

FISHES, FISH ASSEMBLAGES, AND THEIR SEASONAL MOVEMENTS IN THE LOWER BAY OF FUNDY AND PASSAMAQUODDY BAY, CANADA

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ABSTRACT

Five fish assemblages, dominated by pleuronectids, cottids, gadids, clupeids, and rajids, were identified from collections taken during a 5-year survey in the lower Bay of Fundy region, Canada. Individual assemblages occurred in each of estuarine, beach, pelagic, and offshore hard- and soft-bottom habitats. Species and/or age-class components within assemblages varied seasonally but, in general, each assemblage was distinct. There was a progressive seaward displacement of these assemblages from shallow, inshore to deeper, offshore habitats in winter followed by a reversal during summer. Yearly changes in species occurrence and abundance during the study period were predominantly attributable to variation in ocean climate. Long-term changes in abundance of two commercial species at one of the sampling sites, since a similar study there in 1965, appear related to population fluctuations in the Bay of Fundy and the Gulf of Maine. The beach habitat apparently served as a major nursery area for juvenile gadids, pleuronectids, and clupeids.

Although the fish fauna of the Bay of Fundy-Gulf of Maine system is well documented (Bigelow and Schroeder 1953; Leim and Scott 1966), few studies have examined long-term spatial and temporal changes or interrelationship among the fish assemblages. Previous studies in this region were concerned with the biology and seasonal movements of a single species (McCracken 1959, 1963; McKenzie and Tibbo 1961; Wise 1962) or the occurrence and composition of communities at a single site (Bigelow and Schroeder 1939; Tyler 1971).

Moore (1977) and Quinn (1980) have emphasized the need for long-term research to establish baseline information and estimates of natural variability for fisheries assessments and pollution impact studies. This is particularly true for inshore regions because of their importance as nurseries and feeding grounds (Warfel and Merriman 1944; Rauck and Zijlstra 1978). The increasing interest in trophic rela-

tionships among entire communities of fishes is further reason to document movement, abundance, and co-existence of fishes potentially utilizing the same food resource (Richards 1963; Keast 1970; Tyler 1972; Steiner 1976; Hacunda 1981).

Long-term changes in fish assemblages have been attributed to overexploitation of one or more of the species within the assemblage (Brown et al. 1973; Burd 1978; Sherman et al. 1981) and climatic variations (Dow 1964; Sutcliffe et al. 1977). However, it is usually difficult to separate natural fluctuations from those caused by imbalance in competitive and predator-prey relationships due to exploitation (Cushing 1980; Daan 1980; Sissenwine et al. 1982). With the view in mind of assessing these long-term changes to properly assign cause and effect, repetitive, in-depth studies of well-known or type localities are needed.

This study examines spatial and temporal variation in fish diversity and abundance over a 5-yr period at two offshore stations within Passamaquoddy Bay, one offshore station in the Bay of Fundy, and at inshore and beach stations in Passamaquoddy Bay. One offshore station was the same station sampled by Tyler (1971) during 1965-66, allowing documentation of changes that have occurred over the intervening 10-15 yr.

METHODS

Three offshore stations in the Bay of Fundy (B) and in Passamaquoddy Bay (A, C) (Fig. 1) were sampled

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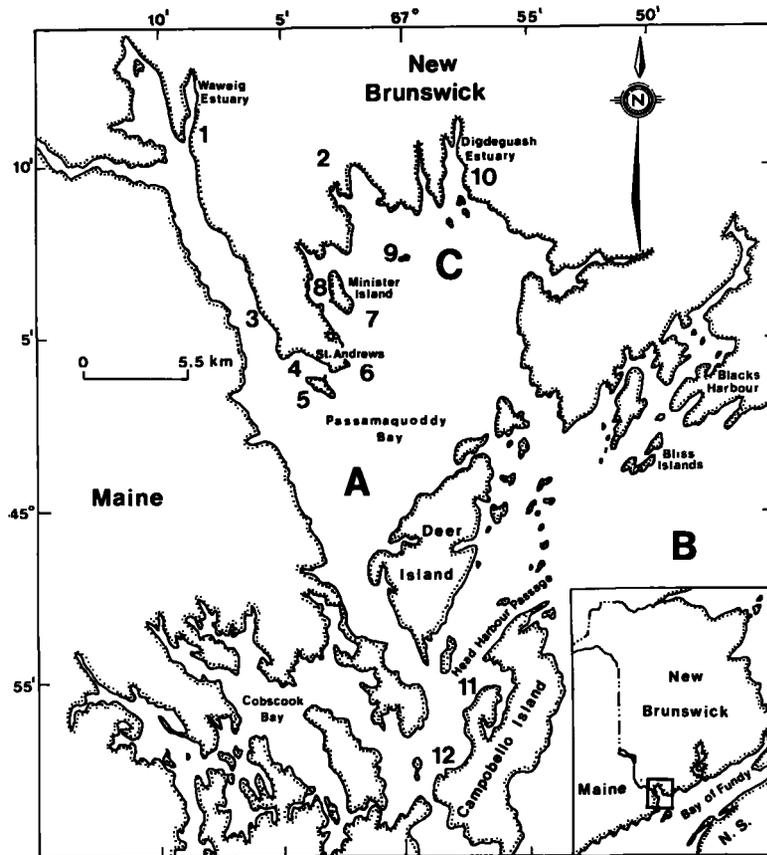


FIGURE 1.—Passamaquoddy Bay and the adjacent Bay of Fundy indicating sampling stations occupied during the study.

at approximately monthly intervals over a 5-yr period, 1976-81 (Table 1). Station A was the same site sampled by Tyler (1971) during 1965-66. Fish were collected using a $\frac{3}{4}$ -35 shrimp trawl (3.8 cm stretch mesh nylon; 15.5 m foot rope), similar to the $\frac{3}{4}$ -35 Yankee trawl used by Tyler (1971), towed by the 150-hp, 14 m stern trawler, Fisheries and Oceans' RV *Pandalus II*. Tows at each station were along a 1.6 km transect at about 4 km/h. Stations A and B were sampled once per trip between 1976 and 1979, and station C was sampled sporadically. From 1979 to 1981, tows at stations A and B were replicated and station C was sampled regularly. Captured fishes were identified to species, and adults and juveniles were categorized by size and enumerated separately. During the final year of collecting, fork length of all fishes was recorded to the nearest centimeter and otoliths were collected from Atlantic cod, ocean pout, American plaice, winter flounder, and witch flounder for age determination. Atlantic cod otoliths were sec-

tioned for aging, other species were aged using the whole otolith. Results reported are the empirical length at age.

Between June and September 1976, 12 estuarine, intertidal, and inshore marine stations were sampled within Passamaquoddy Bay and Head Harbour Passage (Fig. 1). In addition, station 3 was sampled monthly during the period May 1976-November 1977, station 8 was sampled at approximately weekly intervals from May to September 1981, and stations 1 and 10 were sampled in December 1980 (Table 1). Fish were collected using a 9 m, 1.3 cm mesh beach seine, a 3.7 m shrimp trawl with a 3 mm cod end towed behind a 5 m Boston whaler, or bottom-set gill nets with stretched mesh sizes ranging from 7.6 to 17.8 cm. Standard fishing efforts employed with each gear type were shore seine hauls of 5 min during the 2-h period before and after low water, trawl tows of 10 min, and overnight gill net sets of 16 h.

Temperature, salinity, and substrate type were

TABLE 1.—Physical and chemical characteristics and sampling history of stations in the Bay of Fundy and Passamaquoddy Bay. Gear: ST = shrimp trawl; S = seine; GN = gill net. Bottom type: M = mud; Sa = sand; Rk = gravel or rock.

Station	Gear	Maximum depth (m)	Bottom type	Sampling temp. range (C)	Sampling salinity range (‰)	Collection period	Sampling trips
A	ST	80	M-Rk	0-15	29.5-32.5	1976-81	39
B	ST	80	M	1-12	31.0-32.5	1976-81	37
C	ST	20	M	0-15	—	1978-81	15
1	S	1.5	M-Rk	14.5-20.0	22.1-26.0	06-08/76, 12/80	3
2	S	1.5	M-Rk	15.5-22.5	28.0-29.5	06-08/76	4
3	S	1.5	Sa-Rk	0.0-16.0	21.0-30.0	05/76-11/77	16
4a	S	1.5	Rk	12.5	29.0	06, 07/76	2
4b	ST	7.5	Rk	12.5	—	07/76	1
5a	S	1.5	Sa	14.5	30.0	07, 08/76	2
5b	GN	33	Sa-M	—	—	08/76	1
6	S	1.5	Sa-M	14.0	28.0-30.0	08-09/76	2
7	GN	30	M	13.5	28.0	06/76	1
8a	S	1.5	M-Sa	11.0-18.5	28.7-30.7	06, 07/76	2
						05-09/81	23
8b	ST	12	Rk-Sa	—	—	06, 07/76	2
9	S	1.5	Sa	14.0	29.5	06, 08/76	2
10	GN	3	M-Rk	13.0	28.0	06, 09/76, 12/80	3
11	S	1.5	M	—	—	07/76	1
12a	S	1.5	Sa-Rk	15.0	28.0	07, 09/76	2
12b	ST	15	Sa-Rk	—	—	07/76	1

recorded for most sampling sites (Table 1). Bottom temperature and salinity data inside and outside Passamaquoddy Bay came from routine monthly sampling by the Department of Fisheries and Oceans at a site opposite the Biological Station (near Station A) and at "Prince 5" 3.2 km south of Bliss Islands in the Bay of Fundy (near station B). Temperatures at deep stations were taken with a reversing thermometer attached to a Nansen bottle and at shallow stations with a hand thermometer. Salinities were determined with a laboratory salinometer from samples collected in the field. Substrate samples at deep stations were obtained with a PONAR grab. At shallow stations, substrate type was assessed visually.

