SPRING AND SUMMER MOVEMENTS OF SUBADULT STRIPED BASS, MORONE SAXATILIS, IN THE CONNECTICUT RIVER¹

The Connecticut River has no known spawning population of striped bass, Morone saxatilis, but there is an annual run of subadults in the late spring and summer from Long Island Sound to Holyoke Dam, 140 km upstream (Moffitt et al. 1982). In 1980-82, 80-90% were age II (the remainder were age III); about 60% were males (Warner 1983). The biological reason for such a run is unknown, but feeding may be an important attractant to the river. The major foods of striped bass collected at Holyoke Dam are spottail shiners, Notropis hudsonius, and the scales and body parts of adult American shad, Alosa sapidissima, and blueback herring, A. aestivalis, that result from injury or death at the hydropower dam and fish lifts or from angling (Warner and Kynard 1986). Factors other than food are un-

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doubtedly important influences on the riverine migration.

The migration of subadult striped bass into natal or nonnatal rivers was documented by Raney et al. (1954) and Nicholas and Miller (1967), but the reasons for the movement are not clear. We hypothesized that detailed studies of subadult movements in the Connecticut River could help reveal some of the environmental factors that effect the movements. We used radio telemetry of subadults captured at Holyoke Dam to observe the use of river habitats, diel activity, and the rates of upstream and downward movements. We also investigated the passage of striped bass at the Holyoke fish lifts in relation to river temperature during 1979-86.

Study Area

Radio-tagged striped bass were observed after they were transferred above Holyoke Dam into the 53 km of the Connecticut River, between the Holyoke Dam and the Cabot Station hydroelectric facility which is below Turners Falls Dam (Fig. 1). The upstream 23 km reach is relatively straight, with few areas deeper than 4 m; the lower 30 km reach meanders, creating a deep channel and shoals (Fig. 1). Bottom type is rubble and gravel in the

FIGURE 1.—The 53 km of the Connecticut River above the Holyoke Dam where the movements of radio-tagged striped bass were observed in 1981-82. The 13 holding areas where striped bass stopped are on the left side of the river (number of stops in parenthesis).

upper stretch; and sand and areas of exposed rock ledge are in the lower section (Armour 1966).

Methods

The number of striped bass passed daily by the Holyoke fish lifts from 1979 to 1986 was counted by personnel of the Massachusetts Cooperative Fishery Research Unit (MCFRU). Maximum daily river temperature recorded at the dam was used to characterize the temperature regime for the striped bass lifted each day. The daily records of each year's run were used to make frequency distributions of the number of fish lifted and the daily maximum temperature. We used the statistics of mean, median, standard deviation, and range of temperatures to visually compare the temperatures when striped bass entered the lifts.

All striped bass used for telemetry were captured during 1981 and 1982 in the fish trap at the lifts. To help reduce mortality caused by handling, we marked only the largest fish captured (280-365 mm fork length). Fish were held at the dam for a maximum of 5 d in a 1,325 L circular tank supplied with river water. At the release sites (Fig. 1), we inserted into the fish a transmitter which went directly through the mouth and into the stomach, a procedure that did not interfere with subsequent feeding (Warner 1983).

Radio transmitters were constructed using the design of Knight (1975) or with the modifications of Buckley (MCFRU). The transmitters measured 12 mm in diameter and 45 mm long, weighed 3.5-5.5 g in air, and transmitted for 7-21 d. Weight of the transmitters never exceeded 3.4% of the body weight of the fish. Individual fish were identified by 12 frequencies (30.05-30.25 MHz) and by variations in the pulse rate of each frequency.

We tracked striped bass from a boat using an omnidirectional antenna (1/8-wave, base loaded) to locate fish to within about 100 m and a directional, tuned-loop antenna to locate fish to within about 10 m. Locations of fish were noted on contour maps of the river. Initially, we tracked striped bass from 4 to 30 h, but tracking each fish was not continuous and depended on the speed of dispersal. Later, we surveyed the study area daily. Some striped bass moved actively and others were sedentary; therefore, we tracked the active fish continually for as long as 6 h, but only periodically noting the locations of others. In addition to the daily surveys, we observed some fish continually for 24 h to determine the diel movement; we conducted three diel surveys in 1981 and nine in 1982.

