Estuarine, Coastal and Shelf Science (2000) **51,** 201–213
doi:10.1006/ecss.2000.0636, available online at http://www.idealibrary.com on IDEAL®

Fish Assemblage Structure of the Shallow Ocean Surf-Zone on the Eastern Shore of Virginia Barrier Islands

C. A. Layman

Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, U.S.A.

Received 16 August 1999 and accepted in revised form 24 February 2000

This study provides an in-depth description of the fishes in the shallow surf-zone (<0·4 m), a little-studied micro-habitat of the ocean surf. Fish assemblages were examined with respect to three temporal cycles (seasonal, diel and tidal) and at both large and small spatial scales. Sampling was conducted at the Virginia barrier islands using an 8 m bag seine dragged parallel to the beach in water with an average depth of 0·2 m. The fish assemblage was relatively species poor, in fact, there were only two year-round residents, *Membras martinica* (rough silverside) and *Mugil curema* (white mullet). Three species, *M. martinica*, *Trachinotus carolinus* (Florida pompano) and *Menticirrhus littoralis* (gulf kingfish), comprised 94% of all species captured. Both fish species richness and total abundance peaked in the late summer and were lowest in the winter. Multidimensional scaling analysis failed to identify a distinct nighttime fish assemblage. However, univariate analyses found there was a significant increase in species richness at night, due to an influx of predatory adult fishes. Further, significantly more species were collected at high than low tide. Higher species richness and total fish abundance occurred in the shallow water (<0·4 m) of runnels, low wave energy habitats on the backside of small sand bars. The increased richness and abundance suggests a small-scale movement of fishes parallel to the beach face as fishes seek sheltered runnel habitats. This study quantifies the observation that many fishes do utilize the shallow surf-zone, perhaps to minimize predator encounters and/or take advantage of an under-utilized intertidal food source.

Keywords: surf-zone; fish; beach fauna; community composition; nursery grounds; movement; silversides; Virginia Coast

Introduction

Many fishes and macro-crustaceans of the ocean surf-zone community are larval and juvenile individuals that use the shallow water as a nursery habitat (Lasiak, 1986; Robertson & Lenanton, 1984; Ruple, 1984; Ross *et al.*, 1987; Gibson *et al.*, 1993; Santos & Nash, 1995). Such near-shore shallow water habitats are beneficial to juvenile fishes as refugia from aquatic predators or they may provide potential foraging areas. For example, in east coast salt marshes, fishes (e.g. *Fundulus heteroclitus*, common mummichog and *Fundulus luciae*, spotfin killifish) and invertebrates (*Palaemonetes pugio*, grass shrimp) have been shown to utilize the shallow water on the marsh surface in order to minimize encounters with aquatic predators or to take advantage of an under-utilized food resource (Talbot & Able, 1984; Smith & Able, 1994; Yozzo *et al.*, 1994; Kneib, 1997). If the distribution of fishes in the surf-zone likewise is determined by these factors, it is a logical hypothesis that these organisms should move into the shallowest water possible, given their species-specific size and/or morphological adaptations.

Despite the potential importance of the shallow surf-zone as a habitat for fishes, previous surf ichthyofaunal studies have usually examined fish assemblages in water 0·4 m and deeper; very few have focused on the fishes that utilize water less than 0·4 m. Harvey (1998) specifically examined the shallowest waters on a sandy beach of Sapelo Island, Georgia, and was able to demonstrate that *Fundulus majalis* (striped killifish) exhibits a clear preference for runnels, isolated troughs of water behind small sand bars. However, his sampling was both temporally (i.e. one week) and spatially (i.e. one site on one beach) constrained. Santos and Nash (1995), Abou-Seedo (1990) and Peters and Nelson (1987) included water less than 0·4 m deep in their analyses, but in each study the authors seined perpendicularly to the shoreline,

Present address: Department of Wildlife and Fisheries Sciences, Texas A&M University, 210 Nagle Hall, College Station, TX 77843-2258, U.S.A. Tel: 979-589-1672; E-mail: CAL1634@unix.tamu, edu

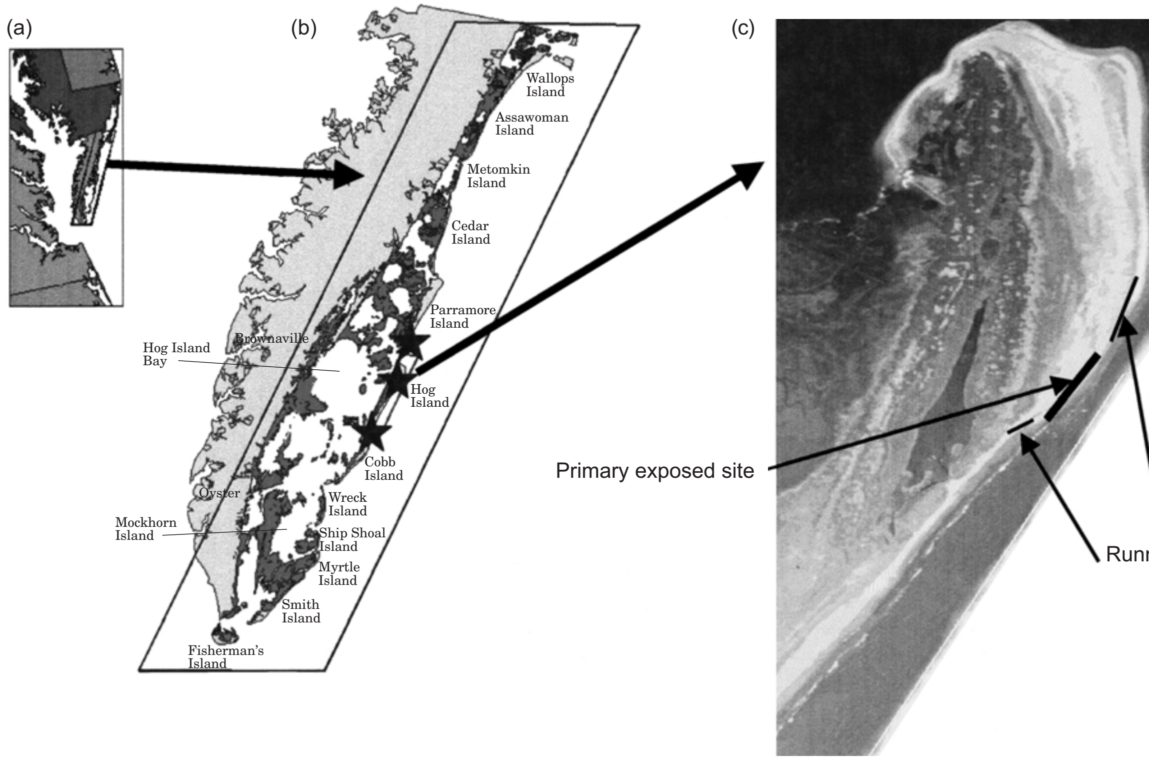

FIGURE 1. The (a) Delmarva Peninsula, (b) Virginia Coast Reserve Long-Term Ecological Research Site, and (c) the north end of Hog Island. The three sampling locations are designated by a star on map (b). At our main sampling site on the north end of Hog Island, the exposed sampling location and adjacent runnel sites are indicated. Primary exposed site: latitude 75·66°W; longitude 37·44°N.

thereby integrating fish collections over a broad range of depths.