Fishes were identified using Leim and Scott (1966) with the exception of red and white hake and redbfish, which were determined by using Musick (1973) and Ni (1982), respectively. Because we were unaware of the problem of distinguishing between young *Raja ocellata* and *R. erinacea* (McEachran and Musick 1973), these determinations may be incorrect.

Coefficients of community were calculated using the formula:

$$\frac{C}{A + B - C} \times 100$$

where C = number of common species, A = number in assemblage 1, and B = number in assemblage 2 (Jaccard 1932; Kontkanen 1957). An index that compared presence and absence of species at each station (binary data) was used because species abundances among stations were not comparable due to different gear used.

RESULTS AND DISCUSSION

Station Environmental Characteristics

Temperature and salinity at stations A and B (Fig. 2) followed the typical, yearly cycle of a cold temperate sea (Fig. 3). Annual temperature range in the Bay of Fundy was less than in Passamaquoddy Bay. Summer temperatures at inshore sites were similar to offshore sites with the exception of higher temperatures at some estuary stations (i.e., 1 and 2) (Table 1). Two notable variations occurred: The early months of 1977 and August 1978 were abnormally warm, particularly at station A (J. Hull³); and throughout the study period there was a generalized cooling trend.

Salinities were highest in late summer through the fall and lowest in spring at both sites. At all times of year, salinities were higher in Bay of Fundy (station B) than at station A (Fig. 2). Inshore sites had salinities of 1-2 ppt less than station B, and salinities at estuarine sites were as low as 21.0 ppt during summer (Table 1).

Substrates of most sites were composed of sand and/or mud (Table 1). Station A had the steepest slope, about 2:100 m. Slopes at stations B and C were 0.4:100 and 0.6:100 m, respectively. Slopes at coastal intertidal sites were gradual, about 1:100 m. Estuarine stations (1, 2, and 10) had extremely soft mud bottoms and station 2 had extensive eel grass beds.

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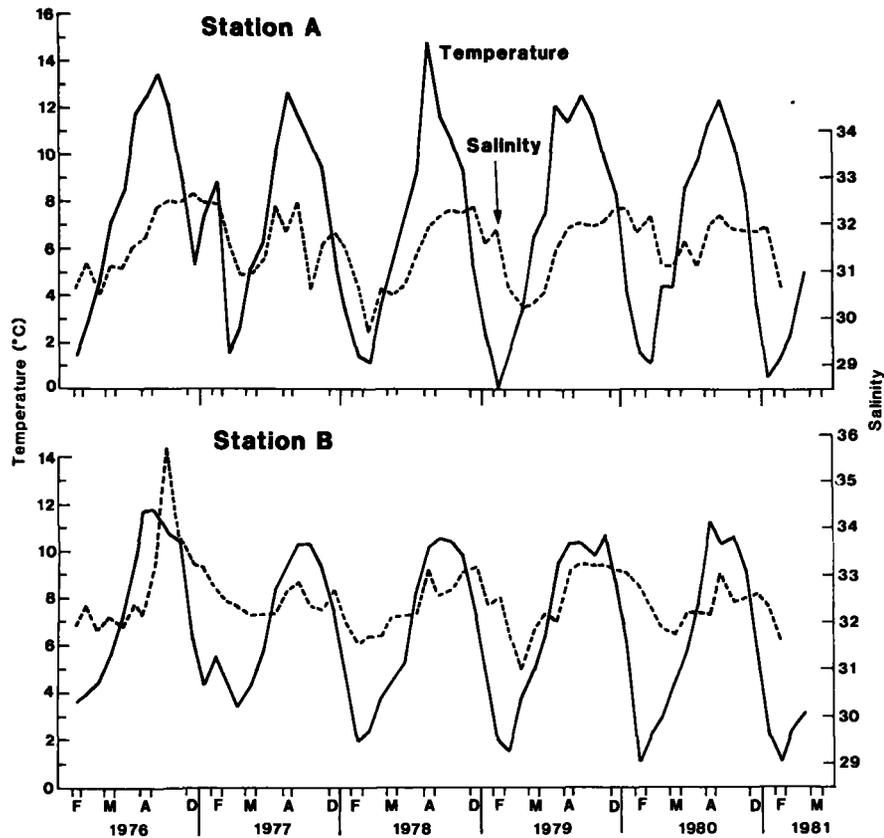


FIGURE 2.—Bottom temperature and salinities at station A in Passamaquoddy Bay and station B in the Bay of Fundy during 1976-81.

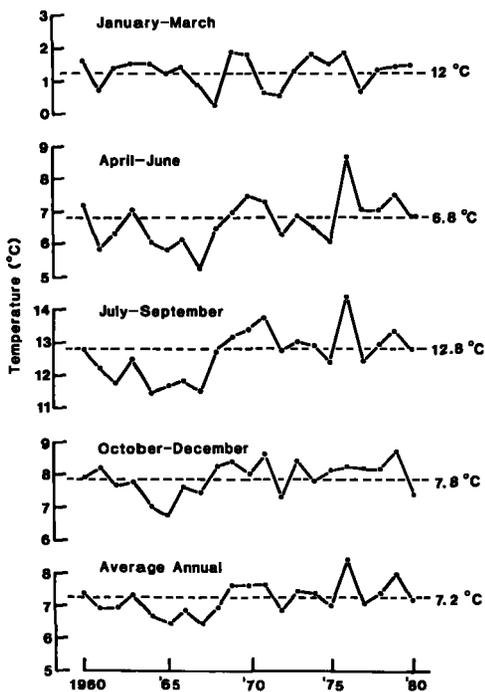


FIGURE 3.—Mean surface sea temperatures at station B by season during 1960-80 as compared with the 50-yr mean at this site.

Fishes and Seasonal Occurrence

Sixty-two species of fish were captured during the study period (Tables 2, 3). For those stations sampled regularly and intensively, residency period and abundance are indicated. Fish occurrence is expressed as part of the summer component (June-October), the winter component (November-May), the regular component (caught year round), or the occasional component. Fishes classified as occasional components show no seasonal abundance pattern and were collected <70 times (specimens captured \times sampling trips) over 5 yr at stations A, B, and C, or <15 times at stations 1-12. We realize that some fish at all stations may have been missed entirely or are listed as rare simply because they were unavailable to the sampling gear used or could avoid capture (e.g., mackerel). Abundance of fishes in the catch was categorized as rare (1-10 specimens), com-

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TABLE 2.—Residency and abundance of fishes occurring at deep sampling stations in the Bay of Fundy and Passamaquoddy Bay. Residency is R = regular; S = summer; W = winter; O = occasional; N = never encountered. Abundance is a = abundant; c = common; r = rare.

Species	Station			Species	Station		
	A	B	C		A	B	C
<i>Mysis glutinosa</i>	Oc	N	N	<i>Lumpenus lumpretaeformis</i>	Or	Or	N
<i>Squalus canthias</i>	Oc	Sa	Oc	<i>Lumpenus maculatus</i>	Or	N	N
<i>Raja radiata</i>	Sc	Rc	Or	<i>Macrozoarces americanus</i>	Ra	Sc	Sc
<i>Raja senta</i>	Or	Rc	Or	<i>Nezumia bairdi</i>	N	Or	N
<i>Raja erinacea</i>	Ra	Wc	Oc	<i>Cyclopterus lumpus</i>	Or	Or	N
<i>Raja ocellata</i>	Rc	Or	Or	<i>Liparis coheni</i>	Wc	Or	N
<i>Raja laevis</i>	N	Or	N	<i>Liparis inquilinus</i>	Wr	N	N
<i>Acipenser oxyrinchus</i>	N	Wr	N	<i>Sebastes fasciatus</i>	Wc	N	N
<i>Alosa aestivalis</i>	N	N	Or	<i>Myoxocephalus octodecemspinosus</i>	Ra	Wc	Oc
<i>Alosa pseudoharengus</i>	Or	Or	Sc	<i>Myoxocephalus aeneus</i>	Wc	Or	N
<i>Alosa sapidissima</i>	Or	Sc	N	<i>Myoxocephalus scorpius</i>	Wc	Or	N
<i>Clupea harengus</i>	Wa	Wa	Wa	<i>Hemirhamphus americanus</i>	Rc	Rc	Or
<i>Osmerus mordax</i>	Rc	Or	Sa	<i>Triglops murrayi</i>	Oc	Or	N
<i>Mallotus villosus</i>	N	N	Or	<i>Artediius uncinatus</i>	Wc	N	N
<i>Enchelyopus cimbrius</i>	Sr	Rc	Or	<i>Aspidophoroides monopterygius</i>	Rc	N	N
<i>Gadus morhua</i> (adult)	Sc	Wc	Oc	<i>Poronotus triacanthus</i>	Oc	Or	Oc
<i>G. morhua</i> (juvenile)	Wa	Wc	Oc	<i>Pseudopleuronectes americanus</i>	Sa	Wa	Sa
<i>Microgadus tomcod</i>	Or	Or	Oc	<i>P. americanus</i> (juvenile)	Wa	Wr	Sa
<i>Pollachius virens</i> (juvenile)	Wa	Or	N	<i>Glyptocephalus cynoglossus</i> (adult)	Or	Sc	N
<i>Melanogrammus aeglefinus</i> (adult)	Sc	Oc	N	<i>G. cynoglossus</i> (juvenile)	Or	Wc	N
<i>M. aeglefinus</i> (juvenile)	Wc	N	N	<i>Hippoglossoides platessoides</i>	Rr	Ra	Sa
<i>Merluccius bilinearis</i>	Sa	Sa	Sc	<i>Limanda ferruginea</i>	Sr	Or	Or
<i>Urophycis tenuis</i>	Sc	Rc	Oc	<i>Liopsetta putnami</i>	N	N	Wc
<i>Urophycis chuss</i>	Sc	Sr	Or	<i>Hippoglossus hippoglossus</i> (juvenile)	Wr	N	N
<i>Anarhichas lupus</i>	Sr	N	N	<i>Paralichthys oblongus</i>	Or	N	N
<i>Ulvina subbifurcata</i>	Wr	N	N	<i>Scophthalmus aquosus</i>	Or	Or	Rc
<i>Cryptacanthodes maculatus</i>	Or	Or	N	<i>Lophius americanus</i>	Sr	Or	N

TABLE 3.—Residency and abundance of fishes occurring at estuarine, intertidal, and shallow marine sites in Passamaquoddy Bay. Residency is R = regular; S = summer; W = winter; O = occasional; N = never encountered (station 3 only). Abundance is a = abundant; c = common; r = rare.

