Movement patterns of winter flounder (*Pseudopleuronectes americanus*) in the southern Gulf of Maine: observations with the use of passive acoustic telemetry

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Abstract—Despite its recreational and commercial importance, the movement patterns and spawning habitats of winter flounder (*Pseudopleuronectes americanus*) in the Gulf of Maine are poorly understood. To address these uncertainties, 72 adult winter flounder (27–48 cm) were fitted with acoustic transmitters and tracked by passive telemetry in the southern Gulf of Maine between 2007 and 2009. Two sympatric contingents of adult winter flounder were observed, which exhibited divergent spawning migrations. One contingent remained in coastal waters during the spawning season, while a smaller contingent of winter flounder was observed migrating to estuarine habitats. Estuarine residence times were highly variable, and ranged from 2 to 91 days (mean=28 days). Flounder were nearly absent from the estuary during the fall and winter months and were most abundant in the estuary from late spring to early summer. The observed seasonal movements appeared to be strongly related to water temperature. This is the first study to investigate the seasonal distribution, migration, and spawning behavior of adult winter flounder in the Gulf of Maine by using passive acoustic telemetry. This approach offered valuable insight into the life history of this species in nearshore and estuarine habitats and improved the information available for the conservation and management of this species.

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Winter flounder (*Pseudopleuronectes americanus*) is a commercially and recreationally important flatfish species that is distributed along the east coast of North America from North Carolina northward to Newfoundland (Bigelow and Schroeder, 1953). Within U.S. waters, this species is managed as three stock units: the southern New England and Mid-Atlantic (SNE–MA); Gulf of Maine; and Georges Bank. To date, there has been less research on the Gulf of Maine stock than on the SNE–MA stock. Seasonal distribution patterns of winter flounder in the Gulf of Maine have emerged from fisheries catch data (McCracken, 1963), mark recapture experiments (Perlmutter, 1947; Howe and Coates, 1975) and annual trawl surveys. However, these sources of data offer limited insight into patterns of estuarine residence and nearshore habitat use for winter flounder because trawl fisheries and research surveys in the Gulf of Maine are typically limited to coastal and offshore waters. In addition, these traditional sampling sources for obtaining distribution data cannot identify individual variability in movement or spawning behavior. In the present study, we sought to investigate spawning patterns and seasonal distribution of winter flounder in nearshore and estuarine waters in the southern Gulf of Maine using passive acoustic telemetry.

The magnitude of variability in individual migration patterns remains poorly understood for even the most economically valuable fish species (Able and Grothues, 2007), in part because we have yet to recognize the importance of contingent behavior. Contingents are cohesive groups of fish within a population that exhibit a common migration pattern (Cadrin and Secor, 2009). Acoustic telemetry offers new opportunities to investigate the fine-scale movements and behavior of individual fish. This technology allows for the recognition of contingent groups within populations (Secor, 1999) and offers insight into the amount of connectivity between estuarine and coastal populations (Able, 2005). Acoustic telemetry has been used to gather high resolution data on the behavior of juvenile winter flounder in the Gulf of Maine (Fairchild et al., 2009). However, before the present study, this technology had not been used to study adult winter flounder in the Gulf of Maine.

Traditionally, winter flounder spawning in the Gulf of Maine was thought to be restricted to estuarine habitats (Bigelow and Schroeder, 1953). This assumption was subsequently reflected in designations of Essential Fish Habitat (EFH) for this species (NMFS, 1999). However, other observations indicate that winter flounder in the Gulf of Maine also use coastal waters as spawning grounds (i.e., Howe and Coates, 1975). If a proportion of individuals spawn in coastal, rather than estuarine habitats, these fish would represent contingents within the larger population. Contingents may provide populations with enhanced stability and resilience because of the variable survival rates of early life history stages in different habitats (Secor, 2007; Kerr et al., 2010). Divergent spawning migrations increase the distribution of eggs and larvae, which may reduce the probability of a failed recruitment event (Lambert, 1990). For winter flounder that spawn demersal eggs, the conditions encountered by the early life history stages are largely determined by the locations where the adults spawn. Therefore, divergent spawning migrations may have a large effect on the recruitment success of local populations.

We chose to monitor adult winter flounder in Plymouth Bay and the adjacent Plymouth Harbor, Kingston Bay, and Duxbury Bay estuary. Plymouth Harbor, Kingston Bay, and Duxbury Bay estuary are commonly referred to as the Plymouth Estuary, and that name will be used throughout this article. Winter flounder is a dominant member of the groundfish community in the Plymouth Estuary, and the estuary serves as an important nursery area for this species (Lawton et al., 1984). Winter flounder are known to spawn in the Plymouth Estuary, where peak spawning occurs in March and April (Entergy[1]). In addition, Plymouth Bay has been identified as an area where coastal spawning likely occurs (NMFS, 1999).

The goal of this study was to obtain high-resolution data on the seasonal distribution, migrations, and spawning behavior of winter flounder in the southern Gulf of Maine. In particular, three primary objectives were addressed during this study: 1) to determine if adults in this region exhibit divergent spawning migrations; 2) to investigate the seasonal distribution of winter flounder in the region, in association with water temperature; and 3) to compare the seasonal distribution observed in this study to that observed in past research in the Gulf of Maine where static sampling methods were used.

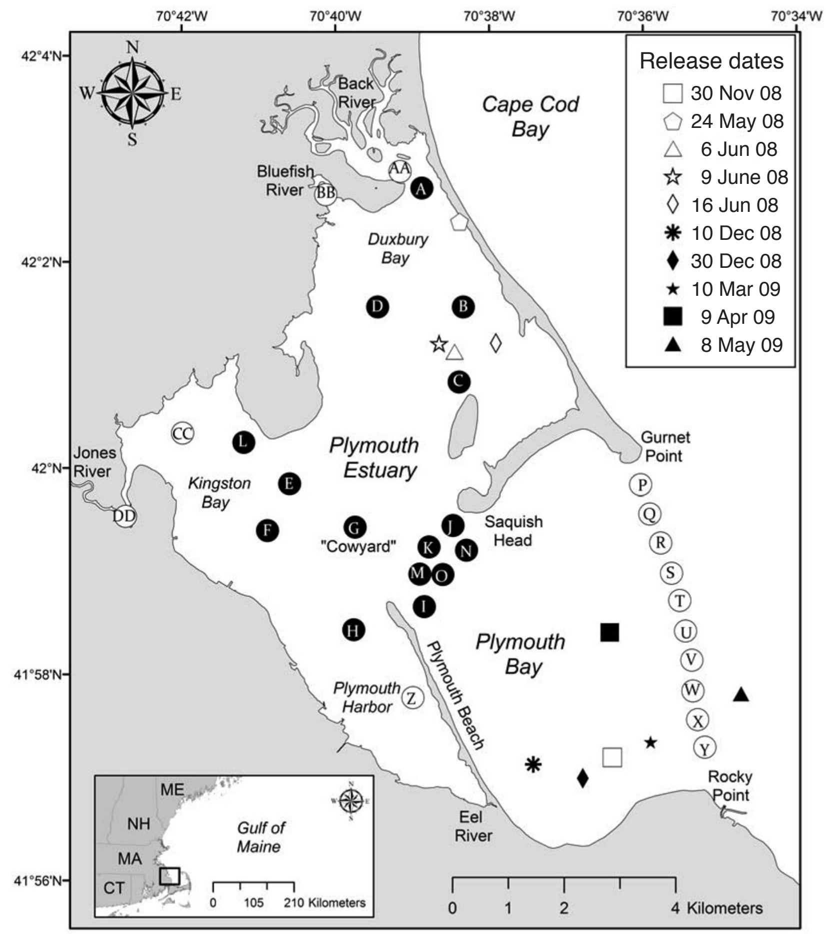

Figure 1

Map of the study site showing the locations of Plymouth Bay and Plymouth Estuary in the Gulf of Maine where the movements of winter flounder (*Pseudopleuronectes americanus*) were tracked with passive acoustic telemetry. Locations of tag releases and acoustic receivers are shown. Receivers used to track winter flounder movements from November 2007 to November 2008 are shown as solid black circles and receivers added to the array in December 2008 are shown as open circles. Circles are not drawn to scale and do not represent the detection radii of acoustic receivers.

