Characterizing Pacific halibut movement and habitat in a Marine Protected Area using net squared displacement analysis methods

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ABSTRACT: We characterized small-scale movement patterns and habitat of acoustic-tagged adult (68 to 220 cm total length) female Pacific halibut during summer and fall in Glacier Bay National Park, Alaska, a marine protected area (MPA). We used net squared displacement analysis methods to identify 2 movement states, characterize individual dispersal patterns, and relate habitat variables to movement scales. Movement states identified for 32 of 43 halibut consisted of (1) a non-dispersive 'residential' movement state (n = 27 fish), where movement was restricted to an average movement radius of 401.3 m (95% CI 312.2–515.9 m) over a median observation period of 58 d, and (2) a 'dispersive' movement state (n = 15 fish), where movements of up to 18 km occurred over a median observation period of 27 d. Some fish (n = 10) exhibited both movement states. Individual fish demonstrated primarily non-random dispersal patterns including home range (n = 17), site fidelity (return to previously occupied locations following forays, n = 6), and shifted home ranges (n = 5). However, we also observed a random dispersal pattern (n = 4) with an estimated mean ± SE diffusion rate of 0.9 ± 0.05 km^2 d^{-1}. Home range size increased with depth but not fish size. Home range locations were associated with heterogeneous habitat, intermediate tidal velocities, and depths <100 m. Observations of non-dispersive movement patterns, relatively small home ranges, and site fidelity for adult females suggest that MPAs such as Glacier Bay may have utility for conservation of Pacific halibut broodstock.

KEY WORDS: Movement ecology · Home range · Site fidelity · Net Squared Displacement · Dispersal · Marine Protected Area · Flatfish · Pacific halibut

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INTRODUCTION

Knowledge of fish movement patterns at multiple spatial and temporal scales can benefit the management of mobile fish species. For example, even highly migratory species that move thousands of kilometers are capable of philopatry at very small spatial scales (Jorgensen et al. 2010). Thus, understanding small scale movement patterns and habitat associations can be an important part of achieving a holistic understanding of stock dynamics and assessing the potential effectiveness of spatial management techniques such as marine protected areas (MPAs) for migratory fish species.

The Pacific halibut *Hippoglossus stenolepis* (hereafter referred to as 'halibut') is an economically, ecologically, and culturally important flatfish species in the North Pacific Ocean. Based on observations of

large-scale seasonal and ontogenetic movements during larval, juvenile, and adult life history stages (Valero & Webster 2012), halibut in North America are managed on a large scale (Clark & Hare 2006) where a single stock assessment is conducted for a region that ranges from California to the Bering Sea before the allowable harvest is apportioned into smaller management units (Webster & Stewart 2014). Some proportion of adult halibut conduct seasonal spawning migrations from summer foraging locations in near-shore areas to winter off-shore spawning areas in deeper waters on the continental slope of the Pacific Ocean (Loher & Seitz 2006, Loher 2011, Seitz et al. 2011). Recent pop-up satellite archival tagging and conventional tagging research has demonstrated that a large proportion of adult halibut exhibit inter-annual site fidelity and homing to summer foraging locations (Loher 2008). These observations suggest that knowledge of movement patterns at smaller scales will be important for understanding the spatial sub-structure of the halibut stock, potential local effects of intense fishing, and the utility or effectiveness of MPAs as a management tool for halibut.

In addition to coast-wide, large-scale management through area-specific harvest rates, halibut are also regulated at smaller spatial scales through catch sharing plans as well as the existence of MPAs. For example, halibut harvest is restricted in the interior waters of Glacier Bay National Park in southeastern Alaska, where commercial fishing for halibut is being phased out (36 CFR 13.1130-1146) over several decades and sport fishing is limited by daily vessel quotas (36 CFR 13.1150-1160) during the summer months. Glacier Bay National Park was added to the National System of Marine Protected Areas in 2009. As a large, high-latitude MPA, Glacier Bay may eventually protect halibut that reside within its boundaries from commercial harvest. However, obtaining information on the scale and patterns of halibut movement and habitat associations is critical for understanding Glacier Bay's potential effectiveness at retention of adults (Kramer & Chapman 1999) and specific benefits that may result from protection.

Here, we present information on the spatial and temporal scales of movement by adult halibut in Glacier Bay National Park during summer and fall that may be valuable for assessing the potential effectiveness of Glacier Bay National Park as an MPA. We use net squared displacement (NSD) analysis techniques to (1) identify and characterize 2 distinct movement states, 'residential' and 'dispersive', (2) classify and quantitatively describe dispersal patterns for individual tagged halibut, and (3) describe habitat associa-

tions and relationships between habitat variables (depth, average tidal speed, habitat complexity, and substrate type) and scale of movement for the residential movement state. We interpret these results in terms of spatially explicit fisheries management applications such as MPA design and effectiveness. We conclude by addressing the potential contribution of NSD analysis methods for characterizing the movement patterns and dispersal scales of fishes and facilitating MPA design.

MATERIALS AND METHODS

Study area

The study was conducted in the northern portion of southeastern Alaska within the inside waters of Glacier Bay National Park (Fig. 1). The technical boundary for the Glacier Bay National Park Marine Protected Area extends to the outside waters, but in this document we refer to the functional MPA of the interior waters, known as 'Glacier Bay Proper', within which commercial fishing and vessel traffic are regulated by the National Park Service. Glacier Bay is a glacial fjord that is influenced by both current and historical glacial activity. Glaciers have receded more than 100 km in the last 300 yr in Glacier Bay,
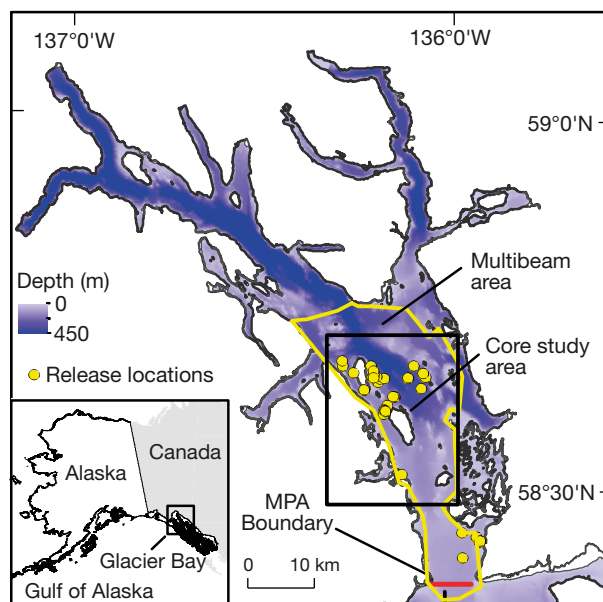

Fig. 1. Study area within the inside waters of Glacier Bay National Park. Map depicts the MPA boundary (red line), multibeam survey area for habitat analyses (yellow line), tagged fish release locations (yellow circles), and core study area (black square) where most tagged halibut were released and tracked

leaving behind a Y-shaped body of water with deep (200 to 450 m) marine basins interspersed with shallow moraines and tidewater glaciers at the heads of the fjords. Substantial glacial freshwater runoff influences the oceanography with high sedimentation and areas of cold water upwelling. Strong tidal currents mix the water column completely in the shallow lower portion of the bay, but deeper upper reaches are largely stratified. Primary productivity levels are highest in a transition zone in the central portion of the bay that is characterized by intermediate stratification. Salinity, temperature, and light penetration decrease towards the heads of the fjords (Etherington et al. 2007b).

Fish tagging and tracking

A total of 43 halibut were captured on longlines, tagged and released in Glacier Bay during the summers of 1991 to 1993 (Table 1, Fig. 1). Longlines were set at 4 general release locations within the study area using snap-on gangions designed for the commercial halibut fishery and were 'soaked' for 6 h. Capture locations were determined when each fish was brought on board the capture vessel using a PLGR GPS that removed selective availability errors. We generally selected larger fish (>100 cm total length, TL) for tagging because we were primarily interested in fish that were vulnerable to the commercial fishery (≥82 cm) and we wanted to minimize possible effects of large, long-life acoustic tags on behavior.

Acoustic transmitters (Sonotronics) that transmitted a unique identifying sonic pulse were attached to halibut externally during 1991 and 1992 (n = 26) and internally during 1992 and 1993 (n = 17). Externally attached acoustic tags were secured to fish by inserting 2 Teflon-coated stainless steel wires through the dorsal musculature immediately ventral to the dorsal fin, with a backing plate of neoprene rubber and fiberglass. A sterilized needle was used to thread the wire. For the internal attachment, tags were surgically implanted in the coelomic cavity using sterile methods. Tags were inserted into the coelomic cavity through a 5 cm incision on the eyed-side, parallel and 2 to 3 cm dorsal to the long axis of the fish. The incision was closed with 7 to 8 external sutures (2-0 Braunamid non-absorbable). During the 5 to 15 minute surgery, the gills of the fish were irrigated with ambient seawater which was well-mixed and high-saline in the study area. When possible, information on the sex of the tagged fish was obtained through cannulation or observation during surgical implantation. Tagged

fish were released within 500 m of the location where they were brought on board.

Acoustic tag transmission frequency and size varied during the study. Acoustic tags attached during the first year (n = 9) transmitted at a frequency of 80 kHz, whereas 35 kHz acoustic tags (n = 34) were used in the 2 subsequent years due to their increased detectability in Glacier Bay's waters. We used 2 sizes of acoustic tags in the study. The smaller tags (n = 17) were 95 mm long × 18 mm diameter, weighed 16 g in water, and had an observed lifetime of 1.3 to 2 yr. The larger tags (n = 26) were 95 mm long × 34 mm diameter, weighed 34 g in water, and had an observed lifetime of 2.5 to 3.4 yr. Details of tag attributes for individual tagged fish are provided in Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m517p229_supp.pdf.

