	*	*	*	*	*	*	*	*	*	R	BI/BM	Te
Mugil cephalus	*	*	**	*	*	*		*	*	*	N	O	C
Torquigener pleurogramma	*	**	**	**	*	**		*	*		N	O	Te
Sillago schomburgkii	*	*	*	*	*	*	*				R	BM	Te
Atherinomorus ogilbyi	**	**	**	**	**	*					R	Z	Tr
Hyperlophus vittatus	*	*	**	**	*	*					N	Z	Te
Leptatherina presbyteroides	*	***		**	***	***	**	**	***	*	R	Z	Te
Platycephalus speculator	*	*		*	*	*		*	*	*	N	BM/P	Te
Pelsartia humeralis	*	*		*	*	*	*		*		N	BM	Te
Syngnathus phillipi	*	*									R	BI	Te
Scorpis georgianus	*		*	*	*				*		T	BM	Te
Hyporhamphus melanochir	*		*		*			*			R	O	Te
Spratelloides robustus	*			*	**	*	*	*	***	***	N	Z	Te
Cnidoglanis macrocephalus	*			*	*	*	**	*		*	R	BI/BM	Te
Paraplagusia unicolor	*			*	*			*			R	BI/BM	Te
Cristiceps australis	*			*	*					*	T	BM/P	Te
Cynoglossus broadhursti	*			*							R	BI/BM	Te
Polyspina piosae	*				*	*			*		N	O	Te
Ammotretis elongatus		*	*	*	*	*		*	*	*	R	BI/BM	Te
Pseudorhombus jenynsii		*	*	*	*	*		*			R	BI/BM	C
Apogon rueppellii		*	*	*	*	*					R	BI/BM	Te
Penicipelta vittiger		*	*	*	*						R	O	Te
Gerres subfasciatus		*	*	*					*		T	BM	C
Favonigobius lateralis		*	*		*	*					R	BI	Te
Pomatomus saltatrix		*	*	*							N	P	Te
Haletta semifasciata		*		*	*	*				*	R	O	Te
Pelates quadralineatus		**		*	*	*					N	BM	Tr
Filocampus tigris		*		*	*	*					R	BI	Tr
Scobinichthys granulatus		*		*	*	*					R	O	Te
Pseudolabrus parilus		*		*	*	*					R	BI/BM	Te
Pelates sexlineatus		**		*	*						N	BM	Te
Rhabdosargus sarba		*		*	*						T	BM/P	Te
Siphamia cephalotes		*			*						R	BI/BM	Te
Aploactisoma milesii		*			*						T	BM	Te
Monacanthus chinensis		*			*						R	O	Tr
Parequula melbournensis		*					*				T	BM	Te
Siganus fuscescens		**									R	H	Te
Penicipelta penicilligera		*									R	O	Te
Sphyraena novaehollandiae		*									T	P	Te
Helcogramma decurrens		*									T	BI/BM	Te
Elops machnata		*									T	BM/P	Te
Trachurus novaezealandiae		*									T	P/Z	Te
Pentapodus vitta		*									T	BM	Te
Pagrus auratus		*									T	BM/P	Te
Upeneus tragula		*									T	BM	Tr
Anacanthus barbatus		*									R	O	Te
Ostracion cubicus		*									T	O	Tr
Sillago burrus			**	*	*	*					N	BM	Tr
Arripis georgianus			*	*	*	*		*		*	T	BM	Te
Sillaginodes punctata			*		*	*					N	BM	Te
Pseudocaranx dentex			*			*		*			T	P/Z	Te
Centropogon latifrons				*	*	*					R	BM/P	Te
Acanthalutes spilomelanurus				*	*	*					R	O	Te
Enoplosis armatus				*	*	*	*				R	BM	Te
Sillago vittata				*	*						N	BM	Te
Brachaluteres jacksonianus				*	*						R	O	Te

Table 1 (continued)

