Feeding Habits of Young Winter Flounder (*Pseudopleuronectes americanus*): Prey Availability and Diversity

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Made in United States of America
Reprinted from Transactions of the American Fisheries Society
Vol. 103, No. 2, April 1974
pp. 261–269

Feeding Habits of Young Winter Flounder (*Pseudopleuronectes americanus*): Prey Availability and Diversity[1]

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ABSTRACT

The principal diet of age I+ winter flounder *Pseudopleuronectes americanus* captured in the Weweantic River Estuary, Wareham, Massachusetts was comprised of polychaetes, bivalves, gastropods, and crustaceans. During spring, flounder fed on planktonic crustaceans found within the estuary and during the summer and fall on mollusks and polychaetes at the estuary's mouth.

A new technique, percent overlap, is described for the comparison of the volume percentages of food species in Peterson grabs and stomachs. Percent overlap values were progressively higher with each season: March, 1.8%; June, 29%; July, 47%; October, 47%. The low overlap values, occurring when fish were within the estuary, indicated that the benthic community was not an important food source.

Diversity indices (Shannon-Weaver, Simpson and McIntosh) calculated for mollusks and macrocrustaceans were more variable at stations within the estuary than at the mouth.

Many investigators (Ayers 1843; Verrill 1873; Linton 1921; Bigelow and Schroeder 1953) have described the feeding habits of adult winter flounder (*Pseudopleuronectes americanus*), but few (Pearcy 1962; Richards 1963) have described the feeding habits of young winter flounder. In this paper I describe the feeding habits of young (age I+) winter flounder in relation to the availability of benthic estuarine invertebrates.

The importance of shallow estuaries to the early life stages of winter flounder has been discussed by Greeley (1939); Perlmutter (1947); Saila (1961); Coates, Howe, and Peterson (1970); and others. Although the winter flounder's life history has been adequately described, factors which permit its development in an estuary remain to be explored. Because estuaries are highly productive, food availability may be as important as temperature and salinity in controlling the animal's estuarine existence (Frame 1973 a,b).

Groups of adult flounder move into shallow bays and estuaries during fall and winter. In southern New England spawning takes place from January to May with peak spawning during February and March (Bigelow and Schroeder 1953). The progeny remain in the confines of the embayment until they are 2 yr old.

STUDY AREA AND METHODS

The Weweantic River Estuary in Wareham, Massachusetts is a shallow salt-wedge estuary lined with moraine sediments (Fig. 1). The channel, less than 3.5 m deep, is centrally positioned except for a 0.8-km section that traverses the estuary's western border. A coarse sand-cobble flat east of this section restricts tidal currents. Gravel and shell fragments line the channel bed and fine sand or mud border the channel.

In the lower half of the estuary where I knew flounder were available (Topp 1967), I established three transects (A, B, C), and on each transect I selected three stations that had different depths and substrates (Fig. 1). The substrate of transect A was fine sand-shell (station 1), mud (station 2), and coarse gravel-shell (station 3). At mean low water (MLW) station 1 was 1.5 m deep; station 2, 0.5 m deep; and station 3, 3.0 m deep. At transect B the substrate was mud-silt

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[1] Contribution No. 38 of the Massachusetts Cooperative Fishery Unit jointly supported by the U.S. Bureau of Sport Fisheries and Wildlife, The Massachusetts Division of Marine Fisheries, The Massachusetts Division of Fisheries and Game, and the University of Massachusetts.

[2] The author lost his life while this paper was being revised. The final draft was kindly completed by William R. Nicholson, National Marine Fisheries Service, Beaufort, North Carolina 28516. Reprints will be available from Mr. Nicholson.—Editor.

