

Abstract—Depth data from archival tags on northern rock sole (*Lepidopsetta polyxystra*) were examined to assess whether fish used tidal currents to aid horizontal migration. Two northern rock sole, out of 115 released with archival tags in the eastern Bering Sea, were recovered 314 and 667 days after release. Both fish made periodic excursions away from the bottom during mostly nighttime hours, but also during particular phases of the tide cycle. One fish that was captured and released in an area of rotary currents made vertical excursions that were correlated with tidal current direction. To test the hypothesis that the fish made vertical excursions to use tidal currents to aid migration, a hypothetical migratory path was calculated using a tide model to predict the current direction and speed during periods when the fish was off the bottom. This migration included limited movements from July through December, followed by a 200-km southern migration from January through February, then a return northward in March and April. The successful application of tidal current information to predict a horizontal migratory path not only provides evidence of selective tidal stream transport but indicates that vertical excursions were conducted primarily to assist horizontal migration.

Manuscript submitted 29 July 2008.
Manuscript accepted 19 December 2008.
Fish. Bull. 107:221–234 (2009).

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Evidence of the selection of tidal streams by northern rock sole (*Lepidopsetta polyxystra*) for transport in the eastern Bering Sea

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Northern rock sole (*Lepidopsetta polyxystra*) in the eastern Bering Sea off Alaska reportedly migrate from summer feeding grounds to deeper spawning grounds in winter (Shubnikov and Lisovenko, 1964; Fadeev, 1965). Although migration routes are poorly understood, at least some individuals are thought to migrate long distances between summer and winter grounds. Shubnikov and Lisovenko (1964) suggested that some northern rock sole migrate from Unimak Island in the Aleutian Islands to areas northeast of the Pribilof Islands between April and July, covering a distance of more than 500 km. As a means to understand better how this migration occurs, we focus here on one potential mechanism that northern rock sole use, that is, the opportunistic or exclusive use of selective tidal stream transport.

Selective tidal stream transport is a mechanism by which aquatic animals can assist their horizontal migration by actively changing their vertical position in the water column, timed to coincide with tidal currents flowing in a preferred direction. Selective tidal stream transport has been documented for a variety of aquatic animals (Forward and Tankersley, 2001; Gibson, 2003) and has been extensively documented in the North Sea for European plaice (*Pleuronectes platessa*) (Kuipers, 1973; Rijnsdorp and van Stralen, 1985; Metcalfe et al., 1990; Fox et al., 2006; Metcalfe et al., 2006). Even before the use of electronic fish tags, it was recognized that some flatfish species selectively

leave the bottom during periods of a preferred tidal current direction (De Veen, 1967; Harden Jones et al., 1979). More recent work with archival tag data, used in combination with tide data (e.g., Hunter et al., 2004b), has highlighted the importance of both tide and diurnal factors in flatfish migration. For plaice and other flatfish species, the vertical movements (i.e., selective tidal stream transport) vary diurnally; most excursions are made away from bottom during the night (De Veen, 1967; Cadrin and Westwood, 2004; Hunter et al., 2004b; Walsh and Morgan, 2004). Juvenile flatfishes (Champalbert et al., 1992; Burrows, 1994), including northern rock sole (Hurst and Duffy, 2005), also show some preference for nighttime activity.

When flatfishes use selective tidal stream transport, the timing of vertical excursions away from the bottom can be combined with predictions of tidal current velocity to construct hypothetical migration trajectories (Arnold and Holford, 1995). For this estimation to be successful, vertical excursions need to be accurately identified and all directed horizontal movement must be restricted to those off-bottom periods. For species known to use tidal currents, selective tidal stream transport may not be used in all habitats because the strength or direction of the currents may be unsuitable for migration. For example, when European plaice inhabit areas of weak tidal currents in the North Sea, they migrate horizontally, staying near the seafloor where there is

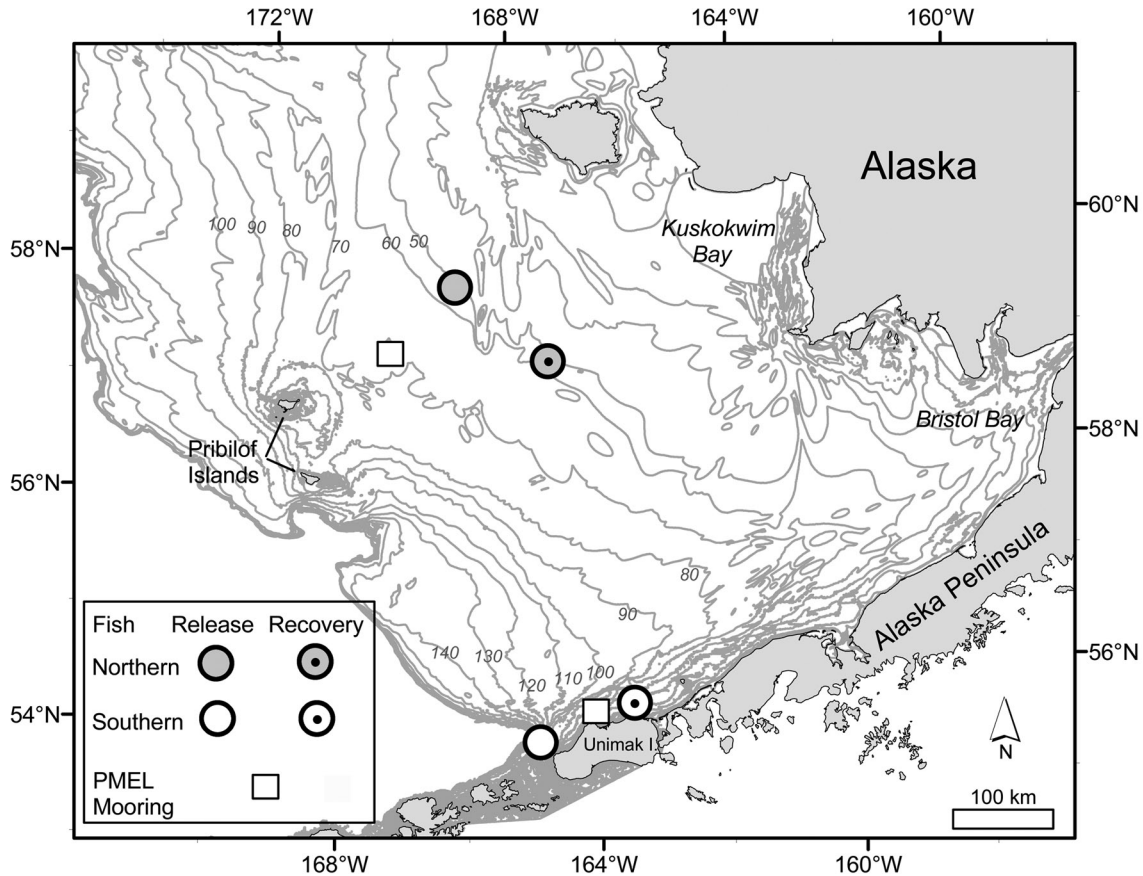


Figure 1

Map of release and capture locations for two female northern rock sole (*Lepidopsetta polyxystra*) tagged with archival tags in the eastern Bering Sea off Alaska in 2003. The locations of the Pacific Marine Environmental Laboratory (PMEL) subsurface moorings where tidal current velocity data (speed and direction) were collected are also shown. Gray lines with numbers indicate the bathymetric contours (in m) in the area.

no tidal assistance (Hunter et al., 2004a; Metcalfe et al., 2006). In addition to accurately determining periods when a fish is off-bottom, successful selective tidal stream transport modeling also requires the ability to accurately predict tidal currents.