Previous authors have extensively described the invertebrate assemblages of United States east coast beaches (Anderson *et al.*, 1977; Leber, 1982; McDermott, 1983), but similar comprehensive ichthyofaunal analyses have not been conducted. McDermott (1983), in New Jersey, and DeLancey (1989), in South Carolina, focused primarily on the food web relationships of shallow surf-zone fishes. The most common fish species were found to be either planktivores (*Menidia menidia*, Atlantic silverside, *Anchoa mitchilli*, bay anchovy, and *Anchoa hepsetus*, striped anchovy), benthic invertivores (*Menticirrhus littoralis*, gulf kingfish, and *Trachinotus carolinus*, Florida pompano) or benthic omnivores/detritivores (*Mugil curema*, white mullet). Peters and Nelson (1987) and Peters (1984) have reported that a similar low diversity fish assemblage is found in the surf-zone on the east coast of Florida.

The objective of this study was to conduct an in-depth analysis of the Virginia barrier island surf, focusing on the fish assemblage in water shallower than 0·4 m. The dynamics of the fish assemblages are described with respect to three temporal scales: (1) seasonal, (2) diel, and (3) tidal. In addition, spatial assemblage structure variation was examined on two scales: (1) small scale spatial differences between exposed beach sites and adjacent runnel habitats, and (2) large scale variations among island sites.

Materials and methods

Study site

The study took place at the Virginia barrier islands, part of the Virginia Coast Reserve Long-Term Ecological Research Site (Figure 1). The primary North Hog sampling location was an exposed beach site with no offshore sandbars. This site was characterized by moderate to heavy wave action (waves typically exceed 1 m in height), no permanent macrofaunal burrows within the intertidal zone, a rather wide surf-zone, presence of relatively deep reduced sediment layers, and intermediate beach particle size. Based on the classification system of McLachlan (1980), the North Hog Island Site is rated 12 (assessed from data collected by Harris, 1988, and Layman, unpubl. data) and falls within the range of beaches described as ‘ moderately exposed ’. Salinity in the Hog Island

TABLE 1. The average temperature of the shallow surf-zone taken coincident with the fish samples each month. All temperatures are reported in °C

1997					1998									1999
Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Feb
29·3	27·2	23·0	9·8	7·8	6·2	11·5	14·1	16·0	19·1	25·8	27·1	26·5	21·5	6·1

surf-zone ranged from 32 to 36 (using the Practical Salinity Scale) during the study period.

General shallow surf-zone sampling protocol

The ' shallow surf-zone ' was the area of the surf immediately adjacent to the beach that is less than 0·4 m deep. All collections were made with a seine 8 m long and 1·5 m deep, with a 1 m square bag and three-sixteenths of an inch (0·48 cm) square mesh throughout. A single seine haul was made by two persons through the shallow swash area parallel to the beach face. One person pulled the outer wing of the seine at a depth of ~0·4 m (estimated at the troughs of passing waves) and the other person pulled the opposite wing along the edge of the shoreline. This procedure sampled an average depth of 0·2 m. During each haul, the net was pulled 15 m along the beach into the prevailing longshore current. The next haul within each seine series was conducted 5 m further up the beach to sample a different section of the shallow surf. Each individual seine was estimated to have swept an approximate area of 120 m^2. Fishes were held in an aerated holding bucket until all seines at a sampling site or time were completed; this ensured that no individuals were captured more than once in a set of seine hauls. Adult fishes were identified based on the descriptions of Murdy *et al.* (1997) and juveniles using Development of Fishes of the Mid-Atlantic Bight (1978). Voucher specimens are held at the Virginia Coast Reserve Long-Term Ecological Research laboratory.

Temporal analyses

Sixteen seine hauls (8 at high and 8 at low tide) were made on each of two days within a month. Sampling began 30 min prior to high or low tide. Because surf-zone fishes school, and individual hauls are highly variable (Lasiak, 1982; Ross *et al.*, 1987; Gibson *et al.*, 1993; Clark *et al.*, 1996*a*), the 32 individual seines were pooled to represent a monthly sample. Samples were taken each month from August 1997 to October 1998 (except January 1998) and in February 1999, each on the same 150 m stretch of beach on Hog Island.

Depending on fish abundance, each series of eight seine hauls took 30 to 90 min. Since the sampling protocol was consistent (i.e. 32 seines of equal distance, at the same site and standardized by tide), no richness index was necessary to compare the number of species collected among months. Instead, collections conducted in an identical manner can most accurately be compared using direct species counts; this approach avoids problems inherent to richness indexes (Ludwig & Reynolds, 1988). Evenness was calculated using the following equation:

$$E=((1/\lambda)-1)/(e^{H'}-1)$$

where $\lambda=\Sigma(n_i/N)^2$ [Simpson's diversity index (Simpson, 1949)] and $H'=-\Sigma p_i \ln(p_i)$ [Shannon's diversity index (Shannon, 1949)]. This evenness index is less biased than the more commonly used J' of Pielou (1975, 1977) because of its independence from sample richness (Ludwig & Reynolds, 1988). Clark *et al.* (1996*a*) suggested that seasonal fluctuations in the faunal abundance of the surf-zone are especially important on beaches in which temperature change exceeds 20 °C annually, a criterion that was met in our study. In order to elucidate the potential relationship between temperature and fish abundance in the shallow surf, species richness, total number of individuals, and evenness were correlated with the average monthly temperature (see Table 1). Temperature of the shallow surf was measured with a YSI model 30 SCT meter.

For day/night comparisons, sampling was conducted on three nights: 7/8 July, 30/31 July, and 12/13 August. Over the three nights, eight series of samples were collected. Each series of samples consisted of eight consecutive seine hauls, as is described in the monthly sampling protocol. Each series of seine hauls was compared to a set of daytime hauls conducted at the identical tide on the previous day. Comparisons between high and low tide fish collections were made using the monthly data. Within a month, the 16 high and 16 low tide seines were pooled and compared on a pairwise fashion.

Spatial analyses

Small-scale spatial variations in fish assemblage structure were analysed by comparing collections at the north Hog Island site to those in shielded ' runnel ' habitats (Komar, 1998). The width and depth of the runnels, as well as the height of the shielding sand bar, varied considerably due to tidal conditions, recent sediment transport, and various other factors. Unlike the study of Harvey (1998), runnels were sampled that were not completely isolated from wave exposure, for example at high tide when small waves moved across the bar and through the runnel. Even so, for every runnel sample there was a clear bar that dissipated wave energy, and the runnel itself was always a well-formed depression. Eight seine collections at the main North Hog site were compared with eight seine collections in one of two runnel habitats immediately adjacent to the exposed site (runnels were within 100 m of the exposed site). Each series of seines were taken at random times within the tidal cycle, but the eight paired runnel seines and exposed site seines were always taken consecutively. The seine was deployed in the same manner at the runnels and at the exposed site.

In order to evaluate fish assemblages at different locations on the Virginia barrier islands, two additional sites were sampled (the southern end of Hog Island and Parramore Island) in July and August, 1999 (See Figure 1). All three locations were exposed beach sites with similar wave energy, surf-zone width, beach slope and particle size. Thirty-two seines were taken each month at these sites, following the collection protocol used in the monthly sampling.

Sampling efficiency

Due to mesh size and net length, capture efficiency varies among species (Parsley *et al.*, 1989; Monteiro-Neto & Musick, 1994; Allen *et al.*, 1995). Thus our use of only a single sampling gear likely resulted in bias against certain fish species. For example, catch efficiency was probably rather low for larger species. Earlier studies have discussed the effect that net efficiency can have on beach seine collections (Gulland, 1983; Lasiak, 1984*a*; Lyons, 1986; Nash, 1986; Parsley *et al.*, 1989; Pierce *et al.*, 1990; Romer, 1990; Monteiro-Neto & Musick, 1994; Nash *et al.*, 1994; Lamberth *et al.*, 1995). In this study, net collection efficiency may have been lower in the turbulent water of the exposed beach site than in the calm runnel water, despite a focused effort to minimize among site sampling variations. Conversely, fishes may be more likely to detect and avoid the net in the calm water. Similarly, earlier studies have debated the validity of making direct day and night collection comparisons (e.g. Horn, 1980; Nash, 1986; Wright, 1989; Gibson *et al.*, 1996). In an attempt to minimize these sampling problems, numerous individual samples were taken at a given site or sampling time; a minimum of 16 individual seines were conducted for any particular comparison.

