Seasonal distribution of river herring *Alosa pseudoharengus* and *A. aestivalis* off the Atlantic coast of Nova Scotia

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Abstract.–The seasonal distribution and relative abundance of river herring *Alosa pseudoharengus* and *A. aestivalis* off Nova Scotia is examined using Canadian Department of Fisheries and Oceans data from bottom-trawl surveys (1970–89) and the International Observer Program (1980–89). River herring occurred throughout the year in regions characterized by strong tidal mixing and upwelling in the Bay of Fundy and off southwestern Nova Scotia. During spring, river herring were most abundant in the warmer, deeper waters of the central Scotian Shelf, particularly between Emerald and Western Banks, and in areas of warm slope water intrusion along the Scotian Slope, the western and southern edges of Georges Bank, and in the eastern Gulf of Maine–Bay of Fundy. Most catches occurred at bottom temperatures of 7–11°C offshore at mid-depths in spring (101–183 m), in shallower nearshore waters in summer (46–82 m) and in deeper offshore waters in fall (119–192 m). Diel variation in catch occurred during summer and fall but not during spring, with largest catches during daylight. Seasonal distribution patterns of small (<19 cm FL) and large (>19 cm FL) river herring overlapped geographically. Small fish preferred shallow regions (<93 m) during spring and fall, while large fish occurred in deeper areas (>93 m) during all seasons. The temporal and spatial distribution of river herring off the coast of Nova Scotia is likely influenced by zooplankton concentrations and occurrence of bottom temperatures >5°C. The pattern of seasonal movement is generally inshore and northward during spring, and offshore and southward in the fall.

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River herring (a collective term for the alewife *Alosa pseudoharengus* and the blueback herring *A. aestivalis*) are anadromous clupeids native to the Atlantic coast of North America. These closely-related species are remarkably similar in morphology and life history and differ only slightly in terms of meristics, morphometrics, growth parameters and time of spawning (Bigelow and Schroeder 1953, Leim and Scott 1966, Messieh 1977, Loesch 1987). Alewives and blueback herring are sympatric; alewife range from Newfoundland to North Carolina, and blueback herring from the Gulf of St. Lawrence to Florida (Bigelow and Schroeder 1953). They are fished commercially in the Maritime provinces of Canada and Atlantic coastal United States during their spring spawning migrations and are often marketed together as alewife, gaspereau, or river herring, depending on local convention.

Both species often co-occur in freshwater (Loesch et al. 1982, Jessop and Anderson 1989), estuarine (Stone and Daborn 1987), and marine (Neves 1981) habitats. While the freshwater life histories of alewives and blueback herring have been well documented (reviewed by Loesch 1987), less information is available on their distribution and movements at sea, particularly in Canadian coastal areas. Off the Atlantic coast of Nova Scotia, bottom trawls have caught river herring on the western Scotian Shelf, with alewives collected during spring and fall (Vladykov 1936, Neves 1981, Vinogradov 1984) and blueback herring in spring and summer (Netzel and Stanek 1966, Neves 1981). In the inner Bay of Fundy, river herring aggregate during summer in the turbid estuarine waters of Minas Basin (Rulifson 1984, Stone and Daborn 1987) and Cumberland Basin (Dadswell et al. 1984). In the outer Bay of Fundy, alewives and blueback herring have been captured during summer and autumn in herring weirs, purse seines (Jessop 1986), and during bottom-trawl surveys (Neves 1981). Neves (1981) examined the marine distribution and seasonal movements of river herring along the continental shelf from Cape Hatteras, North Carolina, to southwestern Nova Scotia. In this paper, we describe the seasonal marine distribution and relative abundance of river herring off Nova Scotia based on 20 years of combined alewife and blueback herring catch data from Canadian research vessel surveys, thereby extending northward the analysis by Neves (1981) of their distribution off the Atlantic coast of the United States. Offshore distributions are interpreted in relation to water depth and temperature within the survey area.

Although marine exploitation of alewives and blueback herring in the Maritime provinces by incidental

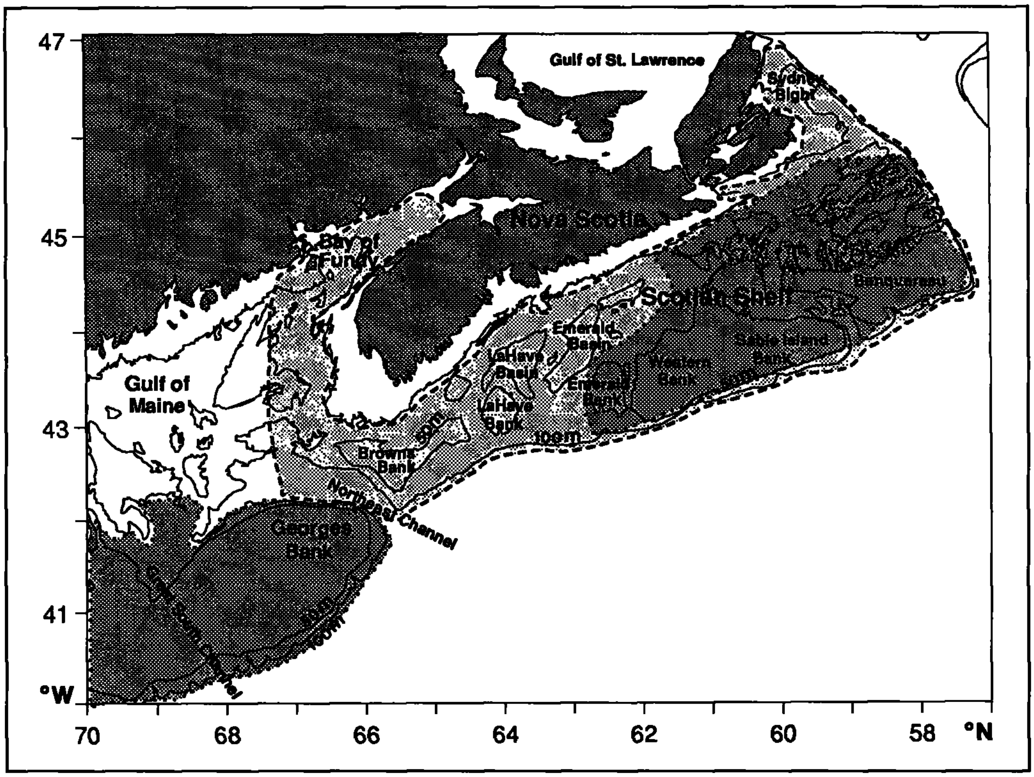

Figure 1
Topographical map of Canadian groundfish survey areas (1970–89) and geographic features mentioned in text. Spring (1979–85), summer (1970–89), and fall (1978–84) survey coverage of the Scotian Shelf and Bay of Fundy (- - -) is shaded light-gray. Spring (1986–89) survey coverage of the eastern shelf and Georges Bank (. . .) is shaded dark-gray. Offshore banks are delineated by the 100 m depth contour; basins and the outer edge of the continental shelf are delineated by the 200 m depth contour.

catches in offshore bottom-trawl fisheries from 1984 to 1989 has averaged 1,400t, which is <17% of the freshwater exploitation (Statistics Branch, Dep. Fish. Oceans, P.O. Box 550, Halifax, Nova Scotia B3J 2S7), only a limited amount of information on marine distribution is available from commercial fishing operations. More comprehensive information comes from the bycatch of the annual bottom trawl surveys of the Scotian Shelf–Bay of Fundy region conducted by the Canadian Department of Fisheries and Oceans (DFO) to monitor temporal changes in the abundance of commercially exploited groundfish species and associated environmental conditions (Halliday and Koeller 1981). Additional information on river herring distribution was obtained from 10 years of bycatch data from foreign and domestic fishing operations compiled by the DFO International Observer Program.