Tagged halibut were tracked from a vessel using a bow-mounted dual hydrophone assembly lowered 2 m beneath the surface of the water and capable of rotating 360°. One hydrophone faced forward and −10° from horizontal and the other hydrophone pointed downward. These directional hydrophones (Sonotronics DH-2) had a beam width of ±6° and a sensitivity of 84 dBV and were connected to manual receivers (Sonotronics USR-4D). With this configuration, *in situ* range tests indicated that tags could be detected at distances of up to 2 km. When a tag was detected, the vessel operator maneuvered the vessel in a circular pattern in the vicinity of the tag until signal strength was uniform at all points on the circle and the signal received on the downward-facing hydrophone in the middle of the circle was highly amplified. A GPS was used to obtain the location of the vessel at this position, which served as the estimated position of the tagged fish. Positions of tagged fish were obtained daily to weekly during tracking periods that lasted 3 to 6 mo, mostly in the summer and fall, of each year. Searches for tagged fish were conducted in an outward spiral starting from each individual's last known position. Consequently, if a tagged halibut moved more than a few kilometers away, it was not necessarily found during the subsequent search. An example of the spatial distribution of tracking effort (number of days tracked per season) in the study area during 1991 is shown in Fig. S2 in Supplement 1.

The precision of position estimates for tagged fish was likely to decrease with increasing water depth. We estimated the precision of each observation based on a linear regression of error radii vs. depth for (1) known positions of tags recovered by SCUBA divers (n = 3) and (2) root mean squared distances

Table 1. ID number of tagged halibut *Hippoglossus stenolepis*, release date (dd/mm/yy), total length, maximum horizontal displacement observed ('max disp.'), net horizontal displacement at last observation ('net disp.'), dispersal pattern model code (see Table 2), tracking year, date of each observation, and movement state code (see key in table). (–) No data

Fish ID	Release Date	Length (cm)	Max disp. (m)	Net disp. (m)	Model code
1	7/24/91	136	13334	6369	FSHR
2	7/30/91	91	2172	1475	HR
3	8/20/91	136	1492	150	HR
4	8/20/91	115	–	–	N
5	8/20/91	140	9796	9614	SHR
6	8/20/91	78	1778	984	HR
7	8/20/91	90	2031	319	HR
8	9/9/91	96	14177	14177	R
9	9/9/91	117	9619	8023	SHR
10	6/3/92	157	3691	2027	FSHR
11	6/17/92	128	16658	11472	U
12	6/19/92	94	–	–	N
13	6/19/92	68	4558	4558	U
14	6/19/92	76.5	762	762	U
15	6/23/92	153	874	378	HR
16	7/1/92	129	9291	418	SF
17	7/1/92	104	2390	2390	R
18	7/8/92	146	2269	1497	HR
19	7/8/92	127	2163	2163	U
20	7/8/92	132.5	13393	13393	SHR
21	7/8/92	121	1848	213	HR
22	7/8/92	124	8184	1909	SF
23	7/8/92	142.5	237	237	U
24	7/8/92	134	16478	16478	R
25	7/8/92	125	12616	3993	SF
26	7/8/92	129	12494	3839	SF
27	7/31/92	201.3	2014	1296	HR
28	11/17/92	130.6	9188	207	SF
29	11/17/92	149	10872	496	SF
30	11/17/92	132.5	1652	497	U
31	11/17/92	168	614	73	HR
32	6/2/93	220	3190	1949	HR
33	6/18/93	154	17954	15963	R
34	6/18/93	162	–	–	N
35	6/18/93	151.2	–	–	N
36	6/19/93	140	1170	567	HR
37	6/19/93	182.8	3526	2614	HR
38	6/19/93	155	859	843	HR
39	6/19/93	151.6	–	–	N
40	6/20/93	152.8	2269	507	HR
41	6/20/93	149.8	1109	726	HR
42	6/20/93	164.4	1296	359	HR
43	8/11/93	77.6	807	619	HR

Legend: # Release / Unknown — Residential — Dispersive

Tracking year: 1991, 1992, 1993

Day of the year

between repeated observations of motionless tags (n = 6). The depth of each observation was multiplied by the resulting slope coefficient, 0.65 (r^2 = 0.83, p = 0.0005), to obtain error buffers for each observation that ranged from approx. ±10 m at depths of 10 m to approx. ±100 m at depths of 150 m.

Data analysis

Due to the large study area and the opportunistic nature of the fish resightings, the dataset was characterized by irregular sampling intervals, unequal sample sizes among fish, and small numbers of observations for some fish. Because most movement analysis methods require regular and frequent observations of tagged fish, we employed an alternative analysis framework that is robust to missing data and small sample sizes. This analysis framework, based on the net squared displacement (NSD) statistic, is based on the identification of patterns of dispersal over time that correspond to different behaviors such as foraging or migration (Börger & Fryxell 2012). NSD, also commonly referred to as R^2_n, is the square of the distance between the origin of a given trajectory and each subsequent position.

$$\text{NSD}_t = \left| \mathbf{x}_t - \mathbf{x}_0 \right|^2 \qquad (1)$$

where $\mathbf{x}_t$ is the coordinate vector at time t (i.e. the

latitude and longitude of a fish on day t), and $\mathbf{x}_0$ is the coordinate vector for the origin of the trajectory (i.e. a fish's release location). For random movement, e.g. Brownian motion, the NSD statistic increases linearly with time (Kareiva & Shigesada 1983) and the slope is proportional to the rate of diffusion (Börger & Fryxell 2012). For non-dispersive movement, such as home range behavior, the NSD statistic reaches a constant value over time that represents the spatial scale of the area in which the fish moves (Turchin 1998, Moorcroft & Lewis 2006). For directed movement toward a specific location, such as during migration or moving between foraging locations, the relationship between NSD and time is exponential (Nouvellet et al. 2009).

Movement states

We defined 2 different movement states using the NSD statistic. The first movement state, 'residential,' reflects non-dispersive movement and was defined when the slope of NSD vs. time = 0 (p > 0.05 for the slope coefficient in a linear regression) for a minimum sample size of 4 consecutive observations (Fig. 2). For this movement state, the intercept of NSD vs. time provides information about the spatial scale at which NSD values do not increase or decrease over time, thus providing an estimate of home range size that is robust to small sample sizes and
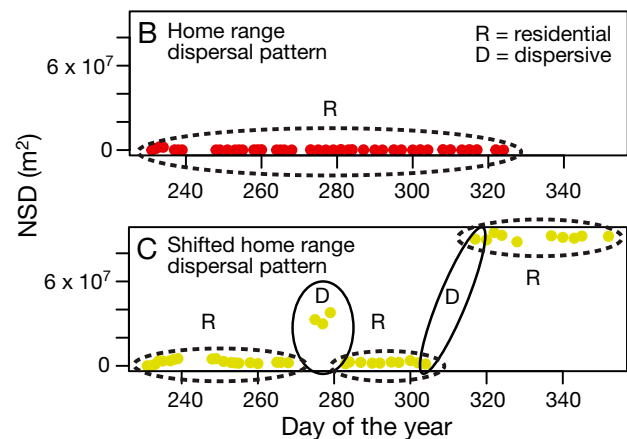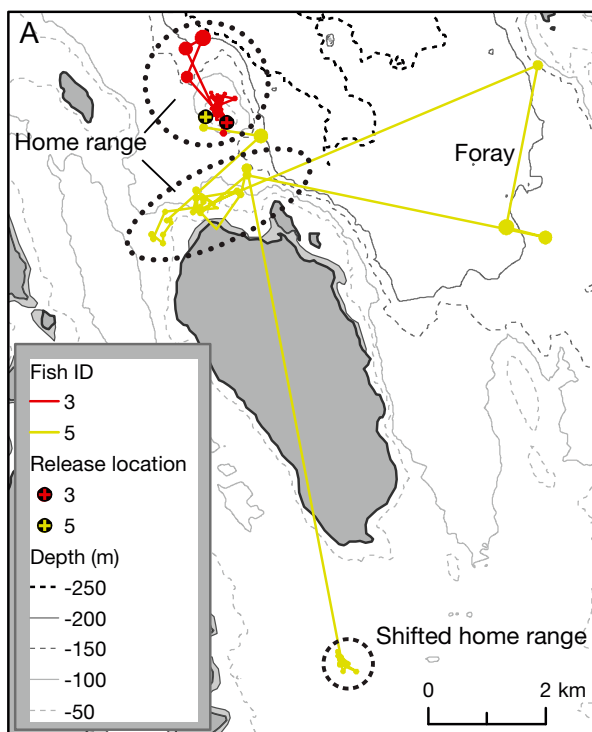

Fig. 2. *Hippoglossus stenolepis.* (A) Different dispersal patterns as shown by 2 tagged halibut (ID#3 and ID#5). The size of solid red and yellow circles represents estimated telemetry position error (in m). Dotted elipses: home ranges. (B,C) Corresponding plots of the net squared displacement (NSD) statistic vs. time for (B) a home range dispersal pattern with all observations classified as residential movement (ID#3), and (C) a shifted home range dispersal pattern with observations classified as residential or dispersive (dashed and solid-line elipses, respectively) movement states (ID#5)

infrequent observations (Moorcroft & Lewis 2006). Consecutive observations classified as residential are subsequently referred to as 'home ranges'. We estimated typical home range size for the residential movement state using an intercept-only linear mixed-effects model:

$$\log(\text{NSD})_{ij} = \alpha + a_i + \varepsilon_{ij}$$
$$a_i \sim N(0, \sigma_a^2), \ \varepsilon_{ij} \sim N(0, \sigma^2) \tag{2}$$

where α is the fixed-effects estimate of mean home range size for the population of i home ranges, a_i is a random variable that represents the variation of individual home range estimates around the fixed-effects mean, and within-group error ε_{ij} is assumed to be independent and normally distributed with a mean of zero. The model was fit using restricted maximum likelihood. NSD values were log-transformed to account for heteroscedasticity prior to modeling. We applied the bias-correction for a log-normal distribution to back-transform the estimated mean to the original scale:

$$\text{Home range size (NSD)} = \exp(\alpha + s^2/2) \tag{3}$$

where α is the mean home range size for the population as described above and s^2 is the estimated variance for α. To provide a more intuitive linear description of movement scale, the square root of intercept coefficients were reported as a 'home range radius.' To minimize potential bias of capture and tagging on the scale of home range movement patterns (e.g. temporary tagging effects, uncertainty in longline position during capture vs. release location, or travel from release position back to the home range), observations within 3 d of tagging were not used for home range analyses.

The second movement state, 'dispersive,' was classified as all observations where the slope of NSD vs. time $\neq$ 0 (Fig. 2C). This movement state generally contained observations from both random and directed movement types. Because fish with more mobile movement patterns were more difficult to relocate, observations were not collected frequently enough to determine whether individual observation sequences were random (linear relationship for NSD vs. time) or directed (exponential relationship for NSD vs. time). Therefore, we did not summarize this movement state using a mixed-effects model, as we did for the residential movement state, because it likely contained a mix of both movement types.