Statistical analyses

All data sets used in univariate tests (comparing species richness, total number of individuals, or fish lengths among months, site, day/night or high/low tide samples) which met assumptions of normality and homogeneity of variance were compared using analysis of variance (ANOVA), or with paired *t*-tests when data were collected in paired fashion. Comparisons which did not meet variance or distributional assumptions were carried out with the Kruskal-Wallis (multiple comparisons) or Wilcoxon Signed Rank (paired comparisons) non-parametric tests. There is much concern over the ' experimentwise ' error rate when multiple comparisons are made within a given study; however, the objective of this study was to make a series of individual comparisons. For example, day/night and runnel/exposed site analyses are considered separately. Therefore, significance of each experiment was evaluated at the 0·05 level following the precedent set by Carmen and Walker (1982) and Soto and Hurlbert (1991). All univariate statistical analyses were conducted with SigmaStat Statistical Software® (1997).

For analyses in which sufficient samples were available (seasonal, day/night and exposed/runnel comparisons), the multidimensional scaling (MDS) technique proposed by Field *et al.* (1982), Clark (1993), and Clark and Ainsworth (1993) was also used to compare fish assemblage structure. In all multivariate analyses, fish abundances were first root-root transformed in order to decrease the influence of the most abundant species (Clark & Green, 1988). Similarity matrices were calculated using the Bray-Curtis similarity index (Bray & Curtis, 1957). Ordination plots based on these pairwise similarities were constructed by the MDS technique using the SPSS statistical software package.

TABLE 2. The total number of individuals captured in 32 seines conducted each month at the main exposed beach site on Hog Island, Virginia from August 1997 to February 1999. Density is expressed as number of fish m^{-2}. Species abbreviations are as follows: *Membras martinica*=Mm; *Menticirrhus littoralis*=Ml; *Trachinotus carolinus*=Tc; *Fundulus majalis*=Fm; *Mugil curema*=Mc; *Menticirrhus saxatilis*=Ms; *Cyprinodon variegatus*=Cv; *Fundulus heteroclitus*=Fh; *Sphyraena* sp.=Ssp.; *Sciaenops ocellatus*=So; *Paralichthys dentatus*=Pd; *Syngnathus fuscus*=Sf

Month	Mm	Ml	Tc	Fm	Mc	Ms	Cv	Fh	Ssp.	So	Pd	Sf	Total	Average Density
Aug-97	419	372	31	34	—	9	3	—	—	—	—	1	869	0·226
Sep-97	14	528	2	6	4	16	—	—	—	—	—	—	570	0·148
Oct-97	145	260	4	7	—	7	—	—	—	—	—	—	424	0·110
Nov-97	40	15	—	4	2	2	20	—	—	2	—	—	83	0·022
Dec-97	12	—	—	—	—	—	—	—	—	—	—	—	12	0·003
Feb-98	18	—	—	—	—	—	—	—	—	—	—	—	18	0·005
Mar-98	104	—	—	—	3	—	—	—	—	2	—	—	107	0·028
Apr-98	141	—	—	—	17	—	—	—	—	—	—	—	158	0·041
May-98	46	—	—	—	2	—	—	—	—	—	—	—	48	0·013
Jun-98	17	—	5	1	12	—	2	—	—	—	—	—	37	0·010
Jul-98	340	17	249	1	30	2	1	3	1	—	1	3	643	0·167
Aug-98	1027	221	81	30	3	14	2	—	—	—	—	—	1378	0·359
Sep-98	2	118	14	3	—	2	—	—	—	—	—	—	139	0·036
Oct-98	10	84	5	1	—	—	—	—	—	—	—	—	100	0·026
Feb-99	19	—	—	—	2	—	—	—	—	—	—	—	21	0·006
Total	2354	1615	391	87	75	52	29	3	3	2	1	1	4607	
(%)	51	35	8	2	2	1	1	<1	<1	<1	<1	<1		

Results

Seasonal analysis

The fish assemblage of the shallow surf-zone on the Virginia barrier islands had low diversity and was dominated by three species, *M. martinica, M. littoralis*, and *T. carolinus*, which accounted for 94% of all fishes collected. The seven most common species accounted for 99·9% of the catch (Table 2) and *M. martinica* was the most abundant fish species (51% of all individuals). There was a distinct seasonal trend in species richness and abundance (Figure 2). Most fishes were collected June through October, with the largest collection in August 1998 (1378 total fish; estimated density=0·36 fish m^{-2}). Fish species richness was highest in the summer and early fall. The lowest species richness and overall fish abundance occurred during the winter and spring. Species evenness was also at a minimum during winter months. Seasonal abundance trends were further supported by distinct positive correlations of species richness, total number of individuals and evenness with temperature (Figure 3). Both richness ($R^2=0{\cdot}54$; $P=0{\cdot}002$) and total number of individuals ($R^2=0{\cdot}51$; $P=0{\cdot}003$) were found to be significantly correlated with temperature.

A MDS ordination plot (Figure 4) revealed distinct groupings of monthly fish samples. Winter and spring samples are in close proximity in ordination space because each of these months was characterized by low species richness and low overall fish abundance. The second major grouping corresponds to the late summer and early fall samples (August through to October) in which species richness and abundance were high. The June sample is differentiated by low abundance despite a relatively high species richness. The July and November samples are differentiated in ordination space because of the presence of species that were not captured in other months.

Almost all fishes collected were less than 100 m in total length. Table 3 gives the average monthly size of the three dominant members of the fish community during the summer months. There was a trend of increasing size from the early to late summer. This trend was most pronounced for *T. carolinus*, which had an average size of 22·7 mm in June and 90·1 mm in August. The average length of *M. littoralis* decreased slightly from July to August, but both months had a significantly higher mean length than June. For these three species there was a significant difference in mean length among months (*M. martinica*, ANOVA, $F_{2,134}=38{\cdot}8$; *T. carolinus*, Kruskal-Wallis, df=2, $H=119{\cdot}2$; *M. littoralis*, Kruskal-Wallis, df=2, $H=45{\cdot}2$; $P<0{\cdot}001$ for all cases).

Day/night analysis

Although significantly more fish species were collected at night (paired *t*-test, df=7, $t=4{\cdot}2$, $P=0{\cdot}004$), the

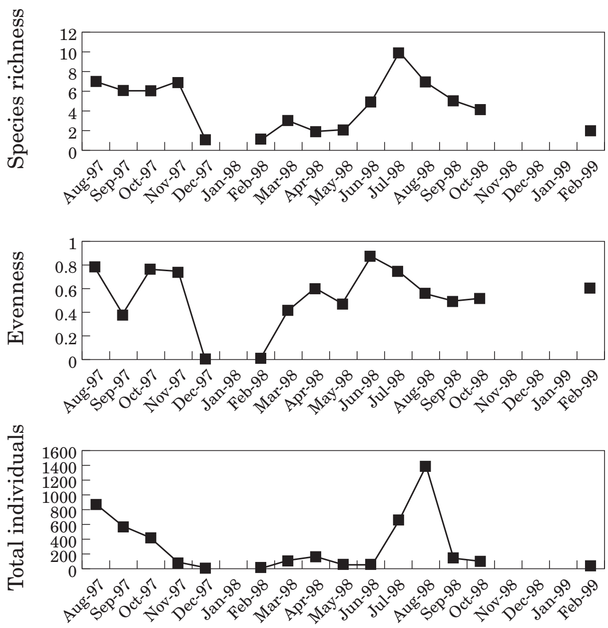

FIGURE 2. Fish species richness, evenness and total number of individuals at the main sampling site on the north end of Hog Island over the 15 month study period. Richness is expressed as total number of species and evenness calculated using the index given in the Methods section (Ludwig & Reynolds, 1988).