Description of survey area

The survey area, which includes the Scotian Shelf, eastern Gulf of Maine, Bay of Fundy, and, recently, Georges Bank, is topographically and hydrographically complex (Fig. 1). The oceanographic and biological characteristics of this area influence the distribution of other species (Sinclair 1988) and are assumed to do so for river herring.

The Scotian Shelf is characterized by deep central basins (>200 m) and shallow offshore banks (<50 m). Over the deeper parts of the shelf, three distinct vertical layers occur: a surface mixed layer with seasonal temperature changes, an intermediate layer with temperatures <5°C regardless of season, and a warm bottom layer derived from cross-shelf intrusions of slope water (Hatchey 1942, Smith et al. 1978). The coldest water at any depth occurs in the northeastern Shelf and the warmest in the bottom waters of the central Shelf (also termed the Scotian Gulf) where intrusion of warm slope water to adjacent Emerald and LaHave Basins is a persistent feature (McLellan 1954). Nutrient-rich upwellings along the shelf-slope interface sustain high levels of biological productivity (Fournier et al. 1977). Consequently, pelagic fish production on the shelf-slope is much higher than on the shelf (Mills and Fournier 1979).

The Bay of Fundy and eastern Gulf of Maine regions are vertically well mixed due to the action of strong tidal currents (Greenburg 1984). Strong, persistent summertime fronts in sea-surface temperature occur near the mouth of the Bay and off southwestern Nova Scotia (Loder and Greenburg 1985). The upwelling of nutrient-rich deep water from the Gulf of Maine and Scotian Shelf supports high biological productivity during spring and summer (Fournier et al. 1984). Secondary production in the outer Bay of Fundy occurs

Table 1

Summary of river herring (*Alosa* spp.) catch (in numbers) and effort for spring, summer, and fall groundfish surveys conducted off Nova Scotia by the Canadian Department of Fisheries and Oceans, 1970–89. Parentheses enclose percentages of total numbers of sets containing catch. SD = sample standard deviation.

Season	Year	No. of surveys	No. of sets	Catch-per-set $\bar{x}$	Catch-per-set SD	Total no. of fish	Sets with catch
Spring (Feb–Apr)	1979–89	11	1231	6.6	73.85	8117	268 (21.8)
Summer (June–July)	1970–89	20	1892	2.0	18.05	3703	214 (11.3)
Fall (Sept–Dec)	1978–84	7	982	1.6	9.47	1537	120 (12.3)
Total	1970–89	38	4105	3.3	42.53	13357	602 (14.7)

predominantly within the water column and provides forage to pelagic fish species (Emerson et al. 1986).

On Georges Bank, frontal regions generated by tidal mixing along the northern and southern edges are highly productive due to advection of nutrients from deeper waters on both sides of the bank (Cohen et al. 1982). Intrusions of warm, saline slope water occur into the southern Gulf of Maine through the Great South Channel (Mountain et al. 1989) and the Northeast Channel (Ramp and Wright 1979).

Materials and methods

Survey design and sampling

River herring catch and length-frequency data were obtained from 38 bottom-trawl surveys conducted between 1970 and 1989 (Table 1). The main study area (Scotian Shelf, eastern Gulf of Maine, and Bay of Fundy; Fig. 1) was surveyed at least once annually during this period. A single summer (June–July) survey was conducted annually between 1970 and 1977; spring (February–April), summer, and fall (September–December) surveys were made from 1978 to 1984; and spring and summer surveys from 1985 to 1989. Changing research requirements shifted spring survey effort to Georges Bank and the eastern Scotian Shelf in 1986, thereby excluding the western shelf region and the Bay of Fundy (Fig. 1). Recent (1987–89) summer surveys also included some coverage of northeastern Georges Bank.

All surveys used a stratified random design with trawl stations allocated to depth strata in proportion to stratum area and randomly positioned within strata. Stratum depth ranges were 0–92 m (0–50 fm), 93–183 m (51–100 fm), and 184–366 m (101–200 fm). Before 1981, summer cruises used a No. 36 Yankee bottom trawl with a 10 mm stretched-mesh liner in the cod end; all other cruises used a Western IIA trawl with a 10- or 20 mm stretched-mesh liner. Tows at each sampling station were for 30 minutes. Halliday and Koeller (1981) and Smith (1988) give further details of Canadian groundfish survey methods.

Total number and weight (kg) of river herring in the catch were recorded for each tow as was bottom-water temperature (°C), tow deployment time (Atlantic Standard Time), latitude, longitude, and bottom depth (m). Fork lengths (FL) were measured (to nearest cm) for all fish in catches of <250 fish; otherwise, catches were subsampled (no fixed procedure) for length. Alewife and blueback herring were not differentiated and sex was not determined.

Catches of river herring in Canadian surveys probably consist mainly of alewives since both species tend to be vertically separated by depth. Blueback herring frequent upper levels; alewives frequent mid-depths (Neves 1981) where they are more available to capture in bottom-trawl gear. All of the river herring catch from 1990 spring and summer groundfish surveys (n 1048) were confirmed by examination to be alewives. However, because river herring were not identified to species during the 1970–89 surveys, upon which our analysis is based, we cannot exclude the possibility that the catch included a small proportion of blueback herring captured incidentally when setting or hauling the gear.

Data analysis

Catch-per-set was standardized to a tow length of 1.75 nm with no adjustment for differences between gear types. Only cruises with catches of one or more fish were analyzed; 17 cruises on the eastern Scotian Shelf with no catches were omitted. River herring >33 cm FL were excluded from the data set (<0.5% of all fish measured), since they exceed the maximum fork lengths recorded for alewife and blueback herring (Loesch 1987) and are believed to be incorrectly identified American shad *Alosa sapidissima*.

Seasonal distributions of relative abundance were obtained from plots of average catch-per-set data (including zero catches) aggregated by 20-minute rectangles of latitude and longitude. Seasonal, rather than monthly, distributions gave a more complete picture of offshore distribution patterns. The locations of 2, 5, and 10°C isotherms, generated from plots of the mean bottom-water temperature in 20-minute rectangles, were superimposed on seasonal distribution plots. Differences in the seasonal distribution of two size-groups of river herring (i.e., ≤19 cm and >19 cm FL) were examined by plotting the capture locations of each group. The size-at-first-spawning of Saint John River blueback herring (Jessop et al. 1982), which mature at a smaller size than alewife, was used as the separation criterion.

