

ARTICLE

Vertical Movements of Juvenile Sablefish in Coastal Southeast Alaska

Karson M. Coutré* and **Anne H. Beaudreau**

College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, Alaska 99801, USA

Dean Courtney¹

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Point Lena Loop Road, Juneau, Alaska 99801, USA

Franz J. Mueter

College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, Alaska 99801, USA

Patrick W. Malecha and Tom L. Rutecki

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Point Lena Loop Road, Juneau, Alaska 99801, USA

Abstract

Diel vertical migration is commonly associated with pelagic fish species, but demersal fishes may also undertake vertical movements while managing foraging tradeoffs during their vulnerable juvenile stage. We examined fine-scale vertical movements of age-0 juvenile Sablefish *Anoplopoma fimbria* to better understand behavioral patterns that may affect their survival in nearshore habitats. Thirteen juvenile Sablefish (mean FL = 241.9 mm) were implanted with acoustic transmitters and were monitored by use of two acoustic receivers from October 5 to November 14, 2003, within St. John Baptist Bay, Baranof Island, Alaska. The six fish that remained within range of the receivers spent the majority of their time near the bottom but made periodic vertical excursions. Generalized linear mixed-effects models were used to determine the relationships between excursion frequency and the tidal stage and diel period. For all Sablefish, variation in excursion frequency was related to date and diel period, with the highest excursion frequency observed during dawn and day periods and the lowest frequency observed at night. Over the 40-d period, excursion frequency increased to a peak on day 33 (i.e., early November). Generalized linear models for each individual fish supported the finding that the excursion behavior was primarily related to date and

Subject editor: Anne B. Hollowed, Alaska Fisheries Science Center, Seattle

© Karson M. Coutré, Anne H. Beaudreau, Dean Courtney, Franz J. Mueter, Patrick W. Malecha, and Tom L. Rutecki

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. The moral rights of the named author(s) have been asserted.

*Corresponding author: kmcoutre@gmail.com

¹Present address: National Oceanic and Atmospheric Administration, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, Florida 32408, USA.

Received June 12, 2016; accepted January 13, 2017

diel period; however, tidal stage also explained variation in excursion frequency for three of the six individuals that remained within receiver range. This study is the first to describe vertical migration of juvenile Sablefish in the wild and reveals that environmental conditions have the potential to influence the fine-scale movements of juvenile Sablefish within nearshore habitats.

As mobile consumers, fish have the capability of managing tradeoffs among prey availability, predation risk, and thermal conditions while seeking habitats that benefit their growth and survival. Many planktivorous fishes undergo diel vertical migration (DVM), feeding near the surface during crepuscular periods but remaining near the bottom during the day to avoid visual predators; however, these patterns can vary among species based on physiology and life history traits (Clark and Levy 1988; Quinn et al. 2012). Predator avoidance is often associated with low activity and occupation of low-light areas (e.g., greater depths) to decrease visibility and the chance of encounters with visual predators (Eggers 1978; Loose and Dawidowicz 1994). For example, juvenile Sockeye Salmon *Oncorhynchus nerka* make brief excursions into shallower depths to feed at dusk, a behavior that is thought to minimize exposure to predators while still fulfilling energetic requirements (Eggers 1978). Vertical movement through the water column may also be linked to patterns of prey supply. Availability of zooplankton often fluctuates with tides and currents, thus influencing the foraging-driven vertical migrations of predators (Laprise and Dodson 1989; Frost and Bollens 1992). Fish may also seek optimal thermal conditions for growth by moving in relation to vertical gradients in temperature (e.g., Mehner et al. 2010).

Diel vertical migration is typically associated with pelagic, planktivorous species; however, demersal fishes may make diurnal movements off the bottom that are related to the vertical distribution of their prey or environmental factors (Beamish 1966). For example, Atka Mackerel *Pleurogrammus monopterygius* made more vertical excursions from the bottom with higher light intensity but fewer excursions during high current velocity associated with spring tides (Nichol and Somerton 2002). Many marine species that are demersal as adults undergo ontogenetic shifts in vertical distribution as they settle from pelagic to benthic habitats (e.g., damselfishes: Ohman et al. 1998; rockfishes: Love et al. 2002). Functionally, juveniles undergoing settlement are neither strictly pelagic nor demersal and may undertake vertical movements to manage foraging tradeoffs during this vulnerable life stage. We examined fine-scale vertical movements of juvenile Sablefish *Anoplopoma fimbria* to better understand behavioral patterns that may affect their survival in nearshore habitats. The nearshore residence period for juvenile Sablefish provides an opportunity to document the frequency and magnitude of vertical movements of a demersal marine species during its early postsettlement phase.

Environmental factors and physiological needs have the potential to dictate juvenile Sablefish vertical movement (Sogard and Olla 1998). In an experimental setting, juvenile

Sablefish (≤ 100 mm) varied their vertical distribution according to food availability and were more active during the day than at night; however, this diel pattern was less evident as juveniles increased in size (Sogard and Olla 1998). At night, some juveniles were also observed using structures at the bottom of the tank, potentially as a resting refuge (Sogard and Olla 1998). Furthermore, juvenile Sablefish avoided their lower temperature threshold (2°C) and bright light (Sogard and Olla 1998). It is plausible that within nearshore areas, vertical movement of juvenile Sablefish may be dictated by a range of environmental factors, including temperature, currents, tidal fluctuations, and light conditions. In addition, juvenile Sablefish consume both benthic and pelagic prey (Cailliet et al. 1988; Gao et al. 2004; Coutré et al. 2015), implying potential vertical movement off the bottom to forage. Juvenile Sablefish are vulnerable to predation by larger fishes, birds, and marine mammals. This vulnerability may be greatest when Sablefish are in the water column; therefore, juvenile Sablefish may make temporary vertical movements from the bottom to avoid visual predators while foraging in the water column.