Materials and methods

Study site

The Plymouth Estuary and Plymouth Bay are located in the southern portion of the Gulf of Maine (Fig. 1). The Plymouth Estuary is bordered on its seaward side by two barrier beaches. Tidal exchange between the Plymouth Estuary and Plymouth Bay occurs through a 2020-m opening between Saquish Head and the northern extremity of Plymouth Beach. The estuary is well mixed and approximately 66% of the water is replaced during each tidal cycle, creating strong tidal currents (Davis, 1984). Plymouth Bay is bordered by Cape Cod Bay to the east.

The average depth within Plymouth Estuary is 3.3 m at mean high water and 2.1 m at mean low water, and

[1] Entergy. 2001. Ichthyoplankton entrainment monitoring at Pilgrim Nuclear Station, January–December, 2000. *In* Marine ecology studies related to operation of Pilgrim Station. Report no. 57, 65 p. Entergy Nuclear Generation Company. Plymouth, MA.

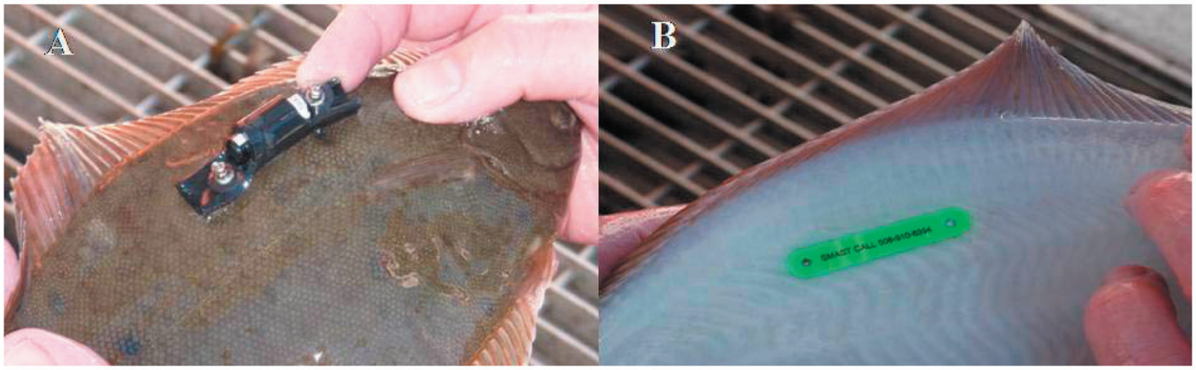

Figure 2

An example of the external attachment method that was used to secure the acoustic transmitters to winter flounder (*Pseudopleuronectes americanus*) to monitor their movements in the southern Gulf of Maine. The Vemco V92L transmitters were fitted into a harness of 9/16" soft latex tubing and secured in the harness with two-part epoxy (**A**). Two nickel tagging pins were passed upwards through the blind side of the fish, through the dorsal musculature (**B**).

salinity in the estuary ranges from 0.0 to 33.0 (Iwanowicz et al.[2]). The bathymetry of the estuary is complex, and extensive sand and mud flats are exposed at low tide when the surface area of the estuary is reduced from 10,057 acres to 5465 acres (Iwanowicz et al.[2]). A deeper channel is present between Saquish Head and Plymouth Beach, where depths reach nearly 26 m. There are four main sources of freshwater input to the Plymouth Estuary: the Back River, Bluefish River, Jones River, and Eel River.

Acoustic telemetry

Adult flounder were captured by using either a small otter trawl, a commercial trawl vessel, or by hook and line. Sampling was nonrandom, and sampling locations were chosen from areas where adult winter flounder have historically been abundant. Tow times with the small otter trawl varied from 10 to 30 minutes, and tows with the commercial vessel were 30 minutes in duration. The total length of each fish was measured to the nearest centimeter, and only adult fish ($\geq$27 cm) in good or excellent condition were fitted with acoustic tags. After tagging, fish were held onboard for observation until they were deemed healthy enough for release. All fish were released in close proximity to the capture site in order to minimize tagging-induced stress.

In total, 72 adult winter flounder (27–48 cm) were fitted externally with acoustic transmitters (model V92L, 69 kHz, 9 mm×21 mm, Vemco Ltd., Halifax, NS, Canada) between November 2007 and May 2009. Each transmitter had an average pulse rate of 80 seconds (range=40–120 seconds) and an expected battery life of 384 days. A novel external attachment method was developed for this study. Acoustic transmitters were secured into a harness of 9/16 inch (14.3 mm) soft latex tubing by using two-part epoxy (Fig. 2). Two nickel tagging pins were passed upwards from the blind side of the flounder through the dorsal musculature. The harness was then secured to the nickel pins on the eyed-side of the fish with plastic earring backings. The tagging procedure took an average of two to three minutes per fish. A laboratory holding study indicated 100% transmitter retention and 100% survival over a seven-month period. A separate holding study conducted at the University of New Hampshire in 2009 indicated that the tag attachment method did not interfere with the swimming or spawning behavior of tagged fish (E. Fairchild, personal commun.[3]).

In November 2007, 24 prespawning winter flounder were tagged in Plymouth Bay, approximately 5 km from the mouth of the Plymouth Estuary (Fig. 1). Three of these winter flounder were observed to be gravid females at the time of release. Repeated efforts were made to capture spawning flounder within the estuary during March, April, and early May of 2008, but we were not able to capture adult fish until late May 2008. Twenty three adult winter flounder were tagged within the Plymouth Estuary between 24 May and 16 June 2008 (Fig. 1). In the second year of the study, an additional 25 winter flounder were tagged in Plymouth Bay between December 2008 and May 2009 (Fig. 1). Eight winter flounder tagged on 8 May 2009 were observed to be gravid females that were in spawning condition.

[2] Iwanowicz, H. R., R. D. Anderson, and B. A. Ketschke. 1974. A study of the marine resources of Plymouth, Kingston and Duxbury Bay. Monograph Series Number 17, 37 p. Division of Marine Fisheries, Boston, MA.

[3] Fairchild, Elizabeth. 2009. Department of Biological Sciences, Univ. New Hampshire, Durham, NH 03824.