Species	Assemblage										Life history	Trophic level	Geographic range
	west coast						south coast						
	A	B	C	D	E	F	G	H	I	J			
Gymnapistes marmoratus				*	*						R	BM/P	Te
Cochleoceps spatula				*	*						R	BI	Te
Microcanthus strigatus				*		*					T	BM	Tr
Parupeneus signatus				*							T	BM	Tr
Cheilodactylus gibbosus				*							T	BM/P	Te
Bovichthys variegatus				*							T	BM	Te
Contusus brevicaudus					*	*		*			N	O	Te
Atherinosoma elongata					*	**					R	Z	Te
Halichoeres brownfieldi					*	*					R	BI/BM	Te
Aptychotrema vincentiana					*	*					T	BM/P	Te
Stigmatophora argus					*	*					R	BI	Te
Histiogamphelus cristatus					*	*					R	BI	Te
Siphonognathus radiatus					*	*					R	O	Te
Neoodax balteatus					*	*					R	O	Te
Callionymus goodladi					*	*					R	BI/BM	Te
Leviprora inops					*	*					N	BM/P	Te
Cristiceps aurantiacus					*	*					T	BM/P	Te
Iso rhothophilus					*					*	T	Z	Te
Parapercis haackei					*						T	BM	Te
Eocallionymus papilio					*						R	BI/BM	Te
Meuschenia freycineti					*						R	O	Te
Urolophus mucosus					*						T	BM	Te
Dasyatis thetidis					*						T	BM	Te
Cheilodactylus rubrolabiatus					*						T	BM/P	Te
Arripis truttaceus					*						N	BM/P	Te
Cirrimuraena calamus					*						T	BM/P	Te
Paraplotosus albilabris					*						T	BI/BM	Tr
Pugnaso curtirostris					*						R	BI	Te
Platycephalus laevigatus					*						N	BM/P	Te
Heteroclinus roseus						*	*				T	BM/P	Te
Allanetta mugiloides						**			***	*	R	Z	Te
Trioris reipublicae						*					T	O	Tr
Diodon nicthemerus						*					T	BM	Te
Amniataba caudavittatus						*					T	BM	Tr
Kyphosus sydneyanus						*					N	H	Tr
Heteroclinus adelaidae						*					T	BM/P	Te
Hippocampus angustus									*		R	BI	Te
Total no. of species	20	41	21	43	66	49	11	16	15	15			

both the west and south coasts. However, over two-thirds of the species caught in the study (65 of 95 species) were restricted to west-coast assemblages, while only one species was recorded exclusively from south-coast assemblages. *L. presbyteroides* showed consistently moderate to high overall mean densities in all assemblages. Species which were characteristic of the west-coast assemblages included *Atherinomorus ogilbyi*, *Hyperlophus vittatus*, *Ammotretis elongatus*, *Pseudorhombus jenynsii* and *Apogon rueppellii* (Table 1).

Assemblage A comprised 20 species, with none of these exclusive to this assemblage (Table 1). With the exception of *Atherinomorus ogilbyi*, all species from this assemblage showed low overall mean densities. Forty-one species were collected in Assemblage B, of which 11 occurred only in this assemblage and were present at low overall mean densities. None of the 21 species in Assemblage C were exclusive to this assemblage, and of the 43 species in Assemblage D there were only three unique species (Table 1).

In contrast, 11 of the 66 species present in Assemblage E were exclusive to this assemblage, and five of the 49 species recorded from Assemblage F were not found in any other assemblage (Table 1). A further nine species were unique to both of these assemblages.

Twenty-one species were restricted to at least two of the three assemblages on the lower west coast (D, E and F). These included three species of monacanthids (*Acanthalutes spilomelanurus*, *Brachaluteres jacksonianus* and *Microcanthus strigatus*) and two species of both syngnathids (*Stigmatophora argus* and

