LIMNOLOGY
and
OCEANOGRAPHY

Limnol. Oceanogr. 9999, 2020, 1–19

doi: 10.1002/lno.11553

Eddy retention and seafloor terrain facilitate cross-shelf transport and delivery of fish larvae to suitable nursery habitats

Esther D. Goldstein,[1*,a] **Jodi L. Pirtle**,[2] **Janet T. Duffy-Anderson**,[1] **William T. Stockhausen**,[3] **Mark Zimmermann**,[1] **Matthew T. Wilson**,[1] **Calvin W. Mordy**[4,5]

[1]Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Washington, Washington, USA
[2]Habitat Conservation Division, Alaska Region, National Marine Fisheries Service, NOAA, Juneau, Juneau, Alaska, USA
[3]Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, Washington, USA
[4]Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, Washington, USA
[5]Pacific Marine Environmental Laboratory, NOAA, Seattle, Washington, USA

Abstract

For marine fish with ontogenetic shifts in habitat requirements, survival is dependent upon oceanographic transport of pelagic larvae from spawning locations and the arrival of settlement-stage larvae to nursery habitats. Settlement success for fish with nurseries on the continental shelf, such as many flatfish, relies on routes of transport that facilitate the delivery of larvae from offshore to suitable inshore habitats. To address spatial and temporal coupling between spawning, transport, and settlement, we utilized an individual-based biophysical model for the years 2000–2011 in combination with a juvenile habitat suitability model for arrowtooth flounder (*Atheresthes stomias*), an abundant predatory flatfish in the oceans off Alaska. Settlement success was inversely related to the availability of nursery habitat, but oceanographic variability dictated interannual patterns in larval supply to nurseries. Paradoxically, the majority of larvae were advected offshore and arrived to nurseries on the continental shelf. Shoreward bathymetric steering through glacial troughs that resulted in directed transport to nurseries was minimal despite the high proportion of larvae that accessed trough features. Based on modeling results and empirical observations, mesoscale eddies and retention near suitable settlement habitats enhanced settlement and recruitment magnitude. In advective ecosystems such as the Gulf of Alaska, settlement success and cross-shelf transport are augmented by transient retentive features that influence recruitment by facilitating the delivery of larvae to nursery habitats on the continental shelf.

Survival for marine fish with a planktonic larval stage and a demersal juvenile stage is restricted by the successful transition from pelagic to benthic habitats, which can create a bottleneck to recruitment. High mortality during this early life-stage transition can be the result of intrinsic costs associated with morphological changes such as muscle and fin development and sensory improvements (Doherty et al. 2004; Almany and Webster 2006), as well as extrinsic processes such as oceanography, food availability, and predation that influence transport, growth, condition, and survival (Johnson 2008; Houde 2016). For organisms that have ontogenetic shifts in habitat requirements such as flatfishes (Duffy-Anderson et al. 2014), mortality can be exacerbated by spatial or temporal decoupling between the larval-juvenile transition and the delivery of larvae to juvenile habitats (Wilderbuer et al. 2002). Settlement success and recruitment are influenced by oceanography that affects access to nursery habitats (Cooper et al. 2013), and by the availability of suitable nurseries (Stier and Osenberg 2010; Pirtle et al. 2019) that promote growth and survival (Gibson 1994; Pirtle et al. 2012). Consequently, juvenile recruitment as well as source-sink dynamics are the end points of multiple junctures, including spawning magnitude, larval quality and supply, settlement success, and post-settlement survival (Cowen and Sponaugle 2009; Pineda et al. 2010).

Settlement success is the culmination of the pelagic larval stage that connects spawning locations with suitable nursery

---

*Correspondence: esther.goldstein@noaa.gov

Additional Supporting Information may be found in the online version of this article.

[a]Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, Washington.

habitats. Many fish species, including most flatfishes in the North Pacific and the Gulf of Alaska (GOA), have life-history strategies that involve spawning in deep waters along the continental slope, a pelagic larval duration that can span multiple months, and late-stage larval settlement to nursery habitats on the continental shelf (Bailey et al. 2005; Doyle et al. 2009). For this life-history strategy, larvae in the offshore pelagic environment must cross the slope, traversing along-shelf currents (Ladd et al. 2005; Janout et al. 2009), and transition to inshore habitats. In advective systems such as the GOA (Stabeno et al. 2016), the delivery of larvae to nursery habitats on the continental shelf may be augmented as a result of transient oceanographic features that disrupt the prevailing currents, increase retention, or enhance cross-shelf exchange. Near continental slopes, eddies, internal tidal bores, fronts, and temporary relaxations in along-shelf flows may be mechanisms that both concentrate larvae and enhance shelfward transport (Pineda 1991; Shanks et al. 2000), leading to fluctuations and pulses in settlement and recruitment magnitude (Sponaugle et al. 2005).

Settlement success and recruitment may also be influenced by seafloor terrain features that affect transport trajectories and routes of larval ingress from offshore to inshore habitats. The margins of the continental shelf and slope are often punctuated by broad-scale (> 1 km) bathymetric depressions (Greene et al. 1999; Harris et al. 2014*a*). These features include glacial troughs, valleys, and canyons that disrupt along-shelf flow (Ladd et al. 2005; Allen and Durrieu de Madron 2009), and can be sites of cross-shelf exchange that focus flow (Hickey 1997) and transport nutrients, zooplankton, and potentially fish larvae from offshore to inshore waters (Bailey et al. 2008; Vestfals et al. 2014). Larvae of slope-spawning flatfish are found in high abundance near troughs in the GOA (Bailey and Picquelle 2002; Siddon et al. 2016), and shelfward flow through troughs typically corresponds with the pelagic larval stage of many fish taxa (Mordy et al. 2019), suggesting potential benefits of larval access to these features.

For ecologically important species, variability in recruitment and coupling between the timing and location of spawning, transport, and settlement can have substantial impacts on community structure and potential economic ramifications (Anderson and Piatt 1999). In the GOA and the North Pacific, recent increases in the biomass of an abundant predator (ATF; arrowtooth flounder; *Atheresthes stomias*) (Spies and Turnock 2013) have led to concern regarding predation pressure on the juvenile stages of commercially important species such as walleye pollock (*Gadus chalcogrammus*) (Hollowed 2000). Ecological and economic consequences of population or community restructuring, and the movement toward ecosystem approaches to management (King et al. 2015), highlight the value of understanding the processes that influence recruitment and survival of marine fish. Large year classes of slope-spawning species such as ATF and Pacific halibut (*Hippoglossus stenolepis*) have been linked to climatic events and the El Niño Southern Oscillation (Bailey et al. 1995; Anderson and Piatt 1999; Clark et al. 1999), yet many of the direct mechanisms influencing recruitment of commercially and ecologically important species are primarily unresolved.

We utilize an individual-based biophysical model (IBM) paired with a habitat suitability model (HSM) to develop and test mechanistic hypotheses regarding physical processes that influence dispersal, transport, and the delivery of settlement-stage larvae to nursery habitats. To address these hypotheses, we focused on ATF due to its ecological significance. We hypothesize that refined designations of suitable nursery habitats will reduce and alter interannual settlement success. However, disruptions in along-shelf currents such as eddies and seafloor terrain features that affect patterns of flow may reduce advective loss of larvae and enhance access to the nursery habitats on the continental shelf. Persistent bathymetric depressions such as glacial troughs may be reliable conduits of cross-shelf transport that deliver larvae to nurseries and buffer the impacts of oceanographic variability on settlement success and recruitment. Increased understanding of interactions between transient oceanography, larval transport and ingress, and the delivery of larvae to suitable nursery habitats will contribute to determining population fluctuations of an ecologically important predator as well as a broader understanding of recruitment variability for organisms with pelagic larvae and obligate nursery habitats.

Methods

Study region

The GOA marine ecosystem is bordered by the Alaskan coastline and the North Pacific Current (Fig. 1b, inset) (Zador and Yasumiishi 2016). The continental shelf of the GOA is incised by glacial troughs and valleys (henceforth troughs) that were formed by erosional glacial processes during the Pleistocene ice ages (Carlson et al. 1982) and extend from inshore areas along the coastline to the shelf break and slope (Fig. 1a,b) (Carlson et al. 1982; Harris et al. 2014*b*). The prevailing currents in the GOA flow counter-clockwise and include the Alaska Coastal Current (ACC) that flows over the continental shelf, and the northward flowing Alaska Current (AC) that originates in the eastern GOA and turns westward to form the Alaskan Stream (AS), following the isobaths along the continental slope (Fig. 1b, inset) (Stabeno et al. 2004). The AC, formed from the bifurcation of the North Pacific Current, is an eastern boundary current that is often associated with eddy formation and meanders (Okkonen et al. 2001; Stabeno et al. 2004). The AS is a typically fast-flowing (> 50 cm s^{-1} near Kodiak Island) western boundary current (Stabeno et al. 2004). Circulation on the shelf is dominated by the westward flowing ACC with the majority (~ 95%) of the ACC transport flowing through Shelikof Strait (Fig. 1a,b, inset) (Stabeno et al. 2016).

Study species

Arrowtooth flounder (ATF) is a piscivorous flatfish with a distribution that encompasses Cape Navarin in Russia, the

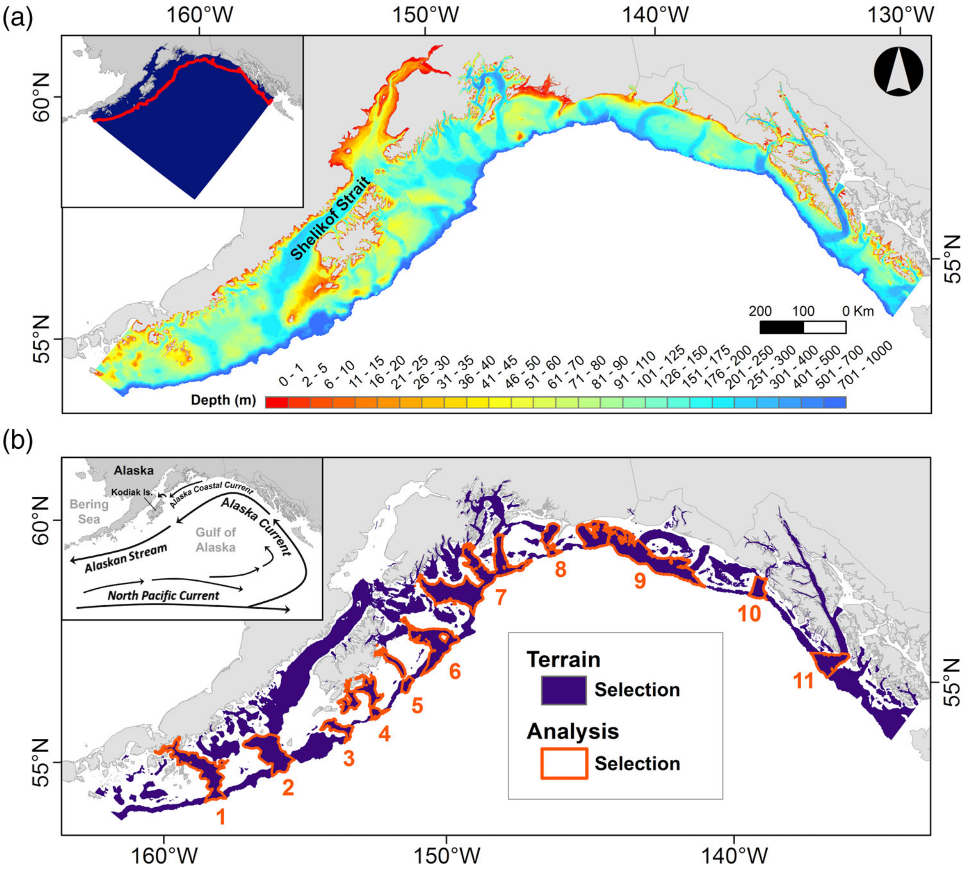

Fig. 1. Maps showing (**a**) bathymetry of the Gulf of Alaska (GOA) study domain from shore to the 1000 m isobath; and (**b**) bathymetric depressions characterized by terrain analysis (purple), to identify glacial troughs and valleys (orange outline). Glacial troughs and valleys are numbered to identify: 1) Shumagin Trough; 2) Shelikof Sea Valley entrance; 3) Sitkinak Trough; 4) Barnabas Trough; 5) Chiniak Trough; 6) Stevenson Trough; 7) complex of the neighboring Amatuli, Knight Island, and Hinchinbrook troughs; 8) Kayak Trough; 9) complex of the bathymetric depressions in the vicinity of the Pamplona zone and the entrances to the neighboring Bering Trough and the Yakutat and Alsek valleys; 10) Yakobi Valley; and 11) Chatham Valley. The inset in (**a**) shows the spatial domain of the Regional Ocean Modeling System (ROMS) model that determined the extent of the habitat suitability model and the individual-based biophysical model (IBM; blue polygon) along with IBM spawning locations from 300 to 600 m depths (red line). The inset in (**b**) shows the prevailing oceanographic currents in the GOA adapted from Stabeno et al. (2004).

eastern Bering Sea, the GOA, and the temperate Pacific Ocean (Blood et al. 2007). In the GOA, ATF are primarily found on the continental shelf as immature fish and then migrate (starting at ~ 4 years) to deeper waters along the continental slope to spawn (~ 7 years for females) (Stark 2008; Wilderbuer et al. 2008). ATF are group-synchronous batch spawners, and spawning primarily occurs along the slope during the winter months (Zimmermann 1997). After a pelagic larval duration of up to ~ 180 d, late-stage larvae settle to obligate juvenile nursery habitats on the shelf in the late summer and early fall (Bouwens et al. 1999*b*; Stockhausen et al. 2019), where they reside as early post-settlement stage juveniles (Norcross et al. 1999; Pirtle et al. 2019).