Approximate randomization tests, with 1000 permutations (Edgington 1987) were used to examine the following relationships: (a) effects of season (spring, summer, fall) and depth (<93 m, 93–183 m, >183 m) on mean catch-per-set (including sets with no catches), (b) diel variability in seasonal catch-per-set (day and night, based on gear deployment times in relation to monthly morning and evening civil twilight times for the appropriate geographic location), and (c) mean fork length by season and depth. All comparisons used catch or fork-length data from a 6-year time-series (1979–84) in which annual sampling occurred during spring, summer, and fall. Each dependent comparison (i.e., depth effect within season, season effect within depth), used a Bonferroni significance level (α 0.05, divided by the number of dependent comparisons) (Day and Quinn 1989).

Randomization procedures were used for the analysis because statistically significant heteroscedasticity in the variances of (a) transformed (ln X + 1) catch per set data by season and depth (Cochran's C = 0.372, $P<0.0001$, df 239, 9), (b) transformed (ln X + 1) diel catch-per-set by season (Cochran's C = 0.365, $P<0.0001$, df 359, 6), and (c) fork length by season and depth (Cochran's C = 0.293, $P<0.0001$, df 637, 9) violates an assumption of parametric statistics. This violation is compounded by unequal sample sizes.

Bycatch data

Set locations and fork lengths of river herring bycatch in foreign and domestic commercial groundfish operations (1980–89) obtained from the DFO International Observer Program database were compared with research survey data. Catch locations were plotted for spring (February–May) and summer (June–August), when fishing effort and bycatch were highest. Fork length distributions were truncated at 33 cm due to assumed misclassification (4% of fish measured exceeded this length). Annual landings of alewife in metric tons (t) for the Scotian Shelf–Bay of Fundy region (4VWX) from 1970 to 1989 were obtained from Northwest Atlantic Fisheries Organization (NAFO) Statistical Bulletins and correlated (Spearman rank) with catch indices from research vessel surveys. The analysis was conducted to determine if survey indices (i.e., mean number and mean weight per set · season^{-1} · year^{-1}) were consistent with bycatch landings as an indicator of relative abundance.

Results

Seasonal distribution and abundance

A total of 13,357 river herring were captured in 602 (15%) of 4105 bottom-trawl sets conducted between 1970 and 1989 (Table 1). Spring survey catches were the highest and most variable, followed by summer. The proportion of sets with river herring from spring surveys was nearly double that from the other two seasons. A maximum catch of 2292 river herring occurred on 17 March 1980 in the Scotian Gulf region, south of Emerald Basin.

During spring surveys, river herring dominated in three regions: the Scotian Gulf, southern Gulf of Maine, and off southwestern Nova Scotia from the Northeast Channel north to the central Bay of Fundy (Fig. 2). Catches also occurred along the southern edge of Georges Bank and in the canyon between Banquereau and Sable Island Banks. Relative abundance was highest in the Scotian Gulf between Emerald and Western Banks, and on the southern slope of Georges Bank. Most catches of river herring occurred where bottom temperatures exceeded 5°C (Fig. 2), although in the Bay of Fundy, captures occurred at lower temperatures.

Summer distributions of river herring were less extensive than in spring and were limited mainly to the eastern Gulf of Maine (off southwestern Nova Scotia) and the Bay of Fundy, with a few occurrences nearshore in the central Shelf region (Fig. 2). Catches were highest along the northern shore of the Bay of Fundy, with very few fish captured in the Scotian Gulf and on the eastern Scotian Shelf. Bottom temperatures exceeded 5°C at all capture locations.

Fall distributions of river herring were more extensive than in summer (Fig. 2). Moderate to large catches were obtained from southwestern Nova Scotia to the Bay of Fundy, the central Scotian Shelf, and Sydney Bight. As in the case of spring and summer surveys, very few fish were captured on the eastern half of the Scotian Shelf. All catches occurred at bottom temperatures exceeding 5°C.

Bycatch of river herring from foreign fishing fleets (1980–89) occurred mainly during spring in a narrow

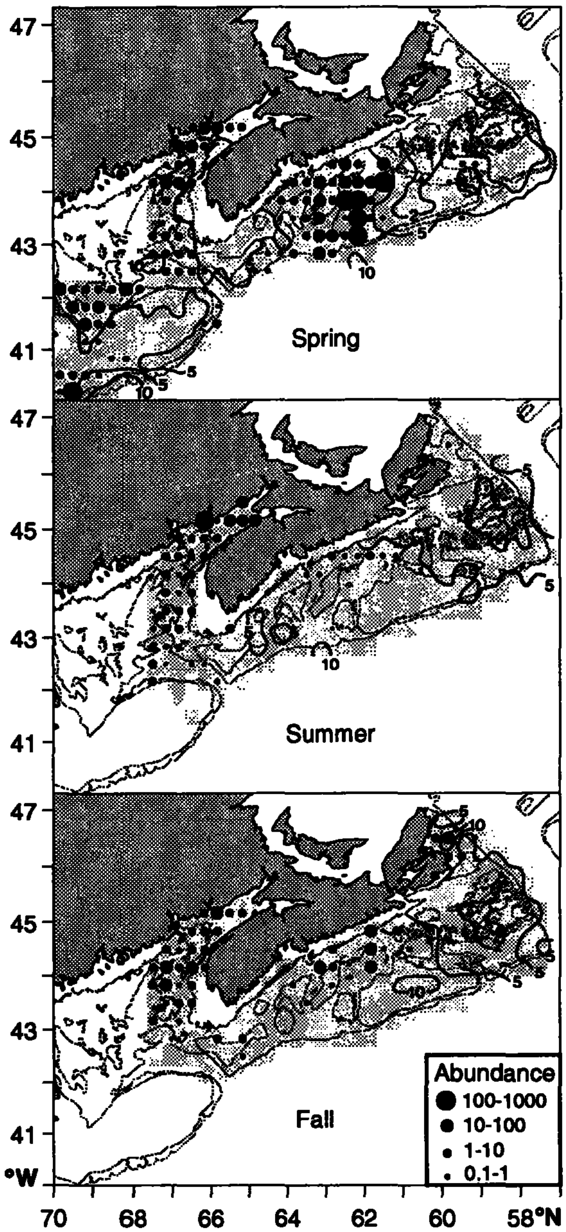

Figure 2
Distribution and relative abundance ($\bar{x}$ catch per 20-min square) of river herring from spring (1979–89), summer (1970–89), and fall (1978–84) groundfish surveys conducted off the Atlantic coast of Nova Scotia. Area sampled is indicated by shading, and mean catch (*n*/tow) for each 20-min square is represented by a solid circle, scaled to catch level. Isotherms for 2, 5, and 10°C of bottom temperature are also indicated.