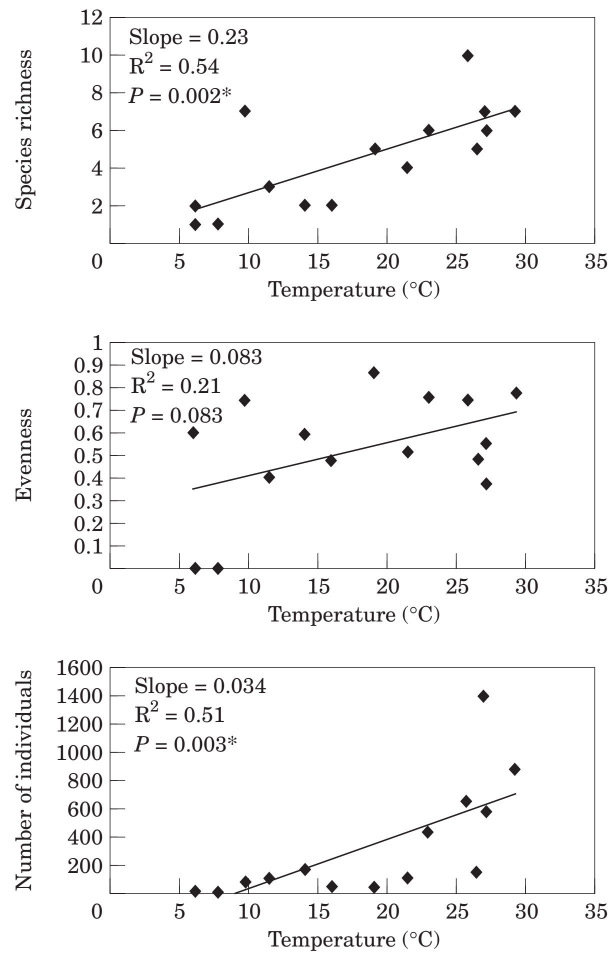

FIGURE 3. Fish species richness, evenness, and number of individuals correlated to temperature of the shallow surf-zone on the monthly sampling dates. Slopes of the lines, r-squared values and P-values are indicated on the plots. Significant regressions are indicated with a *.

total numerical abundance did not differ (paired t-test, df=7, t=0·35, P=0·74). The significant increase in species richness was due primarily to three adult fish species, none of which was collected during the daylight hours (*Paralichthys dentatus*, summer flounder, *Leiostomus xanthurus*, spot, and *Astroscopus guttatus*, northern stargazer). The size of these fishes ranged from 15·1 to 37·1 cm. The three most commonly collected species at night were the same as during the day, *M. martinica*, *T. carolinus*, and *M. littoralis*. These three species made up 90% of the total number of fishes at night, compared to 98% in the paired daytime samples. A MDS ordination plot did not reveal distinct day/night groupings of fish samples (Figure 5); the sampling dates are clustered to a much greater extent than are the day or night samples.

Tidal analysis

For both high and low tide samples, richness peaked in the summer or early fall and declined to a single species in the winter (Table 4). Species richness was significantly greater at high tide (paired t-test, df=14, t=3·86, P=0·002), but numerical abundance did not differ (paired t-test, df=14, t=1·24, P=0·23). For individual species, only *T. carolinus* was more commonly collected at high tide (Wilcoxon Signed Rank, P=0·02).

Runnel analysis

There were clear differences in species richness and total abundance between the main North Hog site and adjacent runnel habitats (Figure 6). On eight of the 10 days in which these comparisons were made, richness was greater in the runnel habitats; on nine of the sampling days, total fish abundance in the runnels was higher. Both species richness (paired t-test, df=9, t=3·0, P=0·014) and total abundance (paired t-test, df=9, t=2·6, P=0·027) were found to be significantly greater at the runnel site. The significant increase in species richness was due to the occurrence of rarely collected species including *Anchoa* sp. (anchovies),

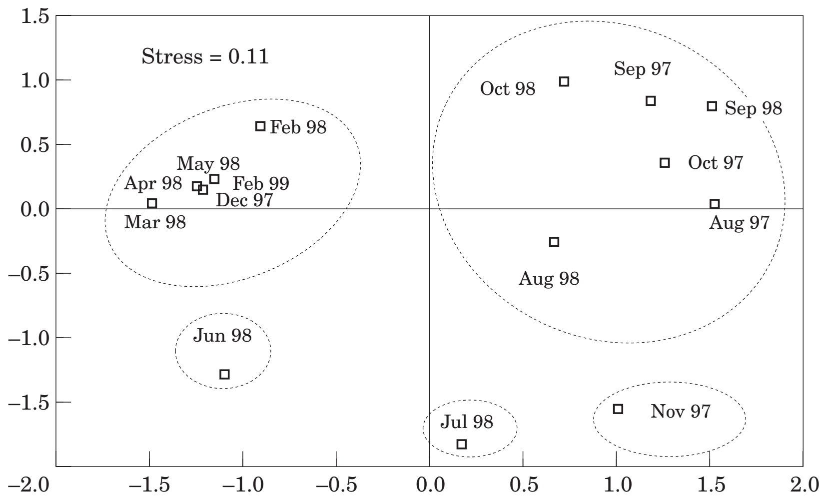

FIGURE 4. Multidimensional scaling ordination plot of the seining data at the main exposed Hog Island sampling location for the fifteen monthly collections. Groups of samples are delineated at the 60% level of similarity.

TABLE 3. The average monthly size of the three most common fish species during June, July and August 1998. Sizes are given in mm

	Membras martinica	*Trachinotus carolinus*	*Menticirrhus littoralis*
June	44·1	22·7	30·1
July	63·9	48·0	66·8
August	67·8	90·1	53·1

Fistularia tabacaria (bluespotted cornetfish), *Hyporhamphus unifasciatus* (halfbeak), *Sphoeroides maculatus* (northern puffer) and juvenile *Anguilla rostrata* (American eels), as well as resident marsh fish species, including the *Fundulus heteroclitus* (common mummichog) and *Cyprinodon variegatus* (sheepshead minnow). In contrast, the significant increase in total abundance of fishes was primarily due to large collections of the three most common shallow surf residents, *M. martinica*, *M. littoralis*, and *T. carolinus*. Despite the clear trends in univariate statistical analyses, there were no distinct groupings of the exposed

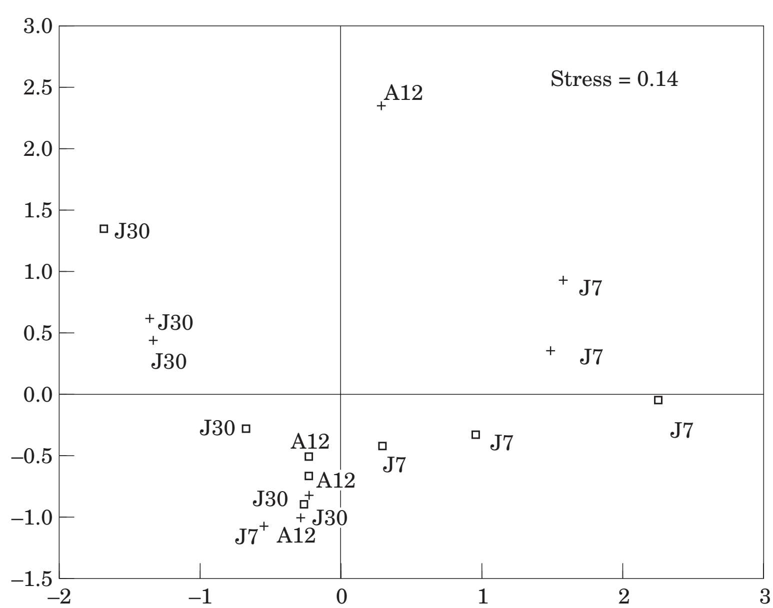

FIGURE 5. The multidimensional scaling ordination plot of the 16 day/night sampling data sets. The dates of sampling are abbreviated as follows: 7/8 July=J7, 30/31 July=J30, and 12/13 August=A12. Crosses: day samples; squares: night samples.

