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First use of satellite tags to examine movement and habitat use of big skates *Beringraja binoculata* in the Gulf of Alaska

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ABSTRACT: Big skate *Beringraja binoculata* is the most frequently landed skate in the Gulf of Alaska portion of the Northeast Pacific Ocean, with recent stock assessment surveys showing relatively healthy skate stocks and continued interest from the commercial fishing industry to increase skate landings. Considered a data-poor species, there is a need for additional ecological information on big skates, including movement patterns and habitat use. We deployed pop-up satellite archival transmitting (PSAT) tags on 8 big skates in the Gulf of Alaska and set the tags to release 1 yr after deployment. The minimum distance traveled by big skates varied between 6 and 205 km, with 1 individual traveling at least 2100 km based on light geolocation data. Three individuals showed evidence of having made long-range movement and crossed at least 1 management boundary, and 3 remained relatively close to their tagging locations. Two tags did not report. The PSAT tags also extended the maximum documented depth of big skates to over 500 m and confirmed that they are thermally tolerant, occupying waters between 2 and 18°C. Because the total catch of big skate is divided into multiple areas and limited movement between areas is assumed, information from this study will aid in the development of appropriate spatial management plans for this species.

KEY WORDS: Satellite telemetry · PAT · Depth utilization · Temperature tolerance · Fisheries management · Connectivity

INTRODUCTION

Skates (Rajiformes: Rajoidei) are dorsoventrally compressed cartilaginous fishes related to sharks and rays and are increasingly recognized as an important part of the benthic ecosystem (Coll et al. 2013). They are captured in directed fisheries and retained in other fisheries as non-targeted catch, mainly for their pectoral fins, or wings. Recently, there has been interest in further developing skate fisheries in Alaska (ADCCED 2009), where skate stocks are not currently listed as overfished or threatened by overfishing (NMFS 2013). Of the 15 most common species of skates captured in the Gulf of Alaska (GOA), the big skate *Beringraja binoculata* (formerly *Raja binoculata*) is the largest (Eschmeyer et al. 1983) and most commonly retained species in state and federal waters (Ormseth 2015). The North Pacific Fishery Management Council, the management body responsible for federal fisheries management in the exclusive economic zone (3–200 nautical miles [nmi]) off Alaska, currently treats big skates as a data-poor species. It has designated skates as a research priority and determined that stock assessment and management of data-poor stocks such as skates requires basic life history information and better estimation of

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fishery interactions (NPFMC 2015). Likewise, the Alaska Department of Fish and Game recognizes the important role of big skates in coastal ecosystems and as a species captured in state-managed fisheries within 3 nmi of the coast and, therefore, seeks to collect more biological and ecological information about this species (Wessel et al. 2014).

The knowledge base of big skates has been growing over the past decade, including studies on diet (Bizzarro et al. 2007, Ormseth 2011), age and growth (McFarlane & King 2006, Gburski et al. 2007), reproductive biology (Ebert et al. 2008), and distribution (Stevenson et al. 2008, Bizzarro et al. 2014). In the GOA, big skates aggregate in certain hot spots along the coast of Alaska (Bizzarro et al. 2014). Most studies indicate that big skates primarily occupy depths between the surface and 200 m (Love et al. 2005, Ormseth 2011), although bottom trawl surveys have retrieved big skates from hauls occurring as deep as 376 m in Alaska (Stevenson et al. 2008) and 459 m along the west coast of the US (Bizzarro & Summers 2015). Big skates are also considered to have a wide thermal niche (Bizzarro et al. 2014).

However, there have been no studies to identify habitat use (such as depth and temperature occupancy). One study has examined movement of big skates in the Pacific Ocean using conventional tags in waters off British Columbia, Canada (King & McFarlane 2010). In that study, over 18 000 big skates were tagged, of which 17 traveled between 800 and 2370 km and were recaptured in the GOA, the Aleutian Islands, or the Bering Sea. However, about 75% of these tagged big skates were recaptured within 21 km of the release location by the commercial fishing fleet, indicating that the majority of skates may not undergo long-distance movements. Whereas conventional tagging efforts are informative, they rely on recaptures in commercial fisheries, which in turn depend on the temporal and geographic coverage of fishing fleets (Bolle et al. 2005). Consequently, conclusions regarding movement and distribution of fishes may be biased by unequal spatial and temporal commercial fishing efforts. Moreover, conventional tags do not provide information about movement or habitat utilization by tagged fish while at liberty. Lacking information to the contrary, management agencies assume that big skates do not make extensive movements or cross management boundaries and that they are restricted to relatively shallow waters, where fishing occurs.

Satellite tagging provides a fisheries-independent solution for examining movement patterns and habitat use of big skates in the GOA region. Pop-up satellite archival transmitting (PSAT) tags measure and record temperature, depth, and ambient light data at user-specified intervals while externally attached to the fish (Arnold & Dewar 2001). On a user-programmable date, the tag releases from the fish, floats to the surface of the ocean, and transmits summarized data to orbiting satellites such as the Argos satellite system. PSAT tags do not need to be physically recovered and are therefore a fisheries-independent means of studying fishes and a valuable tool for studying the biology and ecology of elasmobranchs (Conrath & Musick 2008, Weng et al. 2008) as well as other benthic species, such as Pacific halibut *Hippoglossus stenolepis* (Seitz et al. 2003, Loher & Seitz 2006).

This study provides the first documentation of the movement, swimming depth, and ambient temperature occupancy for big skates in the GOA. Based on previous studies, we hypothesized that no more than 25% of tagged skates moved beyond the area where they were tagged, that big skates occupied depths up to 500 m, and that they utilized a wide temperature range. Although the information from PSAT tags may not be easily extrapolated to populations, it can be used to determine how far individuals are able to travel and what temperatures and depths they can tolerate and may prefer, independent of fishing effort. Results from this research will help advance our understanding of the biology and ecology of big skates and will be valuable in assisting in the evaluation of assumptions currently made in stock assessment models used for managing fisheries in the GOA.

