Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 11:202–212, 2019

ISSN: 1942-5120 online
DOI: 10.1002/mcf2.10070

ARTICLE

First Observations of Long-Distance Migration in a Large Skate Species, the Winter Skate: Implications for Population Connectivity, Ecosystem Dynamics, and Management

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Abstract

The overexploitation and decline of groundfish populations throughout the 1980s and 1990s resulted in a regime shift on Georges Bank and southern New England, which was characterized by subsequent exponential increases in the observed biomass of Winter Skate *Leucoraja ocellata* in the region. Recent work suggested that the rate of the Winter Skate biomass increase cannot be fully explained by internal population dynamics of a population without immigration from other regions and/or populations and that adult-mediated population connectivity (AMPC) with neighboring regions is required to fully explain biomass trends. Despite this, no evidence of long-distance dispersal has been observed for Winter Skate, with individuals assumed to display high endemicity to specific regions of the continental shelf. Annual movements of 58 Winter Skate captured off coastal New York were examined using passive acoustic telemetry, revealing seasonal long-distance dispersal capabilities exceeding 1,000 km. In total, 88,783 unique acoustic detections were observed. Telemetered individuals had an average time at liberty of 199.73 d and collectively traveled 17,576.9 km. Individuals tended to migrate south during summer/fall and north during winter/spring. Movement rates of individuals averaged 9.88 km/d (95% confidence interval = 9.25–10.92 km/d) but ranged from 0.13 to

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Subject editor: Debra J. Murie, University of Florida, Gainesville

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Received November 12, 2018; accepted March 18, 2019

41.38 km/d. An additional 51 recaptured Winter Skate from a total of 3,416 marked with Floy tags suggested greater offshore movement than was observed in acoustically tagged individuals. Our results illustrate that the Winter Skate is a highly mobile species that moves extensively throughout its large geographic range, consistent with its observed ability to rapidly invade neighboring habitat via AMPC. This study has important implications for our understanding of the role of Winter Skate in northwest Atlantic communities and for management strategies therein.

Understanding a species' capacity for dispersal can offer insight into a suite of ecological processes, such as population connectivity and structuring (Frisk et al. 2014; Neat et al. 2014; Sippel et al. 2015; Barkley et al. 2018), ecological niche dynamics (Matich and Heithaus 2015), and energy flow regimes (Papastamatiou et al. 2015; Doughty et al. 2016). Information on dispersal can also be used to identify populations that are particularly vulnerable to extrinsic stressors, such as commercial fisheries interactions, pollution, and habitat fragmentation (e.g., Knip et al. 2010; Urban et al. 2013; Queiroz et al. 2016; Byrne et al. 2017). For many marine species, acquiring movement data is often challenging due to poor access to study sites and low encounter success (Lennox et al. 2017). The rapid technological development of biologging devices (e.g., satellite/acoustic telemetry and acceleration data loggers) in more recent years, however, has revolutionized the study of animal dispersal (Hussey et al. 2015; Crossin et al. 2017). Furthermore, coupling broad-scale patterns of dispersal with biogeophysical parameters (e.g., temperature, primary production, and dissolved oxygen; Vaudo et al. 2016; Howey et al. 2017) has allowed scientists to unravel otherwise cryptic components of organismal life histories, which is imperative to improving the conservation of highly threatened populations, communities, and ecosystems (Hussey et al. 2015; Lennox et al. 2017; Brooks et al., in press).

The Winter Skate *Leucoraja ocellata* is a common benthic predator that is found extensively throughout the temperate northwest Atlantic Ocean, with a range extending from Labrador to the Carolinas (Kulka et al. 2009). Despite populations displaying distributional shifts across seasons (Zacharias 2013), individuals have been traditionally assumed to exhibit limited dispersal and high fidelity to localized regions of the continental shelf. Over the last 40 years, the Winter Skate has received increased attention in the scientific literature, as exponential increases in the biomass of "economically unfavorable" elasmobranchs were observed across the northwest Atlantic in a so-called "elasmobranch outburst" that followed the exploitation and subsequent crash of groundfish populations on Georges Bank and southern New England (Murawski 1991; Mayo et al. 1992; Fogarty and Murawski 1998; Frisk et al. 2008). Although the idea of a "regime shift" is accepted, debate remains over its ultimate causation, particularly as fine-scale population dynamics of the predominant species base (i.e., the Spiny Dogfish *Squalus acanthias* and Winter Skate) remain poorly defined (Frisk et al. 2008, 2014). Significant support, however, suggests that the most extreme biomass changes occurred in Winter Skate compared to other skate species. Further understanding of the population dynamics of Winter Skate is therefore fundamental in assigning causation to the patterns of biomass increase that led to the regime shift hypothesis (Frisk et al. 2008, 2014).