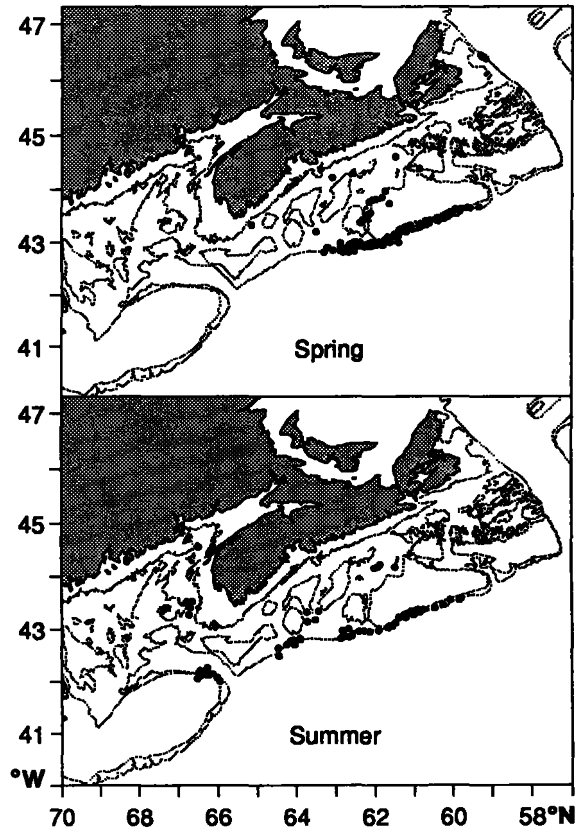

Figure 3
Spring and summer set locations of river herring bycatch from foreign and domestic fishing operations on the Scotian Shelf recorded by Canadian International Observers, 1980–89.

band along the edge of the Scotian Shelf from Emerald Bank east to Sable Island Bank (Fig. 3). This distribution reflects the location of the Soviet and Cuban silver hake fishery (M. Showell, Bedford Inst. Oceanogr., Dartmouth, N.S. B2Y 4A2, pers. commun., Jan. 1991) and indicates a more widespread occurrence of river herring along the shelf break than was apparent from bottom-trawl surveys. Bycatch from domestic fishing operations during spring occurred on the edge of Western and Emerald Banks and corresponds with catch locations from spring groundfish surveys.

Summer bycatch locations were similar to spring but extended further south and west along the shelf edge, with clusters of catches on the northern edge of Georges Bank, off southwestern Nova Scotia, and in the mouth of the Bay of Fundy (Fig. 3). River herring distribution along the shelf break, as indicated from spring and summer bycatches in the silver hake fishery, reflects the spatial distribution of that fishery. The number of summer observations from a reduced foreign fishing effort (*n* 86) was much less than spring (*n* 460). In both seasons, most bycatches occurred in

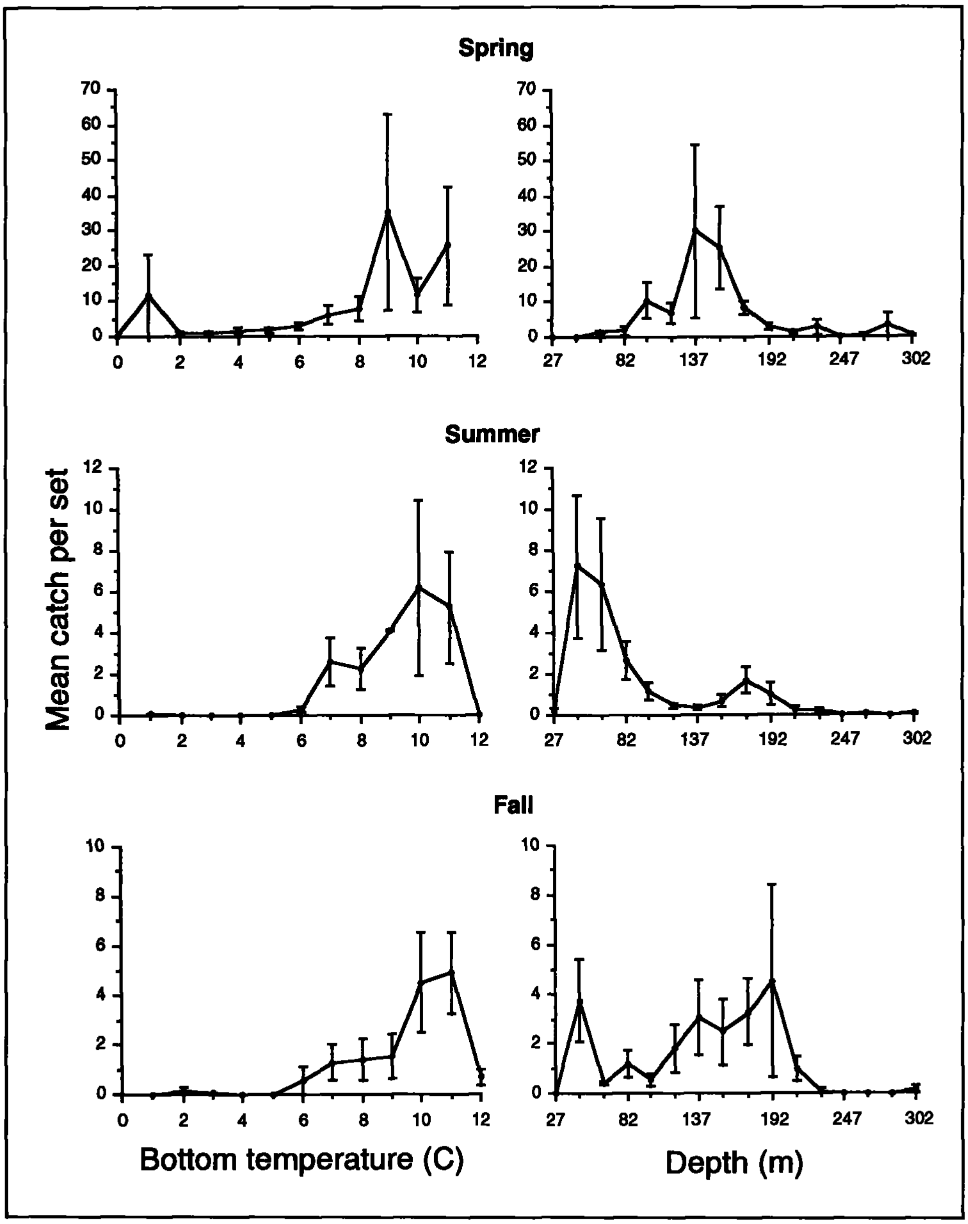

Figure 4
Mean catch-per-set of river herring within 1°C intervals of bottom temperature and 18.2 m (10 fm) depth intervals from spring, summer, and fall groundfish surveys, 1979–84, conducted off the Atlantic coast of Nova Scotia. Vertical bars represent ±1 SE. Sample sizes are ≥10 sets for each temperature and depth interval.

regions where bottom temperatures from groundfish surveys exceeded 5°C.

Temperature, depth, and diel effects on catch

The relationship between catch, bottom temperature, and depth was examined by plotting mean catch-per-set by season for intervals of 1°C and 18.3 m (10 fm) (Fig. 4). Despite much variability in the data, most catches occurred within the 7–11°C range regardless of season, with maximum catches within 9–11°C from spring through fall. An exception is the moderate catches at bottom temperatures <2°C during spring surveys in the Bay of Fundy (Figs. 2 and 4). The depth distribution of catches was more variable; spring catches occurred mainly at intermediate depths of 101–174 m, summer catches in shallow areas (46–82 m), and fall catches at mixed depths (i.e., 46 m, 119–192 m).