Species	Station											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Squalus canthias</i>	—	—	N	—	Sc	—	Sc	—	—	—	—	—
<i>Raja radiata</i> (juvenile)	—	—	Sr	—	Oc	—	O	—	—	—	—	—
<i>Raja erinacea</i>	—	—	Sc	—	O	—	—	—	—	—	—	—
<i>Raja ocellata</i>	—	—	N	—	O	—	O	—	—	—	—	—
<i>Alosa aestivalis</i>	—	—	N	—	—	—	Sa	—	Sa	—	—	—
<i>Alosa pseudoharengus</i>	—	—	Sr	—	—	O	—	Sa	—	Sa	—	—
<i>Clupea harengus</i>	Sc	O	O	O	—	O	O	Sa	—	Sa	O	—
<i>Salmo salar</i>	—	—	S	—	—	—	—	—	—	O	O	—
<i>Osmerus mordax</i>	Rc	Rc	Wa	—	—	—	O	Sa	—	Wa	—	—
<i>Mallotus villosus</i>	—	—	N	—	—	—	—	—	—	Oc	Oc	—
<i>Fundulus heteroclitus</i>	Sa	Sc	Wc	—	—	—	—	Or	—	Sc	—	—
<i>Gasterosteus aculeatus</i>	Sc	Sa	Oc	O	O	O	—	Sc	—	Sc	O	O
<i>Gasterosteus wheatlandi</i>	Oc	Sa	Sr	—	—	—	—	Sr	—	Sr	—	—
<i>Apeltes quadracus</i>	—	—	Sc	N	—	—	—	—	—	—	—	—
<i>Pungitius pungitius</i>	—	—	Sa	N	—	—	—	—	—	—	—	—
<i>Anguilla rostrata</i>	Or	Sc	N	—	—	—	—	—	—	Sr	—	—
<i>Enchelyopus cimbrius</i> (larvae)	—	—	Sc	—	—	—	—	—	—	—	—	—
<i>Gadus morhua</i> (adult)	—	—	N	—	O	—	O	Sr	—	—	—	—
<i>G. morhua</i> (juvenile)	—	—	Sr	—	Sc	—	Sc	Sr	—	—	—	—
<i>Microgadus tomcod</i>	Wc	Wc	Wc	O	O	—	Sc	O	Wc	O	—	—
<i>Pollachius virens</i> (juvenile)	O	O	Sa	O	O	O	—	Sa	O	—	O	—
<i>Urophycis tenuis</i> (juvenile)	—	—	Sc	—	—	—	—	Sc	O	—	—	—
<i>Ammodytes americanus</i>	—	—	N	—	—	—	—	—	—	O	—	—
<i>Scomber scombrus</i>	—	—	Sr	—	Sc	—	Sc	—	—	—	—	O
<i>Pholis gunnellus</i>	O	—	Rc	O	—	—	—	S	—	—	—	O
<i>Ulvina subbifurcata</i>	—	—	N	—	—	—	—	—	O	—	—	—
<i>Cyclopterus lumpus</i> (juvenile)	—	—	Sc	—	—	—	—	O	O	—	—	—
<i>Macrozoarces americanus</i>	—	—	N	—	—	—	—	O	O	—	—	O
<i>Myoxocephalus octodecemspinosus</i>	—	—	Sr	—	—	O	O	S	—	O	O	O
<i>Myoxocephalus aeneus</i>	—	—	Sc	—	—	—	—	Sc	O	—	—	—
<i>Myoxocephalus scorpius</i>	O	—	O	—	—	—	—	Sc	—	—	—	O
<i>Hemirhamphus americanus</i>	Oc	—	Sc	O	—	—	O	O	—	—	—	—
<i>Menidia menidia</i>	Sa	Sa	Wc	—	—	—	—	O	—	—	—	—
<i>Pseudopleuronectes americanus</i> (adult)	Sr	—	Sr	O	Sa	—	Sa	O	O	—	—	—
<i>P. americanus</i> (juvenile)	O	—	Sa	O	Sa	—	Sa	Sa	O	—	—	—
<i>Liopsetta putnami</i>	Sc	O	Sr	—	—	—	—	—	—	Sc	—	—
<i>Syngnathus fuscus</i>	O	Sc	N	—	—	—	—	—	—	—	—	—

mon (11-100), and abundant (+100). Because of gear differences further quantification of catches was unjustified.

Eight species of flatfishes were captured during the study period (Table 2). The winter flounder, *Pseudopleuronectes americanus*, was the numerically dominant species (Figs. 4, 5). Juveniles (<22 cm, 2+ age group; Fig. 6) were abundant in shallow water during summer (Fig. 5) and at deep station over hard bottom in Passamaquoddy Bay during winter (Fig. 4). Adult winter flounder were abundant during summer in Passamaquoddy Bay, both inshore and offshore, but rare at the Bay of Fundy site (Fig. 4). During winter they were rare or absent inside

Passamaquoddy Bay but common to abundant at the Bay of Fundy station. This pattern reflects the winter movement of this species into offshore water in the northern part of its range (Saila 1961; McCracken 1963; Van Guelpen and Davis 1979), which is probably triggered by temperature. Adults were seldom present in Passamaquoddy Bay when temperatures were below 6°C. McCracken (1963) found a similar relationship between minimum flounder catch-per-effort and minimum temperature. Surges of adult flounder abundance at offshore sites, which coincided with rapid temperature change in spring and fall, were evident in most years (Fig. 4; Tyler 1971) and may have been related to rapid onshore or

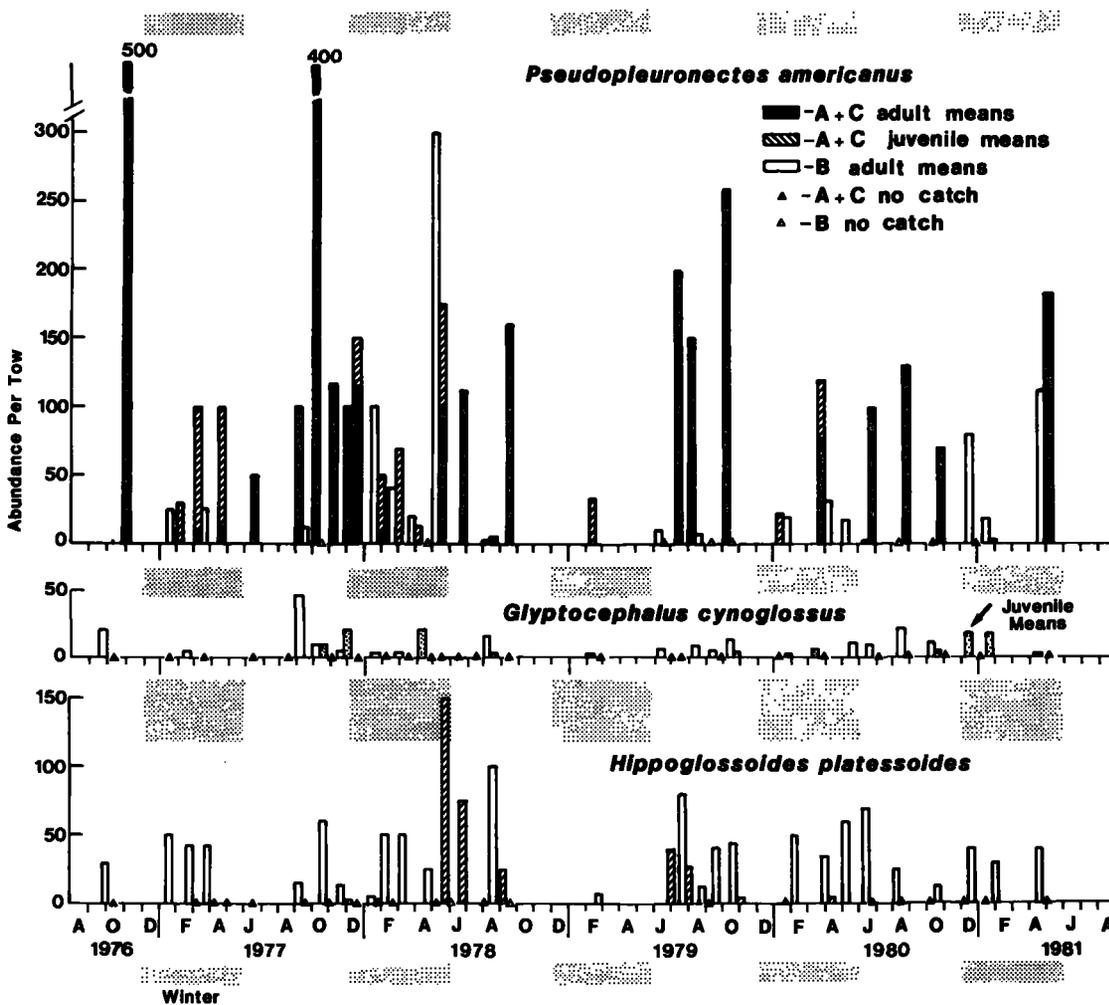


FIGURE 4.—Seasonal occurrence and abundance of juvenile and adult flatfishes (*Pseudopleuronectes americanus*, *Glyptocephalus cynoglossus*, and *Hippoglossoides platessoides*) at offshore station in the Bay of Fundy and Passamaquoddy Bay. For witch flounder (middle) dark bars are adults and lined bars are juveniles at site B. For American plaice (bottom) open bars are site B and lined bars are site C (all juveniles).