The upstream and downstream rates of movement (ground speed) were determined by using the continuous observations of striped bass that had been free longer than 1 h. Locations where striped bass remained longer than 90 min were designated as "holding areas". The physical characteristics of these areas were determined from visual observations and contour maps.

Results and Discussion

Passage in the Lifts and Temperature

Activity at the fish lifts appeared to be related to temperature (Fig. 2). Striped bass first entered the lifts when river temperatures were $17^{\circ}-19^{\circ}$ C (late May or early June), and in some years a few were still entering the lifts at $25^{\circ}-28^{\circ}$ C when lift operation ceased. The mean temperature of activity when striped bass entered the lifts ranged from a low in 1980 of 10.0°C to a high in 1983 of 23.4°C (Fig. 2). For the 7-yr period, the mean temperature of peak movement was 21.3°C (SD, 1.7°C) with 72% of the fish passage from 20°C to 24°C (85% of passage between 19° and 24°C).



FIGURE 2.—Mean, median, standard deviation, and range of temperatures when subadult striped bass were passed in the Holyoke Dam fish lifts, 1979-86.

A recent hypothesis proposed that, as striped bass advance in age, they prefer cooler water (Coutant 1985). Further, the thermal niche of subadults (43-68 cm total length) in Tennessee reservoirs was 20°-24°C, when these temperatures were available (Coutant and Carroll 1980). This is essentially the same range as most upstream movement into lifts in this study. Although the movement of striped bass into the lifts is more an indication of general activity than choice of preferred temperatures; nevertheless, the similarity in range of temperatures found in the two studies is remarkable. Striped bass began entering the fish lifts in late May when river temperatures were about 17°C. During mid- to late May 1979-83, the daily maximum temperatures in Long Island Sound near the mouth of the river were much cooler (12°-13°C, Millstone Laboratory, Northeast Utilities Service Co., Hartford, CT). While we do not know whether the striped bass overwinter in the lower river or enter fresh from Long Island Sound each spring, the movement of subadults from the cooler waters of the Sound into the warmer river is consistent with the thermal niche hypothesis of Coutant (1985). The only data from the Connecticut River that appears inconsistent with the hypothesis of Coutant (1985) is the capture of nine subadults in the lifts at Holyoke Dam in the fall of 1979 when river temperatures were 7°-10°C. Although prey abundance is high each fall at Holyoke Dam because of the outmigration and death of many juvenile American shad and blueback herring passed through the turbines (Taylor and Kynard 1985), the temperatures when the striped bass entered the lifts were much colder than preferred. Did the food abundance cause some striped bass to remain in water temperature that would otherwise be avoided? Because no striped bass have been lifted in the fall since 1979, we concluded that the event must be rare, whatever the reasons.

Radio Telemetry

We tagged 63 striped bass with transmitters: 11 in 1981 and 52 in 1982. Three tags failed immediately after release (all in 1982); therefore, 60 fish total were tracked. The study area was surveyed from late June to late July during 13 d in 1981 and 47 d in 1982.

Individual striped bass were tracked for periods of 1-14 d: 35 were tracked for ≥ 1 d; and 25 were tracked for > 2 d. Fish were tracked for an average of 4.3 d in 1981 (range: 1-14 d, N = 11) and 2.2 d in 1982 (range: 1-12 d, N = 46). Tracks of fish ended because of tag regurgitation, tag failure, and movement out of the study area. Operating tags were regurgitated by 15 fish (4 in 1981, 11 in 1982) averaging 3.6 d before regurgitation. There were four known tag failures after an average of 3.5 d of observations. Tracking the remaining 41 fish ended after they moved out of the study area or after undetected tag failure. No striped bass were observed moving upstream of the Cabon Station or into tributaries of the river. Surveys below Holyoke Dam located seven tagged fish, one 75 km downstream of Holyoke Dam near Hartford, CT. None of these fish returned to Holyoke Dam and they may have continued moving downstream to the Long Island Sound. Twenty additional fish were last observed moving downstream toward Holyoke Dam, and we expected that they also continued past the dam and, possibly, to the Sound. Because there was no spillage over the dam when many tagged fish returned downstream to Holyoke Dam, they passed the dam by entering one or more hydroelectric turbines.