Although we were not able to explicitly classify observations as either random or directed, insight into the randomness of the dispersive movement state

was obtained by comparing our observations of average NSD vs. time to expected random values using correlated random walks (CRWs). CRWs are movement paths comprised of a discrete series of movement steps where the expected distance and the expected angle between subsequent steps determines overall movement path characteristics such as diffusion rates (larger for larger step lengths) and directed vs. random movement (more directed for smaller variation in turning angles, more random for larger variation in turning angles). CRWs are usually simulated based on empirical distributions of both step lengths and turning angles obtained from frequent and regular observations of a fish's location over time (Kareiva & Shigesada 1983, Turchin 1998). However, because our dataset was highly irregular, we simulated random movement from a step length distribution comprised of all records that were 1 d apart, but used a theoretical distribution of turning angles (wrapped Cauchy with an autocorrelation coefficient of 0.5) that is typically observed during fish foraging activities (Morales et al. 2004, Bartumeus et al. 2005). This approach allowed us to incorporate empirical information on spatial scales of our tagged fish (daily step lengths) under a specific hypothesis of random movement during foraging. We fit exponential curves (Moorcroft & Lewis 2006) to both the residential and dispersive step length distributions and sampled randomly from these distributions to create 1000 CRWs for a duration of 90 d for each movement state. To account for the effects of movement that occurs within the confined waters of the study area, simulations were conducted on a 20 m bathymetry grid of Glacier Bay (Geiselman et al. 1997) and were initiated at the first location of each observed residential or dispersive movement sequence. If a simulated position for the CRW fell on land, that position was discarded and a new coordinate was chosen. To assess randomness, the mean NSD from observed data was compared to the mean and 95% CI from the CRWs at each time step. NSD values for random movement should fall within the 95% CI for the CRW simulations, whereas values for directed and non-dispersive movement will be greater than the upper bound and less than the lower bound, respectively, of the 95% CI for CRW values (Austin et al. 2004).

## Individual dispersal patterns

In addition to characterization of movement states, knowledge of the way in which NSD changes over

time during non-dispersive, directed, or random movement can be used to formulate theoretical models that describe behavioral phenomena such as home range occupation, directed movements to new locations, migrations or forays, or random movement (Bunnefeld et al. 2011, Börger & Fryxell 2012, Papworth et al. 2012, Singh et al. 2012). We identified 5 models of NSD vs. time, subsequently referred to as dispersal patterns, that we assume represent underlying behaviors for tagged fish in this study (Table 2). (1) The 'home range' dispersal pattern (HR) reflects a restricted range of movements described by a slope of zero for NSD vs. time. (2) The 'random' dispersal pattern (R) reflects diffusion (e.g. Brownian motion) and can be described by a linear increase in NSD vs. time. (3) The 'shifted home range' dispersal pattern (SHR) represents movement from the release location to another location in the study area and consists of a non-linear (sigmoidal) model with parameters for the timing of the midpoint of the travel to the new location (θ, day of the year), a scale parameter (φ, day of the year) to estimate the time to travel between the midpoint and

approximately ¾ of the distance to the destination (Bunnefeld et al. 2011), and the squared distance to the destination (δ, m^2). (4) The 'site fidelity' (SF) dispersal pattern represents departure from the release location and subsequent return to the original location. It consists of a double sigmoidal model, with one sigmoid function to describe the migration start (subscript m) and one to describe the return to the original location (subscript r). The SF dispersal pattern has the same parameters as the SHR model, but with an additional parameter, θ_r, to describe the timing (day of the year) of the midpoint for the return. (5) The 'foray/shifted home range' dispersal pattern (FSHR) reflects departure from the release location and dispersive behavior before resuming HR behavior in another location. The parameters for this model are the same as those for the SF pattern, but an additional parameter (δ_r, m^2) is added to describe the squared distance between the farthest distance traveled during the foray and the SHR.

Dispersal patterns for individual tagged fish were classified by determining which of the 5 models for NSD vs. time described above best described the

Table 2. Model name, code, number of parameters, theoretical example, and formula for dispersal patterns used to classify movement trajectories for halibut *Hippoglossus stenolepis*. t is time, $\propto$ is the intercept of a linear model, β is the slope of a linear model, and δ, θ, and φ are nonlinear model coefficients that describe the spatial extent, timing, and temporal scale respectively. Subscripts — 'm': migration start; 'r': return. See Bunnefeld et al. (2011)

Model (code)	No. params	Ecological-interpretation	NSD vs. time	Formula
1. Home range (HR)	1[a]	Constrained movement, such as home range behavior (residential movement state)		$NSD = \propto$
2. Random (R)	1	Nomadic, diffusive movement such as foraging		$NSD = \beta t$
3. Shifted home range (SHR)	3	Movement to new location		$NSD = \dfrac{\delta}{1 + \exp\left(\dfrac{\theta - t}{\varphi}\right)}$
4. Site fidelity (SF)	4	Migration or foray with return to original location		$NSD = \dfrac{\delta}{1 + \exp\left(\dfrac{\theta_m - t}{\varphi}\right)} + \dfrac{-\delta}{1 + \exp\left(\dfrac{\theta_r - t}{\varphi}\right)}$
5. Foray/shifted home range (FSHR)	6	Migration or foray with return to new location		$NSD = \dfrac{\delta_m}{1 + \exp\left(\dfrac{\theta_m - t}{\varphi_m}\right)} + \dfrac{-\delta_r}{1 + \exp\left(\dfrac{\theta_r - t}{\varphi_r}\right)}$

Time

[a]Home range can be modeled as intercept-only when the sampling interval is greater than the time the fish takes to reach the limits of its range

observed values of NSD vs. time based on model selection techniques. Non-linear models (all models besides HR and random) were fit using a non-linear least squares algorithm (the nls function in the 'stat' package for R). The best-fitting model for each individual trajectory was selected using the Akaike Information Criterion adjusted for small sample sizes (AICc) (Burnham & Anderson 1990) and residual analysis. An example of the dispersal pattern classification process for individual fish is provided in Fig. S3 in Supplement 2 at www.int-res.com/articles/suppl/m517p229_supp.pdf. Once individual fish were classified according to dispersal pattern, we calculated the average for: (1) maximum distance from the release location during the observation period, (2) distance from the release location at the end of the observation period, (3) observation period duration, and (4) fish size for each dispersal pattern.

We used mixed-effects models to summarize model parameters for dispersal patterns to which more than 3 fish were assigned. Because fish with the HR dispersal pattern were included in the mixed-effects model for the residential movement state, mixed-effects models were only used to summarize the random and SF dispersal patterns. For the random dispersal pattern, we quantified the rate of dispersal over time using a linear model with no intercept, as, by definition, dispersal must be zero at the origin of a trajectory, using fish ID as a grouping variable.

$$NSD_{ij} = \beta t + b_i t + \varepsilon_{ij}$$
$$b_i \sim N(0, \sigma_b^2), \ \varepsilon_{ij} \sim N(0, \sigma^2) \tag{4}$$

where β is the fixed-effect variable estimate of the mean slope of NSD vs. time for the population of i random trajectories, b_i is a random variable that represents the variation of individual slopes around the population mean slope, and within-group error ε_{ij} is a random variable that is independent and normally distributed with a mean of 0. The model was fit using restricted maximum likelihood. Because random movement results in the process of diffusion, NSD vs. time for random movement is proportional to diffusion. Therefore, results are presented in the form of the estimated rate of diffusion, in $km^2 \ d^{-1}$, which is calculated by dividing the slope of NSD vs. time by 4 for movement in 2 dimensions (Börger & Fryxell 2012).

For the SF dispersal pattern, we quantified timing, duration, and distance traveled during forays that occurred during the summer with a non-linear mixed-effects model:

$$NSD_{ij} = \frac{\delta + d_i}{1 + \exp\left(\frac{\theta_m - t}{\varphi + f_i}\right)} + \frac{-\delta + d_i}{1 + \exp\left(\frac{(\theta_r + r_i) - t}{\varphi + f_i}\right)} + \varepsilon_{ij} \tag{5}$$

$$d_i \sim N(0, \sigma_d^2), \ f_i \sim N(0, \sigma_f^2), \ r_i \sim N(0, \sigma_r^2), \ \varepsilon_{ij} \sim N(0, \sigma^2)$$

where δ, θ_m, θ_r, and φ are fixed-effects parameters for the asymptote (e.g. migration distance), date of migration, date of return, and scale, respectively (see Table 2), and d_i, f_i, and r_i are random-effects variables assumed to be normally distributed with mean 0 that represent individual variation in the asymptote, scale, and date of return, respectively. Within-group error ε_{ij} is assumed to be independent and normally distributed. The estimate for distance traveled during the foray is reported as the square root of the asymptote, δ. As approx. 95% of the distance between the midpoint of the migration and arrival at the new location occurs over the time span of $3 \times \varphi$ (Börger & Fryxell 2012), timing of migration is estimated by $\theta_m - (3 \times \varphi)$ and timing of return by $\theta_r + (3 \times \varphi)$. Population estimates of average foray duration are calculated as the difference between the two: $[\theta_r + (3 \times \varphi)] - [\theta_m - (3 \times \varphi)]$.

Selection of random-effects variables for the SF model was conducted by first examining the range of coefficient values for each parameter, based on separate fits of the model to each trajectory, and selecting parameters with large variation as random effects in the full model (Pinheiro & Bates 2000). Alternative models with fewer random-effects variables and autocorrelation structures were tested against the null model using maximum likelihood and compared using AIC and likelihood ratio tests. The best model (Eq. 5) also included an AR1 autocorrelation coefficient of 0.3. All mixed-effects models assumed a Gaussian error structure and were fit using the library 'nlme' in the R program. The assumption of a normal distribution in random-effects estimates was checked using the Shapiro-Wilks test for normality.

Habitat relationships

We characterized habitat occupied by tagged halibut during the residential movement state using several habitat metrics available for the study area (depth, slope, habitat complexity, rugosity, substrate type, tidal velocity). Because >90% of the tagged fish observations occurred within a large area of the central portion of the bay that was characterized by a multibeam survey in 2001, we were able to use fine-scale depth (Carlson et al. 2002) and habitat information (Harney et al. 2006) resulting from this survey.