MATERIALS AND METHODS

Study area and skate collection

Eight big skates were captured in either the state of Alaska waters of Prince William Sound (PWS) (n = 7) or the US federal waters of the continental shelf (n = 1) of the GOA (Fig. 1A). Alaska state waters include all of PWS and are managed by the Alaska Department of Fish and Game. US federal waters are managed by the National Marine Fisheries Service (NMFS), which divides the federal waters of the GOA into the western GOA (WGOA), central GOA (CGOA), and eastern GOA (EGOA) (Fig. 1), each with its own allowable biological catch and overfishing level.

PWS is a large (>9000 km^2), productive fjord estuary with seasonally high freshwater input from surrounding glaciers and precipitation runoff (Stabeno

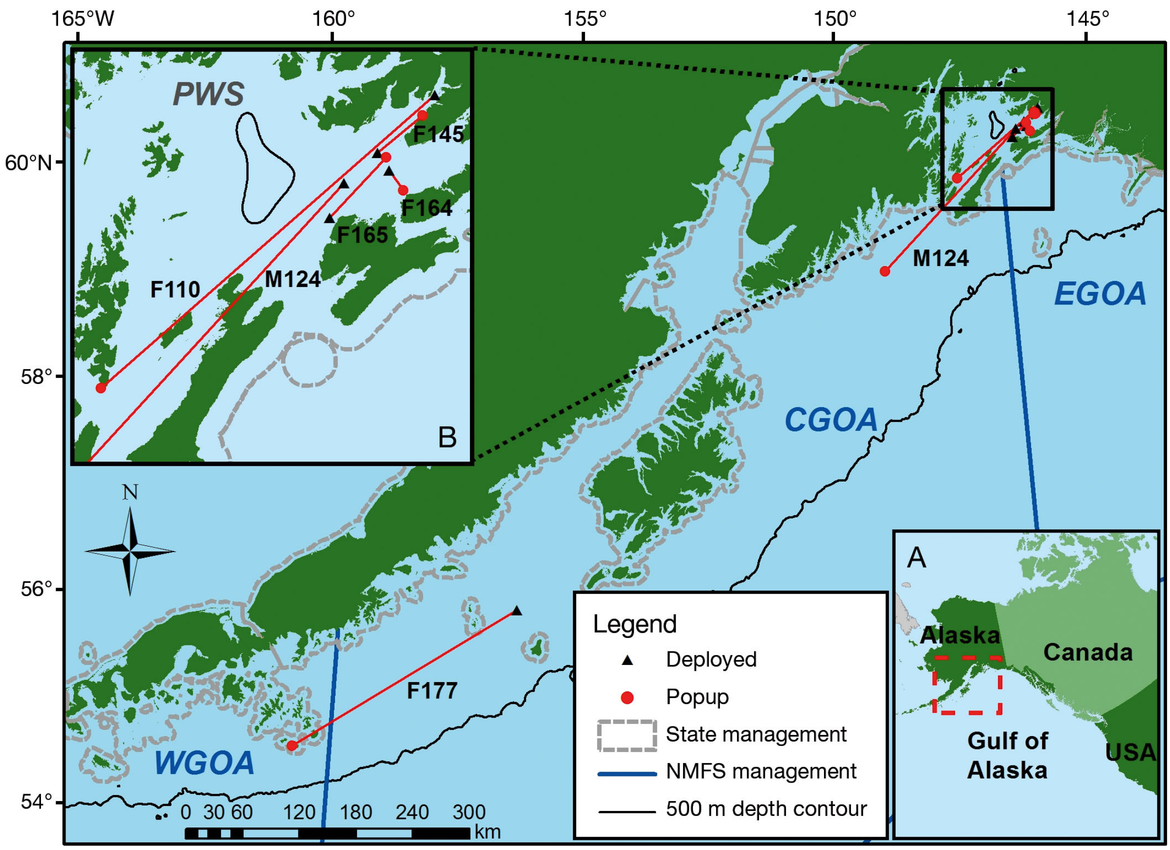

Fig. 1. Deployment and end locations of tagged big skates (designated by their sex and total length; e.g. F177 is the 177 cm female) in the Gulf of Alaska (GOA). Borders of the state management area (3 nautical miles) are shown by the grey dashed line, and borders of the National Marine Fisheries Service (NMFS) federal management areas are shown in blue (WGOA, CGOA, and EGOA represent the western, central, and eastern GOA, respectively). The deployed and pop-up end locations for each skate are denoted by black triangles and red circles, respectively. The lines connecting deployed and end locations are the hypothetical minimum distances traveled by the skate. (A) The GOA in the North Pacific, with the extent of the study area designated by the red dashed box. (B) Prince William Sound (PWS) shown in greater detail

et al. 2004, Harwell et al. 2010, Musgrave et al. 2013). Because of this seasonal melt, mean surface temperatures range from 4 to 13°C, while bottom temperatures range from 4 to 7°C (Vaughan et al. 2001, Musgrave et al. 2013). The bathymetry of PWS is complex, with many islands and steep slopes dropping to 800 m over short distances. Surface circulation in PWS changes seasonally, being a relatively closed system during the spring and summer, while southerly flows in the autumn and winter exit PWS through its 2 main connections to the GOA, both of which have sills shallower than 200 m depth (Harwell et al. 2010, Musgrave et al. 2013). Water temperatures near the surface in the GOA vary seasonally from 3.5 to 13°C, whereas they are fairly constant, around 6°C, near the seafloor. The continental shelf can be as narrow as 5 km in southeastern Alaska to more than 200 km wide around Kodiak Island, Alaska, and varies in depth between 150 and 250 m, after which the continental slope descends rapidly to abyssal depths of 4000 m (Weingartner 2007).