Mean catch-per-set of river herring for annual (1979–84) spring, summer, and fall surveys varied significantly by season and depth (Table 2, Fig. 5). Season effects within depth strata were significant for depths of <93 m and 93–183 m, but not for depths >183 m where all catches were low. Catches were highest within the <93 m strata during summer and within the 93–183 m depth strata during spring. Depth-within-season interaction was significant only during

Table 2

Summary of results from approximate randomization tests used to examine the following relationships: (a) effects of season and depth on mean catch-per-set, (b) diel variability in seasonal catch-per-set, and (c), mean fork length (FL) by season and depth. All comparisons used catch and fork-length data from Canadian groundfish surveys conducted 1979–84. Interaction effects with an asterisk are significant at the adjusted Bonferroni significance level of $P \leq 0.017$.

	Catch by season and depth		Catch by season and time		FL by season and depth	
Source	*n*	*P*	*n*	*P*	*n*	*P*
Main effects						
Season	2157	0.002	2157	0.006	5739	0.001
Depth	2157	0.010	—	—	5739	0.001
Time	—	—	2157	0.80	—	—
Interactions						
Season effect within depth						
<93 m	800	0.008*	—	—	1564	0.001*
93–183 m	836	0.001*	—	—	3769	0.001*
>183 m	521	0.027	—	—	406	0.001*
Depth effect within season						
spring	788	0.002*	—	—	3807	0.001*
summer	565	0.028	—	—	1114	0.001*
fall	804	0.060	—	—	818	0.001*
Season effect within time						
day	—	—	1231	0.228	—	—
night	—	—	926	0.033	—	—
Time effect within season						
spring	—	—	788	0.043	—	—
summer	—	—	565	0.001*	—	—
fall	—	—	804	0.017*	—	—

spring when the range in catches was greatest; summer and fall catches were similar at all depths (Table 2).

Mean catch-per-set of river herring varied significantly by season but not by time-period (Table 2, Fig. 6). Interactions of season effect within time-period were nonsignificant for day and night; interactions of time effect within season were significant for summer and fall but not for spring. For summer and fall surveys, catches from sets conducted during daylight were significantly higher than those conducted at night. While night catches from spring surveys tended to be higher than day catches (but not significantly so), they were extremely variable ($\bar{x}$ 13.4, sample SD 131.32). The proportion of sets with catch during day and night showed a seasonal pattern similar to that for mean catch, i.e., similar in spring (20% vs. 24%) and higher during the day in summer (15% vs. 5%) and fall (16% vs. 9%).

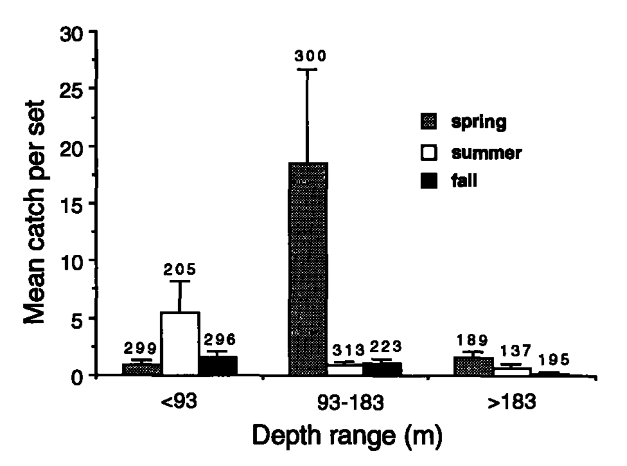

Figure 5

Mean catch-per-set of river herring by depth strata from spring, summer, and fall groundfish surveys, 1979–84, conducted off the Atlantic coast of Nova Scotia. Vertical bars represent +1 SE. Number of tows is indicated above error bars.

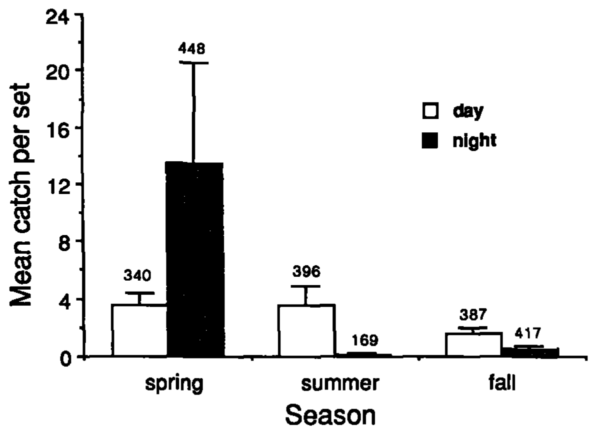

Figure 6
Mean catch-per-set of river herring in day and night collections from spring, summer, and fall groundfish surveys, 1979–84, conducted off the Atlantic coast of Nova Scotia. Vertical bars represent +1 SE. Number of tows is indicated above error bars.

Table 3
Spearman rank correlation coefficients for river herring (*Alosa* spp.) catch indices from spring (1979–89), summer (1970–89), and fall (1978–84) groundfish surveys vs. NAFO landings from the Scotian Shelf–Bay of Fundy (4VWX) and the central and eastern Scotian Shelf (4VW). (n = number of years; * significant at $P<0.05$; ** significant at $P<0.01$).

NAFO areas	Spring (n 11)	Summer (n 20)	Fall (n 7)
Mean catch/set · yr^{-1}			
4VWX	−0.23	−0.15	−0.07
4VW	0.60*	−0.01	−0.18
Mean weight/set · yr^{-1}			
4VWX	−0.19	−0.17	−0.29
4VW	0.74**	−0.05	−0.09

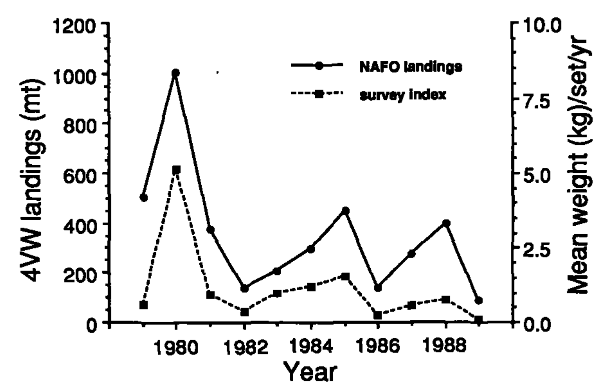

Figure 7
Annual landings in metric tons (t) reported to the Northwest Atlantic Fisheries Organization for the central and eastern Scotian Shelf (4VW), and spring survey catch index (kg/set · yr^{-1}) for 1979–89.