Tidal currents over most of the eastern Bering Sea shelf have characteristics that offer fish a mechanism that assists horizontal movement. Such currents range from rotary motion on the central continental shelf (e.g., east of Pribilof Islands) to bidirectional motion along the Alaska Peninsula (Kowalik, 1999; Pearson et al., 1981), and a strong semidiurnal component everywhere which offers fish two opportunities within a 24-h period to use currents to migrate in a particular direction. Near-bottom tidal current velocities over much of the eastern Bering Sea shelf average approximately 20 cm/s and peak to over 50 cm/s, which if used for transport, could provide a significant increase in migration velocity. Moreover, the rotary nature of the currents offers an intriguing mechanism for transport because it can provide a means of transport in any direction a fish chooses.

Here, we examine depth and time data from archival tags attached to two northern rock sole to determine whether vertical excursions are related to diel and tidal influences, and whether a simple model of selective tidal stream transport can be used to construct a hypothetical horizontal migration path that is consistent with the observed tag release and recovery locations

Methods

Tagging

Two northern rock sole were recovered from among 115 released with attached electronic data storage tags in the eastern Bering Sea between 4 June and 26 July 2003. Release locations were approximately 200 km northeast of St. Paul Island in the Pribilof Islands (northern fish) and 18 km northwest of Unimak Island (southern fish) (Fig. 1). Fish were initially captured with a bottom trawl, tagged, and released during the course of the annual eastern Bering Sea bottom trawl survey (Acuna and

Lauth, 2008). The two recovered fish, both captured by commercial trawlers, were a 34-cm-total-length (TL) (at release) female at liberty for 314 days (northern fish) and a 40-cm-TL (at release) female at liberty for 667 days (southern fish). Both fish were assumed to be mature because they were larger than the reported mean size at maturity of 32.8 cm (Stark and Somerton, 2002).

The fish were tagged with Lotek wireless LTD-1100 (St. John's, NF, Canada) data storage tags. Tags were attached to the eyed-side, just below the anterior end of the dorsal fin with a 0.5-mm diameter stainless-steel wire. The wire was inserted through two points on the tag, through the epaxial musculature above the pectoral fin, and affixed on the blind side of the fish by using oval plastic backing. The two wire ends were fastened on the outside of the backing with a crimped connector sleeve.

Tag data, including depth (pressure) and temperature, were recorded at 0.5-h or 1-h time intervals, totaling 12,015 and 16,346 data pairs for the northern and southern fish, respectively. Two sampling intervals were used because, as a memory management function of the tags, the frequency of recordings decreased with the time at liberty. Depth had a resolution of 0.58 m when fish remained at depths less than 150 m, and 1.2 m if the fish exceeded 150 m; temperature had an accuracy of $\pm 0.3^{\circ}\text{C}$. The northern tag recorded for the entire 314 days the fish was at liberty, whereas the southern tag recorded for 620 of 667 days at liberty before the battery died.

Tide prediction

Tidal height and current speed and direction were estimated at the midpoint location between fish release and recovery (northern fish: $58^{\circ}18'N$, $167^{\circ}02'W$; southern fish: $54^{\circ}55'N$, $164^{\circ}31'W$) for each depth measurement using the OTIS Tidal Inversion Software (Oregon State University, Corvallis, OR) which was created with solutions specifically for the eastern Bering Sea (Egbert et al., 1994; Egbert and Erofeeva, 2002). To test the accuracy of the tide model, speed and direction were also estimated at the site of an oceanographic mooring maintained by the Pacific Marine Environmental Laboratory (NOAA, Seattle, WA) near each fish (Fig. 1) and compared to the measured bottom current data. The northern mooring was located approximately 118 km west of the northern fish location and collected data from October 2004 to April 2005; the southern mooring was located approximately 66 km north of the southern fish location and collected data from March 1995 to September 1995. Each data set consisted of hourly current velocity vectors (u =east-west component, v =north-south component) over a period of 193 days.

Identification of vertical excursions

Time intervals during which the fish were off bottom were identified as follows. Measured tag depths were first corrected for tide height variation by subtracting

the tide height predicted by the tide model. Because along-slope movements can be confused with off-bottom movements, the difference in bathymetric complexity between northern and southern tag release locations dictated differences in the subsequent analysis.

For the northern fish, distance off bottom was calculated as bottom depth minus tag depth where bottom depth was estimated in two stages. First, daily bottom depth was chosen as the maximum tag depth during each 24-h period, on the assumption that northern rock sole contact the bottom at least once a day. Second, bottom depths for each 0.5-h or 1-h recording were estimated by linearly interpolating between the times of daily maxima (proc Expand; SAS, vers. 8.02, SAS Inst., Inc., Cary, NC). Times of vertical excursions were identified as those when the off-bottom distance exceeded 2 m. Discrete excursions away from the bottom were defined as groups of successive off-bottom time recordings.

For the southern fish, which resided in steeper, more rugged terrain, distance off bottom was calculated similarly by using 6-h rather than 24-h time windows. In addition, during times when horizontal movements appeared to be occurring in steep terrain, off-bottom distance was calculated by using estimates of bottom depth for still more frequent intervals, assuming that bottom depth was identical to tag depth during each tag recording if tidal fluctuations were obvious in the original tag depth data (i.e., not corrected for tide). The assumption is that the fish was on bottom when tidal fluctuations were recognized. The southern fish was considered off bottom when off-bottom distances exceeded 3 m. Following the criteria used for the northern fish, each 0.5-h or 1-h depth value was designated as either on or off bottom, and discrete excursions were identified. Analyses of excursions for the southern fish were limited to summary statistics because of the difficulty in accurately identifying off-bottom periods (see *Discussion* section).

Diel and tidal influence on vertical excursions

To determine whether the likelihood of excursions differed between day and night, each 0.5-h or 1-h record collected by a tag was first designated as daytime or nighttime based on the predicted times of sunrise and sunset at the midpoint location between fish release and recovery. Daily sunrise and sunset times were calculated by using an algorithm obtained from the U.S. Naval Observatory, Astronomical Applications Department (Washington, DC). The percentage of off-bottom time recordings occurring during the day and night were then calculated for each fish, and the timing and duration of excursions were plotted with respect to day and night.

To determine if vertical excursions of the northern fish were selectively made with respect to tidal current direction, patterns in tidal current direction were examined using compass plots (function Compass (x,y); Matlab, vers. 7.5.0.342, The MathWorks, Inc., Natick, MA); plots of current direction during hours when the fish was off bottom were compared with plots of all

the available current directions. In addition, the significance of current speed and direction in determining whether the northern fish was off bottom was tested using Generalized Additive Modeling (GAM; Venables and Ripley, 1994). This was done by modeling off-bottom status (coded 0 for on bottom and 1 for off bottom) as a binomial response to a smooth function of current speed and direction, with significance based on analysis of deviance. The test was conducted independently for each month that the fish was at liberty, excluding daytime hours when fish remained on the bottom (see *Results* section).