TABLE 4. The fish species richness, total number of individuals and number of the three most common species at high (H) and low (L) tide. These data are compiled from the monthly seining samples in which eight seines were conducted at high tide and eight at low tide on two days during the month of interest. The high and low tide data were compared with a paired *t*-test and resulting *P*-values are given at the bottom of the table. Significant results are designated with a *. Abbreviations are as follows: *Membras martinica*, Mm; *Menticirrhus littoralis*, Ml; *Trachinotus carolinus*, Tc

Month	Richness		Total Individuals		Mm		Ml		Tc	
Tide	H	L	H	L	H	L	H	L	H	L
Aug-97	7	3	351	518	39	380	238	134	31	0
Sep-97	6	3	262	308	14	0	229	299	2	0
Oct-97	6	4	247	177	23	122	121	48	4	0
Nov-97	7	5	34	51	7	33	2	13	0	0
Dec-97	0	1	0	12	0	12	0	0	0	0
Feb-98	1	1	6	12	6	12	0	0	0	0
Mar-98	3	1	67	42	62	42	0	0	0	0
Apr-98	2	2	49	109	41	100	0	0	0	0
May-98	2	1	26	22	24	22	0	0	0	0
Jun-98	5	3	13	0	6	11	0	0	2	3
Jul-98	8	6	320	325	30	310	8	9	248	1
Aug-98	7	4	452	926	185	842	161	60	64	17
Sep-98	4	4	114	25	0	2	98	20	12	2
Oct-98	4	3	23	77	7	3	12	72	3	2
Feb-99	2	2	10	11	9	10	0	0	0	0
P-values	0·0002*		0·67		0·06		0·25		0·03*	

and runnel sites in MDS space (Figure 7). This suggests that although the richness and abundance of fishes on any given day typically are higher in the runnel than at the adjacent exposed beach site, the fish assemblage is not predictable from day to day.

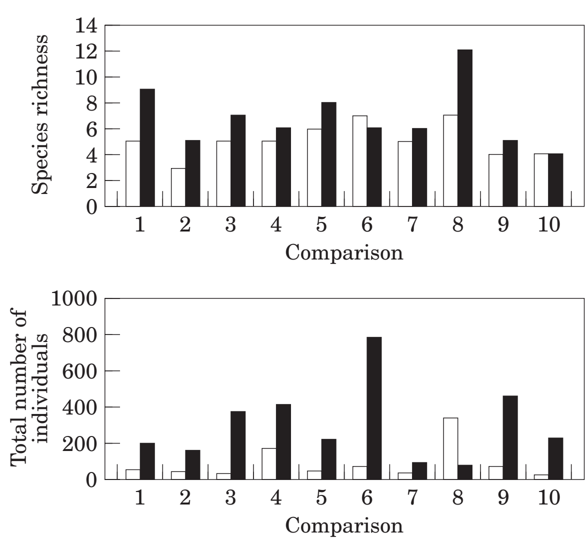

FIGURE 6. Fish species richness and number of individuals collected at the main exposed sampling site on the north end of Hog Island compared to adjacent runnel habitat collections taken immediately before or after. Open bars: exposed site; closed bars: runnel site.

Inter-island analysis

Membras martinica, T. carolinus and *M. littoralis* were the three most commonly collected fish species at the North Hog, South Hog, and Parramore sites during both July and August (Table 5). During each month the rank order (based on abundance of each of these species) was consistent across the three sites. The similarity among sites suggests that the fauna of Hog Island is representative of other Virginia barrier islands.

Discussion

The number of fish species collected in the shallow surf-zone on Hog Island (25) is below the range (26 to 71) reported in previous surf-zone ichthyofaunal studies (Brown & McLachlan, 1990). Importantly, only seven species accounted for 99% of all fishes collected. Although surf-zone habitats are typically dominated by relatively few species (Lasiak, 1984*a*; Ross *et al*., 1987; Brown & McLachlan, 1990; Romer, 1990), the shallow surf-zone was even more species poor. Very few species are able to utilize the turbulent, shallow water. The species that were found in the shallow surf-zone can be classified into one of five life-history categories: seasonal nursery juveniles, adult transients, year-round residents, seasonal or nocturnal migrants, and marsh pond

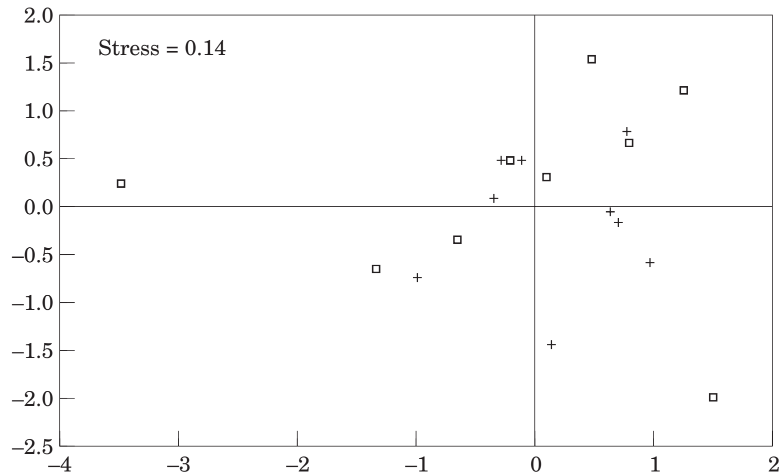

FIGURE 7. The multidimensional scaling ordination plot of samples taken at exposed sites and adjacent runnel habitats during July. Crosses: exposed samples; squares: runnel samples.

TABLE 5. The percent composition of fishes collected at the main site on the north end of Hog Island, the site at the south end of Hog Island, and on Parramore Island in July and August 1998

	July			August		
	Main	South	Parramore	Main	South	Parramore
M. martinica	51	46	80	75	51	51
T. carolinus	37	27	13	6	10	6
M. littoralis	6	24	6	15	36	42
M. curema	4	—	—	<1	—	—
F. majalis	<1	—	—	—	2	2
C. variegatus	<1	<1	—	<1	—	—
M. saxatilis	<1	<1	<1	<1	<1	<1
Sphyraena sp.	<1	—	—	—	—	—
F. heteroclitus	<1	<1	—	—	—	—
P. dentatus	<1	—	—	—	—	—

residents (Table 6). The majority of the species collected in this study were either seasonal juveniles that utilize the shallow waters as a nursery area or adult transient species that are much more common in other marine habitats. These fishes are typically invertivores or planktivores, and are common in the shallow surf-zone during the warmer months of the year. Only two species, *M. martinica* and *M. curema*, were year-round residents. Other adult marine species occasionally moved into the shallows either at night (e.g. *L. xanthurus*) or during a particular season (e.g. *S. ocellatus*). Finally, some of the fish species were residents of marsh ponds on the Virginia barrier islands. These fishes are swept into the ocean as the ponds periodically drain (Layman *et al.*, in press).

