

Annual Occurrence, Abundance and Diversity of Fish in a South Carolina Intertidal Creek*

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Abstract

An intertidal creek in North Inlet Estuary, South Carolina, USA, was sampled monthly for 1 year to determine the occurrence, abundance and diversity of fish species. Sampling was so conducted as to reduce sampling bias to a minimum and all individuals caught were weighed and measured. A total of 16,611 individuals weighing 202.45 kg and comprising 51 species and 25 families of fish was collected. Three diversity indices were calculated for species number. Analysis of variance revealed that season had a highly significant effect on all indices and the number of species, but had no effect on the number of individuals caught.

Introduction

All of the major estuarine habitats must be critically examined to understand the distribution of species in an estuary. Most of the fish population studies in southeast USA have sampled the channels, major creeks and sounds by use of the otter trawl (Tagatz and Dudley, 1961; Dahlberg and Odum, 1970; Freeman, 1971, personal communication; Hicks, 1972; Turner and Johnson, 1972), although a few studies utilized multiple collecting devices (Massmann *et al.*, 1954; Richards and Castagna, 1970; McErlean *et al.*, 1973). The otter trawl is a biased collecting device and selects for larger, slower demersal species and is limited to areas deep enough for navigation. For example, Richards and Castagna (1970) caught 13,800 *Fundulus heteroclitus* by seine and none by trawl when sampling the same area. In many estuaries, large areas are intertidal, and many species of fish follow the tide into these areas to feed on detritus and numerous invertebrates. However, very little is known about the distribution of these species or their utilization of the habitat, probably be-

cause of sampling difficulty. Otter trawls are useless except for the larger creeks, while seining is impossible due to the soft mud and oyster beds. Drop nets are suitable for intertidal sampling, but are biased against larger, more scattered species (Kjelson and Colby, in press).

The objectives of this study were (1) to adequately sample an intertidal creek with as little sampling bias as possible, (2) to determine the seasonal distribution of the species that utilize the habitat, (3) to determine the length and weight ranges of the species caught, and (4) to determine the diversity of these fish.

Materials and Methods

North Inlet Estuary (Fig. 1) is located approximately 6 miles east of Georgetown, South Carolina. A large portion of this estuary is controlled by the Belle W. Baruch Foundation which maintains it for research purposes. The estuary is undeveloped and is classified by the South Carolina Department of Health and Environmental Control as "highest quality". It is a semi-tropical, high-salinity estuary with little fresh-water inflow except from land runoff. The salinity during the course of this study ranged from 31 to 35‰, the water temperature from 9°C to 28°C (Fig. 2). The tidal amplitude of

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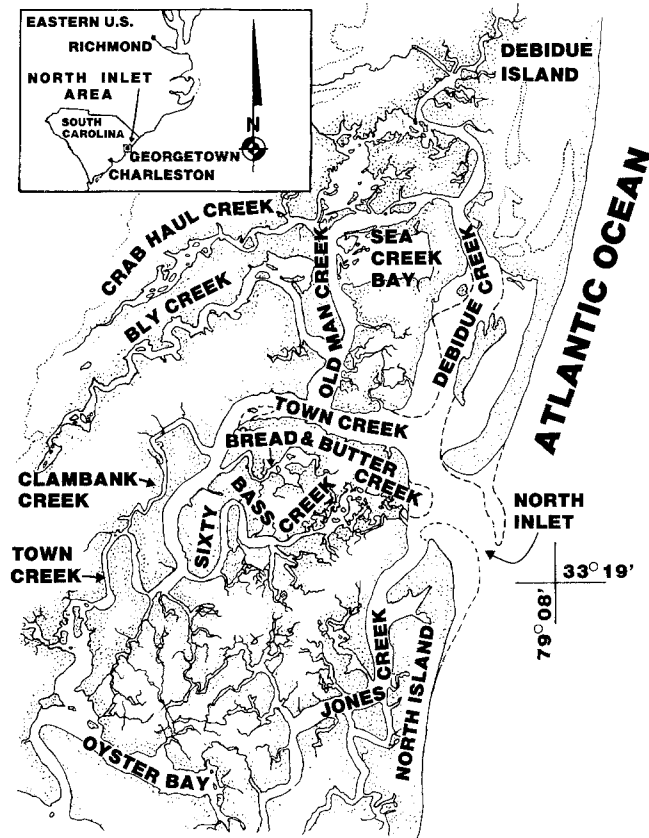