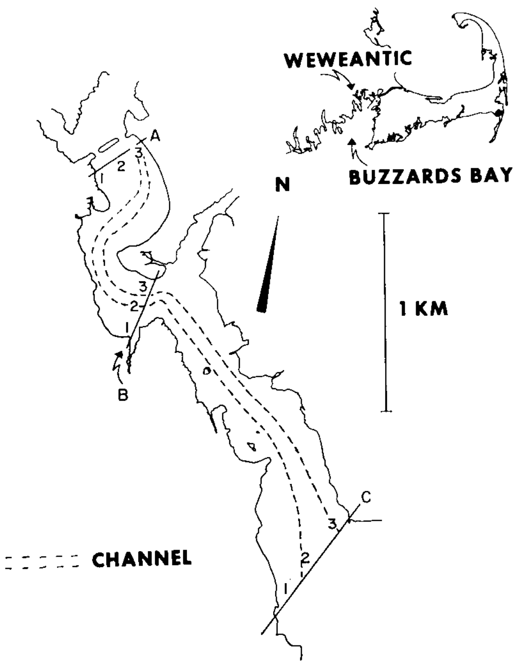

FIGURE 1.—The Weweantic River Estuary, Wareham, Massachusetts: Sampling transects (A–C) and stations (1–3).

(station 1), shell fragments (station 2), and coarse sand-cobble (station 3). Station 1 was 1.0 m deep; station 2, 3.0 m; and station 3, 0.4 m. The substrate at transect C was a variety of mud-silt combinations. Station 1 was 2.5 m deep; station 2, 3.5 m; and station 3, 1.5 m.

Fish were collected with a 5-m otter trawl, and hydrographic measurements were taken during a 24-hr sampling period in April, July, August 1968, and January, March, June, and October 1969. Temperatures and salinities were recorded once every 4 hr during the 24-hr period. Although flounder were captured at all stations of each transect, only those caught at the station having the highest catch per unit of effort (age I+ flounder/10-min haul at 2 knots) were retained. For each sampling period 10 fish were selected randomly from the total catch, packed in mylar bags, placed on ice, and transferred after about 1 hr to a freezer maintained at –30.0 C. Later they were weighed and measured. A subsample of the fish collected during each 4-hr period was taken for analysis of stomach contents. For each subsample I calculated the mean volume percentage (Larimore 1957) of food items in the stomach.

Benthic invertebrates were sampled with a Peterson grab. Approximately five grabs were taken at each station once during January, March, June, July, and October 1969 (transect A and B sampling was omitted in January). The contents of each grab were screened to 1.0 mm, intact specimens were removed, and samples were stored in a freezer at –30 C. All invertebrates were identified to the lowest possible taxonomic level so that the average volume percentage per grab could be determined for each taxon. Since invertebrate numbers were stable throughout each season, I lumped all samples at each station.

The overlap between the volume percentages of food items in grab and stomach samples may be calculated for any taxonomic level. Each stomach and grab may be treated separately, or several stomachs or several grabs may be combined into a single sample. For each sample the sum of the percentages must equal 100. When a grab sample and a stomach sample are compared, the overlap value is calculated by summing the lower percentage values for each item. An overlap value of 100 shows perfect agreement, whereas a value of 0.0 shows no agreement.

By overlap analyses I compared (1) the four classes of invertebrates in grabs and stomachs for each month, March, June, July, and October, for all stations combined, and (2) the food species of invertebrates in grabs and stomachs for station 1, transect C only. I chose this station because the series of data was more complete than that for the other stations.

I calculated diversity indices for the molluscan and crustacean populations with a program written by Mawson and Godfrey (1971) for the C.D.C. 3600 Computer at the Research Computing Center, University of Massachusetts, Amherst. Three indices were computed for all dredge samples and pooled for each station within sampling periods. The following indices were used:

I. Shannon-Weaver Information Index

$$H = -C \sum_{i=1}^{S} \frac{N_i}{N} \log_{10} \frac{N_i}{N}$$

II. Simpson Index

$$D = 1 - \sum_{i=1}^{S} \frac{N_i(N_i - 1)}{N(N-1)}$$

III. McIntosh Index

$$\Delta = N - U$$

where:

$$U = \sqrt{\sum_{i=1}^{S} N_i^2}$$

to reduce variability resulting from sample size, Δ was computed as:

$$\frac{\Delta}{\max \Delta}$$ (see Mawson and Godfrey 1971, p. 7).