Most species utilize the shallow surf during the summer and early fall and then migrate to deeper waters or southward during cooler months, as has been shown in other studies (Gunter, 1945; McFarland, 1963; Modde & Ross, 1981; Guillen & Landry, 1982; Leber, 1982; Lasiak, 1984*b*; Peters, 1984; Peters & Nelson, 1987; Ross *et al.*, 1987; Santos & Nash, 1995; Clark *et al.*, 1996*a*). This seasonal migration is supported by the significant relationship between species abundance and average monthly temperature. Although not directly demonstrated here, it seems likely that temperature either directly, or indirectly (i.e. by influencing the timing of spawning), is the underlying mechanism of seasonal shallow surf-zone dynamics.

MDS revealed no distinct grouping that would suggest distinct day and night fish assemblages. However, the univariate statistics clearly showed a significant increase in species richness at night. This agrees with other studies which have shown that the abundance of relatively rare species may increase at night,

TABLE 6. List of species captured in the shallow surf zone of Hog Island during sampling conducted from August 1997 until February 1999. Each species is classified according to site(s) of capture, time of capture, surf utilization, and trophic level. Trophic level classifications (for the age class of fish which we specifically collected) are based on the descriptions of Murdy *et al.* (1997). *Site*: E=exposed: R=runnel; B=Both. *Time*: D=Day; N=Night; B=Both. *Surf utilization*: Y=year-round resident; J=seasonal nursery juvenile; M=island marsh pond resident; T=adult transient common in other marine habitats. *Trophic level*: P=planktivore; W=water column macroinvertebrates; I=benthic invertivore; F=piscivore; A=algavore; D=detritivore

Scientific name	Common name	Site	Time	Surf utilization	Trophic level
Fish species					
Anchoa sp.	Anchovy	R	B	J	P
Anguilla rostrata	American eel	R	D	J	P/I
Astroscopus guttatus	Northern stargazer	E	N	T	F
Brevoortia tyrannus	Atlantic menhaden	R	D	J	P
Caranx hippos	Crevalle Jack	R	D	J	I/W
Cyprinodon variegatus	Sheepshead minnow	B	B	M	A
Fistularia tabacaria	Bluespotted cornetfish	R	D	T	W/F
Fundulus heteroclitus	Common mummichog	B	B	M	I/W/D
Fundulus majalis	Striped killifish	B	B	T	I/W
Hyporhamphus unifasciatus	Halfbeak	R	D	T	W/F
Leiostomus xanthurus	Spot	B	N	T	I/F
Membras martinica	Rough silverside	B	B	Y	P
Menticirrhus saxatilis	Northern kingfish	B	B	J	I
Menticirrhus littoralis	Gulf kingfish	B	B	J	I
Mugil curema	White mullet	B	B	Y	A/D
Paralichthys dentatus	Summer flounder	B	B	J/T	W/F
Peprilus sp.	Butterfish	B	B	J	P/W
Psenes sp.	Driftfish	B	D	J	P/W
Sciaenops ocellatus	Red drum	E	D	T	F/I
Sphoeroides maculatus	Northern puffer	R	D	T	I
Sphyraena sp.	Barracuda	B	B	J	W/F
Strongylura marina	Atlantic needlefish	B	D	T	W/F
Sygnathus fuscus	Northern pipefish	B	B	T	P/I
Trachinotus carolinus	Florida pompano	B	B	J	I/W

but the main changes in fish assemblage structure were due to variability of the most common fish species (Romer, 1990; Gibson *et al.*, 1996). Additionally, I was able to identify a significant trend of increased richness, as well as a significant trend in increased abundance of *T. carolinus*, in high tide samples. Gibson *et al.* (1998) identified three main reasons for such diel, tidal, or similar fish migrations: (1) foraging considerations, (2) predator avoidance, and (3) selection of suitable environmental conditions. The former two explanations are most likely in the shallow surf-zone.

Nocturnal increases in species richness are related to the shoreward movements of piscivorous fishes (e.g. *Leiostomus xanthurus*), forcing prey fishes into shallower water (Girsa & Zhuravel, 1983; Brown & McLachlan, 1990; Ansell & Gibson, 1990; Gibson *et al.*, 1996). In contrast, tidal migrations within the shallow surf are likely related to the availability of food (Brown & McLachlan, 1990; Gibson *et al.*, 1996). High tides allow some fishes to move into the uppermost ' zones ' of intertidal invertebrate distributions, an area inaccessible to other fishes (Brown & McLachlan, 1990). This foraging explanation may explain the increased abundance of *T. carolinus*, a benthic invertivore (Armitage & Alevizon, 1980), at high tide. In contrast, fishes that do not migrate with tidal cycles may be utilizing food items that are available at various intertidal depths (e.g. the zooplanktivorous *M. martinica*), and their presence in the shallow surf-zone is due primarily to predator avoidance. Movements based on the selection of optimal environmental conditions is unlikely, as the shallow surf-zone actually necessitates increased energy expense in order to maintain position and move freely in such a dynamic, turbulent area (Clark *et al.*, 1996*a*).

Previous studies have made surf-zone wave exposure comparisons among sites separated by many hundreds of metres (Hillman, 1977; Brown & McLachlan, 1990; Romer 1990; Pihl & van der Veer, 1992; Gibson, 1994; Clark *et al.*, 1996*b*; Clark, 1997).

One drawback of such large-scale comparisons is that many factors, including substrate type, sediment size, distance from potential sources of colonization, temperature, and presence of structure, are likely to vary among the sites. The present study minimized these spatial differences by examining the effects of wave exposure on a much smaller scale; fish assemblages were compared in runnel and exposed sites immediately adjacent to one another.

Due to variable collections of common species and the sporadic occurrence of relatively rare fish species, there was no distinct runnel fish assemblage identifiable in MDS space. However, the univariate statistical approaches reveal a very important trend in the data; both species richness and overall fish abundance were significantly higher in the runnels. This statistical result further substantiates the observations of Harvey (1998), who documented the preference of *F. majalis* for runnels. Overall the data suggest that even though there were not distinct runnel and non-runnel fish assemblages (i.e. assemblages varied more among days than between runnel and exposed sites on a single day), there were typically more species and a higher number of species in the runnels on any given day. This concentration of fishes in the runnels may be in direct response to the decreased physical wave energy (Romer, 1990; Clark *et al*., 1996*b*), or an indirect effect resulting from turbidity preferences (Lasiak, 1984*b*; Clark *et al*., 1996*b*), avoidance of predation (Robertson & Lenanton, 1984; Gibson *et al*., 1998; Harvey, 1998), increased food availability (DeLancey, 1989; Gibson *et al*., 1998; Harvey, 1998), or the benefits of macrophyte/debris accumulation (Lenanton, 1982; Robertson & Lenanton, 1984; Peters & Nelson, 1987; Lenanton & Caputi, 1989). A combination of all these factors likely contribute to the preference for runnel habitats.

A convergence of shallow surf-zone fishes into runnels emphasizes a much debated question in surf-zone ecology; what factors actually cause differences in fish assemblage structure among sites with varying levels of wave exposure? The shallow surf-zone may provide the ideal habitat in which this question can be evaluated. The abundance of runnel systems on many beaches (Komar, 1998) provides a natural experiment in which there is significant wave exposure variation among sites (i.e. runnel and exposed locations) in close proximity. Close sampling locations helps minimize the influence of confounding variables inherent to spatial comparisons. Furthermore, the shallow surf-zone is more easily sampled (i.e. it does not require the use of a boat or extensive trawl system) and multiple samples can be taken in a short time period.

Earlier studies have documented the movement of fishes in and out of the surf-zone on seasonal, diel, or tidal cycles (Lasiak, 1984*a*,*b*; Peters, 1984; Senta & Kinoshita, 1985; Ross *et al*., 1987; Wright, 1988, 1989; Abou-Seedo, 1990; Brown & McLachlan, 1990; Gibson *et al*., 1993; Lamberth *et al*., 1995; Santos & Nash, 1995; Clark *et al*., 1996*a*,*b*; Gibson *et al*., 1996; Gibson *et al*., 1988). These patterns may be defined as perpendicular movements, towards or away from the beach. The present study has provided evidence that the same perpendicular movements occur in the shallow surf-zone. For example, this study demonstrates the importance of seasonal movements in the shallow water, due primarily to the influx of juveniles during the summer months. Also important are perpendicular movements on diel and tidal cycles, as fish species richness increases at night and during high tide.