Selective tidal transport model

To determine if the selective use of tidal currents by northern rock sole was an important component of their seasonal horizontal migrations, we developed a selective tidal stream transport model similar in its basic design to that discussed in Arnold and Holford (1995). Assuming that all horizontal movement occurred during off-bottom periods, we constructed a migration path as follows. Starting from the release location, the fish was assumed to drift at the current speed predicted for each off-bottom time and in the mean current direction during each vertical excursion. In addition, the fish was allowed to swim at a specified speed, also in the mean current direction during each vertical excursion. The specified fish swimming speed was held constant over the entire path, but because the true swimming speed was unknown, this speed was iteratively varied until the distance between the final path location and the actual capture location was minimized. Thus, for each 0.5-h or 1-h recording time starting with the release location, latitude and longitude positions were advanced by using the combined drift and swimming speed and mean current direction for each excursion. Tag locations along the selective tidal stream transport path were converted to latitude and longitude positions using great circle formulae.

To verify the accuracy of the predicted migration path, the predicted depth at each location along the path was plotted against the bottom depth (maximum 24-h depth) measured by the tag. Path depths were predicted with inverse distance-weighted surface interpolation (ArcMap 9.2 with Spatial Analyst Extension, ESRI, Redlands, CA) using National Imagery and Mapping Agency (NIMA) depth sounding data for the eastern Bering Sea continental shelf.

Results

Depth data and vertical excursions

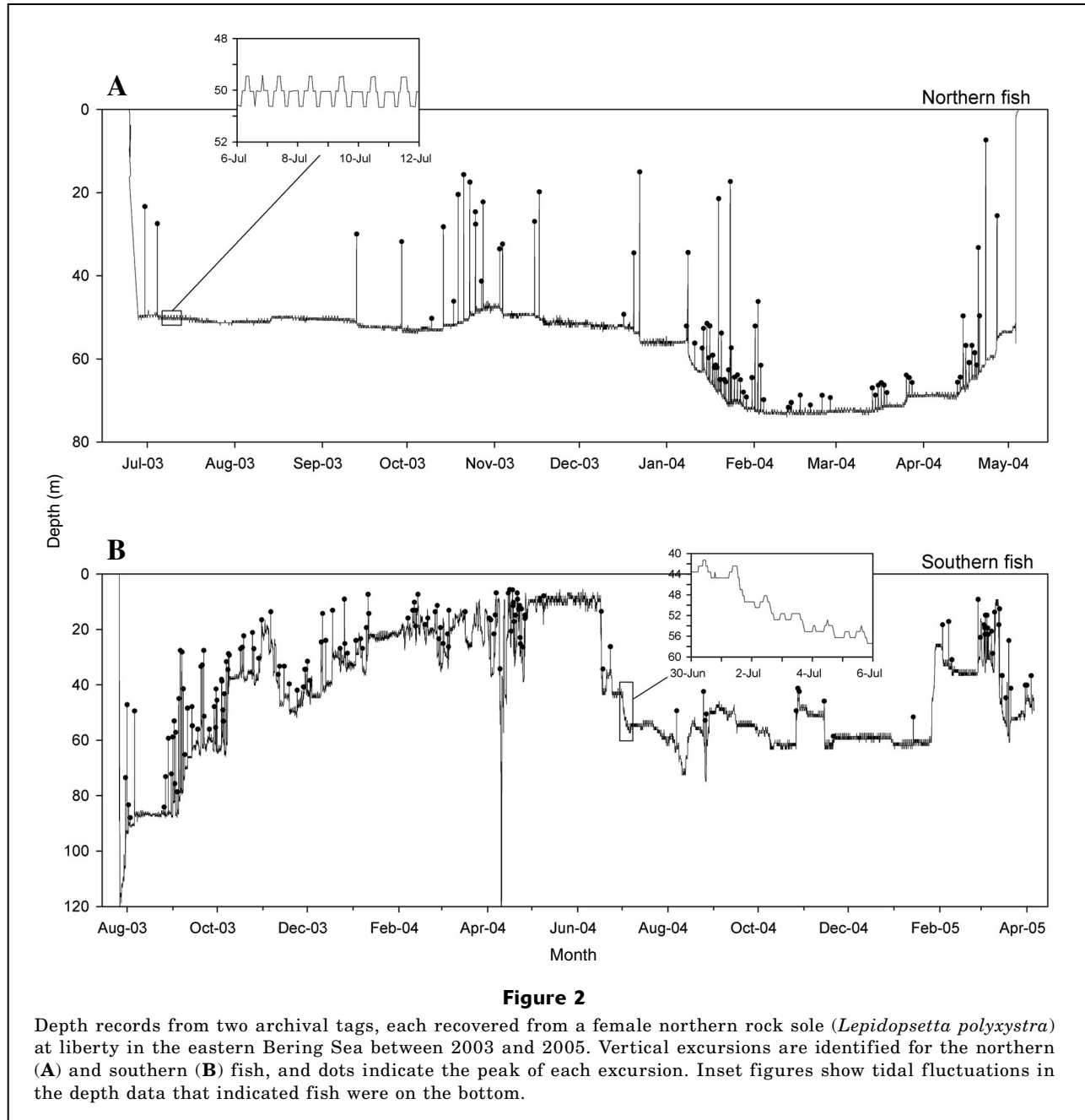
The archival tag depth data contained relatively high frequency variation from three sources. First, vertical excursions away from the bottom were identifiable by sharp decreases in tag depth (Fig. 2). Second, tidal height fluctuations were evident in the tag depth record

(Fig. 2A inset), an indication that fish were settled on the bottom. Third, rapid changes in depth resulted from horizontal movements along steep bottom gradients.

The identification of vertical excursions was clearer for the northern fish than for the southern fish. The northern fish inhabited areas of relatively flat bottom where estimated tag bottom depths ranged from 48 to 74 m; therefore rapid depth changes clearly reflected vertical excursions away from the bottom. The southern fish, by comparison, inhabited an area of complex bathymetric contours where bottom depths collected from tags ranged from 9 to 161 m. Movements along a steep bottom gradient were evident for the southern fish, particularly during April 2004 when fish depth increased and decreased more than 100 m within a 24-h period (Fig. 2B). Because of this complexity, there were occasions when it was unclear whether changes in tag depth resulted from a vertical excursion or a quick movement along a bottom gradient. For this reason, not all vertical excursions were identifiable for this fish. More gradual movements across bottom gradients were observed for both fish, and most often coincided with periods of vertical excursions, indicating that the excursions were related to the horizontal movement of the fish. In a few cases with the southern fish, however, movements across bottom gradients occurred in the absence of vertical excursions (Fig. 2B inset).

The frequency, duration, and distance of vertical excursions away from the bottom were similar for the two fish. A total of 78 distinct excursions away from the bottom were identified for the northern fish during a period of 314 days, and 154 excursions were identified for the southern fish during a period of 620 days (Table 1). These excursions were relatively rare, accounting from 2.0% (southern fish) to 2.6% (northern fish) of the time at liberty. Average excursion durations were 2.6 hours (northern fish) and 2.1 hours (southern fish); average excursion extent (i.e., maximum distance off bottom) was 14 m with a maximum of 64 m (Table 1). The frequency of vertical excursions varied seasonally; most excursions occurred from winter to spring for the northern fish and during fall and spring for the southern fish. Excursions were infrequent during summer months (Fig. 2).