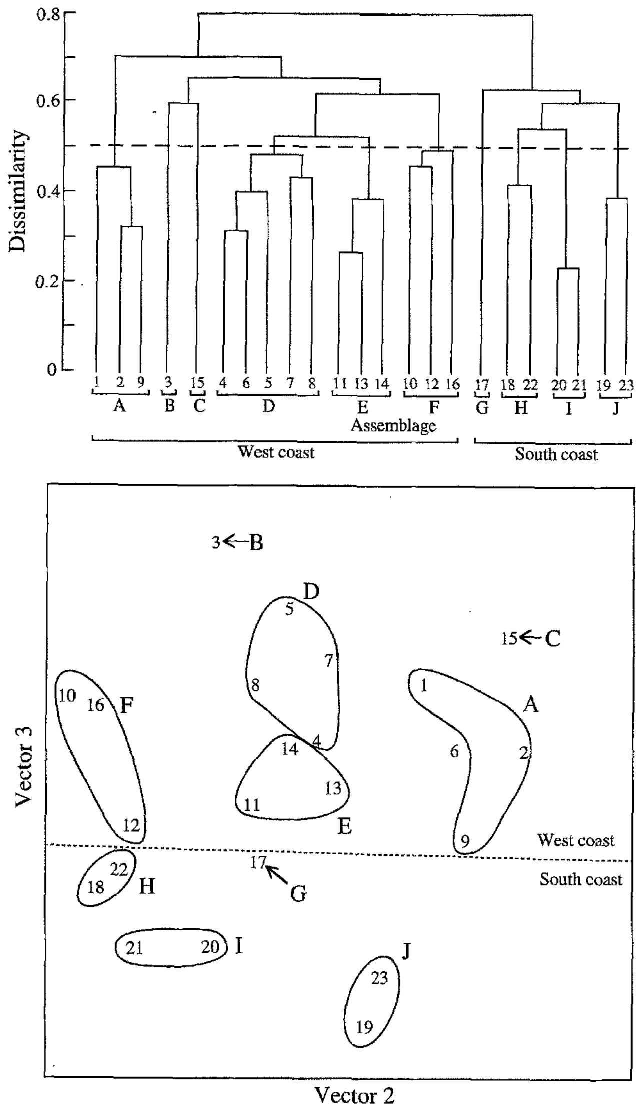

Fig. 2 Results from UPGMA classification (*top graph*) and HMDS ordination (*bottom graph*), using species composition and density data for fish species found in ten surf-zone assemblages (*A–J*) in south-western Australia