Survey catch indices and NAFO landings

Seasonal catch indices (annual mean number and weight of river herring per set) from research vessel surveys were uncorrelated with NAFO bycatch data for the Scotian Shelf–Bay of Fundy area (4VWX) (Table 3). However, landings from the central and eastern shelf (4VW) were significantly correlated with spring (1979–89) survey indices. The relationship between mean weight index and 4VW NAFO landings (Fig. 7) gave the highest Spearman rank correlation coefficient (r_s 0.74).

Seasonal length-composition and distribution

River herring from bottom-trawl collections measured 5–33 cm FL ($\bar{x}$ 23.7 cm; Table 4). Mean fork length in spring catches was less than in summer or fall. Fork lengths of river herring from foreign and domestic fisheries were 22–33 cm ($\bar{x}$ 29.6 cm) and were of comparable size in spring and summer sample collections. The larger size of bycatch fish compared with those from bottom-trawl surveys is probably due to the larger cod end mesh size (6 cm stretched) of commercial gear permitting escapement of smaller fish.

In all seasons, large river herring (>19 cm FL) were more abundant than small (≤19 cm) fish (Fig. 8). Polymodal length-frequency distributions indicated the

Table 4
River herring (*Alosa* spp.) fork-length statistics by season from groundfish surveys conducted by the Canadian Department of Fisheries and Oceans and from foreign and domestic bycatches recorded by Canadian International Observers. All fork lengths were truncated at 33 cm (see 'Materials and methods' for explanation). SD = sample standard deviation.

		Fork length (cm)			
Season	Years	n	$\bar{x}$	SD	range
Groundfish survey data					
Spring (Feb–Apr)	1979–89	7543	22.7	5.08	5.0–33.0
Summer (June–July)	1970–89	3167	25.4	3.77	9.0–33.0
Fall (Sept–Dec)	1978–84	1512	24.8	4.92	5.0–33.0
Combined	1970–89	12213	23.7	4.91	5.0–33.0
Bycatch data					
Spring (Feb–May)	1980–89	1754	29.4	2.14	20.0–33.0
Summer (June–Aug)	1980–89	249	30.4	1.45	26.0–33.0
Combined	1980–89	2032	29.6	2.13	20.0–33.0

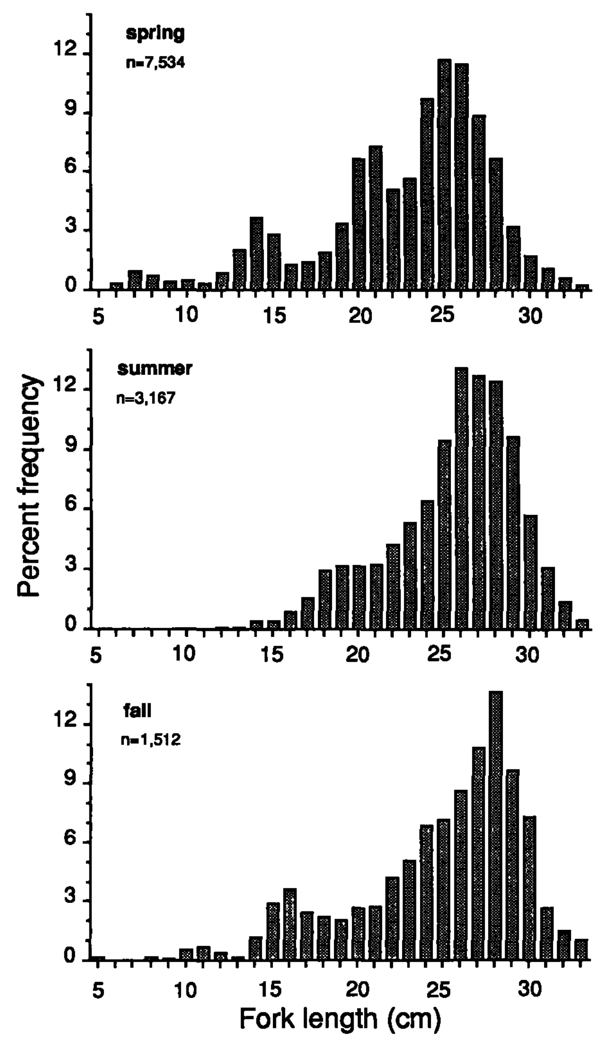

Figure 8

Length-frequency distributions of river herring from spring (1979–89), summer (1970–89), and fall (1978–84) groundfish surveys conducted off the Atlantic coast of Nova Scotia.

presence of at least three year-classes in the fall and four in the spring. Smaller individuals (≤19cmFL) represented a larger proportion of the overall length composition in spring and fall than in summer.

River herring >19cmFL were more densely and extensively distributed in all seasons than smaller fish. During summer and fall, most river herring ≤19cm long were captured within the Bay of Fundy, although a few occurred in the central Shelf region and in Sydney Bight (fall only) (Fig. 9). The greatest overlap in the spatial distribution of both size-groups was during spring, especially in offshore regions (i.e., central Scotian Shelf, southern Gulf of Maine).

The mean fork length of trawl-caught (1979–84) river herring varied significantly by season of capture and depth (Table 2, Fig. 10). Interactions of season effect within depth strata and depth effect within season were all significant. Smaller fish were caught more frequently at depths <93m during spring and fall. Larger fish occurred at all depths during summer (more numerously at <93m depth) and at depths ≥93m during spring and fall. In all three depth strata, river herring from spring surveys averaged smaller in length than those captured in summer and fall because of the greater occurrence of fish ≤19cm throughout the survey area during spring (Fig. 9).

Discussion

Canadian groundfish survey data indicate persistent patterns in the temporal and spatial distribution of river herring off the Atlantic coast of Nova Scotia which appear to be greatly influenced by oceanographic features. In spring, river herring were most abundant in the warmer, deeper waters of the Scotian Gulf, particularly along the edges of Emerald and Western Banks and within the channel separating them, and in regions of warm slope-water intrusion along the Scotian Slope, the western and southern edges of Georges Bank, and the eastern Gulf of Maine. In all seasons, river herring occurred in the Bay of Fundy and off southwestern Nova Scotia, regions characterized by strong tidal mixing and upwelling, but were rarely present on the eastern Scotian Shelf.

Water temperature evidently influences temporal and spatial patterns in river herring depth distribution. In all seasons, most catches occurred within the 7–11°C range but shifted from mid-depths offshore in spring (101–183m) to shallower, nearshore waters in summer (46–82m), and to deeper offshore waters in fall (119–192m). River herring were not present in colder regions on the eastern and western Scotian Shelf. Catches of river herring along the U.S. continental shelf were most frequent at bottom temperatures of 4–7°C and depths <92m (Neves 1981). Spring catches of river herring at bottom temperatures <5°C in the Bay of Fundy indicate some flexibility in thermal selection, as might be expected of a migratory anadromous fish. American shad, which are closely related to alewives and blueback herring, can remain for extended periods in temperatures outside their usual range (7–13°C) and migrate rapidly between areas with different temperature regimes (Dadswell et al. 1987).