The timing of vertical excursions was related to both diel and tidal factors. For the northern fish, 90% of the excursions occurred at night, whereas for the southern fish, 85% occurred at night (although not all vertical excursions could be identified with certainty). Both fish underwent vertical excursions that sometimes occurred over a series of consecutive nights (Fig. 3). In addition to being limited to nighttime, vertical excursions occurred during particular stages of the tide cycle. For example, during the beginning of September 2003, the southern fish made consecutive nightly excursions, but only before the dominant low tide (Fig. 3B). Examination of tidal current directions (northern fish only), revealed the fish did not indiscriminately choose nighttime periods, but made nightly vertical excursions only when tidal currents were in certain directions. For ex-



ample in January, when the northern fish made vertical excursions with greatest frequency, it did so when tidal currents were southerly directed, yet the prevailing nighttime tidal currents were directed toward the west and northeast (Fig. 4). During months with frequent excursions, the probability of being off-bottom was not significantly related to current speed but was highly significantly related to current direction (Table 2; GAM (generalized additive modeling) test). Considering the rotary nature of the tidal current where the northern fish resided, the timing of vertical excursion was selective, as opposed to random, with respect to tidal current

direction. This selection was particularly evident during January when nighttime periods were sufficiently long to allow for two separate southerly directed currents in a single night. Coincident to these dual nightly southern currents, the fish sometimes made two separate nightly vertical excursions (Fig. 3A).

Migration path

The predicted migration path based on selective tidal stream transport for the northern fish extended for 503 km and ended 0.26 km from the reported capture

Table 1

Excursion duration and distance away from the bottom for two northern rock sole (*Lepidopsetta polyxystra*) released with archival tags and recaptured in the eastern Bering Sea between 2003 and 2005. Minimum durations were limited to the collection frequencies of the tags which were 0.5 hour and 1.0 hour, respectively, for the northern and southern fish. Mean distances were weighted by the sampling frequency for the tags. Numbers in parentheses indicate the average maximum distance off bottom among excursions. Not all excursions could be identified with certainty for the southern fish because of the variable bathymetric terrain in the area where the southern fish resided.

	Duration away from bottom (h)			Distance away from bottom (m)			Identified excursions	Time recordings
	Min.	Max.	Mean	Min.	Max.	Mean		
Northern fish	0.5	6.5	2.6	2.2	54.2	10.4 (13.8)	78	316
Southern fish	1.0	7.0	2.1	3.0	63.7	12.2 (13.4)	154	332

Table 2

Significance of tidal current direction and speed on the probability of a northern rock sole (*Lepidopsetta polyxystra*) being off the bottom. Data are from one fish tagged in the more northerly area of the eastern Bering Sea shelf. Generalized additive modeling (GAM) with a binomial error term (0=on bottom, 1=off bottom) was used to test probabilities for each month, during nighttime. n = the total number of timed tag depth recordings per month. Number in parentheses indicates the number of recordings when the fish was away from the bottom. Months of fewer than 10 nighttime off-bottom observations are excluded.

Month	Chi-square		P-value		n
	Direction	Speed	Direction	Speed	
Oct. 03	15.0	1.3	0.0018	0.7310	855 (28)
Nov. 03	9.2	8.6	0.0236	0.0329	969 (12)
Dec. 03	10.9	2.7	0.0106	0.4057	1079 (12)
Jan. 04	75.9	2.0	<0.0001	0.5364	1041 (126)
Feb. 04	40.7	3.4	<0.0001	0.3313	587 (36)
Mar. 04	14.5	2.8	0.0022	0.3991	373 (22)
Apr. 04	17.6	4.8	0.0005	0.1794	288 (39)

location (Fig. 5). A seasonal migration is apparent in this path. After its release in July, the fish remained in the general vicinity of the release location for about 5 months, then abruptly in January and early February 2004, it migrated south approximately 200 km (straight line) from the release location to the southern most point of the path. In March and April, the fish nearly reversed direction and migrated to the north where it was recaptured. During the migration, the fish traveled an average of 6.4 km and maximum of 17.3 km per vertical excursion. The swimming speed which minimized the distance between the final migration path position and the reported capture location was 47 cm/s or 1.4 body lengths per second (BL/s) for the 34-cm fish.

The bottom depths predicted at the locations along the migration path were very similar to the bottom depths (maximum depth within each 24-h period) measured by the archival tag (Fig. 6) and had a mean absolute difference of only 2.5 m, thus corroborating the predicted migration path. The maximum depth during this migration occurred at the beginning of March when

the fish abruptly changed its migration direction from the south to the northeast.

Although a migration path for the southern fish could not be formulated, depth data from the archival tag (Fig. 2B), indicated that the fish must have remained along the Alaska Peninsula and did not migrate west toward the continental slope, or into the central Bering Sea shelf. Because predicted bottom depths gradually decreased from 90 m to 10 m over the first 10 months at liberty, the fish could not have migrated toward the slope. In addition, abrupt changes in bottom depth such as the 10-m to 40-m increase from 16 through 17 June 2004 (Fig. 2B), indicated that the fish remained in an area of relatively steep bathymetry—an area that does not exist on the central shelf.

Accuracy of tidal current prediction

Overall, current direction was more accurately predicted at the northern mooring site, where direction errors were less than 40 degrees during periods of the

most frequently observed current speeds (10–40 cm/s; Fig. 7A). By comparison, errors of over 40 degrees were common at the southern mooring site, particularly when current speeds were less than 20 cm/s (Fig. 7B). Model prediction of current direction improved with increasing observed current speed at both northern and southern mooring sites (Fig. 7). Model estimates of current speed at the northern mooring displayed progressive underestimation of the observed speed with increasing speed (Fig. 8A). When the observed current speeds were 33 cm/s, for example, the model underestimated these speeds by an average of 10 cm/s. At the southern mooring, observed speeds were underestimated at slow speeds and overestimated at faster speeds (Fig. 8B).

Discussion

Archival tag data from two northern rock sole released and recaptured in the eastern Bering Sea provide evidence that selective tidal stream transport can be used to aid horizontal migration. Vertical excursions, although infrequent, were correlated to both diel and tidal factors. Not only did both fish undergo vertical excursions during mostly nighttime hours, the northern fish did so during select periods of the tidal cycle when tidal currents were moving in a particular direction. The significance of current direction as a determinate of vertical movement for the northern fish indicated that the fish did not randomly leave the bottom, but did so only when the current was moving in a specific direction. The successful application of tidal current information to predict a migration path for the northern fish validates that at least some northern rock sole use tidal currents for transport, and also may indicate that their vertical excursions are conducted primarily for the purpose of horizontal migration.