Fig. 1. Map of North Inlet, showing its relationship to the sample area

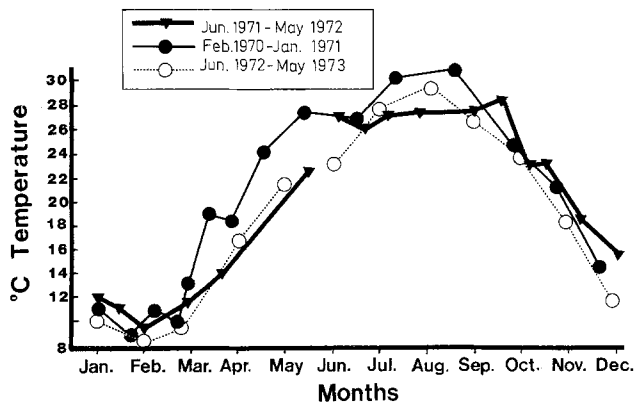


Fig. 2. Seasonal temperature variations at South Clambank Causeway Creek

approximately 1.6 m was very dependent on the wind direction. The tidal marsh is characterized by numerous shallow, labyrinthine, tidal creeks with extensive intertidal oyster beds (*Crassostrea virginica*), and expanses of mud flats and higher ground where *Spartina alterniflora* and *Juncus roemerianus* prevail.

The major sample site was a small intertidal creek, South Clambank Causeway Creek, which was dredged in 1954 to make the causeway. The creek extends the length of the causeway, approximately 150 m, and empties into Clambank Creek. Extensive *Spartina alterniflora* flats are drained by the creek but the actual drainage area is not easily defined. The bed of the creek (approximately 0.15 ha) is soft mud, varying in thickness from 75 mm to 1 m or more, with scattered oyster clumps and shells.

The creek is flooded on every tide and completely dry on low tides which are below mean low water. Thus, during most tidal cycles, there is at least 1.4 m of water at the mouth and 0.6 m at the upper end of the creek. During the sampling period, the creek was never observed to be dry for more than 2 h. Four other creeks were sampled for comparison; but due to their geomorphology, all proved impossible to sample on a regular basis.

The collecting net was a 3.3 x 33 m nylon-bag seine with 1/4-inch (0.64 mm) square mesh and an 8-m bag. The net was placed across the creek at high tide when the incoming tide appeared to be slack, and anchored on each bank by 3 m poles. Other poles were used at intervals to hold the net above the water. The lead line was pushed into the mud so no fish could escape under the net. When the creek was dry, approximately 5 h later, the fish were removed from the net and the creek bottom, washed and preserved in 10% formalin.

Preliminary attempts using the above method proved unsatisfactory for two reasons. First, although the net was held at least 0.3 m above the water at all times, many *Mugil cephalus* (striped mullet) jumped the net and escaped. Second, many small fish escaped through small holes created by *Callinectes sapidus* (blue crabs). In order to reduce these losses, a fish toxin, rotenone, was introduced at the upper end of the creek after the tide had dropped below the bank of the creek. This significantly reduced the loss of the striped mullet and small fish; however, many fish died in the upper part of the creek and had to be picked up by hand. The preliminary samples, collected without the use of

rotenone, were not used in the analysis for this study.

Sampling was attempted in a bi-monthly schedule from June, 1971 to May, 1972. However, because of the many problems associated with the sampling, this could not always be done; but at least one sample was taken in every month.

Sampling was also conducted during the summer of 1973 to determine the effects of repetitive sampling on the diversity and abundance of fish in the same creek. The creek was sampled on 4 consecutive days (July 15-18) and 1 month later. The sampling method was the same, except that a different fish toxin, Antimycin A (Fintrol), was used.

Three diversity indices were calculated for species number. The Shannon-Weaver function ($H' = -\sum P_i \log_e P_i$ natural bel/individual, where P_i is the proportion of individuals in the i th species), is a widely used function that measures both changes in number of species and species evenness or equitability (Bechtel and Copeland, 1970; Dahlberg and Odum, 1970). Two other indices that treat the two components of diversity separately were calculated. For the "species richness" component, the function $D = (S - 1) / \log_e N$ was used (Margalef, 1968; Dahlberg and Odum, 1970). S is the number of species and N is the number of individuals. The last index used was the "evenness" index of Pielou (1966): $J = H' / H \max = H' / \log_e S$. These indices were used by Dahlberg and Odum (1970) for fish diversity studies in a Georgia estuary, and by McErlean *et al.* (1973) for a Maryland estuary.