However, observations for 2 tagged fish were removed from habitat analyses because a majority of their observations fell outside of the multibeam study area. Continuous rasters for slope, change-in-slope (an indicator of slope interfaces and measure of habitat complexity), and rugosity (a measure of surface roughness) were derived from 5 m resolution depth data using ArcGIS 10.0 Spatial Analyst and ArcGIS 10.1 Benthic Terrain Modeler (Wright et al. 2012, ESRI 2011). Continuous rasters for soft sediment and moderate habitat complexity were derived from discrete habitat map polygons by calculating Euclidean distance from each grid cell to each type of polygon. Continuous information on time and depth averaged (monthly) tidal velocity was available from a 2-dimensional circulation model (ADCIRC) of Glacier Bay (Etherington et al. 2007b, Hill et al. 2009). We used information from these 7 continuous rasters (depth, slope, change-in-slope, rugosity, distance from soft sediment, distance from moderate complexity habitat, and tidal velocity) to identify habitat associations and quantify the effects of habitat variables on HR size. Study area maps and additional details on habitat raster characteristics are available in Supplement 3 (Fig. S4, Table S3) at www.int-res.com/articles/suppl/m517p229_supp.pdf.

Habitat associations. To provide a simple description of the predominant habitat characteristics observed for the residential movement state relative to all available habitat types in the study area, we adapted an approach used to detect habitat associations based on the spatial distribution of catch during trawl surveys (Perry & Smith 1994). This method involves comparing the cumulative distribution function (CDF) of habitat values (e.g. depth) where tagged fish were observed to the CDF of available depths in the study area. Because halibut are large-bodied fish capable of a high degree of movement, we assumed they could have moved anywhere in the study area over the course of the observation period. To obtain CDFs for available habitat in the study area, a 20 m grid of the study area was created in ArcGIS (1.08×10^6 points) and values from each habitat raster were extracted at each grid point.

To account for telemetry error in the habitat analyses, a buffer with a radius of the estimated error was drawn around each tagged fish observation and all grid values within the buffer were averaged. 'Observed' CDFs were then calculated using the median value of all observations in each HR to avoid pseudo-replication from treating repeated, irregular observations of 1 fish at 1 location as independent events (Rogers & White 2007). Confidence intervals for observed CDFs were generated by bootstrapping, where the median observation for each HR was sampled with replacement 1000 times, and the 0.975 and the 0.025 quantile values were selected as the upper and lower confidence intervals.

We defined habitat associations by quantitatively comparing the CDFs for observed and available fish habitat. Specifically, for each habitat variable, we used the bootstrapped confidence levels for the observed CDFs to test for differences between observed and available habitat using the Kolmogorov-Smirnov (K-S) test. The K-S test is frequently used to test for differences between CDFs based on the maximum vertical difference (D) between the CDFs (Conover 1999). To determine whether positive differences existed between the observed and available CDFs (e.g. an association with shallower depths), we found the greatest positive difference (D^+) between the upper CI of the observed CDF and the available CDF. To determine whether negative differences existed between the observed and available CDFs (e.g. an association with deeper depths), we found the greatest negative difference (D^-) between the lower CI of the observed CDF and the available CDF. We determined D^+, D^-, and p-values for each habitat variable using one-tailed Kolmogorov-Smirnov tests.

Habitat and home range size. We used a generalized additive model (GAM) to determine whether HR sizes were related to habitat variables or fish total length. Intercept coefficients from the mixed-effects model for the residential movement state (in log format) were used as the response variable. Explanatory habitat variables were selected from the 7 continuous habitat rasters used for habitat association analyses. In addition to habitat variables, we also included fish total length and year of study as explanatory variables for HR size. The GAM approach was used to allow for potential non-linearities in the relationship between response and explanatory variables. Prior to analysis, all variables were checked for covariance with the Pearson correlation coefficient; if a set of variables were found to be correlated, only the variable with the strongest relationship with the response variable was used in the model. After assessing correlation and linearity of habitat variables, 2 full models were tested:

Model 1: $y = \alpha + s_1$ (depth, k = 2) + s_2 (fish total length, k = 3) + s_3 (distance from moderate complexity, k = 3) + β_1 change-in-slope + β_2 tidal velocity + year + ε (6)

Model 2: $y = \alpha + s_1$ (depth, fish total length, k = 3) + s_3 (distance from moderate complexity, k = 3) + β_1 change-in-slope + β_2 tidal velocity + year + ε (7)

where $\textbf{y}$ is the vector of estimated intercepts from the mixed-effects model for all residential trajectory segments (n = 29), α and β_i are regression coefficients, s_i are smooth functions of the predictor variables, k represents the degree of smoothing in the smooth functions, and ε are the residuals, assumed to be independent and normally distributed. GAM models were fit using maximum likelihood methods with a Gaussian error structure in the mgcv package in R (Wood 2006). Variables were sequentially removed from a full model based on the highest p-value (i.e. larger than 0.05) and the best model was chosen based on the AICc criterion and residual analysis.

RESULTS

Fish tagging and tracking

A total of 43 fish were tagged between 1991 and 1993 (Table 1). Most fish were tagged between June and September of each year, but 4 fish were tagged in November 1992 and tracked during the following summer, and all were released in good condition. Tagged fish TL (mean ± SD) was 133 ± 32 cm. Almost all (16 of 18) of the fish that we were able to sex were female; however, sex could not be determined for the majority (n = 25) of tagged halibut in this study. Based on fish size and maturity ogives from International Pacific Halibut Commission (IPHC) records during this time period, the majority of the halibut tagged in this study were likely to be adult females (T. Loher pers. comm.).

Five fish were never relocated following tagging (Table 1). For the remaining 38 fish, the mean (±SD) number of relocations per fish was 17.4 ± 14.3 and ranged from 1 to 49. More than half of the relocations for individual fish were obtained within 3 d of the previous observation, and 90% of the subsequent observations in each tracking period were within 8 d of the previous observation. Thus, the temporal scale of tagged fish observations during each tracking period can be characterized as daily to weekly. In total, 706 acoustic tracking position estimates were obtained for all tagged fish in all years. Tracking effort differed among years, with most intense tracking during 1991 (32.5 observations per fish) and decreasing during 1992 (13.4 observations per fish) and 1993 (14.8 observations per fish). Tagged fish were observed over a mean tracking duration of 79.5 d (range 1 to 290 d) each year.

The average (±SE) distance that individual tagged fish (n = 38) moved between the release location and the location of the last observation was 3.5 ± 0.8 km. The average (±SE) maximum distance traveled during the entire observation was 5.8 ± 0.9 km. The maximum distance from release location recorded during the study was 17.9 km (Table 1). There were no significant relationships between the maximum distance traveled for each fish and fish size (linear regression, p = 0.709), tag size: body weight ratio (linear regression, p = 0.637), tag size (small vs. large; ANOVA, p = 0.146), or tag attachment method (interval vs. external; ANOVA, p = 0.797).

Movement states

The residential movement state was observed most frequently (27 of 43 tagged halibut; Fig. 3A). A total of 31 residential movement sequences (some fish had more than 1 residential sequence) were observed with a median duration of 58 d. The mixed-effects model population estimate (mean ± SE) for the intercept of NSD vs. time was $12.0 ± 0.3$ m^2, with a standard deviation for random effects of 1.4 on the log scale (Fig. 4A). This corresponds to an estimated population HR radius of 401.3 m (95% CI = 312.2–515.9 m) and 95% CIs for individual HR radii that range from 104.3 to 1493.9 m on the untransformed scale.

The dispersive movement state was observed for 15 of 43 tagged halibut (Table 1, Fig. 3B). A total of 18 dispersive movement sequences were observed with a median duration of 27 d. This duration was significantly shorter than that of the residential movement state (t-test, p < 0.0001). The average maximum distance from the release location for fish that exhibited the dispersive movement state was 10.9 km.

The step length distribution for the residential movement state (Fig. 5A) was significantly different than the step length distribution for the dispersive movement (Fig. 5B). Based on a randomization test with 1000 permutations, the median daily movement step length for observations from the residential movement state (330.4 m, n = 193 observations) was significantly less (p < 0.0001) than the median daily movement step length for observations from the dispersive movement state (861 m, n = 19 observations). The rate parameter for the exponential curve that was fit to each step length distribution for use in the CRW analyses was 0.000213 ± 0.000015 (SE) for observations from the residential movement state and 0.0008059 ± 0.000184 for observations from the dispersive movement state.
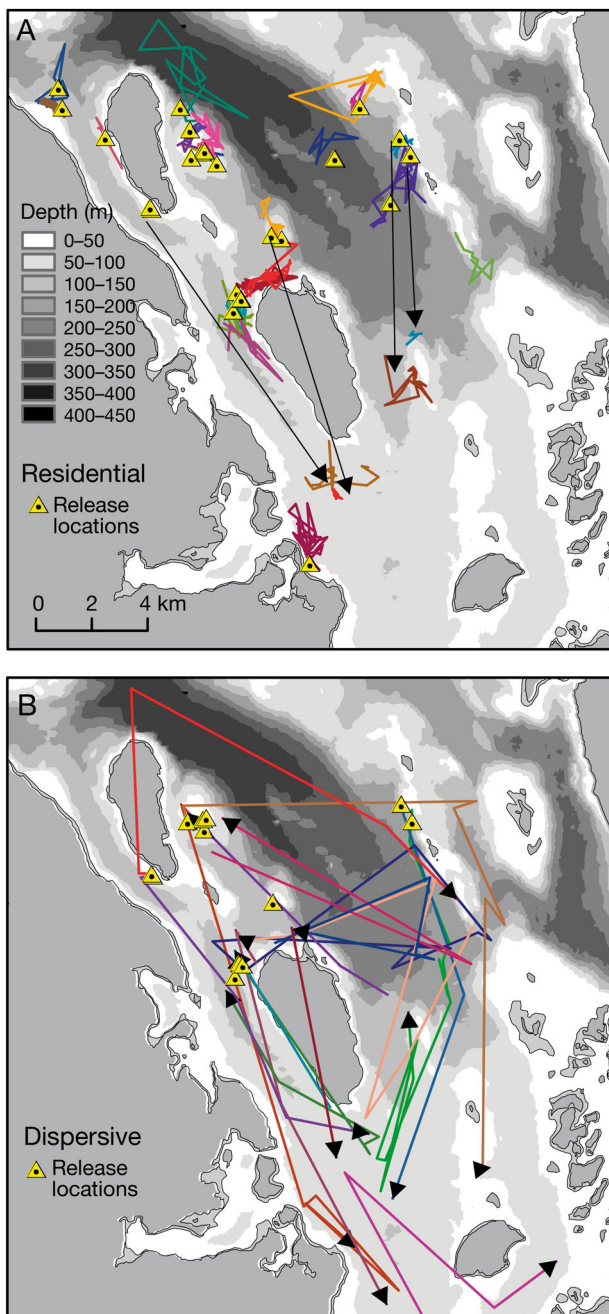
Fig. 3. *Hippoglossus stenolepis.* Movement patterns of tagged halibut exhibiting (A) residential movement (colored lines: movement sequences; black arrows: shifted home ranges from release locations) and (B) dispersive movement (colored arrows) within the core study area