Although the range of depths inhabited by Sablefish throughout their life history has been documented, very little is known about fine-scale patterns in their habitat use. Adults are demersal, inhabiting deep continental slope and outer shelf waters in the Gulf of Alaska and Bering Sea, where they are caught by commercial longlines and pot gear (Rutecki and Varosi 1997; Sigler et al. 2001). They spawn offshore near the continental shelf, and eggs have been found at depths over 200 m (Kendall and Matarese 1987). Larval and presettlement juvenile Sablefish are caught in surface trawls within shelf waters and are associated with the neuston layer (Kendall and Matarese 1987). We analyzed fine-scale vertical movement patterns of postsettlement juvenile Sablefish during their nearshore residence period using an acoustic telemetry data set collected by the National Oceanic and Atmospheric Administration (NOAA) in 2003. Specifically, we aimed to (1) quantify the depth distribution of tagged juvenile Sablefish in St. John Baptist Bay (SJBB), Southeast Alaska; and (2) describe vertical movement patterns in relation to diel and tidal cycles within SJBB. We hypothesized that juvenile Sablefish would be detected at a range of depths, reflecting their use of both benthic and pelagic prey resources in SJBB (Coutré et al. 2015). Furthermore, we hypothesized that Sablefish would be more active during crepuscular periods to exploit prey while avoiding predation and that they would display higher rates of vertical movement in the water column during flood events due to the potential influx of pelagic prey.

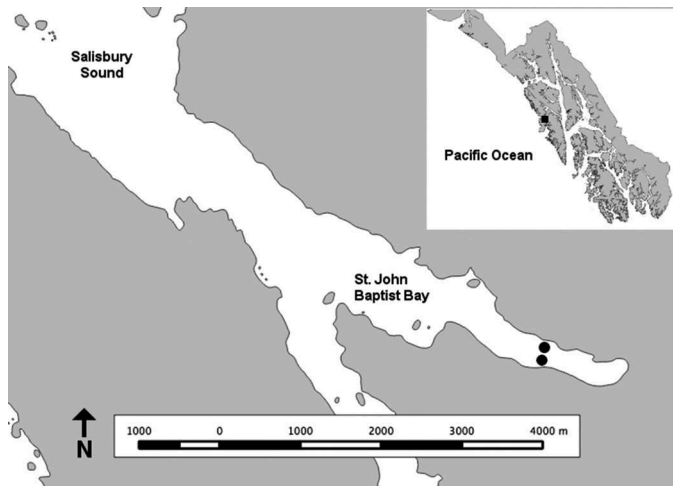


FIGURE 1. Map of study area in St. John Baptist Bay (SJBB), Baranof Island, Alaska. Gray-shaded areas represent land; black dots represent the locations of acoustic receivers at the head of SJBB. The inset map depicts the location of the study area (black square) within Southeast Alaska.

METHODS

Data collection.—St. John Baptist Bay is a small bay (~3 km long; <1 km wide) located on the northwestern side of Baranof Island, 39 km north of Sitka, Alaska ($57^{\circ}17'0''$ – $57^{\circ}17'50''$ N, $135^{\circ}33'0''$ – $135^{\circ}35'0''$ W; Figure 1). This bay was identified as a potential hot spot for postsettlement juvenile Sablefish in Southeast Alaska (Rutecki and Varosi

1997) and has been the focus of Sablefish tagging studies conducted by the NOAA Alaska Fisheries Science Center since 1985. Acoustic telemetry was used to record Sablefish movement within SJBB from October 2 to November 18, 2003 (study duration was determined by the battery life of the acoustic transmitters). Field techniques, including acoustic receiver setup, range testing, and fish tagging procedures, were described in detail by Courtney and Rutecki (2011).

Age-0 Sablefish were captured by angling, anesthetized by using tricaine methanesulfonate (MS-222), and surgically implanted with acoustic transmitters (LOTEK CTP-M11-12; length = 45 mm, diameter = 11 mm, frequency = 77 kHz, transmission rate = 5 s, typical operational life = 33 d). Tagged fish were held in flow-through seawater tanks on the research vessel for at least 24 h to recover and were released near their capture location on October 1–2, 2003 (release location: $57^{\circ}17.178$ N, $135^{\circ}33.723$ W; Courtney and Rutecki 2011). A total of 13 juvenile Sablefish (225–260 mm FL) were tagged and released within SJBB ($57^{\circ}17.178$ N, $135^{\circ}33.723$ W; Table 1). To remotely detect tagged fish, two acoustic receivers (LOTEK MAP-SDL) were moored near the head of SJBB in bottom depths of 18 and 21 m at low tide (receiver 1: $57^{\circ}17.200$ N, $135^{\circ}33.659$ W; receiver 2: $57^{\circ}17.120$ N, $135^{\circ}33.648$ W; Figure 1). For each tag detection, acoustic receivers recorded the unique tag identification number, the ambient pressure of the fish (converted to depth, m), the date, and the time to the nearest 5-s interval. Range detection tests on deployed receivers showed an average detection range of 206 m (Courtney and Rutecki 2011), and all 13 tags released were detected at least once after release. Of the 13 tagged Sablefish, 2

TABLE 1. Summary description of tagged Sablefish by acoustic tag identification number (fish ID), postsurgery release date, size (FL, mm), detection period, status, mean depth (SD in parentheses), median depth, and excursion rate in St. John Baptist Bay. Status describes initial fish activity (L = the tag signal was lost; R = the fish remained in detection range; M = suspected mortality due to the lack of tag movement). The tag release date, FL, and status information are from Courtney and Rutecki (2011). Mean depth, median depth, and excursion rate were only calculated for the six fish that remained in detection range (status = R). The excursion rate was calculated as the total number of 10-min time bins classified as containing an excursion (see Methods) divided by the number of days of detection for individual fish from October 5 to November 14, 2003.