Individual-based biophysical model

To address the influence of oceanography on pelagic larval dispersal and settlement success, a three-dimensional IBM coupled with daily averaged output from the Regional Ocean Modeling System (ROMS) was developed using the Dispersal Model for Early Life Stages (DisMELS) framework (Stockhausen et al. 2019) for the years 2000–2011. The ROMS hydrodynamic model is a terrain-following, primitive equation, three-dimensional ocean circulation model that is driven by atmospheric forcing (Shchepetkin and McWilliams 2005; Haidvogel et al. 2008). This study utilized a series of nested ROMS models (North Pacific [Npac]: 20–40 km resolution, North Eastern Pacific [NEP]: 10 km resolution, and Central GOA [CGOA]: 3 km resolution), where coarser resolution models set boundary conditions for finer resolution nested grids (Hermann et al. 2009; Hinckley et al. 2009; Coyle et al. 2012). Output from the nested models was saved in daily increments to provide ocean circulation information and physical properties for the IBM throughout the model domain (Fig. 1a, inset). This model output was paired with Lagrangian particle tracking using DisMELS and followed the same life-history parameterization described in Stockhausen et al. (2019). Daily ROMS output was interpolated spatially using bilinear interpolation to obtain environmental variables associated with individual modeled larvae. Movement (latitude, longitude, and depth) and biological processes (age, size, and developmental stage) of each virtual larva were based on 20-min time steps, and the locations of larvae were updated using a fourth-order predictor–corrector algorithm that incorporates swimming, buoyancy, and horizontal or vertical random walks for diffusive motion. Larval information (location, depth, age, size, and developmental stage) and interpolated temperature and salinity were saved at daily time steps.

To simulate spawning, eggs were released along the continental slope between 300 and 600 m deep using a 1 km × 1 km grid (Fig. 1a, inset) during three 15-d intervals, for a total of three cohorts per year starting on the first of January. The number of individuals released for each cohort was weighted to reflect measured temporal patterns in larval abundance with 600 individuals km^{-2} released for the first two cohorts and 480 individuals km^{-2} for the final cohort during each year (Stockhausen et al. 2019). Thus, we tracked a total of 49,359 particles in each year, representing 27,641,040 simulated larvae. Simulated ATF developed through a series of life-history stages (Table 1). Upon transitioning to settlement-stage larvae, individuals were allotted an 8-d settlement competency window to encounter suitable habitat and "settle" as juveniles. A mortality rate was not included in the model. The only sources of mortality were exiting the model domain (Fig. 1a, inset) and individuals that did not encounter suitable settlement habitat during their competency window.

Habitat suitability models

The delivery of simulated larvae to nursery habitats was determined by developing a static predictive map of suitable habitat for ATF early post-settlement stage juveniles using maximum-entropy models (MaxEnt) (Phillips et al. 2006). MaxEnt is a method for modeling probability of species occurrence with presence-only data (Phillips et al. 2006) and is appropriate for small sample sizes (Elith et al. 2006; Guisan et al. 2007). Habitat covariates were based on the seafloor terrain and ecology of juvenile ATF (see Supplemental Table 1 for details). Covariates included: (1) depth (Fig. 1a), (2) slope, (3) aspect "eastness," (4) aspect "northness," (5) bathymetric position index (BPI: describes the elevation of a location relative to neighboring locations) (Wilson et al. 2007; Pirtle et al. 2019), (6) sand substrate (Supplemental Fig. 1), (7) sea whips, (8) tidal current speed, and (9) bottom temperature. Habitat predictor variables were produced as 100 m^2 resolution rasters from shore to the 1000 m isobath (Fig. 1a) and were applied to the HSM, following examination for autocorrelation (threshold of < 0.5 correlation).

ATF typically settle to the benthos at ~ 40 mm SL (Stockhausen et al. 2019) and reach ~ 80 mm SL at ~ 300 d post-hatch (Bouwens et al. 1999*a*). Therefore, we confined the HSM to individuals < 80 mm in length (minimum available size was 40 mm) to target individuals soon after settlement. As observations of ATF early post-settlement juveniles were limited, we combined presence-only catch locations from fishery-independent bottom-trawl data from May through September 1989–2013. Catch locations were available from offshore areas of the continental shelf from a groundfish survey (3.2–12.7 cm mesh size gear; n_{ATF} = 48) (von Szalay and Raring 2016), and inshore locations from small-mesh gear surveys (3.2 cm) on the central and western shelf (n_{ATF} = 56) (Jackson and Ruccio 2003) and the central shelf (n_{AT} = 20) (Wilson et al. 2016). All ATF observations were combined for the HSM (n_{ATF} = 124) and partitioned by randomly selecting 70% as training data and 30%

Table 1. Arrowtooth flounder (ATF) parameterization for the individual-based biophysical model (IBM).

Life stage	Age in stage (days)	Growth rate (mm d^{-1})	Transition (SL, mm)	Preferred depth (m)	Swimming speed (body lengths s^{-1})	Diffusivity $\text{m}^2\ \text{s}^{-1}$ (vertical, horizontal)
Egg (19 substages)	~8.3–25	Temperature-dependent	4.4	300–600	Buoyancy-controlled	0.0001, 0.001
Small yolk sac	~41	0.008	6.1	300–600	0.1	0.0001, 0.001
Large yolk sac	~17	0.008	7	150–300	0.1	0.0001, 0.001
Small feeding preflexion	~36	0.01	10	40–80	0.1	0.0001, 0.001
Large feeding preflexion	~29	0.01	13.4	10–30	0.1	0.0001, 0.001
Postflexion	~57	0.01	42	10–30	0.1	0.0001, 0.01
Settlement	8 (max)	—	—	10–30	0.1	0.0001, 0.01

Life stage refers to the developmental stage of simulated larvae in the model. Age in stage is the approximate number of days that a larva remained within each stage based on the growth rate and transition size assigned to each stage in the model. Growth rate is the growth rate of the larvae at each stage. Values were constant for all stages except for the egg stages which included 19 substages with temperature-dependent development. Transition refers to the standard length (SL) at which a larva completed the life stage and transitioned to the next subsequent stage in the model. Preferred depth is the empirically informed or literature-inferred depth range of each life-stage, and was maintained by either buoyancy (eggs) or swimming speed. Diffusivity refers to vertical and horizontal random walk movement at the sub-grid scale. The settlement stage, just prior to transitioning to juveniles, maintained the parameterization of the postflexion stage, but was given an 8-d competency window to encounter suitable habitat. See Stockhausen et al. (2019) for additional details.

to test the resulting models. We implemented the HSM in R (R Core Team 2017) with the MaxEnt software (3.3.3) and the dismo and raster packages (Hijmans et al. 2014*a*,*b*). ATF presence locations were applied to the models over $n = 1000$ iterations with $n = 100{,}000$ randomly selected locations from the covariates. Models were developed and evaluated to determine optimal settings for the regularization multiplier (β) that controls model complexity in steps of 0.5 between values 0.5–5 with automatic feature selection (Warren and Seifert 2011; Merow et al. 2013). The value of β for the final model was determined based on Akaike Information Criterion for small sample sizes (AICc). Final models were produced using k-fold cross validation ($k = 10$) and model fit was evaluated using the area under the receiver operating characteristic curve (ROC, AUC). Jackknife analysis was applied to determine covariates with the greatest contribution to the final models. We produced two sets of models because the extent of the sand substrate data was less than the other variables (Fig. 1a; Supplemental Fig. 1) (Pirtle et al. 2019). We developed a final HSM map of the averaged mosaic of the mean predicted probability of suitable habitat for overlapping areas produced to the bathymetry data extent.

Combining the IBM and HSM

To determine settlement success, we coupled the HSM map with the daily IBM output using simulated larval spatial locations (latitude and longitude). For each larva, the habitat with the highest suitability that was encountered during the 8-d settlement competency window was designated as the settlement habitat, and the trajectory was terminated. We assumed habitat specificity based on evidence of selectivity for preferred settlement habitat for other flatfish species (Wennhage and Pihl 1994; Laurel et al. 2015). For subsequent analyses, rather than assuming that habitat suitability probability was proportional to mortality, the continuous metric was designated as suitable or not-suitable, using a threshold rule of equal training sensitivity and specificity (Pirtle et al. 2019). The threshold value is the break point in the probability distribution where the proportion of presences correctly predicted is equal to the proportion of absences correctly predicted.

Glacial trough designations

To investigate the importance of troughs as routes of cross-shelf transport, we applied seafloor terrain analysis to characterize broad-scale (> 12 km) and elongated (length > width) bathymetric depressions relative to location and feature morphology (Carlson et al. 1982; Harris et al. 2014*b*). We derived BPI from bathymetry at two spatial scales that were roughly equivalent to 13 km (BPI129) and 26 km (BPI257). We applied a conditional statement to the bathymetry (meters) and BPI rasters to create a selection of terrain features from shore to the 1000 m isobath, the seaward extent of the HSM (Eq. 1).

$$\begin{aligned}\text{Selection} = {} & ((\text{Depth} \geq 100)\ \text{AND}\ (\text{BPI257} \leq 0))\ \text{OR}\ (\text{Depth} \geq 180) \\ & \text{OR}\ ((\text{Depth} \geq 100)\ \text{AND}\ (\text{BPI129} \leq 0))\end{aligned} \tag{1}$$

We refined this selection to include troughs and associated bathymetric depressions that are connected to the continental shelf break and slope in order to capture troughs that may be important for cross-shelf transport (Fig. 1b; Carlson et al. 1982; Harris et al. 2014*b*).

We applied a secondary trough selection method using thalweg locations derived from bathymetry using ArcMap (v.10.2.2) to test the sensitivity of simulated larval presence in troughs to feature size and location (*see* Supplemental Fig. 2a for details of the method). The two methods showed agreement regarding the location of most troughs (Supplemental Fig. 2a). Trough size and the number of larvae accessing troughs was reduced using the thalweg method, but interannual patterns of larval presence in troughs were similar (Supplemental Fig. 2b). This agreement between methods indicates that conclusions associated with larval access to troughs are likely robust to minor differences in spatial designations of the features. The conditional terrain analysis designations were utilized for subsequent analyses based on spatial agreement with bathymetry and the incision of troughs from the 1000 m isobath to the continental shelf, which connects the shelf and the basin (Fig. 1; Supplemental Fig. 2a).

Glacial troughs and larval transport

To identify larval access to troughs and ingress to nursery habitats, IBM trajectories were selected such that the simulated individuals met the following criteria: (1) were offshore of the continental shelf (defined by the 1000 m isobath; Fig. 1a) during at least one time step in their trajectory and (2) traversed through a trough (defined by simulated larval latitude, longitude, and a depth > 150 m). Individuals had the potential to traverse multiple troughs and to be advected off of the shelf following occurrence in a trough. Therefore, to quantify the contribution of cross-shelf transport via troughs to settlement success, and directed transport to nurseries, we also identified the successful individuals that were retained on the shelf following their last trough observation time point. The influence of trough or canyon flow on the overlying water column is limited by water column stratification and weaker at the surface (Hickey 1997; Allen and Durrieu de Madron 2009). A 150 m designation, based on the depth of the continental shelf (Fig. 1a) and the ∼ 200 m depth of the shelf break (Okkonen et al. 2001), provided a conservative minimum depth to ensure that larvae were passing through a trough rather than the water column above these features. Thus, only ATF with preferred depth ranges deeper than 150 m could be present in troughs (Table 1).