Central to the regime shift hypothesis is the notion that a rapid biomass increase in Winter Skate was underpinned by competitive release and subsequent increases to fundamental niche space, coupled with internal life history dynamics (e.g., growth and reproduction). However, recent work has argued that the conservative internal population dynamics (i.e., slow growth, late maturation, and low fecundity) of Winter Skate cannot fully explain biomass trends, especially if the population is assumed to be closed (Frisk et al. 2008, 2010, 2014). Frisk et al. (2008) proposed that an elevated complexity of population dynamics is required to fully explain increases in biomass, potentially facilitated by high mobility of adults from other regions, such as the Scotian Shelf. Evidence for this hypothesis (hereafter, the "adult-mediated population connectivity [AMPC] hypothesis"; Frisk et al. 2014) was supported by survey data and was explored in modeling frameworks (Frisk et al. 2011). Specifically, Frisk et al. (2011) compared statistical catch-at-age models that tested model structures representing the AMPC and competitive release hypotheses. Results strongly suggested that adult movement was responsible for the large increase in Winter Skate biomass on Georges Bank and southern New England. However, no observations of long-distance movement in Winter Skate have been published, leaving a critical gap in the notion of large-scale adult movement.

In the present study, acoustic telemetry and mark–recapture data were used to evaluate the AMPC hypothesis by examining long-term movement patterns of individual adult Winter Skate captured throughout the New York Bight and coastal New Jersey regions. Specifically, our objectives were to (1) determine dispersal capabilities, (2) estimate movement rates, and (3) examine seasonal migration patterns. These observations have implications for existing hypotheses regarding the northwest Atlantic regime shift and can be directly applied to contemporary management, as refining dispersal capabilities will further inform stock structure and broader population and ecosystem dynamics.

METHODS

Acoustic telemetry array.— An array of acoustic receivers (VR2W, 69 kHz; Vemco, Bedford, Nova Scotia, Canada) was deployed and maintained by Stony Brook University along the coast from Delaware Bay to Montauk, New York (for further details, see Melnychuk et al. 2017). Each array consisted of a string of at least eight receivers (8–26), spaced approximately 1.0–1.2 km apart, which extended from 0.5 to 9 km offshore (Figure 1). Each acoustic receiver was anchored to the seabed at depths ranging from 7 to 31 m. Array locations were maintained during the study period from 2012 to 2014. Array coverage was usually higher than 70% (i.e., more than 70% of the receivers were active at any one time) but occasionally dropped to 50% for brief periods (Melnychuk et al. 2017). Previous studies estimated detection probability of each array at greater than 40%, with a range from 20% to 90% (Melnychuk et al. 2017). To gain additional coverage beyond the arrays maintained by Stony Brook University, opportunistic acoustic detections were also gathered from collaborators in the Atlantic Cooperative Telemetry Network.

Animal capture and tagging.— Winter Skate were tagged opportunistically aboard the RV *Seawolf* during scientific bottom trawl surveys along the coast of Long Island between 2012 and 2014 (see Dunton et al. 2010, 2015 for complete methods). Winter Skate that were selected for tagging were immediately placed in a 757-L holding tank with flowing raw seawater and aeration. All individuals were measured for TL (nearest cm), sexed, and tagged (n = 3,416) with a unique Floy T-bar anchor tag (Model FD-94 or FD-94HD; hereafter, “Floy tag”; Floy Tag & Manufacturing, Seattle). A subset (n = 58) of captured individuals were either externally tagged or surgically implanted with Vemco V16-4H ultrasonic transmitters (69 kHz; high-power output = 158 dB re 1 μPa at 1 m; random transmitter delay = 50–130 s [1,952-d tag life] or 70–150 s [2,331-d tag life]). External transmitters were attached using stainless-steel wire inserted through both ends of the external tag case and the pectoral fin lateral of the pectoral girdle by using a 16/0 hypodermic needle to ensure placement through the pectoral radials. Wire was given a cradle made from an oval laminate Floy tag to ensure that the wire would not pull through. Individuals were placed into tonic immobility during surgical implantation of acoustic tags, in accordance with the recommendations of Henningsen (1994) and Kessel and Hussey (2015).

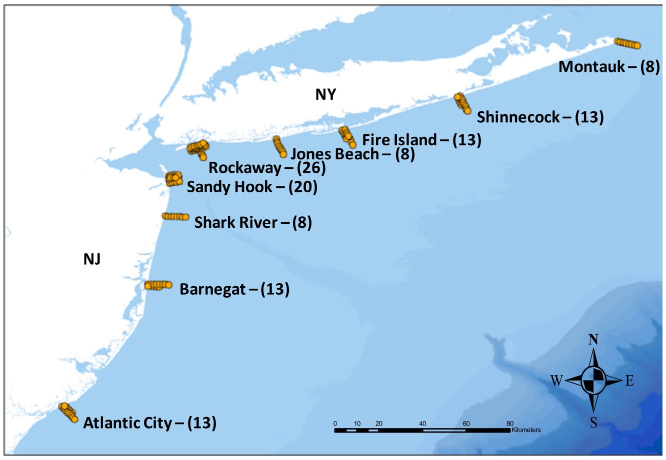

FIGURE 1. Map of acoustic listening arrays maintained by Stony Brook University. The number in parentheses represents the number of receivers in the array.