Fish ID	Tag release date (2003)	FL (mm)	Detection period (d)	Status	Mean depth (m)	Median depth (m)	Excursion rate (number/d)
29500	Oct 1	245	1	L			
29700	Oct 2	260	41	R	23.7 (3.9)	24.7	5.4
29800	Oct 1	245	35	R	25.2 (1.9)	25.4	0.8
29900	Oct 1	240	40	R	24.5 (3.0)	25.0	2.6
30000	Oct 1	230	33	R	24.8 (5.7)	27.4	4.6
30100	Oct 1	250	38	R	23.4 (4.0)	24.7	0.8
30200	Oct 1	240	5	L			
30300	Oct 1	245	2	L			
30500	Oct 1	230	35	R	22.8 (4.6)	23.6	5.4
30600	Oct 1	225	27	M			
30700	Oct 1	240	1	L			
30800	Oct 2	245	12	L			
30900	Oct 2	250	7	M			

individuals remained within the receiver detection range but did not show any depth changes (i.e., possible mortality or tag expulsion), 5 fish either moved outside the detection range of the receivers or their tags malfunctioned shortly after release, and 6 fish remained in the area and were used for the analyses in this study (Table 1).

To determine the tidal stage for each fish detection, tidal predictions for October–November 2003 in Neva Strait, adjacent to SJBB, were acquired from the University of South Carolina Biological Sciences tide predictor (Pentcheff 2003). The reported times of nautical dawn, sunrise, sunset, and nautical dusk were obtained for October–November 2003 from U.S. Naval Observatory archives for Sitka, Alaska (U.S. Naval Observatory 2003).

Analytical methods.—The depth frequencies of tag detections were compared among individual fish and were combined to assess group-level depth distributions of Sablefish in SJBB. Analyses of tagged fish were performed for the period October 5–November 14, 2003, which excluded the initial acclimation period after release (October 1–4, 2003). Apparent depth changes of tagged fish due to tidal fluctuations were corrected by subtracting depth anomalies that were obtained from a stationary transmitter attached to the receiver buoy (Beaudreau and Essington 2011). Depth detections for every tagged fish were assigned to one of four diel periods: dawn (nautical dawn to sunrise), day (sunrise to sunset), dusk (sunset to nautical dusk), or night (nautical dusk to nautical dawn; e.g., Beaudreau and Essington 2011). Each detection was also assigned one of three tidal stages: slack (2 h surrounding the transition between high tide and low tide), ebb (time from slack associated with high tide to slack associated with low tide), or flood (time from slack associated with low tide to slack associated with high tide). High tides ranged from 2.1 to 4.0 m, and low tides ranged from –0.8 to 1.7 m.

We quantified vertical movement of individual Sablefish by analyzing the frequency of excursions to depths at least 5 m shallower than the mean depth across all detections (i.e., cutoff = 19 m). For each fish, detections were grouped into 10-min increments, and the increment was assigned a value of 1 if one or more detections within the increment were shallower than the cutoff; otherwise, the increment was assigned a value of 0 (Nichol and Somerton 2002). On rare occasions, a single excursion may have spanned the end of one time increment and the beginning of the next increment, resulting in both increments being classified as excursions for the analysis. Relationships between excursion frequency and environmental variables (diel period and tidal stage) were evaluated using generalized linear mixed-effects models (GLMMs), with fish identity as a random effect. Models were implemented using the package “lme4” (Bates et al. 2015) in R (R Core Team 2015). The probability p that an excursion occurred within a given 10-min interval was estimated across all six fish by modeling the log-odds ratio (logit-transformed probabilities) as a linear function of the predictors. To account for the observed dome-shaped temporal trend in excursion frequency over the sampling period

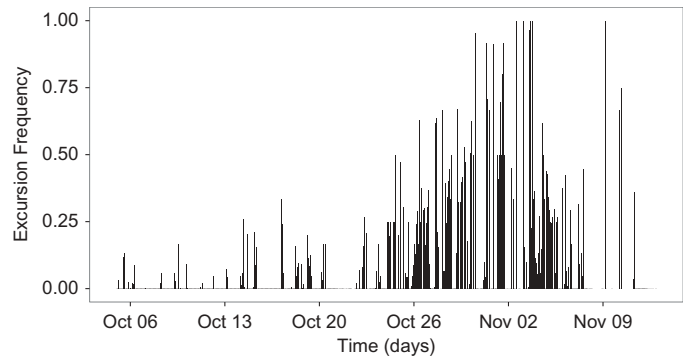


FIGURE 2. Time series of mean excursion frequency (proportion of 10-min intervals classified as 1; see Methods) across six tagged Sablefish in St. John Baptist Bay for 1-h time bins from October 5 to November 14, 2003.

(Figure 2), a Gaussian trend (quadratic trend on the logit scale) for date was included as a variable in the GLMMs. To provide insight into the individual variability in excursion frequency, generalized linear models (GLMs) were also fitted to the data for each fish separately. The full GLMM and GLM, respectively, had the forms

$$\log[p/(1-p)] = \alpha + a_i + \gamma_j + \delta_k + \beta_{jk} + \zeta_l^2 + \zeta_l$$

$$\log[p/(1-p)] = \alpha_i + \gamma_{ij} + \delta_{ik} + \beta_{ijk} + \zeta_{il}^2 + \zeta_{il} \text{ for fish } i,$$