The symbols have the following meanings: H = information; Δ and D = diversity; U = uniformity; S = species; N = number of individuals; N_i = number of individuals in the i^{th} species; C = positive constant.

Diversity in the paper refers to the numerical percentage composition of species as used by Simpson (1949). Both Simpson and McIntosh indices are maximal at 1.0 when each individual belongs to a different species, and minimal at 0.0 when all individuals belong to the same species. The nearer equal the number of individuals in a series of species groupings, the more diverse the fauna; hence the name dominance diversity is often applied to these two parameters (Whittaker 1965). The Shannon-Weaver information function is influenced by both numbers of species and the evenness with which the individuals are distributed among species in a sample. This index, therefore, is said to be influenced by dominance diversity as well as species diversity, which is simply a list of species present in a given environment. The longer the list, the greater the diversity (Sanders 1968).

In all indices the fauna sampled must be evenly or randomly distributed (Sanders 1968). The Simpson and McIntosh indices are sample-size dependent; the Shannon-Weaver index is sample-size independent.

RESULTS AND DISCUSSION

Although age I flounders occurred throughout the study area, they were not equally abundant at all times and places. In winter and early spring they were more abundant between transects A and B, but in late spring and summer they were more abundant at transect C. During summer they were found occasionally over mud flats between transects A and B in the evening, whereas during winter and spring they sometimes were caught at transect C during daylight. During the summer at transect C, station 1, they were caught more easily in the evening than in the day.

In the grab samples, mollusks were more abundant than other taxa (Table 1). Of the genera represented, *Macoma balthica, Mya arenaria, Mulinia lateralis, Hydrobia totteni,* and *Nassarius obsoletus* were most abundant at transect A. The same species plus *Nucula proxima* were most abundant at transect B. At transect C, *Macoma tenta, Nucula proxima, Yoldia limatula, Tellina agilis, Nassarius trivittatus, Natica pusilla,* and *Turbonilla interrupta* were most numerous.

The most numerous invertebrates other than mollusks were the annelid worm, *Pectinaria gouldi,* found throughout the estuary but more abundant at transect C, and the macrocrustacean, the mud crab, *Neopanope texana sayi,* found primarily in the sand at transect B.

The principal foods in stomachs were polychaetes, bivalves, gastropods and planktonic crustaceans (Table 2). Planktonic copepods were more numerous in spring; bivalves, amphipods and polychaetes were more numerous in summer and fall. The most numerous mollusks were *Laevicardium mortoni, Nucula proxima, Tellina agilis,* and *Retusa canaliculata.* Bivalve siphons were also encountered in the stomachs of fish taken in midsummer.

The diversity of mollusks and macrocrustaceans was consistently greater at the mouth of the estuary than within the estuary. Stations 2 and 3 (transect C) had slightly greater index values than station 1 but all indices were relatively constant between sampling periods (Fig. 2). All stations in transects A and B had correspondingly greater variability than

TABLE 1.—*Summary of food items identified in age I+ winter flounder stomachs. Numbers in parentheses refer to the number of stomachs containing the food item*