Table 2. Simulated larval trajectory categorizations based on the arrowtooth flounder (ATF) individual-based biophysical model (IBM) coupled with the habitat suitability model (HSM).

Category	Description
Larval supply	1. Arrived as settlement-stage larvae to a habitat with a suitability >0
Successful settlers	1. Arrived as settlement-stage larvae to a habitat with a suitability ≥0.36
Off-shelf supply	1. Advected off the continental shelf during at least one time point in the trajectory 2. Arrived as settlement-stage larvae to a habitat with a suitability >0
Off-shelf success	1. Advected off the continental shelf during at least one time point in the trajectory 2. Arrived as settlement-stage larvae to a habitat with a suitability ≥0.36
Off-shelf trough success	1. Advected off of the continental shelf during at least one time point in the trajectory 2. Present in a trough during at least one time point in the trajectory 3. Arrived as settlement-stage larvae to a habitat with a suitability ≥0.36
Off-shelf trough success and retention	1. Advected off of the continental shelf during at least one time point in the trajectory 2. Present in a trough during at least one time point in the trajectory 3. Subsequently remained on the continental shelf 4. Arrived as settlement-stage larvae to a habitat with a suitability ≥0.36
On-shelf supply	1. Remained on the continental shelf 2. Arrived as settlement-stage larvae to a habitat with a suitability >0
On-shelf success	1. Remained on the continental shelf 2. Arrived as settlement-stage larvae to a habitat with a suitability ≥0.36
On-shelf trough success	1. Remained on the continental shelf 2. Present in a trough during at least one time point in the trajectory 3. Arrived as settlement-stage larvae to a habitat with a suitability ≥0.36

Habitat suitability was defined based on a binary threshold value of 0.36 applied to the HSM logistic continuous probability prediction (0–1). Glacial troughs, valleys, and associated bathymetric depressions along the Gulf of Alaska continental margin (troughs) were characterized from shore to the 1000 m isobath. Offshore environments were designated as basin areas beyond the 1000 m isobath. Transport through a trough was determined based on latitude, longitude, and a depth > 150 m.

Table 3. Maximum entropy (MaxEnt) habitat suitability model (HSM) results for arrowtooth flounder settlement-stage and early post-settlement stage juveniles in the Gulf of Alaska.

	HSM	HSM with substrate
Training (*n*)	112	74
Test (*n*)	12	8
RM	3.5	3.5
AUC test mean±SD	0.75±0.07	0.81±0.07
H1 (%)	Depth (37.4)	Depth (42.5)
H2 (%)	BPI 6.5 km (25.0)	BPI 6.5 km (31.6)
H3 (%)	Tidal current speed (13.8)	Tidal current speed (9.2)
H4 (%)	Bottom temperature (8.6)	Sand (5.2)
H5 (%)	Sea whips (7.0)	Slope (3.9)
H6 (%)	Aspect northness (3.5)	Sea whips (3.5)
H7 (%)	Slope (3.2)	Bottom temperature (2.0)
H8 (%)	Aspect eastness (1.5)	Aspect eastness (1.9)
H9 (%)	*N/A*	Aspect northness (0.1)

Results are shown for models using all habitat predictor variables and the bathymetry data extent (HSM) and models using all habitat variables and sand substrate (HSM with substrate), including sample size of presence locations for the training and test partitions (*n*), value of the regularization multiplier (RM), AUC (area under the curve) value for test locations, mean ± SD of *k*-fold replicates (*k* = 10), and percent individual contribution of each habitat predictor variable (e.g., H1 (%)) in decreasing order of contribution, as determined by jackknife analysis. BPI is the Bathymetric Position Index.

Recruitment

Mechanistic hypotheses regarding the influence of retention and eddies on settlement success were developed from the IBM and tested using two separate data sources. Age-1 recruitment data were obtained from the 2016 ATF stock assessment for the GOA (Spies et al. 2016) and Eddy Kinetic Energy (EKE; $cm^2\ s^{-2}$) was calculated from satellite-derived altimetry. EKE provides a metric of mesoscale variability (Ladd 2007) to identify features such as eddies or current meanders. Gridded merged satellite data (TOPEX/Poseidon, ERS-1/2, Jason, and Envisat) for EKE calculations had a 1/3° spatial resolution with a map every 7 d and EKE was calculated following (Ladd 2007). Average EKE was also calculated from the ROMS model for comparison. EKE was calculated from the start (spawning) to the end (settlement) dates of the IBM years (01 January to 23 October ± 3 d), and from 01 January to 22 October for additional years. The spatial extent of EKE calculations ranged from −160° to −135° longitude, from the 1000 m isobath to 200 km offshore of the 1000 m isobath. This spatial extent was selected to exclude on-shelf regions that are poorly resolved by satellite data (Dohan and Maximenko 2010) and to focus on EKE associated with cross-shelf transport.

Data analysis

To assess transport routes to suitable nursery habitats, IBM trajectory analyses only included individuals that arrived to settlement habitats within the HSM domain, and IBM results were subdivided into trajectory categories (Table 2). Maps of settlement locations (endpoint of individual larval trajectories), larval density maps, and connectivity matrices were constructed to identify dispersal and settlement variability among regions, years, and trajectory categories. Larval density calculations included all time points throughout each model year and were quantified as the sum of the number of larvae (individuals counted only once in each cell) that traversed 3 km × 3 km ROMS CGOA grid cells (densities as count per 9 km^2) for each trajectory category. Larval densities were then averaged across 0.08° latitude and longitude to avoid obscuring data points.

Connectivity matrices were constructed by dividing the GOA longitudinally (from −132° to −163°) into 50 equal-sized subregions. The values that populate the matrices were calculated as:

$$\%\text{ of settlers} = \frac{\text{spawned}_i\ \&\ \text{settled}_j}{\sum \text{settled}_j} \times 100 \tag{2}$$

where the numerator corresponds to the number of larvae that were spawned from location i and settled in location j out of the total number of larvae that settled in location j (Eq. 2). This metric does not account for differences in the number of larvae released from each spawn location, thus providing general patterns of connectivity, but limiting the ability to compare larval contributions between spawning locations. Connectivity matrices were constructed for years with above average and below average larval supply and settlement by averaging values across years.

The importance of each trough to larval ingress was addressed by quantifying counts of simulated individuals within troughs and the average number of days that individuals were retained within each trough (numbered 1–11; Fig. 1b). Analyses for heat maps included only the final trough in which an individual was observed prior to retention on the continental shelf (based on *off-shelf trough success and retention*; Table 2). The assumption of shoreward transport through troughs was visually assessed by plotting the locations of simulated larvae up to 40 d after the final time point within a trough, and by calculating directionality of transport using the first time point at which a larva entered a trough and the last time point before the larva exited

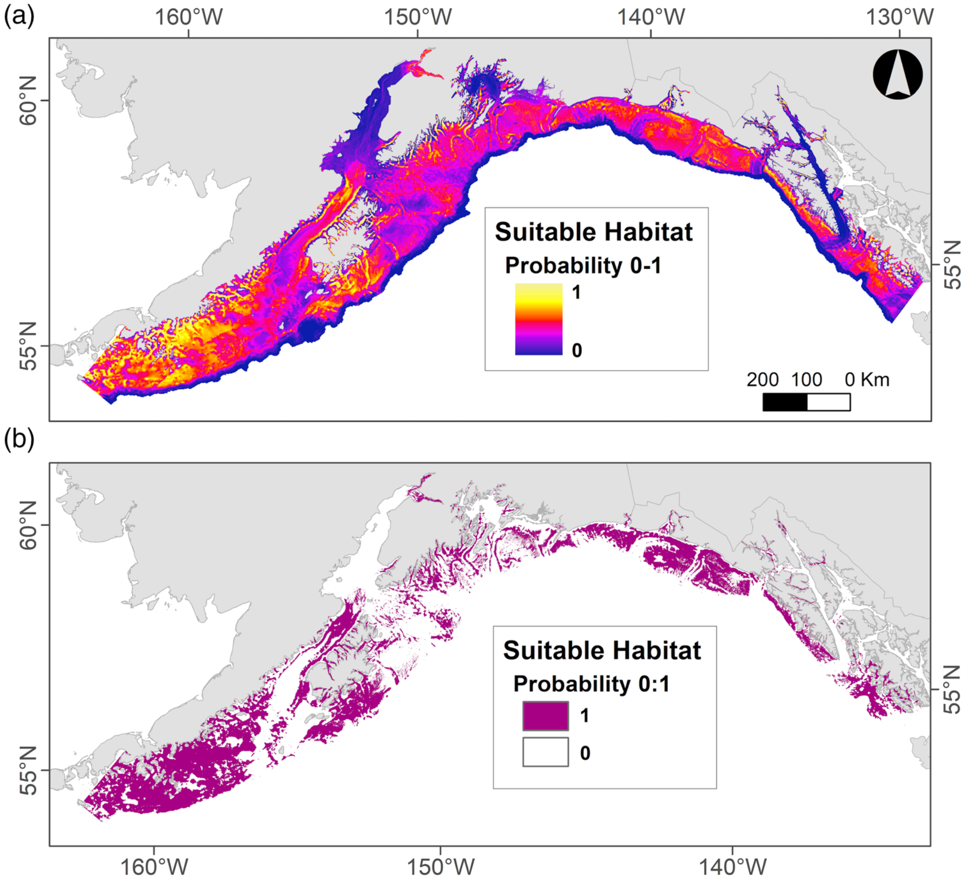

Fig. 2. Maps of the maximum entropy (MaxEnt) habitat suitability model (HSM) results for the study domain, depicted with continuous suitable habitat probabilities from the logistic output (0–1) (**a**), and binary suitable habitat probabilities (0:1) (**b**), where 1 is suitable and 0 is not suitable. Suitable settlement habitat (**b**) was calculated from the total HSM area (**a**) by applying a threshold value (0.36) to the HSM continuous logistic output.

the feature. Directionality of transport did not capture meandering or changes in direction between the two time points.

Hypotheses regarding the mechanistic relationship between eddies and recruitment were assessed based on the relationship between satellite-derived EKE and age-1 recruits as well as ROMS-derived EKE and *successful settlers* (Table 2) using ordinary least squares (OLS) and quantile regression. The influence of eddy location was incorporated into the analysis by calculating mean ROMS-derived and satellite-derived EKE in the eastern and western GOA (breakpoint at −146° longitude), during a time span that corresponded to the pelagic larval stage of ATF. This spatial scale was selected based on evidence of regional discontinuity between the eastern and western GOA (Goldstein et al. 2019), and the lack of agreement between the specific location of eddies in the ROMS model compared to empirical data (Coyle et al. 2012). For satellite-derived EKE and stock assessment-based recruitment, regression analyses used lagged age-1 recruitment for the GOA from 1994 to 2015 (Spies et al. 2016). IBM-based settlement focused on younger fish, therefore, years were not lagged in relation to ROMS-derived EKE. Separate models were fit for the relationship between ATF abundance across the entirety of the GOA with mean EKE in the eastern GOA and the western GOA. For the purposes of visualization, the regional annual EKE was calculated as deviations from the respective regional EKE means across all study years. In addition to OLS, relationships between regional EKE and ATF across the entire GOA were examined using quantile regression in R (R Core Team) with the quantreg package (Koenker et al. 2018) focusing on the lower (25th) and upper (75th) quantiles of settlement or recruitment. This method is ideal when the relationships between predictor variables and observations may not be consistent for all quantiles or when all explanatory variables, or limiting factors, were not measured (Cade and Noon 2003). For this study, the upper quantile provides insight into whether the upper bounds (threshold) of settlement or recruitment are correlated with regional EKE. The lower quantile describes whether regional EKE has a different relationship with ATF survival during years of low settlement or recruitment, or if unmeasured factors influence the relationship. The significance of quantile relationships are presented as bootstrapped *p* values and the fit was determined using the coefficient of determination, $R^1(\tau)$ (Koenker and Machado 1999; Cade et al. 2005).