where α is the overall mean log-odds ratio; γ_j is a fixed effect for diel period j ; δ_k is a fixed effect for tidal stage k ; β_{jk} is the interaction between period j and tidal stage k ; ζ_l^2 and ζ_l are coefficients of the Gaussian function describing the fixed effect for date l ; and a_i is a random effect for the difference in the mean log-odds ratio of fish i from the overall mean, which is assumed to be normally distributed with a mean of 0 and a variance of σ_a^2 . All parameters for the GLM include subscript i because all parameters are specific to individual fish i . Parameters were estimated by maximum likelihood; the best-fitting model(s) was determined based on Akaike’s information criterion (AIC) and was used to identify influential predictors. Candidate models included the full model, a model without a diel period \times tidal stage interaction, and models with all combinations of the fixed effects. For the GLMM, a random-effects-only model was also included in the set of candidate models. The AIC for each candidate model was subtracted from the minimum AIC (among all models) to determine the AIC difference (Δ AIC), and the best model or set of models was identified based on Δ AIC values of 2 or less (Burnham and Anderson 2002). To determine the relative importance of each predictor variable, we first calculated the Akaike weight (w_i) for each model i ; these values sum to 1 across the full set of candidate models and provide the weight of evidence that model i is the best-approximating model for the data (Burnham and Anderson 2002). Akaike parameter weights for each predictor j were then calculated as the sum of w_i across all models in the set that included variable j ;

the closer the sum of Akaike parameter weights ($w_{+}[j]$) is to 1, the more important the variable is for predicting the response across all models (Burnham and Anderson 2002).

RESULTS

For the six Sablefish that remained within range of the receivers from October 5 to November 14, 2003, the majority of detections occurred near the bottom, but the fish made periodic movements into shallower depths (Figure 3). Within the 40-d detection window, the number of days on which individual fish were detected ranged from 27 to 37 d. The bottom depths covered by the receivers ranged from 0 m (shoreline within receiver range) up to 27–32 m, with the majority of the area covered being 20–25 m in depth (the latter two ranges are from low to high tide). Across fish, the mean (\pm SD) depth was 24.1 ± 4.2 m, and the median depth was 25.0 m. The mean depth for individuals ranged from 22.8 ± 4.6 to 25.2 ± 1.9 m, and the median depth for individuals ranged from 23.6 to 27.4 m (Table 1). The depth of tagged fish was plotted through time to visualize vertical movement patterns, revealing the occurrence of excursions into shallower depths (e.g., movements by fish 29700 and 30000 over a 2-d period are shown in Figure 4). The mean (\pm SD) duration of excursions to depths less than 19 m (excluding >5-min gaps in detection) was 1.3 ± 4.1 min. Excursions occurred in 6.6% of the 10-min intervals for all fish combined across the time series. The proportion of detections that were classified as excursions for individual fish ranged from 1% (fish 29800) to 9% (fish 30500; Figure 5). Within the 6-week detection period, the highest frequency of excursions across fish (weighted by total detections per individual) occurred from October 30 to November 9 (Figure 2). There were no 10-min time intervals in which more than four fish underwent an excursion simultaneously.

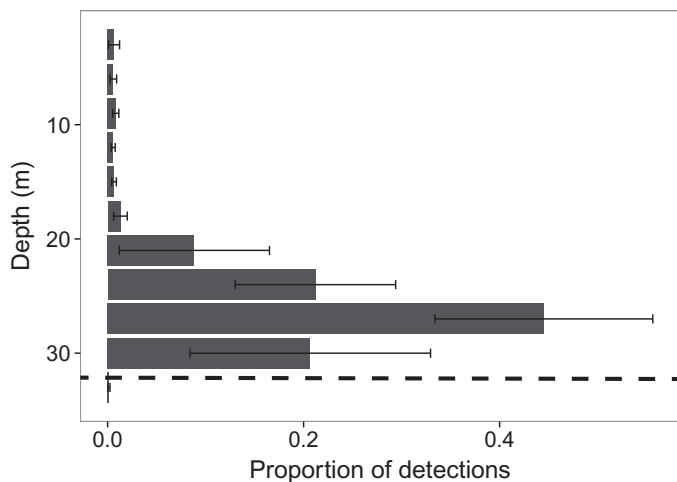


FIGURE 3. Mean (\pm 2 SEs) proportion of detections across tagged Sablefish ($n = 6$) at 3-m depth increments in St. John Baptist Bay. Dashed line represents the greatest bottom depth within receiver range (32 m).

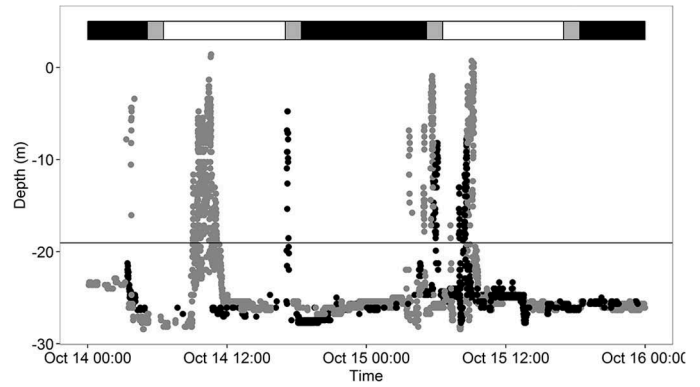


FIGURE 4. Depth distribution over a selected 48-h period for tagged Sablefish (gray dots = fish 29700; black dots = fish 30000) in St. John Baptist Bay. Horizontal bar above the plotted time series represents diel period (black = night; gray = dawn or dusk; white = day). Excursions were defined as movements to depths shallower than the cutoff depth (19 m; depicted by the black horizontal line).