Movement analyses.— Raw acoustic data were organized in Microsoft database organizing software (Access and Excel). A detection was considered valid if three or more acoustic signals were recorded on a listening array; all other detections were considered false positives. Telemetered individuals were tracked and analyzed following their first detection at a listening array between May 9, 2012, and June 4, 2016. If an individual was only detected by a single listening array, mortality was assumed. The first and last detections of an individual's residence at a single listening array were recorded along with the date, latitude, and longitude. Upon detection at another listening array, the direction of movement (north or south) and the number of days at liberty were recorded. The distance between receivers was estimated as the shortest spherical distance based on latitude and longitude measured in degrees. The orthodromic distance between arrays was estimated using the spherical law of cosines:

$$d = \text{acos}[\sin(\varphi_1 \cdot c) \cdot \sin(\varphi_2) + \cos(\varphi_1 \cdot c) \cdot \cos(\varphi_2 \cdot c) \\ \cdot \cos(\varphi_2 \cdot c) - \cos(\varphi_1 \cdot c)] \cdot r,$$

where φ are latitude and longitude coordinates, c is $\frac{\pi}{180°}$, and r is the earth's radius (6,369 km) calculated for a latitude of 40°.

To characterize potential migration rates and seasonality of movement, we estimated the rate of movement and associated directionality. A movement event was defined by detection of an individual between two consecutive listening arrays (i.e., north to south or south to north). Movement rates (km/d) were then estimated and averaged across the sampled population. Some individuals may contribute to multiple movement events as they migrate through the arrays, and each event was assumed independent. No attempt was made to eliminate periods when an individual was not actively moving; thus, the estimate represents periods during times of residency as well as active migration.

Seasonality of detected movements for all events was assessed by examining the number of northerly and southerly movements by month. The average rate of directed movement was estimated for individuals over the monitored period, where directed movement is defined as an individual that traversed three listening arrays in a consistent direction (northward or southward). Movement rate data were not normally distributed, and 10,000 bootstrapped replicates of the mean were utilized to provide uncertainty estimates for all analyses. The 2.5th and 97.5th percentiles were reported as confidence intervals (CIs) along with estimates of the mean. All statistical analyses were performed in R software (R Core Team 2018). To estimate whether movement direction (north versus south) differed from a 50:50 ratio during the spring and fall, an exact binomial two-tailed test was conducted. The spring season included April, May, June, and July, and the fall included September, October, November, and December; combined, these months accounted for 97% of detected movement events.

In Floy-tagged individuals, the distance traveled, rates of movement, and days at liberty were calculated as described above. However, recaptures were based on voluntary returns from recreational, commercial, and research fishers. Locations were provided by the fisher and ranged in accuracy from Global Positioning System-estimated coordinates to general regions, such as Cox's Ledge or Fire Island Inlet, New York. If the location was not discernible based on fisher-supplied information, it was removed from further analyses.

RESULTS

Overall, 58 Winter Skate (25 females and 33 males) were acoustically tagged and released with external ($n = 20$) and internal acoustic tags (Table 1). The TL of telemetered Winter Skate ranged from 58.5 to 104 cm, with an average of 80.7 cm. Weights ranged from 1.46 to 8.53 kg, with an average of 4.32 kg. In total, 88,783 unique detections were observed (Stony Brook array: $n = 88{,}557$; Atlantic Cooperative Telemetry Network: $n = 226$). Of the 58 tagged individuals, 53 were detected across multiple acoustic receivers. Four individuals (28879, 28880, 28909, and 28910; see Table 1) were only detected at initial tagging locations (Rockaway) and were assumed to have suffered mortality. The earliest detection occurred on December 8, 2012, and the last detection was observed on June 4, 2016. Mean time at liberty was 199.73 d but ranged from 3.42 to 1,122.54 d. Collectively, the 53 Winter Skate traveled 17,576.9 km, with an average of 331 km per individual; one notable individual moved 1,376.97 km in 375.77 d.

A total of 3,416 individuals (1,416 females, 1,526 males, and 463 fish of unknown sex) were fitted with Floy tags along the south shore of Long Island, New York, between 2007 and 2016. Additionally, 138 Winter Skate were tagged opportunistically during the North Carolina Cooperative Cruise in January 2013 (see Laney et al. 2007 for details). Overall, 51 Winter Skate were recaptured by fishers (31 by commercial fishers, 6 by researchers, 5 by recreational fishers, and 8 by fishers of unknown type). Additionally, one Winter Skate was reported from a carcass found on the beach. Winter Skate were recaptured as far north as Cape Cod and as far south as New Jersey. On average, Floy-tagged Winter Skate were at liberty for 230.9 d (range = 6–1,167 d). Collectively, the 51 recaptured Floy-tagged Winter Skate traveled an observed 7,599.69 km, with an average of 161.67 km.

Movement Rates

Movement rates for 53 acoustically telemetered individuals averaged 9.88 km/d (95% CI = 9.25–10.92 km/d) and ranged from 0.13 to 41.38 km/d. The northward movement rate ($n = 145$ unique events) averaged 9.1 km/d (95% CI = 8.0–10.34 km/d) and ranged from 0.131 to 41.38 km/d (Figure 2). The southern movement rate ($n = 89$ unique events) averaged 8.5 km/d (95% CI = 7.26–9.80 km/d) and ranged from 0.26 to 26.44 km/d. Migration showed peak periods during the spring and fall seasons. Winter Skate were detected moving northward and southward throughout the year. However, spring movements were primarily in a northward direction, while most fall movements were southward (Figure 3). During the spring, northerly movement was significantly different from a 50:50 ratio ($P \leq 0.000$), with a probability of northern movement equal to 0.77 (95% CI = 0.69–0.83). During the fall, southerly movement was significantly different from a 50:50 ratio ($P \leq 0.000$), with a probability of southern movement equal to 0.74 (95% CI = 0.61–0.84). For Floy-tagged Winter Skate, the average individual movement rate was 4.1 km/d (95% CI = 3.67–5.6 km/d), with a range of 0.01–19.5 km/d.