Our attempt to predict a migration path for the southern fish was unsuccessful for several reasons. First, the identification of vertical excursions was less certain because of the variable bathymetric contours in the area. Second, model estimates of current direction were considerably less accurate when compared to the measured current direction at the location of the southern fish than for the location of the northern fish. Finally, the assumption for the model was that all horizontal movements occurred only during periods when the fish left the bottom; however, for the southern

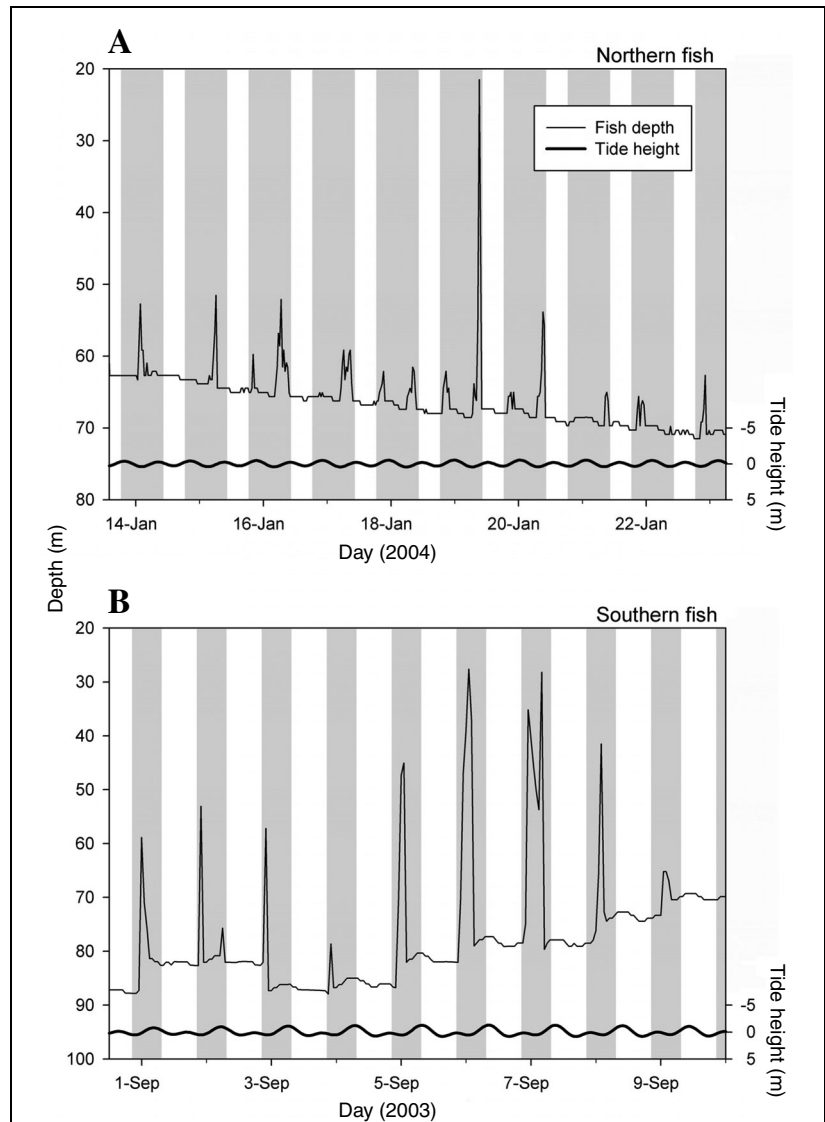
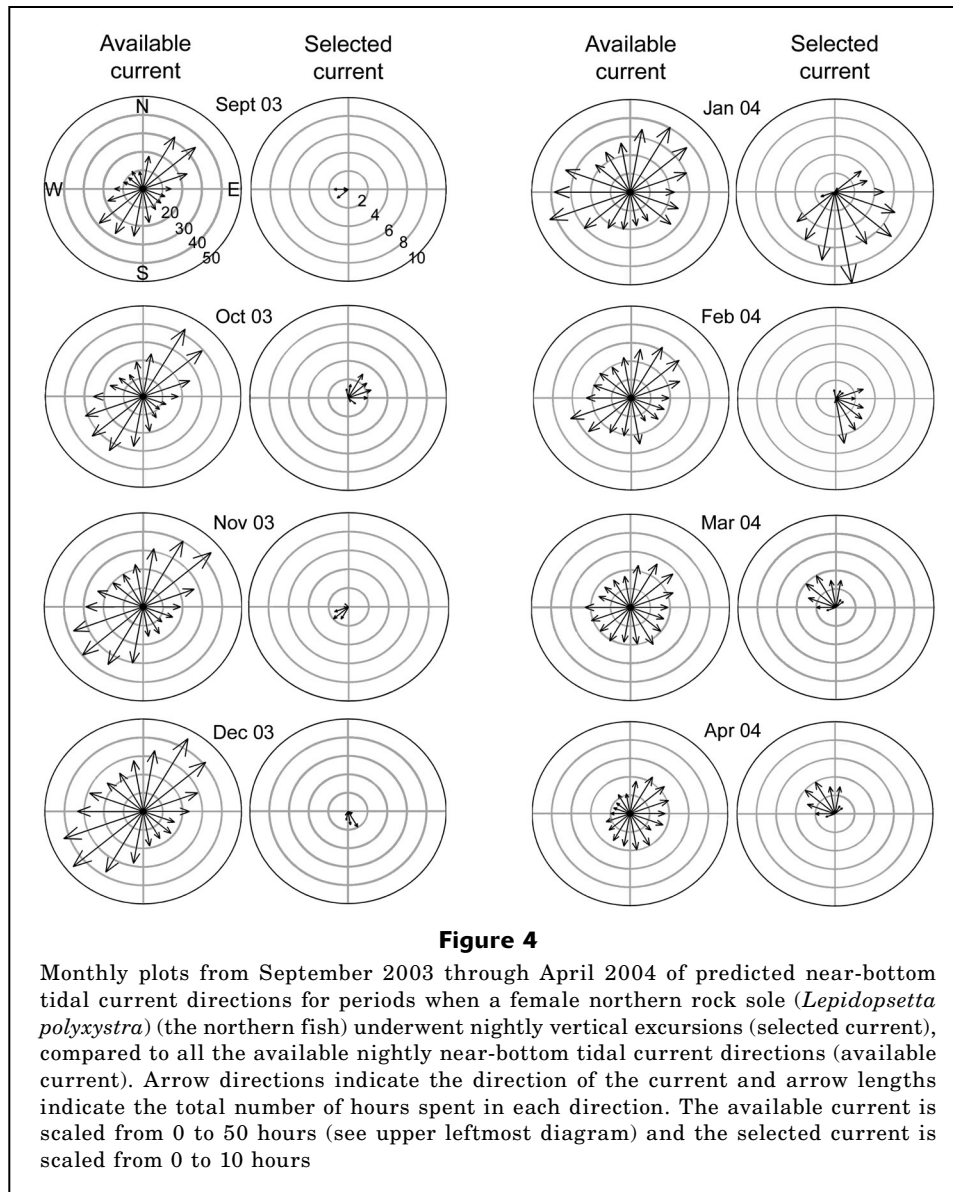


Figure 3

Consecutive nightly vertical excursions (shown as peaks) recorded for two female northern rock sole (*Lepidopsetta polyxystra*) tagged with archival tags in the eastern Bering Sea. Examples for both northern (A) southern fish (B) are presented. Nighttime periods are shaded. Model estimates of tide height (heavy line) at a position midway between fish release and recovery positions are provided to highlight the tidal fluctuation recorded by the tag and show that the timing of vertical excursions is related to tidal factors in addition to diel factors.

fish there was evidence of additional horizontal movement. Gradual decreases in fish depth sometimes occurred during periods in which tidal fluctuations could be recognized in the depth record, indicating that the fish migrated to some extent while it remained on or close to the seafloor. With no way to account for these movements in the model, we were unable to accurately calculate the projection of the path.