Winter flounder tagged between November 2007 and June 2008 (n=47) were tracked within the Plymouth estuary by using a moored array of 15 wireless receivers (model VR2 and VR2W, Vemco Ltd.; Fig. 1). Six of these receivers (I, J, K, M, N, and O; referred to as the "inner gate") were configured as a parallel curtain that spanned the mouth of the Plymouth estuary, allowing the movements of fish traveling between Plymouth Bay and Plymouth estuary to be recorded precisely. Parallel curtain arrays are advantageous because they allow the direction of movement for each fish to be obtained (Heupel et al., 2006). Range testing was performed at the mouth of the estuary by placing transmitters on the bottom in different locations for ten-minute intervals. After range testing, receivers within the parallel curtain were positioned to ensure that overlap existed between the detection radii of adjacent receivers. Tagged winter flounder were monitored within the upper reaches of the Plymouth estuary by using nine receivers positioned in a nonoverlapping grid array. These receivers were placed within the deeper channels of the Plymouth estuary to maximize their detection radii.

During the second year of the study, the receiver array was expanded from 15 to 30 wireless receivers (Fig. 1). Ten receivers (P–Y; referred to as the "outer gate") were deployed across the mouth of Plymouth Bay, from Gurnet Point in Duxbury southward to Rocky Point in Plymouth. This arrangement allowed us to track the movement of tagged winter flounder between Cape Cod Bay and Plymouth Bay. An additional five receivers (Z–DD) were placed within the upper reaches of the Plymouth estuary. Expanding the receiver array allowed us to test more directly our hypotheses about the spawning behavior of the 25 winter flounder that were tagged between 10 December 2008 and 8 May 2009.

Before their retrieval in 2009, six of the 30 acoustic receivers were lost, likely because of boat traffic, interactions with commercial fishing gear, or because of winter storms. Receivers P and Y were lost from the outer gate between Cape Cod Bay and Plymouth Bay. Receivers I, M, and O were lost from the parallel curtain between Plymouth Bay and the Plymouth estuary. Subsequently, receiver G was moved from the "Cowyard" and placed adjacent to the position of receiver M to improve the coverage in this area. Receiver H in Plymouth Harbor was also lost, likely because a high volume of boat traffic in the area.

Data analysis

The movement track of each tagged fish was visualized by using GIS software (ArcMap vers. 9.3, ESRI, Redlands, CA). Estuarine residence time was calculated as the time elapsed between the first and last detection for each individual within the Plymouth estuary. If a tagged winter flounder was recorded within the estuary on more than one occasion, the total days spent within the estuary during each visit were combined to calculate residence time for that individual.

Winter flounder were classified as either estuarine or coastal spawners on the basis of their observed locations during the peak spawning months of March through May. Fish that were detected within the Plymouth estuary at any time over this three month span were classified as estuarine spawners, whereas winter flounder that remained in coastal waters were classified as coastal spawners. A G-test for independence (Sokal and Rohlf, 2001) was performed to examine whether significant interannual variability was present in the proportion of tagged winter flounder that were classified as estuarine spawners in 2008 and 2009. The ratio (with 95% confidence intervals) of estuarine to coastal spawners observed over the two-year period was calculated (Sokal and Rohlf, 2001).

Abiotic monitoring

During the study, bottom water temperature was monitored at four locations within the study site. Three temperature loggers (Vemco Ltd.; 8-bit minilog TR) were attached to the moorings of receivers A, E, and K within the Plymouth Estuary. These temperature loggers were placed 0.5 meters above the bottom and were programmed to record bottom water temperature every 30 minutes. A temperature logger placed in the southeastern portion of Plymouth Bay recorded bottom water temperature once every two hours in 2007 and 2008. In September 2008, another temperature logger was placed on the mooring of receiver T to record bottom temperature in Plymouth Bay. In 2009 some of the temperature loggers failed. When available, bottom water temperature data were averaged weekly at each site.

Results

With passive acoustic telemetry, we successfully gathered high-resolution data on the migration, spawning behavior, and seasonal distribution of adult winter flounder in the southern Gulf of Maine. Twenty eight of the 47 winter flounder tagged during the first year of the study were later detected within the Plymouth estuary, yielding a total of 16,956 detections in our array of acoustic receivers. Twenty two of the 25 fish tagged during the second year of the study were later detected in the receiver array, resulting in 97,394 unique detections. A summary of data for each tagged winter flounder that was later detected is given in Table 1.

Spawning behavior

Based on the observed movements of tagged winter flounder during the spawning season, the presence of two contingent spawning groups of flounder was evident in the region: coastal spawners and estuarine spawners. In both years of the study, the majority of tagged winter flounder exhibited coastal spawning behavior. Only five of the 24 winter flounder (21%) tagged in Plymouth Bay in 2007 were classified as estuarine spawners. Seven of

Table 1

Summary of information for tagged winter flounder (*Pseudopleuronectes americanus*) that was detected during the study. For each tagged winter flounder, the date of release and date of last location are given. The total number of detections, and receivers at which that winter flounder was detected, is provided. For the release locations, PB=Plymouth Bay and PE=Plymouth Estuary.

Tag ID	Length (cm)	Release date	Release location	Last detection	No. of detections	Receiver stations
5837	34	11/30/2007	PB	8/26/2008	27	Outer Cape
5839	28	11/30/2007	PB	10/30/2008	63	C,F,G,N
5850	30	11/30/2007	PB	11/19/2008	2030	C,J,K,M,N,O
5852	32	11/30/2007	PB	6/1/2008	735	J,K,N,O
5862	29	11/30/2007	PB	6/12/2008	100	C,D,K,M,O
5867	36	11/30/2007	PB	5/28/2008	1	K
5868	34	11/30/2007	PB	8/25/2008	1458	J,K,M,N,O
5877	32	11/30/2007	PB	6/22/2008	799	E,F,G,I,M,O
5832	29	5/24/2008	PE	6/17/2008	44	B,C,J
5833	27	5/24/2008	PE	9/30/2008	3227	B,C,J,K,N
5840	33	5/24/2008	PE	6/10/2008	1681	C,J
5844	27	5/24/2008	PE	6/12/2008	957	C,J,K,M,O
5845	35	5/24/2008	PE	6/13/2008	338	C,J,N
5847	42	5/24/2008	PE	7/30/2008	3198	C,J,K,M,N,O
5855	36	5/24/2008	PE	5/26/2008	90	D
5858	29	5/24/2008	PE	6/15/2008	30	K,M
5859	35	5/24/2008	PE	7/7/2008	18	C,J,N
5866	42	5/24/2008	PE	6/15/2008	119	A,C,J
5873	27	5/24/2008	PE	6/13/2008	267	B,K,M
5878	35	5/24/2008	PE	6/13/2008	217	B,C,J
5835	39	6/6/2008	PE	6/10/2008	55	J,K,M,O
5846	30	6/6/2008	PE	6/21/2008	18	C,J
5856	33	6/6/2008	PE	8/18/2008	211	C,J
5864	27	6/6/2008	PE	6/23/2008	27	B,I,M
5874	38	6/6/2008	PE	6/15/2008	636	B,C,J,N
5871	27	6/9/2008	PE	6/14/2008	9	M,O
5876	36	6/9/2008	PE	9/14/2008	546	C,J,K,N,O
5843	28	6/16/2008	PE	10/6/2008	18	C,K
5872	27	6/16/2008	PE	7/24/2008	37	C,N
53876	33	12/10/2008	PB	5/2/2009	10346	G,K,N,X
53877	31	12/10/2008	PB	8/26/2009	6750	G,Q,R,T,U,V,W,X, MA Bay
53879	36	12/10/2008	PB	7/25/2009	19394	V,W,X
53884	36	12/10/2008	PB	5/13/2009	1484	Q,R,S,T,U,V,W,X
53886	31	12/10/2008	PB	7/8/2009	14089	G,K,N,S,T,U
53887	30	12/10/2008	PB	7/20/2009	5061	Q,R,S,T,U,V,W,X
53888	31	12/10/2008	PB	6/14/2009	23842	G,J,K,N,R,S,T,U
53890	29	12/10/2008	PB	6/27/2009	57	X
53891	32	12/10/2008	PB	5/22/2009	443	G,K,N,R,S,T,U.V
53894	41	12/10/2008	PB	7/28/2009	3611	C,E,Q,R,S,T,U,V,W,X
53896	31	12/10/2008	PB	6/26/2009	361	X
53892	37	3/10/2009	PB	6/18/2009	1215	R,U,V,W,X
53893	34	3/10/2009	PB	7/8/2009	288	X
53874	33	4/9/2009	PB	4/11/2009	1061	R,S,T,U
53883	35	4/9/2009	PB	5/4/2009	3018	Q,R,S
53885	31	4/9/2009	PB	7/14/2009	2074	G,K,J,N,Q
53873	39	5/8/2009	PB	5/24/2009	620	Q,U,S,T,U,V,W,X
53875	37	5/8/2009	PB	5/12/2009	177	Q,R,S,T,U,V,W
53878	36	5/8/2009	PB	6/12/2009	2230	G,K,Q,R,S,T,U.X
53881	36	5/8/2009	PB	7/25/2009	479	Q,R,S,T,U,V,W,X
53895	36	5/8/2009	PB	6/25/2009	701	B,C,G,J,N,W,X
53897	48	5/8/2009	PB	5/10/2009	93	V,W,X