Long-Distance Movements

Winter Skate that were acoustically tagged off the coast of New York were detected as far north as Cape Cod, Massachusetts, and as far south as coastal North Carolina. Long-distance movement was reported in mature and immature individuals and in both males and females. Specific examples for four individuals are reported in Figure 4. A 68-cm TL male was tagged on June 1, 2014; traveled north to Cape Cod; migrated southward along the coast to the mouth of the Chesapeake Bay; and moved north along the coast, returning to Cape Cod (Figure 4A). The telemetered period lasted 374 d, and the individual completed 1,377 km of travel at a rate of at least 19 km/d. A 75-cm TL male completed a similar coastal route,

TABLE 1. Summary information for acoustic-tagged Winter Skate, including the unique identification code (Tag), TL (cm), date of tagging (Date), first date of valid detection (Detected), number of days at liberty (Liberty), distance (km) of detected travel (Total), average rate of movement (km/d; Avg. rate), and maximum rate of observed travel events (Max. rate).

Tag	Sex	TL (cm)	Date	Detected	Liberty (d)	Total (km)	Avg. rate (km/d)	Max. rate (km/d)
A69-9001-28865	Male	89.0	May 6, 2013	May 6, 2013	353.06	707.64	4.76	19.27
A69-9001-28867	Female	80.8	May 9, 2012	Nov 16, 2012	225.19	297.07	1.93	3.24
A69-9001-28868	Female	75.0	May 10, 2012	May 10, 2012	10.45	390.00	14.65	21.75
A69-9001-28869	Female	75.5	May 9, 2012	May 15, 2012	3.42	202.00	4.80	9.60
A69-9001-28870	Female	85.8	May 9, 2012	May 21, 2012	177.93	405.00	5.30	14.01
A69-9001-28871	Male	79.5	May 10, 2012	May 14, 2012	20.26	609.00	6.98	11.66
A69-9001-28872	Female	81.3	May 9, 2012	May 16, 2012	707.38	857.03	8.01	18.80
A69-9001-28873	Male	84.6	May 9, 2012	May 12, 2012	419.24	153.74	6.62	24.26
A69-9001-28874	Male	89.0	May 10, 2012	May 19, 2012	5.95	80.73	7.46	14.92
A69-9001-28875	Male	86.7	May 9, 2012	May 30, 2012	336.03	351.44	6.61	19.23
A69-9001-28876	Female	82.5	May 9, 2012	May 9, 2012	6.00	59.51	7.54	12.97
A69-9001-28877	Male	75.4	May 10, 2012	May 17, 2012	409.10	991.70	7.81	26.44
A69-9001-28878	Male	97.4	May 9, 2012	May 9, 2012	380.51	488.92	4.91	11.60
A69-9001-28879	Male	90.5	May 9, 2012	May 9, 2012				
A69-9001-28880	Female	77.7	May 9, 2012	May 18, 2012				
A69-9001-28881	Male	89.7	May 9, 2012	May 9, 2012	18.34	180.95	9.02	13.52
A69-9001-28882	Male	96.8	May 9, 2012	May 9, 2012	15.33	108.53	9.22	21.38
A69-9001-28883	Male	95.0	May 7, 2013	May 16, 2013	184.79	148.90	0.73	1.46
A69-9001-28884	Male	88.0	May 7, 2013	May 7, 2013	17.01	180.73	8.87	13.69
A69-9001-28885	Male	88.5	May 7, 2013	May 7, 2013	28.27	108.53	6.95	13.19
A69-9001-28886	Male	90.0	Oct 31, 2011	May 8, 2013	189.02	148.96	5.98	11.41
A69-9001-28887	Female	64.0	Oct 31, 2011	May 9, 2013	25.45	180.95	8.07	13.10
A69-9001-28889	Female	71.4	May 29, 2014	Jun 3, 2014	367.43	699.26	7.46	18.40
A69-9001-28890	Female	78.5	May 29, 2014	May 29, 2014	6.79	108.31	10.99	16.89
A69-9001-28891	Male	89.5	May 29, 2014	Jun 12, 2014	510.81	470.28	1.70	4.54
A69-9001-28892	Male	76.5	May 29, 2014	May 29, 2014	5.00	59.29	6.16	12.31
A69-9001-28893	Female	77.5	May 29, 2014	May 29, 2014	383.35	548.53	8.87	26.81
A69-9001-28894	Female	72.8	May 29, 2014	May 29, 2014	15.83	180.68	10.79	17.74
A69-9001-28895	Male	74.5	May 29, 2014	May 29, 2014	731.99	510.45	5.62	13.92
A69-9001-28896	Male	68.0	May 29, 2014	Jun 1, 2014	375.77	1,376.97	14.30	41.38
A69-9001-28897	Female	75.2	May 29, 2014	May 30, 2014	736.10	660.20	9.27	20.53
A69-9001-28898	Female	70.5	May 29, 2014	May 30, 2014	143.96	361.77	12.42	21.81
A69-9001-28899	Male	66.0	May 29, 2014	Jun 2, 2014				
A69-9001-28900	Female	67.0	May 29, 2014	May 30, 2014	353.03	831.60	5.63	14.80
A69-9001-28901	Female	58.5	May 11, 2012	May 11, 2012	1,122.54	648.13	4.13	11.73
A69-9001-28902	Male	73.5	May 11, 2012	May 11, 2012	392.51	356.63	5.80	14.30
A69-9001-28903	Female	69.0	May 29, 2014	May 29, 2014	170.42	407.55	6.25	14.61
A69-9001-28904	Female	79.0	May 29, 2014	May 29, 2014	9.55	59.51	4.32	6.67
A69-9001-28906	Male	77.0	May 10, 2012	May 10, 2012	14.42	108.31	5.42	8.72
A69-9001-28907	Male	88.8	May 10, 2012	May 10, 2012	6.83	108.53	15.19	24.23
A69-9001-28908	Male	81.4	May 10, 2012	May 10, 2012	107.46	180.95	9.92	21.34
A69-9001-28909	Male	76.5	May 10, 2012	May 10, 2012				
A69-9001-28910	Female	77.8	May 10, 2012	May 10, 2012				
A69-9001-28911	Female	77.2	May 10, 2012	May 10, 2012	49.50	180.73	9.97	15.30
A69-9001-28912	Female	74.3	May 10, 2012	May 10, 2012	46.40	180.95	5.95	10.69
A69-9001-28913	Female	76.5	May 10, 2012	May 14, 2012	40.05	76.54	1.59	3.07
A69-9001-28914	Male	78.2	May 10, 2012	May 10, 2012	34.53	180.95	4.43	6.91