Results

Habitat suitability and settlement success

The best-fit models ($\beta = 3.5$) had an average test AUC of 0.78 with low variability among replicates ($SD = 0.07$; Table 3). The top covariates in both sets of models were depth, BPI at a 6.5 km spatial scale, and tidal current speed. Habitat for settlement-stage and early post-settlement stage juvenile ATF in the GOA is likely to occur within a depth range from shore to roughly 215 m in low gradient and low-lying areas such as channels within bays that extend to deeper depths on

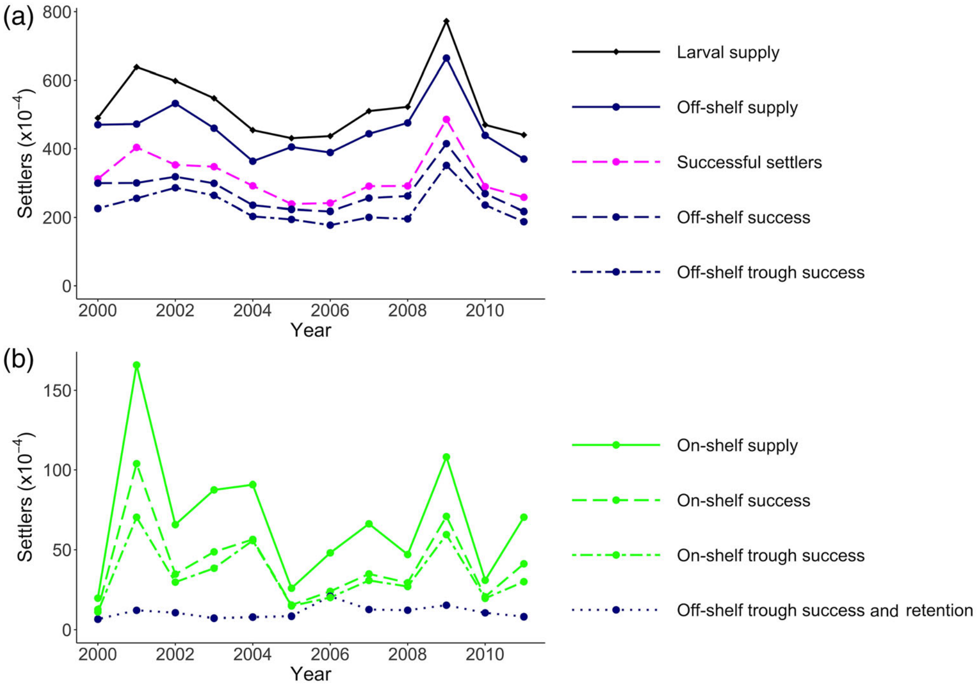

Fig. 3. Model output from the combined analysis of the individual-based biophysical model (IBM) and the habitat suitability model (HSM). The values correspond to the number of simulated larvae that settled (settlers) to habitats on the continental shelf in each model analysis category in each study year (*see* Table 2). Results were separated into (**a**) higher values and (**b**) lower values to allow for different y-axis scales.

the continental shelf. These habitats are also likely to be in areas of lower tidal current speeds with sand substrate present (Table 3; Fig. 2a).

For subsequent analyses, a logistic threshold of 0.36 defined binary suitability indices as nonsuitable (0: < 0.36) and suitable (1: ≥ 0.36) habitats (Fig. 2b). Suitable habitats encompassed a total area of 1.15×10^5 km^2 in contrast to a total area of 3.17×10^5 km^2 for the HSM domain. This binary designation excluded much of the continental shelf near the central GOA, where covariates (ex: reduced sand) were unfavorable for juvenile ATF (Table 3; Supplemental Fig. 1). The majority of the habitat with the highest likelihood of suitability is located in the western GOA (Fig. 2).

The combination of the IBM trajectories and the HSM revealed substantial variability in supply and settlement of larvae throughout the 12-yr study period and among trajectory categories. Enhanced nursery habitat restrictions (*successful settlers*) suppressed settlement when compared to potential *larval supply*. *Larval supply* and *successful settlers* showed generally concomitant fluctuations among years and the same patterns of above (high: 2001–2003, 2009) and below (low) average settlement (Fig. 3a). The majority of simulated larvae were off of the continental shelf at some point in their trajectories (*off-shelf supply*; Fig. 3a). *Successful settlers*, *off-shelf success*, and *off-shelf trough success* showed similar interannual variability in settlement that differed from on-shelf categories. Interannual patterns in *off-shelf trough success and retention* were decoupled from both on- and off-shelf categories with a peak in 2006 followed by 2009 (Fig. 3).

A large portion of settlers that arrived to suitable nursery habitats were observed within troughs regardless of on- or off-shelf transport routes (*on-shelf trough success* and *off-shelf trough success*; Fig. 3). In contrast, when retention on the continental shelf following trough transport was considered, the number of individuals was greatly reduced (*off-shelf trough success and retention*; Fig. 3b). For successful larvae that were advected off of the continental shelf, the number of individuals that were present within troughs was comparatively consistent among years (coefficient of variation: *off-shelf success* = 20.39; *off-shelf trough success* = 21.93), but variability in shelf retention following trough transport was high (coefficient of variation: *off-shelf*

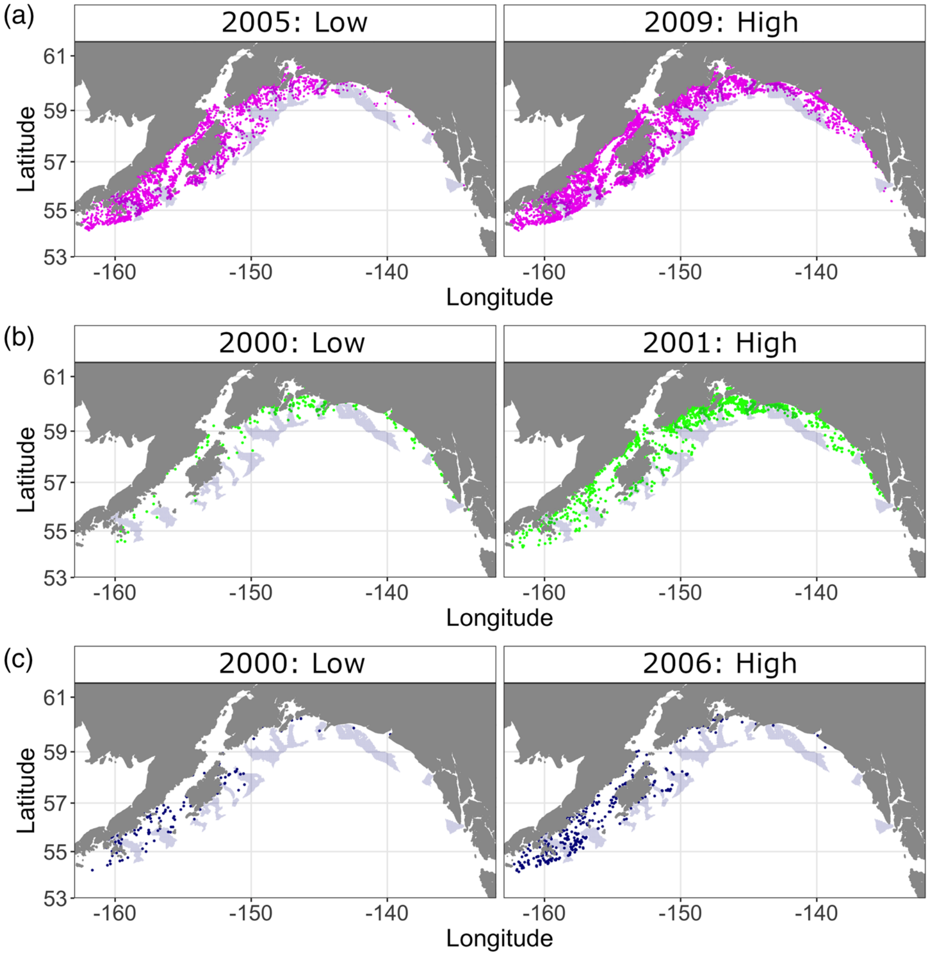

Fig. 4. Simulated larval settlement endpoints during the lowest (low) and highest (high) settlement years for (**a**) *successful settlers*, (**b**) *on-shelf success*, and (**c**) *off-shelf trough success and retention* (*see* Table 2 for details of trajectory categories). Troughs are blue semi-transparent overlays.

trough success and retention = 36.92). *On-shelf success* had the greatest variability among years (coefficient of variation: 63.89).

Settlement success, transport, and retention

Settlement locations spanned the majority of the continental shelf, with differences in extent among trajectory categories. Three major patterns emerged: (1) *successful settlers* typically settled across the entire GOA but were often concentrated in the western GOA, (2) *on-shelf success* settlement locations were primarily nearshore, and (3) settlement locations for *on-shelf trough success and retention* were concentrated in the western GOA (Fig. 4). Settlement habitats were predominantly located westward of spawning locations (Fig. 5; Supplemental Figs. 3, 4). Spawning locations ~ 42–47, in the eastern GOA, supplied larvae to settlement areas throughout the GOA (Fig. 5). As a result of the constraints of the ROMS model domain (Fig. 1a, inset), some locations in the eastern GOA showed high proportional self-recruitment because there were no upstream spawning locations. Despite these constraints, there was evidence of settlement eastward of spawning locations in the eastern GOA (~ 41–47) and the central/western GOA (~ 17–28; Fig. 5).

Patterns of connectivity were similar among trajectory categories and numeric reductions corresponded with restrictions in suitable nursery habitats and transport trajectories. There were some notable distinctions among categories, and between years of high and low settlement (Fig. 5). For *off-shelf trough success and retention*, fewer individuals spawned or

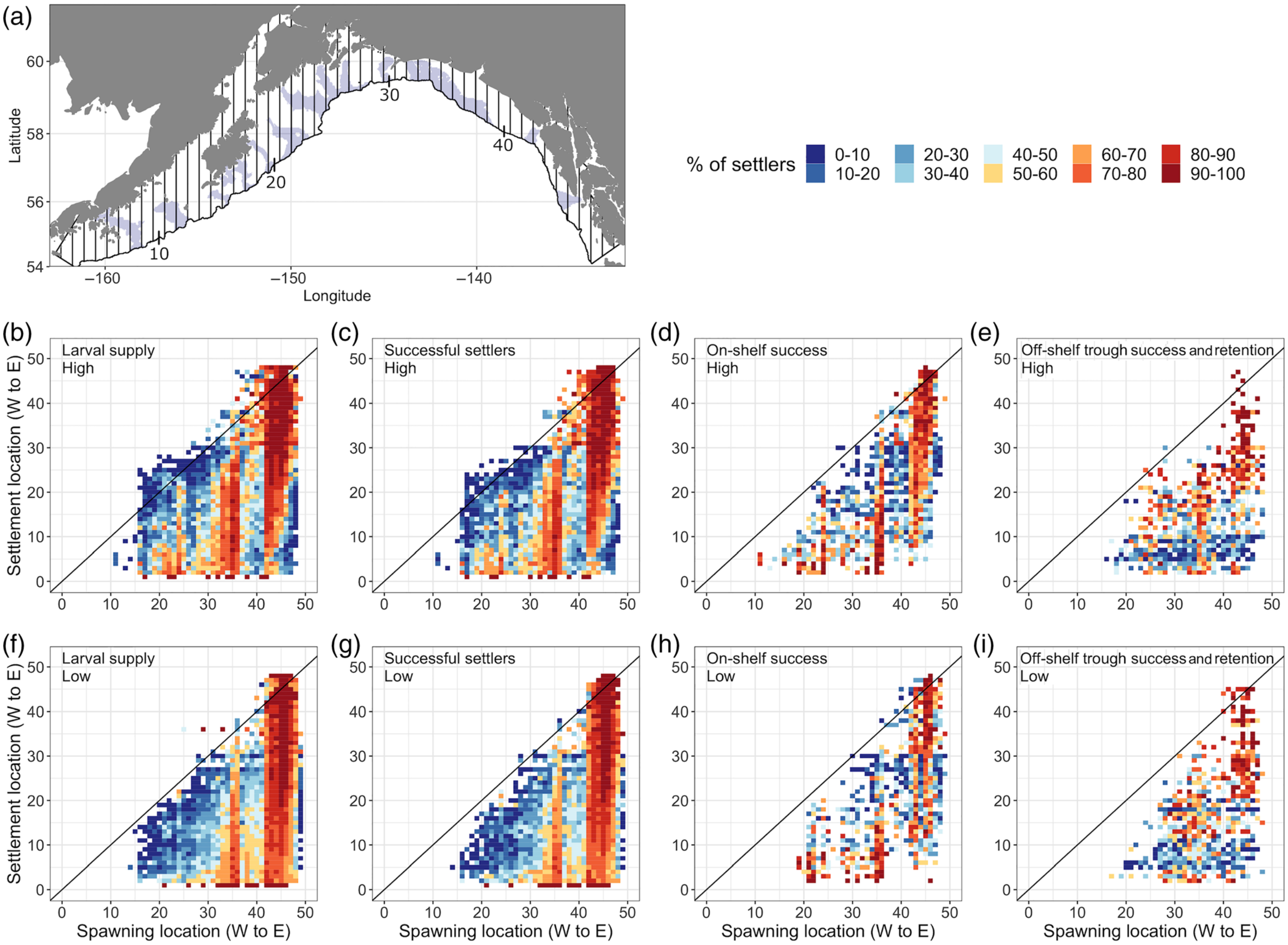

Fig. 5. Simulated larval connections between spawning and settlement locations. The map (**a**) shows the 50 divisions (1–50 from west to east) as well as trough designations (blue). Heatmap connectivity matrices are shown for four trajectory categories (*see* Table 2 for descriptions): *larval supply* (**b**, **f**), *successful settlers* (**c g**), *on-shelf success* (**d**, **h**), and *off-shelf trough success and retention* (**e**, **i**). The color scale shows the percent of individuals that were spawned and settled to each numbered location out of the total number of individuals sourced from all spawning areas that arrived to each settlement location. Grid cells below the diagonal line correspond to westward movement from spawning to settlement locations, and those above show eastward movement. Each analysis category is separated into years with above average (high) and below average (low) settlement. Percentages depicted in the heatmaps (color scale) are calculated as means among high (*larval supply* and *successful settlers*: 2001–2003, 2009; *on-shelf success*: 2001, 2003, 2004, 2009, 2011; *off-shelf trough success and retention*: 2001, 2006–2009) or low years.