The mean frequency of excursions (proportion of 10-min intervals classified as 1) was evaluated for each tidal stage (slack, ebb, and flood) and diel period (dawn, day, dusk, and night) across all six fish combined (Table 2). We used GLMMs to quantify differences in excursion frequency among tidal stages, among diel periods, and through time (Table 3). The model that provided the best fit to the data based on AIC included diel period and date (Table 3), and Akaike parameter weights equal to 1 suggested that these variables were important predictors of variation in excursion frequency, while tidal stage ($w_{+}[j] = 0.31$) was relatively

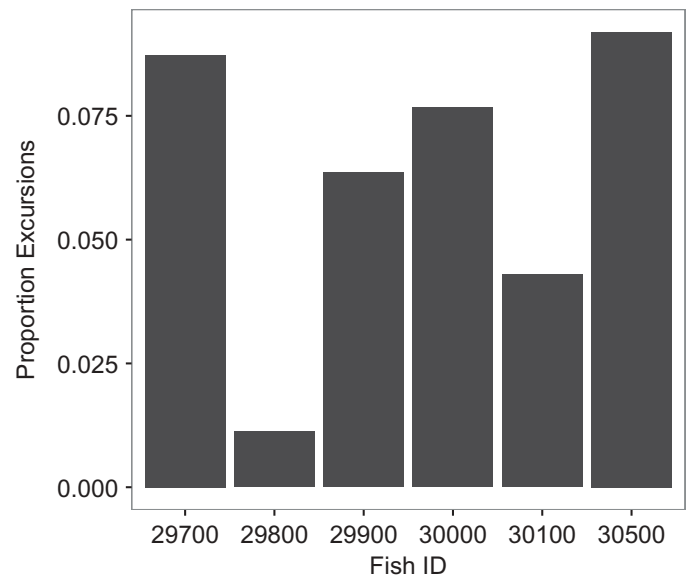


FIGURE 5. Proportion of excursions into shallower water by six Sablefish (fish ID = unique acoustic tag number for each individual) in St. John Baptist Bay from October 5 to November 14, 2003.

TABLE 2. Mean (\pm SEs) excursion frequency by six tagged Sablefish in St. John Baptist Bay at each tidal stage and diel period. Excursion frequency for each fish was calculated as the proportion of 10-min intervals in which at least one detection was classified as an excursion (see Methods).

Environmental condition	Excursion frequency
Diel period	
Dawn	0.09 \pm 0.05
Day	0.07 \pm 0.03
Dusk	0.05 \pm 0.05
Night	0.05 \pm 0.02
Tidal stage	
Ebb	0.06 \pm 0.03
Flood	0.06 \pm 0.03
Slack	0.07 \pm 0.03

unimportant (Table 4). The best-fit model was used to calculate the probability of an excursion for each diel period by date, revealing a peak in predicted excursion probability on day 33 (November 7) during the dawn period (Figure 6). Across diel periods, the highest mean excursion frequency was observed at dawn (Table 2). This pattern was supported by the model results, as the predicted probability of an excursion was highest during dawn and day periods and lowest at night (Figure 6).

Individual GLMs also supported the finding that the excursion behavior was primarily related to date and diel period based on the inclusion of those predictors in the set of best models for all individuals and the high parameter weights ($w_{+[j]} = 0.7-1.0$; Table 4). The model that included diel period and date was identified as the best model ($\Delta AIC = 0$) for three of the six fish (fish 29700, 29800, and 30000; Table 5). In addition to diel period and date, the tidal stage and/or the diel

TABLE 4. Akaike parameter weights ($w_{+[j]}$) calculated from all candidate models describing relationships between Sablefish excursion frequency and the following predictors: diel period (Diel), tidal stage (Tide), the Diel \times Tide interaction, and date as a polynomial. Separate generalized linear models were run for the six tagged individuals (Fish ID = acoustic tag identification number), and a generalized linear mixed-effects model was run for all fish combined (All fish).

Fish ID	Diel	Date	Tide	Diel \times Tide
29700	1.000	1.000	0.537	0.139
29800	0.695	1.000	0.189	0.008
29900	1.000	1.000	0.997	0.965
30000	0.998	1.000	0.424	0.182
30100	0.944	0.953	0.948	0.937
30500	1.000	1.000	0.822	0.027
All fish	1.000	1.000	0.313	0.084

period \times tidal stage interaction were included in the best model and had relatively high parameter weights for three individuals (fish 29900, 30100, and 30500; Tables 4, 5).

DISCUSSION

This study fills the gap in knowledge of Sablefish early life history by providing insight into movements and depth distributions of juveniles in the wild. Of the 13 tagged Sablefish, 5 individuals were detected for only a brief period. The tags on those fish may have malfunctioned or the fish may have left the detection range of the receivers (~ 0.27 km²) either by their own volition or due to predation. Six fish remained in receiver range throughout the sampling period, showing site fidelity to the head of SJBB during the study period. Annual hook-and-line sampling by NOAA in SJBB since 1985 has yielded the highest juvenile Sablefish catch rates in the head of the bay in the vicinity of the two receivers (Rutecki and Varosi 1997). Juvenile Sablefish may

TABLE 3. Parameter estimates from fitted generalized linear mixed-effects models predicting the probability of an excursion by tagged juvenile Sablefish in St. John Baptist Bay, with the following predictors: diel period (Diel), tidal stage (Tide), the Diel \times Tide interaction, and date. Parameter symbols are defined in Methods. All possible combinations of fixed effects were considered, along with a random effect for the difference in the mean log-odds ratio of individual fish from the overall mean. The difference in Akaike's information criterion (DAIC) between the given model and the model with the lowest AIC value is presented. Dashes indicate values that were not applicable due to the interaction term.

Model	ΔAIC	α	γ_{day}	γ_{dusk}	γ_{night}	δ_{flood}	δ_{slack}	ζ_l	ζ_l^2
Date + Diel	0.0	-3.041	-0.049	-0.359	-0.708			113.602	-35.623
Date + Diel + Tide	2.2	-3.041	-0.038	-0.366	-0.705	-0.081	0.057	113.677	-35.829
Date + Diel + Tide + (Diel \times Tide)	4.2	-3.427	-	-	-	-	-	113.102	-36.048
Date	53.1	-3.361						110.392	-34.490
Date + Tide	55.5	-3.408				0.021	0.120	110.239	-34.457
Diel + Tide + (Diel \times Tide)	594.4	-3.057	-	-	-	-	-		
Diel	605.6	-2.437	-0.281	-0.539	-0.703				
Diel + Tide	606.3	-2.499	-0.289	-0.521	-0.707	0.028	0.166		
Intercept	634.4	-2.886							
Tide	634.7	-2.962				0.043	0.181		