Seasonal shifts in zooplankton abundance, which are influenced by local oceanographic features, may also influence river herring distribution patterns off Nova Scotia. Both alewives and blueback herring are zoo-

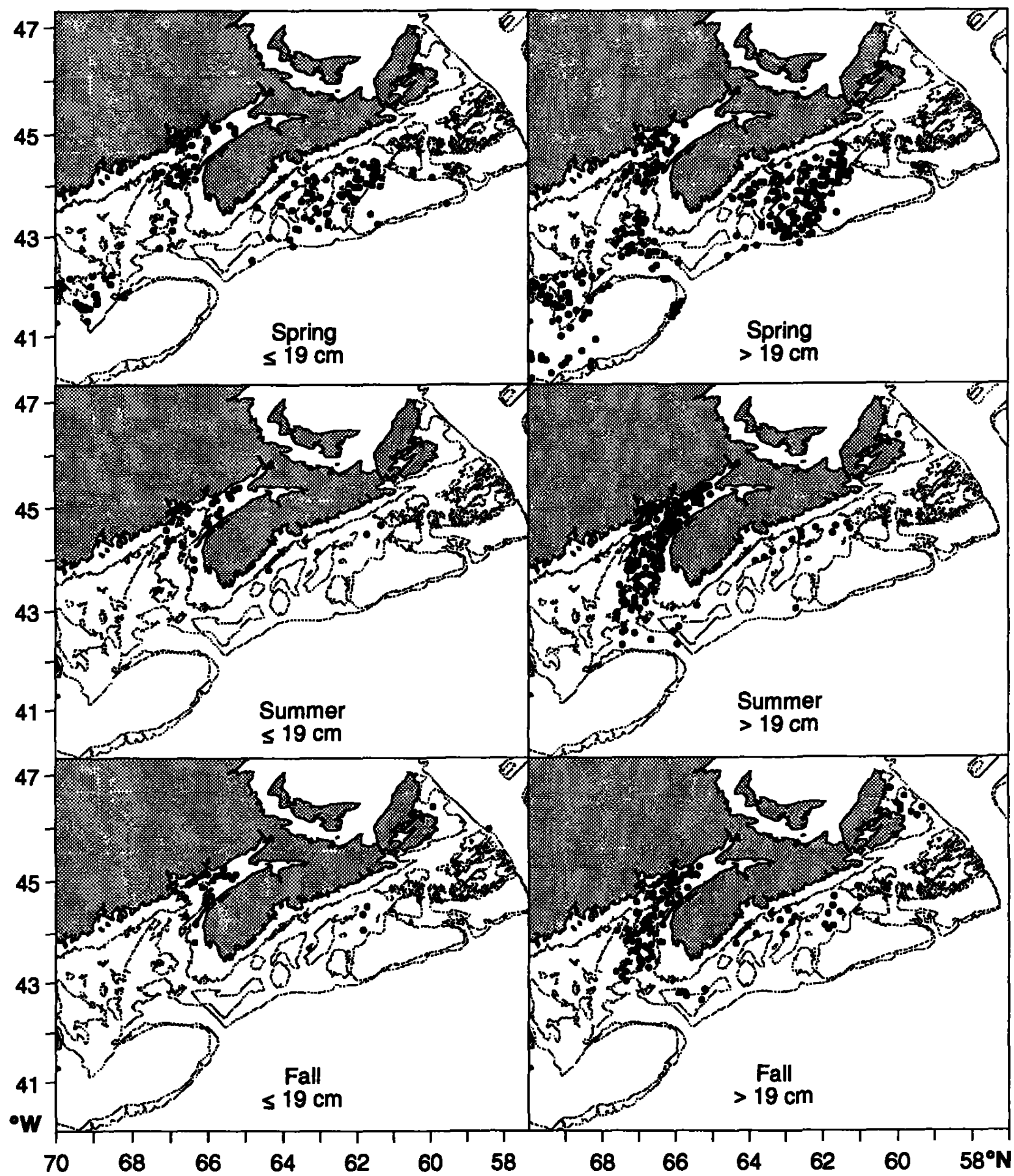

Figure 9

Set locations for catches of river herring ≤19 cm FL and >19 cm FL from spring (1979–89), summer (1970–89), and fall (1978–84) groundfish surveys conducted off the Atlantic coast of Nova Scotia.

planktivores. Stomach contents of river herring collected on Georges Bank and the Scotian Shelf consisted mainly of euphausiids and calanoid copepods (Vinogradov 1984). These prey items are concentrated during winter and spring in deep basins of the Scotian Shelf (Sameoto and Herman 1989, Herman et al. 1991) as well as the outer Shelf and Shelf Slope (Sameoto 1982). Calanoid copepods dominate zooplankton production on Georges Bank during spring (Sherman et al. 1987) and are abundant during summer and fall in the eastern Gulf of Maine–outer Bay of Fundy region (Emerson et al. 1986) along with large populations of euphausiids (Kulka et al. 1982). Aggregations of river herring during spring on the central Shelf, Shelf Slope, and Georges Bank, during summer in the Bay of Fundy–eastern Gulf of Maine, and during fall in the

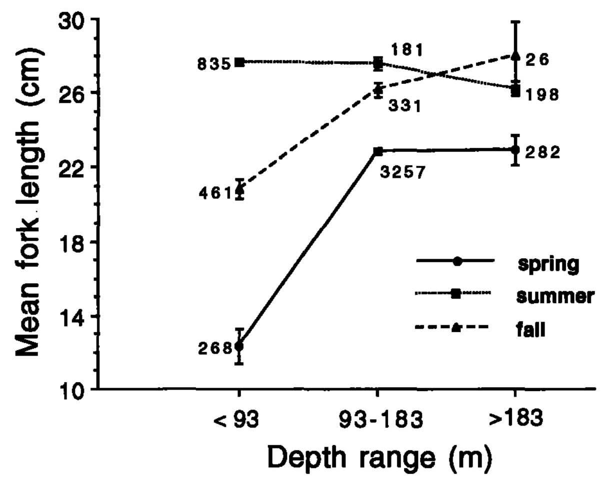

Figure 10
Mean fork length (cm) of river herring by depth strata from spring, summer, and fall groundfish surveys, 1979–84, conducted off the Atlantic coast of Nova Scotia. Vertical bars represent 95% CI. The number of fish in each category is adjacent to symbols.

outer Bay of Fundy and central Scotian Shelf coincide with high secondary productivity and an abundance of prey. River herring may move inshore in summer and offshore in winter in order to exploit seasonally available food resources.

The diurnal pattern of vertical migration by river herring accounts for the higher catches and proportion of sets with catches during daylight hours in summer and fall. Alewives and blueback herring that are closer to the bottom during the day are more susceptible to capture in bottom-trawling gear (Neves 1981, Loesch et al. 1982). Diel migrations, involving an upward movement at dusk followed by a downward movement at dawn, occur in landlocked adult alewives (Janssen and Brandt 1980), as well as anadromous juvenile (Jessop 1990) and adult river herring (Neves 1981). While spring catches did not follow this pattern, the presence of a cold (<5°C) intermediate water mass over warmer, deeper waters on the Scotian Shelf (Hatchey 1942), where the largest catches occurred, may have restricted the extent of vertical migration resulting in more captures at night. Our study indicates that few river herring are captured in areas where bottom temperatures are <5°C during spring; therefore, vertical migrations may be confined by a water temperature inversion.