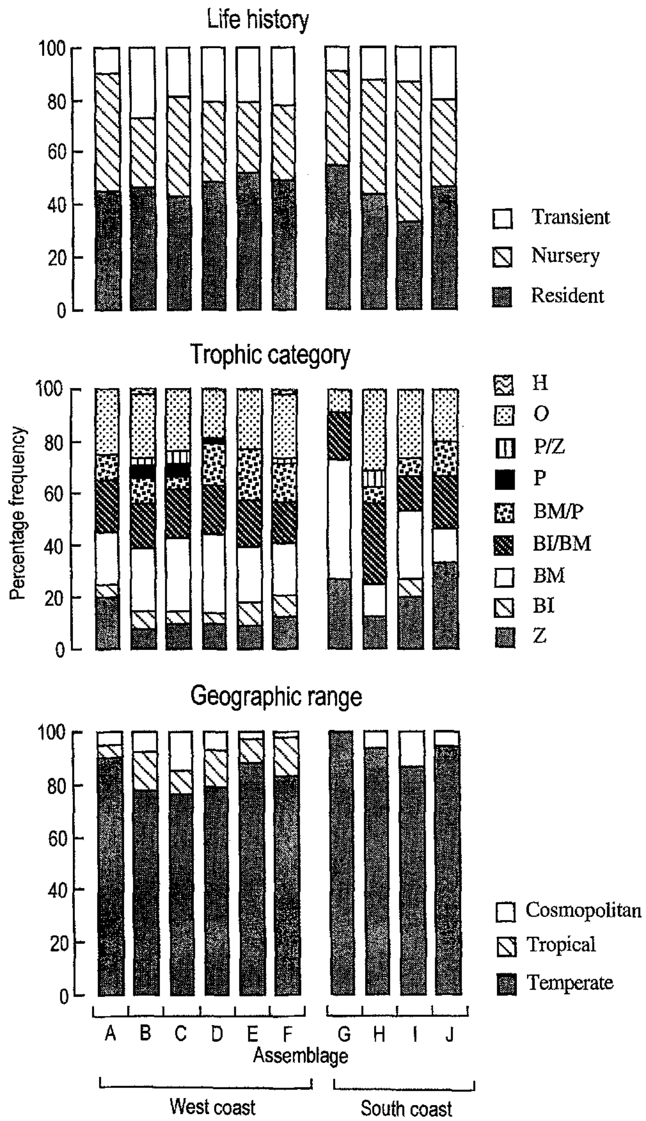

Fig. 3 Percentage frequency of life-history, trophic and geographic-range categories in each of ten surf-zone fish assemblages (*A–J*) in south-western Australia (*Z* zooplanktivores; *BI* benthic microinvertevores; *BM* benthic macroinvertevores; *BI/BM* benthic micro/macroinvertevores; *BM/P* benthic macroinvertevores/piscivores; *P* piscivores; *P/Z* piscivores/zooplanktivores; *O* omnivores; *H* herbivores)

Histiogamphelus cristatus) and odacids (*Siphonognathus radiatus* and *Neoodax balteatus*). Furthermore, other species from these families and species such as *Apogon rueppellii*, *Favonigobius lateralis*, *Pelates sexlineatus* and *Rhabdosargus sarba* were present in the above assemblages and did not extend beyond the west coast.

On the south coast, Assemblage G contained only 11 species, all of which were common to the other assemblages (Table 1). Only three species, *Sillago bassensis*, *Leptatherina presbyteroides* and *Cnidoglanis macrocephalus*, were collected at moderate overall mean densities. Assemblage H contained 16 species and a similar number of species (15) were found in Assemblages I and J. In addition to *L. presbyteroides*, *Spratelloides robustus* and *Allanetta mugiloides* were found in high overall mean densities. While *S. robustus* was also found in west-coast assemblages, it was generally recorded at low overall mean densities. With the exception of *Hippocampus angustus*, which was unique to Assemblage I, no species were exclusively caught in the four south-coast assemblages.

Life-history categories were assigned to each of the 95 species caught in the study (Table 1; Fig. 3). Approximately 43% (41 species) were classified as resident to the nearshore environment, 21% (20 species) used the nearshore region as nursery grounds, and 36% (34 species) were transient, showing no regular association with nearshore habitats. Resident species contributed to at least 40% of the species in each assemblage, except for Assemblage I. Of the resident species, *Lesuerina sp.* and *Leptatherina presbyteroides* were the only two recorded from ≥ 90% of the assemblages.

While nursery species contributed the least number of species overall, they were the second most important group of fishes in the majority of assemblages, comprising between 27.3% (Assemblage J) and 53.3% (Assemblage I) of the total number of species in each assemblage (Table 1; Fig. 3). Nursery species, *Aldrichetta forsteri* and *Sillago bassensis*, were recorded from all assemblages, and *Spratelloides robustus*, *Platycephalus speculator* and *Pelsartia humeralis* occurred in 7 of the 10 assemblages. The contribution of transient species represented between 10% (Assemblages A and G) and 26.8% (Assemblage B) of the total number of species in each assemblage. In general, the proportional contribution of transient species was greater for west-coast assemblages than south-coast assemblages (Table 1 and Fig. 3).

The proportional contribution of each of the nine trophic levels to the total species composition was 25.3% benthic macroinvertevores (24 species), 20.0% omnivores (19 species), 17.9% benthic macroinvertevores/piscivores (17 species), 14.7% benthic micro/macroinvertevores (14 species), 8.4% benthic microinvertevores (8 species), 7.4% zooplanktivores (7 species) and 2.1% piscivores, zooplanktivores/piscivores and herbivores (2 species each) (Table 1; Fig. 3). Assemblage B contained all 9 trophic categories, while the remaining west-coast assemblages possessed 6 to 8 categories and south-coast assemblages generally had the fewest with between 4 and 6 categories. The benthic invertevores and omnivores comprised the greatest proportion of species in most assemblages. Piscivores, zooplanktivores/piscivores and herbivores made a minor contribution to each west-coast assemblage and were virtually absent from the south-coast assemblages. In south-coast assemblages there was a decrease in the proportion of benthic invertevores and an increase in zooplanktivores (Fig. 3).