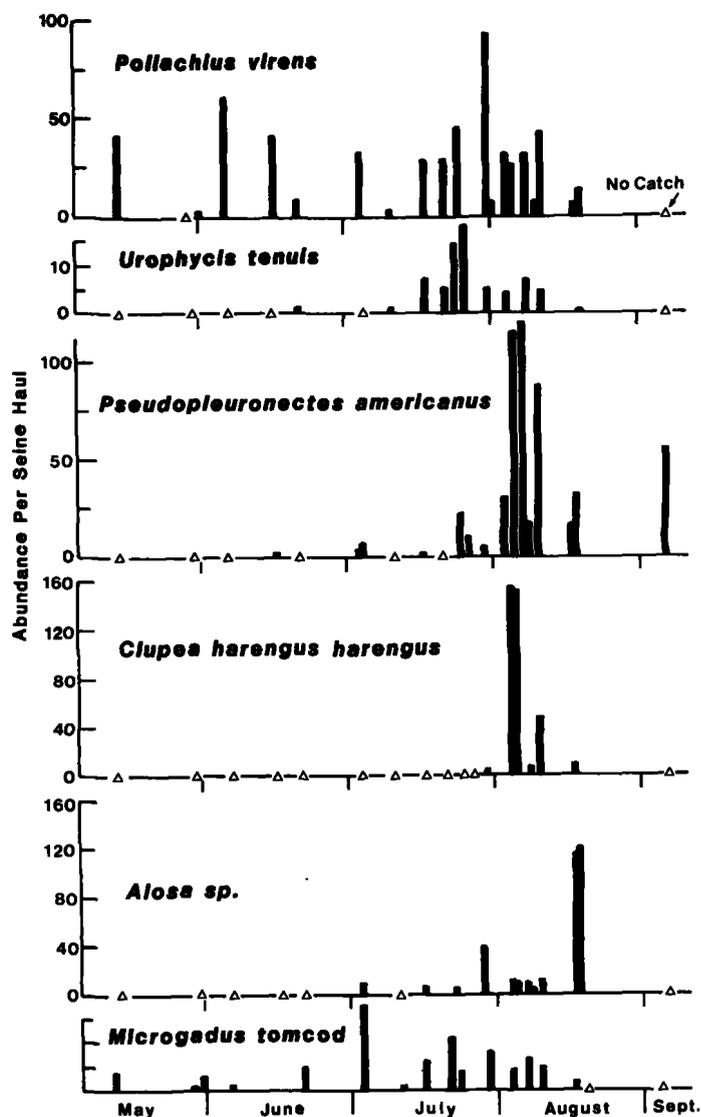


FIGURE 5.—Seasonal occurrence and abundance of fishes captured by seine at beach station 8 from May to September 1981.

offshore movement of the population.

The witch flounder, *Glyptocephalus cynoglossus*, was absent or rare at all times inside Passamaquoddy Bay, but was a regular component at the soft-bottom Bay of Fundy station (Fig. 4). Catches from June to October consisted of large adult witch flounder (30-60 cm, >6+ age group), but catches from November to May were 6-25 cm juveniles (0-6 yr) (Figs. 6, 7). Adult witch flounder on the Scotian Shelf also move from intermediate depths (100 m) in summer to deeper water in winter (Powles and Kohler 1970). Both Powles and Kohler (1970) and Markle (1975) reported juvenile witch flounder from deep water (150-1,000 m) over hard bottom, quite unlike the

situation we encountered except for similar temperature regimes. Also, replacement of adults by juveniles during winter seems peculiar to our study, but may have been observed because of year-round sampling.

Juvenile American plaice, *Hippoglossoides platessoides*, were a major summer component of station C and a regular component of the Bay of Fundy station (Fig. 4), both soft-bottom habitats, but was only occasional at the hard-bottom station (A). Age-2 plaice (6-14 cm; Fig. 6) were first captured with our shrimp net in April. By the following year, recruitment to the gear appears complete at an average size for the age-class of 17 cm (Fig. 7). Juvenile plaice are

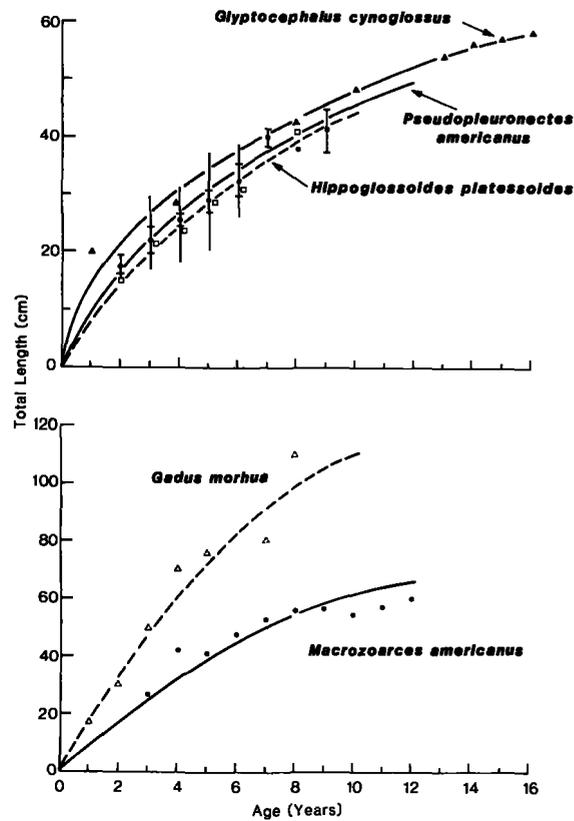


FIGURE 6.—Fish length versus age for five fish species caught at stations A and B; December 1980-June 1981. Lines are fitted by eye.

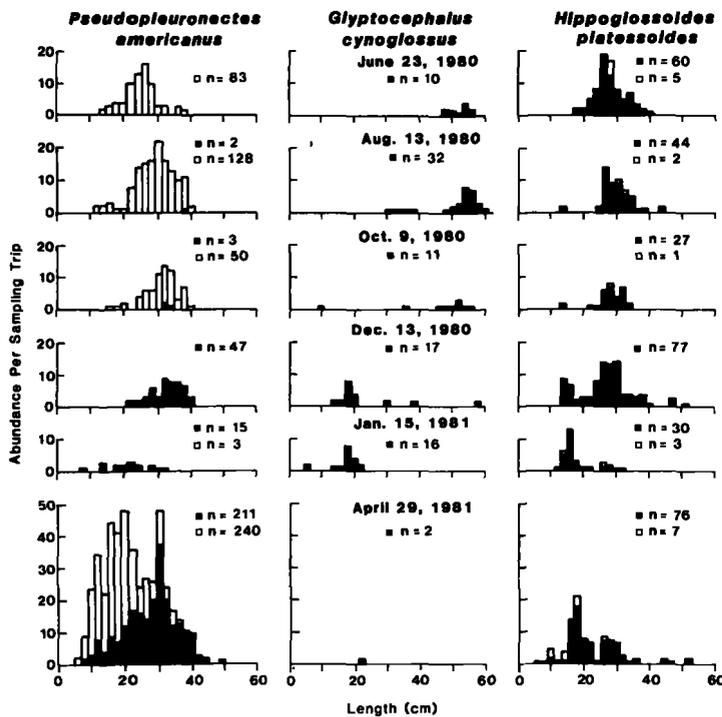


FIGURE 7.—Seasonal size distributions of flatfishes (*Pseudopleuronectes americanus*, *Glyptocephalus cynoglossus*, and *Hippoglossoides platessoides*) from offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1980 and 1981. Shaded area is captures at station B; unshaded, station A inside Passamaquoddy Bay.

sedentary, soft-bottom dwellers, that exhibit little seasonal movement, and migration from nursery ground to adult stock is diffusive (Bigelow and Schroeder 1953; Leim and Scott 1966). However, some seasonal movement does occur when plaice leave soft-bottom, middepth habitat (30 m) for winter and return in summer (present study). Plaice were a regular, low-abundance component at station A in 1965 (Tyler 1971), but we found they were virtually absent between 1976 and 1981. The difference may be attributable to the general decline of groundfish abundance in the Bay of Fundy after 1970 (Hare 1977).

Among other flatfishes, windowpane, *Scophthalmus aquosus*, was a regular component at station C and the smooth flounder, *Liopsetta putnami*, was common among the inshore-estuarine communities during summer (Tables 2, 3). Yellowtail flounder, *Limanda ferruginea*, was a rare member (4-5/tow) of

the summer assemblage at station A and occasional at the other two deep stations. Juvenile Atlantic halibut, *Hippoglossus hippoglossus*, was a low-abundance member (2-3/tow) of the winter assemblage at station A. The fourspot flounder, *Paralichthys oblongus*, was captured once at station A during the abnormally warm fall of 1978.