The CRW simulations highlighted major differences in the scale and nature of dispersal between the residential and dispersive movement patterns. Average values of NSD observed for the dispersive movement state were generally within the 95% CI for the CRWs, however these tended to be closer to
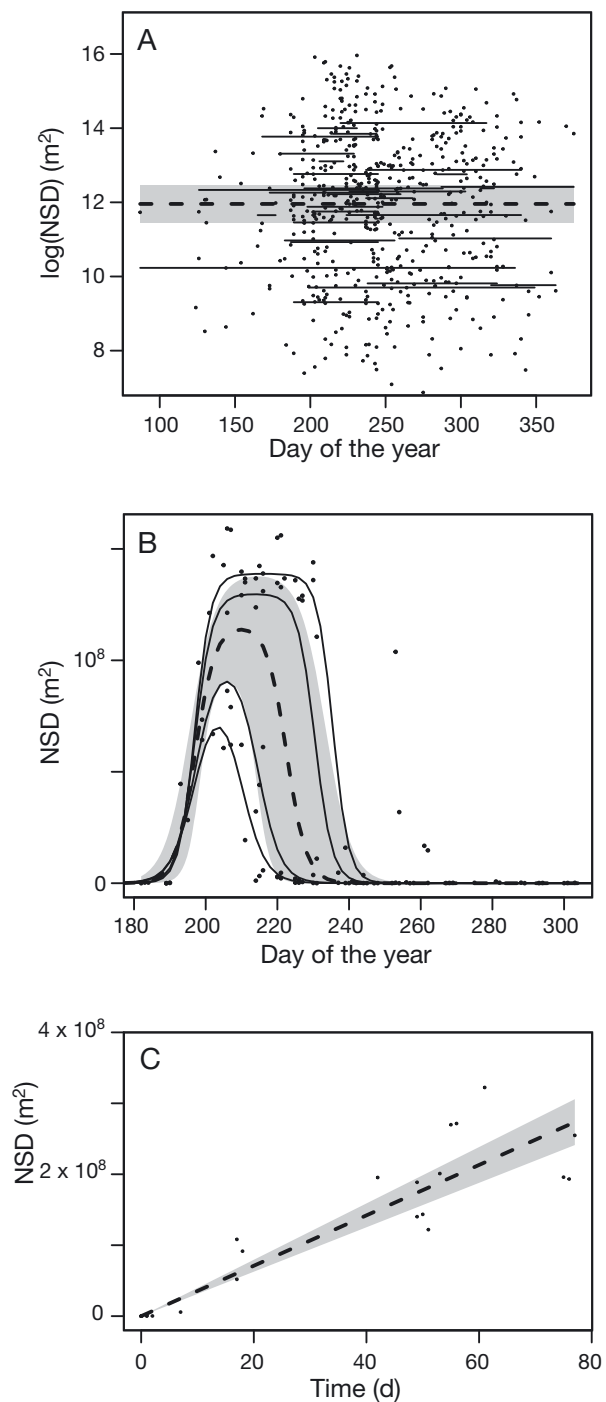

Fig. 4. *Hippoglossus stenolepis.* Observed (points) and estimated (lines) of the net squared displacement (NSD) statistic from mixed-effects models for (A) the residential movement state (n = 31 home ranges) on log-scale, (B) the site fidelity dispersal pattern (n = 4 ind., as 2 ind. with winter observations were not included), and (C) the random dispersal pattern (n = 4 ind.). Population (fixed-effect) means are shown with thick dashed lines, 95% CIs are shown as gray polygons, and thin black lines represent individual (random-effects) estimates (in A, the length of these lines represents the period observation for each individual)
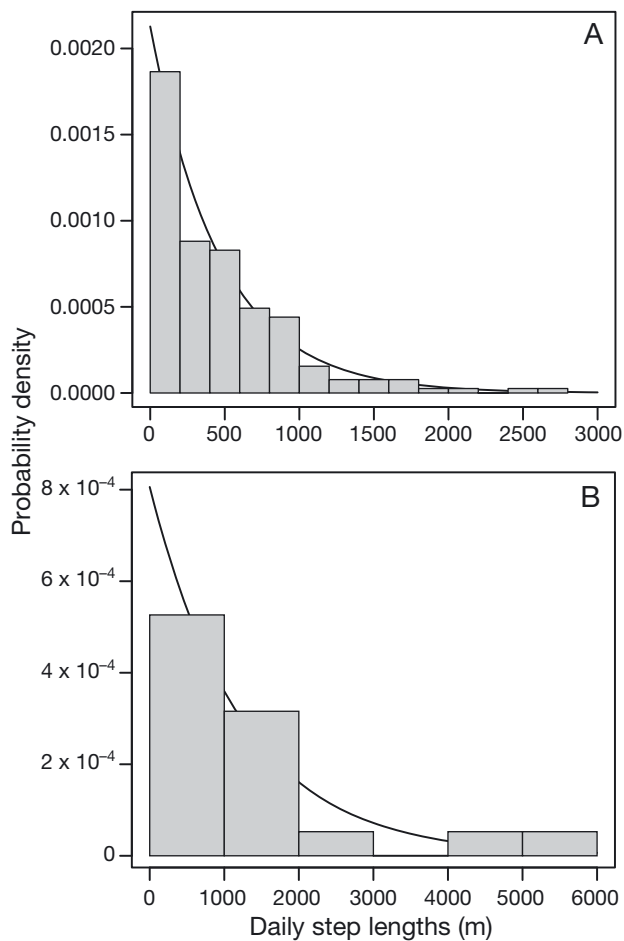
Fig. 5. *Hippoglossus stenolepis.* Daily step length distributions for (A) residential and (B) dispersive movement states along with exponential curves fitted to each distribution

the upper confidence level for the first 20 d (Fig. 6A). Like the CRWs, observed values of NSD for the dispersive movement state exhibited a general trend for increased NSD values over time. In contrast, observed values of NSD vs. time for residential movement pattern were located along the lower 95% CI for the simulations, and some observed values were smaller than the CRW confidence intervals after ca. 30 d (Fig. 6B).

Individual dispersal patterns

Of the 38 fish that were relocated at least once following release, 32 produced a sufficient number of observations to allow classification of their dispersal pattern. More than half of these fish (n = 17) remained in the vicinity of the release location and demonstrated an HR dispersal pattern, where the
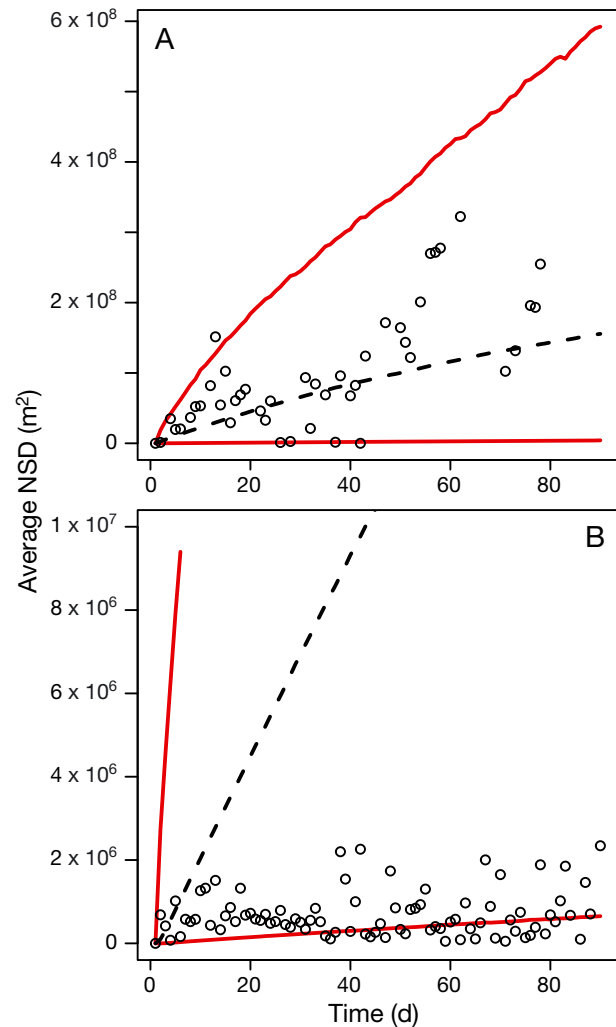

Fig. 6. *Hippoglossus stenolepis.* Observed mean net squared displacement (NSD) statistic (circles) compared to the mean (dotted line) and 95% CIs (red lines) of 1000 correlated random walk simulations for (A) dispersive and (B) residential movement states. Note the difference in scales for the *y*-axes

average net displacement over average tracking durations of >3 mo was <1 km (Table 3). Five fish demonstrated SHR dispersal patterns (SHR, n = 3 and FSHR, n = 2) with average net displacements of 10 and 4 km, respectively, over similar time periods. Six fish demonstrated the SF dispersal pattern by moving an average maximum displacement of approx. 10 km, but eventually returning to locations that were an average net displacement of <2 km from the release location over average time periods of >4 mo. Two of these fish established HRs at other locations in the study area during the foray. Three fish classified with the SF dispersal pattern returned to within hundreds of meters (range 200 to 500 m) of their release locations after moving an average (±SE)

maximum distance of 9.8 km ± 0.5 km. One fish classified as SHR (ID#5, Fig. 2) also demonstrated a SF pattern during a temporary foray of 6 km and duration of 16 d followed by a return to within 200 m of the location occupied prior to the foray. Four fish exhibited the random (R) dispersal pattern, moving an average maximum and average net displacement of approx. 12 km over observation periods that averaged <2 mo (approximately half of the typical durations observed for the fish assigned to other dispersal patterns). The 6 fish for which only a few observations were collected (U) had very short observation durations (average 13.5 d), yet the average net displacement of approx. 3 km for these fish was greater than that observed for the HR dispersal pattern. There was no significant difference among the total lengths of fish in each of the 5 dispersal patterns, unclassified movements, or the fish that were never observed after tagging (Kruskal-Wallis test, p = 0.3679, df = 6).