Catch indices by number and weight from spring groundfish surveys (when relative abundance is greatest) both appear to be useful indicators of river herring bycatch in foreign and domestic trawl fisheries on the eastern and central shelf regions (4VW). Poor correlations, obtained when the Bay of Fundy–eastern Gulf of Maine bycatch landings (NAFO area 4X) were included in the analysis, were puzzling. Survey data indicate the presence of river herring in this area from spring through fall. Underreporting of river herring bycatches in domestic fishing operations (i.e., bottom trawl, gillnet, purse seine) may explain the poor correlations when landings from 4X and 4VW were combined. Catches from the central and eastern shelf region (4VW) are largely bycatches from the silver hake fishery. The frequent presence of DFO observers aboard these vessels may reduce the incidence of misreporting. Another possibility is the seasonal immigration of American-origin river herring into the Bay of Fundy–eastern Gulf of Maine region (Rulifson et al. 1987) which would increase the variability in the NAFO landings for area 4X.

The small proportion of fish ≤19 cm in summer collections, relative to spring and fall collections, may reflect their movement outside the survey area into coastal embayments and estuarine habitats in Maine and the inner Bay of Fundy. These areas serve as important summer feeding areas for river herring (Stone and Daborn 1987) and other anadromous fish species (Haedrich and Hall 1976). Summer resident river herring generally leave the inner Bay of Fundy in autumn when secondary production declines (Stone 1985).

Both large (>19 cm FL) and small (≤19 cm FL) river herring occurred nearshore from spring through fall, but were widely distributed offshore during spring (i.e., southern Gulf of Maine, Scotian Gulf). Most river herring ≤19 cm FL are sexually immature while those >19 cm FL are generally mature fish which have spawned previously or are maturing to spawn for the first time. Smaller, immature river herring evidently migrate offshore seasonally as do larger, mature fish. Size-related differences in depth distribution were such that small river herring occurred in shallow regions (<93 m) during spring and fall, while larger fish occurred in deeper areas (≥93 m) in all seasons. Janssen and Brandt (1980) reported that the nocturnal depth distribution of adult landlocked alewife differed by size-class, with the smaller fish at shallower depths.

Both Canadian and American marine survey data provide evidence of distinct seasonally and geographically separate aggregations of river herring. Off the Atlantic coast of the United States, the Middle Atlantic Bight is an important overwintering area for river herring, while in summer they concentrate further north in the Nantucket Shoals and on Georges Bank (Neves 1981). Aggregations of river herring in spring and fall on the central Scotian Shelf and in the eastern Gulf of Maine–Bay of Fundy suggest that these areas are important overwintering sites off Nova Scotia, although the Scotian Shelf has not been surveyed during winter months (i.e., November–February). The main summer concentration extends northward from southwestern Nova Scotia into the Bay of Fundy.

Other members of the clupeid family also exhibit spatial and temporal discontinuity in marine distribution patterns. American shad winter off Florida, the mid-Atlantic Bight, and in the Scotian Shelf–Bay of Fundy region (Neves and Depres 1979, Dadswell et al. 1987), while summer concentrations occur off Newfoundland and Labrador (Hare and Murphy 1974), the inner Gulf of St. Lawrence (Dadswell et al. 1987), the Gulf of Maine (Neves and Depres 1979), and in the inner Bay of Fundy (Dadswell et al. 1983). Atlantic herring populations in the Gulf of Maine–Scotian Shelf region have several geographically separate areas for summer feeding (southwest Nova Scotia, Georges Bank, Bay of Fundy) and overwintering (Long Island Sound, Chedabucto Bay) (Sinclair and Isles 1985).

Seasonal movement patterns of river herring inferred from American and Canadian survey data involve a north-south progression and an inshore-offshore movement similar to that described for American shad populations along the Atlantic coast of North America (Neves and Depres 1979, Dadswell et al. 1987). During spring, river herring from the Middle Atlantic Bight move north as far as the Nantucket Shoals, Georges Bank, coastal Gulf of Maine and even the inner Bay of Fundy for the summer, then return south to the mid-Atlantic coast in winter and early spring (Neves 1981, Rulifson et al. 1987). The spring aggregation of mature river herring observed in Canadian survey catches from the southern Gulf of Maine likely consists of fish which will move inshore to spawn in rivers along the eastern seaboard of the United States, although some may enter Canadian rivers. A large component of the overwintering population on the Scotian Shelf moves inshore during spring to spawn in rivers along the Atlantic coast of Nova Scotia, the Bay of Fundy, and perhaps the Gulf of Maine. American shad tagged in rivers in Nova Scotia (Melvin et al. 1986) and in Quebec (Vladykov 1956) were recaptured on the Scotian Shelf in winter. The large aggregation of river herring in the eastern Gulf of Maine, apparent during spring surveys, may include fish in transit from overwintering areas on the Shelf to spawning rivers along the Bay of Fundy–Gulf of Maine coast. Considering their preference for water temperatures above 5°C, the migration route would occur along the Shelf Slope and into the eastern Gulf of Maine through the Northeast Channel. Postspawning river herring probably feed during summer in the Bay of Fundy–eastern Gulf of Maine before returning offshore to the central Shelf in the fall to overwinter. Somé may move offshore soon after spawning, as indicated by the presence of large fish ($\bar{x}$ FL 30.4 cm) in the summer bycatch from the silver hake fishery along the shelf slope. Another component of the Shelf overwintering population may move north around Cape Breton to the Gulf of St. Lawrence in spring to spawn in natal rivers, returning in autumn to the Scotian Shelf to overwinter. This hypothesis is supported by the fall concentration of river herring in the Sydney Bight area and movement of an alewife accidently tagged in the Sydney Bight fall fishery for Atlantic herring, to the Margaree River (southern Gulf of St. Lawrence) where it was recaptured the following spring (Jessop, unpubl. data).

Most river herring overwintering on the Scotian Shelf probably originate in the Canadian Maritime Provinces and U.S. Gulf of Maine region. Some river herring of Canadian Maritime origin evidently migrate south to overwinter off the Middle Atlantic Bight as do American shad (Melvin et al. 1986, Dadswell et al. 1987). The tagging of over 50,000 river herring in the Saint John River, New Brunswick, produced two recaptures off North Carolina the following spring and other recoveries along the intervening coast (Jessop, unpubl. data). In another study, most recaptures from over 19,000 river herring tagged during summer and fall in the upper Bay of Fundy occurred in spring fisheries in Nova Scotia rivers, but one occurred off Massachusetts and several came from North Carolina (Rulifson et al. 1987). Summer aggregations of river herring in the Bay of Fundy–eastern Gulf of Maine may therefore consist of a mixture of stocks from the entire Atlantic coast, as do similar aggregations of American shad (Dadswell et al. 1987).

An understanding of the seasonal movements, stock composition, and exploitation of river herring populations which overwinter on the Scotian Shelf may help fishery managers to explain high variability in the returns of spawning fish regionally and to particular river systems. Stock composition and migratory routes remain to be examined.

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