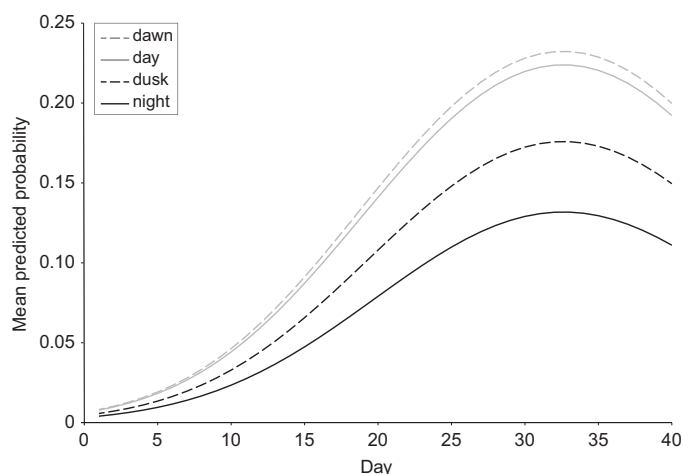


FIGURE 6. Mean predicted probability of an excursion across six tagged Sablefish in St. John Baptist Bay for each diel period through time (day 1 = October 5, 2003; day 40 = November 14, 2003) based on the best-fit binomial generalized linear mixed model.

exhibit site fidelity to a small area of the bay; however, the area covered by the two receivers was insufficient to resolve the horizontal movements of Sablefish or their residence time within core use areas. These fish maintained an affinity for demersal habitat, with average detection depths at or near the deepest depths within the detection range during the majority of the study period; however, all six fish undertook excursions to shallower depths (mean excursions per day ranged from 0.8 to 5.4). The estimated mean probability of excursions in a given 10-min interval ranged from 3% to 15%.

It is unclear whether apparent changes in vertical distribution were changes in depth associated with horizontal movements along the bottom into shallower water or vertical

movements into the water column. However, we hypothesize that most excursions reflect movement into the water column due to the rapid rates of ascent and descent (mean excursion duration was 1.3 min from depths below 19 m to near-surface waters). Based on our knowledge of the bathymetry in SJBB and coarse-scale NOAA charts, bottom depths of 19 m or greater occur in the immediate vicinity of the receiver sites, and the slope increases monotonically to shore; therefore, we calculated the shortest horizontal distance from shore for each receiver and used the Pythagorean theorem to estimate the distance a tagged Sablefish would have to travel along the slope to move from a depth of approximately 19 m to the surface (114.1 m for receiver 1; 76.5 m for receiver 2). Assuming an excursion distance of 19 m and a duration of 1.3 min, a tagged Sablefish would have to swim a minimum of 98.1–146.3 cm/s depending on the receiver to which it was in closest proximity. An experimental study of age-1 and older Sablefish (183–266 mm TL) that were similar in size to those in our study showed unimpaired swimming speeds of 25–30 cm/s (Ryer et al. 2004). Given the much faster swimming speed needed to undergo a depth change of 19 m by moving along the bottom, combined with our field observations of Sablefish moving vertically in the water column (i.e., from depth sounder readings and hook-and-line sampling), we suggest that vertical movement is the most parsimonious explanation for Sablefish excursions into shallow depths. Our ability to differentiate vertical and horizontal movements was limited by the use of just two receivers. Better resolution of the directionality of movements would be possible with a larger receiver array, potentially in combination with mobile tracking of fish tagged with pressure-sensing transmitters.

There are many environmental and ecological factors that could play a role in the vertical movements of juvenile Sablefish, including temperature, salinity, current speed,

TABLE 5. Values of the difference in Akaike's information criterion (DAIC) for generalized linear models (GLMs) predicting the probability of an excursion by Sablefish, with the following predictors: diel period (Diel), tidal stage (Tide), the Diel \times Tide interaction, and date as a polynomial. A separate GLM was run for each tagged individual (Fish ID = acoustic tag identification number), and all possible combinations of fixed effects were considered. The Δ AIC was calculated as the difference in AIC between the given model and the model with the lowest AIC value.

Model	Fish ID					
	29700	29800	29900	30000	30100	30500
Diel + Date	0.0	0.0	11.48	0.0	10.2	3.0
Diel + Tide + Date	0.3	2.803	6.82	1.73	13.31	0.0
Date	29.2	1.503	24.36	12.34	5.91	31.2
Diel + Tide + Date + (Diel \times Tide)	2.4	8.543	0.0	2.3	0.0	6.8
Diel + Tide + (Diel \times Tide)	102.1	93.103	40.82	358.24	5.92	185.7
Diel + Tide	105.9	96.563	50.08	353.04	20.51	179.2
Diel	107.1	106.163	54.35	354.34	17.72	183.6
Tide	136.1	118.233	59.34	356.54	17.1	192.5
Tide + Date	28.1	5.003	22.46	14.04	9.1	26.4