In PWS, big skates were collected from 5 to 14 July 2011 during the Alaska Department of Fish and Game multispecies large-mesh bottom trawl survey. The trawls were conducted during daylight hours for approximately 26 min, covering a distance of 1.85 km at depths between 0 and 500 m, following standardized agency methods (Rumble et al. 2014). The big skate tagged in US federal waters was collected on 25 August 2013 during the annual NMFS longline survey, which covered over 16 km of groundline deployed down the slope and left to soak for 4 to 8 h at each station, following standardized NMFS methods (Lunsford & Rodgveller 2013). The University of Alaska Fairbanks (UAF) Institutional Animal Care and Use Committee (IACUC) has approved the collection and tagging of big skates under UAF IACUC protocol no. 217575.

PSAT tag attachment and deployment

Immediately after bringing the skates on deck, they were placed in a 1 × 2 × 1 m (length × width × depth) holding tank equipped with flowing seawater for at least 10 min to recover. They were then weighed to the nearest 0.1 kg, measured to the nearest 1 cm (total length [TL] from the tip of the snout to the tip of the tail, measured in a straight line, and disc width, from one wing tip to the other, measured in a straight line), and sexed based on the presence or absence of claspers. Males were also assessed for maturity using clasper length and calcification (Ebert et al. 2008). We only tagged big skates that displayed regular spiracle breathing, had no visible wounds, and were larger than 8 kg (corresponding to approximately 100 cm TL). This size was selected based on an analysis of the drag caused by PSAT tags attached to cownose rays *Rhinoptera bonasus* over 7.8 kg that showed they could carry a PSAT tag at moderate speeds with an extra energy exertion of only about 5% (Grusha & Patterson 2005). Because of the similar body shape and swimming mode shared by cownose rays and big skates, a big skate larger than 8 kg was assumed to be able to carry a PSAT tag with minimal effects on its swimming efficiency.

Skates were tagged with Mk10 PSAT tags (Wildlife Computers) measuring 175 mm in length and 40 mm in diameter, weighing 75 g in air, and pressure-rated to 2000 m. The attachment system was based on one developed for Pacific halibut (Seitz et al. 2003), consisting of a titanium dart that was connected to the corrodible link of the PSAT tag by a short length (15 cm) of monofilament fishing line (250 lb test) covered with heat-shrink plastic tubing to minimize abrasion to the skin of the skate (Seitz et al. 2003). Immediately before tag deployment, the dart and tether were disinfected with 95% ethanol. To attach the tag, the dart was inserted into the wing of a big skate dorsoventrally midway between the eye orbit and the insertion of the pectoral fin and one-third of the distance between the spine and the wing tip (Fig. 2). The dart was pushed through the pectoral radials so that it locked in the radials, immediately above the skin on the ventral side of the skate. Total measuring and tagging time for the skates was less than 10 min, with skates being out of water for a maximum of 2 min at a time. The skates were not anesthetized during the process (UAF IACUC protocol no. 217575).

Once tagged, the skates were immediately released back into the ocean as close to the site of capture as possible (between 0 and 2 km). Release of tagged big skates in state waters was accomplished by placing the individual in a 1 × 1 m square of netting attached to 4 lines. While the trawl vessel was stationary, the net was lowered in the water and left in place until the skate voluntarily exited the net (Fig. 2). In federal waters, the tagged skate was released by hand over the side of the longline vessel and observed until it swam out of sight.

Data collection

The tags were programmed to collect 3 types of data at 5 s intervals: depth (range: –40 to 1000 m, resolution: 0.5 m), ambient water temperature (range: –40 to 60°C, resolution: 0.05°C), and ambient light intensity (sensitivity: 5×10^{-12} to 5×10^{-2} W cm^{-2}). For tags deployed in 2011, the archived depth and temperature data were summarized into 4 h bins (00:00–03:59 h, 04:00–7:59 h, etc.) for transmission to satellites. For each time bin, the tag transmitted data representing the percent of time the tag spent in each of 9 temperature bins (<0, 0–2, 2–4, 4–6, 6–8, 8–10, 10–14, 14–18, >18°C) and 11 depth bins (<–1, –1 to 25, 25–50, 50–75, 75–100, 100–125, 125–150, 150–175, 175–200, 200–500, >500 m). More depth bins were created between 0 and 200 m because big skates were expected to spend the majority of their time in shallower waters. Satellite transmissions of tag data also included daily maximum and minimum temperatures and depths. One tag was physically recovered, and the complete archived 5 s interval data set was retrieved. It was sent back to the manufacturer, refurbished, and redeployed on a big skate in 2013 in the GOA (Table 1).

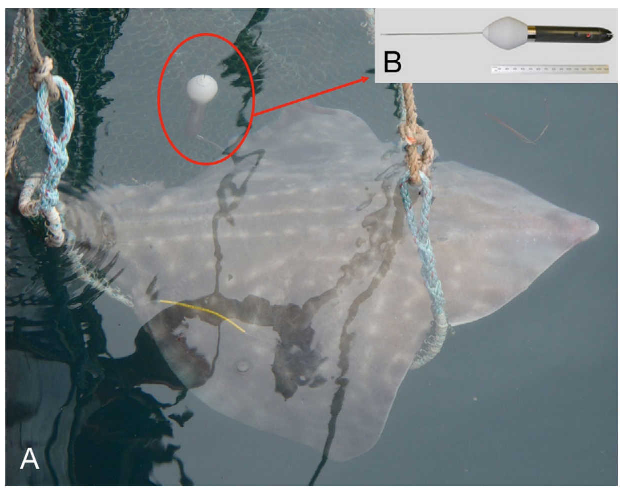

Fig. 2. (A) Tagged big skate F145 being released, with a satellite tag attached. (B) Satellite tag shown in greater detail

Table 1. Deployment summary for pop-up archival transmitting tags attached to big skates in the Gulf of Alaska (GOA), including sex, total length (TL), disc width (DW), age, tagging and pop-off date, location and management area, days at liberty, and percent data reported to the satellite. The sex and TL are used to identify the skate. Age is based on the von Bertalanffy growth curve determined for GOA skates by Gburski et al. (2007). Horizontal movement is the shortest straight-line distance between the tagging and end location and represents the minimum distance the skate could have traveled while at liberty. F: female; M: male; PWS: Prince William Sound; CGOA: central Gulf of Alaska; WGOA: western Gulf of Alaska. –: tag did not report