A mixed-effects model was fit to NSD data from 4 of 6 tagged fish that were classified as having a SF dispersal pattern (Fig. 4B). Movements for the 2 fish that were not included occurred over the winter, so the timing of their movements could not be compared to fish that were observed only during the summer. For the 4 remaining fish in this group, the fixed effect estimate for the distance traveled during their forays (the asymptote, δ) was a movement radius of 10.5 ± 4.0 km (SE) (p < 0.0001) (Fig. 4B). The SD for individual fish from the population mean (d_i) was 5.1 km. The scale parameter φ was estimated to be 2.4 ± 0.5 d (SE) (p < 0.0001), and the SD for the corresponding random-effects variable f_i was 0.0001 d. The population estimate for the timing of departure was July 8 ± 1 d (SE) (p < 0.0001), and the estimate for the timing of the return to the original location was August 17 ± 5 d (SE) (p < 0.0001) with a standard deviation for the random-effects variable r_i of 10.1 d. The overall population estimate for duration of the forays was 40 ± 5.1 d (SE). The value of the AR(1) autocorrelation coefficient (referred to in the nlme package as Phi) for the model was 0.61.

Table 3. Number of individuals of halibut *Hippoglossus stenolepis* assigned to each dispersal pattern (see Table 2; HR: home range; SHR: shifted home range; FSHR: foray/shifted home range; SF: site fidelity; R: random; U: unknown; N: not relocated after release) along with average (±SE) maximum horizontal displacement, average net displacement at the end of the observation period, average observation period duration for each pattern, and total length. (–) No data

Model	No. of fish	Max displacement (km)	Net displacement (km)	Obs. duration (d)	Total length (cm)
HR	17	1.7 (0.02)	0.9 (0.2)	102.5 (14.3)	142.7 (10.0)
SHR	3	10.9 (1.2)	10.3 (1.6)	101.7 (26.4)	129.8 (6.8)
FSHR	2	8.5 (4.8)	4.2 (2.2)	110.0 (8.0)	146.5 (10.5)
SF	6	10.4 (0.8)	1.8 (0.7)	146.5 (46.5)	131.1 (3.7)
R	4	12.8 (3.5)	12.3 (3.3)	48.3 (14.8)	122.0 (13.4)
U	6	4.3 (2.5)	3.3 (1.8)	13.5 (11.7)	134.8 (12.9)
N	5	–	–	–	112.4 (12.9)

Table 4. Habitat associations and habitat occupancy ranges for the residential movement state of halibut *Hippoglossus stenolepis*. **Bold**: significant Kolmogorov-Smirnov test statistics (D). One-tail test sign: positive: the upper 95% CI for the observed CDF is greater than the available CDF; negative: the lower 95% CI for the observed CDF is less than the available CDF). Habitat value given only where significant D^+ or D^- statistics were obtained. NS: not significant

Habitat variable	D	p	1-tail test sign	Habitat value at D
Depth (m)	**0.1701**	0.003	+	104
Slope (°)	**0.2674**	<0.001	−	1.0
Change in slope (°)	**0.3234**	<0.001	−	3.6
Rugosity (ratio)	**0.2066**	<0.001	−	0.00015
Tide speed (m s^{-1})	**0.2114**	<0.001	−	0.07
Tide speed (m s^{-1})	**0.2189**	<0.001	+	0.34
Distance to soft bottom (m)	0.0127	0.968	+	NS
Distance to moderate complexity (m)	0.0785	0.288	+	NS

The population (fixed effect) estimate of the slope of NSD vs. time for the random dispersal pattern was 3.6 ± 0.2 km d^{-1} (SE) (p < 0.0001) which corresponds to an estimated diffusion constant D of 0.9 ± 0.05 km^2 d^{-1} (SE) (Fig. 4C). In contrast to the HR dispersal pattern, there was very little difference between the individual estimated movement rates because most of the variation was attributed to residual variation around the fixed effect.

Habitat relationships

Habitat associations. Significant habitat associations were observed between tagged fish in the residential movement state and available habitat
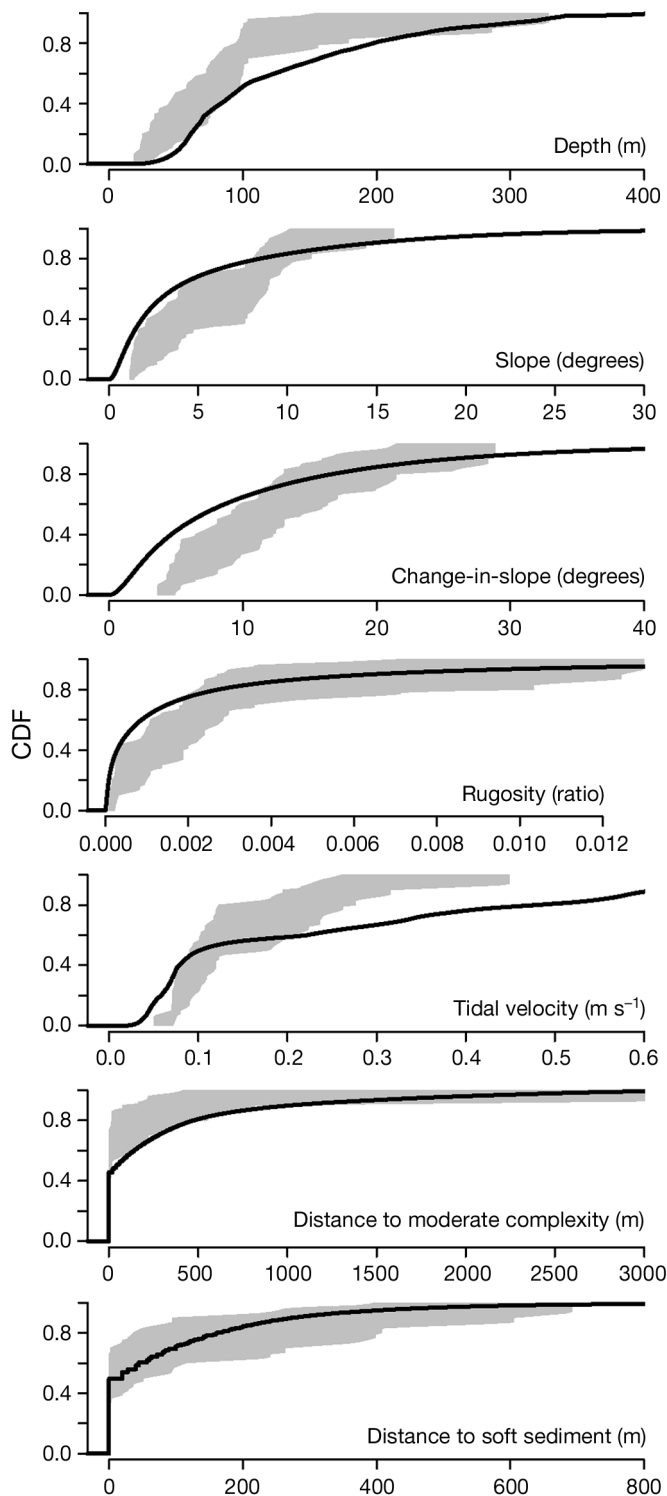
Fig. 7. *Hippoglossus stenolepis.* Observed cumulative distribution functions (CDFs) for the residential movement state (gray polygons: 95% CIs) compared to CDFs of available habitat values within the study area (thick black lines) for depth, slope, change-in-slope, rugosity, tidal velocity, distance to moderately complex habitat, and distance to soft substrate habitat. See Table 4 for habitat association test statistics

in the study area (Table 4, Fig. 7). Relationships were strongest for the habitat heterogeneity variables of change-in-slope, slope, and rugosity, with tagged fish tending to occupy areas of higher habitat heterogeneity relative to the range of values available in the study area. HRs were also associated with intermediate values of tidal velocity, where significant differences between observed and available habitat occurred at both high and low values of tidal velocities. Finally, HRs were associated with shallower depths relative to the range of available depths in the study area, with approximately 75% of HRs occurring in depths less than 100 m. No significant differences were observed between tagged fish and distance to moderate complexity or distance to soft substrate variables.

Habitat and home range size. The results from the GAM analysis indicate that of the variables examined, HR size varied most strongly with depth. The best model contained only a depth term with an estimated degrees of freedom of 1.8 (p = 0.007). For depths less than ~150 m, HR size increased with increasing depth (Fig. 8). The deviance explained by the selected model was 30.0%. No other models with all significant terms were within ±2 ΔAICc of the best model. No patterns were observed in the residuals, which were consistent with a normal distribution (Shapiro-Wilk test, p = 0.65).
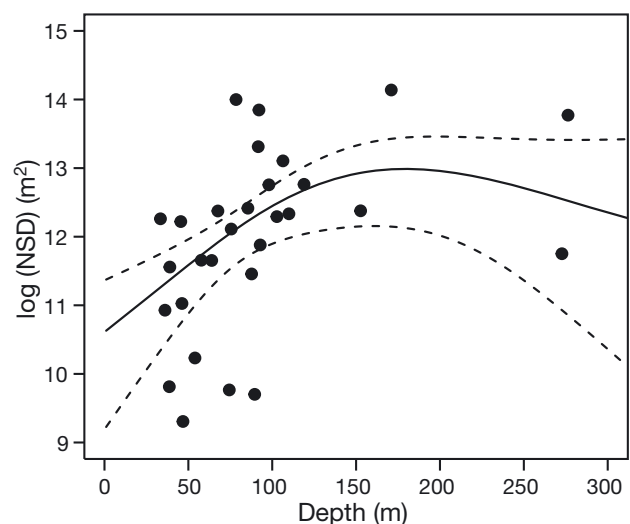

Fig. 8. *Hippoglossus stenolepis.* Predicted relationship between depth and home range size from the best generalized additive model (solid black line); 95% CIs are shown with dashed lines. NSD: net squared displacement

DISCUSSION

Although halibut are large-bodied fish capable of moving thousands of kilometers during winter spawning migrations (Skud 1977, Loher & Seitz 2006), our results suggests that limited dispersion at very small spatial scales may be a common phenomenon for adult female halibut in Glacier Bay during the summer and into the fall. The residential movement state was demonstrated by the majority (27 of 43) of the fish tagged in this study. The HR dispersal pattern (which consists of residential movement in the vicinity of the release location throughout the observation period) was also the most frequently observed dispersal pattern (n = 17) among the 32 ind. for which dispersal patterns could be determined. Although fish that exhibited the dispersive movement state moved more broadly around the study area, these movements were still relatively small (<20 km) compared to the distances moved during winter migrations.