Eight species of gadoid fishes were captured during the study (Tables 2, 3). Adult Atlantic cod, *Gadus morhua*, was an abundant member of the summer component at offshore sites in Passamaquoddy Bay, particularly station A, but was absent from there in winter. It was a common member of the early winter assemblage in the Bay of Fundy but rare thereafter (Figs. 8, 9). During summer, juvenile Atlantic cod (10-20 cm) were captured occasionally while seining beach sites, but were more common in gill net catches at intermediate depth (30 m) inshore (stations 5 and 7; Table 3). The shallow water abundance maxima of

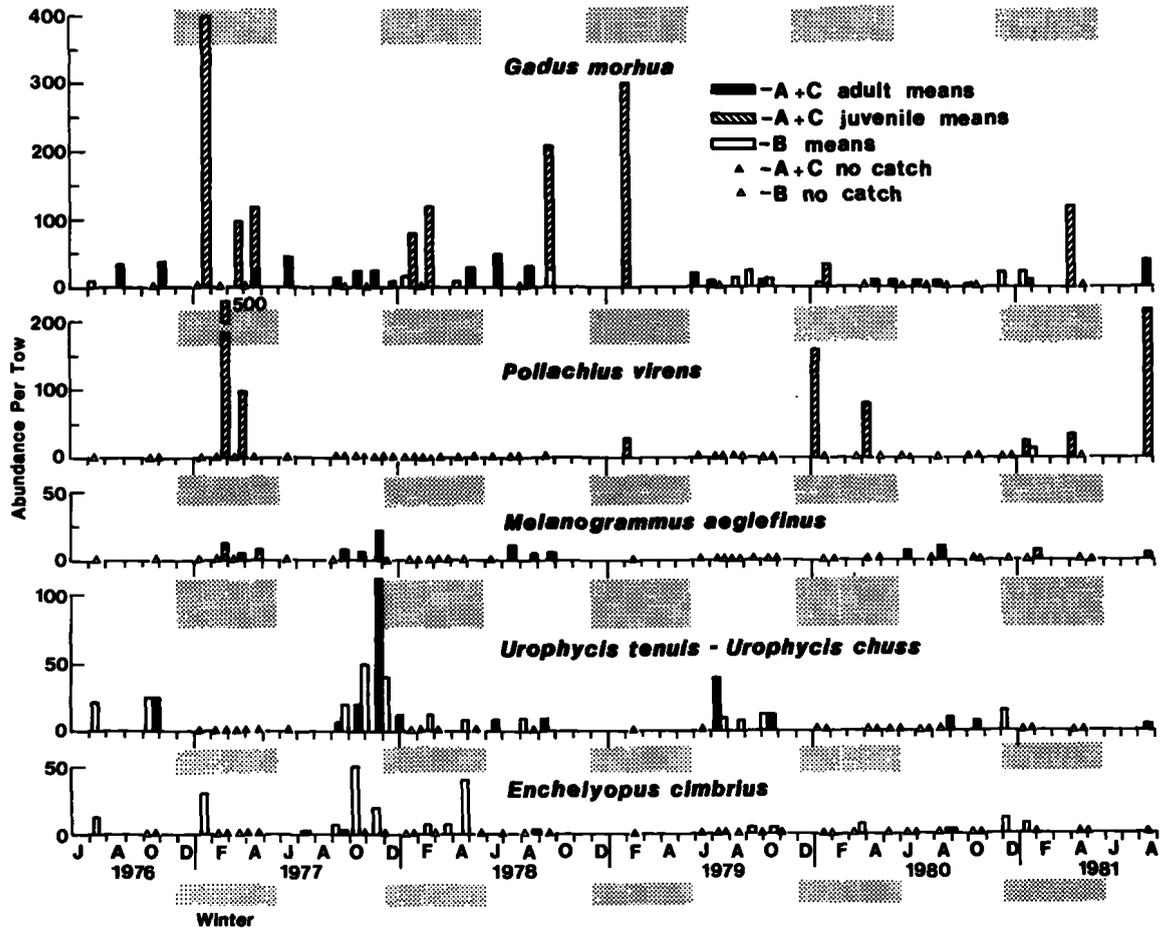


FIGURE 8.—Seasonal occurrence and abundance of gadoids at offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1976-81.

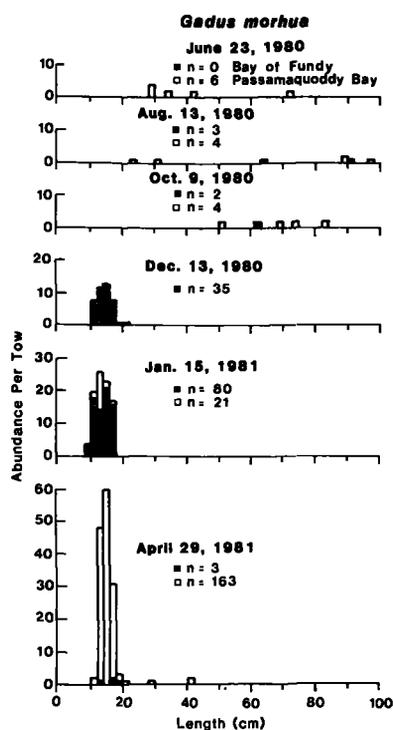


FIGURE 9.—Seasonal size distributions of *Gadus morhua* at station B in the Bay of Fundy and station A in Passamaquoddy Bay, 1980 and 1981.

young cod (0+, 1+, <17 cm) has been previously reported in the western North Atlantic (Schroeder 1930) but is not well documented. On the other hand, this occurrence of young cod in the North Sea is well known (Daan 1978). During winter, juvenile cod were abundant at station A or in colder winters at station B (Fig. 8, 1980 and 1981). Both juvenile and adult cod were more abundant at station A during our study than during 1965 (20-70/tow, Tyler (1971); 1976-81, 50-400/tow).

Haddock, *Melanogrammus aeglefinus*, were never abundant during our study. Adults were captured only at the hard-bottom station A during summer (Fig. 8) and juvenile haddock (1+) were occasionally captured at the same site in winter. Catches of haddock declined from a maximum of 25/tow to <5/tow during the study period (Fig. 8). However, up to 260 haddock/tow were caught at station A during 1965 (Tyler 1971). Decline in abundance after 1965 might be the cause for the collapse of the Gulf of Maine haddock stock in 1970 (Hare 1977; Clark et al. 1982).

Only juvenile pollock, *Pollachius virens*, were captured during the study. Pollock of the annual year class (0+) were either rare or extremely abundant at

beach sites (100+/seine haul) in a given year, depending perhaps, on the size of the annual year class. Pollock dominated beach catches during early summer but disappeared from this region by September (Fig. 5). In years when 0+ pollock were abundant along the beach in summer, members of the same year class were also abundant the following winter at station A (1976-77, 1981) and, in summers of low abundance on the beach, they were correspondingly rare offshore in winter (1977-78; Fig. 8). Large numbers of pollock larvae were present in the plankton during March 1979 (Scott 1980), and we again encountered large number of 0+ juveniles at station A in the winter of 1979-80. Present findings suggest there may have been three large year classes produced during our study period, 1976, 1979, and 1981.

Adult white, *Urophycis tenuis*, and red, *U. chuss*, hakes were common summer components at offshore stations A and B (Markle et al. 1982). Juvenile white hake (<15 cm) were a summer component at beach stations (Fig. 5), but were rarely captured thereafter and only then at offshore sites in winter. Also in 1965 few small hake were captured after December (Tyler 1971). Apparently hake leave Passamaquoddy Bay in winter (Markle et al. 1982). In the present study, the one time hake were observed during winter was at station B in the Bay of Fundy (Fig. 8).

The fourbeard rockling, *Enchelyopus cimbrius*, was a regular component at station B in the Bay of Fundy and occasional in summer at station A (Fig. 8). The mesh size of our gear was just small enough to capture large individuals of this species, and it was probably more abundant than indicated. Larval rockling were a rare summer component of inshore sites (Table 4). Battle (1930) and Tyler (1971) both considered rockling a summer occasional in Passamaquoddy Bay, occurring there during spawning migration. Tyler's catch rate at station A (2-3/tow) was similar to ours at that site. Larger catch rates at station B (10-50/tow) may be due to rocklings preference for soft-bottom habitat (Bigelow and Schroeder 1939).

Silver hake, *Merluccius bilinearis*, was often the most abundant gadoid found at offshore stations during summer, and juveniles were a regular component at station B year round (Fig. 10). Large numbers of adult silver hake were present during fall (Fig. 10) in company with other migratory summer occasionals, including American shad, *Alosa sapidissima*; spiny dogfish, *Squalus acanthias*; and butterflyfish, *Poronotus triacanthus*. All these fishes may carry out counterclockwise spring to fall migrations around the Bay of Fundy similar to the shad (Dadswell et al. 1983).

The Atlantic tomcod, *Microgadus tomcod*, was a regular component of the inshore assemblage and was particularly abundant at beach sites during early

summer (Fig. 5) and in estuaries in early winter (Table 3).

Clupeids and osmerids made up a major portion of

TABLE 4.—Catch of fishes at intertidal seining station 3 (Brandy Cove) during period May 1976–November 1977. Fish captured during three 5-min seine hauls (100 × 15 m) ([j] = juvenile; [l] = larvae).