Sex	TL (cm)	DW (cm)	Age (yr)	Tagging date	Tagging location Lat. (°N)	Tagging location Long. (°W)	Tagging area	Pop-off date	End location Lat. (°N)	End location Long. (°W)	Pop-off area	Horizontal movement (km)	No. of days at liberty	Data reported (%)	No. of light locations
F	145	111	10	5 Jul 2011	60.6194	146.4038	PWS	23 Jun 2012	60.692	146.173	PWS	15	354	80	31
F	165	133	13	5 Jul 2011	60.4846	146.6588	PWS	7 Jun 2012	60.607	146.366	PWS	21	338	0	0
M	124	101	10	8 Jul 2011	60.5595	146.5758	PWS	17 May 2012	59.327	149.300	CGOA	205[a]	314	69	44
F	164	126	13	9 Jul 2011	60.5755	146.3595	PWS	18 Jun 2012	60.527	146.303	PWS	6	345	89	47
M	121	88	10	12 Jul 2011	60.8153	146.8493	PWS	–	–	–	–		–	0	0
F	110	81	6	14 Jul 2011	60.7347	146.1065	PWS	12 Oct 2012	60.152	147.791	PWS	113	90	99	62
F	157	117	12	14 Jul 2011	60.6442	145.6787	PWS	–	–	–	–		–	0	0
F	177	134	15	25 Aug 2013	56.1867	155.9883	CGOA	1 Jun 2014	54.775	159.589	WGOA	278	280	72	40

[a]Based on light geolocation data, this skate actually traveled over 2000 km

The refurbished tag was programmed slightly differently because general habitat use data had already been acquired with the first round of tagging. Instead of binning depth and temperature data, it was programmed to collect time-series data of the ambient water temperature and depth at 10 min intervals. In both years, ambient light intensity data collected by the tags were processed by the onboard computer to produce light curves for sunrise and sunset each day.

All PSAT tags were programmed to release 323 to 365 d after deployment to provide approximately 1 yr of data and to release during the summer months, when more fishing vessels are present, to increase the likelihood of recovering the tags. The tag's programming sent a small electrical signal through the corrodible wires attaching the tags to the skates, causing them to corrode. The PSAT tags then released from the skates, leaving behind only the dart tags. After releasing, the slightly positively buoyant PSAT tags floated to the surface and transmitted the summarized data and light curves to the Argos satellite system. The surface locations of the tags were determined from the Doppler shift of the radio frequency transmitted in successive uplinks received during 1 Argos satellite pass (Keating 1995). The first location for each tag with an Argos class of 1, 2, or 3 (indicating an accuracy <1.5 km) was considered the end location of that skate track. Summarized depth and temperature data, and light curves produced from ambient light intensity data, were downloaded from the Argos satellite system data servers. The number of days during which the tag was attached to the skate is termed 'days at liberty'.

Data analysis

Tag transmission performance was assessed to examine the representativeness of each tag's data record for describing each skate's behavior and environment during its entire time at liberty. Tag transmission performance was defined as the proportion of data retrieved by Argos satellites from each transmitting tag and was calculated by dividing the number of data packets retrieved by Argos by the hypothetical number of packets the tag could have transmitted under ideal conditions. The hypothetical number of packets depended on the duration of tag deployment and the number of data summaries per day.

To investigate the movement of skates while at liberty, the minimum horizontal movement was calculated as the shortest great-circle distance between the tagging and end locations, allowing for this distance to pass over land. In addition, light-based geolocation was used to examine whether skates travelled farther while at liberty than might be shown by their release and end locations alone. Longitude estimates are usually more accurate than latitude estimates for approximating positions of demersal fishes (Seitz et al. 2006), so we focused our analyses on the longitude estimates alone. To obtain longitude estimates, the downloaded light curve data were processed by the proprietary program Data Analysis (Wildlife Computers), which estimated times of sunrise, sunset, and local noon, followed by the Global Position Estimator (Wildlife Computers), which calculated the longitude. These light-based longitude geolocations were examined visually by assessing the slope of the light curve for both dawn and dusk (Seitz et al. 2006). Poor light curves (asymmetrical dawn and dusk curves and/or very shallow slopes in the curve) and highly uncertain positions were discarded. Each longitude estimate was associated with a measure of uncertainty based on the quality of the light curve, and the longitude estimates of a tag, along with the uncertainty estimates, provided a measure of the east–west movement of the tagged skate. We considered applying filters to improve these position estimates; however, these are primarily based on environmental variables, which either do not apply to skates (e.g. sea surface temperature) or do not have sufficient data available (e.g. bottom temperature).

The movement of skates could have management implications if skates moved frequently between management areas. Since each area has its own catch limit, biomass transferring from one area to another could influence the proportion of the stock that is available to harvest in those areas. To infer whether skates crossed management boundaries, we examined the end locations, light-based longitude estimates, and temperature and depth records. The management areas in the GOA are mostly oriented east to west, meaning that changes in light-based longitude estimates can be used to infer movement between management areas, as seen in several Pacific halibut studies (Seitz et al. 2003, 2011, Loher & Seitz 2006, Loher 2008, Loher & Blood 2009). A skate was considered to have crossed a management boundary if the longitude estimates crossed the longitudinal boundary of the management area and the uncertainty range did not overlap with the management boundary. In addition, different management areas (i.e. PWS vs. the CGOA shelf) have different temperature-at-depth characteristics, so all of the depth and temperature records from the 1 physically recovered tag were examined to provide coarse inference on whether the skate moved between these different bodies of water.

Finally, to examine seasonal depths and water temperatures occupied by tagged big skates, data from both satellite transmissions and the physically recovered tag were grouped into summer (July–September), autumn (October–December), winter (January–March), and spring (April–June) seasons. Differences in time spent in depth and temperature bins among seasons were analyzed using a chi-squared test (Zar 1999).