Results

A total of 16,611 individuals weighing 202.45 kg and comprising 51 species and 25 families of fish were collected (Table 1). On a seasonal basis, the number of species was greater in the summer and fall (41 and 32, respectively) than in the winter and spring (20 for both). The number of individuals, however, was not significantly affected by season. The number of specimens caught in a sample depended primarily on the presence of three species, *Fundulus heteroclitus* (mummichog), *Leiostomus xanthurus* (spot), and *Menidia menidia* (Atlantic silverside). In two of the largest samples, these three species constituted over 90% of all individuals caught.

Only one species, the striped mullet *Mugil cephalus*, was present in every collection, but 11 other eurythermal species were regularly collected (Table 1). Seventeen species were collected only

during the warmer months (Table 1), while just one species, *Fundulus majalis* (striped killifish), was collected only during the colder months.

On a yearly basis, the 10 most numerous species totaled 94.3% of the individuals caught. The mummichog was the most numerous species, 4,929 individuals or 29.7%, and the spot and Atlantic silverside, 19.5 and 19.3% respectively, were other abundant species on an annual basis. Other species such as the silver perch *Bairdiella chrysura* (24.8% in June, 1971) and the bay anchovy *Anchoa mitchilli* (18.5% on September 4, 1971) were occasionally abundant. Striped mullet and spot contributed 29.6 and 27.3% of the total biomass, respectively, and were by far the most important species in terms of biomass. The 10 most important species in terms of number of individuals and biomass are listed in Table 2.

Analysis of variance revealed that season had a highly significant effect on all indices (Table 3). The Shannon-Weaver index peaked in the late summer, with a high of 2.30 in August. After August the function gradually decreased, and dropped to a low of 0.42 on February 15. The changes in the diversity of the sample as measured by the Shannon-Weaver function closely corresponded to temperature changes (Fig. 2). The "species richness" index (D), and the "species evenness" index (J), also showed a pronounced seasonal change, indicating that the number of species, and their equitability, significantly influenced the changes in the Shannon index. An analysis of variance test also revealed that season had a highly significant effect on the number of species. The number of species reached a maximum during the summer and fall (34 on September 4) and a minimum during the winter (8 or less from January through March). Again, the changes seem to be directly related to temperature. The analysis of variance test revealed that season had no effect on the number of specimens caught, supporting the assumption that the number of specimens largely depended on the availability of a very few species. These species, spot, mummichogs, and Atlantic silversides are schooling fish and thus exhibit a clumped distribution.

During the follow-up study conducted in 1973, there were no trends evident in any of the diversity indices (Table 4). The Shannon-Weaver index varied from 2.00 to 1.47 during 4 consecutive days, indicating either that the diversity of the creek is not normally constant from day to day, or that the sampling affected subsequent samples. Although the former is probably true, the latter expla-

Table 2. Annual rank and percentage of 10 most abundant species, and annual rank and percentage of 10 species that contributed the most biomass

Species	% of individuals in total collection	Species	% of biomass
<i>Fundulus heteroclitus</i>	29.7	<i>Mugil cephalus</i>	29.6
<i>Leiostomus xanthurus</i>	19.5	<i>Leiostomus xanthurus</i>	27.3
<i>Menidia menidia</i>	19.3	<i>Dasyatis americana</i>	11.0
<i>Mugil curema</i>	5.5	<i>Paralichthys lethostigma</i>	6.0
<i>Anchoa mitchilli</i>	4.8	<i>Mugil curema</i>	4.6
<i>Bairdiella chrysura</i>	4.1	<i>Fundulus heteroclitus</i>	3.8
<i>Mugil cephalus</i>	3.7	<i>Menidia menidia</i>	3.7
<i>Eucinostomus argenteus</i>	3.5	<i>Bairdiella chrysura</i>	2.6
<i>Anchoa hepsetus</i>	2.1	<i>Lepisosteus osseus</i>	2.0
<i>Fundulus majalis</i>	<u>2.1</u>	<i>Archosargus probatocephalus</i>	<u>1.4</u>
Total %	94.3		92.0