The estimated average swim speed of 1.4 BL/s (47 cm/s) that minimized the distance between the final



migration path position and the recovery position is considerably higher than values of 0.6 BL/s reported for European plaice and Japanese flounder (*Paralichthys olivaceus*) during tidally assisted migration (Kawabe et al., 2004; Metcalfe et al., 1990). We offer several explanations. First, estimates of current speeds in the model were lower than actual current speeds, a bias that would inflate our estimated swimming speed. Second, the northern fish may have been capable of maintaining a more consistent direction; that is, more aligned to the destination of the migration than the current directions. We assumed the fish traveled in the average direction of the current during each excursion event. However, if the fish had a predetermined destination and the ability to navigate, it may have actively deviated slightly from the average current direction. More efficient overall swimming directions would have reduced the overall dis-

tance traveled, and again would have resulted in lower swimming speeds necessary to complete the migration path. Finally, some vertical excursions may not have been identified because of the frequency of collection of archival tag data (0.5 hour or 1 hour), or the fish may have migrated toward its destination without undergoing vertical excursions (e.g., it swam while near the bottom). Evidence of this type of movement was clear for the southern fish, which appeared to use tidal currents, but its horizontal migration was not limited to periods of vertical excursions. The northern fish may also have migrated without undergoing vertical excursions, but because the bathymetric terrain was fairly flat on the central eastern Bering Sea shelf, such movements could not be detected.

Although we demonstrate the preference for nighttime vertical activity for only two adult northern rock

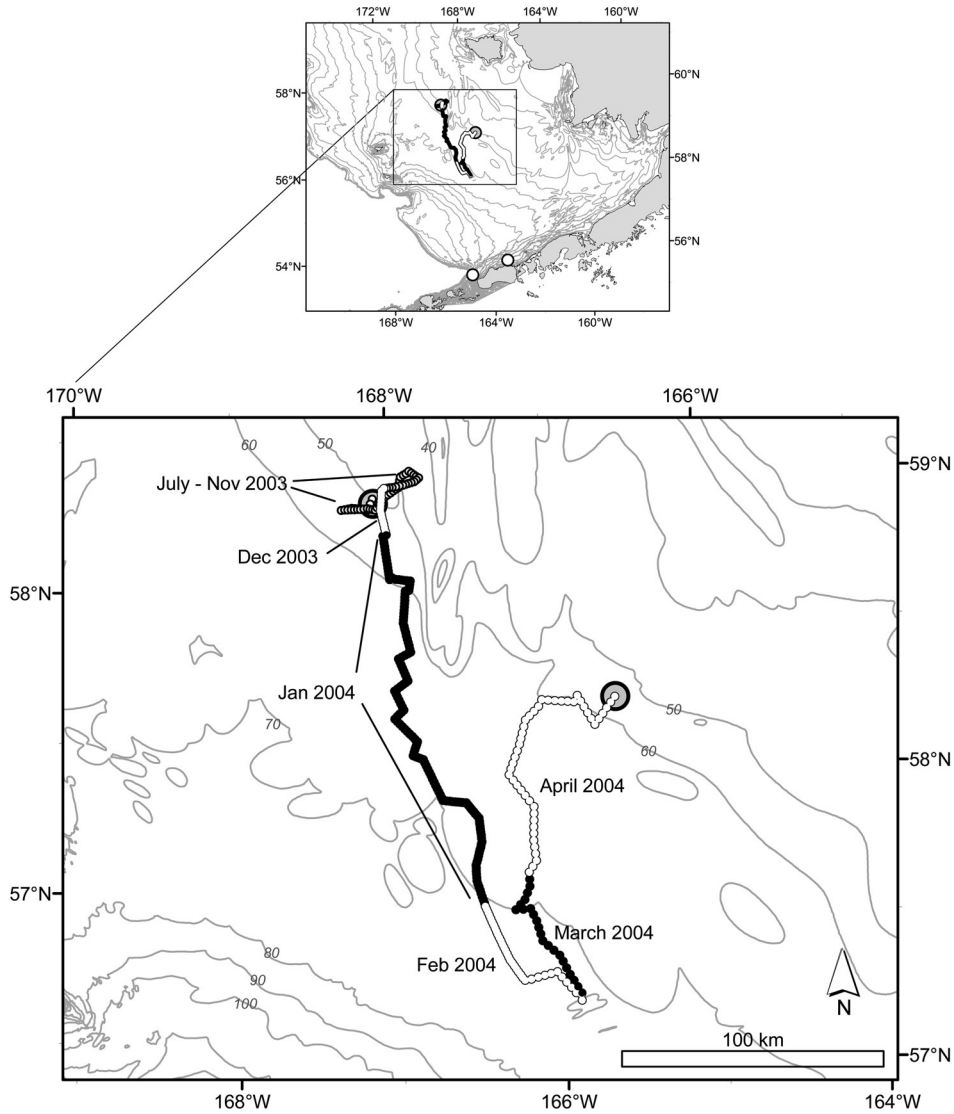
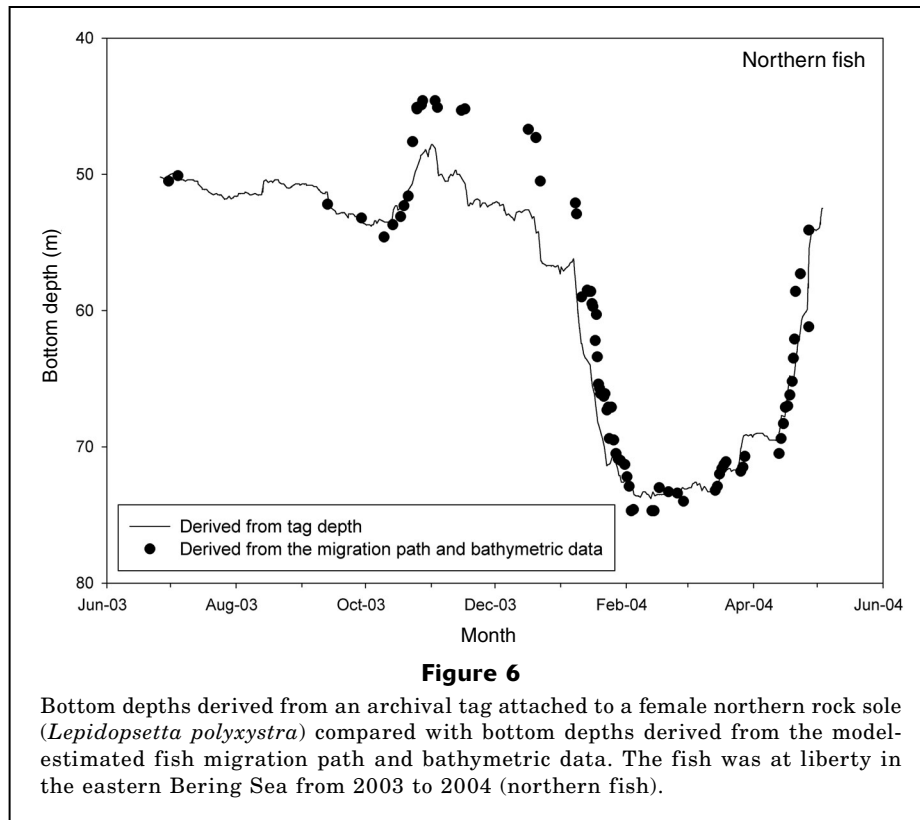


Figure 5

Migration path of one female northern rock sole (*Lepidopsetta polyxystra*), tagged and recaptured in the eastern Bering Sea, released in 2003 and captured in 2004. The migration path is based on current velocity vectors predicted during periods when the northern fish underwent excursions away from the bottom. Circles identify the release and recovery positions. Gray lines with numbers indicate the bathymetric contours (m). Months are indicated by the alternating black and white paths.