All statistical analyses were conducted with R (R Core Team 2014), using a significance level of α = 0.05. Mapping and distance measurements were performed in ArcGIS (v.10.2, ESRI). The depth and temperature plot of the recovered tag was produced with MatLab (v.R2014b, MathWorks). For identification purposes, the tagged skates are identified in the figures and table by a 4-character code designating their sex and TL (e.g. M124 for a male skate measuring 124 cm TL).

RESULTS

Five female and 2 male big skates (range: 110–165 cm TL) were captured and tagged between 49 and 190 m water depth in the eastern part of PWS in 2011 (Table 1). The tag deployed on a 164 cm TL female was recovered on a beach by a commercial fisherman and was returned in 2012. After the full data set was downloaded, the tag was refurbished and re-deployed in 2013 on an eighth big skate, a 177 cm TL female captured at a depth of 205 m southwest of Kodiak Island (Fig. 1).

Tag performance

Six of the 8 PSAT tags deployed on big skates in the GOA reported to satellites upon pop-up, whereas the other 2 failed to report (Table 1). Of these, 5 transmitted 69 to 99% of their summarized depth, temperature, and light level data; the sixth tag (F165) only reported its final location through the Argos satellite system but did not transmit any other data (Table 1). The tag on F110 prematurely released after 90 d at liberty, but the other 4 tags remained attached nearly a full year. In all, we recovered 931 d of depth data and 922 d of temperature data. While at liberty, the tags collected light level data, but only 31 to 62 acceptable daily light curves were produced per tag (Table 1).

Movement

The 6 tags for which Argos-calculated end locations were available popped up in 3 different management areas (Table 1). Four of the tags deployed in PWS had end locations in PWS (minimum horizontal movement: 6–113 km), and 1 had an end location in the CGOA (minimum horizontal movement: 205 km). The tag deployed in the CGOA transmitted its data from the WGOA (minimum horizontal movement: 278 km; Fig. 1). The 3 tagged skates that moved a

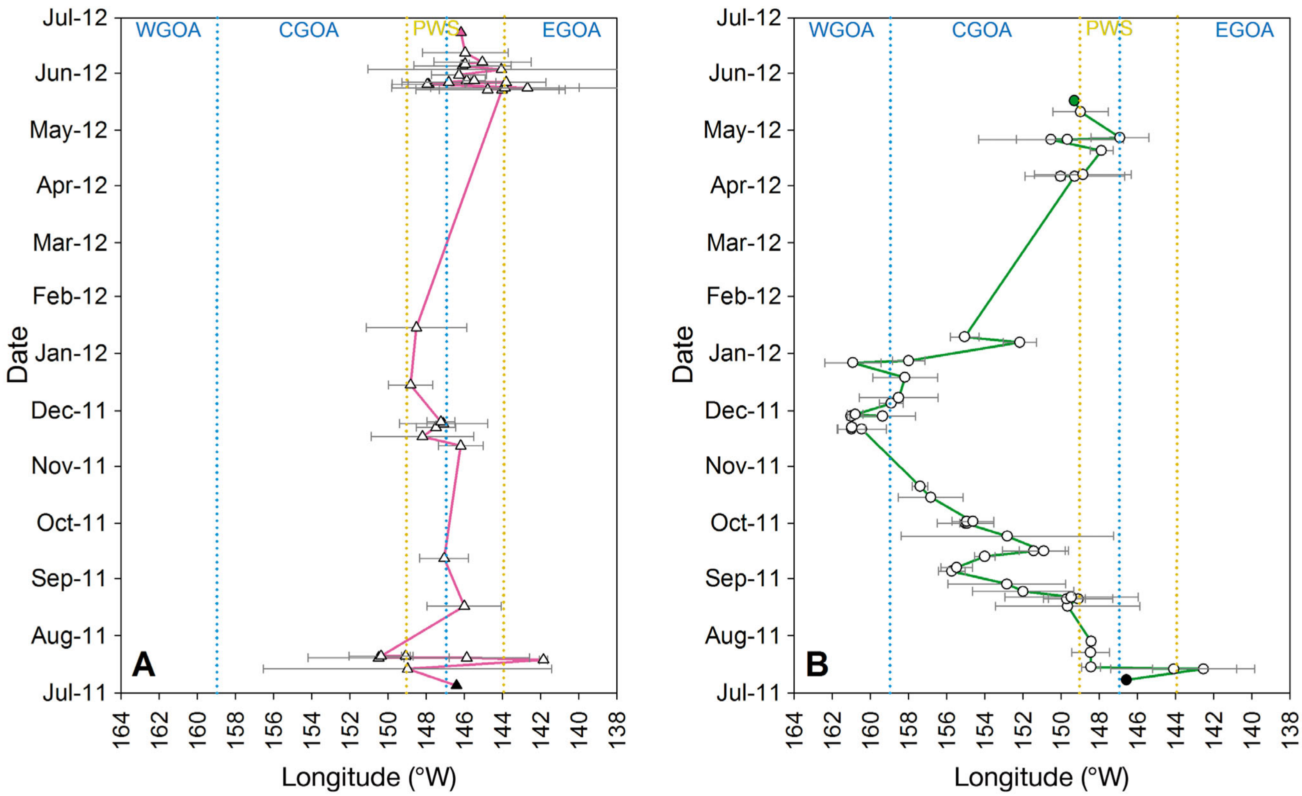

Fig. 3. Example of 2 dispersal types, showing the longitude tracks of tagged big skates (A) F145 (pink line) and (B) M124 (green line) while at liberty. The initial black symbols represent the known tagging locations, and the final colored symbols represent the Argos position of the first location upon pop-up. Open symbols are the estimated longitudes produced by Wildlife Computers software, with the uncertainty of each location represented by the grey horizontal error bars. Dotted vertical lines represent the longitudinal boundaries of the US federal (blue) and state of Alaska (yellow) management areas. WGOA: western Gulf of Alaska; CGOA: central Gulf of Alaska; PWS: Prince William Sound; EGOA: eastern Gulf of Alaska

minimum of 100 km travelled to the southwest, whereas the other 3 travelled to the southeast and northeast while remaining in the eastern PWS.