TABLE 1. Continued.

Tag	Sex	TL (cm)	Date	Detected	Liberty (d)	Total (km)	Avg. rate (km/d)	Max. rate (km/d)
A69-9001-28915	Male	84.4	May 10, 2012	May 15, 2012	180.87	371.75	5.61	13.13
A69-9001-28916	Female	77.1	May 10, 2012	May 12, 2012	152.60	148.96	8.41	14.16
A69-9001-28917	Female	85.8	May 10, 2012	May 10, 2012	13.23	180.95	13.28	22.66
A69-9001-28918	Male	77.0	May 10, 2012	May 11, 2012	393.49	421.19	5.24	9.30
A69-9001-28919	Male	85.8	May 10, 2012	May 10, 2012	421.30	468.19	3.59	10.10
A69-9001-28920	Male	86.3	May 10, 2012	May 13, 2012	4.05	27.52	4.62	9.24
A69-9001-28921	Female	79.2	May 10, 2012	May 10, 2012	37.51	180.95	6.40	14.64
A69-9001-28922	Male	88.5	May 11, 2012	May 14, 2012	19.93	148.90	5.86	10.13
A69-9001-28923	Female	76.4	May 11, 2012	May 11, 2012	19.57	180.95	10.14	16.90
A69-9001-28924	Male	72.2	May 11, 2012	May 12, 2012	178.96	361.55	4.49	8.55
A69-9001-28925	Male	79.9	May 11, 2012	May 11, 2012	7.21	108.53	12.23	20.24

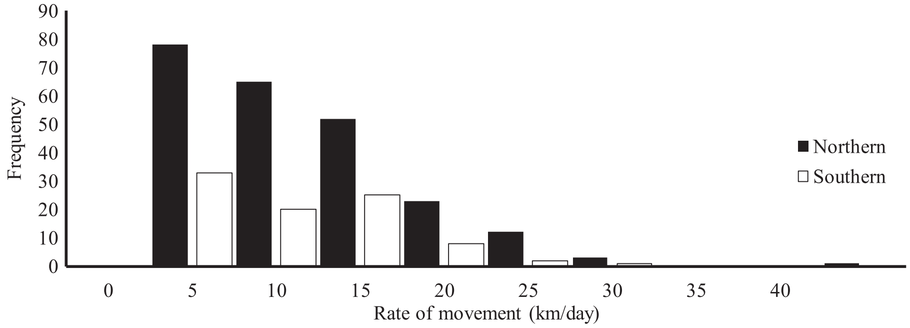

FIGURE 2. Movement rate (km/d) frequencies for northern and southern migrations by acoustically tagged Winter Skate.

moving 1,011 km in 404 d (Figure 4B). A commonly observed path involved northerly spring movement along the coast of New York followed by a southerly fall migration (Figure 4C). A 67-cm TL female was detected as moving 831 km in 350 d, completing a southern fall migration and northern spring migration (Figure 4D).

Individuals tagged with Floy tags showed similar movement trends, with the addition of offshore movement to areas without acoustic coverage (Figure 5). The majority of recaptures occurred in the vicinity of New York, with longer-distance movement to offshore waters. One individual that was tagged during the North Carolina Cooperative Cruise (36°55′4.7994″N, −75°44′5.9994″W) was recaptured off Cape Cod (Figure 5).