the 25 winter flounder (28%) released in Plymouth Bay during 2008 and 2009 were observed to be estuarine spawners. A G-test for independence revealed no significant interannual variability (P=0.56) in the ratio of coastal and estuarine spawners between the two years. In total, only 12 of the 49 (25%) tagged winter flounder were noted to be estuarine spawners. The 95% upper confidence limit for this proportion was calculated to be 0.70. If spawning was restricted to estuaries, the proportion of winter flounder classified as estuarine spawners would be one (100%). Therefore, our results demonstrate that in the Plymouth Bay region of the Gulf of Maine, winter flounder spawning is not restricted to estuaries.

Eleven winter flounder were observed to be gravid females at the time of release. Only one of the three gravid females tagged in Plymouth Bay in November 2007 was later detected in the estuary, but not until May of the following year. Eight gravid females were tagged in Plymouth Bay on 8 May 2009. Two of these individuals migrated rapidly to the mouth of the estuary. These females were detected at the mouth of the estuary six and ten days after release, respectively. Whether these individuals spawned in the estuary, or migrated to the estuary after spawning in coastal waters is unknown. It was apparent that the six of eight gravid winter flounder remained in Plymouth Bay after being tagged.

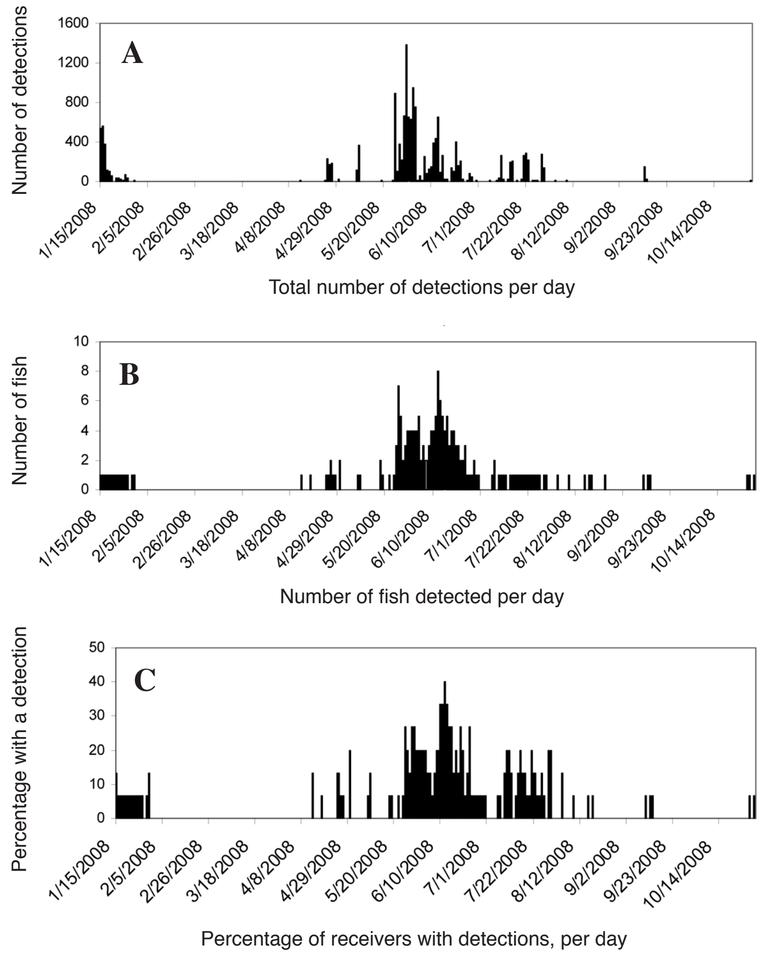

Figure 3

Temporal patterns of winter flounder (*Pseudopleuronectes americanus*) detections obtained by using passive acoustic telemetry in the Plymouth Estuary, MA, between January 2008 and October 2008. (**A**) The total number of detections each day. (**B**) The number of tagged winter flounder that were detected each day. (**C**) The percentage of acoustic receivers that detected a tagged winter flounder during each day of the study.

Seasonal distribution

The seasonal distribution of tagged winter flounder in the Plymouth Bay region became apparent after two years of passive telemetry. Adult winter flounder were largely absent from the Plymouth estuary during the winter months in both years. Only four of the 38 tagged winter flounder at large during the winter of 2008 and 2009 were detected in the Plymouth estuary (Figs. 3 and 4). In the winter of 2008, temperatures were warmer and more stable in Plymouth Bay (range=1.2–5.0°C) than in the Plymouth estuary (range=-1.24–5.2°C) (Fig. 5). In the winter of 2009, the observed temperature ranges were similar in Plymouth Bay (–0.6–5.0°C) and the Plymouth estuary (–0.9–5.9°C).

The movement of winter flounder into the Plymouth estuary began during the spring and was coincident with an increase in water temperature. Some tagged winter flounder began to migrate into the estuary in mid-April, when estuarine temperatures ranged from 9° to 12°C. In 2008, the mean temperature observed when winter flounder migrated from Plymouth Bay in to the Plymouth Estuary was 10.9°C. Tagged flounder were most abundant within the estuary between May and early June (Figs. 3 and 4) when temperatures ranged from 9° to 16°C, and this was also the only period when we were able to capture adult flounder in the estuary. The majority of winter flounder tagged in 2009 remained in the coastal waters of Plymouth Bay in late spring, where water temperatures ranged from 9° to 13°C.

We observed an emigration of tagged winter flounder from the Plymouth estuary during the onset of summer, as water temperatures increased. The mean observed temperature when tagged winter flounder emigrated from the estuary was 13.9°C, and 89% of all recorded departures from the estuary occurred when bottom temperatures were >12°C. In 2008, 18 of the 23 (78%) winter flounder tagged within the estuary migrated to coastal waters over a three week period from 30 May to 19 June (Fig. 6). This emigration coincided with a sharp increase in water temperature throughout the estuary. As of 19 June 2008, water temperatures exceeded 15°C in all but the deepest portion of the estuary. During July and August of 2008 when temperatures reached their seasonal maxima, no winter flounder were detected in the upper reaches of the estuary, and six winter flounder were detected at the mouth of the estuary, where temperatures were the coolest. In July 2009, only one winter flounder was detected in the estuary, for a period of one day.