Only striped bass tagged in 1982 moved upstream; the average upstream rate was 0.7 km/h (range: 0.30-1.2 km/h, N = 11). The mean rate of downstream movement was 1.9 km/h in 1981 (range: 1.0-3.2 km/h, N = 9); and 2.3 km/h in 1982 (range: 1.0-3.8 km/h, N = 21). Mean rates during the 2 years did not differ significantly (Student's *t*-test:P >0.05). One striped bass, which was located nine times during July 1982, traveled at least 143 km in the study area during 14 d.

Nine fish moving downstream in 1981 followed the channel of the river; 61 of 68 locations were in the channel at depths of 3-17 m. Although the actual proportion of deep-channel habitat compared with shoal habitat is unknown, there is much less channel than shoal area. Therefore, the preference for the channel appears strong, as was also found in telemetry studies of adult striped bass in Watts Bar Reservoir, TN (Cheek et al. 1985).

A total of 29 striped bass localized for periods of 90 min to 6 d in 13 different holding areas (Fig. 1). (Two localized at more than one area; therefore, a total of 33 such events were recorded.) Two fish were rarely found simultaneously at the same site. All holding areas, except the Route 202 Bridge site, were located near a bank of the river. The Cabot Station site accounted for 8 of the 33 localized periods and for most of the longest periods, i.e., two fish stayed at Cabot Station for 6 d each, one for 3 d, and three for 2 d.

Fish activity in holding areas was highly variable. Fish at Cabot Station moved in a stop-and-go manner during the day and night, in shallow and in deep water, and in the fast water of the power station discharge and in the slackwater upstream of the station. They appeared to be feeding in the discharge of the hydroelectric station—we have observed striped bass feeding in the discharge water of the Hadley Falls Hydroelectric Station at Holyoke Dam. Five fish were tracked at the outlet of the Northampton Oxbow (Fig. 1). All stayed in the main stem within 0.5 km of the outlet, moved in a stop-and-go manner, and used three habitats: a low-flow turbid area, a 10 m deep channel, and sandy shoals upstream from the outlet. Movements at the S-curve (Fig. 1) and at other holding areas were highly variable: some remained in a small discreet area, others were inactive for long periods, and the rest moved actively within a 0.5 km reach of the river similar to the movements at Cabot Station and at the Northampton Oxbow.

Striped bass followed several patterns of diel behavior. At Cabot Station, which has outside illumination at night, four moved actively during both the day and night. Koo and Wilson (1972) also found that adult striped bass were active at night in illuminated areas. At sites with natural illumination, the movements of 10 striped bass were as follows: 9 moved actively during the day; 6 stopped and 3 were less active at night; and 1 moved only at night. Of the 14 striped bass that we observed for 24 h, 10 increased their activity at dawn, dusk, or both. Dudley and McGahee (1983) found that adults were most active in late afternoon or evening, but noted an increased activity at dawn. Because striped bass feed most actively at dawn and dusk (Raney 1952). the increase in activity during these periods was probably related to feeding.

Based on the results of fish passage at Holyoke Dam, behavioral observations using telemetry, and the general thermal niche of subadults reported by Coutant and Carroll (1980) and Coutant (1985), we hypothesize that the movement of subadult striped bass into the Connecticut River is due in part to thermal preferences. The upriver migration in May-July places subadults in temperatures closer to their preferred range than those found in Long Island Sound. Tracking of fish in the river indicates a diverse behavioral range of active swimming, resting, and feeding that is consistent with a springsummer period of high activity and growth. Local attraction to dam tailwaters provides access to abundant food (Warner and Kynard 1986), a feature that reinforces the advantages of following thermal cues into the riverine environment. The feeding advantages for striped bass will likely increase as the restoration program for American shad and blueback herring results in an increased abundance of juveniles.