Table 3. Analysis of variance for effect of seasons on sample composition and diversity

Index	Season's F values	FO.01	FO.001
No. of species	16.82	5.95	10.80
No. of individuals	0.75	5.95	10.80
H'	12.09	5.95	10.80
D	13.66	5.95	10.80
J	8.67	5.95	10.80

Table 4. Diversity indices for Clambank Causeway Creek July 15-18 and August 14

Index	15 July	16 July	17 July	18 July	14 Aug.
H'	1.831	2.005	1.473	1.732	1.231
J	0.622	0.723	0.484	0.890	0.398
D	2.428	2.623	3.328	1.971	2.990

nation is borne out by examination of the abundance of individual species. The abundance of a few species was directly affected by repetitive sampling which indicated that those species exist in small, relatively fixed populations which are restricted to specific habitats and that exchange between adjacent areas is slight. After 1 month, stocks of most species had returned to approximately the levels of the first samples. The following species (followed by the number present in each daily sequential sample) appeared to be affected by repetitive sampling: *Fundulus heteroclitus* (521-5-39-2), *Bairdiella chrysura* (246-7-14-6), *Mugil cephalus* (61-28-12-6), *Gobionellus boleosoma* (darter goby) (83-0-1-0), *Myrophis punctatus* (speckled worm eel (108-0-0-0)). The last species, the speckled worm eel, was not recorded during earlier creek samples. In earlier samples, it is possible that rotenone did not affect this fish, for it could retreat into its burrows. Antimycin A, probably because it is undetectable by fish, killed many of this species. Most of the eels, though moribund, would still attempt to retreat into their burrows when touched and more eels were seen than captured. After 1 month, no speckled worm eels had returned to the creek. Two other species were collected that had not been captured in the earlier study, *Poecilia latipinna* (1), and *Arius felis* (2).

Samples taken from creek areas, other than South Clambank Causeway Creek, were not analyzed in as much detail, but all of these samples were similar to those taken from the major sample site when collections were made at the same time. Only three different species were found in the other creeks that were not in Clambank Causeway Creek. Two of these species, *Aluterus schoepfi* (orange filefish) and *Prionotus scitulus* (leopard sea-robin), were frequently trawled in deeper water, while the third species, *Rachycentron canadum* (cobia), is rarely captured in North Inlet (Freeman, 1971, personal communication) and then only in the larger creeks.

Descriptive notes of the most numerous species, and those for which unreported or unusual observations were made follow:

Anchoa mitchilli (Valenciennes) - Bay Anchovy

This species was present throughout the year but peaked in abundance during the fall and spring (Table 1). According to Hildebrand (1963), bay anchovies spawn at Beaufort, North Carolina, in early spring to at least midsummer and reach

45 to 60 mm total length (TL) by early August. Very small specimens collected in September (27 mm standard length, SL) indicate that the breeding season in North Inlet extends into late summer.

Rissola marginata (DeKay) - Striped Cusk Eel

Four specimens of the striped cusk eel, weighing 21.1 to 50.0 g and 153 to 200 mm SL, were caught on April 9, 1972. This species is usually caught over sandy bottoms, and it is surprising that they were caught so far from their natural habitat.

Fundulus heteroclitus (Linnaeus) - Mummichog

The mummichog was captured in every month and was the most numerous species (Table 1). This species has been reported to spawn from April to August (Hildebrand and Schroeder, 1928), but some gravid fish were present throughout the year. The majority of the fish collected in March and April were gravid.

The mummichog, known for its wide tolerances to temperature, salinity, and low dissolved oxygen, was very resistant to rotenone. Few mummichogs died from the rotenone, but most were sufficiently affected to be carried into the net.

Bigelow and Schroeder (1953) reported the mummichog to be omnivorous. We found it to be extremely predatory on larval fish, since many specimens contained over 100 larval spot.

Fundulus majalis (Walbaum) - Striped Killifish

The striped killifish was the only species collected solely during the winter and spring (Table 1). This species seemed to undergo a seasonal migration, inshore during the winter along the beaches during the summer. It could be collected in large numbers along nearby beaches during the summer and fall. The striped killifish has been reported to spawn from April to September (Hildebrand and Schroeder, 1928), and therefore the inshore movement may be a spawning migration. Most of the specimens collected in March and April were gravid.