Species	1976								1977								
	15/05	14/06	13/07	18/08	15/09	10/10	08/12		15/02	20/03	10/04	30/05	29/06	15/07	18/09	10/10	17/11
<i>Raja radiata</i> [l]	—	—	—	—	—	1	—		—	—	—	—	1	—	1	2	—
<i>R. erinacea</i> [l]	—	4	—	—	—	—	—		—	—	—	—	—	—	—	—	—
<i>Alosa pseudoharengus</i>	—	—	—	—	25	2	—		—	—	—	—	—	4	—	—	—
<i>Clupea harengus</i>	—	—	2	2	—	—	—		—	—	—	2	—	15	10	—	—
<i>Salmo salar</i> [j]	—	—	—	—	—	—	—		—	—	—	1	—	—	—	—	—
<i>Osmerus mordax</i>	3	—	—	11	—	5	1		—	—	4	—	—	3	—	6	4
<i>Fundulus heteroclitus</i>	—	—	—	—	—	—	5		3	1	—	—	—	—	—	—	1
<i>Gasterosteus aculeatus</i>	—	5	51	5	2	4	—		—	—	5	26	32	5	27	3	—
<i>G. wheatlandi</i>	—	—	1	—	—	—	—		—	—	—	—	—	3	1	—	—
<i>Enchelyopus cimbrius</i> [l]	—	—	—	2	1	—	—		—	—	—	—	—	—	3	—	—
<i>Gadus morhua</i> [j]	—	—	—	1	—	—	—		—	—	—	—	—	—	—	—	—
<i>Microgadus tomcod</i>	1	2	3	—	—	—	—		—	—	4	8	—	3	—	—	—
<i>Pollock virens</i> [j]	115	132	15	12	2	—	—		—	—	2	—	—	—	—	—	—
<i>Urophycis tenuis</i> [j]	—	1	2	—	—	—	—		—	—	—	3	6	11	—	—	—
<i>Scomber scombrus</i>	--- observed never captured ---																
<i>Pholis gunnellus</i>	—	1	2	—	—	3	1		1	—	4	—	2	3	1	2	—
<i>Cyclopterus lumpus</i>	—	1	—	—	—	2	—		—	—	—	—	1	2	—	—	—
<i>Myoxocephalus aeneus</i>	1	—	—	—	—	1	—		—	—	—	1	1	—	3	—	1
<i>M. scorpius</i> [j]	—	—	—	—	—	—	1		—	—	—	2	—	—	—	—	—
<i>M. octodecemspinosus</i> [j]	—	3	—	—	—	2	—		—	—	—	—	—	—	—	—	—
<i>Hemirhamphus americanus</i>	—	1	—	1	—	1	—		—	—	—	1	—	—	3	1	1
<i>Pseudopleuronectes americanus</i>	—	10	9	—	4	—	3		—	—	—	12	22	8	2	—	2
<i>Liopsetta putnami</i>	—	—	1	—	—	—	—		—	—	—	—	2	—	—	—	—
<i>Menidia menidia</i>	1	—	—	3	—	—	15		4	1	—	—	—	—	—	2	4

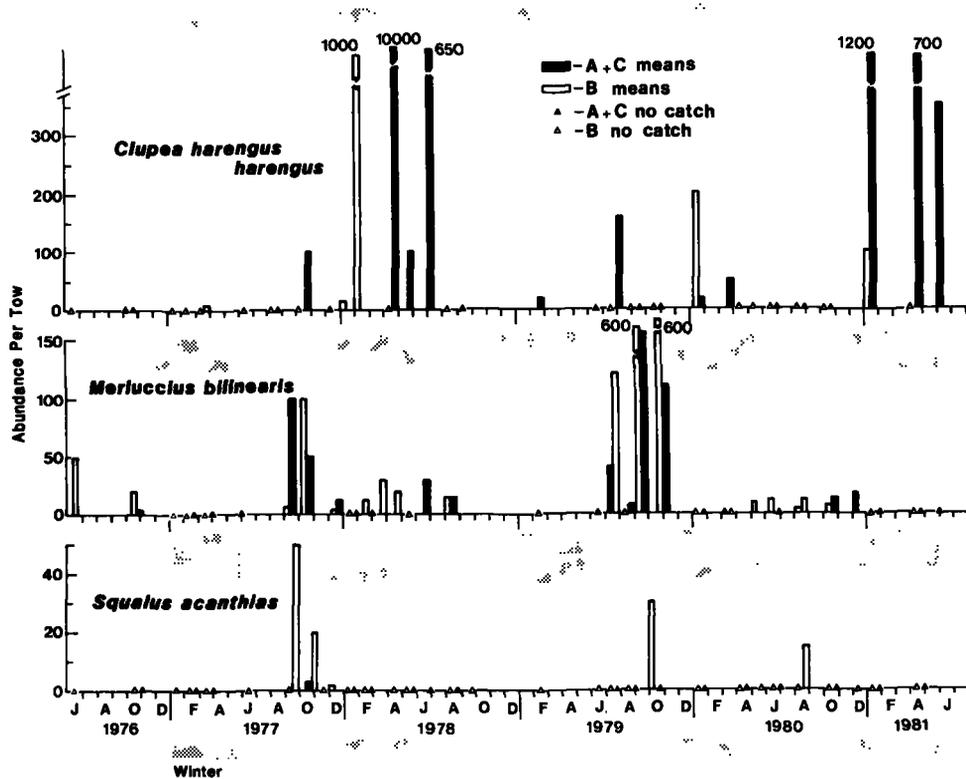


FIGURE 10.—Seasonal occurrence and abundance of pelagic fishes and dogfish at offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1976–81.

the fishes caught at inshore sites (Table 2). At beach station 8, alewives, *Alosa pseudoharengus*; Atlantic herring, *Clupea harengus harengus*; and American smelt, *Osmerus mordax*; appeared in mid-July and increased in abundance during August (Fig. 5). Herring were abundant in estuaries during summer and were replaced there by smelt in winter (Table 3). Large American smelt were present at offshore sites in Passamaquoddy Bay in mid-summer as observed by Tyler (1971). During most winters, juvenile Atlantic herring (10-20 cm) were abundant at offshore sites, particularly inside Passamaquoddy Bay at intermediate depths (station C; Fig. 10). Catches were variable, possibly because of schooling behavior (Brawn 1960). Tagging experiments indicate herring move from inshore during summer to deeper water in winter (McKenzie and Tibbo 1961).

Six species of sculpin (Table 2) were commonly encountered at offshore station of which two—longhorn sculpin, *Myoxocephalus octodecemspinosus*, and sea raven, *Hemitripteris americanus*—were abundant, regular components (Fig. 11). Juveniles of

most species were common at beach sites in summer (Table 4) and at station A in winter (Table 2). Increases in abundance of longhorn sculpins at station B during winter were observed (Fig. 11) and may be the result of migration out of Passamaquoddy Bay. Two small species, Arctic hookear sculpin, *Arctediellus uncinatus*, and mailed sculpin, *Triglops murrayi*, were winter occasional at station A. They were perhaps more abundant than catch rates indicated (2-5/tow) because their maximum size range was at the lower limit of catchability for our trawl.

The blennioid-like fishes were represented by seven species (Tables 2, 3) of which ocean pout, *Macrozoarces americanus*, was regular at offshore stations in Passamaquoddy Bay (Fig. 11), and rock gunnel, *Pholis gunnellus*, was a regular component at beach sites (Table 4). Ocean pout abundance in Passamaquoddy Bay was generally highest in early summer and declined thereafter (Tyler 1971; Fig. 11). Abundance of ocean pout usually increased at station B in late summer and fall, suggesting movement from Passamaquoddy Bay to the Bay of Fundy.

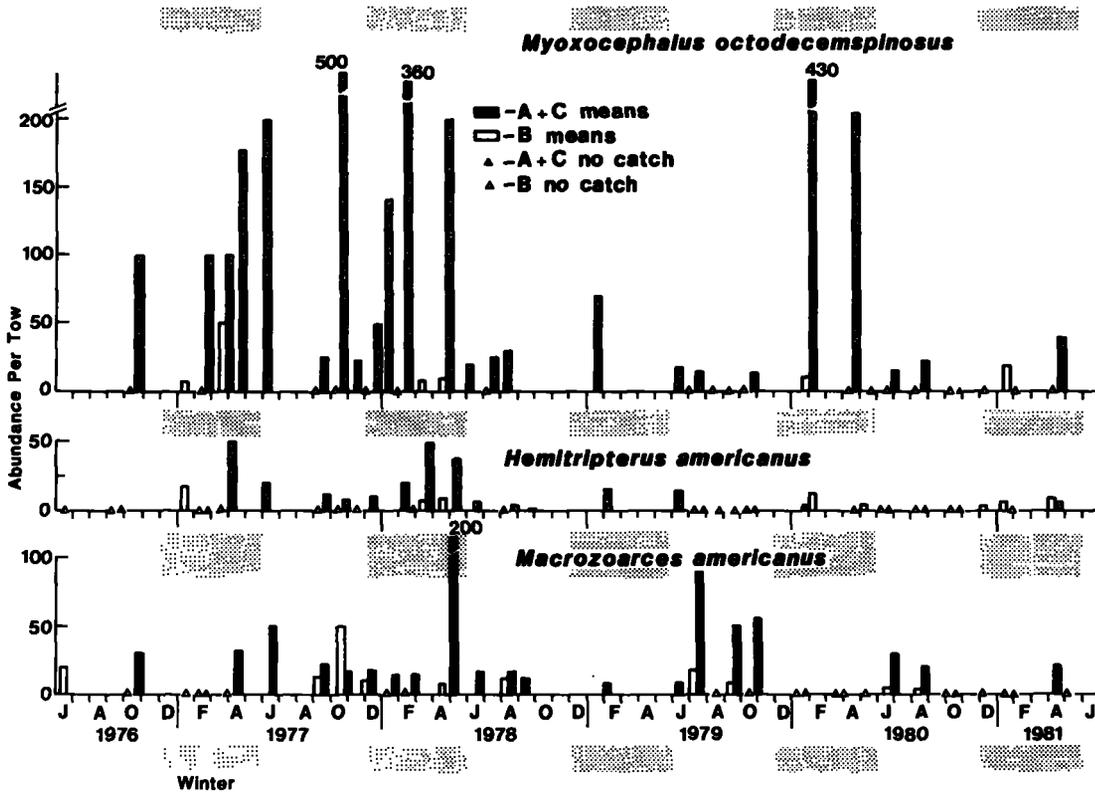


FIGURE 11.—Seasonal occurrence and abundance of sculpins and ocean pout at offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1976-81.