	Date							
	4/68	7/68	8/68	1/69	3/69	6/69	10/69	
	Transect/Station							
Food item	B/2	C/1–C/3	C/1–C/3	A/3	A/3–B/2	C/1–C/3	C/1–C/3	Total
Invertebrata								
Cnidaria								
Hydrozoa (hydroid stage)	—	—	—	—	5(1)	—	—	5(1)
Annelida								
Polychaeta (unidentified)	—	53(30)	4(4)	4(2)	2(1)	11(8)	19(12)	93(57)
Pectinariidae	—	4(3)	—	—	—	4(4)	9(7)	17(14)
Mollusca								
Bivalvia								
Bivalve siphons	—	14(5)	—	—	—	—	—	14(5)
Cyrtopleura costata	—	1(1)	—	—	—	—	—	1(1)
Laevicardium mortoni	—	29(5)	7(1)	—	—	—	15(5)	51(11)
Macoma tenta	—	1(1)	—	—	—	2(2)	—	3(3)
Mercenaria mercenaria	1(1)	1(1)	—	—	—	—	—	2(2)
Mulinia lateralis	—	—	—	—	—	—	1(1)	1(1)
Nucula proxima	—	4(3)	—	—	—	5(5)	3(3)	12(11)
Tellina agilis	—	9(4)	1(1)	—	—	3(3)	7(5)	20(13)
Yoldia limatula	—	9(8)	—	—	—	2(2)	—	11(10)
Gastropoda								
Bittium alternatum	—	4(1)	—	—	—	—	—	4(1)
Crucibulum striatum	—	4(4)	—	—	—	—	—	4(4)
Mitrella lunata	—	—	—	—	—	1(1)	1(1)	2(2)
Natica pusilla	—	1(1)	—	—	—	—	—	1(1)
Retusa canaliculata	—	7(1)	25(1)	—	—	—	9(2)	41(4)
Seila adamsi	—	1(1)	—	—	—	—	—	1(1)
Turbonilla interrupta	—	1(1)	—	—	—	—	2(2)	3(3)
Arthropoda								
Crustacea								
Isopoda	33(5)	—	—	—	1(1)	4(2)	—	38(8)
Amphipoda	7(1)	93(31)	18(4)	7(4)	8(4)	12(5)	18(5)	163(54)
Decapoda								
Crangon septemspinosus	—	5(5)	—	—	—	—	9(5)	14(10)
Neopanope texana sayi	—	1(1)	1(1)	—	—	—	4(4)	6(6)
Pagurus longicarpus	—	—	—	—	—	—	2(2)	2(2)
Polyonyx macrocheles	—	—	—	—	—	—	4(2)	4(2)
Copepoda	112(5)	—	—	—	—	—	—	112(5)
Echinodermata								
Ophiuroidea								
Amphipholis squamata	—	—	—	—	—	—	1(1)	1(1)
Algae								
Rhodophyta								
Ceramium sp. (*rubrum/rubriforme*)	—	—	—	2(1)	—	—	5(1)	7(2)
Chlorophyta								
Enteromorpha sp.	—	2(1)	—	—	—	—	—	2(1)
Total number of fish	25	53	9	21	15	33	20	176

those of transect C (Figs. 3 and 4). At transect A the diversity indices for stations 1 and 2 decreased progressively with sampling periods, whereas index values for station 3 were variable. Transect B index values generally increased with each sampling period and therefore exhibited a trend opposite that of transect A. During January and March at transect A and July and October at transect B, diversity indices approached the constant values derived for transect C. The high spring diversity at transect A stations 1 and 2 was caused by the abundance of *Nassarius obsoletus*, *Mya arenaria* and *Mulinia lateralis*. Species which were rare in spring samples were absent from fall grabs. Increases in diversity during the summer and fall were due to the presence of *Mya arenaria*, *Nucula proximia*, *Anomia simplex* and some infrequently sampled forms like *Solemya velum* and *Mitrella lunata*.

The benthic invertebrates in the upper estuary were never as important a food supply as the invertebrates in the lower part of the estuary. None of the dominant invertebrates in grab samples taken at transect A were found in flounder stomachs during spring, and only one dominant mollusk was found in one fish stomach during the fall. Most of the benthic food species found in stomachs were obtained from the lower estuary, transect C, during late spring, summer and fall.

Flounders appeared to feed more selectively in spring when they were not demersal than in midsummer and fall when they were demersal. Overlap values were 1.8 in March, 29.0 in June, but 47.0 in July and October (Table

TABLE 2.—*Summary of the numbers of live invertebrates identified in 197 Peterson dredge samples (1/16 m²) taken from the Weweantic Estuary in 1969*