Our observations on the autumn distribution of winter flounder in the Plymouth estuary were limited to 2008. Results indicated that five tagged individuals returned to the estuary as water temperatures decreased below their seasonal maxima.

For tagged winter flounder that were detected in the estuary, residence times within the estuary ranged from 2 to 91 days (mean=29 days). The estuarine residence times of fish tagged in Plymouth Bay (mean=40 days) were significantly greater than the residence times for winter flounder tagged in the estuary (mean=22 days) (single-factor ANOVA; P=0.025). No relationship was found between fish size and estuarine residence time (P=0.88). For winter flounder tagged within the Plymouth estuary in 2008, the observed residence time is almost certainly an underestimate because it is unknown how long these fish were present in the estuary before being tagged.

Detections of tagged winter flounder were not uniformly distributed throughout the study site. In the first year of the study, the inner gate of acoustic receivers typically detected more flounder and had more detections than receivers located within the estuary (Fig. 7, A and B). Tagged winter flounder were detected throughout the estuary, and seven of the nine receivers inside the estuary detected at least one tagged flounder. In the second year of the study, tagged winter flounder were most commonly detected in the coastal waters of Plymouth Bay. The outer gate of receivers in Plymouth Bay typically detected the greatest number of winter flounder and had the largest number of detections (Fig. 7, C and D). Two tagged winter flounder (Tags 53876 and 53886) remained at the inner gate for long periods of time within the detection radii of receivers G and K, which accounted for the large number of detections by these receivers (Fig. 7D). In 2009, tagged winter flounder were detected at only three of the 12 receivers inside the estuary, and the low number of detections (<1000) at these three receivers indicates that residence within the estuary was brief. The bimodal distribution of receiver detections (e.g., Fig. 7C) supports the inference of divergent habitat use, spawning behaviors, and contingent structure.

Two tagged winter flounder were detected at receivers used by other

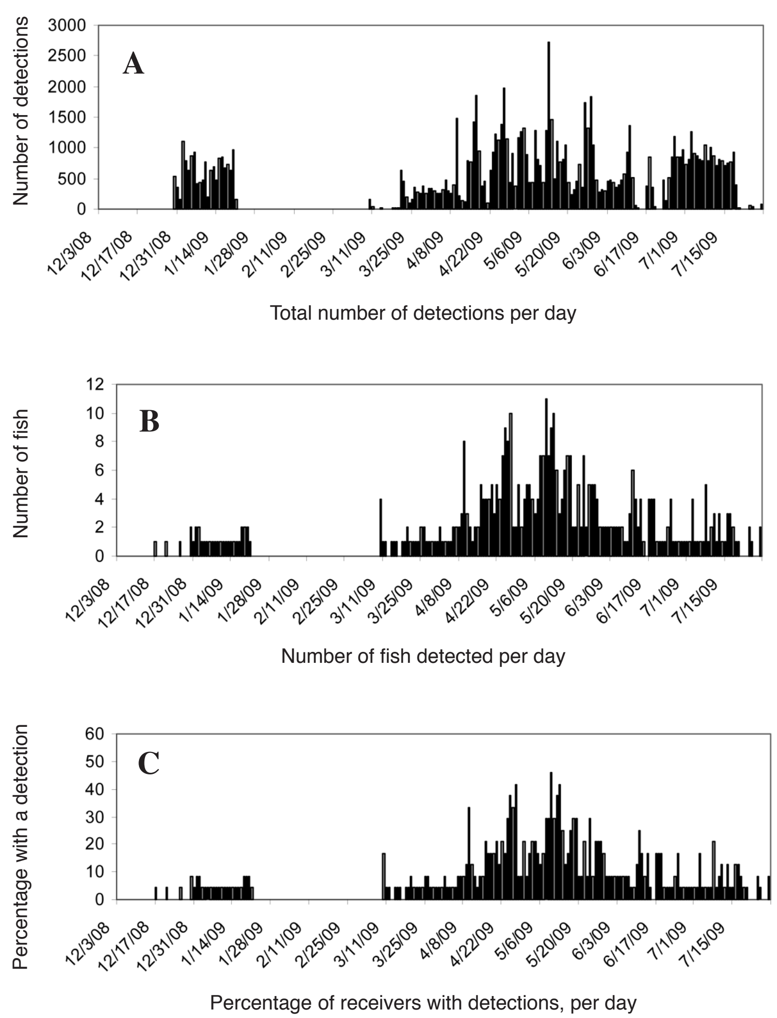

Figure 4

Temporal patterns of winter flounder (*Pseudopleuronectes americanus*) detections obtained by using passive acoustic telemetry in the Plymouth Estuary and Plymouth Bay, MA, between December 2008 and July 2009. (**A**) The total number of detections each day. (**B**) The number of tagged winter flounder that were detected each day. (**C**) The percentage of acoustic receivers that detected a tagged winter flounder during each day of the study.

researchers (W. Hoffman, personal commun.[4]), documenting more substantial movements beyond the study area. One tagged winter flounder (tag 5837) moved from the Gulf of Maine stock area to the SNE–MA stock area and was detected east of Cape Cod on 26 August 2008 (Table 1). This individual was tagged in Plymouth Bay on 30 November 2007 and was never detected in our receiver array. Tag 53877 was detected throughout our array in 2009 and was later detected in Massachusetts Bay on 26 August 2009 (Table 1).

Receiver efficiency

Despite the loss of some receivers, it appears that the array was efficient for the detection of the migrations of winter flounder. Twenty eight winter flounder released during the first year of the study were later detected in the estuary. Each fish was detected in the estuary an average of 416 times (range=1–3227 detections) at an average rate of 1.9 detections/day at liberty. Seventeen of the 24 winter flounder released in Plymouth Bay were never detected inside the estuary. These 24 winter flounder were released outside the receiver array that was used in the first year (Fig. 1); therefore, if these fish remained in coastal waters they would not have been detected by our array. Twenty two of the 25 winter flounder released in the second year of the study were later detected in our array. On average, each tagged winter flounder was detected 2861 times (range 57–23,842 detections) at an average rate of 14.1 detections/day at liberty. Winter flounder tagged on 8 May 2009, were released slightly eastward of the receiver array (Fig. 1), and this location may explain why two of these tagged fish were never detected again.