It may be a response to avoid warm temperatures (Olsen and Merriman 1946). Movement of ocean pout is generally thought to cover only short distances (Orach-Maza 1975; Sheehy et al. 1977).

Other blennioids occurred infrequently at station A (Table 2). Selectivity of our shrimp trawl may have been a factor in these low catches. One species, radiated shanny, *Ulvaria subbifurcata*, which was thought to be rare in Passamaquoddy Bay (Leim and Scott 1966), was often captured (5/tow) at station A during winter. Scuba searches during summer revealed radiated shanny were abundant inshore, under rocks in 6-9 m of water (Dadswell and Melvin, pers. obs.).

Five species of skate were captured during the study (Table 2): Two species, thorny skate, *Raja radiata*, and smooth skate, *R. senta*, were common, regular components of the offshore site in the Bay of Fundy; two little skate, *R. erinacea*, and winter skate, *R. ocellata*, were regular components of station A in Passamaquoddy Bay; and one species, the barndoor skate, *R. laevis*, was encountered occasionally at station B. The species cooccurrences of skates and their habitat selection are as described by McEachran and Musick (1975). Some seasonal movement into Passamaquoddy Bay was exhibited. Abundance of smooth and thorny skates at station A increased during summer and declined after late fall. Juveniles of thorny, little, and winter skates were often captured at beach sites during summer (Table 3).

Several smaller fishes were captured at inshore sites only, but again this may be an artifact of sampling gear. Threespine stickleback, *Gasterosteus aculeatus*, was a regular component at most beach sites (Table 4). Other sticklebacks were more or less confined to estuarine areas (Table 3). Mummichog, *Fundulus heteroclitus*, and Atlantic silversides, *Menidia menidia*, occurred mainly in estuaries during summer but were part of the winter community at beach sites (Table 4).

Assemblages and Diversity

Species assemblages in the study area varied according to site and season. If juveniles and adults of some dominant species are considered as separate taxonomic units (Table 2), calculated coefficients of community show similarity between similar habitat types (e.g., soft bottom) at a given season, and between the summer assemblage of one habitat and the winter assemblage of the next seaward habitat (Table 5). In general, movement of assemblages was from inshore in summer to offshore in winter with some return movement in spring (Fig. 12). Some species, however, exhibited a partial reverse of this pattern (Atlantic tomcod, ocean pout).

Specific groupings of fish were segregated among the available habitats according to season. The "estuarine" assemblage was dominated by warmwater, euryhaline species, including sticklebacks, Atlantic silversides, mummichogs, and juvenile clupeids. Most of this group moved to adjacent, inshore marine habitat in winter (Tables 3, 4), but Atlantic tomcod and American smelt moved in the reverse direction to form a winter estuarine group (Table 3).

The summer "beach" assemblage consisted of regulars such as threespine stickleback and rock gunnel and a summer component including juvenile gadids, juvenile sculpins, flounders, and juvenile alosids. Juvenile gadids (pollock, white hake, and Atlantic tomcod) were most abundant in early summer but were replaced by steadily increasing numbers of clupeids in late summer (Fig. 5). Numerous other postlarval and juvenile fishes, including four-beard rockling and lumpfish, *Cyclopterus lumpus*, appeared in the beach zone during the summer (Table 3). In late fall, most of this assemblage left the beaches and occupied offshore sites in Passamaquoddy Bay. Atlantic herring concentrated at the soft-bottom station C and the gadids, sculpins, and winter flounder (juveniles) at the hard-bottom station A. Threespine stickleback and rock gunnel

TABLE 5.—Coefficients of community among seasonal fish assemblages in the lower Bay of Fundy.

	Seaward									
	Estuarine winter	Estuarine summer	Beach winter	Beach summer	C winter	C summer	A winter	A summer	B winter	B summer
Estuarine winter	—	10.0	20.0	7.0	0.0	12.5	0.0	2.0	0.0	0.0
Estuarine summer	—	—	50.0	12.5	20.0	0.0	0.0	0.0	0.0	0.0
Beach winter	—	—	—	6.6	14.3	3.8	4.2	0.0	0.0	0.0
Beach summer	—	—	—	—	6.6	33.3	36.1	17.3	21.2	0.0
C winter	—	—	—	—	—	12.5	4.2	5.7	6.6	0.0
C summer	—	—	—	—	—	—	4.8	40.0	40.0	47.0
A winter	—	—	—	—	—	—	—	20.9	43.0	26.3
A summer	—	—	—	—	—	—	—	—	36.4	42.8
B winter	—	—	—	—	—	—	—	—	—	25.8

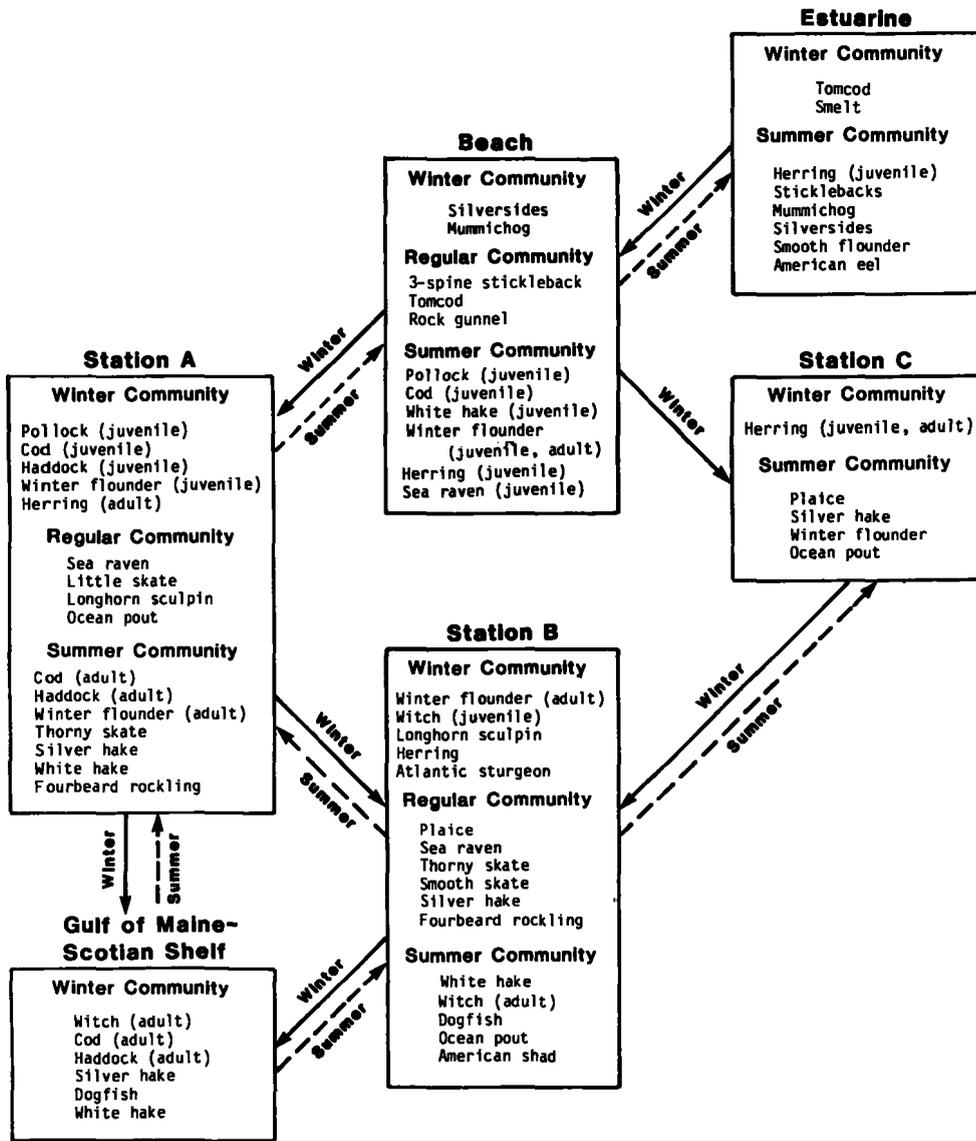


FIGURE 12.—Communities of fishes occurring at each site divided into summer component (SC), winter component (WC), and regular component (RC). Arrows indicate direction of seasonal movement.

remained at beach sites over winter and were joined by Atlantic silversides and mummichog to form a winter assemblage (Table 4).