Scientific name	Transect A Station 1	Transect A Station 2	Transect A Station 3	Transect A Total	Transect B Station 1	Transect B Station 2	Transect B Station 3	Transect B Total	Transect C Station 1	Transect C Station 2	Transect C Station 3	Transect C Total	Grand Total
Annelida													
Polychaeta													
Pectinariidae	11	3	3	17	2	—	4	6	8	5	6	19	42
Polynoidae	1	—	—	1	—	—	—	—	—	—	—	—	1
Phyllodocidae	—	2	—	2	—	—	—	—	1	—	—	1	3
Sabellariidae	—	—	—	—	—	1	—	1	—	1	5	6	7
Sabellidae	—	—	—	—	—	—	—	—	8	7	2	17	17
Serpulidae	—	2	—	2	—	7	1	8	4	10	5	19	29
Bivalvia													
Aequipecten irradians	—	—	—	—	4	—	1	5	—	1	—	1	6
Anomia simplex	—	—	1	1	—	5	17	22	—	—	—	—	23
Cumingia tellinoides	—	—	—	—	—	2	—	2	3	—	—	3	5
Cyrtopleura truncata	1	—	5	6	1	11	20	32	3	2	16	21	59
Laevicardium mortoni	1	—	—	1	—	—	—	—	—	—	—	—	1
Lunarca ovalis	—	—	—	—	—	—	—	—	4	1	—	5	5
Lunarca transversa	1	—	—	1	—	—	—	—	—	2	1	3	4
Lyonsia hyalina	—	—	—	—	—	—	1	1	—	—	—	—	1
Macoma balthica	4	173	—	174	—	54	—	54	—	—	—	—	231
Macoma tenta	4	1	—	5	—	—	—	—	24	32	19	75	80
Mercenaria mercenaria	4	—	4	8	—	2	3	5	—	—	—	—	13
Mulinia lateralis	6	12	1	19	1	—	—	1	3	3	—	6	26
Mya arenaria	15	133	43	191	27	5	4	36	2	1	1	4	231
Mytilus edulis	—	—	—	—	1	1	—	2	—	—	—	—	2
Nucula proxima	—	—	—	—	2	75	126	203	126	50	38	208	411
Crassostrea virginica	1	—	—	1	—	1	—	1	—	—	—	—	2
Siliqua costata	1	—	—	1	—	—	—	—	—	—	—	—	1
Solemya velum	—	—	—	—	—	—	2	2	21	—	6	27	29
Tagelus divisus	—	—	1	1	—	3	1	4	—	2	—	2	7
Tellina agilis	1	—	1	2	4	2	2	8	11	3	22	36	46
Yoldia limatula	—	—	—	—	—	—	—	—	16	11	9	36	36
Gastropoda													
Anachis avara	—	—	—	—	—	3	—	3	—	1	8	9	12
Bittium alternatum	—	1	—	1	—	1	—	1	6	8	3	17	19
Buccinum undatum	—	—	—	—	—	—	—	—	2	—	2	4	4
Busycon canaliculatum	—	—	—	—	—	—	—	—	1	—	—	1	1
Busycon carica	—	—	—	—	—	—	—	—	—	—	1	1	1
Cerithidea sp.[a]	—	—	—	—	57	2	2	61	7	5	—	12	73
Crepidula convexa	—	—	—	—	—	—	9	9	—	1	—	1	10
Crepidula fornicata	1	—	1	2	—	7	96	103	—	—	—	—	105
Crepidula plana	—	—	—	—	—	—	1	1	—	—	—	—	1
Cylichna oryza	—	—	1	1	—	—	—	—	—	8	1	9	10
Epitonium rupicola	—	—	—	—	—	—	1	1	—	—	—	—	1
Hydrobia totteni	4	6	1	11	1	—	1	1	—	—	—	—	12
Littorina obtusata	—	—	—	—	—	—	—	—	1	—	—	1	1
Mangelia plicosa	—	—	—	—	—	—	1	1	—	—	—	—	1
Melampus bidentatus	—	—	—	—	1	—	—	1	—	—	—	—	1
Mitrella lunata	3	1	1	5	8	3	5	16	3	6	4	13	34
Nassarius obsoletus	46	72	142	260	317	136	238	691	1	2	1	4	955
Nassarius trivittatus	—	—	3	3	—	4	—	4	20	28	17	65	72
Nassarius vibex	1	—	1	2	—	3	3	6	4	6	3	13	21
Natica pusilla	2	—	1	3	—	—	6	6	11	2	10	23	32
Retusa canaliculata	—	8	8	16	4	1	—	5	—	7	2	9	30
Seila adamsi	1	—	—	1	1	1	1	3	—	10	4	14	18
Thais lapillus	—	—	—	—	—	—	—	—	—	1	—	1	1
Turbonilla interrupta	—	—	1	1	1	2	3	6	17	16	7	40	47
Urosalpinx cinerea	5	—	5	10	1	3	4	8	1	1	1	3	21
Arthropoda													
Crustacea													
Balanus eburneus	—	—	—	—	—	—	1	1	—	—	—	—	1
Balanus improvisus	—	—	—	—	—	—	—	—	—	—	5	5	5
Carcinus maenas	—	—	—	—	—	—	1	1	—	—	—	—	1
Libnia dubia	—	—	—	—	—	1	—	1	—	—	—	—	1
Neopanope texana sayi	5	—	—	5	—	43	40	83	1	—	4	5	93
Pagurus longicarpus	—	—	—	—	—	—	—	—	3	2	—	5	5
Panopeus herbsti	—	—	—	—	—	1	—	1	—	—	—	—	1
Polyonyx macrocheles	—	—	—	—	—	—	—	—	—	—	2	2	2
Arachnoidea													
Limulus polyphemus	—	1	—	1	—	—	—	—	—	—	—	—	1
Echinodermata													
Ophiuroidea													
Amphipholis squamata	—	—	—	—	—	—	—	—	—	8	2	10	10
Holothuroidea													
Leptosynapta tenuis	—	—	—	—	—	—	1	1	—	—	—	—	1
Chordata													
Ascidiaceae													
Molgula sp.	—	—	—	—	2	—	—	2	—	—	—	—	2