settled in the eastern GOA (~ 40–50), and the contribution of eastern spawning locations (~ 42–47) to settlement in the west (~ 5–23) was reduced compared to the other transport categories (Fig. 5). For successful individuals that remained on the shelf, spawning locations extended farther west in high settlement years compared to low (~ 11–19; Fig. 5d,h). Retention, self-recruitment, and eastward movement were enhanced during high settlement years for *larval supply* and *successful settlers* (Fig. 5b,c,f,g). The retentive regions encompassed spawning and settlement locations in the central GOA to just eastward of Kodiak Island (~ 17–27; Fig. 5a,b,c,f,g). *Off-shelf trough success and retention* also showed higher self-recruitment in the western and central GOA (~ 20–30) during high settlement years, and some evidence of retention farther east during low settlement years (~ 30–40; Fig. 5e,i).

Regions of high larval densities and accumulation differed among years with high and low settlement (Fig. 6; Supplemental Figs. 5–7). During years of high settlement, *successful settlers* were concentrated on the continental shelf in the eastern GOA or offshore of the central GOA (Fig. 6a; Supplemental Fig. 5). These offshore larvae were often concentrated in a circular pattern in either the central (~ −142° to −147° Longitude) or western (~ −148° to −155° Longitude) GOA (ex: 2001 and 2002; Fig. 6a; Supplemental Fig. 5), highlighting eddy entrainment. In 2009, the year of peak settlement success, simulated larvae were again concentrated in the eastern GOA on the continental shelf, but there were additional hotspots along the continental slope and in the central GOA (Fig. 6a; Supplemental Fig. 5). On the shelf, simulated larvae were concentrated near and within troughs and banks (Fig. 6a; Supplemental Fig. 5). Areas of high larval densities for *on-shelf success* were primarily in the eastern and central GOA, but extended farther west during years of above average settlement success (2001, 2003, 2004, 2009, and 2011; Fig. 6b; Supplemental Fig. 6). Transport through troughs was contingent upon offshore advection in our analysis, and therefore IBM trajectories through troughs did not show the same degree of larval accumulation on the continental shelf as other categories (Fig. 6; Supplemental Figs. 5–7). Regions of accumulation associated with trough transport during high settlement years were generally on the shelf in the western GOA near trough features 3–6 (Fig. 1b), or offshore near the central or western GOA (2001, 2008, and 2009; Fig. 6c; Supplemental Fig. 7).

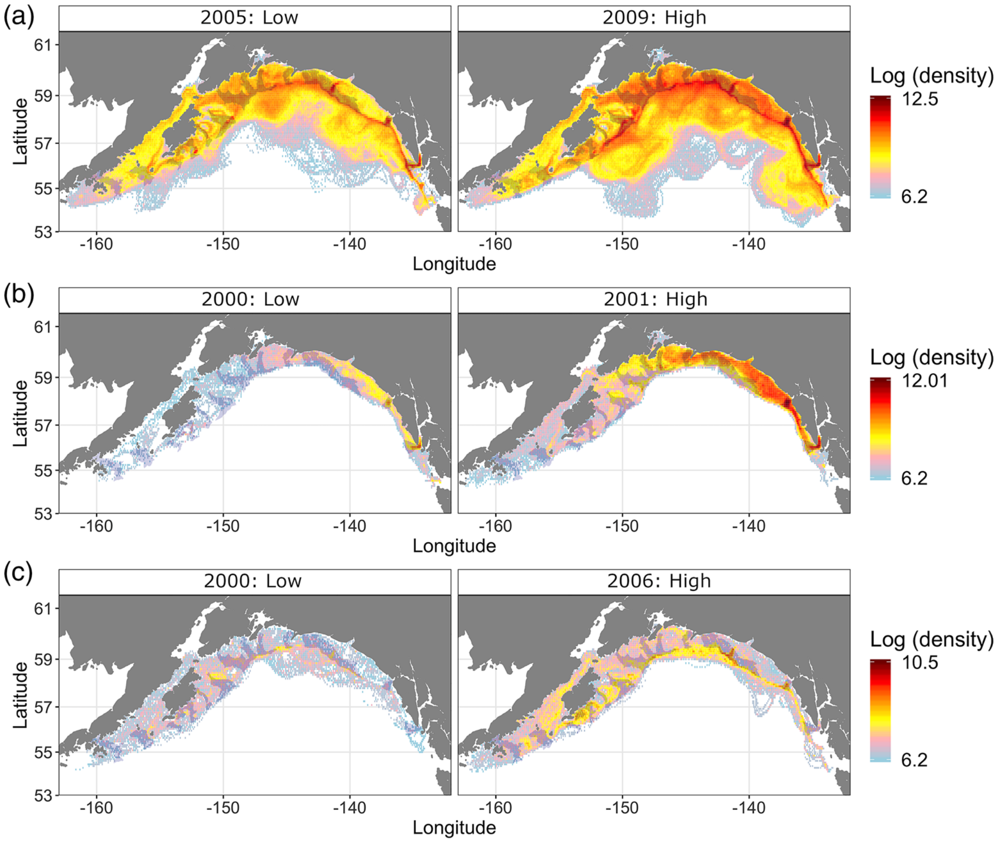

Fig. 6. Maps of simulated larval densities from the individual-based biophysical model (IBM) showing the lowest (low) and highest (high) settlement years for (**a**) *successful settlers*, (**b**) *on-shelf success*, and (**c**) *off-shelf trough success and retention* (*see* Table 2 for trajectory category details). Larval densities (color scale) are the number of unique individuals in 3 km × 3 km grid cells (resolution of the Regional Ocean Modeling System grid), averaged over 0.08° latitude and longitude, throughout the course of the simulation in each study year. Troughs are blue semi-transparent overlays. Note that the color scale differs among subplots.

Directionality of transport through troughs was variable, but modeled larvae generally traveled shelfward following the seafloor terrain (Supplemental Figs. 8–10), and few larvae were advected along the continental slope after accessing trough features (Supplemental Fig. 11). Years of high *off-shelf trough success and retention* (2001, 2006–2009) showed enhanced average trough transport in the western GOA (Fig. 7a). A large number of individuals traversed trough 6 during 2001 and 2008, trough complex 7 during 2006, and troughs 2–6 in 2009 (Fig. 7a). During 2007, the number of individuals within each trough was not notable; however, average residence time in trough 6 was high (Fig. 7b). Larval counts in troughs were influenced by the area of the feature, but larger feature size did not necessarily correspond to longer residence times (Figs. 1b, 7).

Retention and recruitment

Yearly IBM-based settlement success (age-0) was not significantly correlated with lagged stock assessment-based recruitment (age-1; OLS $p > 0.05$). Visual inspection of satellite-derived and ROMS-derived EKE showed differing interannual patterns, and limited similarities in spatial patterns (Supplemental Fig. 12). Despite a lack of temporal agreement between IBM model results and recruitment from the stock assessment model, hypothesized mechanisms of eddy retention and settlement success were corroborated by the relationship between EKE and recruitment. Regional satellite-derived EKE in the western GOA was positively correlated with age-1 recruitment based on OLS regression if 1999, a year with unusually high recruitment, was excluded from the analysis ($y = 0.03x + 8.53$, $r^2_{\text{adjusted}} = 0.20$, $p = 0.03$; Fig. 8). The slope of this relationship increased ($y = 0.06x + 10.85$, $R^1(\tau) = 0.17$, $p = 0.03$; Fig. 8) for the upper (75th) quantile. This quantile relationship indicates that EKE in the western GOA determines years of high recruitment such that it constrains the upper magnitude of recruitment for the entire large marine ecosystem. This threshold relationship is reinforced by the lower (25th) recruitment quantile that did not show a significant relationship between EKE in the western GOA and recruitment during years of low recruitment. OLS and the 75th quantile relationships between EKE and recruitment were not significant in the eastern GOA, indicating that high EKE in the eastern GOA did not lead to years of substantially high recruitment (Fig. 8). However, EKE in the eastern GOA did have a significant relationship with recruitment for the 25th quantile ($y = 0.03x + 6.86$, $R^1(\tau) = 0.18$, $p = 0.02$). Thus, during low recruitment years, EKE in the eastern GOA influenced the magnitude of recruitment. Analyses using ROMS-derived EKE and *successful settlers* (age-0) using the subset of modeled years (2000–2011) showed similar, but nonsignificant trends (Supplemental Fig. 13).

Discussion

Settlement and recruitment success of ATF indicate that oceanographic retention increases access to suitable settlement habitats for fish with pelagic larvae and juvenile nurseries on the continental shelf. Previous work in the GOA has

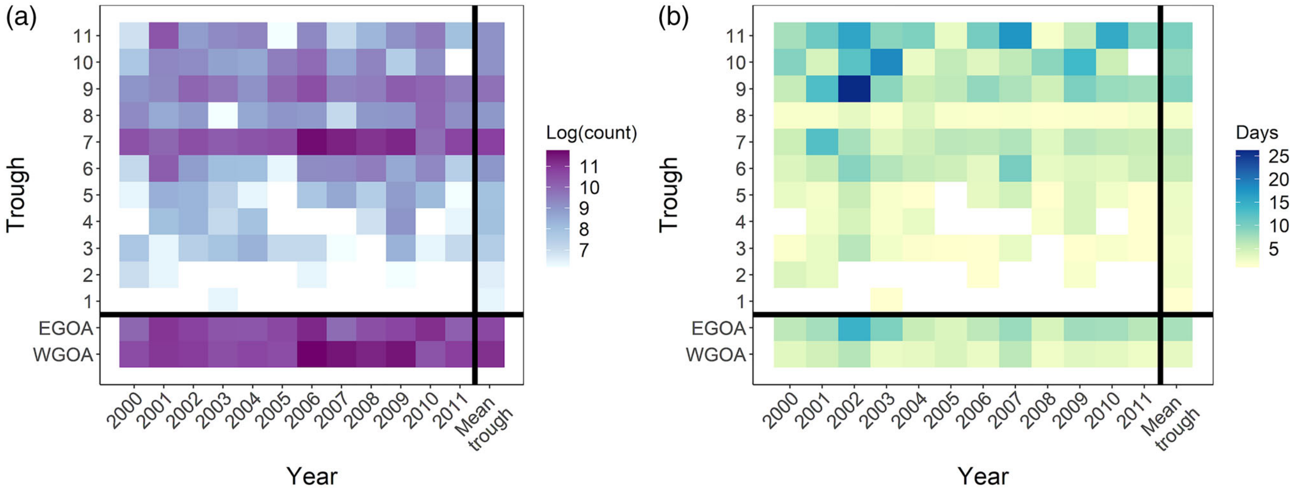

Fig. 7. Heatmaps showing results from *off-shelf trough success and retention* (*see* Table 2). (**a**) The count of individual simulated larvae that traversed each trough (numbered 1–11 from west to east; *see* Fig. 1b) is shown for the study years from 2000 to 2011. Counts only include the final trough observation prior to retention on the continental shelf for each individual. *Mean trough* on the x-axis refers to the average number of simulated individuals that traversed each trough across all study years. On the y-axis, *EGOA* and *WGOA* refer to the total number of simulated larvae in each year that traversed through troughs in the eastern and western Gulf of Alaska, respectively. (**b**) A heatmap of average residence time in days for simulated larvae within troughs is shown for each study year. Values only include observations within the final trough prior to retention on the continental shelf. *Mean trough* on the x-axis refers to the average residence time of simulated individuals that traversed each trough across all study years. *EGOA* and *WGOA* refer to the average residence time of larvae within the eastern and western Gulf of Alaska, respectively. In (**a**) and (**b**), summarized values among years and troughs are separated from other values by the horizontal and vertical black lines. *WGOA* includes troughs 1–7 that are primarily westward of −146° longitude, and *EGOA* includes troughs 8–11.