DISCUSSION

Passive acoustic telemetry and mark–recapture data revealed long-distance, seasonal migration patterns in Winter Skate, with tagged individuals moving distances exceeding 1,000 km across the northeast U.S. continental shelf. The seasonality of Winter Skate movement patterns was characterized by individuals generally moving southward during summer/fall and northward in winter/spring. Individual movement rates were also considerable, with some Winter Skate moving at speeds of up to 20–40 km/d. The display of long-distance dispersal capabilities in Winter Skate individuals prompts questions regarding the current understanding of their population dynamics, which suggested that individuals do not make long-distance migrations and exhibit high endemicity to specific regions of the continental shelf (Kulka et al. 2009). Additionally, while we did not observe compelling evidence of differences in mobility between male and female Winter Skate, the presence of sexually dimorphic pectoral fin shapes in this species (Martinez et al. 2016b) suggests that further work is needed to confirm whether more fine-scale or subtle patterns of spatial differentiation exist.

Although we provide the first evidence of long-distance and seasonal movements for this species, the extent of individual dispersal is not too surprising; rather, it is consistent with patterns observed in other studies. Recent work has begun to document large-scale movements in other species, such as the Thornback Skate *Raja clavata* (Hunter et al. 2005) and Big Skate *R. binoculata* (Farrugia

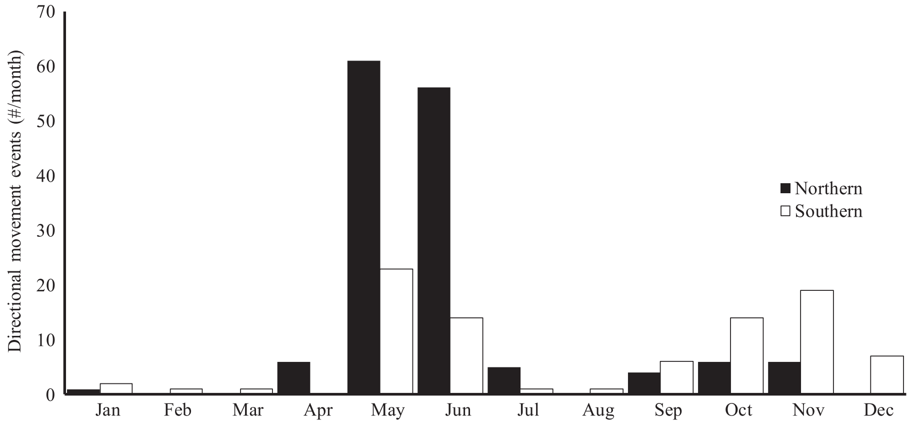

FIGURE 3. Seasonal trends in the number of directional movement events (northern and southern) for acoustically telemetered Winter Skate.