sole, this behavior is common among various flatfish species and juvenile northern rock sole. Nighttime vertical excursions have been reported for a variety of flatfishes from postlarval through adult stages (e.g., De Veen, 1967; Weinstein et al., 1980; Cadrin and Westwood, 2004; Hunter et al., 2004). Nighttime periods are thought to offer flatfishes a reduced risk of predation by visual predators (Burrows, 1994). In laboratory experiments, the swimming activity of juvenile northern rock sole (20–40 mm TL) away from the bottom occurred most often during nighttime (Hurst and Duffy, 2005). This activity involved vertical excursions to the

surface, followed by horizontal swimming and gliding. It follows that, like adult northern rock sole, juveniles undergo vertical excursions away from the seafloor for the purpose of horizontal migration. Considering northern rock sole juveniles inhabit areas with tidal influence, it follows that they also use tidal currents for transport. Although it is unlikely that small juveniles migrate extensive distances, as some adults do, juveniles may use tidal current for short-term migrations as a mechanism to locate better feeding grounds within nursery areas (Hurst and Duffy, 2005). We believe that at least some adult northern rock sole employ this



feeding strategy, albeit on a larger spatial scale. The so called “feeding months” for northern rock sole in the eastern Bering Sea reportedly occur during summer when they disperse across the shelf after aggregating for spawning during winter and spring (Fadeev, 1965; Shubnikov and Lisovenko, 1964). This feeding period may well be represented by the first five months that the northern fish was at liberty (July–November), during which migration was less frequent and not in a consistent direction.

As suggested by the migration path presented here, at least some adult northern rock sole undergo vertical excursions for the purpose of tidally assisted horizontal migration, as opposed to vertical movements into the water column for feeding or spawning. Both juvenile and adult northern rock sole feed during daylight hours, but rarely during the night (Corcobado Oñate, 1991; Hurst et al., 2007) when off-bottom swimming occurs. Unlike other eastern Bering Sea flatfish species such as arrowtooth flounder (*Atheresthes stomias*), which feed high in the water column (Yang, 1995), northern rock sole feed close to the bottom. Northern rock sole feed almost exclusively on benthic invertebrates, such as polychaete worms and other marine worms (Corcobado Oñate, 1991; Lang et al., 1995; McConnaughey and Smith, 2000). In addition, northern rock sole likely do not leave the bottom to spawn because, along with their congener, southern rock sole (*L. bilineata*), they are the only northeast Pacific flatfishes to spawn de-

mersal adhesive eggs (Matarese et al. 1989; Stark and Somerton, 2002).

If most northern rock sole prefer to undergo vertical excursions during the night, winter offers greater opportunity to travel in a preferred direction because of the increased hours of darkness. For the northern fish, vertical excursions were most frequent during January, when it travelled in a southerly direction. Southerly directed tidal currents were sometimes available at two different periods within a single night because of the semidiurnal nature of the tides (e.g., a full clockwise rotation of tidal currents every 12 hours). Hunter et al. (2004b) noted similar nocturnal behavior for European plaice in the North Sea during winter when two “transporting tides” sometimes occurred within a night because of the longer periods of darkness lasting up to 15 hours.

The northern rock sole vertical movements examined here appear shorter in both duration and extent (Table 1) in comparison with other flatfish for which vertical behavior has been studied, with the exception of yellow-tail flounder (*Limanda ferruginea*) whose excursions average 1.5 hours and 6 m off bottom (Cadriin and Moser, 2006). Some European plaice (*P. platessa*) in the North Sea reportedly spend from 6 hours to 12 hours a night swimming in midwater during winter months (Hunter et al., 2004b). Common sole (*Solea solea*) in the North Sea are thought to use the upper half of the water column for selective tidal stream transport during which

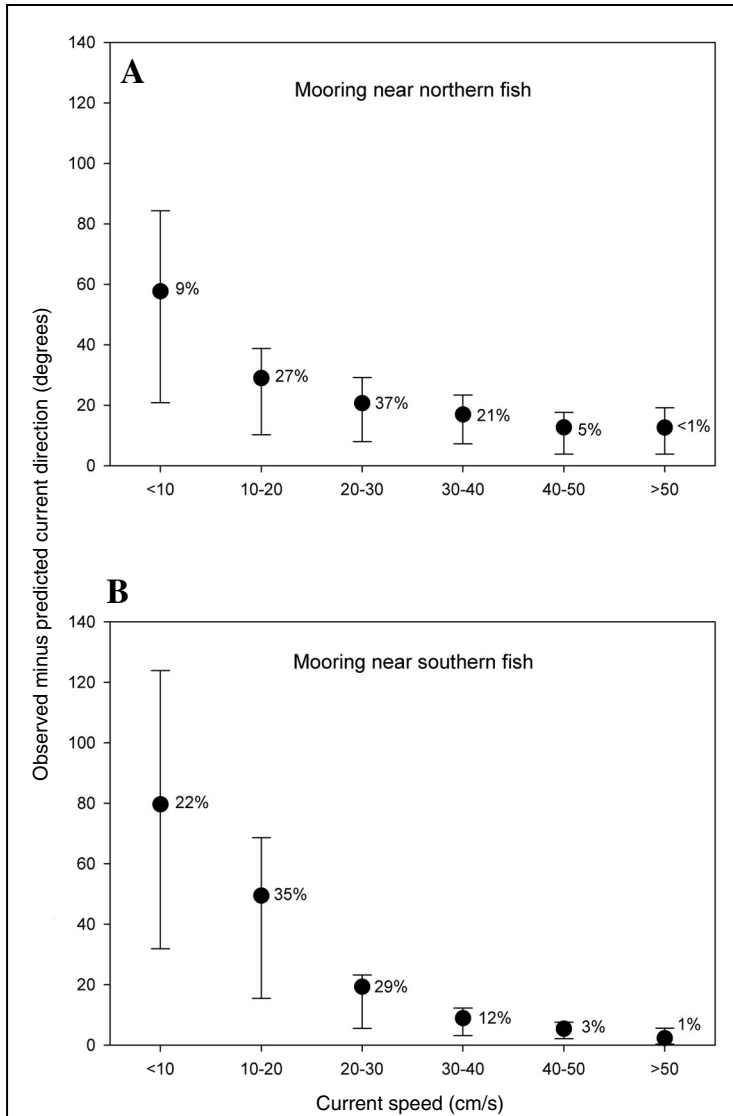


Figure 7

Angle difference between observed and predicted (model) near-bottom tidal current directions at the mooring site near the northern fish (A) and at the mooring site near the southern fish (B) in the eastern Bering Sea, plotted at different observed current speeds. The y-axis is expressed as the mean absolute value of the angle difference between observed and predicted current directions (in degrees). Error bars indicate 25th and 75th percentiles. Percentages next to the means (circles) indicate the percentage of time that each grouping of observed current speed represented during the 193 days of collection.

they frequently approach the surface (De Veen, 1967; Greer Walker et al., 1980). By comparison, the northern rock sole examined here only occasionally approached the surface; most vertical excursions occurred in the bottom half of the water column. Even during periods of active migration (e.g., January; northern fish), vertical excursions averaged only 2.6 hours in duration and were a maximum extent of 11.6 m away from the