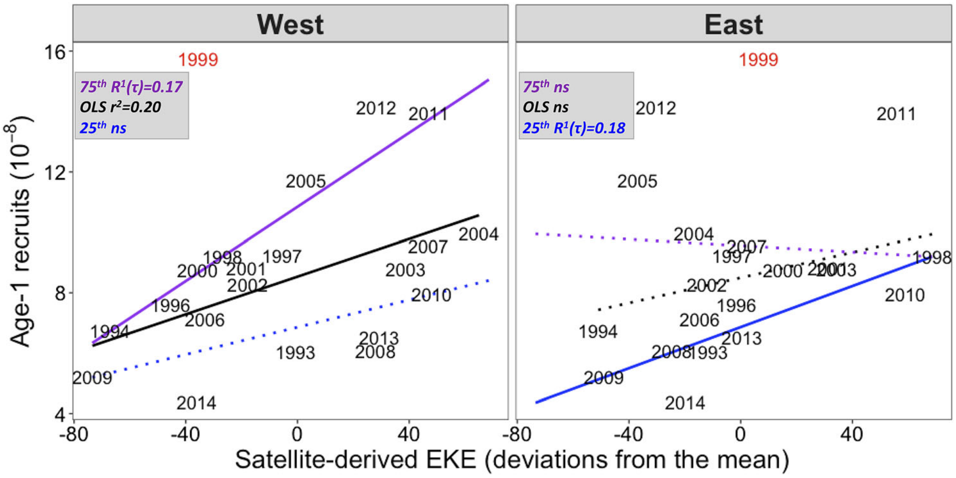

Fig. 8. Relationships between satellite-derived eddy kinetic energy (EKE) in the western (west) and eastern (east) Gulf of Alaska (GOA) and the recruitment of age-1 arrowtooth flounder (ATF) across the entire GOA based on the 2016 stock assessment. The years listed correspond to a one-year lag for ATF recruitment to ensure that EKE values temporally correspond to the pelagic larval stage. Relationships are linear models, including quantile regressions for the 75th and 25th quantiles and ordinary least-squares regressions (OLS). All regression relationships exclude the lagged year 1999, when recruitment was highest. Correlation coefficients (OLS) or the coefficient of determination (quantile regression) are listed for significant relationships (solid lines), and "ns" denotes non-significant relationships (dotted lines). Satellite-derived EKE is shown as deviations from the regional mean to highlight years of above and below average EKE.

pointed to the influence of climate on flatfish recruitment (Bailey et al. 1995) as well as associations between flatfish and troughs (Bailey et al. 2008). Here, we identify mechanistic links between local oceanography and interannual variability in recruitment. Larvae benefitted from regions of accumulation and retention to augment delivery to suitable on-shelf settlement habitats. On the continental shelf and slope, high concentrations of larvae were associated with glacial troughs and broad-scale bathymetric depressions. Offshore accumulation of larvae was influenced by mesoscale oceanography and eddies. Mechanistically, eddies and regions of retention minimize advective loss, increase self-recruitment, and enhance larval ingress and access to nursery habitats on the shelf.

Habitat suitability and settlement success

The recruitment bottleneck between the pelagic larval stage and the demersal juvenile stage for many marine fish is regulated by larval supply to nursery habitats and post-settlement mortality (Cowen and Sponaugle 2009; Pineda et al. 2010). Arrowtooth flounder are nursery habitat generalists in comparison to many other flatfish species (Wilson et al. 2016). Accordingly, suitable habitat for early juvenile ATF encompassed a broad expanse of low-lying and low gradient terrain from inshore to offshore areas on the continental shelf. Even for a species that is tolerant to a range of environmental conditions, the availability of suitable habitat within the study domain represented only 36% of potential habitat on the shelf. This decline in suitable settlement habitat availability resulted in an average estimate of *successful settlers* that was 60% of the total potential *larval supply*. The relationship between habitat availability and settlement success was concomitant but not one-to-one, suggesting that ATF settlement success is also influenced by processes beyond nursery habitat availability.

Geographic constraints on nursery habitats should presumably decouple the relationship between potential larval supply and realized settlement success as a result of differences in advantageous oceanographic transport trajectories. In contrast to this assumption, *larval supply* and *successful settlers* fluctuated in unison among years. These results indicate that the arrival of larvae to suitable settlement habitats is mechanistically linked to the total supply of larvae to the continental shelf. Marine fish must adapt their life-history strategies to maximize fitness (Burgess et al. 2017; Shima et al. 2018), and flatfish species such as ATF are adapted to take advantage of spawning times and locations that interact with oceanographic features to enable directed transport to settlement habitats (Bailey et al. 2005; Duffy-Anderson et al. 2014). The concurrent interannual fluctuations in *larval supply* and *successful settlers* indicate that ATF settlement magnitude is not sensitive to the patchiness of nursery habitats, but is primarily influenced by oceanographic variability. In unpredictable environments, "bet-hedging" spawning strategies often evolve to maximize the chances of offspring survival given variable environmental conditions, with fitness benefits that are evident across multiple spawning events (Burgess et al. 2017). The IBM did not incorporate small-scale variability in spawning locations, but spawning in deep waters along the continental slope during the winter months may, on average, maximize the likelihood of offspring survival. Indeed, the spawning strategy of ATF resulted in eventual off-shelf advection for the majority of larvae that led to high settlement success with low interannual variability. Additionally, larvae that were advected offshore accessed a greater portion of available settlement habitats in comparison to on-shelf trajectories that primarily delivered larvae to inshore nurseries. A "bet-hedging" spawning strategy hypothesis is also supported by the offset between the reductions in settlement success (~ 40% lower than *larval supply*) that resulted from a 64% decrease in available nursery habitat (suitable nurseries compared to the area of the continental shelf). ATF transport trajectories fluctuated as a result of interannual oceanographic variability, but the spawning strategy of ATF may exploit reliable transport routes or oceanographic features that maximize larval delivery to nursery habitats.

Settlement success, transport, and retention

The prevailing currents in the GOA flow from east to west along the continental shelf and slope (Stabeno et al. 2004), creating the potential for larval loss from the ecosystem. IBM results indicate that settlement success is highest in years when there is high larval accumulation, retention, and self-recruitment. The importance of larval retention in proximity to the shelf is supported by negative correlations between ATF recruitment and gap winds that enhance off-shelf transport (Ladd et al. 2016). Based on IBM results, the majority of larvae are dispersed offshore, yet many successfully arrive to nursery habitats. Larvae in these offshore environments must eventually traverse the slope current in the eastern GOA or the intensified along-shelf currents in the western GOA (Ladd et al. 2005; Janout et al. 2009) where the majority of ATF nursery habitat is located. Troughs are hypothesized to be conduits of cross-shelf transport for fish larvae (Bailey et al. 2008) through recirculation and accumulation of larvae as well as shelfward flow (Hickey 1997). ATF distributions from empirical studies show high densities of larvae along the slope and in the western GOA, particularly near troughs (Ichthyoplankton Information System http://access.afsc.noaa.gov/ichthyo/index.php [accessed 22 August 2019]; Siddon et al. 2016). These empirical spatial patterns and IBM-based regions of larval accumulation near troughs support the role of seafloor terrain and troughs in concentrating and accumulating larvae along the continental shelf and margin.

Troughs could serve as ecologically important routes of cross-shelf transport for fish larvae via several mechanisms: (1) through directed transport to nursery habitats; (2) by disproportionately contributing to settlement success in some years; (3) as routes of cross-shelf transport despite oceanographic variability; (4) by disrupting along-shelf flow and reducing advective loss of larvae; and (5) by providing high quality larval habitat. A large portion of ATF larvae accessed the continental shelf domain through troughs and arrived to suitable settlement habitats. Additionally, regions of larval accumulation over the continental shelf and margins (*off-shelf trough success and retention*), and reduced connectivity from eastern spawning locations to western settlement locations, suggest that trough access is associated with disruptions in along-shelf flow, meandering, cross-shelf movement, and bathymetric steering that could maintain larvae near settlement habitats. Yet, retention over the continental shelf following trough transport was low and variable among years, suggesting that directed transport from troughs to nurseries was limited.

Nevertheless, we suggest that troughs probably do serve as important links between the slope and the shelf. Settlement success associated with troughs is influenced by modeling methods and limitations including the resolution of the model, feature designations, and biological processes. This study focused primarily on physical mechanisms, and other factors not included in the model could retain larvae over the continental shelf post-trough. Burgeoning behavioral, developmental, and sensory capabilities of growing larvae permit directed movements in response to coastal environmental cues that could amplify their on-shelf retention in a way that is not captured using the present modeling approach (Staaterman and Paris 2014). Based on ecological evidence for ATF and many other fish taxa (Auth et al. 2007; Stockhausen et al. 2019), larvae were restricted to preferred depth ranges, which could be a limitation of the approach given ontogenetic development of directed swimming in relation to environmental cues (Staaterman and Paris 2014; Leis et al. 2015). Troughs and canyons are also regions of high productivity and biomass of organisms, creating potentially risky but high quality larval habitats (Brodeur 2001; Genin 2004). Larval behavior and the influences of food availability and predation in troughs could have lasting impacts on survival, settlement, and recruitment (Cowen and Sponaugle 2009; Shulzitski et al. 2016).

Retention and recruitment

Mesoscale features such as eddies are important to the settlement (Limouzy-Paris et al. 1997; Nakata 2000), growth, and survival (Logerwell and Smith 2001; Shulzitski et al. 2016) of fish larvae, and there is evidence of life-history strategies that maximize larval access to these features despite potentially higher mortality risk (Richardson et al. 2009; Bakun 2013). Additionally, retention and self-recruitment for marine fish have a presumed evolutionary advantage of remaining in favorable habitats (Cowen et al. 2000; Armsworth et al. 2001). The hypothesized relationship between retention near the continental shelf and successful settlement based on the IBM was supported by the correlation between satellite-derived EKE and stock assessment-based recruitment. Surprisingly, the strength of the mechanistic relationship between retention and recruitment was evident despite the lack of agreement between satellite- and model-derived EKE (Coyle et al. 2012), and the temporal discrepancies between IBM-based settlement magnitude and stock assessment-based recruitment.

The impact of eddies on age-1 recruitment suggests that eddy-enhanced settlement propagates into the following year despite high mortality associated with the transition from the pelagic larval phase to the juvenile stage. (Tupper and Boutilier 1995; Almany and Webster 2006). This relationship was less pronounced based on the IBM that focused on settlement magnitude rather than recruitment. While the IBM did capture the prevalence of retention and eddies in western GOA (Ladd 2007), there are several potential explanations for the weaker relationship between eddies and settlement in the IBM: (1) the analyses of ROMS-based EKE and settlement success spanned only 12 yr rather than 21 yr; (2) the ROMS model may not resolve EKE patterns to the same degree as satellite-derived data; (3) post-settlement processes that affect survival may alter the relationship between EKE and age-1 recruitment compared to age-0 settlement. There is evidence to suggest that food availability for larval fish may be higher in productive eddy environments (Nakata 2000; Hitchcock et al. 2005) and entrainment in eddies enhances growth and survival of fish larvae, which can provide a post-settlement selective advantage (Shulzitski et al. 2016). Therefore, the strength of the relationship between EKE and recruitment may reflect physical processes that enhance settlement success as well as biological advantages and increased post-settlement survival.