Of the 5 tags from which daily geolocation longitude estimates could be derived, 2 dispersal types were observed. The first dispersal type was defined as having start and end locations in the same management area and with no evidence that the tagged skates crossed management boundaries while they were at liberty (F145 and F110; Fig. 3A). The second dispersal type was exhibited by 3 skates that crossed management boundaries while at liberty. In one case (F177), the light-based longitude estimates showed a direct westward progression from the point of release to the end location, undertaken primarily in the late summer and autumn. In another case (M124), the release and end locations were in relatively close proximity (205 km apart), but the longitude estimates provided evidence that the fish traveled much farther than the minimum horizontal distance between those 2 points. Indeed, the geolocation data suggest that this skate moved at least 2100 km from the release site in PWS (longitude: 146.6° W) through the CGOA and into the WGOA to 160° W (±1°) between July 2011 and January 2012 and then back to 149.3° W in the CGOA by May 2012 (Fig. 3B). In doing so, the skate crossed 3 management boundaries in 314 d, for a minimum average speed of 6.8 km d^{-1}. Finally, evidence of this dispersal pattern was also found using the fine-scale data from the physically recovered tag (F164), which allowed a closer examination of the depth and temperature occupancy of this skate. The data from this tag suggest that the skate moved out of PWS and into the GOA in mid-August and subsequently returned into PWS in late September. In PWS, the tag experienced water at 20 m depth that only reached 8°C in late July, and then as it moved into the GOA, it experienced temperatures above 10°C at 70 m in August and September 2011 (Fig. 4). In addition, the maximum depth of the tag between mid-August and mid-September did not exceed 115 m, more typical of the depths on the continental shelf of the GOA. Starting in late September, the tag again experienced deep depths typical of PWS.

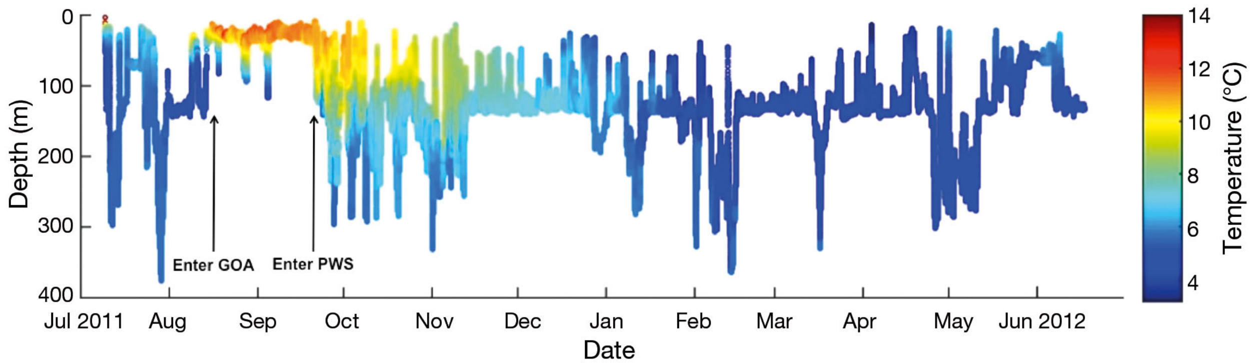

Fig. 4. Depth and temperature profile of the skate for which the tag was recovered (F164) while at liberty in 2011 and 2012. The line represents depth of the skate over time, and the color of the line represents the temperature experienced by the skate. Black arrows show the possible times of movement from Prince William Sound (PWS) to the Gulf of Alaska (GOA) in mid-August and from the GOA back into PWS in mid-September

Depth and temperature range occupancy

Tagged big skates occupied depths from 0 to over 500 m and encountered temperatures between 2 and over 18°C (Fig. 5). Based on depth and temperature occupancy, 3 depth-based behavior types were inferred: local resident, slope transient, and shelf transient. The local resident behavior type was demonstrated by skates that provided no evidence of long-distance movement while tagged (F145 and F164). As mentioned earlier, F164 likely crossed a management boundary, from PWS to the GOA, but based on its location, it did so while still undergoing a small (less than 100 km) horizontal movement (Fig. 1). Local residents occupied different depth ranges in summer and winter, staying above 50 m for most of the summer but spending most of the winter and spring between 100 and 200 m (Fig. 5). Temperatures experienced by these skates were confined to between 4 and 14°C, although they primarily occupied waters between 10 and 14°C during the summer and spent all of winter and spring almost exclusively in 4 to 6°C waters (Fig. 5).

The skate for which we had fine-scale data (F164) experienced a maximum depth of 376 m, with an average of 125.6 m (±60.96 m, 1 SD) and a temperature range between 3.2 and 12.9°C (average of 6.2 ± 2.09°C). Interestingly, despite its wide depth occupation, F164 spent 39.8% of its time at liberty in a 20 m depth range between 122 and 140 m. It returned to that depth range 12 times during the year, each time staying there more than 3 d consecutively (Fig. 4). Often while in this depth range, the depth record changed in a sinusoidal fashion, exactly mirroring the tidal cycle in PWS. For example, during a 4 d bout in April 2012, the water depths of the skate tag and the tidal cycle were not significantly different in amplitude (paired *t*-test: t_6 = 0.95, p = 0.38), cycle length (paired *t*-test: t_6 = 0.75, p = 0.48), and timing (paired *t*-test: t_6 = 1.24, p = 0.98). This suggests that the skate was stationary on the sea floor for 3 to 15 d at a time, while the water column height fluctuated with the tide.

The slope transient behavior type was associated with skates that traveled over 100 km and occupied shallow depths (<175 m) during the summer, spring, and autumn and depths down to 500 m during the winter (i.e. M124, F110; Fig. 5). Based on the longitude estimates while at liberty, it appears these skates undertook their long-range movements in the late summer or early autumn (Fig. 3). Although data for F110 were only available for 90 d, this individual started displaying this long-range movement while spending over 84% of its time between 0 and 50 m in the summer and autumn. During the winter and spring, the slope transients occupied warmer waters (mostly 6 to 8°C) than the other 2 behavior types and never occupied waters colder than 4°C (Fig. 5).