The vast majority of species (83.1%) were classified as temperate species followed by tropical species (13.7%) and lastly, species classified as circum-Australia (3.2%) (Table 1; Fig. 3). All three categories were represented in west-coast assemblages, but only temperate and circum-Australian species were collected from the south coast.

Discussion

Characteristics of surf-zone fish community

The sandy surf zones of the south-western coast of Australia possess a diverse ichthyofauna. Ninety-two teleost and three elasmobranch species from 47 families were found in these waters, with only five teleost species numerically abundant throughout the 1500 km of this study. These trends are consistent with those exhibited in other surf-zone fish assemblages characterised by a dynamic and diverse group of species, with only a few species numerically dominant (Modde and Ross 1981; Lasiak 1983, 1984a, b; Robertson and Lenanton 1984; Ross et al.1987; Romer 1990), and emphasise the importance of this environment in sustaining significant populations of some fish species (see Brown and McLachlan 1990). This generality led Romer (1990) to suggest that surf-zone fish assemblages are "species rich but inequitable communities".

While the total number of species caught in the present study was greater than that recorded in previous studies in the surf zones of South Africa and North America (Modde and Ross 1981; Lasiak 1983, 1984a, b; McDermott 1983; Peters and Nelson 1987; Ross et al. 1987; Romer 1990), the present study was based on a greater number of sites and covered a wider geographic range. The number of species present in each assemblage ranged from 20 to 66 on the west coast and 11 to 16 on the south coast. The numbers of species in these assemblages are comparable to those recorded for surf zones of other continents. Surf-zone fish assemblages in South Africa consisted of 50 species (Lasiak 1984a, b), while the Gulf of Mexico contained 59 and 76 species (Modde and Ross 1981; Ross et al. 1987), and 26 species were collected from the surf zones of the central east coast of North America (McDermott 1983).

Between 8 and 14 families are shared between the present study and at least one of these other studies, with representatives of the Pomatomidae, Mugilidae, Clupeidae and Tetraodontidae cosmopolitan to the surf zones of the three continents, and members of the Atherinidae, Carangidae and Dasyatididae reported from Australia and one other continent (Lasiak 1984a, b; Ross et al. 1987; Lenanton and Caputi 1989). Representatives from these families in the present study include *Aldrichetta forsteri*, *Mugil cephalus*, *Torquigener pleurogramma*, *Leptatherina presbyteroides*, *Atherinomorus ogilbyi*, *Hyperlophus vittatus*, *Spratelloides robustus* and *Pomatomus saltatrix*. The majority of these species were relatively abundant in almost all the assemblages, indicating that the surf zone is an important environment for many species from these families.

Regional differences in number of species and species composition

Classification and ordination showed that the composition of the surf-zone fish faunas on the west coast differed markedly from those on the south coast. While 65 species (68%) were recorded on the west coast, only 29 species (31%) were found in the surf zones on both coasts, and only one species (1%) was collected exclusively from the south coast. A similar reduction in the number of species has also been reported for surf zones over a geographically restricted area along the south-western tip of Australia (Lenanton 1982 and unpublished data) and also for the estuarine environment of south-western Australia (Potter et al. 1990). Of the 46 species common to the present study and Lenanton's (1982 and unpublished data), 25 species were not recorded from the south-coast surf zones. While 11 of these species have been found in estuaries (Potter et al. 1993; Potter and Hyndes 1994) and embayments (Kirkman et al. 1991) along the south coast, the remaining species appear to be absent from southern marine nearshore waters. It would therefore appear that the south-western tip is the most southerly location of the distribution of many west-coast species and is a transitional zone for the fish faunas of these coasts.

The greater number of species recorded from the west coast can probably be attributed to two factors. First, the west coast possesses more complex and heterogeneous habitats than the south coast as a result of different beach morphologies and the presence of adjacent limestone reefs and seagrass beds. Offshore reefs are a prevalent physical feature along the majority of the west coast, but show an irregular and sparse distribution along the south coast (Hegge 1994). Parts of the reef system, and islands in some locations, on the west coast provide a buffering effect for nearby waters which enable large expanses of seagrass to grow along this coast (Kirkman and Walker 1989). However, along the south coast there are fewer and less sheltered nearshore areas as a consequence of the higher wave regime of the region (Sanderson and Eliot 1995).