Regions of larval accumulation and cross-shelf transport are influenced by interactions between mesoscale oceanography and seafloor terrain. The importance of retentive features such as eddies in the western GOA to ATF recruitment across the entirety of the GOA implies that recruitment strength is dependent upon the location of mesoscale features. Eddies located in the western GOA determined the upper limits of recruitment magnitude. Eddies in the eastern GOA also had a positive relationship with recruitment, but only in association with years of lower recruitment. The relationship between EKE and ATF recruitment weakened if the highest recruitment year was included in the analysis. However, 1999 was a unique year with a particularly cold winter associated with La Niña and a strong negative Pacific Decadal Oscillation index (Papineau 2001; Stabeno et al. 2004) that may have influenced recruitment for winter spawning ATF. The differing relationships between EKE in the western and eastern GOA may be the result of interactions between regional processes and eddy frequency or duration. For example, larval accumulation near the start of the ACC (Stabeno et al. 2004) may be a hotspot where bathymetric depressions and high EKE (Ladd 2007) promote cross-shelf exchange (Stabeno et al. 2016). Eddy-induced recirculation or proximity to terrain features upstream or near settlement habitats likely affects settlement success by disrupting along-shelf flow and augmenting shelfward transport or retention (Hickey 1997; Hare et al. 2002). The differing relationship between EKE in the eastern and western GOA and recruitment suggests that the upper limits of recruitment are driven by a confluence of favorable physical and biological processes in the western GOA: retention facilitates the accumulation and ingress of larvae to prevalent and favorable habitats.

Conclusions

We show that mesoscale oceanographic features influence retention and recruitment magnitude across a large marine ecosystem even for an abundant, mobile, fish species with broad nursery habitat requirements. This study focused primarily on transport and settlement, but further research to develop a complete mechanistic understanding of recruitment should incorporate spatial and temporal variability in biological processes during the early life stages such as mortality, predation (Bailey and Houde 1989), patchiness, density-dependence (Shepherd and Cushing 1980), and the influences of food availability on growth and survival (Pepin et al. 2015). ATF, and likely other slope-spawning species with nursery habitats on the continental shelf, rely on off-shelf advection, retention, and disruptions in the prevailing unidirectional currents to enhance access to advantageous larval and settlement habitats. Retention increases recruitment for ATF in the GOA, but with differing regional mechanisms that point to interactions between oceanography, seafloor terrain, and habitat availability. Glacial troughs do not disproportionately direct larvae to nurseries; rather, troughs are associated with disruptions in along-shelf currents that connect the continental shelf and basin, and meandering trajectories that retain larvae on the shelf. Eddy presence in the western GOA, where the availability of suitable settlement habitat is high, enhances the delivery of larvae to nursery habitats, thus providing a threshold mechanism that dictates the upper bounds of recruitment. In advective ecosystems, mesoscale retentive features can facilitate access to favorable habitats for fish larvae and regulate recruitment magnitude for species with obligate nursery habitats on the continental shelf.

References

Allen, S. E. 2009. A review of the role of submarine canyons in deep-ocean exchange with the shelf. Ocean Sci. **5**: 607–620. doi:https://doi.org/10.5194/os-5-607-2009.

Almany, G. R., and M. S. Webster. 2006. The predation gauntlet: Early post-settlement mortality in reef fishes. Coral Reefs **25**: 19–22. doi:10.1007/s00338-005-0044-y

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. **189**: 117–123. doi:10.3354/meps189117

Armsworth, P. R., M. K. James, and L. Bode. 2001. When to press on or turn back: Dispersal strategies for reef fish larvae. Am. Nat. **157**: 434–450. doi:10.2307/3079184

Auth, T. D., R. D. Brodeur, and K. M. Fisher. 2007. Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast. Fish. Bull. **105**: 313–326.

Bailey, K. M., A. A. Abookire, and J. T. Duffy-Anderson. 2008. Ocean transport paths for the early life history stages of offshore-spawning flatfishes: A case study in the Gulf of Alaska. Fish Fish. **9**: 44–66.

Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem, p. 1–83. *In* J. H. S. Blaxter and A. J. Southward [eds.], Advances in marine biology. Academic Press.

Bailey, K. M., et al. 1995. ENSO events in the northern Gulf of Alaska, and effects on selected marine fisheries. Other Report 36:78-96. California Cooperative Oceanic Fisheries Investigations (CalCOFI).

Bailey, K. M., H. Nakata, and H. W. Van der Veer. 2005. The planktonic stages of flatfishes: Physical and biological interactions in transport processes. p. 94–119. In R. N. Gibson [ed.], Flatfishes: Biology and exploitation. Blackwell Science Ltd, Oxford, UK.

Bailey, K. M., and S. J. Picquelle. 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: Potential transport pathways and enhanced onshore transport during ENSO events. Mar. Ecol. Prog. Ser. **236**: 205–217.

Bakun, A. 2013. Ocean eddies, predator pits and bluefin tuna: Implications of an inferred 'low risk–limited payoff' reproductive scheme of a (former) archetypical top predator. Fish Fish. **14**: 424–438. doi:10.1111/faf.12002

Blood, D. M., A. C. Matarese, and M. S. Busby. 2007. Spawning, egg development, and early life history dynamics of arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska.

Bouwens, K. A., A. J. Paul, and R. L. Smith. 1999*a*. Growth of juvenile Arrowtooth flounders from Kachemak Bay. Alaska. Alaska. Fish. Res. Bull. **6**: 35–40.

Bouwens, K. A., R. L. Smith, A. J. Paul, and W. Rugen. 1999*b*. Length at and timing of hatching and settlement for arrowtooth flounders in the Gulf of Alaska. Alsk. Fish. Res. Bull. **6**: 41–48.

Brodeur, R. D. 2001. Habitat-specific distribution of Pacific Ocean perch (*Sebastes alutus*) in Pribilof canyon, Bering Sea. Cont. Shelf Res. **21**: 207–224. doi:10.1016/S0278-4343(00)00083-2

Burgess, S. C., R. E. Snyder, and B. Rountree. 2017. Collective dispersal leads to variance in fitness and maintains offspring size variation within marine populations. Am. Nat. **191**: 318–332. doi:10.1086/695879

Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. Front. Ecol. Environ. **1**: 412–420. doi:10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2

Cade, B. S., B. R. Noon, and C. H. Flather. 2005. Quantile regression reveals hidden bias and uncertainty in habitat models. Ecology **86**: 786–800.

Carlson, P. R., T. R. Bruns, B. F. Molnia, and W. C. Schwab. 1982. Submarine valleys in the northeastern Gulf of Alaska: Characteristics and probable origin. Mar. Geol. **47**: 217–242. doi:10.1016/0025-3227(82)90070-6

Clark, W. G., S. R. Hare, A. M. Parma, P. J. Sullivan, and R. J. Trumble. 1999. Decadal changes in growth and recruitment of Pacific halibut (*Hippoglossus stenolepis*). Can. J. Fish. Aquat. Sci. **56**: 242–252.

Cooper, D. W., J. T. Duffy-Anderson, W. T. Stockhausen, and W. Cheng. 2013. Modeled connectivity between northern rock sole (*Lepidopsetta polyxystra*) spawning and nursery areas in the eastern Bering Sea. J. Sea Res. **84**: 2–12. doi:10.1016/j.seares.2012.07.001

Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: Open or closed? Science **287**: 857–859.

Cowen, R. K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. Ann. Rev. Mar. Sci. **1**: 443–466.

Coyle, K. O., W. Cheng, S. L. Hinckley, E. J. Lessard, T. Whitledge, A. J. Hermann, and K. Hedstrom. 2012. Model and field observations of effects of circulation on the timing and magnitude of nitrate utilization and production on the northern Gulf of Alaska shelf. Prog. Oceanogr. **103**: 16–41. doi:10.1016/j.pocean.2012.03.002

Dohan, K., and N. Maximenko. 2010. Monitoring ocean currents with satellite sensors. Oceanography **23**: 94–103. doi:10.5670/oceanog.2010.08

Doherty, P. J., V. Dufour, R. Galzin, M. A. Hixon, M. G. Meekan, and S. Planes. 2004. High mortality during settlement is a population bottleneck for a tropical surgeonfish. Ecology **85**: 2422–2428.

Doyle, M. J., S. J. Picquelle, K. L. Mier, M. C. Spillane, and N. A. Bond. 2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. Prog. Oceanogr. **80**: 163–187. doi:10.1016/j.pocean.2009.03.002

Duffy-Anderson, J. T., K. M. Bailey, H. N. Cabral, H. Nakata, and H. W. Van der Veer. 2014. The planktonic stages of flatfishes: Physical and biological interactions in transport processes, p. 132–170. *In* R. N. Gibson, R. D. M. Nash, A. J. Geffen, and H. W. Van der Veer [eds.], Flatfishes: Biology and exploitation. John Wiley & Sons.

Elith, J., and others. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**: 129–151. doi:10.1111/j.2006.0906-7590.04596.x

Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. **50**: 3–20. doi:10.1016/j.jmarsys.2003.10.008

Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Neth. J. Sea Res. **32**: 191–206. doi:10.1016/0077-7579(94)90040-X

Goldstein, E. D., J. T. Duffy-Anderson, A. C. Matarese, and W. Stockhausen. 2019. Larval fish assemblages in the eastern and western Gulf of Alaska: Patterns, drivers, and implications for connectivity. Deep-Sea Res. Part II Top. Stud. Oceanogr. **165**: 26–40. doi:10.1016/j.dsr2.2018.09.003

Greene, H. G., M. M. Yoklavich, R. M. Starr, V. M. O'Connell, W. W. Wakefield, D. E. Sullivan, J. E. McRea, and G. M. Cailliet. 1999. A classification scheme for deep seafloor habitats. Oceanol. Acta **22**: 663–678. doi:10.1016/S0399-1784(00)88957-4

Guisan, A., C. H. Graham, J. Elith, and F. Huettmann. 2007. Sensitivity of predictive species distribution models to change in grain size. Divers. Distrib. **13**: 332–340. doi:10.1111/j.1472-4642.2007.00342.x

Haidvogel, D. B., and others. 2008. Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. J. Comput. Phys. **227**: 3595–3624. doi:10.1016/j.jcp.2007.06.016

Hare, J. A., and others. 2002. Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. Limnol. Oceanogr. **47**: 1774–1789.

Harris, P. T., J. V. Barrie, K. W. Conway, and H. G. Greene. 2014*a*. Hanging canyons of Haida Gwaii, British Columbia, Canada: Fault-control on submarine canyon geomorphology along active continental margins. Deep-Sea Res. Part II Top. Stud. Oceanogr. **104**: 83–92. doi:10.1016/j.dsr2.2013.06.017

Harris, P. T., M. Macmillan-Lawler, J. Rupp, and E. K. Baker. 2014*b*. Geomorphology of the oceans. Mar. Geol. **352**: 4–24. doi:10.1016/j.margeo.2014.01.011

Hermann, A. J., S. Hinckley, E. L. Dobbins, D. B. Haidvogel, N. A. Bond, C. Mordy, N. Kachel, and P. J. Stabeno. 2009. Quantifying cross-shelf and vertical nutrient flux in the Coastal Gulf of Alaska with a spatially nested, coupled biophysical model. Deep-Sea Res. Part II Top. Stud. Oceanogr. **56**: 2474–2486. doi:10.1016/j.dsr2.2009.02.008

Hickey, B. 1997. The response of a steep-sided, narrow canyon to time-variable wind forcing. J. Phys. Oceanogr. **27**: 30.

Hijmans, R., J. van Etten, M. Mattiuzzi, M. Sumner, and J. Greenberg. 2014*a*. Raster: Geographic data analysis and modeling, R Core Team.

Hijmans, R., S. Philips, J. Leathwick, and J. Elith. 2014*b*. Species distribution modeling: Dismo package, R Core Team.

Hinckley, S., K. O. Coyle, G. Gibson, A. J. Hermann, and E. L. Dobbins. 2009. A biophysical NPZ model with iron for the Gulf of Alaska: Reproducing the differences between an oceanic HNLC ecosystem and a classical northern temperate shelf ecosystem. Deep-Sea Res. Part II Top. Stud. Oceanogr. **56**: 2520–2536. doi:10.1016/j.dsr2.2009.03.003

Hitchcock, G. L., T. N. Lee, P. B. Ortner, S. Cummings, C. Kelble, and E. Williams. 2005. Property fields in a Tortugas Eddy in the southern straits of Florida. Deep-Sea Res. I Oceanogr. Res. Pap. **52**: 2195–2213.

Hollowed, A. 2000. Including predation mortality in stock assessments: A case study for Gulf of Alaska walleye pollock. ICES J. Mar. Sci. **57**: 279–293. doi:10.1006/jmsc.1999.0637

Houde, E. D. 2016. Recruitment variability. *In* 98–187. Fish reproductive biology: Wiley-Blackwell.