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HABITAT PARTITIONING BY SIZE IN WITCH FLOUNDER, GLYPTOCEPHALUS CYNOGLOSSUS: A REEVALUATION WITH ADDITIONAL DATA AND ADJUSTMENTS FOR GEAR SELECTIVITY

In 1970, Powles and Kohler hypothesized separation of habitats of adult and juvenile witch flounder, *Glyptocephalus cynoglossus*, by depth based on surveys of Nova Scotia Banks and in the Gulf of St. Lawrence. Juveniles were sampled with a small mesh Icelandic shrimp trawl on the Nova Scotia Banks. These data were supplemented by data obtained from Squires' (1961) field records collected during shrimp surveys in the Cabot Strait and Gulf of St. Lawrence in the summers of 1957 and 1958 using a Norwegian deep-sea shrimp trawl. The authors concluded that during the summer months newly metamorphosed and small (<30 cm) witch flounder were found in the 180-288 m depth range.

Adult witch flounder (\geq 30 cm) were sampled with a No. 36 Yankee otter trawl on the Nova Scotia Banks from May to October and from November to April. Powles and Kohler (1970) concluded that adult witch flounder were most abundant at a depth range of 92-162 m. In winter months both adults and juveniles were found together in deeper water while in the summer both groups were separated.

Powles and Kohler (1970) suggested that this deepwater distribution of juvenile witch flounder could prevent direct competition with young of more abundant species such as Atlantic cod, Gadus morhua, and American plaice, Hippoglossoides platessoides, and provide a natural conservation against fishery exploitation. Their otter trawl catches, over a depth range of 36-450 m, yielded few juvenile witch flounder, although many small American plaice were captured. Escapement of juvenile witch flounder through the mesh in the wings of the trawl was ruled out because many small plaice were captured on the same grounds. The authors concluded that juvenile witch flounder were absent unless American plaice and witch flounder differed radically in behavior. Other studies of witch flounder depth distribution on the continental slope off Virginia (Markle 1975) and in the Gulf of St. Lawrence, NAFO (Northwest Atlantic Fisheries Organization) Divisions 4R and 4S (LaFleur and Lussiàa-Berdou 1982) supported the habitat separation hypothesis.

However, recent studies showed that a No. 36 Yankee shrimp trawl was more efficient in catching juveniles whereas a No. 41.5 Yankee otter trawl was more efficient in catching adult witch flounder (Walsh 1984). In that study juvenile American plaice and witch flounder co-occurred in the shrimp trawl catches; differential catches of witch flounder in the otter trawl was due to the escapement of juveniles. Apparent depth separation proposed by Powles and Kohler (1970) may have been based on data biased by gear selection.

Accurate descriptions of life history patterns of witch flounder are important for sound fisheries management, especially with regard to competition with other species and with regard to presumed mechanisms which protect from overfishing. Powles and Kohler (1970) derived their results from summer and winter surveys, and the conclusions were tentative because of potential gear selectivity problem. Therefore, I reevaluated the depth separation hypothesis with additional data taking gear selectivity into consideration.

Materials and Methods

Data used in the analysis were obtained from regular groundfish biomass surveys of the Gulf of St. Lawrence, NAFO Divisions 4R and 4S, by research vessels of the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, during the period 1978-80. In addition, two juvenile flatfish surveys were used: one in the northern Gulf of St. Lawrence, NAFO Division 4R, 1980; and one in the areas of Hermitage Bay and Fortune Bay, NAFO Division 3Ps, in 1981 (Fig. 1).

Fishing Gears and Research Designs

Groundfish surveys in September and October of 1978-80, NAFO Divisions 4R and 4S by the A. T. Cameron (side trawler) were conducted with a standard No. 41.5 Yankee otter trawl with a stretched mesh size of 127 mm in the wings and reducing to 111 mm in the cod end and a 30 mm mesh cod end liner was used. A total of 188-30 min fishing sets