Second, the movement of the Leeuwin Current down the outer continental shelf of the west coast facilitates egg, larval and juvenile finfish dispersal and subsequent recruitment along the west coast, as well as indirectly maintaining the productivity of some coastal habitats (Lenanton et al. 1991). The Leeuwin Current has less effect along the south coast, and as a consequence recruitment of many species is restricted. Its reduced influence is highlighted by the absence of tropical species on the south coast.

Influence of other nearshore habitats

The presence of nearshore seagrass and/or limestone patch reefs is likely to influence the fish assemblages in adjacent sandy surf-zone areas by enhancing the number of microhabitats, providing refugia from predation and foraging area, and moderating wave and swell activity on beaches (Lasiak 1986; Peters and Nelson 1987; Bell and Pollard 1989; Howard 1989). The reduction in habitat complexity along the south coast has not only a major influence on the number of species, but also on the presence of different life-history stages for some species. This is best illustrated by *Aldrichetta forsteri* in the present study, which was represented by both juveniles and adults on the west coast but only sub-adults and adults on the south coast (Ayvazian unpublished data).

The importance of adjacent seagrass and patch reef to the fish fauna of adjacent surf zones is evident when the results of the present study are compared to those of other nearshore habitats in south-western Australia. The sandy-beach surf-zones on the west coast shared 36 species (38.2% of total) with nearshore reefs (Howard 1989; Hutchins 1994) and 40 species (42.5%) with seagrass beds (Scott 1981; Hyndes unpublished data), the proportion of shared species being as high as 50 and 56% for the respective habitats in some assemblages. Furthermore, 21 species (22.3%) were common to all three habitats. Species present in both the sandy surf zone and seagrass included *Haletta semifasciata*, *Pelates sexlineatus* and *Acanthalutes spilomelanurus*, while *Platycephalus speculator*, *Pelsartia humeralis* and *Pseudocaranx dentex* were found in surf-zone and nearshore-reef habitats and *Torquigener pleurogramma*, *Apogon rueppellii* and *Rhabdosargus sarba* were present in all three habitats. Additionally, Assemblages B, E and F each had unique species, suggesting that embayment and island sites provided a productive and protective environment for species with a preferred habitat in either seagrass beds, limestone reef areas or along low-energy surf zones.

The large overlap of species found in both the surf zone and adjacent seagrass beds can, in part, be attributed to the presence of large wracks of detached macrophyte detritus accumulating in the surf zone. The detached macrophytes provide a refuge from diurnal predators and a rich invertebrate food source for, particularly, juvenile *Aldrichetta forsteri*, *Pelsartia humeralis*, *Cnidoglanis macrocephalus* and *Haletta semifasciata* (Robertson and Lenanton 1984; Lenanton and Caputi 1989).

While a number of species present in the surf zone were also affiliated with other nearshore habitats, over 40 species were not recorded from other habitats. These included species such as *Sillago bassensis*, *Lesuerina* sp. and *Mugil cephalus*, which would therefore appear to display some degree of dependence on the sandy surf-zone environment.

Life-history, trophic and geographical categories

The proportion of resident species was high on both the west and south coasts, constituting at least 33% in each of these assemblages. Species such as *Sillago schomburgkii* and *Leptatherina presbyteroides* spend their entire life cycle in or near the nearshore region (Prince and Potter 1983; Hyndes et al. 1995). The high proportion of resident species found in this study challenges previous suggestions that the dynamic and unpredictable nature of the surf-zone environment makes it unsuitable for such species, but adequate only as a short-term nursery area (see Brown and McLachlan 1990).

Many of the species utilising the surf zone as a nursery area were found throughout the study region and, in some cases, in relatively high densities. These species included *Aldrichetta forsteri*, *Sillago bassensis*, *Torquigener pleurogramma*, and *Spratelloides robustus*. Although the proportion of transient species was low in all assemblages, the higher contribution of this group on the west coast is likely to be the result of the localised influences of the Leeuwin Current, where many tropical species migrate down the coast, showing no regular association with surf zones.