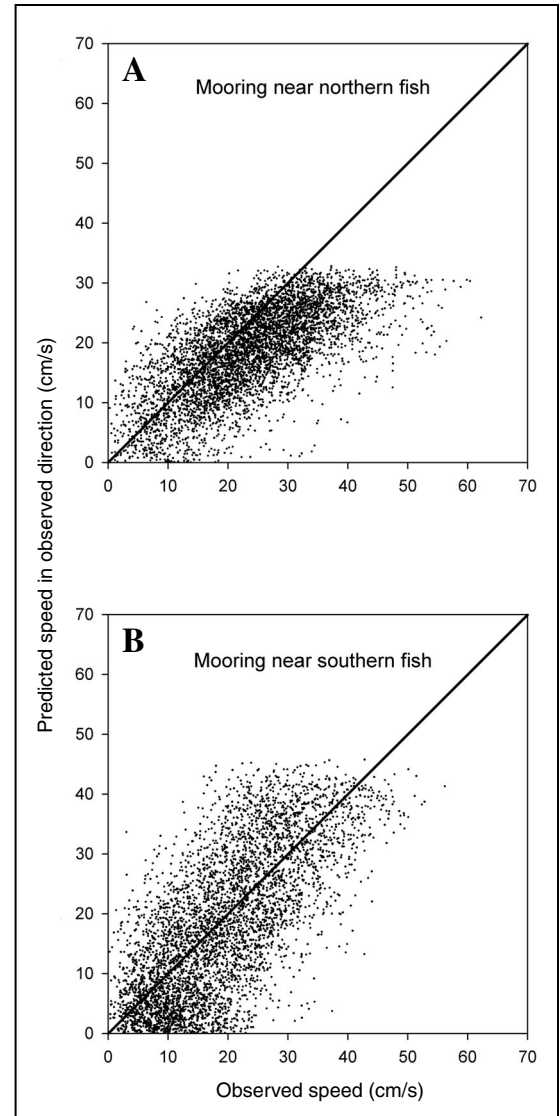


Figure 8

Comparison of observed and predicted (model) near-bottom tidal current speeds at the northern (A) and southern (B) mooring sites in the eastern Bering Sea. Predicted speed is presented as the component of the model speed projected in the observed direction, $MS_o \cos(\theta)$, where MS_o = the model-predicted speed in the observed direction, and θ = the angle difference between observed and predicted current directions. The line indicates a 1:1 ratio. Model estimates of speed do not include residual (e.g., baroclinic) effects that may have been present in observed current speeds.

bottom. These vertical excursions could be of interest to fishery managers if they affect fish availability to bottom trawl surveys (Hunter et al., 2004b). However, the northern rock sole excursions were particularly infrequent during summer daylight hours when the bottom trawl surveys of the eastern Bering Sea are

conducted (Acuna and Lauth, 2008). From the data on the two fish examined here, northern rock sole remain on the bottom 99.8% of the time during summer (June and July) daylight hours.

Although we could not predict a migration path for the southern fish, it was apparent that the migration pattern differed between the two fish. The northern fish clearly used tidal currents to facilitate a southern migration to deeper water during winter and a migration back north during spring. These movements are consistent with the seasonal spawning and post-spawning migrations suggested by Fadeev (1965) and Shubnikov and Lisovenko (1964). As with some European plaice, which migrate south to warmer waters for spawning (Hunter et al., 2004a), northern rock sole that reside on the northern part of the eastern Bering Sea shelf during summer (i.e., the northern fish) may require a migration to more southern or deeper waters to reach temperatures suitable for spawning. Adult rock sole (likely *L. polyxystra*) from the western Bering Sea also undergo a migration to deeper water in winter, and do so presumably to avoid temperatures below 0°C (Shvetsov, 1979). Temperatures experienced by both fish decreased during winter months but stabilized to about 2°C in February and March. Had the northern fish stayed in the vicinity of its release, it would have experienced bottom temperatures below 0°C in February, as recorded by instruments at the northern oceanographic mooring site. The southern fish also underwent nighttime vertical excursions that were tidal in nature, but unlike the northern fish, there was no indication of a spawning migration; excursion frequency did not increase before the known spawning season (winter–spring), and depth records indicated no repeatable pattern from one winter (2004) to the next (2005). It is logical to assume that the extent of migrations is dependent on the proximity of feeding and spawning locations. Thus, the northern fish may require a directed seasonal migration to reach a viable spawning location, whereas the southern fish can remain resident if suitable feeding and spawning locations are within close proximity.

If the northern fish migrated south for the purpose of spawning, the southern extent of the migration route may have been a spawning location. We can infer from the spatial distribution of the fishery for roe of northern rock sole—a fishery that operates in the eastern Bering Sea during February and March just before the spawning season (Stark and Somerton, 2002; Wilderbuer and Nichol, 2007)—that spawning aggregations occur over a wide area of the central and outer continental shelf extending from Unimak Island to west of the Pribilof Islands. This distribution overlaps with the southern point of the migration path.

The eastern Bering Sea shelf offers a multitude of possibilities for tidally assisted transport, and the distribution range that individuals seasonally inhabit may partly depend on the nature of the tidal currents. Based on tidal current ellipses for the M_2 tidal constituent in the eastern Bering Sea, tidal currents are rotary in

nature over the majority the shelf area south of latitude 60°N but become more bidirectional (i.e., 60- and 240-degrees) close to the Alaska Peninsula and into Bristol Bay (Pearson et al., 1981; Kowalik, 1999). Because the northern fish inhabited the central part of the eastern Bering Sea continental shelf, opportunities for selective tidal stream transport were available in all directions, thus enabling a round-trip migration. By comparison, the southern fish resided along the Alaska Peninsula; therefore opportunities for selective tidal stream transport were limited to northeasterly and southwesterly directions. Fish that undergo migrations in northeasterly and southwesterly directions could use selective tidal stream transport over much of the eastern Bering Sea shelf. Adult yellowfin sole (*Limanda aspera*), for example, are known to migrate annually in a northeasterly direction more than 500 km from winter grounds west and southeast of the Pribilof Islands to nearshore summer spawning grounds in Kuskokwim and Bristol bays (Wakabayashi, 1989). Given the extent of this migration and the availability of tidal currents, it is reasonable to assume that yellowfin sole also use selective tidal stream transport.

Results presented here provide the first known evidence of selective tidal stream transport among aquatic animals in the eastern Bering Sea. Among larval flatfish in the eastern Bering Sea, including northern rock sole, passive forms of transport involving wind-driven surface currents and geostrophic flow have been shown to contribute to their horizontal distribution and likelihood of survival (Wilderbuer et al., 2002; Lanksbury et al., 2007). The contribution of more active forms of transport such as selective tidal stream transport may become evident as more is learned about the vertical migration behavior of larvae. Evidence that larval northern rock sole as small as 8 mm can regulate their depth in the water column (Lanksbury et al., 2007) indicates that selective tidal stream transport is a possibility. As we learn about how adult, juvenile, and larval fishes use tidal currents for migration, the need becomes evident for more accurate tide-prediction models that can be used for modeling fish migration. Such models should become available in the near future with the completion of a baroclinic tide model of the eastern Bering Sea.

Acknowledgments

We thank D. Kachel and P. Stabeno for providing tidal information at Pacific Marine Environmental Laboratory (PMEL) mooring sites, and for providing insight concerning tides in the eastern Bering Sea. A. Greig, S. Kotwicki, and J. Benson provided technical support on use of ArcView and circular trigonometry. T. Wilderbuer and J. Gauvin provided productive discussion concerning flatfish spawning and migration. Finally, K. Baily, T. Hurst, T. Wilderbuer, J. Lee, S. Cadrin, and three anonymous reviewers improved the manuscript with insightful suggestions.

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