The results of this study also suggest that an additional movement might occur parallel to the beach face, as fishes move into or among preferred runnel habitats. The dynamic nature of the runnels themselves (due to tidal influences, shifting sediment, etc.) suggests that fishes may undertake frequent small-scale movements seeking runnels that provide maximum benefit. A related observation was made by McLachlan and Hesp (1984) who suggested that fishes prefer lower energy bay habitats over high energy horn areas on beaches with distinct cusp morphology. Fishes may migrate parallel to the beach seeking bay habitats, much as they move into runnels in the shallow surf-zone. The result is a convergence of surf-zone residents and a distinct concentration of food web interactions (McLachlan & Hesp, 1984).

In conclusion, the shallow surf-zone is characterized by low species diversity, and serves as a nursery area (or, in certain cases, a year-round habitat) for those species which are able to utilize the shallow water. Some characteristics of the shallow surf reflect those reported for the overall surf-zone, including seasonal, tidal, and diel trends in richness and abundance. Of these temporal scales, seasonal movements seem to be the most important component of the shallow surf-zone fish dynamics. Additionally, fishes of the shallow surf demonstrate a preference for low energy runnel habitats. The mechanism underlying this phenomena remains unclear, but it may be the end result of small-scale movements parallel to the beach face.

Acknowledgements

Although too numerous to list, I would like to thank everyone who assisted me in the various aspects of my field work. Especially important was Devin Herod, a valuable field and laboratory assistant throughout this project. I received insightful comments that greatly improved earlier versions of this manuscript from Mike Erwin, Devin Herod, Carleton Ray, Brian Silliman, Dave Smith, and two anonymous reviewers. My research was supported by the Virginia Coast Reserve Long-Term Ecological Research Program at the University of Virginia and the Fred Holmsley Moore Research Award.

References

Abou-Seedo, F., Clayton, D. A. & Wright, J. M. 1990 Tidal and turbidity effects on the shallow-water fish assemblage of Kuwait Bay. *Marine Ecology Progress Series* **65,** 213–223.

Allen, D. M., Service, S. K. & Ogburn-Matthews, M. V. 1995 Factors influencing the collection efficiency of estuarine fishes. *Transactions of the American Fisheries Society* **121,** 234–244.

Anderson, W. D., Jr., Dias, J. K., Dias, R. K., Cupka, D. M. & Chamberlain, N. A. 1977 The macrofauna of the surf-zone off Folly Beach, South Carolina. N.O.A.A. *Technical Report NMFS SSRF-704*.

Armitage, T. M. & Alevizon, W. S. 1980 The diet of the Florida pompano (*Trachinotus carolinus*) along the east coast of Central Florida. *Florida Scientist* **43,** 19–26.

Ansell, A. D. & Gibson, R. N. 1990 Patterns of feeding and movement of juvenile flatfishes on an open sandy beach. In *Trophic Relationships in the Marine Environment* (Barnes, M. & Gibson, R. N., ed.). Aberdeen University Press, Aberdeen, pp. 197–207.

Bray, J. R. & Curtis, J. C. 1957 An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27,** 325–349.

Brown, A. C. & McLachlan, A. 1990 *Ecology of Sandy Shores. Elsevier, Amsterdam*, 328 pp.

Carmen, S. G. & Walker, W. M. 1982 Baby bear's dilemma: A statistical tale. *Agronomy Journal* **74,** 122–124.

Development of Fishes of the Mid-Atlantic Bight: An Atlas of Egg, Larval, and Juvenile Stages. Chesapeake Biological Laboratory 1978. Department of the Interior, Fish and Wildlife Service, Office of Biological Services, Power Plant Project.

Clark, B. M. 1997 Variation in surf-zone fish community structure across a wave-exposure gradient. *Estuarine, Coastal and Shelf Science* **44,** 659–674.

Clark, B. M., Bennet, B. A. & Lamberth, S. J. 1996*a* Temporal variations in surf zone fish assemblages from False Bay, South Africa. *Marine Ecology Progress Series* **131,** 35–47.

Clark, B. M., Bennett, B. A. & Lamberth, S. J. 1996*b* Factors affecting spatial variability in seine net catches of fishes in the surf-zone of False Bay, South Africa. *Marine Ecology Progress Series* **131,** 17–34.

Clark, K. R. 1993 Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18,** 117–143.

Clark, K. R. & Ainsworth, M. 1993 A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92,** 205–219.

Clark, K. R. & Green, R. H. 1988 Statistical design and analysis for a " biological effects " study. *Marine Ecology Progress Series* **46,** 213–226.

DeLancey, L. B. 1989 Trophic relationship in the surf zone during the summer at Folly Beach, South Carolina. *Journal of Coastal Research* **5,** 477–488.

Field, J. G., Clark, K. R. & Warwick, R. M. 1982 A practical strategy for analysing multi-species distribution patterns. *Marine Ecology Progress Series* **8,** 37–53.

Gibson, R. N. 1994 Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32,** 191–206.

Gibson, R. N., Ansell, A. D. & Robb, L. 1993 Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. *Marine Ecology Progress Series* **130,** 1–17.

Gibson, R. N., Robb, L. & Ansell, A. D. 1996 Tidal, diel, and longer term changes in the distribution of fishes on a Scottish sandy beach. *Marine Ecology Progress Series* **130,** 1–17.

Gibson, R. N., Pihl, L., Burrows, M. T., Modin, J., Wennhage, H. & Nickell, L. A. 1998 Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* **165,** 145–159.

Girsa, I. I. & Zhuravel, V. N. 1983 Behavioural rhythm of some fishes in the coastal regions of the White Sea. *Journal of Ichthyology* **23,** 138–142.

Guillen, G. J. & Landry, A. M. 1982 Species composition and abundance of ichthyoplankton at beachfront and saltmarsh environments. In *Proceedings of the Annual Conference of the Southeast Association of Game and Fish Agencies*, No. 34, pp. 88–403.

Gulland, J. A. 1983 *Fish Stock Assessment. A Manual of Basic Methods*. John Wiley and Sons, New York, 223 pp.

Harvey, C. J. 1998 Use of sandy beach habitat by *Fundulus majalis*, a surf-zone fish. *Marine Ecology Progress Series* **164,** 307–310.

Gunter, G. 1945 Studies on the marine fishes of Texas. *Publication of the Institute of Marine Science at the University of Texas* **1,** 1–190.

Harris, M. S. 1988 *The Geomorphology of Hog Island, Virginia: A Mid-Atlantic Coast Barrier*. Master's Thesis, University of Virginia.

Helfman, G. S. 1993 Fish behaviour by day, night, and twilight. In *Behaviour of Teleost Fishes* (Pitcher, T. J., ed.). Chapman and Hall, London, pp. 479–612.

Hillman, R. E., Davis, N. W. & Wennemer, J. 1977 Abundance, diversity and stability in shore-zone fish communities in an area of Long Island Sound affected by discharge of a nuclear power station. *Estuarine Coastal and Shelf Science* **3,** 355–381.

Horn, M. H. 1980 Diel and seasonal variation in abundance and diversity of shallow-water fish populations in Morro Bay, California. *Fishery Bulletin* **78,** 759–770.

Kneib, R. T. 1997 Early life stages of resident nekton in intertidal marshes. *Estuaries* **20,** 214–230.

Komar, P. D. 1998 *Beach Processes and Sedimentation*. Prentice Hall, Upper Saddle River, New Jersey, 544 pp.