The high proportion of benthic invertevores in the present study contrasts with that generally described for surf zones in other studies, which have shown zooplanktivores to be dominant (see Brown and McLachlan 1990). The dominance of the former group in the surf zones of south-western Australia may be attributable to the stability of nearshore regions. More sheltered nearshore regions display a greater abundance of benthic invertebrates than exposed regions (Dexter 1984). Such a conclusion is supported by an increase in the proportion of zooplanktivores on the more exposed south coast, where representatives of Atherinidae and Clupeidae are abundant. The prevalence of this group of fishes is similar to that reported for South Africa (see Brown and McLachlan 1990).

In summary, the number of species in west-coast versus south-coast assemblages can be attributed to the more complex and heterogeneous habitat types in close proximity to the relatively sheltered sandy surf-zones of the former coast. This feature is likely to produce a more temporally stable environment than has been attributed previously, and suggests a unique role for surf zones on the lower west coast. While the number of resident species was high in assemblages on both coasts, the greater number of transient species on the west coast may be regulated by the southward-flowing Leeuwin Current. An increase in the proportion of zooplanktivores in south-coast assemblages reflects the increased exposure of surf zones on this coast. While the present study has examined differences in the species composition in relation to geographic region and habitat heterogeneity, differences in beach morphology and other physical variables will be examined in subsequent work to more fully evaluate the determinants of surf-zone fish-fauna composition.

Acknowledgements The authors thank the scores of people who assisted with the collection of fish, especially K. Bakitch, I. Eliot, B. Hegge and D. McGlashan. Stimulating discussion and support were provided by I. Eliot, B. Knott, R. Lenanton and I. Potter. B. Hutchins of the West Australian Museum assisted with the identification of fishes. We acknowledge the financial support of a University of Western Australia Postdoctoral Fellowship to SGA, a Murdoch University Postgraduate Grant to GAH, and the Western Australia Department of Fisheries for partial research funds. The manuscript was much improved by the constructive comments of I. Eliot, R. Lenanton and I. Potter.

References

Allen GR, Swainston R (1988) The marine fishes of north-western Australia. Western Australian Museum, Perth

Belbin L (1988) PATN. Pattern analysis package. CSIRO Division of Wildlife and Rangelands Research, Canberra

Bell JD, Pollard DA (1989) Ecology of fish assemblages and fisheries associated with seagrasses, In: Larkum AWD, McComb AJ, Shepard SA (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, pp 565–609

Brown AC, McLachlan A (1990) Ecology of sandy shores. Elsevier, Amsterdam

Creswell G (1990) The Leeuwin Current. Corella 14: 113–118

Dexter D (1984) Temporal and spatial variability in the community structure of the fauna of four sandy beaches in south-eastern New South Wales. Aust J mar Freshwat Res 35: 663–672

Grant EM (1982) Guide to fishes. The Department of Harbours and Marine, Brisbane, Queensland

Hegge B (1994) Low energy sandy beaches of southwestern Australia: two-dimensional morphology, sediments and dynamics. Ph.D. thesis. The University of Western Australia, Nedlands

Howard RK (1989) The structure of a nearshore fish community of Western Australia: diel patterns and the habitat role of limestone reefs. Envir Biol Fish 24: 93–104

Hutchins B (1991) Dispersal of tropical fishes to temperate seas in the southern hemisphere. J Proc R Soc West Aust 74: 79–84

Hutchins B (1994) A survey of the nearshore reef fish fauna of Western Australia's west and south coasts – The Leeuwin Province. Rec West Aust Mus (Suppl.) 46: 1–66

Hutchins B, Swainston R (1986) Sea fishes of southern Australia. Swainston Publishing, Perth

Hyndes GA, Potter IC, Lenanton RCJ (1995) Habitat partitioning by whiting species (Sillaginidae) in coastal waters. Envir Biol Fish (in press)

Kirkman H, Humphries P, Manning R (1991) The epibenthic fauna of seagrass beds and bare sand in Princess Royal Harbour and King George Sound, Albany, south-western Australia, In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) The marine flora and fauna of Albany, Western Australia. Western Australian Museum, Perth, pp 553–563