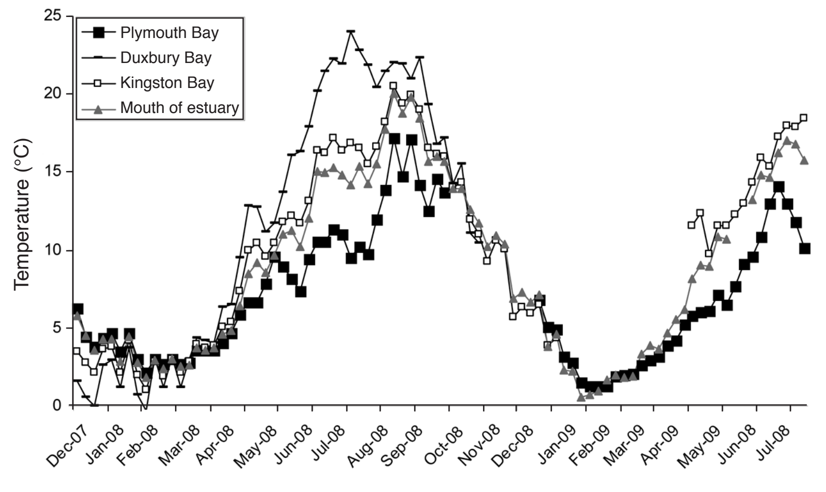

Figure 5

Weekly averaged bottom water temperatures observed between November 2007 and July 2009. Water temperature was recorded every 30 minutes at four locations during the study: Plymouth Bay; the mouth of the Plymouth Estuary; Kingston Bay (western portion of Plymouth Estuary); and Duxbury Bay (northern portion of Plymouth Estuary).

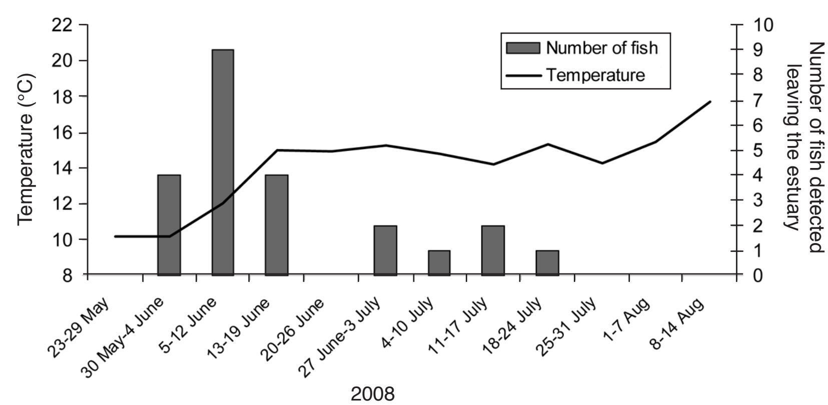

Figure 6

The relationship between water temperature and the emigration of tagged winter flounder (*Pseudopleuronectes americanus*) from the Plymouth Estuary in 2008. Winter flounder emigrated rapidly from the Plymouth Estuary as water temperatures increased from 10° to 15°C at the beginning of the summer.

In the fall of 2008, receivers I and M were lost from the inner gate of receivers that spanned the mouth of the estuary. After these receivers were lost, two tagged winter flounder (tags 5833 and 5873) were detected inside the estuary at the end of September and October, respectively, without being detected at the inner gate of receivers. One flounder (tag 5855) was released inside the estuary on 24 May 2008, and was detected two days later at receiver D. However, this individual was never detected at another receiver during the study. The fate of this fish is unknown. It may have been captured in the recreational fishery, eaten by another animal, or died after having been tagged. This was the only winter flounder that was released and detected inside the estuary (tag 5855) that was never detected at the inner gate. In the second year of the study, only one tagged winter flounder (tag 53894) that was detected inside

[4] Hoffman, William. 2009. Massachusetts Division of Marine Fisheries, Gloucester, MA 01930.

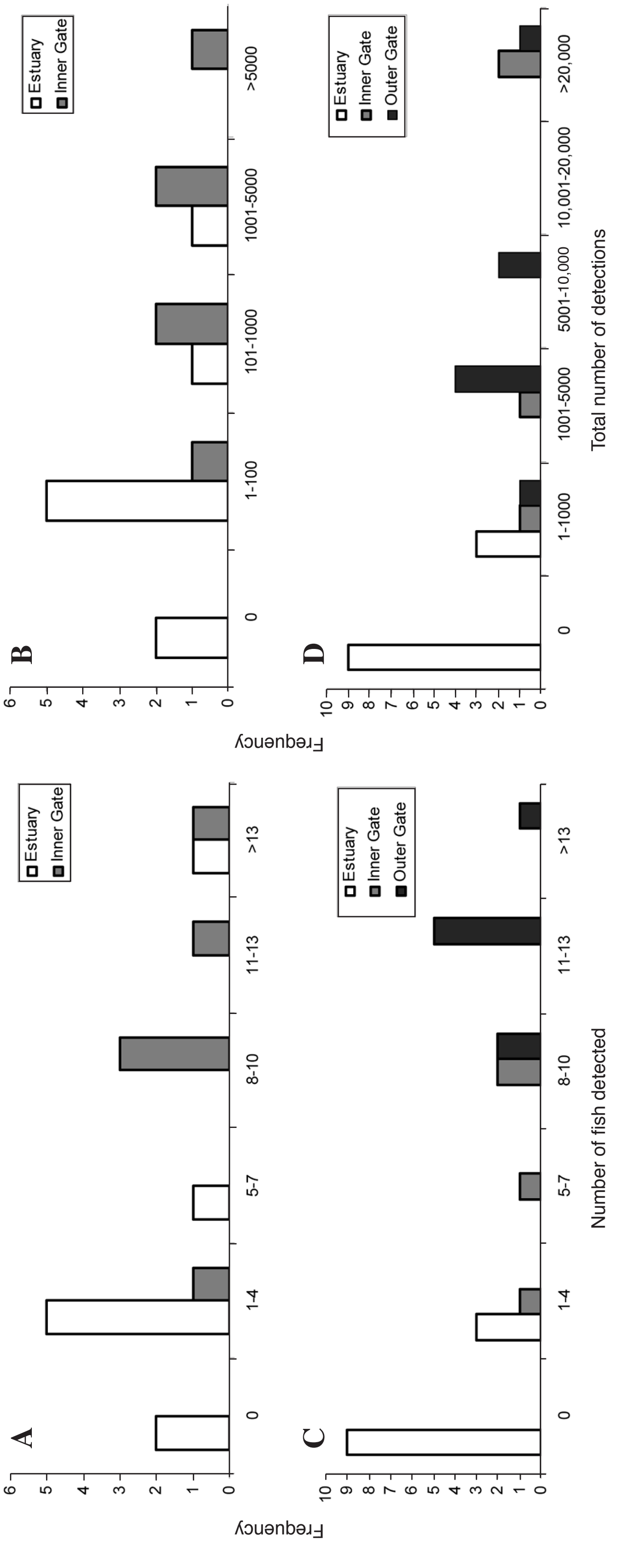

Figure 7

Histograms depicting (**A**) the number of tagged winter flounder (*Pseudopleuronectes americanus*) detected at each receiver, and (**B**) the total number of detections recorded in the Plymouth Estuary between November 2007 and November 2008. Histograms depicting (**C**) the number of tagged winter flounder detected at each receiver, and (**D**) the total number of detections at each receiver in Plymouth Bay and the Plymouth Estuary between December 2008 and July 2009.

of the estuary without first being detected at the inner gate. However, this individual was later detected at the inner gate when it emigrated from the estuary in May.

A quantitative assessment of the efficiency of the outer gate receivers in Plymouth Bay is more difficult. It is unlikely that winter flounder were able to pass between adjacent receivers without being detected, because tagged winter flounder were commonly detected simultaneously at two or three adjacent receivers in Plymouth Bay, indicating that these receivers had overlapping detection radii. Unfortunately, the receivers that were lost (P and Y) were each at the edges of the outer gate. Therefore, it is difficult to assess how many fish may have moved from Plymouth Bay to Cape Cod Bay without being detected.