Lamberth, S. J., Bennet, B. A. & Clark, B. M. 1995 Seasonality and other factors influencing beach-seine catches in False Bay with an assessment of closed periods as a management option. *South African Journal of Marine Science* **15,** 157–167.

Lasiak, T. A. 1982 *Structural and Functional Aspects of the Surf Zone Fish Community of the Eastern Cape*. Ph.D. Thesis, University of Port Elizabeth.

Lasiak, T. A. 1984*a* Structural aspects of the surf-zone fish assemblages at Kings Beach, Algoa Bay, South Africa: short-term fluctuations. *Estuarine, Coastal and Shelf Science* **18,** 347–360.

Lasiak, T. A. 1984*b* Structural aspects of the surf-zone fish assemblages at Kings Beach, Algoa Bay, South Africa: long-term fluctuations. *Estuarine, Coastal and Shelf Science* **18,** 459–483.

Lasiak, T. A. 1986 Juveniles, food, and the surf-zone habitat: implications for teleost nursery areas. *South African Journal of Zoology* **21,** 51–55.

Layman, C. A., Smith, D. E. & Herod, J. D. Seasonal cycle of abiotic and biotic structuring mechanisms in marsh pond fish communities. *Marine Ecology Progress Series* (in press).

Leber, K. M. 1982 Seasonality of macroinvertebrates on a temperate, high wave energy beach. *Bulletin of Marine Science* **32,** 86–98.

Lenanton, R. C. J. 1982 Alternative non-estuarine habitats for some commercially and recreationally important fish species of southwestern Australia. *Australian Journal of Marine and Freshwater Research* **33,** 881–900.

Lenanton, R. C. J. & 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. *Journal of Experimental Marine Biology and Ecology* **128,** 165–176.

Ludwig, J. A. & Reynolds, J. F. 1988 *Statistical Ecology*. John Wiley and Sons, New York.

Lyons, J. 1986 Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. *North American Journal of Fisheries Management* **6,** 288–289.

McDermott, J. J. 1983 Food web in the surf-zone of an exposed sandy beach along the mid-Atlantic coast of the United States. In *Sandy Beaches as Ecosystems* (McLachlan, A. & Erasmus, T., ed.). W. Junk, The Hague, pp. 529–538.

McFarland, W. N. 1963 Seasonal change in the number and biomass of fishes from the surf at Mustang Island, Texas. *Public Institute of Marine Science at the University of Texas* **9,** 91–105.

McLachlan, A. 1980 The definition of sandy beaches in relation to exposure: a simple rating system. *South African Journal of Science* **76,** 137–138.

McLachlan, A. & Hesp, P. 1984 Faunal response to morphology and water circulation of a sandy beach with cusps. *Marine Ecology Progress Series* **19,** 133–144.

Modde, T. & Ross, S. T. 1981 Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. *Fishery Bulletin* **78,** 911–922.

Monteiro-Neto, C. & Musick, J. A. 1994 Effects of beach seine size on the assessment of surf-zone fish communities. *Atlantica* **16,** 23–29.

Murdy, E. O., Birdsong, R. S. & Musick, J. A. 1997 *Fishes of Chesapeake Bay*. Smithsonian Institution Press, Washington D.C., 324 pp.

Nash, R. D. M. 1986 Diel fluctuations of a shallow water fish community in the Inner Oslofjord, Norway. *Marine Ecology* **7,** 219–232.

Nash, R. D. M., Santos, R. S., Geffen, A. J., Hughes, G. & Ellis, T. R. 1994 Diel variability in catch rate of juvenile flatfish on two small nursery grounds (Port Erin Bay, Isle of Man and Porto Pim Bay, Faial, Azores) *Journal of Fish Biology* **44,** 35–45.

Parsley, M. J., Palmer, D. E. & Burkhart, R. W. 1989 Variation in capture efficiency of a beach seine for small fishes. *North American Journal of Fisheries Management* **9,** 239–244.

Peters, D. J. 1984 *Seasonality, Residency and Spatial Distribution of Surf-Zone Fishes of the Florida East Coast*. Master's of Science Thesis, Florida Institute of Technology.

Peters, D. J. & Nelson, W. G. 1987 The seasonality and spatial patterns of juvenile surf zone fishes of the Florida east coast. *Biological Sciences* **50,** 85–99.

Pielou, E. C. 1975 *Ecological Diversity*. John Wiley & Sons, New York, 165 pp.

Pielou, E. C. 1977 *Mathematical Ecology*. John Wiley & Sons, New York, 385 pp.

Pierce, C. L., Rasmussen, J. B. & Leggett, W. C. 1990 Sampling littoral fish with a seine: corrections for variable capture efficiency. *Canadian Journal of Fishery and Aquatic Sciences* **47,** 1004–1010.

Pihl, L. 1982 Food intake of young cod and flounder in a shallow bay on the Swedish west coast. *Netherlands Journal of Sea Research* **15,** 419–432.

Pihl, L. & van der Veer, H. W. 1992 Importance of exposure and habitat structure for the population density of O-group plaice, *Pleuronectes platessa* L., in coastal nursery estuaries. *Netherlands Journal of Sea Research* **29,** 145–152.

Robertson, A. I. & Lenanton, R. C. J. 1984 Fish community structure and food chain dynamics in the surf-zone of sandy-beaches: the role of aquatic macrophyte detritus. *Journal of Experimental Marine Biology and Ecology* **84,** 265–283.

Romer, G. S. 1990 Surf zone fish community and species response to a wave energy gradient. *Journal of Fish Biology* **36,** 279–287.

Ross, S. T., McMicheal, R. H., Jr. & Ruple, D. L. 1987 Seasonal and diel variation in the standing crop of fishes and macro-invertebrates from a Gulf of Mexico Surf Zone. *Estuarine, Coastal and Shelf Science* **25,** 391–412.

Ruple, D. L. 1984 Occurrence of larval fishes in the surf-zone of a Northern Gulf of Mexico Barrier Island. *Estuarine, Coastal and Shelf Science* **18,** 191–208.

Santos, R. S. & Nash, R. D. M. 1995 Seasonal changes in a sandy beach fish assemblage at Porto Pim, Faial, Azores. *Estuarine, Coastal and Shelf Science* **41,** 579–591.

Senta, T. & Kinoshita, I. 1985 Larval and juvenile fishes occurring in the surf-zone of western Japan. *Transactions of the American Fisheries Society* **114,** 609–618.

Shannon, C. E. 1949 *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, Illinois, 117 pp.

SigmaStat Statistical Software® 1997 SPSS, Inc. Version 2.0.

Simpson, E. H. 1949 Measurement of diversity. *Nature* **163,** 688.

Smith, K. J. & Able, K. W. 1994 Salt-marsh tide pools as winter refuges for the mummichog, *Fundulus heteroclitus*, in New Jersey. *Estuaries* **17,** 226–234.

Soto, D. & Hulbert, S. H. 1991 Long-term experiments on calanoid-cyclopoid interactions. *Ecological Monographs* **61,** 245–265.

Talbot, C. W. & Able, K. W. 1984 Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* **7,** 434–443.

Thorman, S. & Wiederholm, A. M. 1986 Food, habitat, and time niches in a coastal fish species assemblage in a brackish water bay in the Bothnian Sea, Sweden. *Journal of Experimental Marine Biology and Ecology* **95,** 67–86.

Wright, J. M. 1988 Seasonal and spatial differences in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. *Marine Biology* **102,** 135–142.

Wright, J. M. 1989 Diel variation and seasonal consistency in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. *Marine Biology* **102,** 135–142.

Yozzo, D. J., Mannino, A. & Smith, D. E. 1994 Mid-summer abundance of resident sub-adult marsh nekton at the Virginia Coast Reserve. *Virginia Journal of Science* **45,** 21–30.