The final depth-based behavior type, the shelf transient (F177), moved long distances along the continental shelf and never experienced depths below 150 m, most likely because it remained on the continental shelf throughout its time at liberty. In contrast with the other 2 depth-based behavior types, this skate occupied shallower depths more often in winter and spring than in summer and autumn (Fig. 5). The shelf transient behavior type generally occupied colder waters than the other behavior types, inhabiting mostly 4 to 6°C waters during the winter and spring. While dispersing in the summer and autumn, it mostly occupied a temperature range of 6 to 8°C.

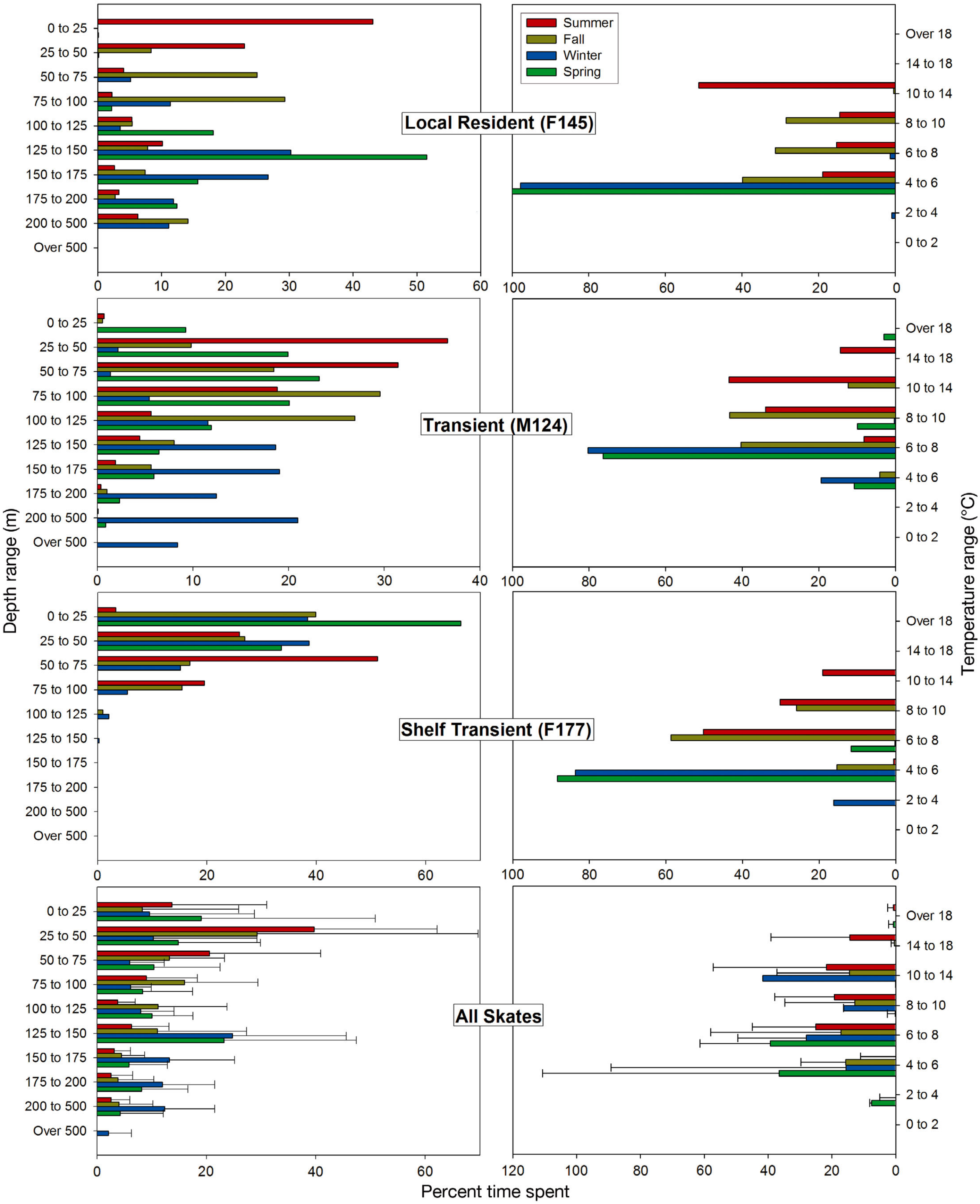

Fig. 5. Percent time spent at different depth (left column) and temperature (right column) ranges for the 3 behavior types (using an example skate identified by sex and TL), as well as all skates, during each of the 4 seasons. Error bars for all skates are 1 SD

DISCUSSION

Satellite tags deployed on big skates provided novel ecological data allowing insight into their behavior that can be used to help evaluate and potentially refine assumptions currently used in the management of this species. Specifically, we found that this species may undergo large horizontal movements and occupy greater depths more often than previously thought. Therefore, it is prudent to reexamine the assumption that big skates undergo limited long-range movements. Interestingly, the area around the Shumagin Islands in the WGOA, to which 2 tagged skates traveled, has been recently identified as a location with high spring and summer big skate abundance based on trawl survey data spanning 1999 to 2012 (Bizzarro et al. 2014). In addition, both tagging locations were within a high-abundance location found by Bizzarro et al. (2014). Together, these findings suggest that there may be multiple areas around the GOA that have relatively high densities of big skates, at least during the spring and summer seasons, and that big skates may travel between them. In other words, these areas are not isolated hot spots or centers of distinct big skate populations but rather are areas that may have seasonal characteristics beneficial to big skates, such as abundant food sources, protection from predators, and optimal temperatures, or hold importance as nursery and mating areas.

Conventional tagging studies almost certainly underestimate the distance travelled and number of management boundaries crossed by skates. One skate in our study traveled a net distance of 21 km between tagging and end locations, but the archived data suggested a much larger-scale movement. Data from another skate showed that tagging and end locations alone underestimated the distance traveled and the number of management boundaries crossed. A conventional tagging study in British Columbia found that only 6.1% of big skates were recaptured over 100 km from the tagging location and that 70% of the skates that traveled over 800 km were females of immature size (King & McFarlane 2010). We found both males and females underwent long movements, and the longest movement (>2000 km) was undertaken by a male of mature size. In the conventional tagging study, big skates traveled at an average speed of 2 to 6 km d^{-1}, similar to what we found in this study.