[a] The author's identification of this species is incorrect. *Cerithidea* spp. do not range farther north than South Carolina, so the correct identity of this gastropod is unknown (editor).

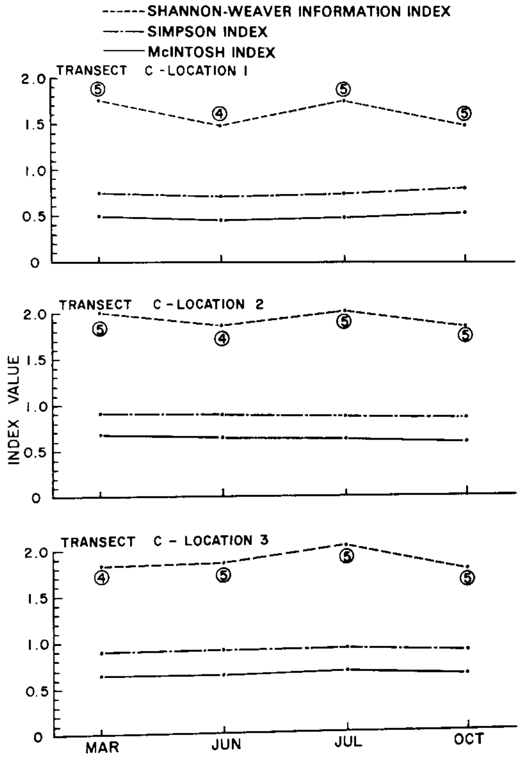

FIGURE 2.—Pooled diversity indices (mollusks and crustaceans) for three stations at transect C in the Weweantic River Estuary: Circled numbers represent the number of Peterson grabs pooled.