Menidia menidia (Linnaeus) - Atlantic Silverside

The Atlantic silverside was extremely common throughout the year except for the summer months (Table 1). Its scarcity in estuaries during the summer has also been reported by Bigelow and Schroeder

(1953). The spawning season has been reported to be from March to August (Hildebrand, 1922), but we collected gravid fish only in March, April, and September. The Atlantic silverside that we collected had fed extensively on larval fish during the winter and early spring months.

Bairdiella chrysura (Lacepede) - Silver Perch

The silver perch was present in all except the coldest months and represented the second most common sciaenid (Table 1). This species has been reported to spawn from April to July and to reach approximately 120 mm TL by the end of their first year at Beaufort, North Carolina (Hildebrand and Cable, 1930). Most of the specimens we collected were young of the year. It appeared that the young utilized the intertidal creeks more than the adults, as adults were common in trawl catches in the larger creeks but not in the intertidal creek.

Leiostomus xanthurus Lacepede - Spot

The most common sciaenid, the spot, was caught in every month except January and February (Table 1). Hildebrand and Cable (1930) and Dawson (1958) reported low levels of abundance for spot in the late spring and summer. Dawson stated that the maximum inshore population should occur in spring and summer since it consisted of recently hatched fish and the older age groups. Dawson was at a loss to explain this anomalous situation and stated "It cannot be assumed that the majority of summer fish frequent unexplored bottoms". The present study indicated that such assumption is not valid, since spot were most plentiful in Clambank Causeway Creek during this period.

Mugil cephalus Linnaeus - Striped Mullet

The striped mullet was the only species to be collected in every sample (Table 1). Striped mullet, which are spawned offshore, first appeared in the catch on December 17. Very little growth was apparent until April as the March larvae were about the same size as those captured in December. By April the striped juvenile mullet were extremely plentiful. Thousands covered the creek bed after the rotenone was applied. Several hundred of these were collected, and used in a comparative growth study by Burns (unpublished data, 1972). His report showed

that the growth for *Mugil cephalus* in a brackish pond was faster than the wild population in North Inlet. The mullet from the brackish pond averaged 12 mm SL longer and 0.82 g heavier than the North Inlet fish in April.

This collection was used as a reference for growth of striped mullet in North Inlet. The striped mullet reached about 50 mm SL by July, 85 mm SL by September, and 100 mm SL by the end of their first year. On October 29 two very large specimens containing roe were collected.

Mugil curema Valenciennes - White Mullet

The young of the year (0 age-class) white mullet were more plentiful than striped mullet throughout the summer and fall, but disappeared after December (Table 1). Early spring-spawned white mullet apparently grew faster than the striped mullet. Although white mullet are reported to move south to Florida at the onset of their first winter and not to return, one sample on July 27, 1971 (Table 1) contained older age groups of this species.

Discussion

If we are to understand a complex ecosystem such as an estuary, the basic biology of organisms that dwell therein must be known. One of the first steps taken when studying any ecosystem is to identify the organisms present, their distribution, and their relative abundance. Although estuarine fish have been sampled for many years, there are large gaps in existing information because of a lack of adequate sampling techniques.

We have compared our results with those obtained by other investigators in similar areas. Freeman (1971, personal communication) sampled with an otter trawl the same general area of tidal creeks of North Inlet as we did, but two fundamental differences between the sampling methods are evident. The most numerous species in our study, the mummichog *Fundulus heteroclitus*, was very rarely caught by Freeman's trawl, probably because of the fish's size and habit of staying very close to the shoreline. Also, the striped mullet *Mugil cephalus*, the species that contributed the most biomass in our study, was practically absent in Freeman's samples because the striped mullet could easily out-swim or jump over a trawl. With the exception of *Trinectes maculatus*, the other common shallow-water species found in Freeman's sur-

veys were present in Clambank Causeway Creek. Either this flatfish buries itself in the mud to avoid capture or does not frequent intertidal areas. If such differences exist in other trawl surveys, then their relevance and generalizations about the distribution of estuarine fish must be accepted with reservation. Dahlberg and Odum (1970) trawled Sapelo and St. Catherine Sounds, Georgia (USA), including four small marsh creeks, but collected only 2 *M. cephalus* and 5 *F. heteroclitus*. Dahlberg and Odum stated that these species are probably common but occupy "unsampled areas". Since both these species are euryhaline and were the most numerous, had the highest biomass and were found everywhere in North Inlet, it is probable that the absence of these two species in Dahlberg and Odum's survey was due to their sampling method.