Discussion

Using acoustic telemetry, we were able observe the movements of adult winter flounder in the southern Gulf of Maine with high spatial and temporal resolution. In particular, we were able to investigate the spawning behavior of tagged winter flounder in the vicinity of Plymouth Bay and assess the seasonal distribution of tagged flounder in the region. This approach yielded valuable insight into the life history of this species.

Spawning behavior of winter flounder

Our observations support the hypothesis that winter flounder spawning in the Gulf of Maine is not restricted to estuaries. Two sympatric contingents of winter flounder were observed, both of which exhibited divergent spawning migrations. The majority of adults tagged in coastal waters (76%) were absent from the estuary during the peak spawning months of March through May. In addition, eight of the eleven tagged winter flounder that were observed to be gravid did not enter the estuary during the spawning period.

Evidence of coastal spawning by winter flounder in Plymouth Bay was also found in previous studies. Ichthyoplankton sampling has been conducted in this region for decades to assess the impacts of the Pilgrim Nuclear Power Station (PNPS), which is on the southeast shore of Plymouth Bay. Researchers at Marine Research, Inc.[5] used a physical model to estimate the time it would take for eggs spawned in the Plymouth estuary to drift to Plymouth Bay near the power plant. They collected and aged eggs at PNPS and found that a proportion of the eggs had been spawned too recently to have originated from the estuary. They concluded that these eggs had been spawned in Plymouth Bay, rather than the estuary.

Evidence for coastal spawning has also been noted in other regions of the Gulf of Maine. Howe and Coates (1975) suggested that coastal spawning groups may exist on the basis of their observations of tagged flounder captured in coastal and offshore waters during the spawning season. Data collected during the NOAA Northeast Fisheries Science Center annual spring trawl survey have shown that the mean depth occupied by winter flounder in the Gulf of Maine has increased significantly over the last 40 years (Nye et al., 2009). This increase in depth may reflect a broad shift from estuarine to coastal spawning in the Gulf of Maine stock.

Winter flounder do not require estuaries as spawning habitat. This is evidenced by the large, self-sustaining stock of winter flounder that is present on Georges Bank (NMFS, 1999). Rather, estuarine spawning appears to be a strategy to maintain localized population structure. Tagging studies have shown that winter flounder display homing to their spawning grounds (Perlmutter, 1947; Saila, 1961). Dispersal is limited or nonexistent during the egg stage. In addition, larval behavior and estuarine hydrographic features promote the retention of larvae within estuarine spawning areas (Pearcy, 1962; Crawford and Carey, 1985; Chant et al., 2000). These characteristics, which promote local population structure, also make winter flounder vulnerable to human impacts.

Anthropogenic impacts such as dredging, pollution, eutrophication, and elevated temperatures often occur in estuaries (Nelson et al., 1991), and these activities can reduce the survival of winter flounder eggs, larvae, and juveniles. Estuaries are relatively small in size and are more susceptible to changes in water temperature than are coastal waters (Abood and Metzger, 1996). Elevated temperatures have been shown to reduce the survival and fitness of winter flounder eggs (Keller and Klein-MacPhee, 2000) and winter flounder has been identified as a species that is particularly vulnerable to global warming (Rose, 2005). A closed population of winter flounder that relies solely on an estuary as a spawning and nursery ground will likely exhibit poor recruitment, if that estuary has been degraded by human activities. Homing to spawning grounds by adults may be unfavorable when conditions do not inhibit the act of spawning but do diminish the survival of eggs and larvae (Harden Jones, 1968). Harden Jones (1968) also concluded that strict natal homing was not a sustainable life history strategy and that diverse migration behaviors are needed for a population to persist in a changing environment.

Divergent migrations impart resilience to populations against spatial variability in mortality (Secor, 1999). Passive telemetry revealed that winter flounder in the southern Gulf of Maine exhibit spatial heterogeneity in their use of spawning habitat and that coastal spawning was prevalent. Compared to estuarine spawning, coastal spawning likely leads to a greater dispersal of larvae. Therefore, a single coastal spawning contingent may provide a larval source for one or more estuarine nursery grounds. Coastal spawning contingents may confer resilience in a regional population during periods when estuarine productivity is low.

Our results indicate that coastal waters may provide essential spawning habitats for winter flounder in the Gulf of Maine. However, future research is needed to identify the prevalence of coastal spawning in other regions of the Gulf of Maine. Acoustic telemetry is a promising tool for conducting this research. For example, receiver gates could be placed across the mouths of estuaries along the coast, in a design similar to the one proposed by Grotheus and Able (2007). Ichthyoplankton studies could also be used to compare the densities of winter flounder eggs in estuarine and coastal waters. High-resolution trawl surveys could be used to sample the reproductive condition of winter flounder throughout the Gulf of Maine. Finally, coupled biophysical models would allow an examination of the dispersal of coastal spawned larvae in the Gulf of Maine.

Seasonal distribution of winter flounder

Bigelow and Schroeder (1953) and McCracken (1963) observed that flounder north of Cape Cod are more abundant in deeper, coastal waters during the winter months. Our observations in one region of the Gulf of Maine support this claim because only 10% of tagged of winter flounder at large during the winter months were detected within the shallow waters of the Plymouth estuary. Contrary to our observations, Howe and Coates (1975) claimed that flounder in the Gulf of Maine moved farther inshore into estuaries during the winter months. However, their analysis may have been hampered by a lack of tag returns during the fall and winter months.

Winter flounder in Newfoundland are thought to move to deeper coastal waters during the winter to avoid ice formation and extreme turbulence during storm events (Van Guelpen and Davis, 1979). Winter flounder may

[5] Marine Research, Inc. 1986. Winter flounder early life history studies related to the operation of Pilgrim Station—A review 1975–1984. Pilgrim Nuclear Power Station Environmental Monitoring Program – Report Series No. 2, 111 p. Boston Edison Company, Boston, MA.

also migrate to deeper waters during the winter to prevent their blood serum from freezing, which occurs between –1.25 and –1.38°C (Fletcher, 1977). Temperatures in the Plymouth estuary dropped to as low as –1.55°C during the winter of 2008, whereas the minimum recorded temperature in Plymouth Bay was 1.2°C. Therefore, the deeper waters of Plymouth Bay may act as a refuge from the extreme cold temperatures and ice formation that are present in the Plymouth estuary during the winter.

Tagged winter flounder were most commonly present in the estuary during the late spring, when water temperatures ranged from 9° to 16°C, which is within the preferred temperature range (12–15°C) of this species (McCracken, 1963; Reynolds, 1977). Although winter flounder were common in the estuary during the late spring, the majority of the tagged winter flounder remained in coastal waters during this period. Howe and Coates (1975) also reported that winter flounder are concentrated in shoal areas during the spring months. Although we were unable to capture adult winter flounder in the estuary from March through early May 2008, we cannot conclude that winter flounder were not present in the estuary during this time. Winter flounder in spawning condition often cease feeding or reduce their food intake (NMFS, 1999) and therefore it is less likely that we would have captured flounder using hook-and-line gear during the spawning season. In addition, flounder that were buried in the sediment may not have been available to the small trawl net that we were using to capture flounder in the estuary.