Kirkman H, Walker DI (1989) Regional studies – Western Australian seagrasses. In: Larkum AWD, McComb AJ, Shepard SA (eds) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, pp 157–181

Kuiter RH (1993) Coastal fishes of south-eastern Australia. University of Hawaii Press, Honolulu, Hawaii

Lasiak TA (1981) Nursery grounds of juvenile teleosts: evidence from the surf zone of King's Beach, Port Elizabeth. S Afr J Sci 77: 388–390

Lasiak TA (1983) The impact of surf zone fish communities on faunal assemblages associated with sandy beaches. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. W. Junk, The Hague, pp 501–506

Lasiak TA (1984a) Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: long-term fluctuations. Estuar cstl, Shelf Sci 18: 459–483

Lasiak TA (1984b) Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay, South Africa: Short-term fluctuations Estuar cstl, Shelf Sci 18: 347–360

Lasiak TA (1986) Juveniles, food and the surf zone habitat: implications for teleost nursery areas. S Afr J Zool 21: 51–56

Lenanton RCJ (1982) Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. Aust J mar Freshwat Res 33: 881–900

Lenanton RCJ, Caputi N (1989) The roles of food supply and shelter in the relationship between fishes, in particular *Cnidoglanis macrocephalus* (Valenciennes), and detached macrophytes in the surf zone of sandy beaches. J exp mar Biol Ecol 128: 165–176

Lenanton RCJ, Joll L, Penn J, Jones K (1991) The influence of the Leeuwin Current on coastal fisheries of Western Australia. J Proc R Soc West Aust 74: 101–114

Lenanton RCJ, Robertson AI, Hansen JA (1982) Nearshore accumulations of detached macrophytes as nursery areas for fish. Mar Ecol Prog Ser 9: 51–57

McDermott JJ (1983) Food web in the surf zone of an exposed sandy beach along the mid-Atlantic coast of the United States. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. W. Junk, The Hague, pp 501–506

Modde T, Ross ST (1981) Seasonality of fish occupying a surf zone habitat in the Gulf of Mexico. Fish Bull US 78: 911–922

Peters DJ, Nelson WG (1987) The seasonality and spatial patterns of juvenile surf zone fishes of the Florida east coast. Fla Scient 50: 85–99

Potter IC, Beckley LE, Whitfield AK, Lenanton RCJ (1990) Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and southern Africa. Envir Biol Fish 28: 143–178

Potter IC, Hyndes GA (1994) Composition of the fish fauna of a permanently open estuary on the southern coast of Australia, and comparisons with a nearby seasonally closed estuary. Mar Biol 121: 199–209

Potter IC, Hyndes GA, Baronie FM (1993) The fish fauna of a seasonally closed Australian estuary. Is the prevalence of estuarine-spawning species high? Mar Biol 116: 19–30

Prince JD, Potter IC (1983) Life-cycle duration, growth and spawning times of five species of atherinidae (Teleostei) found in a Western Australian estuary. Aust J mar Freshwat Res 34: 287–301

Robertson AI, Lenanton RCJ (1984) Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. J exp mar Biol Ecol 84: 265–283

Romer GS (1990) Surf zone fish community and species response to a wave energy gradient. J Fish Biol 36: 279–287

Ross ST, McMichael RH, Ruple DL (1987) Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Estuar cstl, Shelf Sci 25: 391–412

Sanderson P, Eliot I (1995) Shoreline salients on the coast of Western Australia. J cstl Res (in press)

Scott JK (1981) The seagrass fish fauna of Geographe Bay, Western Australia. J Proc R Soc West Aust 63: 97–102

Scott TD, Glover CJM, Southcott RV (1974) The marine and freshwater fishes of South Australia. A.B. James Government Printer, South Australia

Searle DJ, Semeniuk V (1985) The natural sectors of the inner Rottnest Shelf coast ajoining the Swan coastal plain. J Proc R Soc West Aust 67: 116–136

Steedman RK and Associates (1977) Mullaloo marina environmental investigation. Part 1. Physical oceanographic studies. Report to Wanneroo Shire Council, Perth, Western Australia