Fish that were never relocated or were relocated too infrequently to characterize their movement patterns (11 of 43 fish) may have exhibited a more mobile movement pattern and thus moved out of the study area quickly. In this case, they could have moved to areas within Glacier Bay that were not monitored during acoustic surveys or they could have left the interior waters of Glacier Bay entirely. Alternatively, they may have been captured in commercial harvests that were occurring in Glacier Bay, experienced mortality, or the tag could have been shed or ceased to function.

Movement states

Telemetry records often document different behaviors among individuals that are driven by different movement 'states' (Blackwell 1997, Morales et al. 2004). For example, a period of intensive foraging may result in a movement state with little net displacement, while a period of migration may result in a movement state with relatively large net displacement. Typically, ecologists are interested in the spatial and temporal scales of these movement states, as well as habitat attributes with which they may be associated (Papworth et al. 2012).

The 2 movement states, residential and dispersive, that tagged fish exhibited during the summer and fall differed in terms of scale, duration, and potential for dispersion. The residential movement state was associated with average movement scales of <1 km for several months at a time and a sustained, non-random lack of dispersion. In contrast, the dispersive movement state was characterized by greater spatial scales (approx. 10 km), shorter temporal durations (<1 mo), and likely contained a mix of random and directed movement.

Because tracking occurred during the summer foraging season, and large adult halibut have few predators, these 2 movement states could reflect different underlying foraging strategies. Both 'sit-and-wait' ambush and active searching are common foraging tactics for flatfish species (Gibson 2005). The residential movement pattern could be driven by a sit-and-wait tactic, which would require little movement in areas where prey is delivered to the fish. Based on laboratory studies, a closely related congener Atlantic halibut *Hippoglossus hippoglossus* is thought to be an ambush predator that employs a sit-and-wait feeding tactic (Haaker 1975, Nilsson et al. 2010). Other flatfish such as summer flounder *Paralichthys dentatus* have been observed to employ a variety of foraging tactics — including ambush and active pursuit — that change with prey type (Staudinger & Juanes 2010). Thus, switching between the 2 movement states may occur in conjunction with changes in the type, abundance, distribution, and mobility of prey species (see Nakano et al. 1999). However, the dispersive movement pattern could also include fish that are moving in a directed manner from one feeding location to another.

Caveats. It is important to emphasize that the data presented in this study are inherently positive and biased toward the observation of the residential movement state. The experimental design employed in this study, which featured searching for tagged fish in the vicinity of their last known location, resulted in a much better characterization of the residential movement state compared to the dispersive movement state. The tracking procedure was effective for locating tagged fish that were occupying HRs, as the detection range for the acoustic tags (up to 2 km) was larger than the scale of most HRs. However due to the difficulty of tracking more mobile fish for long time periods in the large study area, it is likely that the dispersive movement state occurred more frequently than was observed and its spatial extent was not fully characterized. Although detection ability was adequate for characterizing the residential state throughout the study, changes in tag size and frequency (Table S1) could have improved the detection of fish in the dispersive movement state as the study progressed. It is likely that the largest movement observed (18 km) probably reflects a prac-

tical limit for the area searched during this study, so movements beyond that would have a low probability of detection.

Although it is possible that unknown tagging effects may have affected the behavior of tagged halibut, we feel that tagging effects are unlikely to have affected the scale and nature of halibut movement reported in this study for several reasons. (1) A long-term laboratory study of both internal and external archival tag attachment suggests that both types of attachment are well-tolerated by halibut and do not result in changes in behavior compared to controls (Loher & Rensmeyer 2011). (2) The tags were small relative to the size of the fish (average = 0.1%, maximum = 0.4%). (3) Pacific halibut fitted with much larger pop-up satellite tags have been observed to move more than 1000 km (Loher & Seitz 2006). (4) We found no statistical relationships between fish size or tag:body size ratio and maximum displacement, and no relationship between maximum displacement and tag size (small or large) or type of attachment (internal or external).

Individual dispersal patterns

Non-random dispersal patterns: home range and site fidelity. The majority of tagged fish in this study exhibited distinctly non-random individual dispersal patterns that were dominated by HR, but also included temporary long-distance forays followed by return to previously occupied locations and shifting of HRs to new locations. The prominence of the HR dispersal pattern suggests that regular use of relatively small areas could be a common phenomenon during summer. Several acoustic telemetry studies have demonstrated summer HR behavior for other flatfish species such as adult English sole *Parophrys vetulus* (S. O'Neill pers. comm.) and juvenile California halibut *Paralichthys californicus* (Espasandin 2012) that occurs at scales <1 km. Because some halibut shifted locations for HR behavior, it is possible that some fish may switch HR locations depending on changes in prey distribution and abundance and thus may not have fidelity to specific locations.

However, multiple observations of tagged fish returning to within several hundred meters of previously occupied locations following larger-scale movements (e.g. 10 km distance, 1 mo duration) suggests that some halibut do have SF to specific locations (as defined by Giuggioli & Bartumeus 2012). The SF dispersal pattern was observed for 7 of 43 fish (including 1 fish, ID#5, that was assigned to the SHR

dispersal pattern). It is also possible that temporary departures from HRs were not detected due to the irregular nature of the tracking trips and the difficulty of relocating wide-ranging fish. In that case, subsequent relocation of these same individuals at previously occupied locations would indicate intra-annual SF to established HRs. Therefore intra-annual SF may be a key feature of adult female halibut movement patterns in Glacier Bay during the summer and fall.

The study has also provided some evidence for interannual SF for halibut in Glacier Bay. Of the 4 fish released in November, 3 inhabited HRs at their release locations the following summer. Whether or not these fish left Glacier Bay during winter spawning migrations is unknown, but 2 of these fish were observed at different locations within the park following tagging (thus demonstrating an SF dispersal pattern).

These results complement previous observations of SF for Pacific halibut from a pop-up satellite archival tag (PSAT) study and provide further details on the scales at which it may occur. Approx. 80% of summer-to-summer PSAT pop-up locations (n = 25) were located within 20 km of release locations after 1 yr at liberty (Loher 2008). Most (75%) of these fish had returned to the release location following migrations to deeper water in the Gulf of Alaska during winter, presumably to spawn. Although the displacement from the release locations from the PSAT study matches the scale of the dispersive movement state observed in this study, the demonstrated ability of fish in the current study to return to within a few hundred meters of their original locations after undertaking forays indicates that SF for Pacific halibut likely occurs at much finer spatial scales than can be detected using PSATs. SF has also been observed for many other flatfish species (Hunter et al. 2003, Solmundsson et al. 2005, Sackett et al. 2008, Dando 2011, Moser et al. 2013).

Random movement: diffusion. Although the majority of the fish in this study displayed non-random movement patterns associated with an overall lack of dispersal during summer, some fish did appear to have more mobile movement patterns. The random movement dispersal pattern demonstrated by a small proportion of tagged halibut suggests that some halibut do not establish HRs, but may instead move randomly throughout summer foraging areas. The rate of diffusion associated with random movement in this study, 0.9 km^2 d^{-1}, is comparable to diffusion rates estimated for other flatfish species such as Baltic Sea turbot *Psetta maxima* (Florin & Franzén 2010) and

winter flounder *Pseudopleuronectes americanus* (Saila 1961) based on results derived from conventional tag recaptures. Therefore, random movement appears to be another common behavior of Pleuronectiformes species, likely as a foraging tactic. However, sample sizes were low for this dispersal pattern, so results should be interpreted with caution. For example, these fish could also have been detected during temporary forays to or from HRs in unknown locations.

A large-scale summer-to-summer PIT tag study of 67 000 halibut provided similar observations of both sedentary and mobile movement patterns for adult halibut that occurred over larger scales in space and time. Fish tagged during 2003 and 2004 had not mixed completely with the population by 2006 to 2009 (Webster et al. 2013) and as of 2008, 86% of 132 tags recaptured by annual survey vessels were caught at the same survey station where they were released (Loher 2008). Survey stations were located on an 18.5 km grid, which matches the approximate scale of the dispersive movement state observed in Glacier Bay. These observations support the presence of a long-term sedentary movement pattern for adult fish. On the other hand, the probability for large-scale movement between management units for large (e.g. 130 cm) fish was close to 20% for some units (Webster et al. 2013), which suggests that a more mobile movement pattern with a greater potential for dispersal also exists for adult halibut. In addition to the 4 fish that exhibited the random dispersal pattern in our study, it is possible that some of the 11 fish that were rarely or never detected had more mobile movement patterns. In that case, the proportion of tagged fish with more mobile patterns would range from a minimum of 9% (4 of 43) to a maximum of 35% (15 of 43), assuming no mortality, tag loss, or undetected HR behavior at unknown locations within Glacier Bay had occurred.

Caveats. Our use of a model selection framework to link observed patterns of NSD vs. time to theoretical models of dispersal represents a promising approach for identifying and quantifying fish movement patterns in terms of ecological phenomena such as HR occupation, foraging, and migration. This analysis method is appropriate for data collected at irregular intervals because the analysis is based on positive observations of NSD at a given point in time. However, due to the small sample sizes obtained for fish with more mobile movement patterns in this study, the results for dispersal patterns other than HR should be viewed as providing a preliminary under-standing of the types of behavior and spatial scales of movement that fish may demonstrate during summer.