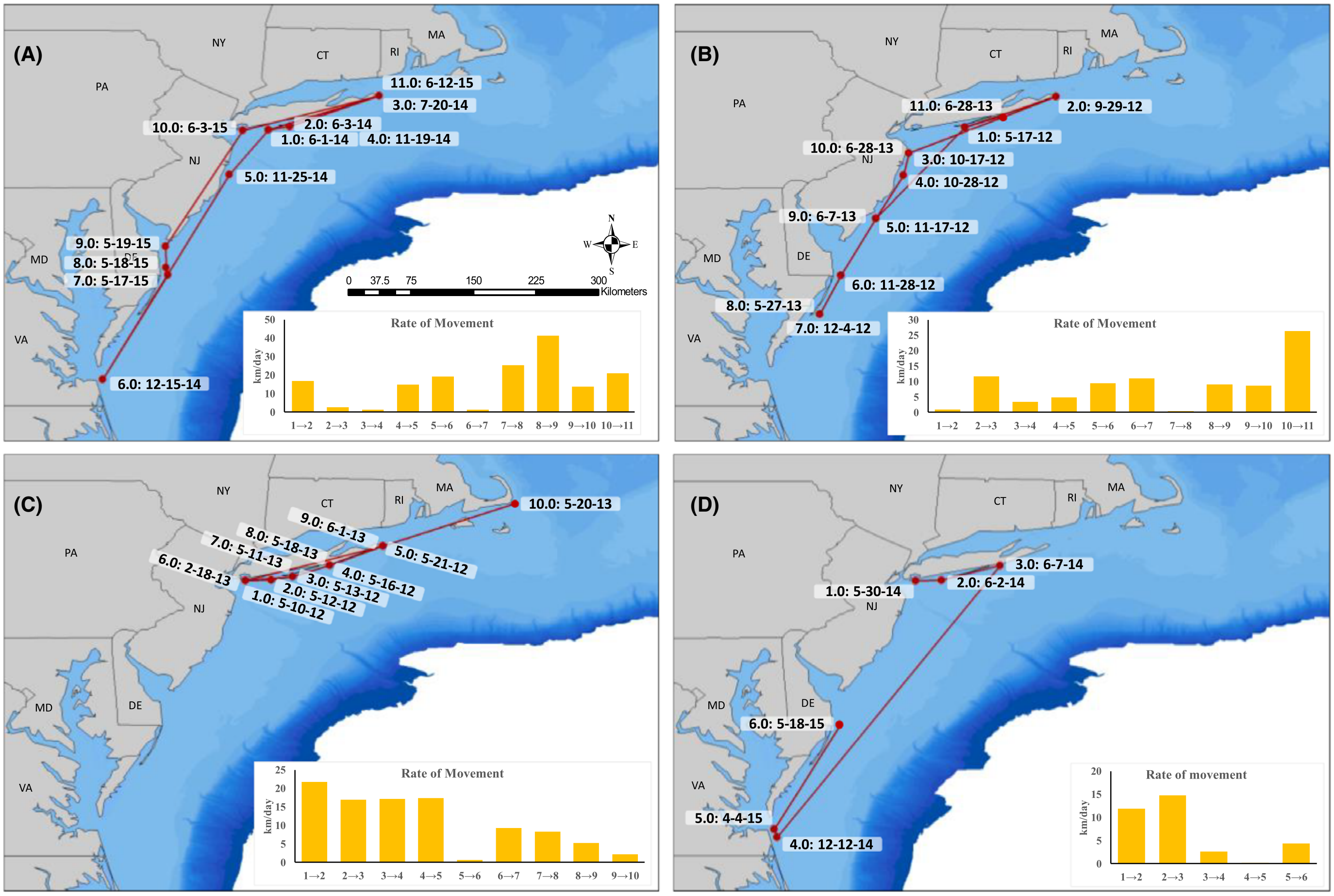

FIGURE 4. Examples of movement patterns for telemetered Winter Skate, with movement paths ordered by number and date (2012–2015). Insets provide the rate of movement (km/d) between listening arrays, identified by the sequentially ordered and numbered detected movement events. The panels represent the tracks of the following individuals: (**A**) a male (68 cm TL) that was detected as traveling 1,177 km over 374 d at liberty; (**B**) a male (75 cm TL) that was detected as traveling 1,011 km over 404 d at liberty; (**C**) a female (75 cm TL) that was detected as traveling 713 km over 379 d at liberty; and (**D**) a female (67 cm TL) that was detected as traveling 831 km over 350 d at liberty.

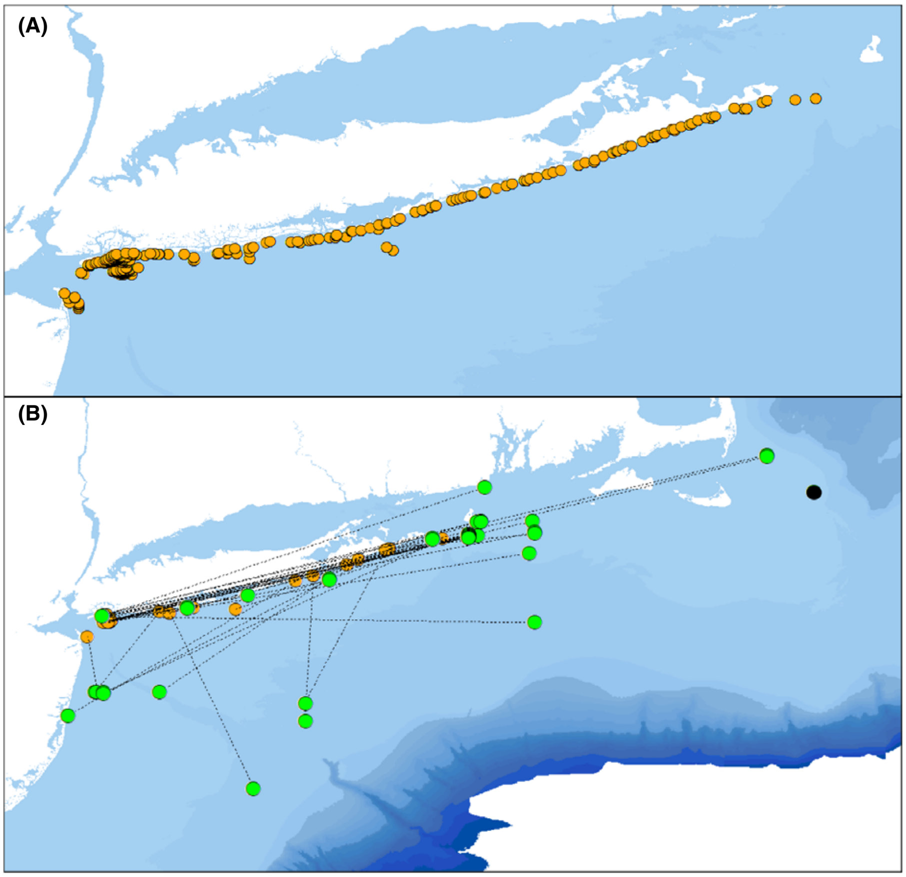

FIGURE 5. (**A**) Release locations of telemetered Winter Skate tagged with generic Floy tags and (**B**) recapture locations. Orange dots represent tagging locations, and green dots represent recapture locations. The black dot represents a Winter Skate tagged off North Carolina during the North Carolina Cooperative Cruise in January 2013 (see Laney et al. 2007 for details).

et al. 2016). Additionally, a recent review of skate movement studies revealed that an inherent lack of biotelemetry approaches compared to conventional tagging has led to significant underestimations of skate dispersal capabilities across many species (Siskey et al. 2019). Lastly, data on pectoral morphology (the primary source of propulsion in most batoids) place skates in an intermediate position between benthic stingrays and highly mobile pelagic rays, with the Winter Skate being average within the skates themselves (Martinez et al. 2016a). Given that batoid pectoral shapes are largely indicative of swimming mode and lifestyle (Rosenberger 2001; Martinez et al. 2016a), the morphological evidence also appears to corroborate an intermediately mobile Winter Skate, as observed in this study. Together, these independent lines of evidence suggest a need for research focused on skate movements and spatial ecology across a broader range of species and locales—especially for data-deficient species.