Jackson, D., and M. Ruccio. 2003. Kodiak, Chignik and South Peninsula shrimp fisheries and their management: A report to the Alaska Board of Fisheries. Alaska Dep. Fish Game Reg. Inf. Rep. 4K03-7.

Janout, M. A., T. J. Weingartner, S. R. Okkonen, T. E. Whitledge, and D. L. Musgrave. 2009. Some characteristics of Yakutat Eddies propagating along the continental slope of the northern Gulf of Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **56**: 2444–2459. doi:10.1016/j.dsr2.2009.02.006

Johnson, D. W. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. Oecologia **155**: 43–52. doi:10.1007/s00442-007-0882-0

King, J. R., G. A. McFarlane, and A. E. Punt. 2015. Shifts in fisheries management: Adapting to regime shifts. Philos. Trans. R. Soc. B: Biol. Sci. **370**: 20130277. doi:10.1098/rstb.2013.0277

Koenker, R., and J. A. F. Machado. 1999. Goodness of fit and related inference processes for quantile regression. J. Am. Stat. Assoc. **94**: 1296. doi:10.2307/2669943

Koenker, R., S. Portnoy, P. Ng, Z. Achim, P. Grosjean, and B. Ripley. 2018. quantreg, R Core Team.

Ladd, C. 2007. Interannual variability of the Gulf of Alaska eddy field. Geophys. Res. Lett. **34**: L11605. doi:10.1029/2007GL029478

Ladd, C., W. Cheng, and S. Salo. 2016. Gap winds and their effects on regional oceanography part II: Kodiak Island, Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **132**: 54–67. doi:10.1016/j.dsr2.2015.08.005

Ladd, C., P. Stabeno, and E. D. Cokelet. 2005. A note on cross-shelf exchange in the northern Gulf of Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **52**: 667–679. doi:10.1016/j.dsr2.2004.12.022

Laurel, B. J., A. J. Basilio, C. Danley, C. H. Ryer, and M. Spencer. 2015. Substrate preference and delayed settlement in northern rock sole larvae *Lepidopsetta polyxystra*. Mar. Ecol. Prog. Ser. **519**: 183–193. doi:10.3354/meps11090

Limouzy-Paris, C. B., H. C. Graber, D. L. Jones, A. W. Ropke, and W. J. Richards. 1997. Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. Bull. Mar. Sci. **60**: 966–983.

Logerwell, E. A., and P. E. Smith. 2001. Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. Fish. Ocean. **10**: 13. doi:10.1046/j.1365-2419.2001.00152.x

Merow, C., M. J. Smith, and J. A. Silander. 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography **36**: 1058–1069. doi:10.1111/j.1600-0587.2013.07872.x

Mordy, C. W., and others. 2019. Patterns of flow in the canyons of the northern Gulf of Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **165**: 203–220. doi:10.1016/j.dsr2.2019.03.009

Leis, J. M., U. E. Siebeck, A. C. Hay, C. B. Paris, O. Chateau, and L. Wantiez. 2015. In situ orientation of fish larvae can vary among regions. Mar. Ecol. Prog. Ser. **537**: 191–203. doi:10.3354/meps11446

Nakata, H. 2000. Implications of meso-scale eddies caused by frontal disturbances of the Kuroshio Current for anchovy recruitment. ICES J. Mar. Sci. **57**: 143–152. doi:10.1006/jmsc.1999.0565

Norcross, B. L., A. Blanchard, and B. A. Holladay. 1999. Comparison of models for defining nearshore flatfish nursery areas in Alaskan waters. Fish. Oceanogr. **8**: 50–67. doi:10.1046/j.1365-2419.1999.00087.x

Okkonen, S. R., G. A. Jacobs, E. Joseph Metzger, H. E. Hurlburt, and J. F. Shriver. 2001. Mesoscale variability in the boundary currents of the Alaska Gyre. Cont. Shelf Res. **21**: 1219–1236. doi:10.1016/S0278-4343(00)00085-6

Papineau, J. 2001. Wintertime temperature anomalies in Alaska correlated with ENSO and PDO. Int. J. Climatol. **21**: 1577–1592. doi:10.1002/joc.686

Pepin, P., and others. 2015. Once upon a larva: Revisiting the relationship between feeding success and growth in fish larvae. ICES J. Mar. Sci. **72**: 359–373. doi:10.1093/icesjms/fsu201

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. **190**: 231–259. doi:10.1016/j.ecolmodel.2005.03.026

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by intertidal bores. Science **253**: 548–551.

Pineda, J., F. Porri, V. Starczak, and J. Blythe. 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. J. Exp. Mar. Biol. Ecol. **392**: 9–21. doi:10.1016/j.jembe.2010.04.008

Pirtle, J. L., G. L. Eckert, and A. W. Stoner. 2012. Habitat structure influences the survival and predator–prey interactions of early juvenile red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Ser. **465**: 169–184. doi:10.3354/meps09883

Pirtle, J. L., S. K. Shotwell, M. Zimmermann, J. A. Reid, and N. Golden. 2019. Habitat suitability models for groundfish in the Gulf of Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **165**: 303–321. doi:10.1016/j.dsr2.2017.12.005

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Richardson, D. E., J. K. Llopiz, K. D. Leaman, P. S. Vertes, F. E. Muller-Karger, and R. K. Cowen. 2009. Sailfish (*Istiophorus platypterus*) spawning and larval environment in a Florida Current frontal eddy. Prog. Oceanogr. **82**: 252–264. doi:10.1016/j.pocean.2009.07.003

Shanks, A., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol. Oceanogr. **45**: 230–236. doi:10.4319/lo.2000.45.1.0230

Shchepetkin, A. F., and J. C. McWilliams. 2005. The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model. **9**: 347–404. doi:10.1016/j.ocemod.2004.08.002

Shepherd, J. G., and D. H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. ICES J. Mar. Sci. **39**: 160–167. doi:10.1093/icesjms/39.2.160

Shima, J., E. G. Noonburg, S. E. Swearer, S. H. Alonzo, and C. W. Osenberg. 2018. Born at the right time? A conceptual framework linking reproduction, development, and settlement in reef fish. Ecology **99**: 116–126. doi:10.1002/ecy.2048

Shulzitski, K., S. Sponaugle, M. Hauff, K. D. Walter, and R. K. Cowen. 2016. Encounter with mesoscale eddies enhances survival to settlement in larval coral reef fishes. Proc. Natl. Acad. Sci. USA **113**: 6928–6933. doi:10.1073/pnas.1601606113

Siddon, E. C., L. G. De Forest, D. M. Blood, M. J. Doyle, and A. C. Matarese. 2016. Early life history ecology for five commercially and ecologically important fish species in the eastern and western Gulf of Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **165**: 7–25. doi:10.1016/j.dsr2.2016.06.022

Spies, I., J. N. Ianelli, A. Kingham, R. Narita, and W. Palsson. 2016. Assessment of the arrowtooth flounder stock in the Gulf of Alaska, p. 507–510. *In* Gulf of Alaska stock assessment and fishery evaluation report to the North Pacific Fishery Management Council, 605 W. 4th Avenue, Anchorage AK 99510.

Spies, I., and B. J. Turnock. 2013. Assessment of the arrowtooth flounder stock in the Gulf of Alaska, p. 542–610. *In* Gulf of Alaska stock assessment and fishery evaluation report to the North Pacific Fishery Management Council, 605 W. 4th Avenue, Anchorage AK 99510.

Sponaugle, S., T. Lee, V. Kourafalou, and D. Pinkard. 2005. Florida current frontal eddies and the settlement of coral reef fishes. Limnol. Oceanogr. **50**: 1033–1048.

Staaterman, E., and C. B. Paris. 2014. Modelling larval fish navigation: The way forward. ICES J. Mar. Sci. **71**: 918–924. doi:10.1093/icesjms/fst103

Stabeno, P. J., S. Bell, W. Cheng, S. Danielson, N. B. Kachel, and C. W. Mordy. 2016. Long-term observations of Alaska Coastal Current in the northern Gulf of Alaska. Deep-Sea Res. Part II Top. Stud. Oceanogr. **132**: 24–40. doi:10.1016/j.dsr2.2015.12.016

Stabeno, P. J., N. A. Bond, A. J. Hermann, N. B. Kachel, C. W. Mordy, and J. E. Overland. 2004. Meteorology and oceanography of the Northern Gulf of Alaska. Cont. Shelf Res. **24**: 859–897. doi:10.1016/j.csr.2004.02.007

Stark, J. W. 2008. Age-and length-at-maturity of female arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska. Fish. Bull. **106**: 328–333.

Stier, A. C., and C. W. Osenberg. 2010. Propagule redirection: Habitat availability reduces colonization and increases recruitment in reef fishes. Ecology **91**: 2826–2832.

Stockhausen, W. T., and others. 2019. Running the gauntlet: Connectivity between spawning and nursery areas for arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska, as inferred from a biophysical individual-based model. Deep-Sea Res. Part II Top. Stud. Oceanogr. **165**: 127–139. doi:10.1016/j.dsr2.2018.05.017

Tupper, M., and R. G. Boutilier. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 1834–1841.

Vestfals, C. D., L. Ciannelli, J. T. Duffy-Anderson, and C. Ladd. 2014. Effects of seasonal and interannual variability in alongshelf and cross-shelf transport on groundfish recruitment in the eastern Bering Sea. Deep-Sea Res. Part II Top. Stud. Oceanogr. **109**: 190–203. doi:10.1016/j.dsr2.2013.09.026

von Szalay, P., and N. Raring. 2016. Data report: 2015 Gulf of Alaska bottom trawl survey. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFCS-325, 249 p.

Warren, D. L., and S. N. Seifert. 2011. Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. Ecol. Appl. **21**: 335–342. doi:10.1890/10-1171.1

Wennhage, H., and L. Pihl. 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): Impact of benthic microalgae and filamentous macroalgae. Neth. J. Sea Res. **32**: 343–351. doi:10.1016/0077-7579(94)90011-6

Wilderbuer, T. K., A. B. Hollowed, W. J. Ingraham Jr., P. D. Spencer, M. E. Conners, N. A. Bond, and G. E. Walters. 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. Prog. Oceanogr. **55**: 235–247.

Wilderbuer, T. K., D. G. Nichol, and K. Aydin. 2008. BSAI arrowtooth flounder. NPFMC Bering Sea Aleutian Islands SAFE 2009: 643–706.

Wilson, M. F. J., B. O'Connell, C. Brown, J. C. Guinan, and A. J. Grehan. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar. Geod. **30**: 3–35. doi:10.1080/01490410701295962

Wilson, M. T., K. L. Mier, and D. W. Cooper. 2016. Assessment of resource selection models to predict occurrence of five juvenile flatfish species (Pleuronectidae) over the continental shelf in the western Gulf of Alaska. J. Sea Res. **111**: 54–64. doi:10.1016/j.seares.2015.12.005

Zador, S., and E. Yasumiishi (editors). 2016. Ecosystems considerations 2016: Status of the Gulf of Alaska marine ecosystem. 145 p. *In* North Pacific Fishery Management Council, 605 W. 4th Avenue, Anchorage AK 99510.

Zimmermann, M. 1997. Maturity and fecundity of arrowtooth flounder, *Atheresthes stomias*, from the Gulf of Alaska. Fish. Bull. **95**: 598–611.

Acknowledgments

We would like to thank the scientists at the National Oceanic and Atmospheric Administration's Alaska Fisheries Science Center (NOAA-AFSC) and the University of Washington who contributed to this research. In particular, we would like to thank Carol Ladd and Wei Cheng for their physical oceanographic help and expertise. We would also like to thank H. Gary Greene and Peter T. Harris for providing guidance regarding the seafloor terrain features of the Gulf of Alaska. We are grateful for helpful reviews of this manuscript provided by Lauren Rogers and Carol Ladd in addition to three anonymous reviewers. This project was funded by the North Pacific Research Board (NPRB), which sponsored the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP), with additional funding from NOAA's Ecosystems and Fisheries-Oceanography Coordinated Investigations Program (EcoFOCI) and the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA15OAR4320063. Esther Goldstein was supported by The National Academies of Sciences, Engineering, and Medicine, National Research Council (NRC) Research Associateship Programs. This research is contribution EcoFOCI-0936 to NOAA's EcoFOCI Program, contribution 2019-1028 to JISAO, and contribution 5018 to NOAA's Pacific Marine Environmental Laboratory. This manuscript is GOAIERP publication number 46 and NPRB publication number 693. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Conflict of interest

The authors declared no potential conflicts of interest.

Submitted 14 March 2019
Revised 12 September 2019
Accepted 21 May 2020

Associate editor: James Leichter