Habitat relationships

The habitat associations observed for tagged fish may be related to a tendency for tagged fish to occupy a specific benthic habitat type in Glacier Bay. Three regions composed of different combinations of depth, tidal velocity, substrate type, and community composition exist in Glacier Bay (Etherington et al. 2007a). The mouth and lower portions of Glacier Bay consist of a large, flat, shallow (50 m), high-current area with sand and cobble substrate associated with a community of horse mussels, scallops, and sea urchins. In contrast, the central and northern portions of the bay are composed primarily of deep fjords (to approx. 450 m) with muddy substrates (Fig. S4) and were associated with Tanner crab (*Chionoecetes bairdi*), shrimp, and flatfish species. However, the majority of fish in this study were tagged and tracked in a transition zone between these 2 areas that is characterized by intermediate depths, intermediate levels of tidal velocity, mixed cobble/soft sediment, and intermediate to high levels of habitat complexity. This region is also occupied by Pacific herring (*Clupea palasii*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*), rockfishes (*Sebastes* spp.), and other common prey items for halibut (Best & St-Pierre 1986, Etherington et al. 2007a, Moukhametov et al. 2008, Renner et al. 2012). This transition area is also a highly productive front where well-mixed water from the mouth of the bay meets nutrient-rich stratified waters from the fjords (Etherington et al. 2007b).

Significant associations between the residential movement state and measures of habitat heterogeneity (change-in-slope, rugosity) and tidal velocity may also be related to a sit-and-wait foraging strategy. For example, complex habitat can aid concealment during ambush and tides may deliver pelagic prey (see Beaudreau & Essington 2011) to ambush predators. The strongest habitat association observed was for the change-in-slope variable, which represents interfaces between shallow and steep slopes as well as areas where depth is frequently changing. Tagged halibut tended to be found in close proximity to high values of the change-in-slope variable where glacial features such as moraines and ice scours interface with large expanses of flat, homogeneous terrain in the lower portion of Glacier Bay

(Fig. S5). Associations with interfaces between different habitat types have been observed for other fish species such as the barred sand bass *Paralabrax nebulifer* which inhabited interfaces between rocky reefs used for hunting and adjacent soft-sediment habitats used for resting or refuge (Mason & Lowe 2010). Although flatfishes are often associated with soft sediments related to their tendency to bury in sediments (Gibson 2005), no significant habitat association with distance to soft substrate habitats was observed here, a result that could be related to the abundance of soft sediment in the study area or a reduced tendency to bury in sediment for adult fish compared to juveniles.

Of the environmental and biological explanatory variables examined, only depth was significantly related to HR size. Increased scales of movement in deeper areas could reflect differences in prey type or prey densities compared to shallow areas (i.e. transition region communities compared to deep fjord bottom communities, as discussed above). A positive relationship with depth has also been observed for temperate reef-associated fishes, where species that occupy deeper depths tend to have larger ranges of movement than those that occur at shallower depths (Freiwald 2012). An increase in telemetry error with depth could confound the relationship between depth and HR size; however, the expected telemetry error is still small (100 m) relative to the distances moved in the larger HRs (1 to 2 km). Note that the 95% CIs reported for the GAM do not include errors associated with uncertainty of position related to depth. Because this model explained only 30% of the variance, HR is probably affected by variables that were either not measured or occurred at different scales in space or time. For example, the movements of many fish species are known to be related to tidal patterns on a daily basis (Tolimieri et al. 2009), so the use of time-and-depth averaged tidal velocity in this study may have been too coarse to detect relationships with tide. Although positive relationships between fish length and HR size have been previously reported (Kramer & Chapman 1999), we found that HR size was not related to fish size in this study. However the size distribution of the fish tagged in this study was relatively homogeneous (Fig. S1), so this result could also be related to low numbers of very small or very large fish. Finally, HR size did not change over time based on the lack of significance of the year variable. This result implies a stability of HR scales over time as well as a lack of effect of changing tag types (frequency, size, longevity, attachment method) as the study evolved (Table S2). Recent

fieldwork by the authors (J. K. Nielsen & A. C. Seitz unpubl. data), where 15 adult female halibut were tracked for 2 mo in Glacier Bay, has provided independent confirmation of the scale and dominance of the residential movement pattern during summer.

Implications for MPAs and spatial fisheries management

Determining fish movement scales relative to MPA size is one of the most important aspects of MPA design (Gruss et al. 2011, Saarman et al. 2013). Scales of both residential and dispersive movement states were smaller than the scale of the Glacier Bay MPA, and most tagged fish were detected regularly inside the MPA boundary. Thus, Glacier Bay is likely to encompass the majority of movements of individual adult female Pacific halibut during the summer and fall. Retention of halibut within Glacier Bay may be encouraged by the enclosed nature of the bay, availability of heterogeneous habitat with which tagged halibut were associated, and the productivity of its waters. Glacier Bay would therefore be expected to serve as a refuge from commercial harvest after the phase-out of commercial fisheries in the park is completed (estimated by the National Park Service to occur sometime between 2040 and 2050). However, understanding the potential for specific benefits of Glacier Bay as an MPA such as change in size structure or abundance (Taggart et al. 2004) will require more information on (1) large-scale movement patterns of halibut over yearly timescales, as fish could be vulnerable to commercial fishing during migrations from summer foraging locations to winter spawning locations outside of Glacier Bay, and (2) the effect of ongoing charter and unguided sport fishing within the park that will continue after commercial fishing is phased out.

In addition to insights into the potential utility of Glacier Bay as an MPA, this study has also yielded information that may be useful for design of MPAs or spatial management in general for halibut. The frequent observations of non-random dispersal patterns such as HR and SF are strikingly similar to dispersal patterns observed for other temperate reef-associated fishes such as lingcod (*Ophiodon elongatus*) and some rockfish species (Matthews 1990, 1992, Pearcy 1992, Starr et al. 2004, Tolimieri et al. 2009, Beaudreau & Essington 2011). Lingcod, yellowtail rockfish (*Sebastes flavidus*), blue rockfish (*Sebastes mystinus*), and California scorpionfish (*Scorpaena guttata*) were found to exhibit non-dispersive movement at spatial

scales that were similar to tagged halibut in this study (Freiwald 2012, his Supplement 1, Fig. S1). Benefits such as increases in biomass and egg production have been observed for multiple temperate reef fish species within MPAs in California (Tetreault & Ambrose 2007). Movement patterns and scales for adult female lingcod tagged in a small MPA near Sitka, Alaska, which were very similar to those of the adult female halibut tagged in our study, suggest that MPAs may facilitate increased egg production through protection of lingcod brood stock (Starr et al. 2004). Our research suggests that MPAs may also provide some degree of protection for Pacific halibut brood stock, and therefore potential enhancement of egg production, based on observations of HR and SF during the summer and fall. The effectiveness of such MPAs would then depend on the timing of winter spawning migrations, which may occur just before and/or after the commercial fishing season (Loher 2011), as well as the proportion of adult females that undertake annual spawning migrations (Loher & Seitz 2008). As the estimated total biomass of Pacific halibut in the eastern North Pacific Ocean has declined by 50 % between 1996 and 2013 and the majority of fish captured in the commercial fishery are females (Stewart et al. 2013), additional time-area closures in areas where large females are found in high abundance could provide some measure of protection during periods of declining stock abundance.

However, additional research will be required to determine the extent to which the movement scales and habitat associations observed in Glacier Bay, a relatively enclosed fjord estuary, may be applicable to other marine environments that occur throughout the range of halibut distribution. For example, limited movement within fjords has been observed for Atlantic halibut (Seitz et al. 2014) and Atlantic cod (Hedger et al. 2011). Movement scales may also be related to the availability of complex habitat and high relief areas in a given location (Matthews 1990, Beaudreau & Essington 2011). Our results indicate that in Glacier Bay, scales of movement tend to be smaller in shallow (<100 m) areas with heterogeneous topography and complex habitat compared to deep, flat areas with low levels of habitat complexity. Thus, although some locations are likely to be more effective than others at retaining the movements of halibut per unit area, more research on halibut movement scales in different habitat types and geographic regions is needed to determine how much of the sedentary movement patterns observed in this study are due to (1) fjord topography, (2) the presence of complex habitat, or (3) inherent behavior of adult halibut.

Finally, the existence of fine-scale SF for some proportion of reproductive females has implications for depletion of mature female fish at local scales. Although the phenomenon of local depletion for Pacific halibut has not been explicitly documented, some evidence from a variety of sources suggests that it may be of concern. For example, declines in commercial catch per unit effort near the Pribilof Islands occurred in conjunction with concentrated local fishing effort (Hare 2005). Localized declines have also been observed near populated areas, where intense charter and sport fishing effort occurs (Trumble et al. 1991). Our findings of HR behavior combined with SF and the ability to return to previously occupied areas suggest a potential mechanism by which Pacific halibut could be vulnerable to local depletion. However, before the potential for local depletion can be characterized, broad geographic-scale dispersal processes, population connectivity, and spatial structure during other life history phases, such as passive planktonic larval drift and contranatant ontogenetic migrations, must be fully assessed (Skud 1977, Conners & Munro 2008).

Benefits of NSD analysis methods

Our use of NSD analyses to describe and quantify movement patterns and scales is a novel, robust approach that can be applied to irregular datasets commonly collected for fishes. Using the analysis of dispersal patterns, telemetry records for tagged fish can be analyzed in the context of movement ecology and potential for dispersal, rather than focusing on the size or location of an area inhabited by the fish. The mixed-effects model framework allows the description of inherent individual variability, as well as borrowing 'strength' from individuals with more observations. Information on movement characteristics is provided in formats such as diffusion rates or HR scales that can be easily used to simulate movement paths for use in other studies. For example, such simulations could be used to estimate energy budgets during residential versus dispersive movement states. In addition, it provides a way to compare results between acoustic and conventional tagging studies. For example, diffusion coefficients have been calculated for American lobsters using the slope of NSD vs. time from conventional tag recovery data (den Heyer et al. 2009). Thus, this method may provide a way to leverage the detailed information provided by acoustic studies with the larger sample sizes available from conventional tagging studies.

Finally, the NSD analysis framework complements information needs for MPA design, where managers are often faced with the task of compiling information on the movement scales of multiple fish species based on data collected using different methods (Saarman et al. 2013). Because HR scales are reported as a movement radius rather than area, NSD methods can be used to compare scales for fish that move in one dimension (e.g. in a river or along a coastline) with those that move in 2 dimensions. Combining different types of movement data (e.g. large-scale acoustic arrays, archival tags, or conventional tags) would also be possible because the only information required for this method is distance moved from the release location over time. Therefore this analysis approach may be particularly valuable because it provides movement data in formats that can be easily combined or compared with results from other studies.

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