In contrast to the skates that traveled away from their tagging areas, 3 of the tagged skates (50%) likely remained in PWS for the duration of the tag deployment and traveled a maximum of 21 km between tagging and pop-up locations. It is noteworthy that this is the same distance within which 75% of the big skates conventionally tagged in British Columbia were recaptured (King & McFarlane 2010). Site fidelity has been found in other electronic tagging studies of skates: common skates *Dipturus batis* in the North Atlantic (Wearmouth & Sims 2009) and Arctic skates *Amblyraja hyperborean* in the Canadian Arctic (Peklova et al. 2014). It has been proposed that persistent food supplies may account for site fidelity in some skates (Wearmouth & Sims 2009) and that high-abundance locations for other species could be linked to niche differentiation between species (Bizzarro et al. 2014). In our study, we did confirm that big skates show site fidelity rather than inferring it based on the tagging and recapture location of conventional tags.

Consistent with findings in other studies (Love et al. 2005, Ormseth 2011), big skates tagged with satellite tags spent the majority of their time at depths ≤200 m. However, they also occupied greater depths more often than previously assumed (Stevenson et al. 2008), most likely as a result of limited coverage of surveys during the winter and spring, when big skates occupy relatively deeper water. The maximum depth of big skates has occasionally been reported in the literature as 800 m, always citing the same unpublished manuscript (by K. M. Howe in 1981). This likely spurious record has not been confirmed as far as we can tell and should not be cited until confirmed. The deepest confirmed records of big skates are 376 m in the GOA (Stevenson et al. 2008) and 459 m along the California coast (Bizzarro & Summers 2015), both from summer bottom trawl surveys. This study has not only confirmed that big skates can travel below 500 m, it has also shown that big skates occupy these greater depths more often than previously thought, with one individual spending nearly 10% of the winter season below 500 m. Ecological knowledge such as this provides evidence for extending the habitat description of big skates.

The temperature range occupied by big skates in this study is similar to that found in previous research (Bizzarro et al. 2014) and confirms that big skates are thermally tolerant, occupying temperatures between 2 and 18°C. Overall, tagged big skates in this study generally occupied deeper and colder waters during the winter and spring seasons. The temperature occupancy was most likely related to available water temperatures, which are usually restricted to between 4 and 7°C in both the GOA and PWS during the winter (Vaughan et al. 2001, Weingartner 2007, Musgrave et al. 2013). During the summer and autumn, when a stronger thermocline is established and a wider range of temperatures is available, the tagged skates tended to occupy warmer temperatures at shallower depths, possibly for the metabolic advantages conferred by warmer temperatures (Wallman & Bennett 2006). Temperature is an important factor in structuring skate assemblages (Arkhipkin et al. 2012, Bizzarro et al. 2014), parsing out the habitat between species based on their thermal optima. However, other factors such as food availability may further refine this distribution, and a thermally tolerant species like the big skate may be found in sub-optimal temperatures to reduce competition if other skate species are present (Bizzarro et al. 2014).

PSAT tags deployed on big skates were able to provide novel and salient ecological information on a potentially important commercial fishery species, but this technology comes with a certain number of caveats and drawbacks. First, 2 tags (25% of deployed tags) did not report, and therefore there was no evidence of the reason for their lack of data transmission. This percentage of tag failure is comparable to other studies that have deployed PSAT tags on demersal high-latitude species like Pacific halibut (19% tag failure; Seitz et al. 2011), Pacific sleeper shark *Somniosus pacificus* (33% tag failure; Hulbert et al. 2006), and Arctic skate (22% tag failure; Peklova et al. 2014). Despite these failures, successful big skate tags reported the majority of their data, providing us with valuable insight into the ecology of this species. Second, only 6 tags provided data, making any population-level extrapolations tenuous. Big skates likely display more than 3 behavior types, and our small sample size is not sufficient to define all behaviors that this species can exhibit. Although we were able to show that big skates are capable of long-range movements, understanding the frequency of this long-range movement at the population level will require a much larger sample of tagged individuals. Third, the size of the PSAT tags restricted us to use only larger individuals (over 100 cm TL) to avoid affecting their behavior, but there is conflicting evidence as to which way this might have biased our conclusions. Wearmouth & Sims (2009) determined that larger common skates were more likely to be vertically active, based on PSAT tag data. However, conventional tags on big skates in British Columbia showed that smaller (<90 cm TL) individuals undertook most of the long-range movements (King & McFarlane 2010).

Finally, some of the capabilities of PSAT tags, namely the ability to determine geolocations based on ambient light levels, are more difficult for a demersal species and at high latitudes. New models are being developed that may help refine positions of fish tagged in high-latitude areas, such as the hidden Markov models that integrate maximum depth, tidal patterns, and activity of the fish (Pedersen et al. 2008). Most other existing models use a sea surface temperature- and/or primary productivity-based approach (Chittenden et al. 2013), which cannot be applied to deeper-water demersal species like skates.

Although the present study only examined a small number of individuals during a relatively short time scale, the results provide initial qualitative evidence that big skates can, and likely frequently do, travel long distances, cross management boundaries within the GOA, and spend more time in deeper waters than previously thought, especially during the winter months. As a result, this information can be used to refine assumptions of stock assessment models, such as the depth selectivity of fishing and survey gear, the area of suitable skate habitat for extrapolating abundance surveys, and movement rates among and out of management areas. Managers may therefore want to consider incorporating catch rates at multiple depths during abundance surveys and developing management strategies for this species at the scale of the entire GOA rather than broken down into smaller management areas (such as the WGOA, CGOA, and EGOA). Future research should be designed to further quantify the connectivity of big skates across the entire GOA to better define their stock structure and to facilitate coordinated management in state and federal waters.

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