spatial and temporal availability of prey resources, and predator distribution and density. Movements may also vary across the ontogeny of juvenile Sablefish; however, the size range of fish tagged in this study was not sufficient to permit evaluation of size-based shifts in movement patterns. Vertical excursion frequency varied in relation to date and diel period, with a higher excursion frequency during dawn and day periods and an overall peak from October 30 to November 9. Diel period and date were the most influential variables in predicting excursion frequency overall and for individual fish, suggesting that the changes over time in excursion frequency and the diel pattern are group-level characteristics that apply to all individuals (Tables 4, 5). Some individuals also exhibited variation in excursion frequency by tidal stage along with date and diel period. Tidal stage and the diel period \times tidal stage interaction were not important across individuals (GLMM), but tidal stage was quite important for some individuals, perhaps suggesting different feeding strategies, with some individuals taking advantage of feeding opportunities during flood or slack tides and others remaining near the bottom. Vertical movements in relation to diel and tidal conditions have been documented for other North Pacific demersal fishes, including the Blue Rockfish *Sebastes mystinus* (Green et al. 2014), Lingcod *Ophiodon elongatus* (Beaudreau and Essington 2011), and Atka Mackerel (Nichol and Somerton 2002). Flood and subsequent slack stages may create an influx of pelagic resources (Aubry and Acri 2004), potentially explaining the more frequent vertical movements of some juvenile Sablefish during those tidal conditions. Juvenile sablefish in SJBB are known to consume forage fish species (Coutré et al. 2015), and predation on forage fish during flood tide has been favored by other predators, such as harbor seals *Phoca vitulina* (Zamon 2001). It is not known why the frequency of excursions by juvenile Sablefish increased in late October 2003 and peaked in early November (Figure 2), but this period coincided with spring tides (the greatest tidal exchange was on October 27) that may have transported allochthonous resources into the bay. The influence of date on excursion probability may be revealing a larger tidal effect that was not captured by assigning a coarse tidal stage category.

Among the six fish that stayed within range of the receivers near the head of the bay, there was individual variation in excursion frequency and the environmental variables explaining this variation. Individual variation in movement has been found in other fishes, including Largemouth Bass *Micropterus salmoides*, Yellow Perch *Perca flavescens*, Pumpkinseeds *Lepomis gibbosus*, and Bluegills *Lepomis macrochirus* (Fish and Savitz 1983); Lingcod (Beaudreau and Essington 2011); and Pacific Halibut *Hippoglossus stenolepis* (Nielsen et al. 2014). Variation among individuals may be related to foraging specialization and social structure (Fish and Savitz 1983; Beaudreau and Essington 2011); however, resolving the extent to which variation in the frequency and timing of excursions

by tagged juvenile Sablefish is related to individual variation in foraging strategies will require movement data coupled with diet sampling, which was not conducted in this study. In addition, our sample size was small, so inferences about the extent of individual variation in juvenile Sablefish movement patterns are limited. A larger sample size, longer study duration, and more extensive receiver array would help to discern the extent of individual variation in movement and space use.

We found a decreased probability of excursions by tagged Sablefish at night, which may correspond to reduced foraging activity during periods of low light availability, as was observed for Sablefish in the laboratory (Ryer and Olla 1999) and for other visual predators (Eggers 1978; Beaudreau and Essington 2011). Although it is difficult to resolve the mechanisms underlying fish movement patterns, it is plausible that Sablefish may make forays off the bottom to actively forage for pelagic species. Periodic vertical excursions may reflect opportunistic foraging on locally available pelagic prey by juvenile Sablefish to meet their energetic needs. In a diet study along the coast of California and Oregon, approximately 65–90% of sampled juvenile Sablefish (300–500 mm FL) consumed midwater species (Laidig et al. 1997). Similarly, juvenile Sablefish in SJBB have been documented to prey heavily on pelagic schooling fishes, (e.g., Pacific Herring *Clupea pallasii* and smelts [Osmeridae]) and pelagic invertebrates (e.g., euphausiids; Coutré et al. 2015). However, postsettlement juveniles also forage near the seafloor, as up to 64% of their diet within SJBB includes benthic invertebrates, such as worms, clams, and amphipods; demersal fishes; and scavenged salmon offal (Coutré et al. 2015). Coutré et al. (2015) discovered a high occurrence of adult salmon *Oncorhynchus* spp. carcasses in the stomachs of juvenile Sablefish collected from SJBB during the fall; those carcasses were likely scavenged off the bottom.

At smaller body sizes, fish are more vulnerable to predation, and many juvenile fish take refuge in benthic habitats to reduce their exposure to predators (Werner et al. 1983; Valdimarsson et al. 2000). Juvenile Sablefish are potentially vulnerable to a wide range of predators, including seabirds (Thayer et al. 2008), adult salmon (Wing 1985), and other piscivorous fishes. In 2015, NOAA researchers observed juvenile Sablefish in the stomachs of Pacific Cod *Gadus macrocephalus* caught in SJBB (D. Hanselman, NOAA, personal communication). We found no clear pattern of DVM to suggest that juvenile Sablefish use low-light conditions to reduce predation risk while foraging; however, they may avoid predators by seeking refuge in benthic habitats. Better characterization of predator and prey abundance and distribution within SJBB and the use of refuge habitats by juvenile Sablefish would provide further insight into the relative importance of predation risk and prey availability in explaining Sablefish vertical movement patterns.

ACKNOWLEDGMENTS

K.M.C. and A.H.B. were supported with NOAA funds administered by the Cooperative Institute for Alaska

Research under Cooperative Agreement NA08OAR4320751 with the University of Alaska. Additional support was provided to K.M.C. by the University of Alaska Fairbanks. The captain and crew of the NOAA vessel *John N. Cobb* assisted with data collection, and Dave Csepp aided in fish surgery technique. We thank two anonymous reviewers for providing comments that improved the manuscript. Lastly, we are grateful to Bryce Mecum for invaluable help with programming.