Turner and Johnson (1972) sampled 5 creeks in Port Royal Sound, South Carolina, with a method very similar to the method used in this study except that the 5 creeks they sampled did not go dry. They relied on rotenone to kill the fish, and the current to carry the fish into the net. Their study showed the importance of the striped mullet (42% of the biomass); but because of the resistance of the mummichog to rotenone, their results may not reflect the abundance of this widely distributed and successful estuarine fish. This method does not collect *Paralichthys* spp. because these flatfish tend to leave the water to flop on the banks after the application of rotenone. In addition, the flatfish are not carried by currents very easily since they lie flat on the bottom or bury themselves in the mud.

From our data, a simple scheme of the fish community structure for an intertidal creek can be developed. In the early spring, the creek was dominated by the mummichog, an omnivore, and the silverside, a carnivore. The diet of both species consisted almost exclusively of the very numerous spot, croaker and striped mullet larvae. Bay anchovies, which fed mostly on planktonic crustaceans, and striped killifish (omnivores) which fed almost exclusively on larval fish, were the only other numerous species. Predators that might have fed on any of those species were not present in the intertidal creeks.

In the summer, young spot were most abundant, followed by juvenile white mullet, silver perch, striped mullet and spotfin mojarra (*Eucinostomus argenteus*). It is assumed that larvae of these species probably feed on planktonic or benthic crustaceans, as larger mullet consumed detritus and the other species

remained secondary consumers. The mummichog was much less common in the summer than in the spring, and the number of large predatory (piscivorous) species increased in the summer: *Strongylura marina* (Atlantic needlefish) - 15, *Pomatomus saltatrix* (bluefish) - 11, *Caranx hippos* (crevalle jack) - 12, *Paralichthys* spp. - 24; however, these species were still not plentiful.

In the fall, a number of species were abundant and the mummichog was again the most numerous fish. Although the largest numbers of spot were collected in December, these fish should probably be considered part of a fall run because of their absence in January and February and because of the unusually extended fall warm weather. If this December sample is included in the analysis of the fall season, which is reasonable on the basis of water temperatures, then the spot was almost as plentiful as the mummichog, but contributed much more biomass. The Atlantic silverside, which had feeding habits similar to the mummichog, was also very numerous and both species consumed small planktonic crustaceans in this season. We also observed that the mummichog consumed quantities of detritus. The silver perch and the silver jenny were also abundant and evidently competed with the spot for food. Both species of anchovies, as well as both species of mullet, were also plentiful. Piscivorous species, *Lepisosteus osseus* (longnose gar) - 4; *Strongylura marina* (Atlantic needlefish) - 3; *Caranx hippos* (crevalle jack) - 35; *Caranx latus* (horse-eye jack) - 48; *Chloroscombrus chrysurus* (Atlantic bumper) - 20; and *Paralichthys* spp. - 25, were abundant in this season although still not common, as over 6,000 fish were caught during this period.

The winter composition of fish species was very simple. The Atlantic silverside was by far the most numerous species, followed by the mummichog, striped killifish, and *Lagodon rhomboides* (pinfish). The first three species fed on spot and mullet larvae. No predators or high trophic-level consumers were collected in the intertidal area, although they are known to be present in the channels of the permanent creeks (Dahlberg and Odum, 1970).

Diversity indices summarize the numerical associations of organisms and allow us to compare populations. Diversity indices are generally a more reliable indicator of environmental health or stress than are individual indicator species. Bechtel and Copeland (1970), studying fish diversity in Galveston Bay, Texas, found that diversity was inversely proportional to the amount of efflu-