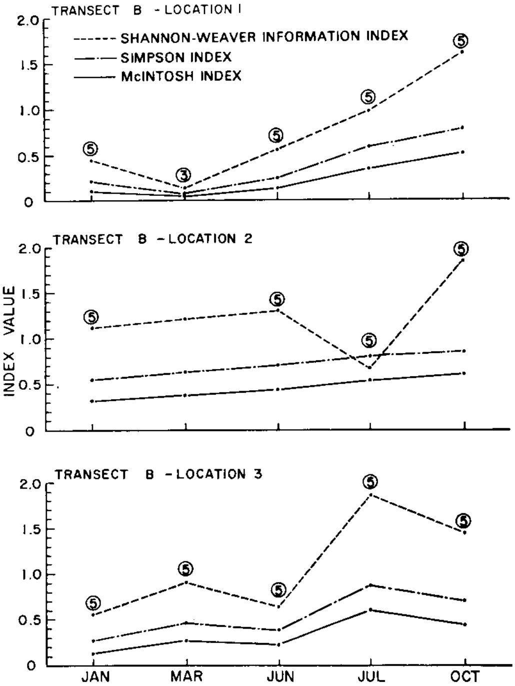

FIGURE 3.—Pooled diversity indices (mollusks and crustaceans) for three stations at transect B in the Weweantic River Estuary: Circled numbers represent samples.

3). They fed primarily on planktonic copepods in spring and shifted to benthic invertebrates in summer and fall. The preference for plankton was revealed by the high incidence of plankton in the stomach. The planktonic food supply has been suggested as an attraction for other species of flatfish that occur in estuaries during the winter and spring. Dovel, Mihursky and McErlean (1969), for example, have demonstrated that the hogchoker, *Trinectes maculatus*, resides in water of low salinity where plankton is abundant during winter.

Winter flounder appear to adapt to a benthic existence after the midpoint of their first year, when their food preference shifts from plankton to benthic invertebrates. Adult flounder prey on the same classes of invertebrates, Crustacea, Polychaeta, Bivalvia, and Gastropoda (Linton 1921; Bigelow and Schroeder 1953; Mulkana 1966) as age I+ flounders, but their seasonal preferences for given taxa differ. Pearcy (1962), who has done the only study of differences in the diet of young winter flounder, shows that planktonic crustaceans in the diet are gradually replaced by polychaetes as the flounder grows older. In the Weweantic estuary flounder seem to prefer mollusks and amphipods to polychaetes. Be-

TABLE 3.—*Average volume percentages invertebrate classes (polychaetes, gastropods, bivalves and crustaceans) in winter flounder stomachs and Peterson grabs compared by percent overlap*

Date	Transect	Station	Number of fish	Number of fish	Percent overlap
March 1969	A B	3 2	11	5	1.8
June 1969	C C	1 3	19	15	29.0
July 1968	C C	1 3	46	15	47.0
October 1969	C C	1 3	20	15	47.0

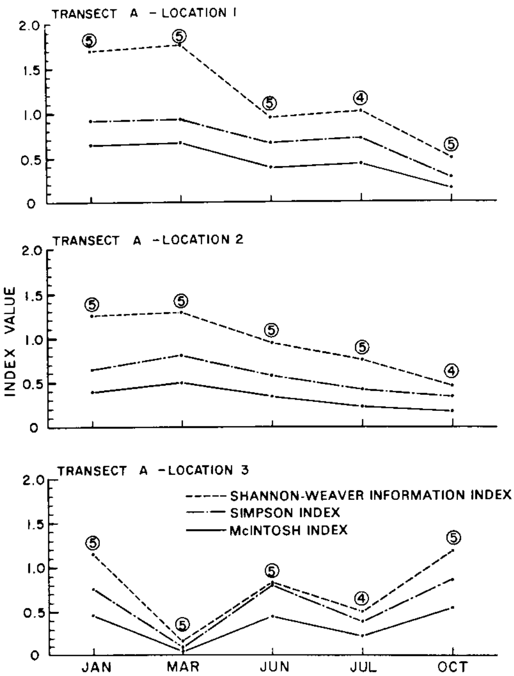

FIGURE 4.—Pooled diversity indices (mollusks and crustaceans) for three stations at transect A in the Weweantic River Estuary: Circled numbers represent samples.