REFERENCES

- Aubry, F. B., and F. Aciri. 2004. Phytoplankton seasonality and exchange at the inlets of the Lagoon of Venice (July 2001–June 2002). *Journal of Marine Systems* 51:65–76.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beamish, F. W. H. 1966. Vertical migration by demersal fish in the Northwest Atlantic. *Journal of the Fisheries Research Board of Canada* 23:109–139.
- Beaudreau, A. H., and T. E. Essington. 2011. Use of pelagic prey subsidies by demersal predators in rocky reefs: insight from movement patterns of Lingcod. *Marine Biology* 158:471–483.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer, New York.
- Cailliet, G. M., E. K. Osada, and M. Moser. 1988. Ecological studies of Sablefish in Monterey Bay. *California Fish and Game* 74:132–153.
- Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile Sockeye Salmon and the antipredation window. *American Naturalist* 131:271–290.
- Courtney, D., and T. Rutecki. 2011. Inshore movement and habitat use by juvenile Sablefish, *Anoplopoma fimbria*, implanted with acoustic tags in Southeast Alaska. National Marine Fisheries Service, Alaska Fisheries Science Center, Processed Report 2011-01, Juneau.
- Coutré, K. M., A. H. Beaudreau, and P. W. Malecha. 2015. Temporal variation in diet composition and use of pulsed resource subsidies by juvenile Sablefish. *Transactions of the American Fisheries Society* 144:807–819.
- Eggers, D. M. 1978. Limnetic feeding behavior of juvenile Sockeye Salmon in Lake Washington and predator avoidance. *Limnological Oceanography* 23:1114–1125.
- Fish, P. A., and J. Savitz. 1983. Variations in home ranges of Largemouth Bass, Yellow Perch, Bluegills, and Pumpkinseeds in an Illinois lake. *Transactions of the American Fisheries Society* 112:147–153.
- Frost, B. W., and S. M. Bollens. 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1137–1141.
- Gao, Y., S. H. Joner, R. A. Svec, and K. L. Weinberg. 2004. Stable isotopic comparison in otoliths of juvenile Sablefish (*Anoplopoma fimbria*) from waters off the Washington and Oregon coast. *Fisheries Research* 68:351–360.
- Green, K. M., A. P. Greenley, and R. M. Starr. 2014. Movements of Blue Rockfish (*Sebastes mystinus*) off central California with comparisons to similar species. *PLOS (Public Library of Science) ONE [online serial]* 9:e98976.
- Kendall, A. W. Jr., and A. C. Matarese. 1987. Biology of eggs, larvae, and epipelagic juveniles of Sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. *Marine Fisheries Review* 49:1–13.
- Laidig, T. E., P. B. Adams, and W. M. Samiere. 1997. Feeding habits of Sablefish, *Anoplopoma fimbria*, off the coast of Oregon and California. NOAA Technical Report NMFS 130.
- Laprise, R., and J. J. Dodson. 1989. Ontogeny and importance of tidal vertical migrations in the retention of larval Smelt *Osmerus mordax* in a well-mixed estuary. *Marine Ecology Progress Series* 55:101–111.
- Loose, C. J., and P. Dawidowicz. 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology* 75:2255–2263.
- Love, M., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the Northeast Pacific. University of California Press, Berkeley.
- Mehner, T., S. Busch, I. P. Helland, M. Emmrich, and J. Freyhof. 2010. Temperature-related nocturnal vertical segregation of coexisting coregonids. *Ecology of Freshwater Fish* 19:408–419.
- Nichol, D. G., and D. A. Somerton. 2002. Diurnal vertical migration of the Atka Mackerel *Pleurogrammus monopterygius* as shown by archival tags. *Marine Ecology Progress Series* 239:193–207.
- Nielsen, J. K., P. N. Hooge, S. J. Taggart, and A. C. Seitz. 2014. Characterizing Pacific Halibut movement and habitat in a marine protected area using net squared displacement analysis methods. *Marine Ecology Progress Series* 517:229–250.
- Ohman, M. C., P. L. Munday, G. P. Jones, and M. J. Caley. 1998. Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology* 225:219–238.
- Pentcheff, D. 2003. WWW tide and current predictor for Whitestone Narrows, Neva Strait, Alaska. University of South Carolina, Columbia. Available: <http://tbone.biol.sc.edu/tide/>. (March 2017).
- Quinn, T. P., C. J. Sergeant, A. H. Beaudreau, and D. A. Beauchamp. 2012. Spatial and temporal patterns of vertical distribution for three planktivorous fishes in Lake Washington. *Ecology of Freshwater Fish* 21:337–348.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.R-project.org. (March 2017).
- Rutecki, T. L., and E. R. Varosi. 1997. Distribution, age, and growth of juvenile Sablefish, *Anoplopoma fimbria*, in Southeast Alaska. NOAA Technical Report NMFS 130.
- Ryer, C. H., and B. L. Olla. 1999. Light-induced changes in the prey consumption and behavior of two juvenile planktivorous fish. *Marine Ecology Progress Series* 181:41–51.
- Ryer, C. H., M. L. Ottmar, and E. A. Sturm. 2004. Behavioral impairment after escape from trawl codends may not be limited to fragile fish species. *Fisheries Research* 66:261–269.
- Sigler, M. F., T. L. Rutecki, D. L. Courtney, J. F. Karinen, and M. Yang. 2001. Young of the year Sablefish abundance, growth, and diet in the Gulf of Alaska. *Alaska Fisheries Research Bulletin* 8:57–70.
- Sogard, S. M., and B. L. Olla. 1998. Behavior of juvenile Sablefish, *Anoplopoma fimbria* (Pallas), in a thermal gradient: balancing food and temperature requirements. *Journal of Experimental Marine Biology and Ecology* 222:43–58.
- Thayer, J. A., D. F. Bertram, S. A. Hatch, M. J. Hipfner, L. Slater, W. J. Sydeman, and Y. Watanuki. 2008. Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Canadian Journal of Fisheries and Aquatic Sciences* 65:1610–1622.
- U.S. Naval Observatory. 2003. Sunrise, sunset, and nautical twilight tables for Sitka, Alaska. Available: <http://aa.usno.navy.mil/data/>. (March 2017).
- Valdimarsson, S. K., N. B. Metcalfe, and S. Skúlason. 2000. Experimental demonstration of differences in sheltering behaviour between Icelandic populations of Atlantic Salmon (*Salmo salar*) and Arctic Char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:719–724.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Wing, B. L. 1985. Salmon stomach contents from the Alaska troll log-book program, 1977–1984. NOAA Technical Memorandum NMFS F/NWC-91.
- Zamon, J. E. 2001. Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. *Fisheries Oceanography* 10:353–366.