During summer an "offshore, hard-bottom" assemblage consisting of adult gadids (Atlantic cod, haddock, white and red hake), adult flounders (winter yellowtail), ocean pout, adult sculpins, and skates assembled inside Passamaquoddy Bay. Sea raven, longhorn sculpin, ocean pout, and little skate remained at this site over winter and were joined by juvenile fishes from the beach zone. The other

species apparently move to offshore sites in the Bay of Fundy and/or to the Scotian Shelf (McCracken 1959; Wise 1962; Edwards 1965; Kulka and Stobo 1981).

The "offshore, soft-bottom" assemblage consisted of American plaice, witch flounder, white hake, fourbeard rockling, and skates as described by Bigelow and Schroeder (1939). This group at station B was the most stable assemblage studied and had the largest regular component. Conversely, similar assemblages which occurred at the shallower, soft-

bottom station C were the most seasonally dynamic (Fig. 12). Adult witch flounder and most hakes left station B in winter for grounds further offshore in the Gulf of Maine (Powles and Kohler 1970; Kulka and Stobo 1981), and this site was occupied by adult winter flounder and longhorn sculpin, perhaps from inside Passamaquoddy Bay or other adjacent inshore sites (McCracken 1963).

Superimposed on the two offshore, essentially benthic fish assemblages was a seasonal semipelagic component. In summer, silver hake was the numerically dominant species. During fall, diversity increased with the arrival of spiny dogfish, butterfish, and American shad. In winter, Atlantic herring numerically dominated the pelagic component at all offshore sites (Fig. 12).

Diversity, expressed simply as number of species captured, varied appreciably at beach sites during the year. Diversity was 2-5 species in winter-spring, 9-13 species in summer, and 4-6 species in fall-winter (Fig. 13). Total number of species captured at inshore sites was 35, compared with 51 species captured at offshore sites.

Diversity of assemblages at deep offshore sites (80+ m) was more stable on an annual basis because of the seasonal influx and departure of species from and to adjacent habitats (Fig. 14). Species number varied between 7 and 17 fishes at station B and 7 and

20 fishes at station A, fluctuating about a mean of 12/sampling trip. During 1965, Tyler (1971) observed a higher mean diversity of 17 species/trip at station A with a maximum occurrence of 24. The difference between his observations and ours may be accounted for partially by the decline in haddock abundance

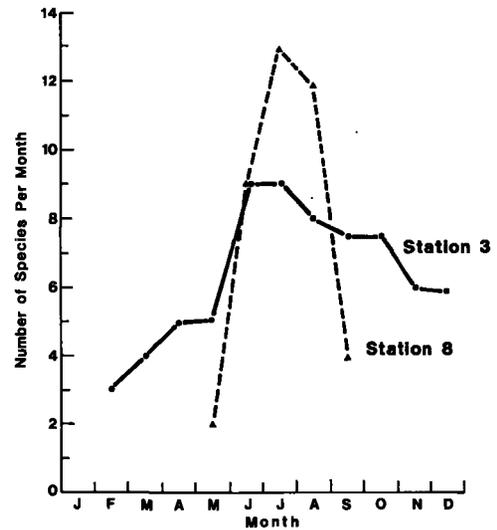


FIGURE 13.—Monthly diversity of fishes at intertidal stations 3 and 8 in Passamaquoddy Bay. Species/month for station 3 is mean of 1976 and 1977 samples.

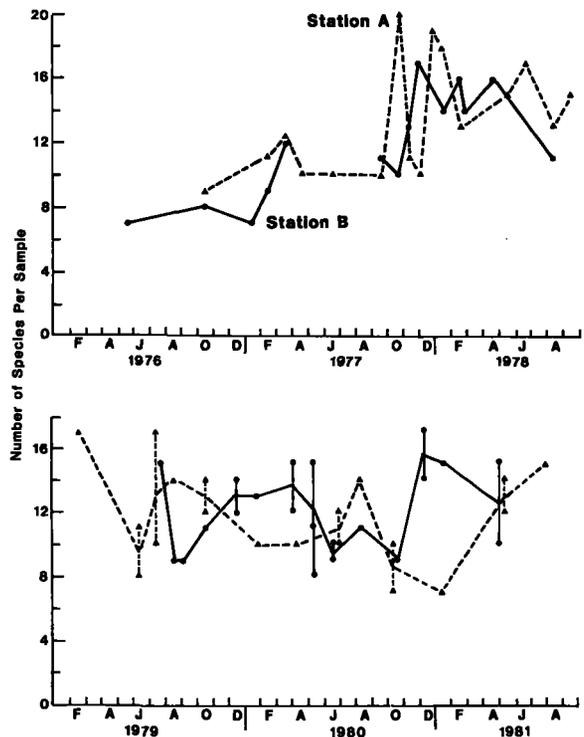


FIGURE 14.—Seasonal diversity of fishes at station A (Passamaquoddy Bay) and station B (Bay of Fundy). Vertical bars represent the range among replicated collections.

since 1965 and the recent absence of American plaice from this site, and partially by his use of a 0.6 cm cod end liner, which would have retained small, occasional species more often than our 2.5 cm cod end.

Highest diversities occurred during winter at station B and during summer at station A (Fig. 14) as a result of seasonal exchange between these sites and the arrival of periodics. The highest diversities recorded during the study period occurred at station A during the fall, coinciding with maximum annual temperatures (Fig. 2). Diversity at station C, the mid-depth site, decreased from 13 species in May 1978 to 4 species in May 1980, perhaps in response to a general decline in lower Bay of Fundy temperatures during the study period (Fig. 3).

GENERAL DISCUSSION

Most authors have related the occurrence and distribution of adult benthic fishes in the North Atlantic to substrate type and temperature (Edwards 1965; Colton 1972; McEachran and Musick 1975; Scott 1976) and have shown that there is a marked seasonal variation (Lux and Nichy 1971; Jeffries and Johnson 1974). Our findings agree and suggest yearly differences at the same site for a given time may be influenced mainly by annual ocean climate perturbation. Species occurrence and abundance appeared to change in response to seemingly small changes in temperature. Jeffries and Johnson (1974) reported a similar observation concerning winter flounder abundance over a 7-yr period in Narragansett Bay. Pelagic and semipelagic species (Atlantic herring, silver hake) demonstrated little or no substrate preference. Occurrence was apparently related to annual migratory behavior.

Seasonal movements of the various species was largely from an inshore, shallow-water locality in summer to an offshore, deepwater locality in winter with a reverse movement occurring in spring. Cause of this movement may have a large physiological component related to temperature effects on the osmoregulation of marine fishes (Potts and Parry 1964). In the southern part of their range, fish such as winter flounder migrate onshore in winter (Bigelow and Schroeder 1953) in response to availability of preferred temperature but never encounter the low temperatures found at northern latitudes. Atlantic tomcod, a species known to produce an antifreeze in its blood (Fletcher et al. 1982), was one of the few fishes exhibiting onshore migration to lower salinities during winter in this area. For many species (pollock, Atlantic herring, white hake), migration

from inshore habitat to offshore is unidirectional for the individual, since each year the beach community consists of the new 0+ year class. For other species (winter flounder, juvenile sculpins, radiated shanny), the return inshore is an annual occurrence, triggered perhaps as much by resource availability and predator avoidance as by physiology.

Tyler (1971) concluded that in Passamaquoddy Bay movements of large fish independent of the small individuals of a species were not evident for fishes other than hake, but we found obvious differences in size-class distributions and abundance between summer and winter populations of winter flounder, witch flounder, Atlantic cod, and pollock at offshore sites and a complete lack of most fish inshore. This suggests marked segregation between juveniles (at least 0+ age group) and adults for these species. The use of shallow water habitat as nursery area by fishes of commercial importance in the Canadian North Atlantic has received little attention. In Europe, this fact has been amply demonstrated for many fish species, including Atlantic cod and pollock (Zijlstra 1972; Daan 1978; Burd 1978; Rauck and Zijlstra 1978). The use of beach habitat as nursery by these fishes makes them susceptible to coastal pollution impacts and puts their adult fisheries at risk to coastal degradation and development.

Decline in haddock abundance in Passamaquoddy Bay since 1965 coincides with increased numbers of Atlantic cod. However, previous studies indicate little interaction between these two species (Tyler 1972; Jones 1978). Catches in 1965 (Tyler 1971) coincided with the largest haddock abundance on record (Clark et al. 1981). Fishermen in Passamaquoddy Bay may only catch haddock consistently during years preceded by large recruitment on Georges Bank, the Scotian Shelf, and the Gulf of Maine.

In the Bay of Fundy region, fish assemblages are segregated according to habitat and, although fish movement is influenced by seasonal climatic regime, assemblages appear cohesive through time. In summer, fishes assembled and exploited the available resources as members of 1) estuarine, 2) beach, 3) offshore, hard-bottom, 4) offshore, soft-bottom, and 5) migratory-pelagic assemblages. With winter, movement of species and/or age groups resulted in different seasonal assemblages in each habitat, but major groupings remained essentially intact and replaced each other seaward. The reverse movement occurred in spring. A large portion of benthic and pelagic components occurring at the offshore, hard-bottom habitat were migratory. In contrast, the offshore, soft-bottom assemblage was more sedentary. Smaller seasonal variation in the water tem-

perature at the Bay of Fundy, soft-bottom site, and the greater seasonal stability of invertebrate food resource production in this type of habitat (Wildish and Dadswell in press) may also be important. The dynamic nature of the hard-bottom community, particularly among commercially valuable species, emphasizes the need for well-designed, seasonal sampling programs in order to properly assess the occurrence of species and abundance of fish stocks in a local area. Long-term changes are apparent from annual assessment data (Brown et al. 1973), but higher resolution surveys at "type" localities are needed to properly determine causative factors, whether physical or biological.

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