TABLE 4.—*The percent overlap of food species within stomachs; within grabs and between stomachs and grabs. Fish were captured at transect C, Station 1 in July 1968; grabs were taken from the same location July 1969*

	Stomachs (% overlap)				
Stomachs	1	2	3	4	5
1		31	6	6	6
2			50	36	50
3				36	50
4					50
5					
Average % overlap Grand average = 31%		31	28	26	39
	Peterson grabs (% overlap)				
Peterson grabs	1	2	3	4	
1		46	58	62	
2			56	70	
3				62	
4					
Average % overlap Grand average = 56%		46	57	65	
	Peterson grabs (% overlap)				
Stomachs	1	2	3	4	
1	14	0	6	6	
2	23	0	6	8	
3	15	18	6	32	
4	15	0	6	8	
5	15	0	6	8	
Average % overlap Grand average = 9.6%	16.1	3.6	6	12.4	

cause mollusks preserve better than annelid worms or other soft-bodied invertebrates, they were easier to identify and therefore may have appeared more numerous than they actually were. Moreover, the dredge sampled only the top 10 cm of the bottom and annelids may have been severed or crushed by the gear.

Because fish may move to areas which may lie well outside the sampling stations, they would be expected to have a more variable diet than if they could not move. A variable diet is indicated by the lower percent overlap between stomachs than between grabs (Tables 4 and 5). The fish were able to select invertebrate foods from a variety of habitats. The overlap values of stomach contents were higher in July than in October, indicating that the fish's diet was more homogeneous in summer. The overlap value of stomach contents and grabs was lower in July than in October, suggesting that the grab samples were less representative of the animal's feeding behavior in the summer. They may have been less representative because the fish utilized very few of the foods available in the summer and did not stray from areas sampled. These interpretations may be confounded by the percent overlap parameter itself, which is sensitive to both species and numbers.

The three diversity models used in my study are frequently employed to measure community structure on a common scale. Each index is restricted to a single range of values. In both the Simpson and McIntosh indices, which measure how equally or unequally the species are divided among the sample, the number of species is important. Therefore, when many species are represented by equal numbers, the Shannon index yields more information about a sample.

The diversity of the dominant mollusks and macrocrustaceans fluctuates seasonally in the estuary but remains constant at the mouth. The assumption of Klopfer (1959) that a stable environment allows space for more niches and enhances diversity seems appropriate in view of my findings. The seasonal variations in salinity and temperature were

TABLE 5.—*The percent overlap of food species within stomachs, within grabs, and between stomachs and grabs. Fish and grab samples were taken from transect C, station 1 in October 1969*

	Stomachs (% overlap)				
Stomachs	1	2	3	4	5
1		17	14	0	100
2			30	0	17
3				14	14
4					0
5					
Average % overlap		17	22	5	33
Grand average = 19%					
	Peterson grabs (% overlap)				
Peterson grabs	1	2	3	4	5
1		62	43	69	50
2			66	53	54
3				60	43
4					43
5					
Average % overlap		62	55	61	48
Grand average = 57%					
	Peterson grabs (% overlap)				
Stomachs	1	2	3	4	5
1	29	0	0	40	0
2	17	0	0	17	8
3	14	0	0	14	14
4	29	29	29	29	29
5	29	0	0	40	0
Average % overlap	24	6	6	28	10
Grand average = 14.8%					

less at the mouth (transect C) than within the estuary. Minimal variation creates a more seasonally stable environment, and therefore a more seasonally stable community with more niches, than does maximal variation. In a boreal estuary oscillations in salinities or temperatures cause oscillations in the number of individuals (Thomas and White 1969) and make measurements of productivity difficult.

There are two possible reasons for the occurrence of age I+ winter flounders in the estuary during winter and spring: a high abundance of planktonic crustaceans, and a greater chance of survival due to metabolic adaptation. The metabolic rate of age I+ flounder held under laboratory conditions decreases by 50% when the salinity is lowered from 30‰ to 20‰ (Frame 1973a). Other investigators (Deubler and White 1962; Poole 1966) have suggested that winter flounder movement is related to salinity.

ACKNOWLEDGMENTS

I am grateful to Charles Cole, James McCann, and Craig Edwards for their guidance and critical review of the manuscript. I especially thank the several persons who helped in field sampling: Fredric Serchuk, David Crestin, Roderick Smith and James Moulton. Johanna Reinhart, Curator of the Gray Museum, Marine Biological Laboratory, Woods Hole, Massachusetts, kindly assisted in invertebrate identification.

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