The emigration of winter flounder from the estuary coincided with rising temperatures at the onset of summer. Between 30 May and 19 June 2008 the majority of tagged winter flounder emigrated from the estuary as water temperature increased from 10° to 15°C (Fig. 6). These observations were consistent with previous reports that revealed that winter flounder will migrate to cooler waters when temperatures exceed 15°C (Bigelow and Schroeder, 1953; McCracken, 1963). Perlmutter (1947) found that the movements of winter flounder north of Cape Cod are typically localized, and Howe and Coates (1975) calculated that the average displacement of winter flounder tagged in Plymouth Bay was only 3 km. They also found that in the Gulf of Maine, winter flounder could find suitable temperatures (between 12° and 17°C) within 2 km of the shore zone during the summer. Weekly averaged temperatures in Plymouth Bay only exceeded 15°C twice in 2008, and did not exceed 15°C in 2009. Therefore, winter flounder leaving the Plymouth estuary were not forced to migrate long distances to reach suitable temperatures.

During the autumn months of 2008 five tagged individuals returned to the estuary as water temperatures decreased below their seasonal maxima. Bigelow and Schroeder (1953) also noted that winter flounder will return to the Plymouth estuary during the autumn months when temperatures start to cool.

Conclusions

By collecting large amounts of high-resolution data, we are able to offer insight into the fine-scale behavior and distribution of winter flounder in the southern Gulf of Maine. Our results indicate that winter flounder exhibit divergent spawning behaviors which support inferences of contingent structure and that coastal waters may provide essential spawning grounds for this species. As such, coastal waters should merit consideration in the assignment of Essential Fish Habitat for this species in the Gulf of Maine. In this region of the Gulf of Maine, estuarine residence appears to be brief, and dependent upon water temperature.

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Literature cited

Able, K. W.
2005. A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. Est. Coast. Shelf Sci. 64:5–17.

Able, K. W., and T. M. Grothues.
2007. An approach to understanding habitat dynamics of flatfishes: advantages of biotelemetry. J. Sea Res. 58:1–7.

Abood, K. A., and S. G. Metzger.
1996. Comparing impacts to shallow water habitats through time and space. Estuaries 19(2A):220–228.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull 53:1–577.

Cadrin, S. X., and D. H. Secor.
2009. Accounting for spatial population structure in stock assessment: past, present and future. *In* The future of fisheries science in North America, fish and fisheries series (R. J. Beamish, and B. J. Rothschild, eds.), p. 405– 426. Springer Science + Business Media B.V., New York.

Chant, R. J., M. C. Curran, K. W. Able, and S. M. Glenn.
2000. Delivery of winter flounder (*Pseudopleuronectes americanus*) larvae to settlement habitats in coves near tidal inlets. Estuar. Coast. Shelf Sci.51:529–541.

Crawford R. E., and C. G. Carey.
1985. Retention of winter flounder larvae within a Rhode Island salt pond. Estuaries 8:217–227.

Davis, J. D.
1984. Western Cape Cod Bay: hydrographic, geological, ecological and meteorological backgrounds for environmental studies. *In* Observations on the ecology and biology of western Cape Cod Bay, Massachusetts (J. D. Davis, and D. Merriman, eds.), p. 1–18. Springer-Verlag, New York.

Fairchild, E. A., N. Rennels, and H. Howell.
2009. Using telemetry to monitor movements and habitat use of cultures and wild juvenile winter flounder in a shallow estuary. *In* Tagging and tracking of marine animals with electronic devices (J. L. Neilsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert, eds.), p. 5–22. Springer Science + Business Media B.V., New York.

Fletcher, G. L.
1977. Circannual cycles of blood plasma freezing point and Na^+ and Cl^- concentration in Newfoundland winter flounder (*Pseudopleuronectes americanus*): correlation with water temperature and photoperiod. Can. J. Zool. 53:197–206.

Grothues, T. M., and K. W. Able.
2007. Scaling acoustic telemetry of bluefish in an estuarine observatory: detection and habitat use patterns. Trans. Am. Fish. Soc. 136:1511–1519.

Harden Jones, F. R.
1968. Fish migration, 325 p. Edward Arnold (Publishers) Ltd., London.

Heupel, M. R., J. M. Semmens, and A. J. Hobday.
2006. Automated acoustic tracking of aquatic animals: scales, designs and deployment of listening station arrays. Mar. Freshw. Res. 57:1–13.

Howe, A. B., and P. G. Coates.
1975. Winter flounder movements, growth and mortality off Massachusetts. Trans. Am. Fish. Soc. 104:13–29.

Keller, A. A., and G. Klein-MacPhee.
2000. Impacts of elevated temperature on the growth, survival and trophic dynamics of winter flounder larvae: a mesocosm study. Can. J. Fish. Aquat. Sci. 57:2382–2392.

Kerr, L. A., S. X. Cadrin, and D. H. Secor.
2010. The role of spatial dynamics on the stability, resilience and productivity of fish populations: an example based on white perch in the Chesapeake Bay. Ecol. Appl. 20:497–507.

Lambert, T. C.
1990. The effect of population structure on the recruitment of herring. J. Cons. Int. Explor. Mer 47:249–255.

Lawton, R. P., R. D. Anderson, P. Brady, C. Sheehan, W. Sides, E. Kouloheras, M., Borgatti, and V. Malkoski.
1984. Fishes of the inshore Cape Cod Bay: studies in the vicinity of the Rocky Point shoreline. *In* Observations on the ecology and biology of western Cape Cod Bay, Massachusetts (J. D. Davis, and D. Merriman, eds.), p. 191–230. Springer-Verlag, New York.

McCracken, F. D.
1963. Seasonal movements of the winter flounder *Pseudopleuronectes americanus* (Walbaum), on the Atlantic coast. J. Fish. Res. Board Can. 20:551–586.

NMFS (National Marine Fisheries Service).
1999. Winter flounder, *Pseudopleuronectes americanus*, Life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-138, 39 p.

Nelson, D. A., J. E. Miller, D. Rusanowsky, R. A. Greig, G. R. Sennfelder, R. Mercaldo-Allen, C. Kuropat, E. Gould, F. P. Thurberg, and A. Calabrese.
1991. Comparative reproductive success of winter flounder in Long Island Sound: a three year study (biology, biochemistry and chemistry). Estuaries 14:318–331.

Nye, J. A., J. S. Link, J. A. Hare, and W. J. Overholtz.
2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar. Ecol. Prog. 393:111–129.

Pearcy, W. G.
1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). Parts I–IV. Bull. Bingham Oceanogr. Coll. 18:1–78.

Perlmutter, A.
1947. The blackback flounder and its fishery in New England and New York. Bull. Bingham Oceanogr. Coll. 11:1–92.

Reynolds, W. W.
1977. Fish orientation behavior: an electronic device for studying simultaneous responses to two variables. J. Fish. Res. Board Can. 34:300–304.

Rose, G. A.
2005. On distributional responses of North Atlantic fish to climate change. ICES J. Mar. Sci. 62:1360–1374.

Saila, S. B.
1961. A study of winter flounder movements. Limnol. Oceanogr. 6:292–298.

Secor, D. H.
1999. Specifying divergent migration in the concept of stock: the contingent hypothesis. Fish. Res. 43:13–34.
2007. The year-class phenomenon and the storage effect in marine fishes. J. Sea Res. 57:91–103.

Sokal, R. R., and F. J. Rohlf.
2001. Biometry. 3rd ed., 887 p. W. H. Freeman and Co., New York.

Van Guelpen, L., and C. C. Davis.
1979. Seasonal movements of the winter flounder, *Pseudopleuronectes americanus*, in two contrasting inshore locations in Newfoundland. Trans. Am. Fish. Soc. 198:26–37.