In contrast to the distances traveled by Winter Skate, the observed rates of movement were more surprising and pose significant questions regarding energy metabolism in this species. For example, fast movement rates could reflect a high nutritional condition of tagged individuals, which may be facilitated by a reliable and productive prey base. Although examination of nutritional condition in elasmobranchs is rare, this hypothesis could be tested by measuring the ratios of free circulating energy metabolites in relation to closely related species (e.g., Little Skate *Leucoraja erinacea*), namely triglyceride and cholesterol, and/or through morphometric body condition indices (Gallagher et al. 2014, 2017). A recent study utilizing carbon and nitrogen stable isotope ratios (δ^{13}C and δ^{15}N) suggested that Winter Skate individuals may predominantly forage within a specific latitudinal range (Shipley et al., in press), a pattern that has also been hypothesized for oceanic sharks (Bird et al. 2018). This result suggests that high rates of movement, particularly off coastal New York and New Jersey, could reflect primary foraging grounds laying outside of the immediate capture and tagging region. Highly productive temperate regions, such as Georges Bank, may serve as a potential foraging hotspot; however, more work is required to augment this claim. Regardless of location, if individuals move quickly to reach specific foraging locations, this may pinpoint more specific regions for targeted conservation efforts.

In addition to north–south migrations, mark–recapture data based on Floy tagging suggest that individuals may also make extensive onshore–offshore movements, thereby allowing individuals to utilize deeper areas of the continental shelf. Although the functional significance of these movements is difficult to ascertain without complementary approaches (e.g., ecogeochemical tracers, direct observation, or additional biotelemetry devices), complex movements may reduce resource competition with sympatric species (sensu Bizzarro et al. 2014), like Little Skate, which are assumed to exhibit lesser dispersal (Shipley et al., in press). This observation also underscores a limitation of passive acoustic telemetry networks that generally remain close to the shore and do not provide adequate coverage in offshore regions. However, expansion of acoustic array systems may be the primary avenue for tracking benthic and demersal species, as light-based geolocation approaches do not work well for bottom-dwelling animals (Siskey et al. 2019). Nevertheless, discerning the full migration routes and identifying “high-use” areas underpin the efficient conservation of critical habitat supporting Winter Skate populations and the discernment of individuals’ vulnerability to fisheries.

Our observations provide support for AMPC in Winter Skate, which was hypothesized as the mechanism underlying the large increase in observed elasmobranch biomass on Georges Bank in the 1990s (Frisk et al. 2014). Specifically, the results not only suggest that Winter Skate are capable of long-distance travel but commonly undertake movements between regions on the geographic scale hypothesized for AMPC (Frisk et al. 2014). The AMPC hypothesis does not assume an underlying population structure but instead argues that regional dynamics, including observed regional biomass fluxes, are influenced and/or driven by the movement of adults. These results add to growing evidence for the importance of long-distance movements that control population connectivity and/or meta-population dynamics and control regional temporal abundance in marine teleosts and elasmobranchs (O’Leary et al. 2013; Rochette et al. 2013; Frisk et al. 2014; Chapman et al. 2015; André et al. 2016; Archambault et al. 2016; Morse et al. 2017; Midway et al. 2018; Wang et al. 2018). However, our observations showed only the capacity for long-distance migration patterns, and this study was not able to detect the large-scale and periodic movement of individuals as envisioned by Frisk et al. (2008). Thus, long-term monitoring of Winter Skate movement is needed to further understand the species’ migration and population connectivity patterns. The ability of Winter Skate to move considerable distances has additional implications for contemporary stock assessment and broader management of populations throughout the northeast U.S. coastal shelf. Earlier observations suggested that high mixing of northeast stocks of Winter Skate was plausible since individuals did not exhibit region-specific life history differentiation (e.g., age at maturity), as seen in sympatric Little Skate (Frisk and Miller 2006, 2009). However, recent research has argued that Winter Skate in the Gulf of St. Lawrence represent a unique population with a smaller size and younger age of maturation (Kelly and Hanson 2013). Additional research is needed to further define movement patterns and population structure of Winter Skate so as to better inform regional management of the species.

An emerging body of evidence has highlighted the growing need for conservation of elasmobranch fishes, including skates, throughout the world’s oceans. These fishes have been subjected to a suite of extrinsic stressors eliciting considerable threats to population viability, including fisheries exploitation, habitat degradation, and marine pollution (Dulvy et al. 2014, 2017; Stein et al. 2018). The integration of acoustic telemetry data into contemporary management of marine fishes and their associated habitats has proven successful in several locations worldwide (Brooks et al., in press). Therefore, we recommend that similar approaches be applied with greater urgency to a broad number of skate species at data-poor locations, especially within the Americas and east Asia, which already house a notable number of threatened species that are subject to high fishing pressure (Dulvy et al. 2017).

ACKNOWLEDGMENTS

The funding for this research was provided by the New York State Department of Environmental Conservation and the NOAA Species Recovery Grant Program NA07NMF4550320. We thank the crew of the RV *Seawolf*, B. Pfeiffer (Island Diving) and N. Stark (Soggy Bottom Diving) for contributing to the success of the research. We especially thank members of the ACT Network for providing detection data outside our receiver coverage. There is no conflict of interest declared in this article.

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