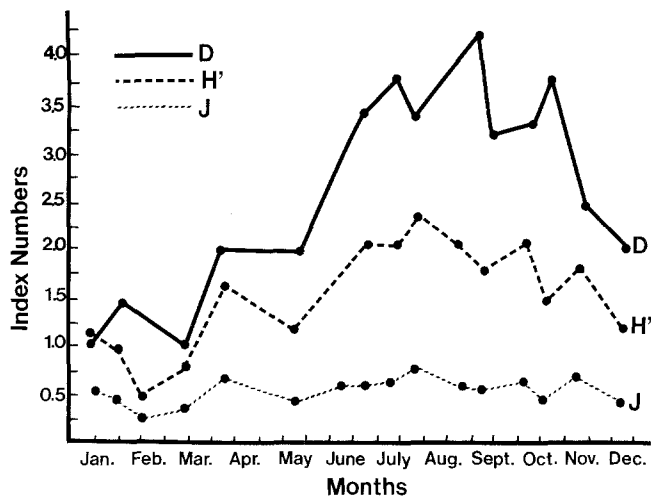


Fig. 3. Annual cycles of species diversity indices Clambank Causeway Creek from June, 1971 to May, 1972

ents and toxic material an area received, the most polluted areas exhibiting the lowest mean annual diversity. The mean annual diversity for Clambank Causeway Creek was higher than any area surveyed by Bechtel and Copeland. Factors that may regulate diversity are (1) variety of niches, (2) size of niches and niche overlap, (3) stability of environment or climate, (4) rigorousness of environment, (5) succession, (6) productivity, (7) biomass accumulation, (8) competition, (9) space, (10) length of food chains, and (11) body size (Dahlberg and Odum, 1970). Except for the influence of temperature and migration, little can be said about these factors since they require data which are not complete for a single population of estuarine fish, much less for an entire community.

The transient nature of many species is one characteristic of an estuarine fish population that influences diversity. Emigration and immigration of adults and young fish can directly affect the population diversity. For example, the drop in H' during the winter (Fig. 3) was directly attributable to the exodus of 6 of the most numerous species (white mullet, spot, silver perch, spotfin mojarra, and the anchovies). Only one species, the striped killifish, immigrated to take their place. The rise in H' in the spring was primarily a result of the immigration of various juvenile fish species, as well as the return of the adults of some species.

In the present study, all diversity indices showed marked seasonal variations. However, Dahlberg and Odum (1970) found, in Georgia estuaries, that the

"species richness" index, D , did not vary with season because numbers of species and of individuals changed simultaneously.

The diversity of fish in Clambank Causeway Creek appeared to be correlated with annual temperature cycles. Only 4 of the 10 most numerous fish would be considered eurythermal species. The other 6 species had disappeared or were sharply reduced in number by November, when the temperature dropped below 20°C. These 6 species (Table 1) did not disappear abruptly, but decreased gradually with very few specimens of each species present in late October and November.

The late stragglers were generally smaller specimens, which are generally considered to be more temperature tolerant.

The species that utilize the intertidal and shallow areas have a distinct advantage over other species in the estuary. First, they have more available habitat since the deep water areas occupy a rather small percentage of the total estuary. It has been extensively documented that the shallow areas are also more productive than creeks, not only because of the extensive cover provided by the *Spartina alterniflora* flats, but also because primary production by *S. alterniflora*, leading to extensive detritus formation, is greater than in the creeks (Odum, 1970; Odum and Heald, 1975). The formation of detritus from *S. alterniflora* provides food and habitat for numerous crustaceans and other detritivores, and detritus is also a direct food source for estuarine fish. The intertidal area of the *S. alterniflora* flats also provides a plentiful food supply for the fish that crop at the primary and secondary consumer levels. Those species that can stand the rigors of intertidal areas are extremely important ecologically, and should receive more attention from researchers.

Odum (1970) and Odum and Heald (1975) discussed the multiple feeding levels of fish occupying the mangrove estuary of Florida. Their results emphasize the need for more critical analyses of feeding patterns of estuarine fish. Our results also reveal that species occupying the intertidal area of the *Spartina alterniflora* marsh shift their energy sources from season to season. The species with the highest annual biomass and absolute numbers are detritivores, omnivores or primary consumers; and none appear to be limited to an exclusive trophic level since they shift their feeding behavior as they grow. The mullet, for example, shifts its trophic level and thus its role in energy flow in estuaries with maturation.

Bioenergetics are known for very few fish and these are primarily measures of temperate, fresh-water, isolated individuals fed a laboratory diet. We lack data on the bioenergetics of estuarine fish, many of which are schooling species, that occupy large areas of the salt marsh ecosystem and channel energy from several sources to other fish, birds, and man. Until these data are obtained, it would seem that we are some distance from understanding the ecology of estuaries.

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